Untangling the effects of fishing effort and environmental variables on benthic communities of commercially fished scallop grounds

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Thesis Abstract

The Isle of Man fishing industry is currently predominated by two lucrative and heavily exploited scallop fisheries, targeting *Pecten maximus* and *Aequipecten opercularis.* The impacts of which have previously been investigated, however without the addition of environmental information. This thesis represents a unique long-term investigation into the impacts of fishing pressure and environmental variables on the benthic invertebrate communities of fishing grounds found around the Isle of Man. A significant positive trend in seawater temperature was found, along with an inverse correlation with chlorophyll-α. Fishing pressure was found to have a small, significant negative effect on indices of diversity; however environmental variables were unable to explain the remaining patterns in diversity. The composition of each of the benthic communities was then investigated in more detail. Fishing pressure had a significant negative effect on densities of benthic invertebrates at some grounds; however this study showed that many of the heavily fished sites were composed of dredge-tolerant species.

Significant relationships were found between the densities of *Asterias rubens* and *Porania pulvillus* and several environmental variables on the south-west fishing grounds, suggesting that environmental variation, rather than fishing pressure was responsible for variations in these species. Further evidence was found of the negative impact of scallop dredging from the long-term analysis of a closed area, implemented in 1989. Recovery of *P. maximus* has occurred within this closure, without the concurrent increase in of the predatory starfish *A.rubens*. Relationships between several benthic species with the closed area and environmental variables were found. However, the results of this study indicate a complex ecosystem, which is also affected by predator-prey interactions. The overall findings of this research indicate that closed area management is a relatively straightforward and effective management measure in this region. Future management decisions will however, have to account for the potential effects of climate change.

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Author's Declaration

The data used in this thesis was collected from a variety of sources over the time period 1989 – 2006. All contributors are acknowledged and any previous published work is referenced within the text. I declare that this body of work is my own, with advice and guidance from my supervisor Dr. Bryce Stewart.

Chapter 1

General Introduction

Throughout the last century marine ecosystems have seen an increasing range of anthropogenic impacts that affect them (Capasso, Jenkins et al. 2009; Miles 2009; Drinkwater, Beaugrand et al. 2010). Eutrophication, pollution, commercial fishing, ocean acidification and global climate change are of concern for resource managers and conservationists alike (Schiel, Steinbeck et al. 2004; Capasso, Jenkins et al. 2009; Frost, Baxter et al. 2012). These impacts rarely exist individually and synergies between their effects are common (Callaway, Engelhard et al. 2007; Miles 2009). On top of this, individual species' responses to each impact may not be as straightforward as some models have previously predicted (Schiel, Steinbeck et al. 2004). Understanding the long-term changes in marine ecosystems is fundamental to understanding, managing and predicting the future effects of these anthropogenic impacts (Capasso, Jenkins et al. 2009; Miles 2009). However, their synergistic nature often makes it difficult if not impossible to measure the effect of each impact individually (Callaway, Engelhard et al. 2007; Miles 2009).

In this first chapter I will begin by outlining the current understanding of this issue in relation to benthic communities and critically reviewing the available literature. Many benthic communities are heavily impacted by human activity, particularly in terms of the effect of towed bottom fishing (Collie, Escanero et al. 1997; Kaiser 1998; Philippart 1998; Kaiser, Cheney et al. 1999; Collie, Escanero et al. 2000; Kaiser, Ramsay et al. 2000; Jennings, Pinnegar et al. 2001; Kaiser, Clarke et al. 2006; Tillin, Hiddink et al. 2006), climate change (Wieking and Kröncke 2001; Philippart, van Aken et al. 2003; Schiel, Steinbeck et al. 2004; Beukema and Dekker 2005; Kirby, Beaugrand et al. 2007; Kirby, Beaugrand et al. 2008; Kirby and Beaugrand 2009) and pollution (Frid, Buchanan et al. 1996; Frid, Clark et al. 1999; Clark 2001; Rees, Pendle et al. 2006). Benthic fauna such as shellfish are also of great commercial importance , for example an estimated 840,876 tonnes of pectinid scallops were caught worldwide in 2010 (Murray, Hinz et al. 2009; FAO 2010). Therefore it is of both great commercial and environmental importance to understand how benthic communities respond to the array of impacts acting upon them. This information can then feed into the management of damaging anthropogenic activities to reduce the negative effects they may have on benthic ecosystems.

I will then focus on the effect of the three specific impacts mentioned above, climate change, pollution and fishing, on benthic communities. Moving on I will specifically discuss the effect of dredging on benthic communities, as this has been described as the most damaging form of towed bottom gear (Currie and Parry 1996; Collie, Escanero et al. 2000; Collie, Hall et al. 2000; Eleftheriou 2000; Jenkins, Beukers-Stewart et al. 2001; Carbines and Cole 2009). Finally, I will explain the focus of this thesis on untangling the effects of fishing and environmental change on marine benthic communities, explain my aims and objectives and thesis organisation. The study site for this thesis is introduced in the following Chapter, where a full review of the area is undertaken.

1.1 Marine Benthic Communities

Marine benthic communities on the continental shelf are naturally structured by a complex array of variable factors (Kaiser 1998; Hill, Veale et al. 1999; Kaiser, Ramsay et al. 2000). These include, among others, temperature (Kröncke, Dippner et al. 1998), substrate type, tidal currents (Kaiser 1998), seasonal currents (Hill, Brown et al. 1997; Hill, Veale et al. 1999), phytoplankton availability (Frid, Buchanan et al. 1996) and the frequency and intensity of storms (Frid, Buchanan et al. 1996; Kaiser 1998; Bradshaw, Veale et al. 2002; Reiss, Meybohm et al. 2006). In addition to these large scale factors, smaller scale disturbances also occur, such as predator feeding activity (Kaiser 1998). Complex benthic communities are not static in time, inter-annual fluctuations can be caused by small-scale changes in local conditions that differentially affect reproduction, recruitment or survival of each species present (Bradshaw, Veale et al. 2002).

Our empirical knowledge of the natural variability of most benthic ecosystems is however, rather limited, as the majority of areas studied have been altered in some way by anthropogenic activity prior to study (Currie and Parry 1996; Capasso, Jenkins et al. 2009). For example in the heavily fished North Sea, it is unlikely that un-fished benthic communities have ever been observed scientifically, due to long-term industrial fishing pressure pre-dating thorough scientific investigation (Frid, Clark et al. 1999). Many studies, therefore do not or cannot assess the disturbance caused by anthropogenic activity against a background of natural disturbance that occurs over the same time scale (Stokesbury and Harris 2006). In addition to this many of the natural factors that structure benthic communities now appear to be affected by human activity (Miles 2009). Temperature is affected by global warming (Schiel, Steinbeck et al. 2004), phytoplankton abundance is affected by pollution (Frid, Clark et al. 1999) and climate change (Shi, Xu et al. 2010; Klauschies, Bauer et al. 2012) and community structure is altered by fishing activities (Kaiser, Ramsay et al. 2000). The next three sections expand this by reviewing studies conducted on benthic communities which highlight these three issues.

1.2 The Effect of Global Climate Change on Benthic Communities

The oceans act as the Earth's heat sink, and as anthropogenic climate change has increased global temperatures, the heat content of the upper layers of the ocean has increased concurrently (Hoegh-Guldberg and Bruno 2010). Over the last 100 years there has been an increase in the average temperature of the upper ocean of 0.6^{o}C (Hoegh-Guldberg and Bruno, 2010; Pachauri, 2007). Ocean warming is expected to cause significant alterations in the structure and composition of marine communities (Schiel, Steinbeck et al. 2004). However, our understanding of how climate change will affect marine ecosystems lags behind that of terrestrial ecosystems, mainly because of the relative difficulty of taking measurements in the marine environment (Hoegh-Guldberg and Bruno, 2010). This difficulty means that long-term studies assessing the impact of climate change in the oceans are rare compared to those on the land (Hoegh-Guldberg and Bruno, 2010; Rosenzweig et al, 2008). In addition to increases in water temperature there are several other changes in the chemical and physical conditions of the world's oceans that have been attributed to anthropogenic climate change. These include ocean acidification as a result of the absorption of anthropogenic CO_2; increased ocean volume and sea level rise as a result of glacial and ice sheet melt water runoff; increased stratification of the water column caused by the warming of the upper layers of the ocean, which affects nutrient availability and primary production; and decreased oxygen concentration in the upper layers of the ocean as a result of increased stratification (Hoegh-Guldberg and Bruno, 2010). For an up-to-date review of the observed and predicted changes to the world's oceans as a result of anthropogenic climate change see Hoegh-Guldberg and Bruno (2010). Below are some examples of the biological responses to climate change that have been observed within benthic communities around the world.

One of the commonly cited examples of such changes is to see a pole-ward shift in the distributional boundaries of species present (Schiel, Steinbeck et al. 2004; Drinkwater, Beaugrand et al. 2010). Such shifts should be more noticeable near the northern or southern boundaries of a species range (Drinkwater, Beaugrand et al. 2010). Examples of northward bound shifts in response to increasing temperature include *Calanus finmarchicus* and *Calanus helgolandicus* in the north-east Atlantic (Beaugrand, Reid et al. 2002), several zooplankton species in the Northeast Pacific (Mackas, Batten et al. 2007) and numerous examples from fish species (Drinkwater, Beaugrand et al. 2010). However, few empirical studies demonstrate this in benthic communities, perhaps because many benthic communities are adapted to fluctuating environments (see previous section and references therein). One possible example comes from the Dogger Bank in the central North Sea, where increased densities of 'southern' benthic species were recorded, accompanied by an increased range of 'northern' species on the northern slope of the Bank (Wieking and Kröncke 2001). This seemed to be linked with the

North Atlantic Oscillation (NAO) index, but was not a clear distributional shift in species' range (Rees, Pendle et al. 2006).

In the southern North Sea there was a shift in the benthic community structure in the late 1980s (Reiss, Meybohm et al. 2006). This was related to a period of mild winters that resulted in an increase in abundance, biomass and species number of the benthic macrofauna, including the sea urchin *Echinocardium cordatum* (Kröncke, Dippner et al. 1998; Kröncke, Zeiss et al. 2001). The mild winters were correlated with the North Atlantic Oscillation (NAO) Index, a climatic index, which describes the difference in atmospheric pressure at sea level between the Icelandic low and the Azores high. The NAO controls the strength and direction of westerly winds and storm tracks across the North Atlantic. Particularly between November and April the NAO is responsible for much of the weather variability in the North Atlantic region, predominantly in Western Europe (Jones et al, 1997; Osborn, 2004; Osborn, 2006; Osborn, 2011), and therefore probably mediated by sea surface temperature (SST) (Reiss, Meybohm et al. 2006). However, this benthic community shift was not in the form of species range shifts as has been predicted.

In another study, Schiel et al (2004) showed that the response of a near-shore benthic community on the California coastline to a 3.5°C increase in temperature over 10 years was mostly unpredicted. The increase in temperature came from an outflow of cooling water from a power station (Schiel, Steinbeck et al. 2004). In this case there seemed to be no distributional range shifts in the species present, as had been expected (Schiel, Steinbeck et al. 2004). That is not to say that there was no change, subtidal communities altered dramatically in this time period, with what were described as lasting, cascading effects (Schiel, Steinbeck et al. 2004). One such effect was a change in the dominant species in the kelp canopy to a species more tolerant of warm temperatures (Schiel, Steinbeck et al. 2004). This in turn changed the light conditions below the canopy and the other algal species that could survive, which then influenced changes in benthic fauna (Schiel, Steinbeck et al. 2004). This particular example illustrates how benthic communities are interconnected with the wider marine ecosystem and as such can be vulnerable to the indirect effects of climate change.

Many ocean warming studies have focused on the effect increasing SST will have on the plankton, which may be the main way that benthic communities are affected (Callaway, Engelhard et al. 2007). An increase in seawater temperature in this way could alter food supply to the benthic community. For example, phytoplankton productivity is controlled by climatic factors; earlier phytoplankton blooms caused by increasing temperature often mean more sinking primary production, therefore more food for the benthos (Frid, Buchanan et al. 1996; Kirby and Beaugrand 2009; Drinkwater, Beaugrand et al. 2010). An alteration in the timing of phytoplankton blooms could therefore mean that vital food sources reach the benthos at the wrong time. For example, a study of surf clams (*Spisula solidissima*) in the Northwest Atlantic proposed that their death was caused by malnourishment (Yungkul and Powell 2004). This was due to an environmental shift, mediated by increasing SST, which led to a mismatch between food supply and demand (Yungkul and Powell 2004). Temperate marine ecosystems are thought to be particularly vulnerable to this phenological mismatch because the recruitment success of higher trophic levels is dependent on synchronization with pulsed planktonic production (Edwards and Richardson 2004).

The North Sea is one temperate marine ecosystem that has experienced such a change. Edwards and Richardson (2004) showed that dinoflagellates have advanced their seasonal peak by almost a month but diatoms have continued to bloom at the same time. This is a good example of the use of cues for phenological events, the two main cues in the marine environment are temperature and light (Drinkwater, Beaugrand et al. 2010). In this case dinoflagellates use temperature as their cue, whereas diatoms use light. The mismatch between these two trophic levels (dinoflagellates consume among other things diatoms) has repercussions further along the food chain, in terms of the transfer of energy. In fact, this observed difference in the plankton is thought to have exacerbated the decline in North Sea cod stocks (Edwards and Richardson 2004). In addition to the above pelagic species many benthic species also use temperature as their cue for spawning (Kirby, Beaugrand et al. 2008). Ocean warming would mean earlier spawning in many cases and a subsequent change in the plankton at particular times of the year (Edwards and Richardson 2004; Kirby, Beaugrand et al. 2008).

A later study in the North Sea using the Continuous Plankton Recorder (CPR) found that there was an increase over 45 years in the larvae of benthic echinoderms in the meroplankton (Lindley and Batten 2002; Kirby, Beaugrand et al. 2007). In addition to this increase there was an advance of 47 days in the peak abundance of the larvae in the plankton over the same time period (Kirby, Beaugrand et al. 2007). This finding represents the largest phenological change found in the plankton of the North Sea so far (Edwards and Richardson 2004; Kaiser, Blyth-Skyrme et al. 2007; Kirby, Beaugrand et al. 2007). The dominant echinoderm in this larvae was *Echinocardium cordatum* and it was found that increasing SST seemed to be responsible (Kirby, Beaugrand et al. 2007). The reproductive cycle of *E. cordatum* is cued by temperature at several stages: gametogenesis in the North Sea begins at the end of winter when temperatures reach 6^{o}C (Nunes and Jangoux 2004); increased temperature during gametogenesis increases the number of eggs spawned and reduces their size, therefore increasing individual fecundity (Kirby, Beaugrand et al. 2007); spawning then occurs between 10 and 13^{o}C (Nunes and Jangoux 2004; Kirby, Beaugrand et al. 2007); and finally increasing temperatures reduce the amount of time spent in the larval stage (a period of high mortality) by speeding up development and therefore increasing survival (Kirby, Beaugrand et al. 2007). It is thought that increased larval abundance of *E. cordatum* will increase recruitment and that warmer winters will aid adult survival (Kirby, Beaugrand et al. 2007). This seems to be supported by underwater benthic surveys which have shown an increase in the density of *E. cordatum* even in the coldest parts of the North Sea (Kirby, Beaugrand et al. 2007; Rees, Eggleton et al. 2007). An increase of adults within the benthic community would further increase reproductive output (Kirby, Beaugrand et al. 2008). Temperature also seems to play a role in adult survival during the winter, with increasing temperatures improving survival of *E. cordatum* particularly in near-shore areas (Zeiss and Kröncke 1997; Reiss, Meybohm et al. 2006; Kirby, Beaugrand et al. 2008).

Not all species react in the same way to increasing temperature, however, further studies in the North Sea have shown that bivalve larval abundance has declined over the same period as the above study (Kirby, Beaugrand et al. 2008). This decline is not thought to be due directly to increasing SST, as there is still a positive relationship between bivalve larvae and SST (Kirby, Beaugrand et al. 2008). Rather it is thought to be caused by a concurrent increase in the predatory decapod species which feed on newly settled bivalve larvae (Philippart, van Aken et al. 2003; Kirby, Beaugrand et al. 2008). Landings of predatory decapods species have increased in the North Sea, whereas bivalve landings have not (Kirby, Beaugrand et al. 2008). Therefore, the reduction in bivalve larvae is thought to represent a dwindling adult population, brought about by poor recruitment due to an increase in predators (Kirby, Beaugrand et al. 2008). This illustrates that although benthic species with similar life histories may respond in the same way to ocean warming, species interactions can lead to very different outcomes (Kirby, Beaugrand et al. 2008). The North Sea has altered considerably in the last century, as a result of both fishing and climate change (Kirby and Beaugrand 2009). The new dynamic regime that exists there has been found to favour jellyfish in the plankton and decapods and detritivores (echinoderms) in the benthos (Kirby, Beaugrand et al. 2008; Kirby and Beaugrand 2009). The main reason for this change is an increase in SST of only 1°C although this has occurred following decades of overfishing (Kirby and Beaugrand 2009).

A warming ocean has also been shown to increase disease outbreaks in some marine species. The fishery for Icelandic scallops (*Chlamys islandica*) in Breidafjordur, West Iceland was halted in 2004 after the stock was unable to withstand fishing pressure and declined to a historically low level (Jonasson, Thorarinsdottir et al. 2007). It was found that a complex interaction of infection, food availability and temperature was the most plausible explanation for the reduced resilience (Jonasson, Thorarinsdottir et al. 2007). An increase in SST has been related to increased parasite prevalence in other shellfish species (Cook, Folli et al. 1998). Therefore this, combined with a possible reduction in food availability, made the *C. islandica* populations less resilient to fishing pressure (Jonasson, Thorarinsdottir et al. 2007). Much of the focus when it comes to marine pathogens is on coral reef disease, however, growth rates of marine bacteria and fungi are both positively correlated with temperature (Harvell, Mitchell et al. 2002). Therefore this may be an emerging threat to benthic communities as ocean warming continues.

In addition to an increase in temperature, global climate change could also increase the frequency of extreme weather events such as seasonal storms (Easterling, Meehl et al. 2000). As has already been mentioned, seasonal storm events are one of the natural variables that structure benthic communities (Kaiser 1998; Bradshaw, Veale et al. 2002). Therefore an increase in their frequency could have important implications. In the North Sea, for example, long-term changes in the benthic macrofaunal communities were not only related to winter temperatures but also the frequency of storm events (Kröncke, Dippner et al. 1998; Kröncke, Zeiss et al. 2001; Reiss, Meybohm et al. 2006). Such things are less easy to measure and predict and it is often the case that increasing temperature is used to signify climate change in many studies (Drinkwater, Beaugrand et al. 2010). It can also be argued that temperature is the most dominant climate variable in terms of its effect on marine ecosystems (Drinkwater, Beaugrand et al. 2010), however, other variables such as storm events should not be forgotten.

1.3 The Effect of Pollution on Benthic Communities

The major sources of anthropogenic organic inputs into near-shore marine systems come from sewage effluent, farm runoff and industrial inputs (Clark 2001). Some studies have looked at the effects of sewage sludge (the product of land-based sewage treatment), which was often disposed of in the sea until a Europe wide ban came into place in 1998 (Rees, Pendle et al. 2006). Sewage and sewage sludge dumped into the marine environment has a direct impact on benthic fauna, which is exposed to the sedimentation of organically rich particulate matter (Frid, Clark et al. 1999; Clark 2001; Rees, Pendle et al. 2006). Sensitive benthic species are excluded from the resident fauna because of smothering by the particulate matter and the reduction of oxygen concentration caused by enhanced bacterial activity (Clark 2001). However, more tolerant species flourish because of the input of extra nutrients, which results in a reduction in overall diversity but an increase in the abundance of organisms (MacKay, Halcrow et al. 1972; Moore and Rodger 1991; Clark 2001). Studies conducted while sewage sludge dumping was ongoing in the Firth of Clyde on the west coast of Scotland showed these classic effects of organic enrichment on the benthic macrofauna (MacKay, Halcrow et al. 1972; Moore and Rodger 1991). In addition to the biological effects it was estimated that 20km^2 of the sediment around the dumping site was contaminated by trace metals (Halcrow, MacKay et al. 1973; Moore and Rodger 1991).

Several studies have looked at the recovery of benthic communities following the cessation of sewage sludge dumping. On the North-east coast of England the presence of artefacts within sediments, such as tomato pips (a good indicator of sewage contamination as they pass through the human digestive system intact) provided evidence of the lasting effects of historical sewage-sludge dumping 5 years after it was stopped (Rees, Pendle et al. 2006). However, the benthic macrofauna seemed to be no longer affected by the marginal enrichment of the sediment caused by the sewage-sludge after 3 years (Rees, Pendle et al. 2006). This was in contrast to a benthic community in the New York Bight, which received a much greater amount of sewage sludge and had not completely recovered after 3 years (Moore and Rodger 1991). There was still a reduction in benthic macrofauna biomass, no shift in the dominance of species to match unaffected areas and evidence of sewage sludge still existed in the sediment (Moore and Rodger 1991). Another study done on a slow-moving, deep-water site at Garroch Head in Scotland showed communities were still altered 14 years after the cessation of sewage sludge dumping (Moore and Rodger 1991). It is clear just from this handful of studies that the effect of sewage sludge and other organic discharges to the marine environment depends a lot on the local hydrography (Clark 2001).

The input of anthropogenic organic matter tends to have specific effects for the benthic community within the area it has been discharged, but wide spread effects are not often reported (Clark 2001). An indirect benthic effect of increased nutrients in the marine environment comes from an increase in phytoplankton (Frid, Clark et al. 1999; Clark 2001). Off the Northumberland coast of England between 1972 and 1999 an increase in phytoplankton was caused by increased organic input into the system (Frid, Clark et al. 1999). Some of the changes in the benthic community structure at both heavily and lightly fished sites during this time period reflected the increase in food supply caused by the increasing phytoplankton (Frid, Clark et al. 1999). Other changes were directly related to fishing pressure (Frid, Clark et al. 1999), which highlights the effect of multiple stressors on the benthic community, as mentioned at the beginning of this chapter. As also mentioned above, changes in the abundance of phytoplankton can also be caused by increasing SST (Edwards & Richardson, 2004). In the North Sea, eutrophication is just one of many anthropogenic impacts (see above and below), but it was considered to be the cause of a shift in the benthic community at Dogger Bank between the 1950s and the 1980s (Kröncke 1990; Callaway, Engelhard et al. 2007). The shift was from long-lived species to opportunistic, short-lived species (Kröncke 1990; Callaway, Engelhard et al. 2007). However, it coincided with an increase in fishing pressure, which could have brought about the same community changes (see below) and it is thought that both impacts could have had a synergistic effect on the benthic community (Callaway, Engelhard et al. 2007).

1.4 The Effect of Bottom Fishing on Benthic Communities

Bottom fishing using towed nets and dredges has occurred for centuries (de Groot 1984; Kaiser, Ramsay et al. 2000; Roberts 2007). There has been concern about the effect that towed fishing gear has on the environment for as long as it has been used (de Groot 1984; Collie, Escanero et al. 1997; Thrush and Dayton 2002; Roberts 2007). In more recent years a greater environmental awareness has resulted in increased concern, as heavier gear is towed deeper and by larger vessels than ever before (Currie and Parry 1996). Bottom fishing has been conducted on such a scale that it is often described as one of the greatest sources of anthropogenic disturbance to marine benthic communities (Dayton, Thrush et al. 1995; Jennings and Kaiser 1998; Thrush, Hewitt et al. 1998; Kaiser, Ramsay et al. 2000; Thrush and Dayton 2002; Carbines and Cole 2009). Bottom fisheries use gear designed to catch species that live within, on, or in close association with the seabed (Kaiser, Ramsay et al. 2000; Veale, Hill et al. 2000). As the gear passes over the seabed, incidental damage can occur to habitats and large amounts of the resident biota can be removed, whether they are target species or not (Kaiser, Ramsay et al. 2000). The damage caused by towed fishing gear to structurally complex habitats and fauna has been likened to forest clear-cutting (Watling and Norse 1998).

Towed fishing gears cause varying levels of disturbance to the seabed, ranging from altering its complexity and topography; removing, damaging or killing benthic fauna; reducing benthic production, and altering sediment characteristics (Caddy 1973; de Groot 1984; Currie and Parry 1996; Ramsay and Kaiser 1998; Thrush, Hewitt et al. 1998; Watling and Norse 1998; Hall-Spencer and Moore 2000; Hall-Spencer and Moore 2000; Bradshaw, Veale et al. 2001; Piersma, Koolhaas et al. 2001; Bradshaw, Veale et al. 2002; Kaiser, Clarke et al. 2006). The impacts of demersal fishing gear on the benthic community include the reduction in abundance of fragile, large-bodied organisms while allowing small, fast growing and opportunistic species to flourish (Jennings and Kaiser 1998; Kaiser, Hinz et al. 2005; Capasso, Jenkins et al. 2009). Many studies have focused on the short-term changes to benthic communities caused by towed fishing gear (Kaiser, Ramsay et al. 2000). This is mainly because long-term changes are difficult to measure when historical datasets do not exist and even when they do sampling methodologies may not be comparable with modern techniques (Callaway, Engelhard et al. 2007). However, given the vulnerability of some benthic fauna to towed fishing gear in the short-term, it seems sensible to assume that changes will be made to the composition of the benthic faunal community when fishing has been conducted over a large time-scale (Callaway, Engelhard et al. 2007). What follows are brief examples from around the United Kingdom (U.K.) where long-term changes in the benthic community caused by a century of fishing, have been observed.

1.4.1 The Irish Sea

Kaiser et al (2000) studied benthic communities in two habitats in the Irish Sea, where chronic fishing disturbance has occurred, and found that the communities present showed responses to this disturbance that concur with theoretical work. Shell scars were studied on a long-lived (>30 years) bivalve *Glycymeris glycymeris* and showed that at least 40% of the samples were from areas of seabed that had been physically disturbed by fishing gear at different intensities over many years (Kaiser, Ramsay et al. 2000). Abundance-biomass curves for infaunal and epifaunal species in areas of high fishing activity tended to converge, whereas in areas less intensively disturbed the biomass curve lay much higher above the abundance curve (Kaiser, Ramsay et al. 2000). That is to say that highly disturbed areas were dominated by smaller-bodied organisms that are more tolerant of physical disturbance and relatively large-bodied fauna had been removed (Kaiser, Ramsay et al. 2000).

1.4.2 The English Channel

In the English Channel a study of benthic community change at Eddystone Reef over 112 years, found similar results to the Irish Sea study (Capasso, Jenkins et al. 2009). In particular, large-bodied, fragile organisms such as sea urchins *Spatangus pupureus* and *Echinus esculentus*, and large starfish *Marthasterias glacialis* and *Crossaster papposus* appeared in one 1895 study but were not found again in 2007 (Capasso, Jenkins et al. 2009). These species are particularly prone to damage from towed fishing gear (Jenkins, Beukers-Stewart et al. 2001) and the fact that prior to the original 1895 study the only fishing that was conducted around Eddystone Reef was long-lining and a few sail trawlers, suggests that the subsequent expansion of towed bottom fishing was largely responsible for this change (Capasso, Jenkins et al. 2009).

1.4.3 The North Sea

The North Sea is an intensively fished marine ecosystem, with the entire North Sea being fished by 1900 (Jennings, Greenstreet et al. 2002). Fishing effort has more or less increased consistently since then (apart from dips during the two World Wars) and dramatic declines in target fish species such as cod (*Gadhus morhua*) have been witnessed (Jennings, Greenstreet et al. 2002; Thurstan, Brockington et al. 2010). In the North Sea the effects of fishing on the epibenthos have been more difficult to untangle from other anthropogenic impacts, particularly climate change and eutrophication (see above) (Callaway, Engelhard et al. 2007). In addition to large bodied commercial species, such as the queen scallop *Aequipecten opercularis* and horse mussel *Modiolus modiolus*, the other species that declined in abundance over the century of study in the North Sea include those that are vulnerable to the effects of bottom fishing (Callaway, Engelhard et al. 2007). In particular, fragile bodied (*S. purpureus, Phaxas pellucidus*, *Echinocyamus pusillus*, *Brissopsis lyrifera*) and long-lived organisms (*Arctica islandicus*) declined in abundance (Callaway, Engelhard et al. 2007), whereas small robust species such as *Psammechinus miliaris* and *Ophiura ophiura* seemed unaffected by fishing (Callaway, Engelhard et al. 2007). In addition, species with regenerative capabilities (e.g. starfish and crabs) that can encounter fishing gear and survive, have increased (Callaway, Engelhard et al. 2007). This suggests that the changes observed in the North Sea are at least partly due to the effects of fishing over the last century, although climate change and eutrophication are both important additional components of this system (Callaway, Engelhard et al. 2007).

This short section has shown that towed bottom fishing can have lasting effects on benthic communities in both the short and long term. Of all the different types of towed bottom fishing gear that are used, dredging for shellfish has been described as the most non-selective and damaging to benthic fauna and substrates (Currie and Parry 1996; Collie, Escanero et al. 2000; Collie, Hall et al. 2000; Eleftheriou 2000; Jenkins, Beukers-Stewart et al. 2001; Kaiser, Clarke et al. 2006; Carbines and Cole 2009). What follows is a section that describes the effect of shellfish dredging on benthic communities in more detail.

1.5 The Impact of Dredging on Benthic Communities

The effect that dredging has on benthic communities depends on a complex set of conditions, including the type of sediment, the level of natural disturbance, the type of fishing gear used, structural complexity and the resident fauna (Collie, Escanero et al. 1997; Løkkeborg 2005; Kaiser, Clarke et al. 2006; Morsan 2009). A meta-analysis of over a hundred different studies on the impact of fishing showed that the magnitude of impact varied significantly among habitats (Kaiser, Clarke et al. 2006). For example, benthic communities that are adapted to sandy substrates are generally more resilient than those living on gravelly and sand/shell substrata (Eleftheriou and Robertson 1992; Guijarro Garcia, Ragnarsson et al. 2006). This is thought to be due to the highly energetic nature of a sandy habitat, which means natural physical processes will have a significant habitat-structuring influence (Kaiser, Clarke et al. 2006). For example, Stokesbury & Harris (2006) studied Georges Bank, northwest Atlantic and suggested that the epibenthic community associated with the scallop grounds there was adapted to living in a highly dynamic environment, and therefore was not so heavily disturbed by the effects of scallop dredging.

Of the different types of towed fishing gear used, the same meta-analysis mentioned above, also showed that scallop dredges produced the largest negative responses, in comparison to other fishing gear (Kaiser, Clarke et al. 2006). Scallop dredges are designed to penetrate the surface layers of the seabed and may dig down as far as 10cm, making benthic epifauna particularly vulnerable (Ramsay and Kaiser 1998). As for all towed bottom gear, the resident fauna exhibiting the characteristics of long-lived, slow-growing epifaunal species, which have a fragile body structure, in general are more sensitive to encounters with dredges than taxa with protective exoskeletons (Hall-Spencer and Moore 2000; Kaiser, Ramsay et al. 2000; Guijarro Garcia, Ragnarsson et al. 2006). Megafaunal species (>10mm) are often more vulnerable to the effects of dredging than macrofaunal species because they tend to be relatively slow growing and take a long time to recover from disturbance (Collie, Escanero et al. 1997). Other characteristics that would make fauna resilient to the effects of dredging include the ability to avoid the dredge by swimming away or burrowing deep into the sediment, as well as life history characteristics which ensure a large supply of young (i.e. highly fecund) (Bradshaw, Veale et al. 2002).

Previous studies have concluded that the effects of dredging are more severe in the early stages of the fishery (Kaiser, Hill et al. 1996; Jennings and Kaiser 1998; Tuck, Hall et al. 1998; Hall-Spencer and Moore 2000; Guijarro Garcia, Ragnarsson et al. 2006). These changes involve the loss of epibenthic biogenic structures and their associated fauna (Guijarro Garcia, Ragnarsson et al. 2006). The most apparent effects of continued dredging are the reduced abundance of species and the alteration of benthic community structure (Kaiser, Ramsay et al. 2000; Carbines and Cole 2009). Scallop dredges can also increase the sediment load, relocate boulders and destroy topographic features (Guijarro Garcia, Ragnarsson et al. 2006). Foveaux Strait, New Zealand, has been dredged for oysters for over 130 years (Carbines and Cole 2009). In un-dredged sites there was a more complex 3D structure inhabited by a more diverse fauna than dredged sites (Carbines and Cole 2009). On the other hand, a study on the northern edge of Georges Bank, northwest Atlantic, showed that sites disturbed by dredging had a higher diversity than un-dredged sites, thought to be because dredging prevents any one species from becoming dominant (Collie, Escanero et al. 1997). However, it was also found that disturbed sites lacked any colonial epifauna (Collie, Escanero et al. 1997).

It is becoming clear that not all benthic species will respond to disturbance in a uniform way and it is difficult to precisely predict the response of individual species to the effects of dredging (Currie and Parry 1996; Collie, Escanero et al. 1997; Hill, Veale et al. 1999). Some species may even benefit from the bycatch and/or damaged organisms that are left behind in the fishing gear’s wake, or in the case of encrusting epifauna (e.g. bryozoans, sponges etc.) flourish in dredged areas where new substrate is continually being uncovered (Currie and Parry 1996; Ramsay, Kaiser et al. 1998; Hill, Veale et al. 1999; Kaiser, Cheney et al. 1999; Bradshaw, Veale et al. 2001; Bradshaw, Veale et al. 2002). Bycatch is a pervasive part of the majority of marine capture fisheries and it spans the spectrum of marine fauna, from turtles on hooks to benthic invertebrates in dredge bags (Davies, Cripps et al. 2009). The role of bycatch in degrading marine ecosystems has made it one of the most significant nature conservation issues in the world today (Davies, Cripps et al. 2009). The typical bycatch from scallop dredges is comprised of species that live on, or near the sediment surface and are sufficiently large enough to be retained by the steel rings of the dredge 'belly' (Kaiser, Armstrong et al. 1998; Veale, Hill et al. 2001). High levels of mortality in certain megafaunal species, as a result of being part of a fishery's bycatch, may result in radical changes in the benthic community structure through effects on trophic relationships and competitive interactions (Jennings and Kaiser 1998; Jenkins, Beukers-Stewart et al. 2001). Bycatch species may also be affected at a population level, for example through local extinctions or reductions in population sizes (Philippart 1998; Veale, Hill et al. 2001).

Several things can happen when animals become bycatch: they can be killed directly; damaged to the point where predation or disease are inevitable, therefore killed indirectly; damaged to the point that there is an energetic cost to recover from, or suffer minor damage that requires little energetic cost to recover from (Jenkins, Beukers-Stewart et al. 2001; Veale, Hill et al. 2001). In heavily fished areas it is likely that capture will happen on more than one occasion, therefore the chance of damage is high (Ramsay, Bergman et al. 2001). Additional stress could also be experienced by those animals escaping predation following capture, which has been described as a chronic effect of bycatch capture (Veale, Hill et al. 2001). Scavengers and predators have been shown to increase due to fishery discards and damaged organisms on the seafloor, which can provide a large food source (Ramsay, Kaiser et al. 1996; Collie, Escanero et al. 1997; Escolar, Diez et al. 2009). In addition to those organisms that are bycatch, there are also high levels of mortality in organisms that encounter the dredges but are not captured (Jenkins, Beukers-Stewart et al. 2001). In the case of spring-toothed scallop dredges like the Newhaven dredge capture efficiency for non-target organisms is quite low, therefore the majority of megafauna that will encounter the scallop dredges will remain on the seabed but in a damaged condition (Jenkins, Beukers-Stewart et al. 2001).

The damage sustained by non-target animals varies depending on the composition of the substratum, the fragility of their body and any behavioural adaptations (Veale, Hill et al. 2001). For example, although the soft body of *Asterias rubens* means that they are easily damaged by bottom fishing (Eleftheriou and Robertson 1992), their regenerative capabilities mean that they are relatively resilient to capture within the dredge (Ramsay, Kaiser et al. 1998; Veale, Hill et al. 2000; Bradshaw, Veale et al. 2002). Autonomy (a nervously mediated shedding of a limb or other body part) and regeneration are common within echinoderms (Ramsay, Bergman et al. 2001), therefore other species within this group may also be able to cope with capture or damage by the dredge (e.g. some species of brittlestars) (Bradshaw, Veale et al. 2002). However, complete regeneration of a lost arm by *A. rubens* can take over a year (Ramsay, Bergman et al. 2001), which may mean in heavily fished areas, repeated capture or damage by the dredge could become an issue. In other types of bottom fishing it has been found that some starfish and brittlestar species are vulnerable to the impacts of the fishery. For example, within the *Nephrops norvegicus* trawl fishery in the Clyde Sea the most vulnerable bycatch species to damage was found to be the brittlestar *O. ophiura* (Bergmann, Beare et al. 2001). Another starfish species (*Astropecten irregularis*) within this fishery also suffered a high amount of damage when caught as bycatch (Bergmann, Beare et al. 2001).

In addition to the physical damage caused by dredging to benthic fauna, individual species responses are determined by behavioural adaptations (Jenkins, Mullen et al. 2004). For example, *A. rubens* is an opportunistic predator within the benthic community, targeting a variety of things including discards from fisheries (Saier, 2001). *A. rubens* has an acute, seasonal chemoreceptive ability, at its peak during the winter months when seawater temperature is between 10-13^{o}C (Anger, Rogal et al. 1977; Saier 2001). If there is super-abundant food within chemoreceptive range, *Asterias* species have been known to migrate to the food source in huge aggregations (Marino, Juanes et al. 2007). These aggregations have been reported on mussel (*Mytilus edulis*) beds in the lower intertidal and shallow subtidal areas of the White Sea coast of Russia, Sweden, Denmark and all around Great Britain (Sloan and Aldridge 1981). Aggregations have also been found feeding on the scallops, *Chlamys islandica* (Brun 1968) and *A. opercularis* (Briggs 1981), clams *Spisula elliptica* (Sloan and Aldridge 1981) and ascidians, *Ciona intestinalis* (Gulliksen and Skjaeveland 1973). However, Barbeau & Scheiling (1994) found that *Asterias* species benefited more from immobile, damaged discards as a food source than from a large standing stock of mobile prey species (Barbeau and Scheibling 1994). As mentioned above, many short-term studies have shown localised influxes of scavengers like *A. rubens* to the dredge spoil (Caddy 1973; Ramsay, Kaiser et al. 1996; Collie, Escanero et al. 1997; Ramsay, Kaiser et al. 1998; Hall-Spencer and Moore 2000; Bradshaw, Veale et al. 2002; Guijarro Garcia, Ragnarsson et al. 2006). From these observations it appears possible that in fisheries where discarded bycatch is high, *A. rubens* may indeed benefit, despite being caught as bycatch itself.

The general effects of dredging on benthic communities have been well documented and overall seem to be negative. However, it is clear that the level of impact depends on several factors and could be described as site specific. In addition, when other variables are influencing benthic communities, such as eutrophication and ocean warming, the effects of dredging may not be as expected. Differential responses to all of the anthropogenic impacts by different taxa will also add to the complexity of the situation. What is clear though is that understanding how the benthic community at a particular location responds to all variables, anthropogenic and natural, is important for managing the ongoing and future human activity that could affect them.

1.6 Thesis Aims and Objectives

This chapter has discussed the complexities of benthic communities and the range of anthropogenic impacts that are affecting them. This thesis aims to untangle the effects of scallop dredging and environmental variables on commercially fished scallop grounds around the Isle of Man in the Irish Sea. A full review of the study site is given in the next Chapter, detailing historical fishing effort and the results of previous work in the area. In addition to what has been published previously, there are now several long-term datasets that can be utilised to attempt to understand the dynamics of these exploited benthic communities. These include 15 years of continuous bycatch data, which has been collected biannually during fisheries-independent scallop surveys at almost every fishing ground. As fishing pressure is not equal at each ground, this creates a gradient of fishing intensity with which to study the benthic community. Alongside this fisheries-independent data, a corresponding dataset of fishing effort exists, which is highly spatially specific, allowing the effects of the Manx scallop fishery on the benthic community to be investigated. Environmental data have also been collected off the south-west of the Isle of Man at the CYPRIS site covering the time series of this study. These long-term environmental data will be used to investigate whether environmental variables are playing a role within the benthic community. Finally, there exist independent benthic community data from an area that has been closed to fishing since 1989. This represents a recovering community that is no longer directly impacted by fishing effort. Therefore this dataset allows the investigation of the effects of environmental variables without the added pressure of scallop dredging.

The primary aim of this thesis is to use these long-term datasets to analyse and understand the benthic community around the Isle of Man. In doing so it is hoped that the long-term effects of anthropogenic activities, particularly scallop dredging, and the effects of environmental fluctuations, can be identified. The main problem in the majority of the work that has already been undertaken in this area is that many causative agents have been interplaying with each other. By analysing several different components of the benthic community it is hoped that the major structuring factors in this set of benthic communities can be identified.

I have four specific objectives:

1) *To investigate temporal and spatial trends in benthic community composition*
   By-catch data will be used as a proxy for benthic community composition and calculated into diversity indices across all eight fishing grounds. Temporal and spatial trends in these indices will then be analysed to determine whether there are significant changes in diversity at any of the fishing grounds over the time period of 1992 - 2006. Individual species densities will be calculated from bycatch abundance data. These will then be used to elucidate temporal trends in the dominant benthic species at each fishing ground and investigate the differences in species composition between fishing grounds.

2) *To analyse the effect of fishing pressure on benthic communities*
   Fishing effort data that are spatially specific for each of the eight fishing grounds will be used to determine whether fishing pressure is influencing benthic diversity across all of the fishing grounds. Then a more in depth analysis will be conducted investigating individual species responses to fishing pressure at each ground. This two pronged approach should give a broad understanding of the effect of fishing pressure on the benthic communities found on these grounds.

3) *To analyse the effect of environmental variables on benthic communities*
   Environmental data will be used in a series of multiple linear regression analyses of diversity at fishing grounds to the south-west of the Isle of Man. This analysis will be used to understand how environmental variables are influencing the benthic community on commercially exploited scallop fishing grounds. As with the fishing effort data, the effect of environmental variables on individual species will then be analysed in more detail.

4) *To investigate benthic community composition within a closed area*
   The 2km^2 closed area to the south-west of the Isle of Man has been sampled by dive surveys from 1989 to 2006. These data will be used to investigate the temporal trends in benthic megafaunal community composition. In addition, the effects of environmental variables on both diversity and individual species density within the closed area will be analysed. This analysis in an area that excludes fishing is likely to give a clearer picture of which environmental variables are playing a role in structuring this benthic community.

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Chapter 2

Review of the Isle of Man: Scallop Fisheries, Benthic Communities and Environmental Trends

2.1 Introduction

The Isle of Man is found in the north Irish Sea, between the coasts of Wales, Ireland, Scotland and England. The waters around the Isle of Man have been both studied and exploited for more than a century. A marine laboratory was established on the island in 1892 at Port Erin and this became part of the University of Liverpool in 1919. Although it was closed in 2006, research has continued through the University of Wales, Bangor since 2007 (Murray, Hinz et al. 2009). The long history of exploitation in the waters around the Isle of Man has in the past included fisheries for herring, Dublin Bay prawn, cod, plaice, whiting, dogfish, monkfish, Dover sole, crabs, lobsters, squid and whelks (Bradshaw, Veale et al. 2002). Currently these waters support five main fisheries, which target great scallops (*Pecten maximus*), queen scallops (*Aequipecten opercularis*), common lobster (*Homarus gammarus*), brown crab (*Cancer pagurus*) and whelks (*Buccinum undatum*) (Murray, Hinz et al. 2009).

The Isle of Man is at the centre of one of the most heavily exploited scallop fisheries in Europe (Kaiser, Ramsay et al. 2000; Bradshaw, Veale et al. 2002). The two species targeted are the great scallop (*P. maximus*) and the queen scallop (*A. opercularis*) (Bradshaw, Veale et al. 2001). The value of the great scallop fishery in 2005 was £1.75 million and the queen scallop fishery was valued at £450k in 2004 (Beukers-Stewart and Beukers-Stewart 2009).These two fisheries make up 85% of all landed seafood on the Isle of Man (Brand, Beukers-Stewart et al. 2005; Beukers-Stewart and Beukers-Stewart 2009) and boats from the Isle of Man (currently about 25), Ireland, Northern Ireland, Wales, England and Scotland (making up to 70 visiting vessels) all engage in the fishery for scallops in the north Irish Sea (Bradshaw, Veale et al. 2001; Beukers-Stewart, Vause et al. 2005; Read 2009). Both fisheries have been extensively researched since they began, with focus mainly being on the target species, although the environmental impact of scallop dredging has also been studied (Brand 2006; Beukers-Stewart and Beukers-Stewart 2009). This chapter aims to describe the history of scallop fisheries around the Isle of Man, including development of the gear used and management measures that have been implemented over the years. Then a review of the current understanding about the effect that the fishery has had on the populations of the two main species of scallops, the by-catch from the fishery and the benthic communities will follow. Finally investigations into the closed area at Port Erin will be reviewed along with recent research into the possible impacts of climate change.

2.2 History of the Isle of Man Scallop Fisheries

Great and queen scallops have dominated the Isle of Man fishing and fish processing industries since the collapse of the herring fishery in the late 1970s (Brand and Prudden 1997; Veale, Hill et al. 2001). However, the fishery for great scallops began in 1937 when Manx fishermen turned their attention to *P. maximus* following the decline of fin-fish stocks in the Irish Sea (Bradshaw, Veale et al. 2001; Bradshaw, Veale et al. 2002; Beukers-Stewart, Mosley et al. 2003). At that stage the fishery consisted of nine small (7.5 – 10.5 m) boats towing between one and three dredges, close inshore off the southwest coast of the Isle of Man (Bradshaw, Veale et al. 2001; Bradshaw, Veale et al. 2002). Up until 1950, little had changed and there were still only 14 boats in the fishery; however, by the mid-1950s a rapid expansion began (Brand 1999; Bradshaw, Veale et al. 2001; Bradshaw, Veale et al. 2002). By the mid-1960s the fleet had doubled in size and new grounds began to be exploited; initial catch rates following this expansion were high (Bradshaw, Veale et al. 2002). In contrast, the fishery for queen scallops did not begin until 1969, mainly to the south and the east of the island, using a range of trawls and dredges to catch this more mobile species (Bradshaw, Veale et al. 2002). The development of the queen scallop fishery prompted further exploitation of previously un-fished grounds (Brand 1999).

As the great scallop fishery developed so did the gear used. To begin with each boat towed a ‘gang’ of relatively large individual dredges (each were approximately 1 – 1.8 metres wide with a fixed tooth bar) (Brand 1999). This changed in 1972 when ‘Newhaven’ spring-toothed dredges were introduced and these quickly replaced the fixed-tooth dredges as the normal gear (Mason 1983; Brand 1999). The new style of dredge has, as the name implies, a spring-loaded tooth bar that allows the dredge teeth to flex backwards, preventing them from snagging on harder ground and improving the efficiency of the gear (Kaiser and Spencer 1996). “Newhaven” scallop dredges are designed to rake up great scallops from their recessed position in the seabed (Beukers-Stewart and Beukers-Stewart 2009). In the 1980s there was also a reduction in the individual dredge frame size to about 80cm wide, but these were typically fished in ‘gangs’ of up to 16 on each side of the boat (Veale, Hill et al. 2001). These gear developments enabled boats to exploit grounds with rougher seabed, so increasing the number of available fishing grounds (Brand, Allison et al. 1991; Brand 1999; Veale, Hill et al. 2000).

Queen scallops are a more mobile species than great scallops (Brand 2006; Beukers-Stewart and Beukers-Stewart 2009; Hinz, Murray et al. 2012). They are active swimmers and do not recess themselves in the seabed, therefore they are fished for with either a skid dredge (on rougher southern and western grounds) or trawls (on eastern and northern grounds) (Brand 2006; Beukers-Stewart and Beukers-Stewart 2009). Skid dredges are similar to Newhaven dredges in their operation, but they have the tooth bar replaced with tickler chains and have skids on either side that are designed to run along the top of the seabed (Vause, Beukers-Stewart et al. 2007; Beukers-Stewart and Beukers-Stewart 2009). The type of gear used also differs between the seasons, in the summer months (1^{st} June – 31^{st} October, during the closed season for *P. maximus*) queen scallops are primarily targeted using otter trawls because during the summer this species is more mobile than during the winter (Hinz, Murray et al. 2012). Although queen scallops are predominantly targeted in the summer months, those fishers that continue to fish them during the winter months tend to switch to using dredges (Hinz, Murray et al. 2012).

Despite the increase in effort and exploitation of new fishing grounds seen through the years, catch rates in the great scallop fishery fell to a very low level by the end of the 1980s when the number of boats engaged in the fishery reached its maximum of about 70 (Brand, Allison et al. 1991; Bradshaw, Veale et al. 2002; Beukers-Stewart, Mosley et al. 2003). Since then several management measures have been introduced (see below for full details of management measures), including closed areas, gear restrictions and minimum landing sizes (Beukers-Stewart, Vause et al. 2005). Annual landings of great scallops in the Isle of Man and Scotland continued to decline through the late 1980s and early 1990s (Murray, Hinz et al. 2009). After 1994, however, annual landings began to increase and although there have been year on year fluctuations some recovery seems to have occurred (Murray, Hinz et al. 2009). The queen scallop fishery has also shown large fluctuations in annual landings into the Isle of Man, but have remained around 1000-2000 tonnes for the past 14 years (Murray, Hinz et al. 2009). However, in comparison to annual landings into the Isle of Man in 1972 (7,600 tonnes) the 2008 landings (770 tonnes) are dramatically reduced (Murray, Hinz et al. 2009). Even the more recent peak in landings in 2010 (2817 tonnes; FAO Fishery and Aquaculture Global Statistics 2013) – the highest seen for several decades – is less than half of what was caught in the early 1970s. The recent fluctuations and reductions in both scallop species landings could be due to changes in fishing effort, stock abundance, or even market demand (Murray, Hinz et al. 2009).

2.3 Management of the Isle of Man Scallop Fisheries

The Isle of Man is a self-governing British Crown Dependency and is not a member of the European Union. Management of both scallop fisheries is the sole responsibility of the Isle of Man Government, Department of Environment, Fisheries and Agriculture (DEFA) (this department was previously known as the Department for Agriculture, Fisheries and Food (DAFF)) within the Territorial Sea, which runs out to 12 miles offshore (Beukers-Stewart and Beukers-Stewart 2009). However, between 3 and 12 miles offshore any management measures must be agreed with the U.K.(Beukers-Stewart and Beukers-Stewart 2009). The management of Manx scallop fisheries is generally considered to be ahead of the U.K. and has evolved considerably since the fisheries began (Beukers-Stewart and Beukers-Stewart 2009).

2.3.1 Management measures in the Great Scallop fishery

The fishery for great scallops has been regulated in a variety of ways, with conservation legislation being in place since 1943 and the most recent update in 2010 (Bradshaw, Veale et al. 2001; Beukers-Stewart, Mosley et al. 2003; Department of Environment 2010). The legislation restricts the fishing of great scallops to an open season that currently runs from 1 November to 31 May inclusive (Bradshaw, Veale et al. 2001; Beukers-Stewart, Mosley et al. 2003). Vessels that want to fish for scallops within Manx waters must be licensed with a U.K. and Manx licence and an additional permit is required for fishing within the first 3 miles offshore (DAFF 2009). There is a minimum landing size of 110mm shell length for great scallops, (Bradshaw, Veale et al. 2002). There are also restrictions on boat size, gear type and gear widths within the Isle of Man 12 mile Territorial Sea (Brand, Wilson et al. 1991; Bradshaw, Veale et al. 2001; Bradshaw, Veale et al. 2002; Department of Environment 2010). Within the first 3 miles offshore the total width of scallop dredges must not currently exceed 762 cm (25ft) and a maximum of five dredges can be towed aside (DAFF 2009; Department of Environment 2010). In addition, a scallop fishing curfew exists, which bans fishing for scallops between 18.00 and 06.00 hours GMT within the 3 mile limit (DAFF 2009).

From 3 – 12 miles offshore the restrictions on total width of scallop dredges has recently (2010) been reduced from 1219cm (40ft), to 1067cm (35ft) (DAFF 2009; Department of Environment 2010). Tow bar diameter has been limited to 185mm within the 3-12 mile limit and a limit on the number of dredges fished per side within this area was introduced in 2010, a maximum of seven dredges aside are now permitted (Department of Environment 2010). Finally, the scallop fishing curfew has also been extended in this area by two hours, from 21.00 - 05.00 hours GMT to 20.00 – 06.00 hours GMT in 2010 (DAFF 2009; Department of Environment 2010). Several other new management measures were introduced in 2010, which although not relevant to this current dataset (1992 – 2006) illustrate how well managed the Isle of Man scallop fisheries are. All scallop fishing vessels within the whole Territorial Sea (0-12 miles) are now required to have satellite tracking devices and only vessels with engine power less than 221kw are allowed to fish for scallops (Department of Environment 2010).

2.3.2 Management measure in the Queen Scallop fishery

Up until 2010 the queen scallop fishery had relatively fewer restrictions than the great scallop fishery, for example it could be fished all year round, but was mainly targeted in the summer months (Brand, Allison et al. 1991; Veale, Hill et al. 2001; Vause, Beukers-Stewart et al. 2007; Hinz, Murray et al. 2012). There was no specific legislation regarding a minimum landing size for this species, although fishing gear was size-selective to target queen scallops that were >55mm shell length, primarily because of the economics of processing (Brand, Allison et al. 1991; Bradshaw, Veale et al. 2002; Vause, Beukers-Stewart et al. 2007). On the 7th August 2010, however, a bye-law was enacted by the Isle of Man government, which was created to deal with certain issues within the then expanding queen scallop fishery (DEFA 2013). The regulations enacted by this bye-law included: the creation of an annual closed season for queen scallops within the Manx territorial Sea between 1 April and 31 May, inclusive; a total ban on tooth bars on queen scallop dredges; a ban on dredging for queen scallops between the 1st June and 31st August; the creation of a queen scallop conservation zone, covering more than half the Territorial Sea, where all forms of queen scallop dredging are banned; an ability to close the fishery if the total catch recommended by fisheries scientists is exceeded; a minimum landing size of 50mm shell length; and a ban on new entrants to the fishery with engine power greater than 221Kw (Department of Environment 2010).

In 2011 the Isle of Man queen scallop trawl fishery was accredited by the Marine Stewardship Council as a sustainable trawl net fishery, the first scallop fishery in Western Europe to achieve this (DEFA 2013). In 2012 the queen scallop fishery was also awarded ‘Protected Designation of Origin’ status under European Union Law (DEFA 2013). This designation means that only queen scallops from Manx waters can be marketed as such and protects the reputation of this regional seafood (DEFA 2013). The fishery is currently managed by an independent Board, which has brought together various stakeholders in the queen scallop fishery and is viewed as a unique co-operative venture (DEFA 2013). Work continues to sustainably manage the queen scallop fishery, including a recent consultation to make amendments to the 2010 Bye-laws (DEFA 2013).

2.3.3 Closed area management

In 1989 an exclusion zone of approximately 2km^2 off the southwest of the Isle of Man was closed to commercial fishing by dredge or trawl under Isle of Man legislation (Beukers-Stewart, Vause et al. 2005). The taking of scallops by any means was also banned. Fishing with static gear such as lobster and crab pots, however, was allowed to continue within the closed area (Beukers-Stewart, Vause et al. 2005).This closed area was heavily dredged in the 50 years prior to closure and is situated near one of the most intensively fished grounds in the Irish Sea, called the Bradda Inshore fishing ground (43% of the seabed at this fishing ground is dredged each year) (Bradshaw, Veale et al. 2001). The closure was initially implemented to allow Port Erin Marine Laboratory scientists to investigate the possibility of scallop cultivation and stock enhancement, but has since given the opportunity to monitor the benthic community after the cessation of dredging (Bradshaw, Veale et al. 2001; Beukers-Stewart, Vause et al. 2005). In 2003 the closed area was increased in size with the support of the Manx fishing industry (Read 2009).

In 2008 Douglas Bay on the east coast of the Isle of Man was designated as the second closed area (Murray, Hinz et al. 2009). There are also currently two restricted areas, where fishing for, taking or killing both species of scallops is prohibited, Laxey Bay on the east coast and Niarbyl Bay on the southwest coast (DAFF 2009). Furthermore, in 2009 the Isle of Man's first Marine Nature Reserve was designated at Ramsay Bay, which is also closed to fishing (Department of Environment 2010). All of these spatial management measures have been made with the support of the Manx fishing industry (A. Read *pers comm.*).

2.3.4 Voluntary log-book scheme

As mentioned at the beginning of this Chapter, a marine laboratory existed at Port Erin from 1892 – 2006 and research continues to this day through Bangor University, Wales. Much of the work has been investigating the dynamics of the scallop stocks on the various fishing grounds, although there are several publications investigating the wider effects of the fishery. To aid this research, data has been collected from Manx fishermen on the effort of the Manx fishing fleet since 1981 in the form of a voluntary logbook scheme (Brand and Prudden 1997; Beukers-Stewart, Mosley et al. 2003). About a third of the Manx fishing fleet record catch and effort data on a precise 5 x 5 nautical mile spatial scale (Brand and Prudden 1997; Veale, Hill et al. 2001). These boxes correspond to individual fishing grounds for the smaller grounds, with larger grounds taking up two or more boxes (Beukers-Stewart, Mosley et al. 2003). This is an unusually small and precise spatial scale given that the standard International Council for the Exploration of the Sea (ICES) fisheries statistical rectangles cover 30 x 30 n.m. (Rijnsdorp, Buys et al. 1998; Veale, Hill et al. 2001). Despite only one-third of the Manx fleet recording their fishing data in this way it can then be multiplied up to give an estimate of the total effort for the whole fleet (Kaiser, Ramsay et al. 2000). The database now contains over two decades of spatially precise effort data that has been used in studies to understand and explain the effects of this fishery (e.g. (Kaiser, Ramsay et al. 2000; Veale, Hill et al. 2001; Beukers-Stewart, Mosley et al. 2003).

2.4 The Effect of Scallop Dredging on Scallop Populations

2.4.1 Effect of the Great Scallop fishery

In general scallop stocks tend to have highly variable recruitment, which leads to "boom and bust" cycles in scallop fisheries (Orensanz, Parma et al. 1991; Beukers-Stewart, Mosley et al. 2003; Vause, Beukers-Stewart et al. 2007; Beukers-Stewart and Beukers-Stewart 2009). Having said that, unsustainable exploitation of scallops causes large reductions in abundance that exacerbates the variability in their recruitment and is often also the reason for such patterns in their fisheries (Orensanz, Parma et al. 1991; Beukers-Stewart and Beukers-Stewart 2009). Recruitment of *P. maximus* around the Isle of Man is not thought to be as variable as has been seen in other fisheries around the world (Brand, Allison et al. 1991; Beukers-Stewart, Mosley et al. 2003). However, the populations of *P. maximus* around the Isle of Man have been subjected to a long history of consistently high exploitation (Beukers-Stewart, Mosley et al. 2003). Prior to the current set of management measures (that were first implemented in the early 1990s) catch rates of *P. maximus* were following a downward trend, suggesting a fishery in continuous decline (Brand, Allison et al. 1991; Brand and Allison 1994; Beukers-Stewart, Mosley et al. 2003). From 1991 to 2001 catch rates stabilised and began to improve, although they were nowhere near those reported at the beginning of the fishery (Beukers-Stewart, Mosley et al. 2003). Catch rates now are at a 20 year high, despite the fact that the Manx fishing fleet is reduced to about half the size it was in the 1980s, although total landings are still much lower (Beukers-Stewart, Mosley et al. 2003; Brand, Beukers-Stewart et al. 2005; Beukers-Stewart and Beukers-Stewart 2009; Murray, Hinz et al. 2009).

Investigations have been undertaken into the affect that the scallop fishery has had on the scallop populations around the Isle of Man. These have shown that the great scallop populations have an altered age structure (Beukers-Stewart, Mosley et al. 2003). There has been a shift from a population, which was once dominated by scallops of ten years or older, to one dominated by scallops of five years or less (Brand, Allison et al. 1991; Brand and Beukers-Stewart 2000; Beukers-Stewart, Mosley et al. 2003). These results are supported by the fact that areas that have low relative densities of scallops do not appear to be targeted by fishermen and support a higher proportion of older scallops (>5 years old) than the heavily exploited fishing grounds (Beukers-Stewart, Mosley et al. 2003). A result of this change is that the fishery is now largely dependent each season on the strength of the recruiting year-class.

In addition to the capture mortality in scallop fisheries, there is evidence that fishing for scallops using dredges, has a range of effects on uncaptured scallops that come into contact with the dredge and juvenile scallops, which are caught and discarded (Beukers-Stewart and

Beukers-Stewart 2009). Undersized great scallops (<110mm) have been shown to make up to 70% of the catch in some areas (Beukers-Stewart, Mosley et al. 2003; Beukers-Stewart and Beukers-Stewart 2009). It is common practise for fishermen to return damaged and undersized scallops to the sea in the belief that they will survive and recruit into the fishery (Maguire, Coleman et al. 2002). However, undersized scallops returned to the sea following capture have been found to be stressed and more susceptible to predation (Caddy 1973; Maguire, Coleman et al. 2002). Research around the Isle of Man has also shown that discarded and disturbed great scallops may attract predators, therefore increasing their chance of predation (Veale, Hill et al. 2001; Beukers-Stewart, Mosley et al. 2003).

Scallop dredging is not a particularly efficient method of capturing great scallops, with spring-toothed dredges (which are used around the Isle of Man) having a capture efficiency of between 6 and 41% for individuals larger than 90mm (Dare, Key et al. 1993; Beukers-Stewart, Jenkins et al. 2001; Jenkins, Beukers-Stewart et al. 2001). In addition to capture mortality, both scallop fisheries around the Isle of Man can also damage the scallops that come into contact with the dredge but are not captured (Beukers-Stewart, Mosley et al. 2003). The teeth of Newhaven scallop dredges can cause significant, sometimes fatal physical damage to scallop shells (Beukers-Stewart, Jenkins et al. 2001; Jenkins, Beukers-Stewart et al. 2001; Beukers-Stewart and Beukers-Stewart 2009; Shephard, Goudey et al. 2009; Beukers-Stewart, Brand et al. in prep). The level of fatality varies greatly, from 2% to more than 20%, in captured and non-captured undersized scallops on different grounds (Beukers-Stewart and Beukers-Stewart 2009; Beukers-Stewart, Brand et al. in prep). This variability seems to be mainly due to spatial differences in the strength of the scallops shells (Beukers-Stewart and Beukers-Stewart 2009; Beukers-Stewart, Brand et al. in prep). Sublethal damage caused to scallops during the dredging process includes chipped valve margins, separation of the hinges, desiccation of and sediment in the mantle cavity (Maguire, Coleman et al. 2002). Survival from such damage obviously depends on the severity and frequency experienced. In areas that are subjected to heavy fishing these indirect effects of scallop dredging can have a significant effect on the productivity of scallop populations (Beukers-Stewart and Beukers-Stewart 2009).

Finally, as discussed in Chapter 1, scallop dredging can have important implications for the structure of the benthic community. It has been shown to reduce habitat complexity by impacting sessile epifaunal species (Auster, Malatesta et al. 1996; Collie, Escanero et al. 1997; Watling and Norse 1998; Bradshaw, Veale et al. 2000; Collie, Escanero et al. 2000; Kaiser, Ramsay et al. 2000; Bradshaw, Veale et al. 2001; Bradshaw, Collins et al. 2003). This is significant in terms of scallop populations because scallop spat (both great and queen) have been reported to settle predominantly on hydroids and bryozoans (Bradshaw, Collins et al. 2003; Howarth, Wood et al. 2011). Bradshaw et al (2003) found that pectinid spat were present in significantly higher numbers (8.4 times as many) in areas with hydroids, than those without, inside the closed area at Port Erin. Hydroids and other upright epifauna are generally less abundant in fished areas of the Irish Sea (Bradshaw, Veale et al. 2000; Bradshaw, Veale et al. 2001; Bradshaw, Collins et al. 2003; Lambert, Jennings et al. 2011). However, hydroids are still present in fished areas around the Isle of Man and Bradshaw et al (2003) suggest that this could be due to the closed season in the scallop fishery. The loss of scallop spat settlement habitat through scallop dredging, compounds the other negative effects that dredging has on the abundance and sustainability of scallop populations (Beukers-Stewart and Beukers-Stewart 2009).

2.4.2 Effect of the Queen scallop fishery

The queen scallop fishery around the Isle of Man is governed mainly by market demand, which saw a downturn in the early part of the 21st century (Vause, Beukers-Stewart et al. 2007; Beukers-Stewart and Beukers-Stewart 2009; Murray, Hinz et al. 2009). There has been high inter-annual variability in total catch rates for queen scallops since the beginning of the fishery (Beukers-Stewart and Beukers-Stewart 2009). Landings from the dredge fishery peaked at almost 8,000 tonnes a year in 1970, however there was a decline from the late 1980s and the stock took many years to recover, with catch rates remaining low but relatively stable (Brand, Beukers-Stewart et al. 2005; Vause, Beukers-Stewart et al. 2007; DEFA 2013). From 2008 onwards, landings of queen scallops by Isle of Man registered vessels began to increase and in 2011 and 2012 were at a 30 year high (DEFA 2013). These recent high rates have caused concern that the fishery is now operating at an unsustainable level (DEFA 2013).

The Isle of Man queen scallop fishery is dominated by scallops aged 2-4 years (Brand, Allison et al. 1991; Vause, Beukers-Stewart et al. 2007). This low number of age classes within the exploited population again indicates that the success of this fishery depends on the strength of the recruiting year class (Vause, Beukers-Stewart et al. 2007). Vause et al (2007) found the fishery to be heavily reliant on recruiting 2 year olds and so potentially vulnerable to recruitment overfishing. However, the persistence of the fishery since 1969 and recent upward trends in stock size and catch rates suggested that the levels of fishing prior to 2008 were sustainable (Beukers-Stewart, Mosley et al. 2003; Vause, Beukers-Stewart et al. 2007).

Reliance on the recruiting year-class leaves both fisheries vulnerable to environmental changes that could reduce the number of recruiting scallops (Beukers-Stewart, Mosley et al. 2003; Shephard, Beukers-Stewart et al. 2010). This is a problem because (as has already been mentioned) recruitment into scallop stocks is notoriously variable and trying to incorporate this variation into a management plan can be very difficult (Orensanz, Parma et al. 1991; Beukers-

Stewart, Mosley et al. 2003). Failure to do this can ultimately lead to the complete collapse of a fishery (Frank and Brickman 2001; Beukers-Stewart, Mosley et al. 2003), something that would have disastrous consequences for the Isle of Man fishing industry.

2.5 The Bycatch from the Isle of Man Scallop Fisheries

2.5.1 Bycatch from the great scallop dredge fishery

Scallop dredges are designed to dig into the sediment and capture great scallops, which live recessed in the seabed (Veale, Hill et al. 2001). This inevitably impacts non-target benthic species, either when encountering the gear on the seabed or by capture and subsequent discarding (Veale, Hill et al. 2001). Removal of biota in the bycatch may contribute significantly to changes in megafaunal densities and the overall benthic community (Veale, Hill et al. 2001). At the population level, heavily impacted bycatch species may undergo changes in population size, size structure or even local extinctions (Veale, Hill et al. 2001).

Bycatch data has been collected around the Isle of Man since 1992 during the bi-annual stock-assessment surveys of the scallop populations (Veale, Hill et al. 2001). These data have shown that there are two distinct bycatch assemblages, one to the south-west of the island and the other on the remaining fishing grounds to the north, south and east of the island (Veale, Hill et al. 2001). Although there are many reasons for this difference in assemblage (including local hydrography, sediment type and other environmental variables), differential exposure to intense dredging could also be playing a key role in structuring these communities (Veale, Hill et al. 2001). The scallop grounds around the south-west of the Isle of Man have been exploited since the beginning of the fishery, whereas the other grounds have shorter and less intense exploitation histories (Brand, Allison et al. 1991; Brand and Beukers-Stewart 2000; Veale, Hill et al. 2001). Most of the species that are affected by the dredges are relatively slow-growing and long lived, so it is thought that the closed season (June-October) for *P. maximus* provides little benefit (Veale, Hill et al. 2001).

In addition to those animals that are captured by the dredge, high levels of mortality may also occur in animals that encounter the dredge but are never caught (Jenkins, Beukers-Stewart et al. 2001). Up until recently these mortalities have been largely ignored as they are so difficult to assess. However, diver surveys have been conducted, which showed that the mean level of damage to benthic megafauna caused by demersal fishing gear around the Isle of Man was similar regardless of whether they were captured or not (Jenkins, Beukers-Stewart et al. 2001). As mentioned above the capture efficiency of the great scallop dredges was estimated at between 6 and 41% depending on ground type (Dare, Key et al. 1993). For bycatch this efficiency is estimated at <25%, which means the majority of the damage and mortality takes place in the dredge tracks (Jenkins, Beukers-Stewart et al. 2001). For example, the mortality of *Cancer pagurus* was actually higher in those individuals not captured by the dredge, as they were crushed by the gear passing over their bodies (Jenkins, Beukers-Stewart et al. 2001). This diver study showed that the majority of the damage to large benthic invertebrate species caused by scallop dredging occurs out of sight on the seabed rather than in the bycatch of the dredges (Jenkins, Beukers-Stewart et al. 2001). If this is the case, scallop dredging around the Isle of Man may have an even greater impact on benthic invertebrate species populations than previously estimated from bycatch studies.

2.5.2 Bycatch from the queen scallop fishery

Queen scallops around the Isle of Man are targeted by two different fishing gears, otter trawls (predominantly in the summer months) and skid dredges (the rest of the year). Queen scallops are more active swimmers during the summer months, due to relatively warmer water temperatures, therefore they are more effectively targeted with trawls rather than dredges (Hinz, Murray et al. 2012). A recent study by Hinz et al (2012) investigated the relative differences in bycatch caught by these different gears. Otter trawls were found to catch fewer bycatch species than the traditional queen skid dredge (Hinz, Murray et al. 2012). There was also a considerable difference in the composition of the bycatch species caught in the two different gears, with otter trawl bycatch dominated by fish species, whilst dredge bycatch was dominated by benthic invertebrate species (Hinz, Murray et al. 2012). Clearly the dredges used to capture queen scallops will have a similar impact on the benthic community as those used to capture great scallops. However, the otter trawls have the potential to affect populations of demersal fish species rather than benthic invertebrate species (Hinz, Murray et al. 2012).

Although the effect of scallop dredging on fish species around the Isle of Man has recently been investigated (Craven, Brand et al. 2012), no long-term studies have been undertaken to investigate the potential long-term effects of the queen scallop otter trawl. This is significant because queen scallops are predominantly targeted during the summer months when the great scallop fishery is closed and therefore otter trawls are the dominant gear-type used in this fishery (Hinz, Murray et al. 2012). Otter trawling hence has the ability to affect predatory demersal fish species such as cod, which may be undesirable in areas where recovery plans for such species are in place (i.e. the cod recovery plan) (Hinz, Murray et al. 2012).

2.6 Effect of Scallop Dredging on Benthic Communities

In 1993 a large research programme was started by the scientists at Port Erin Marine Laboratory, to investigate the environmental impact of scallop dredging around the Isle of Man (Brand 1999). Both the long (weeks, months) and short-term (hours, days) effects were studied, including the effects of dredging on by-catch species (see above), studies with the closed area (see below) and comparisons with historical data sets (Hill, Brand et al. 1997; Brand 1999).

Between 1946 and 1951 Dr Norman Jones sampled the benthos around the south of the Isle of Man at over 200 sites (Jones 1951; Hill, Veale et al. 1999; Bradshaw, Veale et al. 2002). Jones used a wide range of sampling gears, including the naturalist's dredge, scallop dredge, canvas dredge and van Veen grab, to ensure that his collection included the great majority of species present (Jones 1951; Bradshaw, Veale et al. 2002). Jones also qualitatively recorded the substratum type from all of his samples, which were taken mainly during the summer months and are described in more detail in Bradshaw, Veale et al. (2002). Although these samples were taken after the scallop fishery began in the area, they are prior to the onset of the rapid expansion seen in the mid-1950s, and have provided a detailed benthic fauna dataset for around the Isle of Man (Bradshaw, Veale et al. 2002). Hill et al (1999) compared Jones' historical data with samples taken from the same sites 40 years later. Despite a few data limitation issues, the study showed that the benthic community structure had changed considerably since 1950, with decreases in vulnerable tube-dwelling species and fragile echinoids and increases in benthic scavengers (Hill, Veale et al. 1999). However, it was difficult to assign these changes solely to the effect of dredging, particularly when individual species responses to such disturbance were unknown (Hill, Veale et al. 1999). In addition to this, an area that had been exposed to low levels of fishing since 1950 also had a dramatically changed community, which could have been due to other anthropogenic effects or a long-term natural biological cycle (Hill, Veale et al. 1999).

Another attempt to determine the effects of scallop dredging on the benthos around the Isle of Man was made by Bradshaw et al. (2002). All sites sampled, regardless of sediment type or location around the island had experienced broad-scale community level changes over the last ~50 years (Bradshaw, Veale et al. 2002). Evidence that these changes were at least partially caused by scallop dredging comes from the two most heavily fished sites samples (Bradda Inshore and the now Closed Area) (Bradshaw, Veale et al. 2002). The biodiversity of these sites was measured using a Taxonomic Distinctness indicator, which showed community impoverishment at both sites (Bradshaw, Veale et al. 2002). In addition to this evidence, an analysis of the number of species lost at each site over time showed that those sites that had been fished for the longest amount of time had lost the most species (Bradshaw, Veale et al.

2002). Sediments at sites that could be compared with historical samples became finer regardless of sediment type (i.e. stony, gravely, sandy) (Bradshaw, Veale et al. 2002). Anecdotal evidence from local fishermen seems to support the theory that a reduction in at least the larger fraction of the sediment (e.g. shells) is due to fishing activity (Bradshaw, Veale et al. 2002). In conclusion to this study the authors note that the differences between the historical data and modern samples can be assumed to be greater than could be accounted for by natural variability of the system and indicate real long-term change (Bradshaw, Veale et al. 2002). Given that the Irish Sea used to support a myriad of different fisheries (see above) and that most of these are no longer conducted on a significant scale, it could be suggested that the long-term change observed by both Hill et al. (1999) and Bradshaw et al. (2002) is a small proportion of the changes that have occurred since fishing began.

2.7 Investigations with the Closed Area at Port Erin

Five years after the Port Erin closed area was established (1994) an experimental dredging programme began in the northwest corner of the closure (Bradshaw, Veale et al. 2001). This study was to investigate the effect of scallop dredging on both infaunal and epifaunal communities by exposing them to five years of controlled dredging, similar to the level experienced by benthic communities on commercial fishing grounds (Bradshaw, Veale et al. 2001). The cumulative impacts (5 years of dredging) of this experiment led to a more homogenous benthic community, with experimentally dredged sites inside the closed area becoming more similar to fishing grounds than undredged plots within the closure (Bradshaw, Veale et al. 2001). This change has important implications for the level of habitat complexity and the associated success of larval settlement, survival of mobile species and general species diversity (Roberts and Polunin 1991; Auster, Malatesta et al. 1996; Bradshaw, Veale et al. 2001; Howarth, Wood et al. 2011; Lambert, Jennings et al. 2011). The average age of the scallops within the closed area was also higher than those on fishing grounds, however, the authors state that it was still nowhere near as high as the 1937 populations sampled before the onset of fishing (Tang 1941; Bradshaw, Veale et al. 2001).

A more recent study (Beukers-Stewart, Vause et al. 2005) followed on from Bradshaw et al. (2001) and continued the sampling inside the closed area. It showed increases in the density, mean size and mean age of great scallops within the closed area and experimental dredging within the closure confirmed that this was largely a result of decreased fishing activity (Beukers-Stewart, Vause et al. 2005). In addition to this finding, increases in the recruitment at nearby fishing grounds since then were thought to be a result of larval export from the closed area (Beukers-Stewart, Vause et al. 2004; Beukers-Stewart, Vause et al. 2005). The spillover effect of larvae and adults from marine reserves into fished areas has been discussed and demonstrated mainly for tropical marine ecosystems (Russ and Alcala 1996; Roberts, Bohnsack et al. 2001; Harrison, Williamson et al. 2012). In temperate systems, spillover is still open to debate and there is currently insufficient empirical evidence to determine whether this occurs (Neill and Kaiser 2008).

Spillover and connectivity around the Isle of Man has been investigated further through a series of particle tracking models (PTM) (Neill and Kaiser 2008). The PTMs identified considerable connectivity among the different known scallop grounds, supporting the creation of a network of marine protected areas to improve fisheries management (Neill and Kaiser 2008). They also suggested that larvae from the current closure are exported onto the fishing ground known as ‘The Targets’ (Neill and Kaiser 2008), which is further north than the areas suggested by Beukers-Stewart et al. (2005). This fishing ground has seen a large increase in the number of scallops in recent years, which seems to support the findings of the PTM, although other mechanisms could be at work (Murray, Hinz et al. 2009). It is clear that further work is required to understand the precise mechanism of larval dispersal from this closed area and what impact this may have on the nearby fishing grounds.

What both of the above closed area studies have shown is that scallop dredging has had a significant impact on the benthic communities around the Isle of Man. Combined with the historical studies already discussed it is clear that changes have occurred within these communities in the last 60 years. It is also clear that scallop dredging has played a large role in these changes.

2.8 Fluctuations and patterns in environmental variables

The Irish Sea is a semi-enclosed sea, with a well understood oceanographic regime (Kennington, Allen et al. 1999; Gowen and Stewart 2005; Hanley, Gell et al. 2012). The annual cycle of dissolved inorganic nutrients is typical of northern European coastal and shelf seas (Gowen and Stewart 2005). This cycle sees maximum concentrations in the winter months and minimum concentrations in the summer months, following the pattern of biological productivity and breakdown (Gowen and Stewart 2005). It is widely supposed that nitrogen is the nutrient most likely to limit phytoplankton growth in the Irish Sea as a whole (Gowen and Stewart 2005). However, diatoms are a dominant component of the spring phytoplankton bloom around the Isle of and their growth is often limited by silicate availability (Gowen and Stewart 2005; Hanley, Gell et al. 2012).

2.8.1 Temperature and the North Atlantic Oscillation

Since the 1950s, global sea surface temperatures (SSTs) have increased by approximately 0.4^{o}C (Levitus, Antonov et al. 2009; Doney, Ruckelshaus et al. 2012). This warming trend has been associated with anthropogenic climate change (Frost, Baxter et al. 2012). However, ocean circulation and interactions with climate variability, such as the North Atlantic Oscillation, have meant that ocean warming has not been spatially uniform (Ishii, Kimoto et al. 2006; Doney, Ruckelshaus et al. 2012). There is also the additional complexity of natural variability in sea water temperature, which ranges from interannual to multi-decadal time scales and varies between regions (Frost, Baxter et al. 2012).

In the north Atlantic there have been several well defined ‘cool’ and ‘warm’ periods relative to the underlying warming trend (Frost, Baxter et al. 2012). These periods oscillate between each other and have been defined as: a cool period between 1900 and 1930; followed by a similar warm period from 1930 to 1960; from the late 1960s to 1990 there was another cool period; and then a warm period from 1990 to present (Holliday, Hughes et al. 2011; Frost, Baxter et al. 2012). The current warm period has been particularly strong around the UK and Ireland, with the seas surface temperature being up to six times greater than the global average (Frost, Baxter et al. 2012). The North Sea and English Channel experienced the strongest warming trend, with a rate of +0.6 and +0.8^{o}C per decade, respectively (Frost, Baxter et al. 2012). The seas to the west and north of Scotland have seen a slower rate of increase of around +0.2 – 0.4^{o}C per decade (Frost, Baxter et al. 2012). However, long-term datasets from the Port Erin Marine Laboratory have shown an increase in seawater temperature of 0.75^{o}C over the last century (Bradshaw, Veale et al. 2002). This suggests that the Irish Sea around the Isle of Man has experienced a similar warming trend to that found in the English Channel and as such is experiencing one of the greatest increases in temperature around the U.K.

2.8.2 Long-term nutrient trends

Gowen et al (2002) and Evans et al (2003) examined data from 1954 – 1991 taken from the CYPRIS sampling station on the south-west of the Isle of Man, which is also used in this study. Both investigations found that phosphate levels had increased from 1954 to 1988 and then declined from 1989 to 1999, thought to be caused by a decrease in a major anthropogenic, industrial source of phosphate from the Cumbrian coast. Nitrate levels were also found to increase but only from 1954 to 1974, with a period of stabilisation from 1975 to 1999. In terms of silicate, both studies found that there was no trend in the data.

Although the Irish Sea as a whole is thought to be particularly vulnerable to anthropogenic nutrient enrichment (Gowen and Stewart 2005), it seems that no direct anthropogenic cause for the long-term (40 years) trends in nitrate concentration can be found

(Evans, Williams et al. 2003). In fact Evans et al (2003) conclude that the anthropogenic load of nitrate was unlikely to be the sole determining factor. Their conclusion was that the observed decadal changes in both nutrient concentrations and also salinity had occurred because sampling had been done along a salinity/nutrient distribution gradient, which has changed geographic position over time. These shifts in water masses would be represented by the observed local changes in the concentrations of nutrients (Evans, Williams et al. 2003).

2.8.3 Phytoplankton community dynamics

Hanley et al (2012) investigated the phytoplankton community in the Manx territorial sea. They found that the spring bloom was dominated by diatoms and microflagellates and that as the spring and summer months progressed there was a distinct succession of phytoplankton functional groups, which was typical of phytoplankton in the Irish Sea waters as a whole (Hanley, Gell et al. 2012). During the spring bloom both nitrate and silicate become exhausted as the diatom component of the phytoplankton dominates (Hanley, Gell et al. 2012). After this the diatom population crashes and is replaced by a dinoflagellate population, which dominates during the summer and autumn months (Hanley, Gell et al. 2012). Kennington et al (1999) found that in the north-east Irish Sea, winter concentrations of total organic nitrate and silicate were closely associated with variations within the spring phytoplankton community. As both nitrate and silicate are important for diatom growth (Hanley, Gell et al. 2012) it makes sense that fluctuations in their availability in the year prior to the spring bloom, would have an influence on the biomass of phytoplankton in the spring bloom, which is dominated by diatom flora.

2.9 The effect of environmental change on the benthic communities

Only one study has been conducted on the benthic communities around the Isle of Man investigating the effects of environmental variables. Shephard et al (2010) found a significant positive correlation between great scallop (*P. maximus*) recruitment and a time series (1991 – 2007) of spring mean water temperature around the Isle of Man. There is evidence that increasing SST around the Isle of Man is favourable for gonad development in scallops and is leading to greater gamete production (Shephard, Beukers-Stewart et al. 2010). This in turn appears to be increasing recruitment in this commercial scallop population, which is then responsible for recent observed increases in commercial catch rates (Shephard, Beukers-Stewart et al. 2010).

In terms of the rest of the benthic community around the Isle of Man there are no published correlations with increasing SST. However, given the complex interactions that have already been discussed for the North Sea (Chapter 1) it is likely that if any such correlations exist, they will not be straightforward. Shephard et al (2010) also tested for relationships between scallop recruitment and each of oxygen concentration (ml/l) and chlorophyll α concentration (µg/l) and none were found. However, that is not to say that relationships between these variables and the rest of the benthic community do not exist.

2.10 Summary

This review of the history, management and impacts of the scallop fisheries around the Isle of Man highlights that the benthic community structure has been significantly altered over the 70 years the fishery has been conducted. There are many confounding issues to the study of long-term changes in benthic communities, including the effects of environmental variables. Fortunately long-term environmental datasets exist for this part of the Irish Sea and have been investigated for long-term trends (Kennington, Allen et al. 1999; Evans, Williams et al. 2003; Gowen and Stewart 2005). A link has already been found between SST and recruitment in the great scallop (Shephard, Beukers-Stewart et al. 2010) and it is possible that the benthic communities found around the Isle of Man may also be affected by not only temperature but also other environmental variables. The next three chapters of this thesis build upon the extensive body of work that exists for the marine environment around the Isle of Man and explore the temporal and spatial trends in the benthic community and investigate how both fishing pressure and environmental variables affect these trends.

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Chapter 3

Untangling the effects of environmental variables and fishing pressure on the benthic diversity of commercial scallop fishing grounds

3.1 Abstract

Previous work has shown that more than 70 years of scallop dredging have dramatically altered the benthic communities found on the fishing grounds around the Isle of Man. These communities are thought to now be made up of more fishing-tolerant species. This study investigated the patterns in diversity indices on eight different fishing grounds over a fourteen year period. Two grounds (East Douglas and Laxey) found on the east of the Isle of Man showed a significant decrease in diversity over the time series. Whilst two grounds (Bradda Inshore and Targets) on the west of the island, which has been more heavily fished historically than the east, showed significant increases in diversity over the time series. Only a small (<7%) proportion of the patterns in diversity were negatively related to fishing effort, which suggests that the benthic communities are reasonably well adapted to fishing disturbance. Likewise despite several trends and correlations between environmental variables, no clear relationship with diversity was found. It is thought that individual species responses to these variables may be masking a clear relationship and this is investigated in Chapter 4.

3.2 Introduction

Marine benthic communities on the continental shelf are typically structured by various environmental factors and are not static in time (Kaiser 1998; Hill, Veale et al. 1999; Kaiser, Ramsay et al. 2000; Bradshaw, Veale et al. 2002). These range from the large to the small scale. For example temperature (Kröncke, Dippner et al. 1998), tidal currents (Kaiser 1998), seasonal currents (Hill, Brown et al. 1997; Hill, Veale et al. 1999), phytoplankton availability (Frid, Buchanan et al. 1996) and the frequency and intensity of storms (Frid, Buchanan et al. 1996; Kaiser 1998; Bradshaw, Veale et al. 2002; Reiss, Meybohm et al. 2006) all play a role on a large scale. Whereas smaller-scale community factors such as predator feeding activities (Kaiser 1998) and recruitment success (Bradshaw, Veale et al. 2002) can also differentially affect the survival of each species present. It is difficult however, to get an accurate picture of the natural variability within most benthic ecosystems (Currie and Parry 1996; Capasso, Jenkins et al. 2009). This is because the majority of the areas that have been studied have also been impacted by some kind of anthropogenic activity (Currie and Parry 1996; Capasso, Jenkins et al. 2009).

One of the greatest sources of anthropogenic disturbance for benthic communities is bottom-fishing, the effects of which have been well documented in recent years (Dayton, Thrush et al. 1995; Jennings and Kaiser 1998; Thrush, Hewitt et al. 1998; Kaiser, Ramsay et al. 2000; Thrush and Dayton 2002; Carbines and Cole 2009). Towed fishing gears cause varying levels of disturbance for benthic communities, including altering their complexity and topography, removing, damaging or killing benthic fauna, reducing benthic production and altering sediment characteristics (Caddy 1973; de Groot 1984; Currie and Parry 1996; Ramsay and Kaiser 1998; Thrush, Hewitt et al. 1998; Watling and Norse 1998; Hall-Spencer and Moore 2000; Hall-Spencer and Moore 2000; Bradshaw, Veale et al. 2001; Piersma, Koolhaas et al. 2001; Bradshaw, Veale et al. 2002; Kaiser, Clarke et al. 2006). In fact the damage caused by towed fishing gear to structurally complex habitats and fauna has been likened to forest clear-cutting (Watling and Norse 1998).

Of the different types of towed fishing gear used, dredging for shellfish has been described as the least selective and most damaging to benthic fauna and substrates (Currie and Parry 1996; Collie, Escanero et al. 2000; Collie, Hall et al. 2000; Eleftheriou 2000; Jenkins, Beukers-Stewart et al. 2001; Carbines and Cole 2009). The exact effects of dredging on the benthos depends on a complex set of conditions, including sediment type, the level of natural disturbance, structural complexity and the resident fauna (Collie, Escanero et al. 1997; Løkkeborg 2005; Kaiser, Clarke et al. 2006; Morsan 2009). Studies have concluded that the effects of dredging are more severe in the early stages of a fishery, with the loss of epibenthic biogenic structures and their associated fauna (Kaiser, Hill et al. 1996; Jennings and Kaiser

1998; Tuck, Hall et al. 1998; Hall-Spencer and Moore 2000; Guijarro Garcia, Ragnarsson et al. 2006). The most obvious effects of continued dredging are the reduced abundance of fragile, long-lived species, the high mortality of which may result in radical changes in benthic community structure (Hall-Spencer and Moore 2000; Kaiser, Ramsay et al. 2000; Guijarro Garcia, Ragnarsson et al. 2006).

The impact of dredging on benthic communities, however, does not exist in isolation. In addition to a background of natural variability, many environmental variables that structure benthic communities have also been affected by anthropogenic activities. For example temperature is affected by global warming (Schiel, Steinbeck et al. 2004; Doney, Ruckelshaus et al. 2012) and phytoplankton abundance is affected by pollution (Frid, Clark et al. 1999). Synergies between all of the anthropogenic impacts and environmental variables are common (Callaway, Engelhard et al. 2007; Miles 2009). Yet it is these very synergies that make it difficult if not impossible to measure the effect of each impact individually (Miles 2009). An understanding of how a benthic community changes and responds in the long-term to any of these pressures is very useful for the management of activities that impact the community.

This Chapter investigates the temporal and spatial patterns of benthic diversity on scallop fishing grounds around the Isle of Man. The Isle of Man is found in the north Irish Sea, between the coasts of Wales, Ireland, Scotland and England. It is at the centre of one of the most heavily exploited scallop fisheries in Europe (Kaiser, Ramsay et al. 2000; Bradshaw, Veale et al. 2002). There are two scallop species that are targeted, the great scallop, *Pecten maximus* and the queen scallop, *Aequipecten opercularis* (Bradshaw, Veale et al. 2001) (for a full review see Chapter 2).

The effects of scallop dredging on the benthic communities and by-catch species around the Isle of Man, have been studied in the past, with focus on both the short and the long term (Hill, Brand et al. 1997; Beukers-Stewart, Mosley et al. 2003). Hill et al (1999) compared data collected by Norman Jones, prior to the rapid expansion of the *P. maximus* fishery, with samples from the same sites 40 years later. Benthic community structure had changed considerably over that time. There had been a reduction in vulnerable tube-dwelling species and fragile echinoids and an increase in benthic scavengers (Hill, Veale et al. 1999). It was however, difficult to assign these changes solely to the effects of dredging, as an area which had seen low levels of fishing also showed a dramatically changed community (Hill, Veale et al. 1999). These changes could therefore have been due to other anthropogenic effects, a long-term biological cycle, or a combination of all three (Hill, Veale et al. 1999).

A later study by Bradshaw et al (2002), however found that dredging was the most likely cause for the observed long-term changes. At all sites sampled, regardless of sediment type or location around the island, the benthic community had experienced broad-scale community level changes, with particularly low diversity at the sites that had been most heavily fished for the longest period (Bradshaw, Veale et al. 2002). Bradshaw et al (2002) concluded that the differences between historical and modern samples were greater than could be accounted for by the natural variability of the system and indicated real long-term change (Bradshaw, Veale et al. 2002). The benthic community that now exists on the fishing grounds around the Isle of Man seems to have shifted to one composed of more dredge-tolerant species (Bradshaw, Veale et al. 2002).

Although fishing pressure is thought to be the main driver of the changes observed in the benthic communities, it is possible that other factors are playing a role. Long-term environmental datasets have shown a 0.75^{o}C increase in mean seawater temperature around the Isle of Man over the last 100 years (Bradshaw, Veale et al. 2002). A recent study found a significant relationship between *P.maximus* recruitment around the Isle of Man and mean spring temperature in the year of larval settlement (Shephard, Beukers-Stewart et al. 2010). In addition to temperature, there has been statistically significant increase in soluble reactive phosphate and total oxidised nitrogen since 1934 and 1960 respectively, in a site 4km offshore from one of the most heavily fished grounds (Bradda Inshore); both changes are most likely due to anthropogenic inputs (Allen, Slinn et al. 1998; Bradshaw, Veale et al. 2002). Therefore it is possible that the dredge-tolerant benthic communities that are now present (Bradshaw, Veale et al. 2002) are being structured by fluctuations in environmental variables in addition to the impact of fishing pressure.

This first chapter aims to determine whether there are any linear relationships between benthic diversity, fishing pressure and environmental variables on the fishing grounds around the Isle of Man. Changes in biodiversity can be directly caused by exploitation, pollution and habitat destruction or indirectly caused through the effects of climate change (Worm, Barbier et al. 2006). It is widely recognised that marine ecosystems that have a higher biodiversity are not only more robust to exploitation, but they also show increased rates of recovery following exploitation (Worm, Barbier et al. 2006; Hector and Bagchi 2007). Worm et al (2006) found that a loss of biodiversity within regional ecosystems led to impairment of ecosystem services, such as food provision, water filtration and flood defences. Therefore it is possible that heavily fished sites that have lower diversity may be less resilient to the effects of environmental variables.

Diversity can be expressed by any number of indices that emphasize different aspects of species richness and evenness (Magurran 2004). For this study two indices have been selected from the non-parametric heterogeneity measures: Simpson's Diversity Index (Simpson 1949) and Shannon Index (Shannon and Weaver 1949). The Shannon Index is the most enduring of all measures of diversity and takes into account both the species richness and the evenness of a community (Magurran 2004). However, this index is not without flaws; for example an assumption of the index is that all species present have been included, therefore any missing species can lead to bias in the index (see Magurran (2004) for a full review). To ensure that analyses were not affected by this, the Simpson’s Diversity Index (1-D) was also used. The Simpson’s Diversity Index (1-D) is described as one of the most meaningful and robust measures of diversity available (May 1975; Lande 1996; Lande, DeVries et al. 2000; Magurran 2004). There are subtle differences between the two indices, with the Simpson’s Diversity Index (1-D) being less sensitive to changes in species richness than the Shannon Index (Magurran 2004). Therefore by using two indices the effects of both species richness and evenness can be investigated for the benthic communities around the Isle of Man.

Data from 14 years of benthic community sampling were used to determine spatial and temporal trends in benthic diversity of eight commercial fishing grounds around the Isle of Man. Corresponding long-term environmental and fishing effort datasets were used to determine (via linear and multiple linear regression analysis) whether either of these potential impacts was affecting benthic diversity on these grounds. It is thought that although environmental variables should play a role in the patterns of diversity, fishing effort will have a greater influence on the diversity of these benthic communities. This is because it has played an important role in the past in determining the composition of species within the benthic community. Of the environmental variables studied it is thought that those that have had observed trends in the past (temperature and nutrients) are most likely to affect benthic diversity.

3.3 Methods

3.3.1 Study Area

The Isle of Man (58^{o}08’N,4^{o}27’W) is located in the north Irish Sea, between the coasts of Ireland, Scotland, Wales and England. The Isle of Man’s territorial limit stretches to 12 miles offshore and the waters within this limit are shallow, mostly less than 30m deep. The only exception to this is to the south and west of the island, where depths slope to 80-90m at the 12 mile limit. The north-east coast of the island conversely has extensive shallow sandy banks. Sediment type varies around the island, with near shore sediments being mainly fine sand and offshore sediments divided into four categories; coarse sands and gravel, fine sand, muddy sand and mud (Barne, Robson et al. 1996; Craven, Brand et al. 2012).

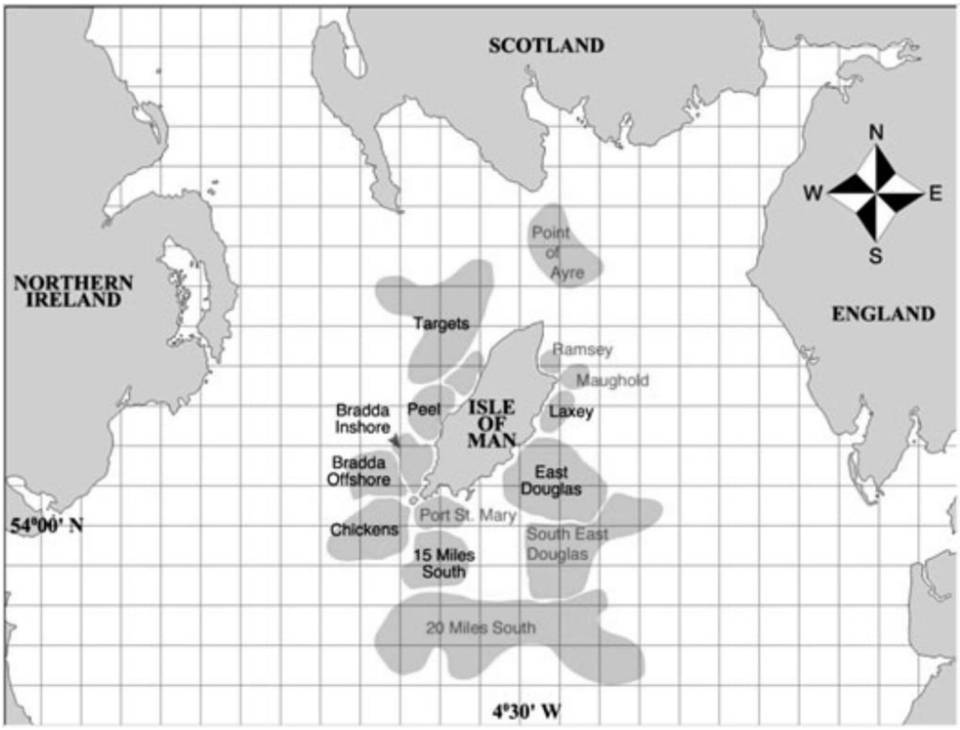

Figure 3.1 Map of the Irish Sea showing the Isle of Man and the main fishing grounds for great and queen scallops. The grounds analysed in this study are labelled in bold.

(Source: Beukers-Stewart *et al.*, 2003)

The waters around the Isle of Man currently support one of the most heavily exploited scallop fisheries in Europe (Kaiser, Ramsay et al. 2000; Bradshaw, Veale et al. 2002). There are two species targeted, the great scallop, *P.maximus* and the queen scallop, *A. opercularis* (Brand and Prudden 1997). For a full review of the history and management of these two fisheries see Chapter 2. Figure 3.1 highlights the various fishing grounds around the Isle of Man. The great scallop dredge fishery predominantly targets grounds to the south and west of the Isle of Man, whilst the queen scallop fishery is focused on the eastern and southern grounds (Beukers-Stewart, Vause et al. 2005; Vause, Beukers-Stewart et al. 2007).

3.3.2 Investigating the effects of fishing & environmental variables on benthic communities

The fishing grounds around the Isle of Man and their benthic communities have been subjected to varying levels of fishing pressure over the last 70 years. A previous study has shown shifts in benthic community structure since the onset of heavy commercial fishing (Hill, Veale et al. 1999), however there were also changes in community structure that could not be explained by fishing pressure alone. This current study aims to untangle the relative influences of fishing pressure and environmental variables on the benthic diversity at the various fishing grounds around the Isle of Man. To do this data was obtained from several different sources, covering the time period of 1992 to 2006 and are outlined below.

3.3.2.1 Fisheries-independent surveys

Benthic community diversity data was obtained from a time-series of catch data taken from fisheries-independent surveys conducted by staff at the Port Erin Marine Laboratory (PEML). Scallop fishing grounds surround the Isle of Man from inshore to beyond the 12-mile limit (Figure 3.1). These are a mixture of great and queen scallop grounds, with the majority of great scallop grounds being to the west and south of the island. From 1992 to 2006 a series of fisheries independent surveys were conducted twice a year on the fishing grounds around the Isle of Man. Surveys were conducted just before the start of the great scallop fishing season (October) and just after the season closed (June). From 1992 to June 2002 a 20m converted beam trawler, the RV ‘Roagan’, was used. From October 2002 several commercial fishing boats of similar size and design were chartered for the surveys.

The surveys were designed to replicate commercial fishing practises and therefore comparable catch (both scallop species) and bycatch (mainly benthic invertebrates and some fish species) was collected. Each ground was surveyed using 3 or 4 replicate tows, of approximately 2nm. in length, of spring loaded Newhaven type dredges. Average tow speed was 2.5 knots (4.63 km h^{-1}) and average tow duration was 45 minutes. Exact tow length and duration was recorded using a differential global positioning system (DGPS) linked with Microplot software (Sea Information Systems, Aberdeen). This ensured that as far as possible the same area of each fishing ground was targeted each year. A gang of 4 standard scallop dredges was fished on one side of the boat whilst a gang of 4 queen scallop dredges was fished on the other side. All dredges were 0.76m in width; the standard scallop dredges had 9 teeth of 110m length and belly rings of 80mm internal diameter, whereas the queen scallop dredges had 10 dredge teeth of 60mm length and belly rings of 55mm internal diameter.

As well as enumerating the scallops caught during the surveys, the bycatch that was also caught was identified to species level where possible. The bycatch consisted of a mixture of fish (Craven, Brand et al. 2012) and benthic invertebrate species. This study focused on the invertebrate component of the bycatch. Any data from non-functioning dredges or where the bycatch was not recorded were removed from the analysis to avoid bias.

3.3.2.2 Environmental data

The environmental data used in this study was taken from a multi-annual time series for water quality around the Isle of Man. The CYPRIS sampling site is located on the west coast of the Isle of Man, where in the summer the water column is transitional in character because it is just inshore of the main western stratified water mass and also offshore of true coastal waters (Evans, Williams et al. 2003). Sea-surface temperature, salinity, chlorophyll-α concentration and nutrient abundance variables were all derived from the CYPRIS data.

In addition to the CYPRIS environmental data, data from the North Atlantic Oscillation (NAO) index was also obtained. The NAO is one of the major modes of variability of the Northern Hemisphere atmosphere (Osborn 2006). There is particular importance of the NAO in winter, when it exerts a strong control on the climate of the Northern Hemisphere (Osborn 2006). A time series of the winter (December – March average) NAO index calculated by (Jones, Jonsson et al. 1997) was calculated by Osborn (2006) and used in this study.

3.3.2.3 Logbooks

Finally, fishing effort data was collected using a voluntary logbook scheme for Manx scallop fishermen, that has been running since 1981 (Brand and Allison 1994). Fishermen filled out details of their daily fishing activity, including hours fished, number of scallops caught and their location within pre-designated 5x5 nautical mile boxes (Beukers-Stewart, Mosley et al. 2003). These boxes corresponded to the whole area of smaller fishing grounds, whereas larger grounds were covered by two or more boxes. This gives unusually precise spatial fisheries data when compared to the usual data available within Europe, which is based on the International Council for the Exploration of the Seas (ICES) rectangles of 0.5^{o} latitude x 1^{o} longitude (Bradshaw, Veale et al. 2000). Over the course of the logbook data collection there have been little or no changes or improvements in the fishing gear design, the average size of vessels or the size of the engines, therefore catch rates were considered to be comparable (Beukers-Stewart, Mosley et al. 2003; Vause, Beukers-Stewart et al. 2007). Approximately 30% (10-25 boats) of the Manx scallop fishing fleet participated in the scheme, although this fluctuated year on year (Beukers-Stewart, Mosley et al. 2003). The total fleet size was recorded for most years of this study, however fleet size was not available for the years 1994/5 – 1999/2000 inclusive. Therefore fleet size was estimated for those years using a linear relationship created from the available data. All effort data was then multiplied up to the size of the total fleet, using a multiplying factor of (total fleet size/sample fleet size). This created an estimate of total fishing effort each year by the Manx scallop fishing fleet.

3.3.3 Data analysis

3.3.3.1 Diversity indices

The catch data from the queen dredges were used to calculate a time-series of two different diversity indices; the Simpson's Diversity Index (1-D) and the Shannon Index for each fishing ground.

Simpsons Index of Diversity (1-D):

$$D = \sum \frac{n(n-1)}{N(N-1)}$$

n = the total number of individuals of a particular species
N = the total number of individuals of all species

Shannon Index (H'):

$$H' = \sum_{i=1}^{s} (p_i)\,(\ln p_i)$$

p_i = proportion of species i in community (= n_i/N; where n is the number of individuals of a given species and N is the total number of individuals in a sample)

Two diversity indices were chosen to incorporate different aspects of the benthic community diversity. The Shannon Index tends to be influenced by changes in both species richness and evenness, whilst Simpson's Diversity Index (1-D) is mainly influenced by the evenness of the community being studied (Magurran 2004). By investigating the trends in both indices a more complete picture of benthic diversity will be examined. The queen dredges were used instead of the scallop dredges because by having smaller belly rings, they retained a greater proportion of the benthic community than the scallop dredges. Data from both the June and October surveys were initially included.

3.3.3.2 Temporal trends in benthic diversity

To investigate whether there were any temporal trends in benthic diversity, the data was separated by fishing ground. The two diversity indices on each were then explored for any trends over time using regression analysis.

3.3.3.3 Effect of the closed season on diversity

The effect of the great scallop closed season (June – October, inclusive) on benthic diversity was analysed using a one-way ANOVA by comparing the diversity indices from June sampling with those taken in October sampling. Data were tested for normality using Shapiro-Wilk Normality Test and tested for homogeneity of variance using Bartlett’s test. Only grounds that had been sampled both in June and October could be included in this analysis.

3.3.3.4 Fishing Effort Data

Estimates of total fishing effort per year were separated into the 5x5 nautical mile boxes used in the logbook scheme. The effort data that best matched the sampling positions of each of the fisheries-independent surveys was then collated to produce estimates of fishing effort for each sample site / fishing ground. For some grounds (Targets, South Port St. Mary and East Douglas) it is known that the fishery moves around from year to year and so the match was not always precise, however it was still highly spatially specific and likely to be a good indicator of general trends in fishing effort. For the fishing ground Peel, although the effort and survey data correspond to the same 5x5 nautical mile square, it is now known that the fishery occurred in the offshore part of this square, whilst the surveys were conducted inshore.

3.3.3.5 Effect of fishing on diversity

Fishing effort data was site specific, therefore an analysis incorporating all fishing grounds was possible. To investigate the effects of fishing on diversity all data were combined and a regression analysis, using all possible combinations of site and year, was performed. Various lags in the fishing effort data were investigated and because the fishing effort data ran from 1981, a greater number of lags could be tested than in the analysis of environmental variables (see below). The lags investigated were: no lag, a 1 year lag, a 2 year lag, a 3 year lag and a 4 year lag. Each lag was investigated for both diversity indices. All data were checked for normality and homogeneity of variance and it was found that the fishing effort data was not normally distributed and therefore was transformed using a square-root transformation to ensure normality. A regression analysis was then performed between square-root transformed fishing effort and diversity. Each model was validated to ensure no pattern in the residuals.

3.3.3.6 Analysis of environmental variables

Environmental data were combined into useable indices by combining several months' worth of samples into seasonal and annual means. Temperature and chlorophyll- α time-series were both converted into spring means. For temperature this meant averaging the April-June data for each year, and for the chlorophyll- α data an average encompassing the varying spring blooms was created by combining April-July data to create an average spring bloom value for each year. The bloom normally occurred in May, however some years peak chlorophyll- α concentration was early (April) and some years it was late (June) and one year it occurred in July.

All other environmental variables were calculated by converting raw data into annual means, which took into account data from June – May, which matched the timing of the scallop survey data. These included nitrate, silicate and soluble reactive phosphate concentrations, chlorophyll- α and temperature. As already mentioned a winter NAO index calculated by Osborn (2006) was also included with the environmental variables.

All possible combinations of environmental variables were then tested for homogeneity of variance and normality using both Bartlett's test and Shapiro-Wilk Normality Test, respectively. Those pairs that fulfilled these criteria were then tested using Pearson's Product Moment for correlations between them. Those that were not normally distributed were tested using Spearman's Rank Correlation Coefficient. Temporal trends in the environmental data were then investigated by performing a regression analysis on each variable.

3.3.3.7 Effect of environmental variables on diversity

To investigate the effect of environmental variables on the two species diversity indices a series of multiple-regression analyses were performed. Due to environmental variables being collected from the south-west of the Isle of Man and a known difference in environmental conditions on the east coast of the island (Veale, Hill et al. 2001; Gowen, Hydes et al. 2002; Evans, Williams et al. 2003; Gowen and Stewart 2005) the data from the two east coast fishing grounds were removed from this analysis. In addition to prevent pseudo-replication of the environmental variables and to overcome some gaps in the diversity index data, a mean diversity index was calculated for all of the remaining grounds (Bradda Inshore, Bradda Offshore, Chickens, Targets, Peel and South of Port St. Mary). As there was no significant difference in the June and October diversity data and the June data was more complete, this was used in this analysis.

It was expected that there would be a lagged effect of the environmental data on the measures of diversity, because if the environmental conditions were influencing species reproduction and settlement (e.g. Shepherd, Beukers-Stewart et al. 2010) then a certain amount of time would be required for these species to grow large enough to be collected by the dredges. Therefore three different time lags were tested for each diversity index: no lag, a 1 year lag and a 2 year lag. Further lags were unable to be tested as each time the data was lagged a year of data was lost. All data were tested for normality and homogeneity of variance. The explanatory environmental variables were then analysed for co-linearity using Variance Inflation Factor (VIF) analysis using the statistical programme R (Team 2012). In all cases this resulted in chlorophyll- α bloom and annual temperature being removed. Remaining variables were then analysed using multiple linear regression and optimum models were selected using Stepwise Model Selection found in the statistical programme R. All final models were then validated to ensure no patterns in the residuals.

3.4 Results

3.4.1 Spatio-temporal patterns in benthic diversity

In total eight fishing grounds had sufficient data to calculate time series of diversity. Figures 3.2 and 3.3 show the temporal trends across all eight fishing grounds in Simpson's Diversity Index (1-D) and the Shannon Index, respectively. The overall pattern was similar for both indices, the main difference between the two indices is that the Simpson's Diversity Index (1-D) gives more weight to dominant or common species and so is likely to fluctuate if there is a sudden increase in abundance of a particular species, it is also less sensitive to changes in species richness than the Shannon Index (Magurran 2004). Figures 3.2 and 3.3 show that although diversity varied temporally at each fishing ground, this variation was not the same for all of the fishing grounds and there were differences spatially as well as temporally.

Figure 3.4 and 3.5 show the temporal variation of the Simpson's Diversity Index and the Shannon Index, respectively, at each fishing ground separately. For each ground a regression analysis was performed to explore trends in each diversity index over time. Four out of the eight grounds had significant temporal changes in both diversity indices. Bradda Inshore had a significant upward trend in Simpson's Diversity Index (1-D) (df = 1, F = 18.84, $P < 0.001$, $R^2 = 0.61$) and in Shannon Index (df = 1, F = 44.64 , $P < 0.001$, $R^2 = 0.79$). Targets also had a significant upward trend in both Simpson's Diversity Index (1-D) (df = 1, F = 9.31, P = 0.01, $R^2 = 0.51$) and Shannon Index (df = 1, F = 14.92, P = 0.004, $R^2 = 0.62$). Laxey on the other hand had a significant downward trend in both Simpson's Diversity Index (1-D) (df = 1, F = 15.39, P = 0.004, $R^2 = 0.64$) and Shannon Index (df = 1, F = 12.82, P = 0.006, $R^2 = 0.59$). East Douglas showed a significant downward trend in Simpson's Diversity Index (1-D) (df = 1, F = 5.74, P = 0.04, $R^2 = 0.42$), however, there was no significant trend in Shannon Index (df = 1, F = 4.32, P = 0.07, $R^2 = 0.35$).

Bradda Offshore showed no significant temporal trend in Simpson's Diversity Index (1-D) (df = 1, F = 0.15, P = 0.7, $R^2 = 0.015$) or Shannon Index (df = 1, F = 0.11, P = 0.75, $R^2 = 0.01$). Chickens showed no significant temporal trend in Simpson's Diversity Index (1-D) (df = 1, F = 1.96, P = 0.19, $R^2 = 0.15$).or Shannon Index (df = 1, F = 0.11, P = 0.75, $R^2 = 0.009$). Peel showed no significant temporal trend in Simpson's Diversity Index (1-D) (df = 1, F = 0.06, P = 0.81, $R^2 = 0.0066$) or Shannon Index (df = 1, F = 4.049, P = 0.075, $R^2 = 0.31$). South of Port St. Mary showed no significant temporal trend in Simpson's Diversity Index (1-D) (df = 1, F = 0.83, P = 0.39, $R^2 = 0.09$) or Shannon Index (df = 1, F = 0.02, P = 0.88, $R^2 = 0.003$).

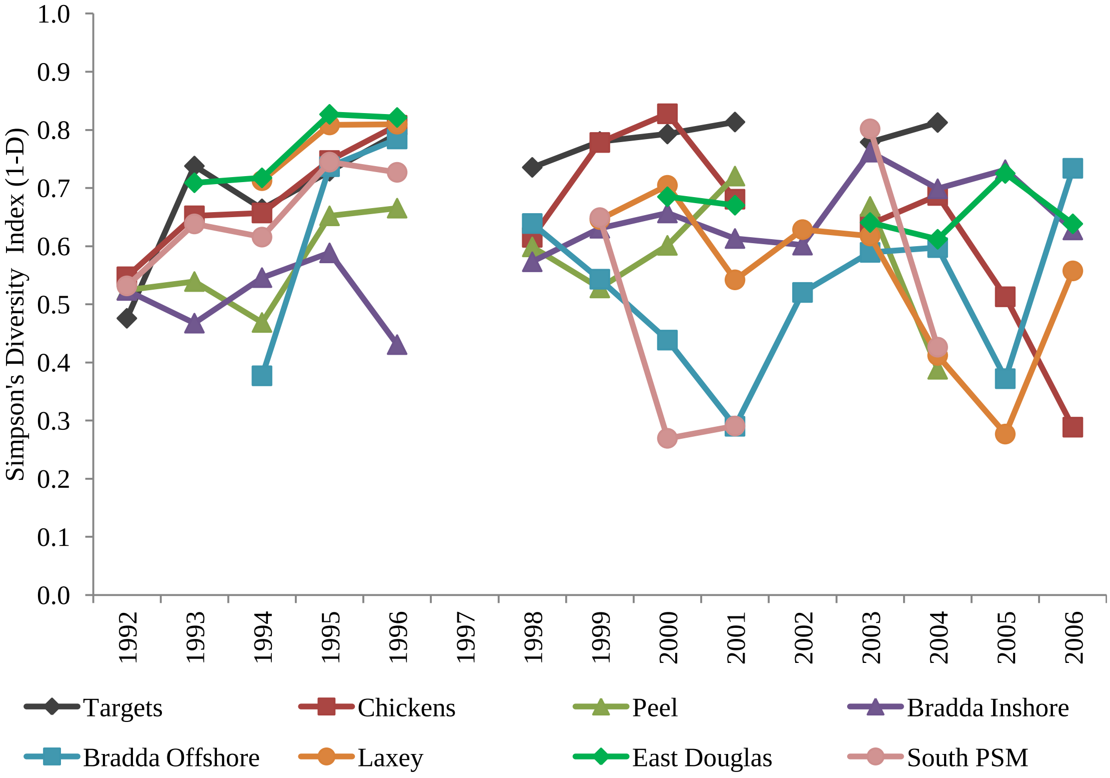

Figure 3.2.Temporal trends in the Simpson's Diversity Index (1-D) of the benthic communities found on eight fishing grounds around the Isle of Man from 1992 to 2006, inclusive.

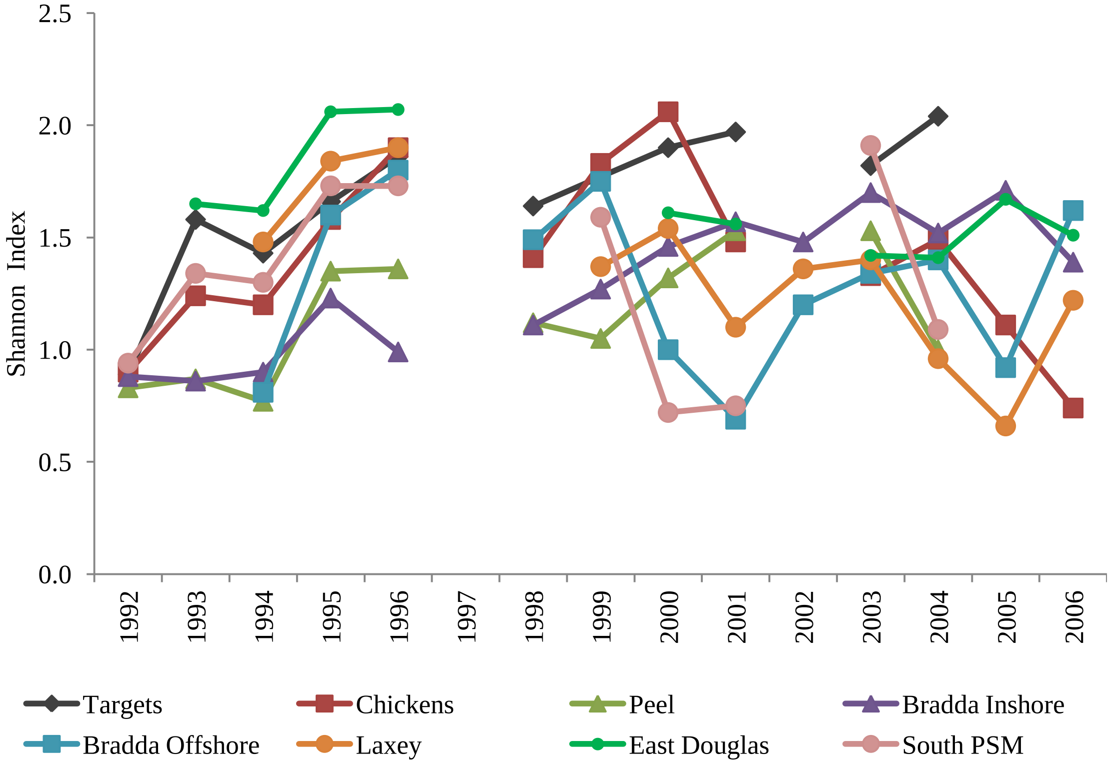

Figure 3.3.Temporal trends in the Shannon Index of the benthic communities found on eight fishing grounds around the Isle of Man from 1992 to 2006, inclusive.

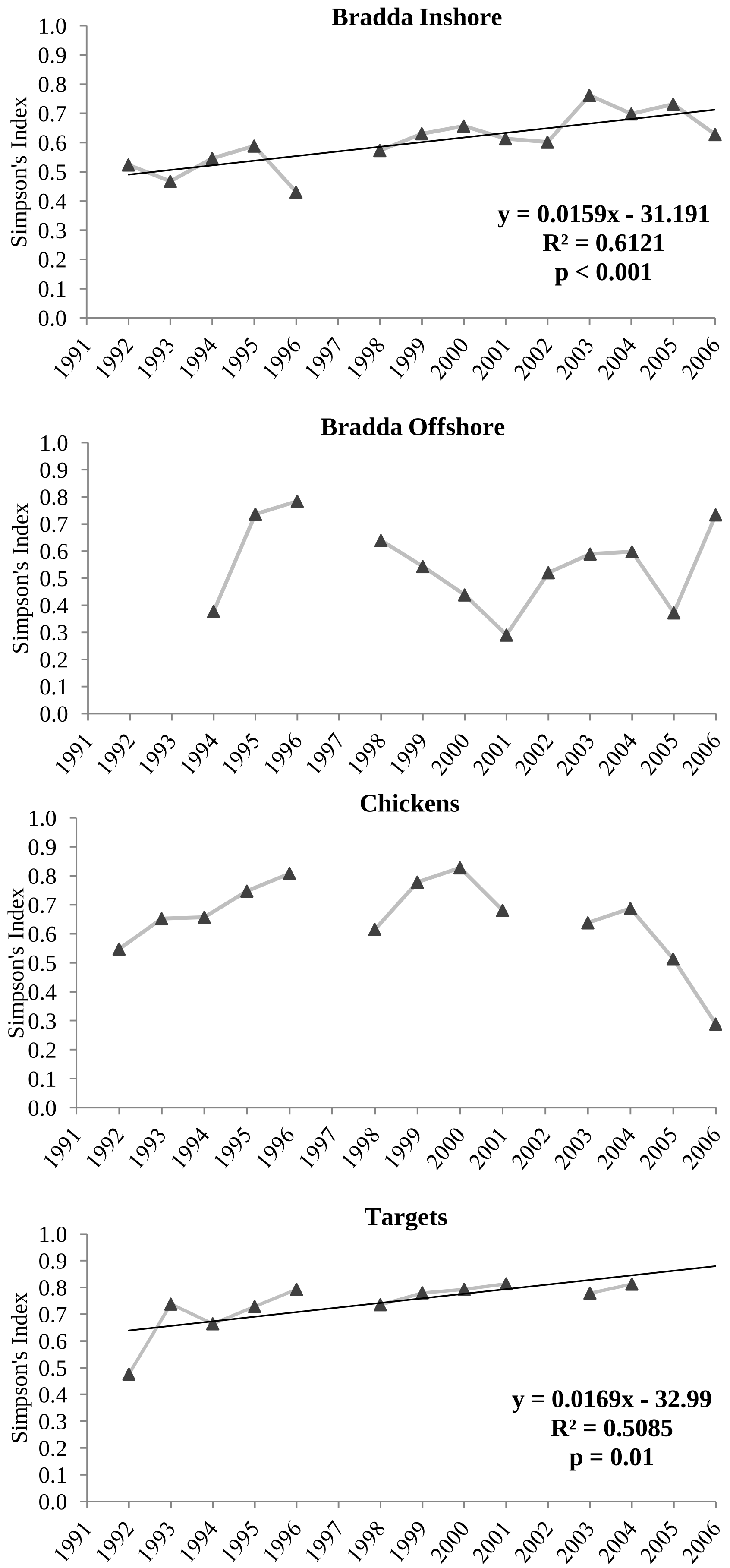

Figure 3.4a. Temporal variation in Simpson's Diversity Index (1-D), calculated from the June, queen dredge catch and bycatch data, at the four fishing grounds around the Isle of Man from 1992 to 2006, inclusive.

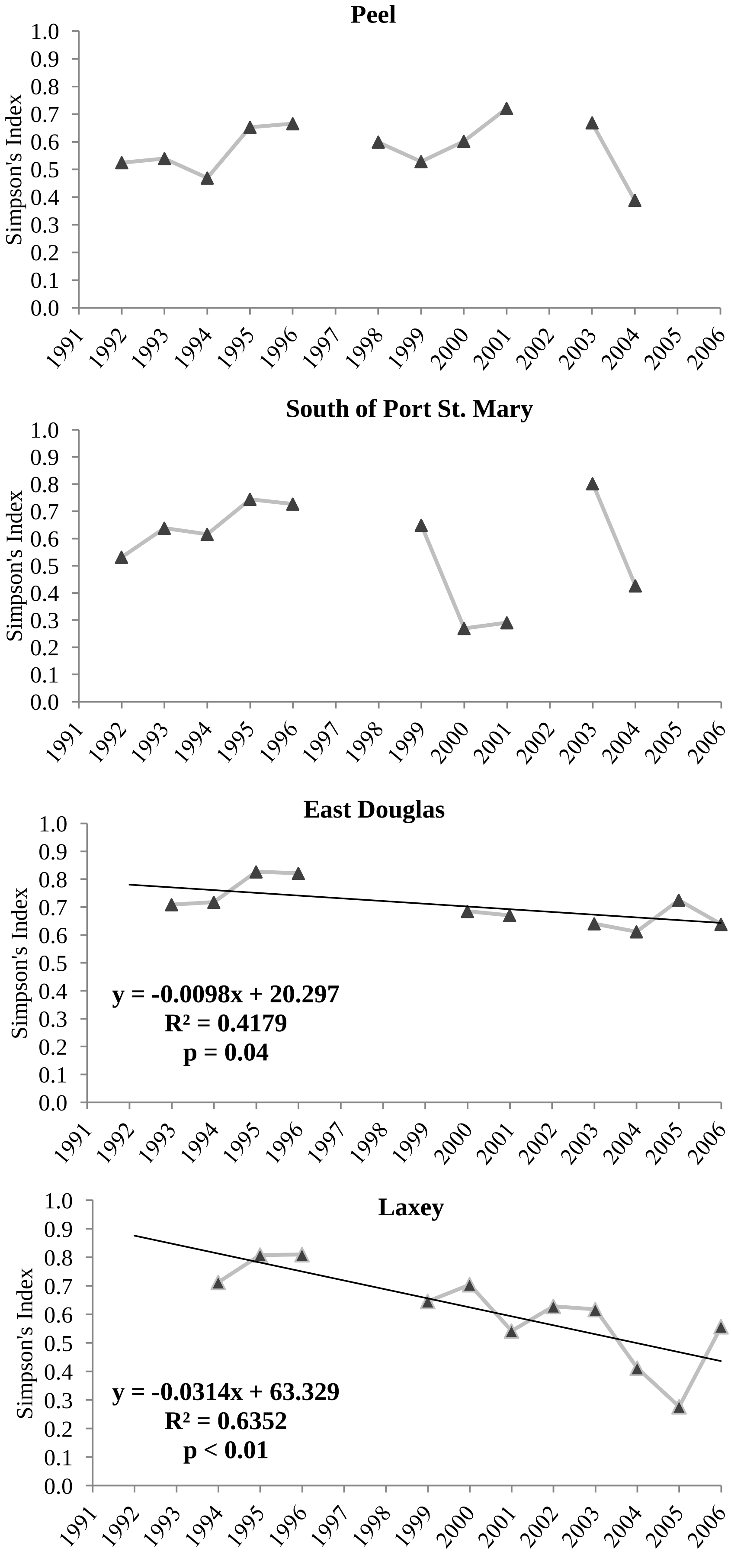

Figure 3.4b. Temporal variation in Simpson's Diversity Index (1-D), calculated from the June, queen dredge catch and bycatch data, at the four fishing grounds around the Isle of Man from 1992 to 2006, inclusive.

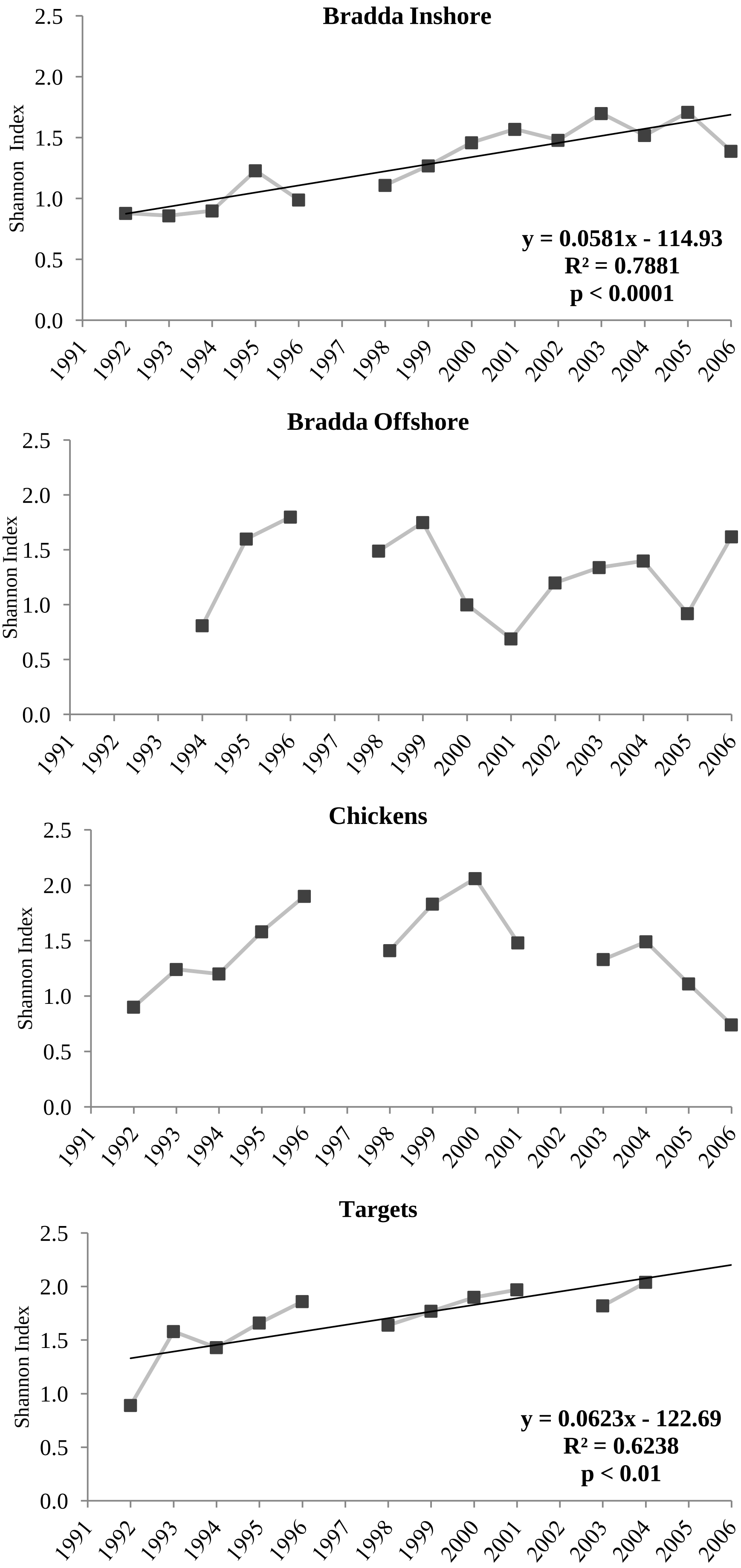

Figure 3.5a. Temporal variation in the Shannon Index, calculated from the June, queen dredge catch and bycatch data, at four fishing grounds around the Isle of Man from 1992 to 2006, inclusive.

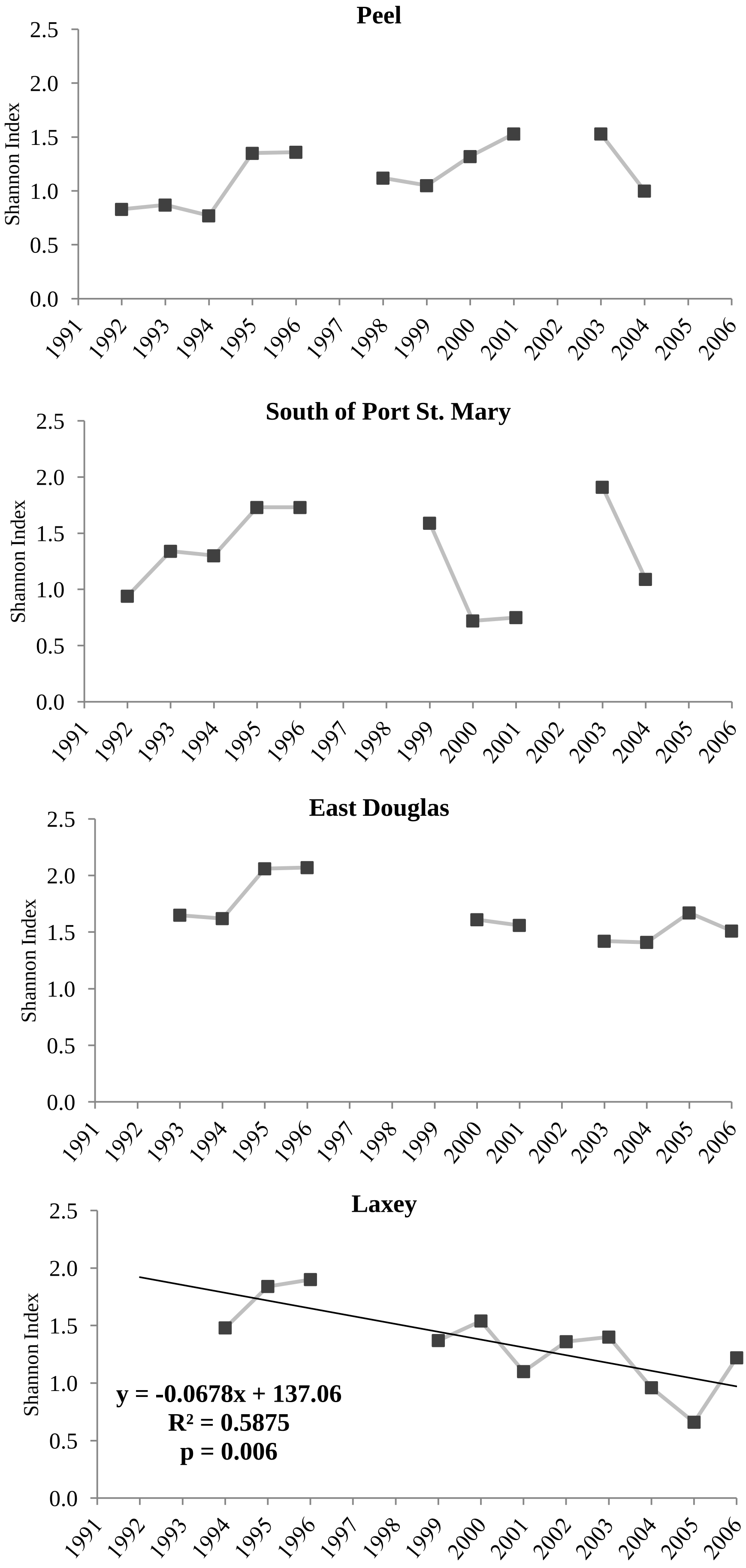

Figure 3.5b. Temporal variation in the Shannon Index, calculated from the June, queen dredge catch and bycatch data, at four fishing grounds around the Isle of Man from 1992 to 2006, inclusive.

3.4.2 Effects of the closed season

There was no significant difference in Simpson's Diversity Index (1-D) between June (the start of the closed season) and October (the start of the fishing season), at any of the eight fishing grounds sampled when tested with one-way ANOVA (Figure 3.6; Table 3.1). Likewise there was no significant difference in Shannon Index between June and October sampling at any of the eight fishing grounds samples when tested with one-way ANOVA (Figure 3.7; Table 3.2).

Table 3.1. Results of one-way ANOVA examining Simpson's Diversity Index (1-D) in June and October (before and after the closed season) at all fishing grounds around the Isle of Man. All data were tested for normality and homogeneity of variances. No fishing ground showed a significant difference in Simpson's index between before and after the closed season.

Ground	df	SS	MS	F-ratio	p-Value
Bradda Inshore	1	0.003	0.003	0.270	0.61
Bradda Offshore	1	0.000	0.000	0.006	0.94
Chickens	1	0.015	0.015	0.793	0.38
Targets	1	0.003	0.003	0.913	0.36
Peel	1	0.000	0.000	0.001	0.98
South PSM	1	0.073	0.073	2.481	0.14
East Douglas	1	0.013	0.013	1.664	0.22
Laxey	1	0.009	0.009	0.243	0.63

Table 3.2. Results of one-way ANOVA examining Shannon Index in June and October (before and after the closed season) at all fishing grounds around the Isle of Man. All data were tested for normality and homogeneity of variances. No fishing ground showed a significant difference in Shannon index between before and after the closed season.

Ground	df	SS	MS	F-ratio	p-Value
Bradda Inshore	1	0.025	0.025	0.322	0.58
Bradda Offshore	1	0.017	0.017	0.149	0.70
Chickens	1	0.041	0.041	0.363	0.55
Targets	1	0.044	0.044	1.149	0.31
Peel	1	0.001	0.001	0.016	0.90
South PSM	1	0.408	0.408	2.783	0.12
East Douglas	1	0.114	0.114	1.722	0.21
Laxey	1	0.077	0.077	0.425	0.52

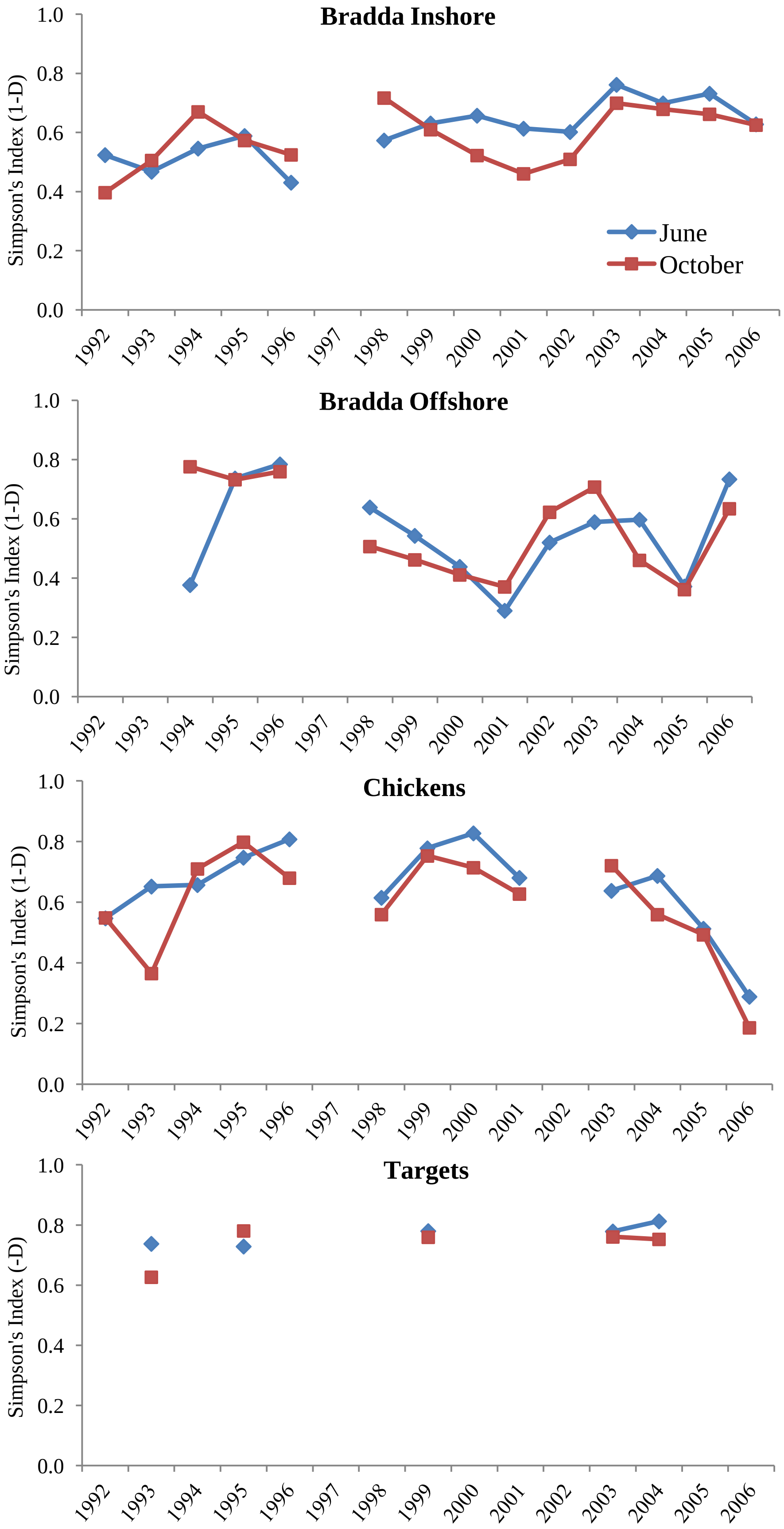

Figure 3.6a. Annual and seasonal variation in Simpson’s Diversity Index (1-D) calculated from queen dredges during surveys on four fishing grounds around the Isle of Man, from 1992 to 2006. Results from June surveys are plotted in line with results from October surveys from that year to coincide with the closed season for great scallop fishing. Only grounds surveyed in both seasons were included.

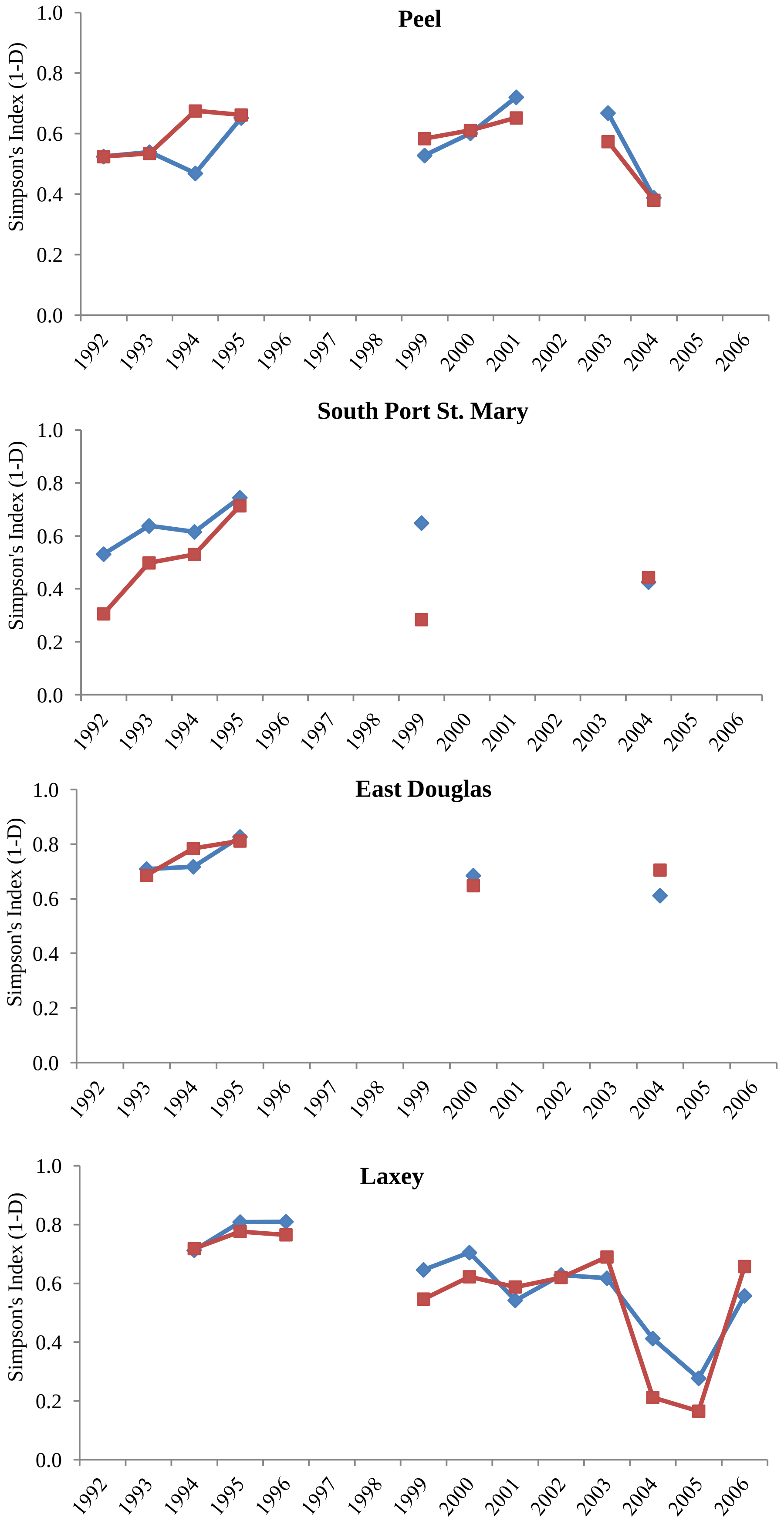

Figure 3.6b. Annual and seasonal variation in Simpson's Diversity Index (1-D) calculated from queen dredges during surveys on four fishing grounds around the Isle of Man, from 1992 to 2006. Results from June surveys are plotted in line with results from October surveys from that year to coincide with the closed season for great scallop fishing. Only grounds surveyed in both seasons were included.

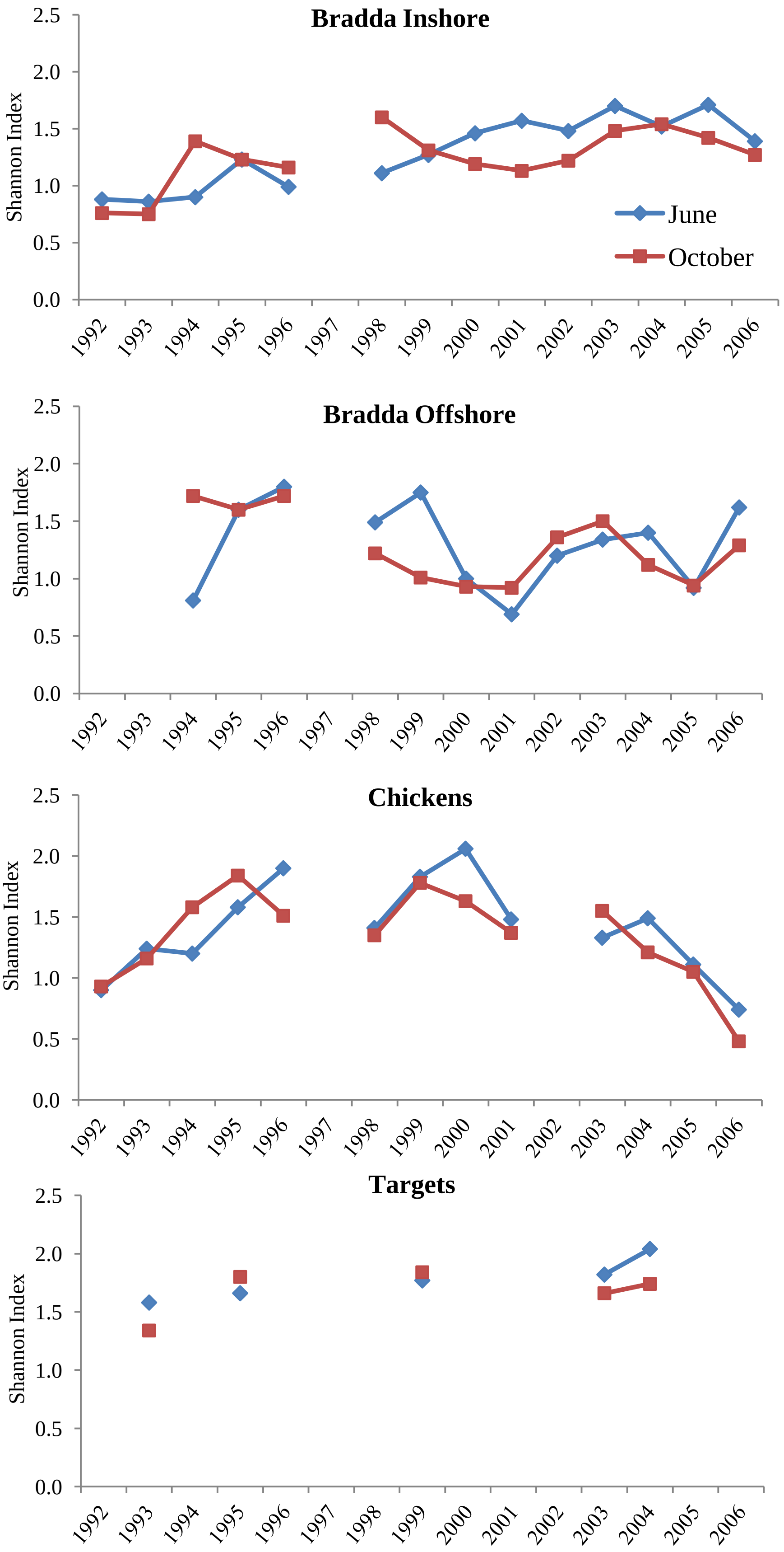

Figure 3.7a. Annual and seasonal variation in Shannon Index calculated from queen dredges during surveys on four fishing grounds around the Isle of Man, from 1992 to 2006. Results from June surveys are plotted in line with results from October surveys from that year to coincide with the closed season for great scallop fishing. Only grounds surveyed in both seasons were included.

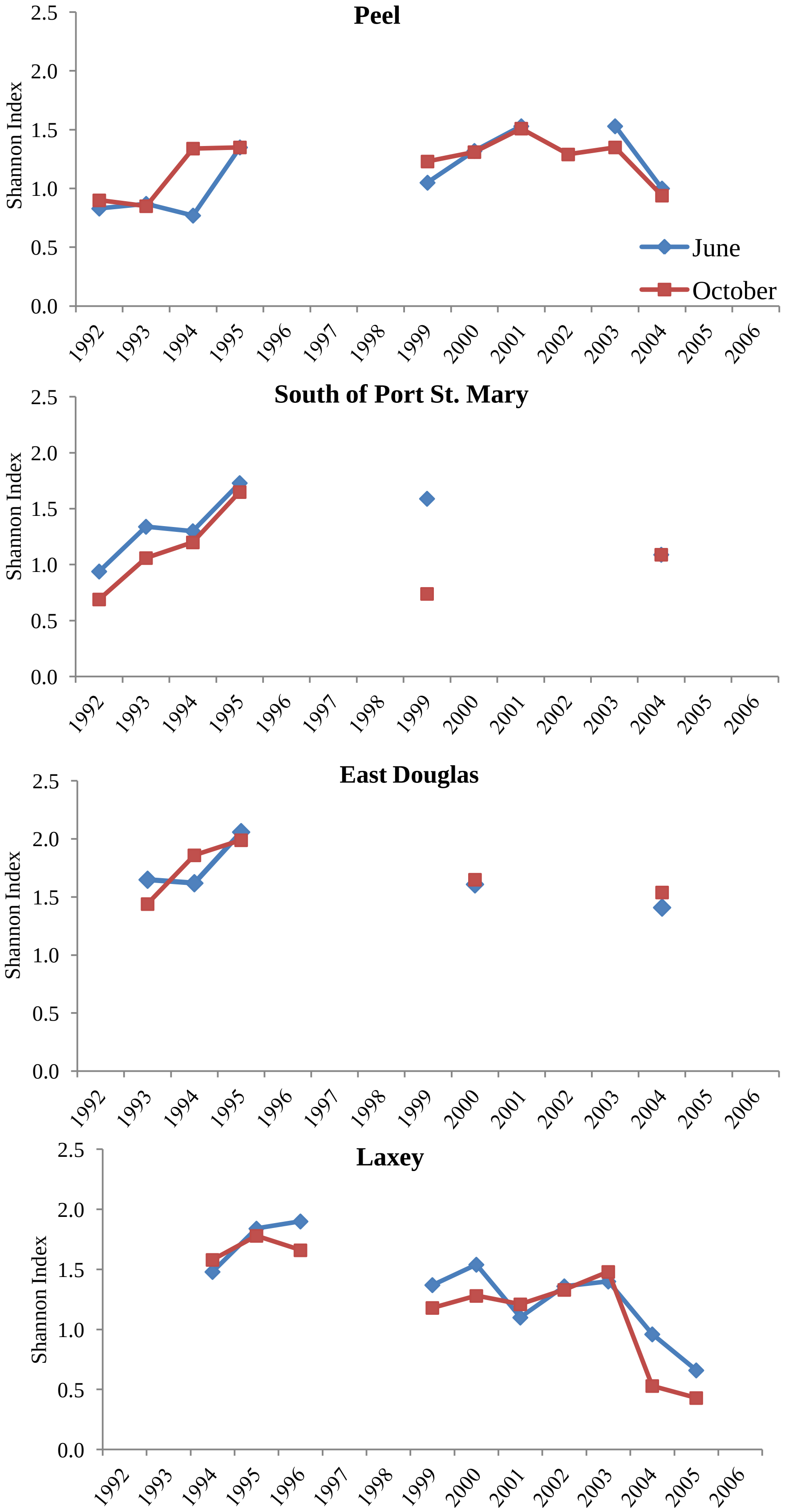

Figure 3.7b. Annual and seasonal variation in Shannon Index calculated from queen dredges during surveys on four fishing grounds around the Isle of Man, from 1992 to 2006. Results from June surveys are plotted in line with results from October surveys from that year to coincide with the closed season for great scallop fishing. Only grounds surveyed in both seasons were included.

3.4.3 Spatio-temporal trends in local fishing fleet effort

Fishing effort by the local Manx great scallop fishing fleet is shown in Figure 3.8. The effort on each ground is shown individually for fishing seasons running from 1991/92 to 2005/06. There were no apparent temporal trends in fishing effort at any of the grounds, although there were large fluctuations from less than 5000 metres of dredge fished per hour at some grounds in the early 1990s to just over 45,000 metres of dredge fished per hour at Targets fishing ground during the 1997/98 fishing season.

3.4.4 The effect of local fishing fleet effort on diversity

A series of linear regression analyses were performed to determine whether there was a relationship between local fishing fleet effort and the diversity indices. Data from all eight grounds were included in this analysis and fishing effort data had to be square-root transformed to ensure normality. Figure 3.9 shows the relationship between Simpson's Diversity Index (1-D) and square-root transformed fishing effort at the three significant time lags. Un-lagged transformed fishing effort had no significant relationship with Simpson's Diversity Index (1–D) (df = 92, F = 0.00003, P = 0.996, $R^2 < 0.0001$). Likewise 1-year lagged transformed fishing effort had no significant relationship with Simpson's Diversity Index (1-D) (df = 95, F = 1.013, P = 0.32, $R^2 = 0.011$). When lagged by 2 years square-root transformed fishing effort had a significant negative relationship with Simpson's Diversity Index (1 – D) (df = 89, F = 3.91, P = 0.051, $R^2 = 0.042$). 3 year lagged square-root transformed fishing effort also had a significant negative relationship with Simpson's Diversity Index (1 – D) (df = 88, F = 5.87, P = 0.017, $R^2 = 0.063$). Finally 4 year lagged square-root transformed fishing effort also had a significant negative relationship with Simpson's Diversity Index (1–D) (df = 90, F = 5.22, P = 0.025, $R^2 = 0.055$).

Figure 3.10 shows the relationship between Shannon Index and square-root transformed fishing effort at the three significant time lags for fishing effort. Un-lagged transformed fishing effort had no significant relationship with Shannon Index (df = 84, F = 0.15, P = 0.703, $R^2 = 0.0017$). Likewise 1-year lagged transformed fishing effort had no significant relationship with Shannon Index (df = 87, F = 0.43, P = 0.516, $R^2 = 0.005$). When lagged by 2 years square-root transformed fishing effort had a significant negative relationship with Shannon Index (df = 87, F = 4.7, P = 0.0331, $R^2 = 0.051$). Three year lagged square-root transformed fishing effort also had a significant negative relationship with Shannon Index (df = 87, F = 6.27, P = 0.014, $R^2 = 0.067$). Finally 4 year lagged square-root transformed fishing effort also had a significant negative relationship with Shannon Index (df = 89, F = 4.32, P = 0.041, $R^2 = 0.046$).

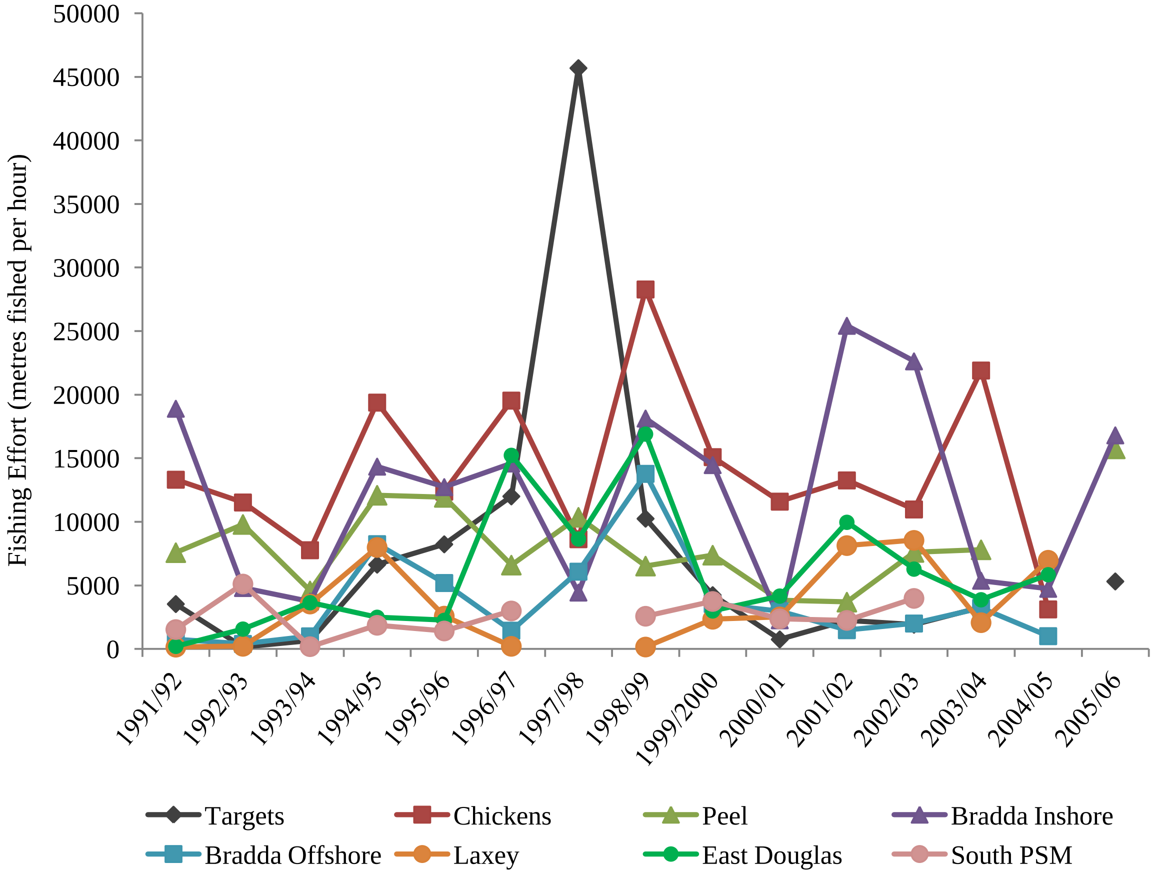

Figure 3.8. Fishing effort for the Great scallop (*Pecten maximus*) at grounds around the Isle of Man from 1991 – 2006. The fishing season runs from 1st November to 31st May each year. Effort data is taken from the Fisherman's Logbook scheme and has been adjusted to take into account the size of the Manx fishing fleet. Data corresponds to the part of each fishing ground that was sampled in the bi-annual scallop surveys, from which diversity indices were calculated for this study.

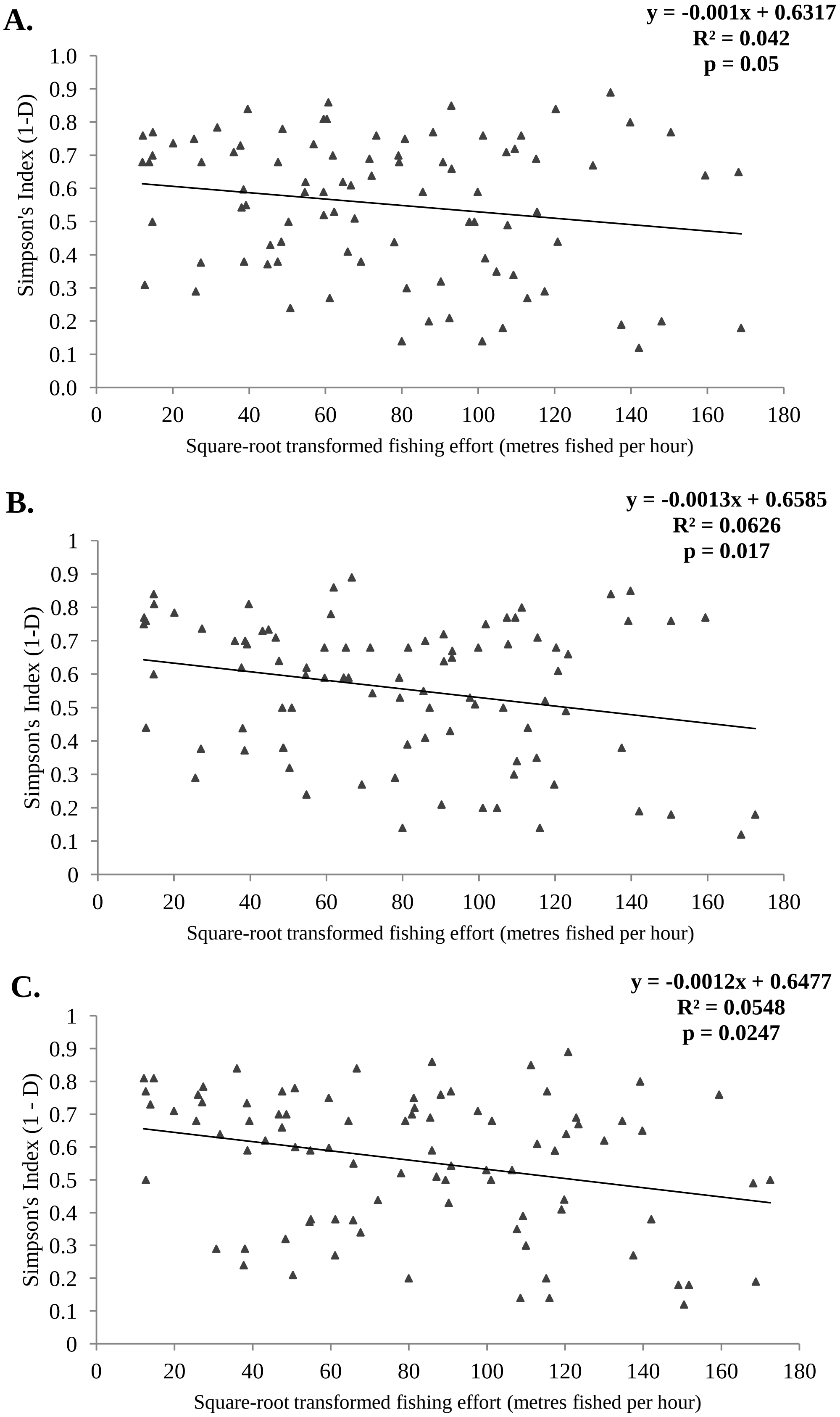

Figure 3.9. The relationship between Simpson’s Index at all scallop fishing grounds around the Isle of Man and (A) 2 year lagged, (B) 3 year lagged and (C) 4 year lagged square-root transformed fishing effort (metres fished per hour). Fishing effort data was transformed to ensure normality and homogeneity of variance.

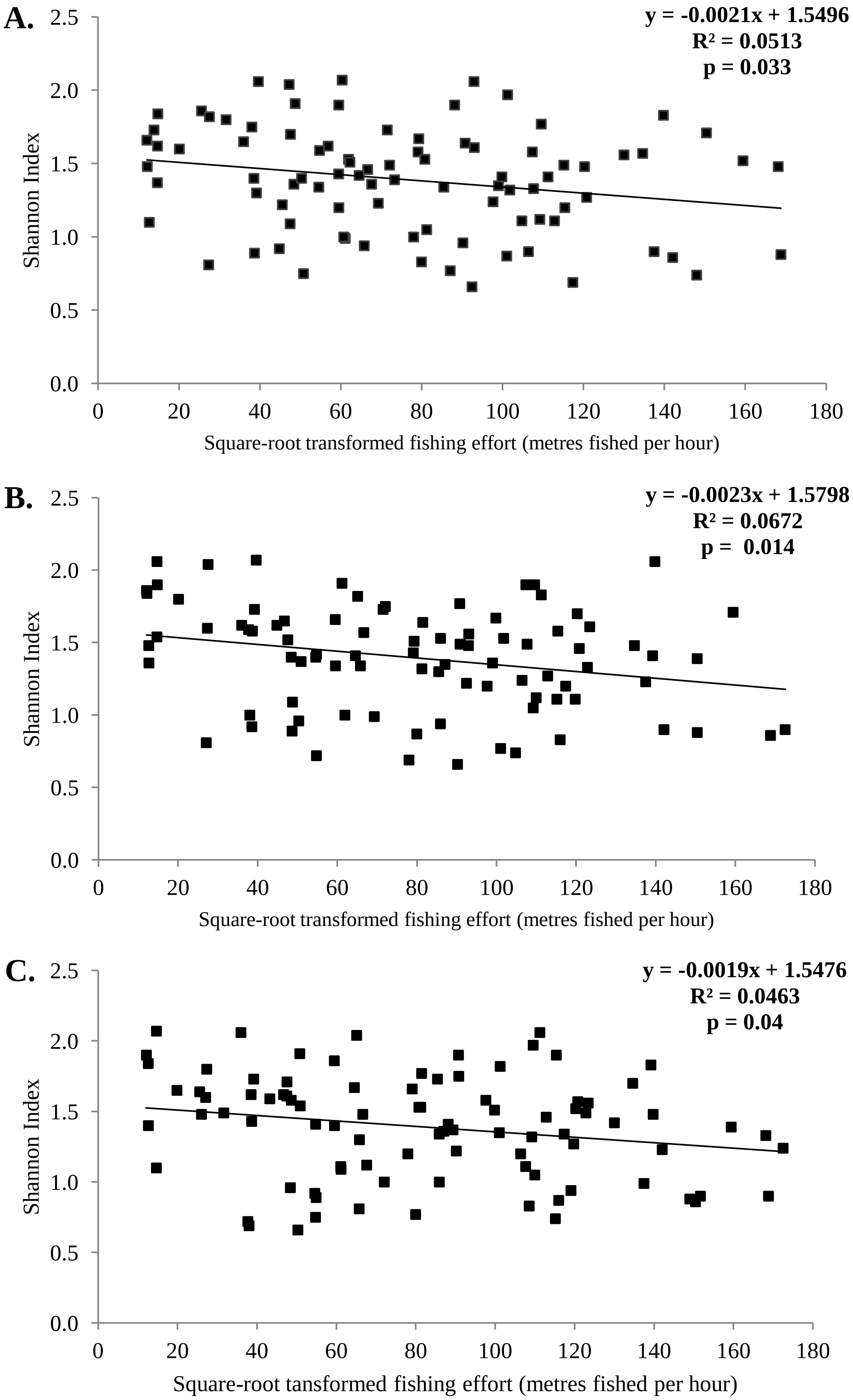

Figure 3.10. Relationship between Shannon Index from all fishing grounds around the Isle of Man and square-root transformed fishing effort, lagged by (A) 2 years, (B) 3 years and (C) 4 years. Fishing effort data was transformed to ensure normality and homogeneity of variance.

3.4.5 Temporal trends in environmental variables

Environmental data collected from the CYPRIS sampling station, to the south-west of the Isle of Man was analysed for temporal trends over the time series studied. Figure 3.11 shows the two significant trends found in the environmental variables. Mean annual chlorophyll-α concentration (μg/L) was calculated from June to May each year and showed a significant downward trend from 1993 to 2006 (df = 1, F = 12.73, P = 0.0039, R^2 = 0.515). Mean annual temperature (^{o}C) was calculated from June to May each year and showed a significant upward trend from 1993 to 2006 (df = 1, F = 9.28, p = 0.01, R^2 = 0.44).

Figure 3.12 shows temporal variation in the three other environmental variables analysed. The North Atlantic Oscillation (NAO) Index (df = 1, F = 3.49, P = 0.084, R^2 = 0.212) and mean spring chlorophyll-α concentration (μg/L) (df = 1, F = 3.49, P = 0.085, R^2 = 0.212) had no significant temporal trend. Conversely, mean spring temperature (^{o}C) showed a significant upward temporal trend (df = 1, F = 5.79, P = 0.0317, R^2 = 0.31).

Figure 3.13 shows the temporal trends of the mean annual concentration of 3 nutrients; nitrate, silicate and soluble reactive phosphate (μM). Mean annual nitrate had no significant temporal trend (df = 1, F = 2.86, P = 0.12, R^2 = 0.19), likewise neither mean annual silicate (df = 1, F = 0.00012, P = 0.99, $R^2 < 0.01$) nor mean annual soluble reactive phosphate (df = 1, F = 0.04, P = 0.85, R^2 = 0.003) had significant temporal trends from 1993 – 2006.

3.4.6 Correlations between environmental variables

All combinations of environmental variable pairs were tested for significant correlations over the time-series of this study (1992-2006). Three combinations had statistically significant relationships and were as follows: mean annual silicate concentration (μM) and mean annual soluble reactive phosphate concentration (μM) (Figure 3.14) were non-normally distributed, and so Spearman’s rank-order correlation was used, which showed that there was a significant positive association between these two variables (r = 0.67, df = 12, P = 0.01). Mean annual temperature (^{o}C) and mean annual nitrate concentration (μM) (Figure 3.15) were both normally distributed and Pearson product-moment correlation indicated a significant negative association between these two variables (r = -0.66, df = 12, $P < 0.01$). Likewise mean annual temperature (^{o}C) and mean annual chlorophyll-α concentration (μg/L) (Figure 3.16) were both normally distributed and Pearson product-moment correlation indicated a significant negative association between these two variables (r = -0.62, df = 12, P = 0.02). All associations between other environmental variables combinations tested were insignificant.

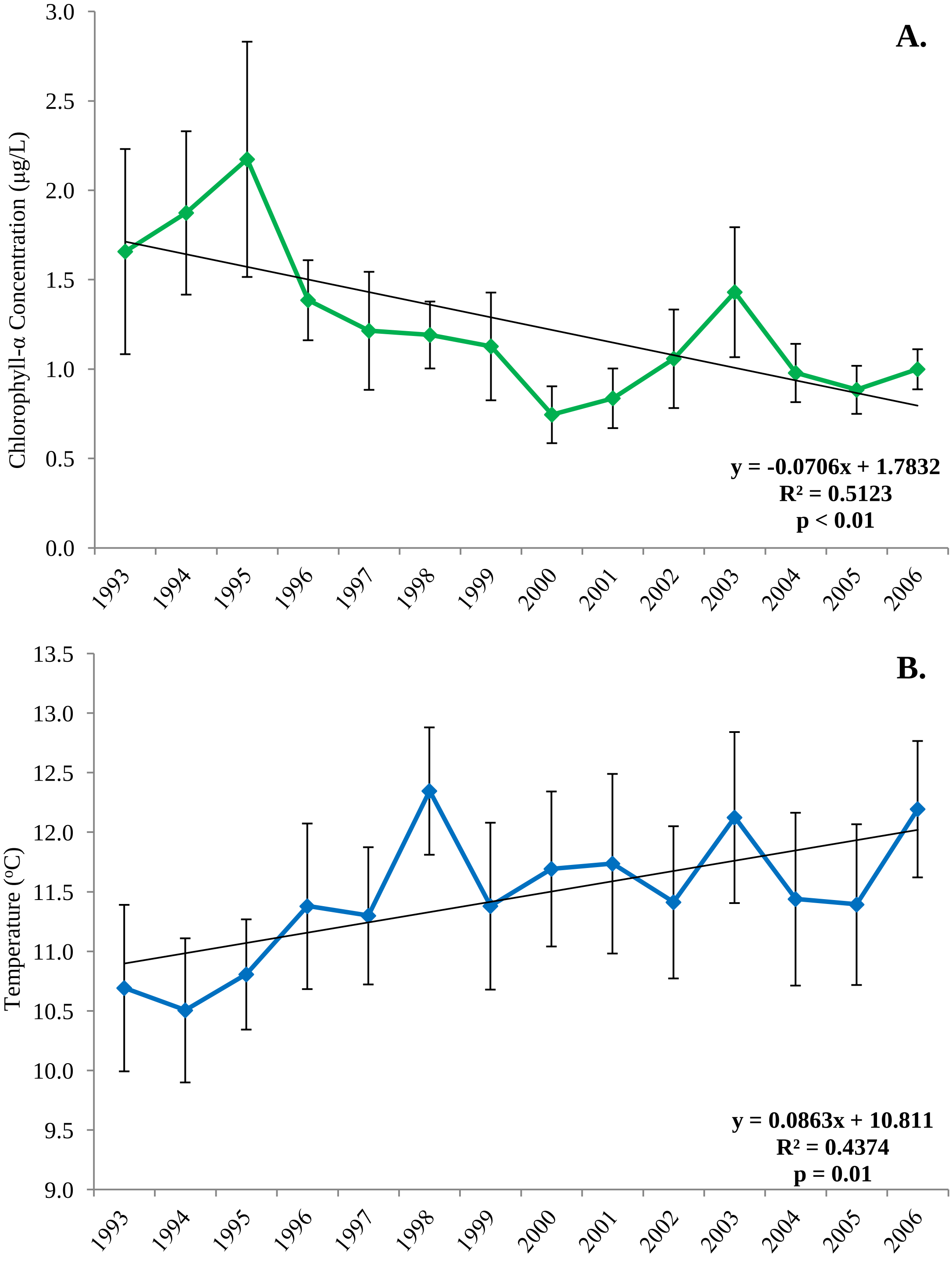

Figure 3.11. Temporal trends in (A) Mean Annual Chlorophyll-α concentration (μg/L) and (B) Mean Annual Temperature taken from the CYPRIS site, south-west of the Isle of Man, from 1993 – 2006 inclusive. Annual values were calculated using data from June the preceding year to May of the year shown. Linear regression trends are shown, with (A) showing a statistically significant negative trend over time ($p = 0.003$) and (B) showing a statistically significant positive trend over time ($p = 0.01$). Standard error bars are shown. Note the truncated y-axis on (B).

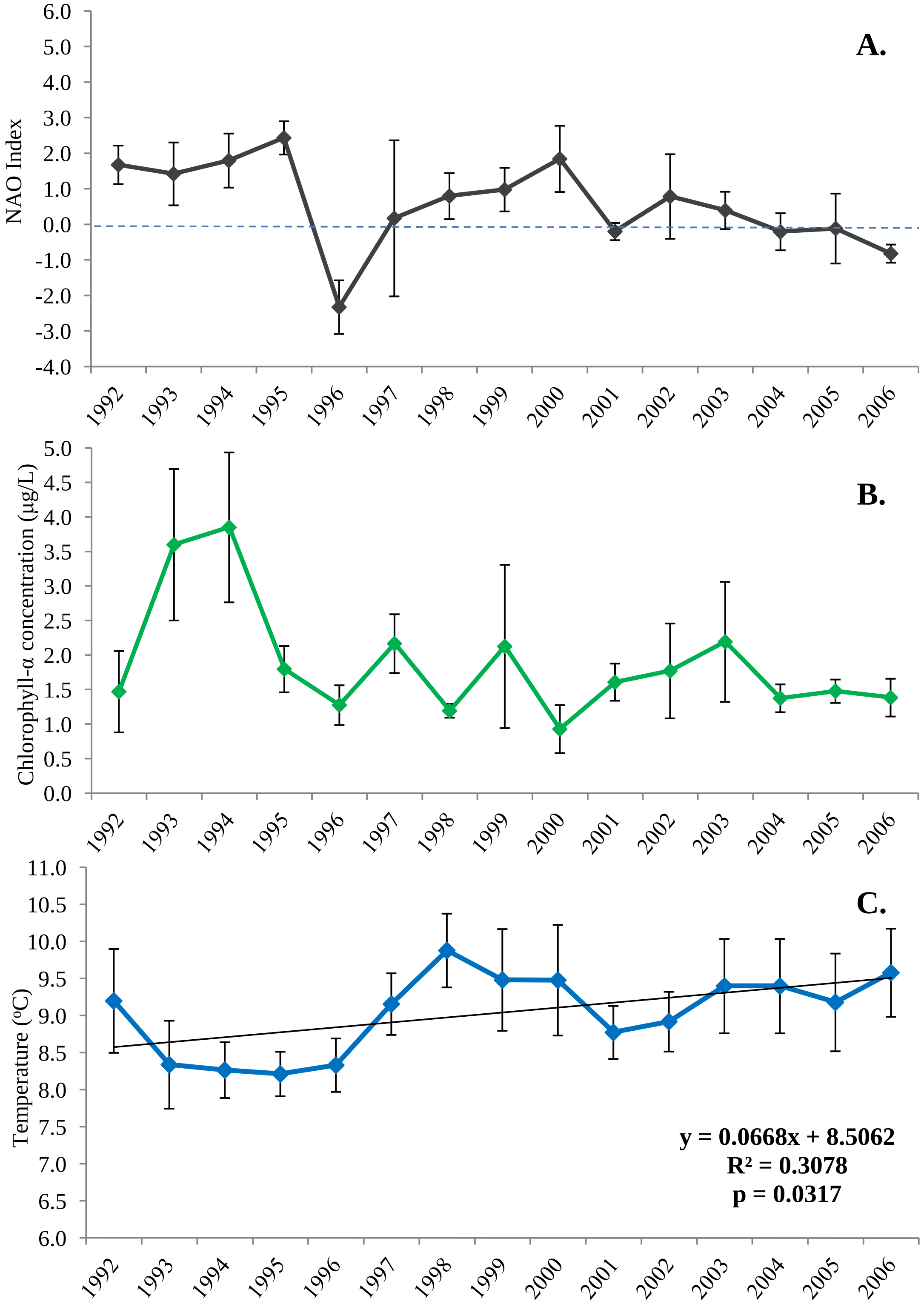

Figure 3.12. Temporal trends in (A) winter (December-March) North Atlantic Oscillation (NAO) Index (B) mean spring chlorophyll-α concentration (µg/L) (calculated from April-June each year) and (C) mean spring (calculated from April-June each year) temperature (°C), from 1992 – 2006, inclusive. NAO data were obtained from the Climate Research Unit, University of East Anglia. Chlorophyll-α and temperature data were collected from the CYPRIS sampling site, south-west of the Isle of Man. Standard error bars are shown on all graphs. Note the negative y-axis on graph A and the truncated y-axis on graph C.

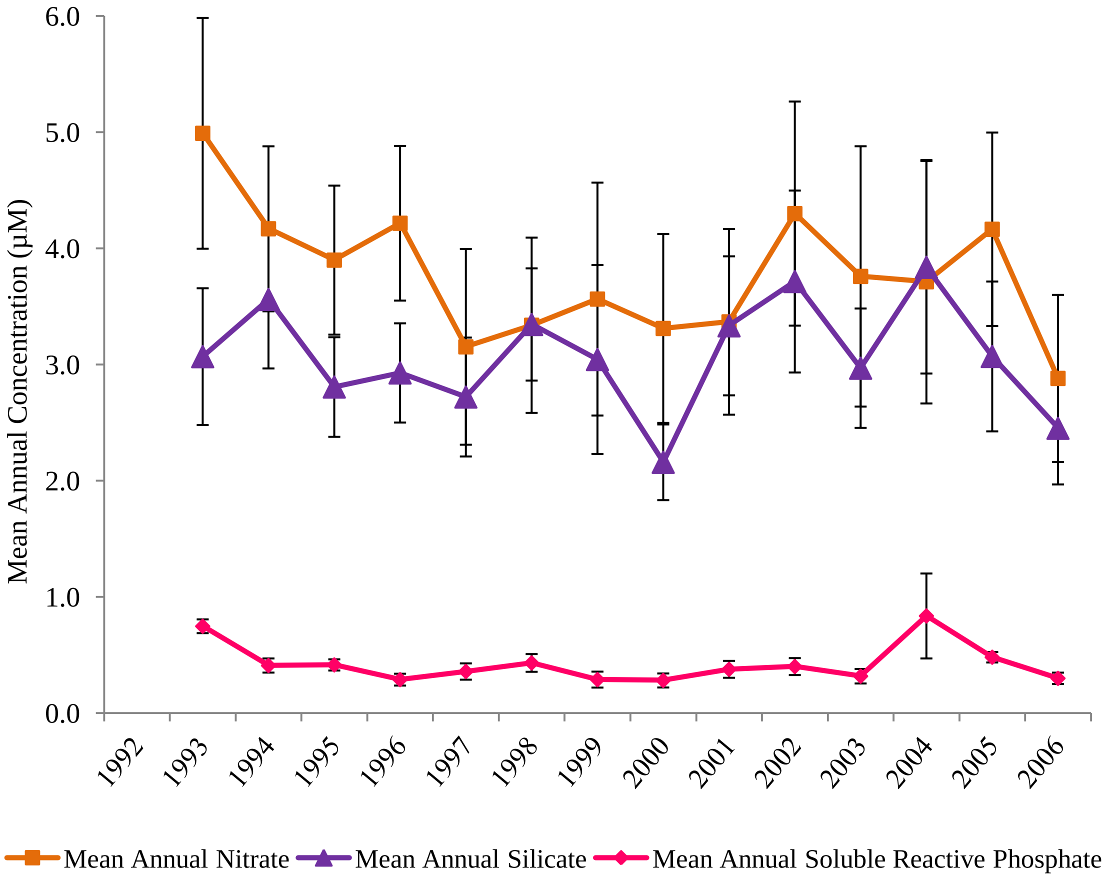

Figure 3.13. Temporal trends in mean annual nutrient concentrations (µM) taken from the CYPRIS sampling station, south-west of the Isle of Man, from 1992 – 2006. Mean annual values were calculated by taking the mean of monthly concentrations from June the preceding year to May of the year shown. Standard error bars are shown.

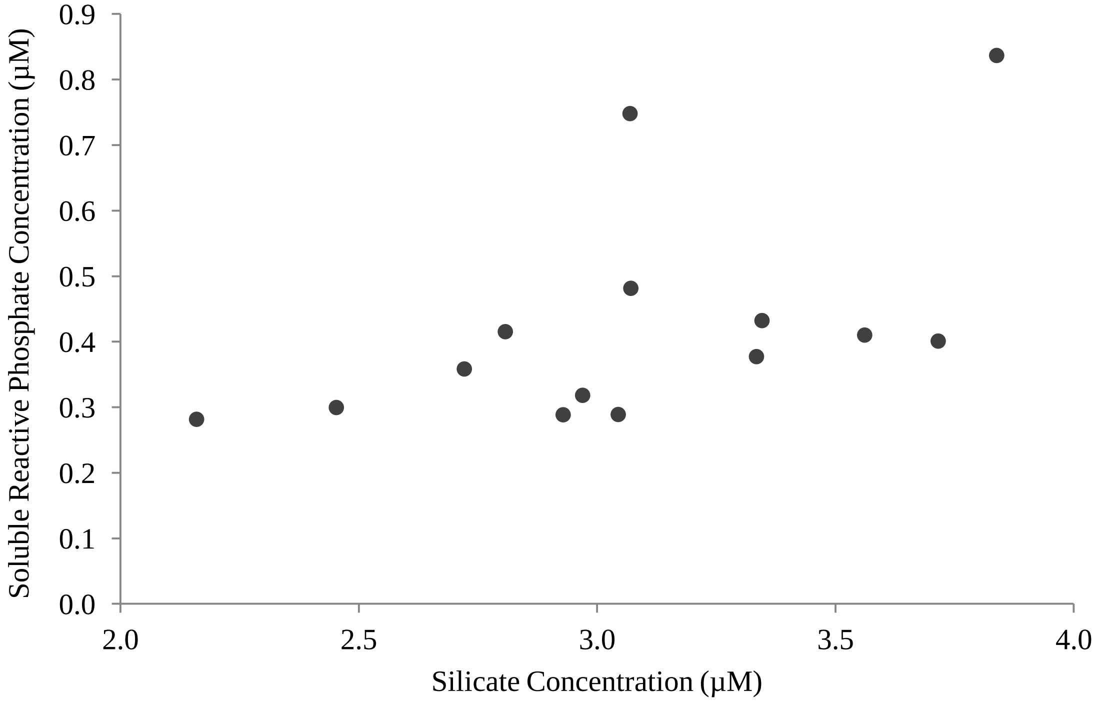

Figure 3.14. The correlation between mean annual silicate concentrations (µM) and mean annual soluble reactive phosphate concentration (µM) from 1992 – 2006 inclusive. Data collected from the CYPRIS site found south-west of the Isle of Man. Note the scaled up x-axis. Data were tested for normality using the Shapiro-Wilk normality test and were found to be non-normally distributed. Spearman's rank-order correlation indicates a significant positive association between mean annual silicate concentration and mean annual soluble reactive phosphate concentration (*r* = 0.67, d.f. = 12, *P* = 0.01).

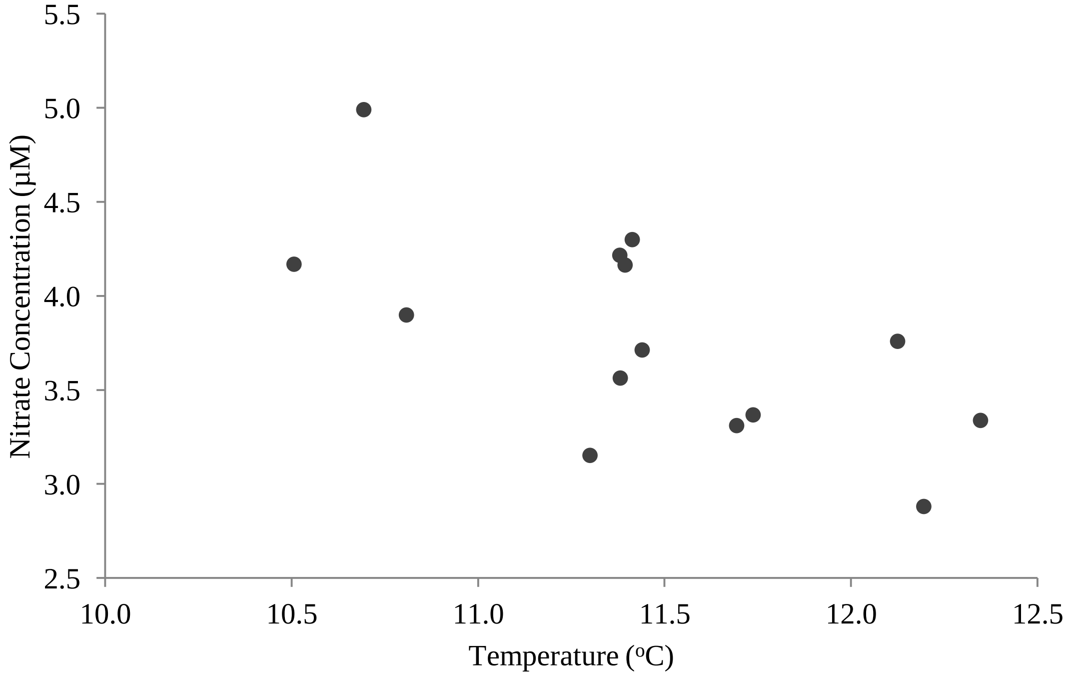

Figure 3.15. The correlation between mean annual temperature (°C) and mean annual nitrate concentration (µM) from 1992 – 2006 inclusive. Data collected from the CYPRIS site, found south-west of the Isle of Man. Note the scaled up x and y-axis. Both datasets were tested for normality using the Shapiro-Wilk normality test and found to be normally distributed. Pearson product-moment correlation indicates a significant negative association between mean annual temperature and mean annual nitrate concentration (*r* = -0.66, d.f. = 12, *P* < 0.01).

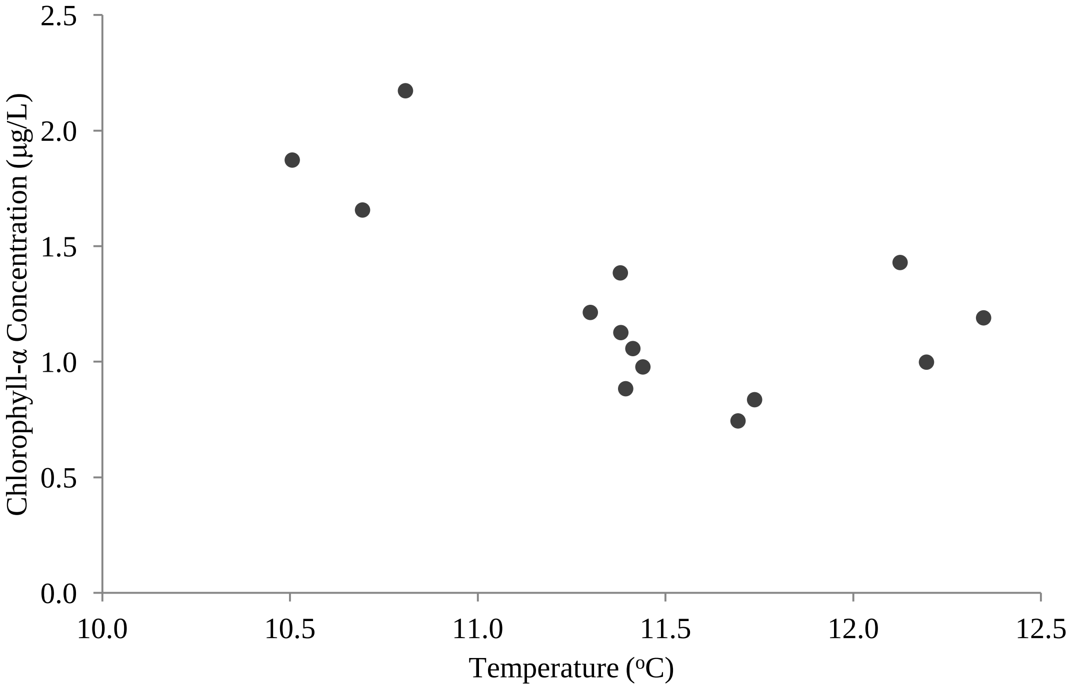

Figure 3.16. The correlation between mean annual temperature (°C) and mean annual chlorophyll-α concentration (µg/L) from 1992 – 2006 inclusive. Data collected from the CYPRIS site, found south-west of the Isle of Man. Note the scaled up x-axis. Both datasets were tested for normality using the Shapiro-Wilk normality test and found to be normally distributed. Pearson product-moment correlation indicates a significant negative association between mean annual temperature and mean annual nitrate concentration (r = -0.62, d.f. = 12, P = 0.02).

3.4.7 The effect of environmental variables on benthic diversity

As with the analysis of fishing effort, the environmental analysis was conducted with different time lags. However, because comparable data was unavailable prior to 1992 only three different lags of the environmental variables were attempted: un-lagged; a 1 year lag; and a 2 year lag. In addition because environmental data was unavailable for each fishing ground individually these lags were tested as a function of mean Simpson's Diversity Index (1-D) and mean Shannon Index, calculated each year for the fishing grounds found on the south and west of the Isle of Man (Bradda Inshore, Bradda Offshore, Chickens, Targets, Peel and South of Port St. Mary). Mean annual soluble reactive phosphate concentration (µM) had a significant positive correlation with mean annual silicate concentration (µM), therefore to reduce possible colinearity the variable for mean annual soluble reactive phosphate concentration (µM) was removed from all analyses. Each analysis also underwent a Variance Inflation Factor (VIF) analysis prior to multiple linear regression. In all cases the only two variables to be removed were mean annual temperature (^{o}C) and mean spring chlorophyll-α concentration (µg/L). Following multiple linear regression and Akaike Information Criteron (AIC) (a measure of the relative quality of the model) model selection the only model to have any significant relationships between any of the environmental variables and either diversity index was the following model with a 1 year lag in environmental variables (Table 3.3) (df = 8, F = 4.801, P = 0.03, $R^2 = 0.64$):

(*Equation 1*)
Mean Shannon Index ~ mean annual nitrate + mean spring temperature + mean annual chlorophyll-α

Table 3.3. Multiple linear regression results for mean Shannon Index modelled as a function of environmental variables lagged by 1 year. Multiple $R^2 = 0.64$, Adjusted $R^2 = 0.51$, F-statistic = 4.801 on 3 and 8 *d.f.* And *P* = **0.03**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Nitrate	-0.200	0.070	-2.687	**0.028**
Mean Spring Temperature	0.083	0.030	2.823	**0.022**
Mean Annual Chlorophyll-α	0.202	0.087	2.333	**0.048**
Intercept	1.567	0.254	6.175	**0.000**

3.5 Discussion

This current study has attempted to untangle the effects of both environmental variables and fishing pressure on the benthic diversity of the commercial fishing grounds around the Isle of Man. Diversity varied spatially between fishing grounds as well as temporally although only four grounds showed significant temporal changes. Bradda Inshore and Targets (found on the west of the island) had significant increases in both diversity indices over the time series. Whereas the fishing grounds Laxey and East Douglas (both on the east of the island) showed significant decreases in diversity. Fishing pressure had a significant negative relationship with both diversity indices when it was lagged by two, three and four years. However, all R^2 values from these analyses were less than 0.07, indicating that less than 7% of the variation in the data was explained by fishing effort. The limited effect of fishing effort on benthic diversity is also shown in the analysis of the effect of the closed season on benthic diversity. Neither diversity index significantly differed between the beginning and the end of the closed season.

Two of the environmental variables investigated showed significant temporal trends; mean annual temperature significantly increased whilst mean annual chlorophyll-α concentration significantly decreased. A significant negative correlation was also found between these two variables. No clear overall relationship between environmental variables and benthic diversity was found. However, when environmental variables were lagged by one year a significant relationship was found between mean annual nitrate, mean spring temperature and mean annual chlorophyll-α concentration and mean Shannon Index. This model had an R^2 value of 0.64, meaning that approximately 64% of the variation seen in mean Shannon Index was explained by this model. This relationship and the rest of this study’s results are discussed in more detail below.

3.5.1 Patterns in diversity

Figures 3.2 and 3.3 show the spatio-temporal patterns in Simpson’s Diversity Index (1-D) and Shannon Index, respectively, at all eight fishing grounds around the Isle of Man. What is most interesting to note is that diversity varied spatially between grounds. In the first half of the time series, from 1992 to 1998, Bradda Inshore, Bradda Offshore and Peel, three of the historically most heavily fished grounds on the west of the Island, showed the lowest diversity for both indices. From 1998 to 2002 Bradda Inshore and Peel’s diversity increased slowly, whilst Bradda Offshore and South of Port St. Mary saw steep declines in both diversity indices. By the end of the time series (2002 – 2006) both diversity indices at Bradda Inshore had continued to slowly increase, whilst Peel, Bradda Offshore and Chickens grounds saw declines in both indices. Of the two grounds on the east coast of the Island, Laxey’s diversity declined steeply in the latter part of the time series for both indices. These patterns indicate factors affected diversity at a ground-specific, rather than regional, scale.

Figures 3.4 and 3.5 show the temporal trends in Simpson's Diversity Index (1 – D) and Shannon Index, respectively, for each fishing ground separately. A regression analysis was performed on all of the grounds, four of which showed significant trends over time. For both indices the fishing grounds Bradda Inshore and Targets showed a significant increase in diversity over the course of the time-series. Whilst Laxey showed a significant decrease in diversity over the course of the time-series for both indices, East Douglas only showed a significant decrease in Simpson's Diversity Index (1-D). All of the other fishing grounds saw fluctuations in both diversity indices over the time series, but exhibited no significant increase or decrease overall.

Benthic communities are not static in time and there could be several causes for the diversity fluctuations exhibited at each fishing ground. Interestingly the two grounds with positive trends (Bradda Inshore and Targets) are found on the west of the Island and the two grounds with negative trends are found on the east of the Island. It is known that there are two distinct bycatch assemblages on either side of the Isle of Man (Veale, Hill et al. 2001). It is also known that the environmental conditions differ between the east and the west of the Island and there is thought to be little mixing of invertebrate populations between each side because of the local hydrodynamic conditions (Evans, Williams et al. 2003; Gowen and Stewart 2005; Hanley, Gell et al. 2012). These factors could play a role in the patterns of diversity shown here, however, not all of the western sites showed increasing diversity over time, so it is likely that there are other factors at play than environmental regime. What is interesting to note is that fishing pressure has historically been higher on the west of the Island and the western fishing grounds have been exploited for longer; the scallop fishery began on Bradda Inshore in 1937 (Brand, Allison et al. 1991). The observed increases in diversity at this site and Targets is therefore surprising, because other work has shown that heavy fishing pressure has a negative effect on diversity (Veale, Hill et al. 2000). It is known that the benthic communities on these fishing grounds have shifted to communities composed of dredge-tolerant species, such as mobile scavengers and species with regenerative capabilities (Bradshaw, Veale et al. 2002). This adaptation of the community to the effect of dredging could then mean that environmental conditions are playing a role in the observed trends in diversity at Bradda Inshore and Targets.

A study of benthic communities on Georges Bank found that although undisturbed sites had a greater abundance of species and overall diversity, disturbed sites had a greater evenness (Collie, Escanero et al. 1997). The reason for this observed trend was thought to be because dredging prevented any single species from becoming numerically dominant (Collie, Escanero et al. 1997). The diversity measures used in this study both take into account evenness within the community, although Shannon Index is more sensitive to increases in species richness (Magurran 2004). If the benthic communities of the fishing grounds to the south-west of the Isle of Man are in fact composed of dredge-tolerant species, then an increase in species evenness may also be an explanation for the observed increases in diversity at these sites.

3.5.2 The effect of the closed season on diversity

Diversity did not vary significantly between the start and end of the closed season. This result is perhaps not surprising because the closed season is only 5 months in duration and recovery times for benthic communities have been found to take years, especially in chronically exploited areas (Kaiser, Clarke et al. 2006; Foden, Rogers et al. 2010). For example, *P. maximus* densities in the closed area near the Bradda Inshore fishing ground took several years to increase after the initial closure (Beukers-Stewart, Vause et al. 2005). In addition to this it takes about 2 years for benthic invertebrates like *P. maximus* to grown large enough to appear in the dredges used in this study (Beukers-Stewart, Mosley et al. 2003). Therefore it is unlikely that a short closed season would directly affect species diversity in the samples analysed. Similar results were also found for the fish component of the bycatch used in this time series (Craven, Brand et al. 2012). Craven et al (2012) noted that although the great scallop fishery is closed during the summer months, throughout this survey the queen scallop fishery remained open. Therefore it is likely that on those grounds that are also used as queen scallop fishing grounds, there is year round impact from some form of bottom fishing.

3.5.3 Effects of fishing effort on diversity

Fishing effort had a significant negative effect on both Simpson's Diversity Index (1-D) and Shannon Index when lagged by 2, 3 and 4 years (Figures 3.9 and 3.10 respectively). When analysed with no lag or only a 1 year lag no significant effect of fishing effort could be seen on either diversity index. All of the significant results had very low R^2 values (<0.07), indicating that fishing effort only explained a small proportion of the pattern in either diversity index. It is clear, therefore, that other factors are having an effect on diversity in addition to fishing effort. It is likely that there is some effect of environmental variables, which were also analysed in this study and are discussed in the next section.

Benthic communities are structured by a range of factors and naturally vary over time (Kaiser, Armstrong et al. 1998; Bradshaw, Veale et al. 2002). Therefore some of the variation seen in diversity at each of the fishing grounds in this study could be due to natural variation within the benthic community. Unfortunately comparable data from before intensive scallop fishing began around the Isle of Man are not available. Earlier studies such as Hill et al (1999) and Bradshaw et al (2002) compared modern datasets with those collected by Norman Jones in the 1950s. Both studies found significant differences in the benthic community composition on the fishing grounds around the Isle of Man, with an increase in more dredge-tolerant species and a decrease in fragile dredge-vulnerable species (Hill, Veale et al. 1999; Bradshaw, Veale et al. 2002). However, fishing effort data has only been collected since the 1980s and therefore the current time series stretches as far back as is possible.

Another reason for the observed small R^2 values may be that fishing effort has a differential effect on each ground. There are differences in the substrate and the depth of the fishing grounds, both of which are known to influence the impacts of fishing (Kaiser 1998). The settlement of spat for both queen and great scallops varies temporally and spatially (Beukers-Stewart, Mosley et al. 2003; Vause, Beukers-Stewart et al. 2007). The sources and sinks for scallops around the Isle of Man are not well understood (Neill and Kaiser 2008). It is therefore likely that many benthic species that have similar reproductive phases and pelagic larvae will also vary in their settlement spatially and temporally, which may explain some of the variation seen in diversity between fishing grounds.

Some of the fishing grounds around the Isle of Man are subjected to fisheries for both great and queen scallops (Targets, Laxey, East Douglas and South of Port St. Mary) (Vause, Beukers-Stewart et al. 2007). The effect of the queen scallop fishery, which utilised both trawls and dredges throughout the time period of this study (Brand 2006; Beukers-Stewart and Beukers-Stewart 2009), is not quantified and therefore represents another area of uncertainty. However, the impact of the queen scallop fishery is unlikely to be on the same scale as the great scallop fishery because it is less widespread and not as intensive (Vause, Beukers-Stewart et al. 2007). In addition to this the fishing gear used is less damaging than the toothed Newhaven dredges used in the great scallop fishery (Vause, Beukers-Stewart et al. 2007; Hinz, Murray et al. 2012)

The time lags (1,2, 3 and 4 years) used to investigate fishing effort were chosen because many of the species that make up the benthic communities (e.g. *Asterias rubens*) around the Isle of Man take approximately two years to become large enough to count in the dredges (Bryce Stewart *pers. comm.*).Therefore it is not surprising that fishing effort showed no effect on diversity when it was not lagged or only given a one year lag. Not all benthic species would have appeared in the dredges in the same year and hence the significance of the 2, 3 and 4 year lag in fishing effort probably reflects these differences. Given the life span of many of the species present, a lag any greater than 4 years would not make biological sense.

The 3-year lag in fishing effort produced the lowest p-values (<0.02) and the greatest R^2 values (0.06) for both diversity indices. However, these values were not greatly different from the 2-year lag and 4-year lag in fishing effort and therefore, although it seems that fishing effort lagged by 3 years fit the pattern in both of the diversity indices best, it must be remembered that even this explained less than 7% of the variation in the data.

3.5.4 Patterns in environmental variables

3.5.4.1 Temperature

Since the 1950s, global sea surface temperatures have increased by approximately 0.4^{o}C (Levitus, Antonov et al. 2009; Doney, Ruckelshaus et al. 2012). This warming trend has been associated with anthropogenic climate change (Frost, Baxter et al. 2012). However, ocean circulation and interactions with climate variability, such as the North Atlantic Oscillation, have meant that ocean warming has not been spatially uniform (Ishii, Kimoto et al. 2006; Doney, Ruckelshaus et al. 2012). There is also the additional complexity of natural variability in sea water temperature, which ranges from inter-annual to multi-decadal time scales and varies between regions (Frost, Baxter et al. 2012). In this current study two different temperature variables were used, mean annual temperature (^{o}C) and mean spring temperature (^{o}C). Both variables showed statistically significant increases over the course of the time series (1992 – 2006) (Figures 3.11B and 3.12C). This finding concurs with an analysis of long-term environmental datasets that have shown a 0.75^{o}C increase in mean seawater temperature around the Isle of Man over the last 100 years (Bradshaw, Veale et al. 2002). A recent study conducted by Shephard et al (2010) also found a warming trend in spring ocean temperatures around the Isle of Man.

Sea temperature is one of the key factors affecting the physiology and ecology of marine fish and shellfish (Portner and Farrell 2008; Drinkwater, Beaugrand et al. 2010; Frost, Baxter et al. 2012). The increases in spring temperature around the Isle of Man have been linked to observed increases in recruitment success and CPUE for the great scallop (Shephard, Beukers-Stewart et al. 2010). However, increases in temperature can have many other complicated effects on marine ecosystems, such as increased stratification leading to decreased nutrient availability, shifts in phenological events leading to mis-matches between predators and prey and changed distributional boundaries of species with low thermal tolerances, to name but a few (Doney, Ruckelshaus et al. 2012).

The temperature variables in this study were examined for correlations with the other environmental variables. Two significant correlations were found (Figures 3.15 and 3.16), one with chlorophyll-α concentration, discussed in the next section and the second was a significant inverse correlation with nitrate concentration. This inverse correlation found between mean annual temperature and mean annual nitrate concentration (Figure 3.15) is one that is generally observed in marine systems (Silio-Calzada, Bricaud et al. 2008). As light levels increase, there is progressive warming of the water occurring simultaneously to nitrate consumption by increases in phytoplankton, which ultimately lead to the spring bloom (Silio-Calzada, Bricaud et al. 2008). This bloom then depletes the nutrients found in the euphotic layer and so during the warm summer months, nitrate concentrations are low (Silio-Calzada, Bricaud et al. 2008). The results of this study, therefore confirm that this is happening around the Isle of Man.

3.5.4.2 Nutrients

In this investigation no statistically significant temporal trends have been found in any of the nutrient concentrations between 1992 and 2006. It should be noted that the data used in this study, although collected from the same CYPRIS site as other long-term studies, was analysed using automated chemical analysis and has been thought by other authors to not be wholly comparable with data collected pre-1992 (Allen, Slinn et al. 1998; Evans, Williams et al. 2003). However, previous studies from the same sampling site, have found long-term significant trends in the concentrations of phosphate and nitrate (Gowen, Hydes et al. 2002; Evans, Williams et al. 2003). These studies were conducted on a much larger temporal scale than this current work, therefore the lack of a significant trend here is likely because of the relatively short nature of this time series.

3.5.4.3 Chlorophyll-α

Chlorophyll-α concentration has been used as a proxy indicator for phytoplankton biomass in this study. No specific information about the species composition of the phytoplankton was collected and this makes understanding the temporal trends a little challenging. In this study mean annual chlorophyll-α concentration showed a statistically significant decrease over time (Figure 3.11A), whereas mean spring chlorophyll-α concentration showed no significant temporal pattern (Figure 3.12B). This suggests that there was no significant temporal change in the spring phytoplankton bloom, but that there was a decrease in phytoplankton during the rest of the year. Both chlorophyll-α variables show much larger concentrations in the first four years of the time series (1992 – 1995). For mean spring chlorophyll-α, concentrations in 1993 and 1994 were approximately 1.5μg/L greater than any other year (Figure 3.12B). This pattern is repeated within the mean annual chlorophyll-α variable, although because it is the annual mean the difference between years is not so great. The reason for these high concentrations is not clear, although it seems likely that nutrient availability is the main cause. The concentration of nitrate was higher in 1993 than any other year, and although there was not a significant temporal trend over the course of the time-series, there was a corresponding decrease in concentration from 1994 – 2000 (Figure 3.13). Silicate also showed a slight increase in concentration for 1994, followed by a slight dip for the years 1995 to 1997 (Figure 3.13). This suggests that nutrient availability was the main factor in determining phytoplankton biomass over the course of this study.

This theory seems to be supported by recent work conducted by Hanley et al (2012) investigating the phytoplankton community in the Manx territorial sea. They found that the spring bloom was dominated by diatoms and microflagellates and that as the spring and summer months progress there was a distinct succession of phytoplankton functional groups, typical of phytoplankton in the Irish Sea waters as a whole (Hanley, Gell et al. 2012). During the spring bloom both nitrate and silicate become exhausted as the diatom component of the phytoplankton dominates (Hanley, Gell et al. 2012). After this the diatom population crashes and is replaced by a dinoflagellate population, which dominates during the summer and autumn months (Hanley, Gell et al. 2012). Kennington et al (1999) found that in the north-east Irish Sea, winter concentrations of total organic nitrate and silicate were closely associated with variations within the spring phytoplankton community. As both nitrate and silicate are important for diatom growth (Hanley, Gell et al. 2012) it makes sense that fluctuations in their availability in the year prior to the spring bloom, would have an influence on the biomass of phytoplankton in the spring bloom, which is dominated by diatom flora.

There were not, however any statistically significant correlations between either of the chlorophyll-α variables and any of the nutrient concentrations in this study. In fact mean annual chlorophyll-α (μg/L) was the only variable of the two to have a statistically significant correlation with anything else and that was a negative correlation with mean annual temperature (^{o}C) (Figure 3.16). A correlation does not infer causality and could be an artefact of the two variables temporal trends, however it is not implausible that temperature may play a role in the concentration of chlorophyll-α found in this time-series.

The two main factors controlling phytoplankton blooms (other than nutrients) are light and temperature (Wiltshire and Manly 2004; Wiltshire, Malzahn et al. 2008; Lohmann and Wiltshire 2012). A theory has developed that suggests that for a constant supply of nutrients (as in this study) and light (for which there are no data available in this study) phytoplankton biomass would decrease with increasing temperature (Brown, Gillooly et al. 2004). This is because of an increased metabolic demand per unit of biomass (Brown, Gillooly et al. 2004; Sommer, Adrian et al. 2012). There is also evidence that heterotrophic plankton species are more sensitive to temperature increases than autotrophic species (Allen, Slinn et al. 1998; O'Connor, Piehler et al. 2009; Sommer, Adrian et al. 2012). Therefore a reduction in the standing stock of phytoplankton within an ecosystem experiencing warming could be a result of stronger consumer-driven control of primary production (O'Connor, Piehler et al. 2009). There is clearly scope for more work investigating the dynamics of the phytoplankton community around the Isle of Man, in particular its relationship with temperature as the results of this study indicate that these two variables have some form of relationship. Given that both *P. maximus* and *A. opercularis*, the two valuable target species of the fisheries around the Isle of Man, are suspension feeders, the results of this study highlight the importance of understanding the dynamics of complex food webs and the impact climate change may have.

3.5.5 Effect of environmental variables on diversity

To attempt to discern any relationships between environmental variables and diversity, a series of multiple linear regression analyses were performed against mean Simpson's Diversity Index (1-D) and mean Shannon Index. The mean diversity indices were calculated from diversity at grounds found on the western side of the Isle of Man (Bradda Inshore, Bradda Offshore, Chickens, Targets, Peel and South of Port St. Mary). This was done because environmental data was only available from the CYPRIS sampling station and different environmental conditions exist on the eastern side of the Island, where Laxey and East Douglas fishing grounds are located (Hanley, Gell et al. 2012). Mean diversity indices were calculated so that data gaps caused by missed sampling seasons were filled, which meant that the full 14 years of data could be analysed. This was also important when lagging environmental variables because a year was lost from the dataset each time they were lagged.

Colinearity between the environmental variables was tested using a VIF analysis and this led to the removal of mean spring chlorophyll-α concentration (μg/L) and mean annual temperature (^{o}C). Mean annual phosphate concentration (μM) was excluded from the analysis because it had a significant positive correlation with mean annual nitrate concentration (μM). It was considered to be the least important of the three nutrient variables and therefore it is not felt that its removal at this stage in the analysis will have had any effect on the outcome of the analyses. Of all the combinations of environmental variables and the two diversity indices only one multiple linear regression model showed any significant relationship with diversity and that was when mean annual nitrate, mean spring temperature and mean annual chlorophyll-α were lagged by 1 year and modelled against mean Shannon Index (Table 3.3). Mean spring temperature (^{o}C) and mean annual chlorophyll-α concentration (μg/L) both had significant positive relationships with mean Shannon Index, whilst mean annual nitrate had a significant negative relationship. The overall R^2 value for the model was 0.64, meaning around 64% of the pattern in mean Shannon Index was explained by these three variables.

The positive relationship between Shannon Index and temperature concurs with the results from Shephard et al (2010) who found a positive relationship between temperature and recruitment of great scallops around the Isle of Man. A positive relationship between diversity and chlorophyll-α is also perhaps unsurprising as this represents an indicator for phytoplankton, a major component at the base of the benthic food chain. Finally given the nutrient cycle in the Manx waters, a negative relationship with nitrate concentration seems to be connected to chlorophyll-α concentration. In other words, when chlorophyll-α concentration is high, so is phytoplankton biomass, which means that nitrate levels should be low (Gowen and Stewart 2005). This might then suggest some level of colinearity, however the model was not improved by the removal of nitrate as a variable. It also confirms what other authors have suggested about nitrate being a limiting nutrient in the Irish Sea (Gowen and Stewart 2005).

Given that these datasets are a time series, auto-correlation may also be inflating the p-values. The overall p-value for this model was p=0.03, below the 0.05 threshold. However, in this case, when it is known that data come from a time series and there is a lack of independence, it seems prudent to reduce the significance threshold. This was suggested by Underwood (1997) and given the low number of data points in this analysis, precluding more complicated procedures it appears to be the best way to avoid a Type I error (an incorrect rejection of a null hypothesis). An acceptable conservative threshold of p=0.01 is suggested, which would mean that even this model is insignificant.

An explanation for finding no significant relationship between the environmental variables and diversity could be the complexity of the benthic ecosystem. With so many different structuring forces at play picking out particular trends is highly challenging. This is particularly the case given that site specific environmental data was not available for each fishing ground and an overall proxy from the CYPRIS site was used. In addition to this although the time scale of this study is 14 years, perhaps that is not long enough to pick up relationships between diversity and environmental variables. As explained above, nutrient levels have been remarkably stable for the period of this study and temperature has increased by 0.75°C over the last 100 years around the Isle of Man (Bradshaw, Veale et al. 2002; Evans, Williams et al. 2003; Shephard, Beukers-Stewart et al. 2010). Therefore this study has only captured 14% of the trend in temperature and perhaps only a similarly small amount of the trend in diversity. Certainly when looking at individual sites on the west coast of the Island, only two (Bradda Inshore and Targets) showed significant positive temporal trends (Figures 3.2 and 3.3). The four other fishing grounds (Bradda Offshore, Peel, Chickens and South of Port St. Mary) showed no significant trend, yet fluctuations were seen over the course of the time-series. Clearly patterns in diversity fluctuate spatially as well as temporally and the relationship between diversity and environmental variables seems to be a complicated one.

Although diversity indices are widely used in ecological studies to assess the effects of disturbance and environmental conditions (Magurran 2004), the choice of such a relatively simple response variable could also be masking more complicated trends within the benthic communities studied. Diversity indices are just that, indices of community composition. Simpson’s Diversity Index (1-D) and Shannon Index take into account both species richness and evenness within a community. They do not, however, give any information about interactions within a community between species, and the effect of an increase in a particular species could be masked by a corresponding decrease in another species. Individual species responses to environmental variables and fishing effort therefore, may be able to provide more insight into the diversity trends seen in this study. These will be studied in more detail in the next chapter.

3.5.6 Conclusions

Two significant trends were apparent in the environmental data in the study; an increase in temperature, and a downward trend in chlorophyll-α concentration. Both of these trends are likely linked to climate change and have been discussed in detail. Fishing effort data showed no clear linear trends over time, but did vary spatially and temporally. Neither fishing effort nor environmental variables fully explained the variation in diversity observed in this study, although significant linear relationships were found between lagged fishing effort and diversity. It is likely that the complexity of benthic community structuring and community level interactions are the reasons for these findings.

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Chapter 4

Species level responses to fishing pressure and environmental change in benthic invertebrate communities on commercial scallop fishing grounds.

4.1 Abstract

The benthic invertebrate communities found on the fishing grounds around the Isle of Man are thought to be composed of relatively dredge-tolerant species. The previous chapter highlighted how fishing effort only had a relatively small negative impact on diversity, and this was thought to be because the species present were adapted to cope with this disturbance. This study, however, found that the effect scallop dredging had on benthic communities was dependent on which ground was being fished. Several benthic invertebrate species on the eastern fishing grounds had significant negative relationships with fishing effort. Whilst on other grounds only *Echinus esculentus* showed a significant negative relationship with fishing pressure. It is suggested that the reason for this difference in impact is because of the underlying substrata of each fishing ground, combined with the background fishing pressure. Two species were investigated for relationships with environmental variables (*Asterias rubens* and *Porania pulvillus*). Both species showed strong relationships with chlorophyll-α and temperature, indicating that environmental variables are playing a role in structuring these commercially fished benthic communities. The implications of these findings are discussed with relation to climate change and fisheries management.

4.2 Introduction

The benthic communities found on the fishing grounds around the Isle of Man have been impacted by scallop dredging for over 70 years (Brand and Prudden 1997, Brand 1999, Bradshaw, Veale et al. 2001, Bradshaw, Veale et al. 2002, Beukers-Stewart, Mosley et al. 2003). The long-term effects of this impact have been documented by several authors and include an increase in the abundance of benthic scavengers, a reduction in diversity, a loss of the relatively large-bodied fauna, a reduced abundance in the least mobile components of the benthos and a reduction in organisms with fragile bodies (Hill, Veale et al. 1999, Kaiser, Ramsay et al. 2000, Veale, Hill et al. 2000, Bradshaw, Veale et al. 2002). Broad-scale, community level changes have occurred between the beginning of the scallop fishery (1930s-1950s) and the early 21st century (Bradshaw, Veale et al. 2002). This has led to the conclusion that the benthic communities that now exist are composed of species that are more tolerant to the effects of scallop dredging (Bradshaw, Veale et al. 2002). Indeed this is backed up by the theory that the greatest damage occurs at the beginning of a fishery and continued fishing leads to more homogeneous communities (Kaiser, Hill et al. 1996, Jennings and Kaiser 1998, Tuck, Hall et al. 1998, Hall-Spencer and Moore 2000, Bradshaw, Veale et al. 2002, Guijarro Garcia, Ragnarsson et al. 2006).

The patterns in diversity studied in the previous chapter were not as expected for areas of high fishing effort. From 1992 to 2006 diversity increased significantly at two fishing grounds on the west of the Isle of Man, whilst it decreased significantly at two fishing grounds on the east of the Island. The remaining four grounds showed no significant trend in diversity over the 14 years of the study. In fact lagged fishing effort data only explained around 7% of the patterns seen in diversity, suggesting that other environmental variables may have been playing a role. However, diversity was not significantly related to any of the environmental variables examined, implying that the situation is more complex than originally thought.

One possible set of confounding factors could be the differential responses of organisms to both fishing pressure and environmental variables. Individual responses to fishing can be predictable, for example *Asterias rubens* is known to be fairly resilient to the effects of fishing because of the flexibility of its test and ability to regenerate (Kaiser and Spencer 1996), whilst fragile or delicate bodied species such as *Spatangus purpureus* and *Anseropoda placenta* are particularly vulnerable to damage from scallop dredging (Veale, Hill et al. 2001). However, sometimes an individual species' response is unexpected; for example the whelk, *Buccinum undatum*, which has a strong shell and may be expected to resist the damaging effects of dredging was found to be more vulnerable to predation by *A. rubens* in areas that were disturbed by scallop dredges (Ramsay and Kaiser 1998). Generally, though organisms that have a robust body type, regenerative powers, are readily mobile and/or has the ability to right or rebury themselves following the passage of a dredge are likely to be more tolerant to fishing pressure (Kaiser, Ramsay et al. 2000, Bradshaw, Veale et al. 2001).

Not only are species differentially affected by fishing pressure overall, damage or mortality to individual species caused by fishing impact is not temporally uniform either. Some species, such as *Cancer pagurus* are more vulnerable at certain times of the year than others (Veale, Hill et al. 2001). *C. pagurus*, has been shown to be more abundant on grounds with high levels of fishing effort and is generally quite robust to capture in scallop dredges (Veale, Hill et al. 2001). However, when ovigerous females have distended abdomens they are more likely to suffer severe damage when captured in a dredge (Veale, Hill et al. 2001). Likewise, despite being relatively resilient to the impacts of towed fishing gear, *A. rubens* may be more vulnerable to damage in the autumn because their bodies become swollen following a summer of warm temperature and higher feeding rates (Veale, Hill et al. 2001). Fishing does not affect each species life history stage equally either. Gastropods such as *B. undatum* and *Neptunea antiqua* with their robust shells may be relatively undamaged by fishing gear (although predation risk increases with fishing effort), however their egg masses, which are attached to the substratum, are vulnerable (Ramsay and Kaiser 1998, Kaiser, Ramsay et al. 2000, Veale, Hill et al. 2001).

The effect of scallop dredging on individual species and communities also varies with substrate type (Bradshaw, Veale et al. 2001). This is an important point, because the fishing grounds around the Isle of Man have very heterogeneous substrates (Bradshaw, Veale et al. 2000). Grounds that are composed of stones rather than sand are likely to increase damage to some benthic species, such as *A. rubens*, *B. undatum* and *Echinus esculentus*, when they are caught in the dredge and subsequently discarded (Veale, Hill et al. 2001). Additionally fishing gear efficiency varies between different substrates, hence the number of benthic animals caught in the bycatch will vary between fishing grounds (Veale, Hill et al. 2001). Therefore the effects of fishing effort may be more pronounced for some species on certain fishing grounds where damage and mortality is higher because of difference in substrate and gear efficiency.

It is clear that the community response of a particular site to dredging (or any other disturbance) depends on many variables, including the life history characteristics of each species present, local hydrography, the time of year fished and the substrate type (Bradshaw, Veale et al. 2001). Information about the effects of dredging on individual benthic species would help to fully explain or predict the effects of dredging on a community (Bradshaw, Veale et al. 2001). High levels of mortality in certain mega-faunal species may result in radical changes in community structure through effects on trophic relationships and competitive interactions (Jenkins, Beukers-Stewart et al. 2001). However, in areas that have been heavily modified by historical fishing effort, like those around the Isle of Man, benthic communities will likely be composed of species adapted to certain levels of disturbance (Kaiser, Ramsay et al. 2000, Bradshaw, Veale et al. 2002). As a result the benthic communities present around the Isle of Man have lower diversity than those found prior to the onset of commercial fishing (Hill, Veale et al. 1999, Bradshaw, Veale et al. 2002). Areas with low species diversity may be less resilient to the loss of further species either by fishing pressure or due to an environmental effect, such as the increasing temperatures currently being observed on a global scale (Harley, Randall Hughes et al. 2006).

It is known that seawater temperature around the Isle of Man has increased by 0.75^{o}C over the last 100 years (Bradshaw, Veale et al. 2002, Shephard, Beukers-Stewart et al. 2010). Although no link between temperature and diversity was found in the previous chapter, increasing temperature has been related to biological performance in at least one important member of the benthic community, the target species of the scallop fishery *Pecten maximus* (Shephard, Beukers-Stewart et al. 2010). Increasing spring temperature was positively correlated with strengthened recruitment and gonad development in *P. maximus* (Shephard, Beukers-Stewart et al. 2010). It is therefore possible that the effects of environmental variables on the benthic communities around the Isle of Man were not shown in the diversity indices because they were masked by interactions between individual species. In fact a recent meta-analysis of the effects of climate change on marine ecosystems found that the interactions between species in a community were as important as the effects of climate change on individual species in mediating community level shifts (Wernberg, Smale et al. 2012).

This chapter aims to investigate the species composition of the commercially exploited fishing grounds around the Isle of Man over a 14 year time period. Veale et al (2001), in a short-term (4 year) study, found that there were two distinct assemblages of benthic species; one centred to the south west of the Island and the other on the remaining fishing grounds to the north south and east of the Island. This study covers a much longer time period than Veale et al (2001), running from 1992 to 2006. Therefore the longer-term impacts of fishing pressure will be investigated on the species composition and density of the fishing grounds around the Isle of Man. In addition to this the effect of environmental variables on the benthic species composition of these fishing grounds will be investigated for the first time, The effects of both fishing effort and environmental variables on key species at each fishing ground will be analysed, to determine whether they are having any influence on the population dynamics and composition of the species present.

4.3 Methods

The previous chapter investigated the effects of fishing pressure and environmental variables on the diversity of benthic communities at eight fishing grounds around the Isle of Man. This chapter extends that investigation by studying the effects of fishing pressure and environmental variables on individual species from the benthic communities at the eight fishing grounds. The benthic species composition at each fishing ground will be explored and several dominant species for further study will be identified. Temporal trends in the abundance of these species will be analysed and the effect of the closed season will be explored. Then the effect of fishing pressure and several environmental variables on each species’ abundance will be investigated using linear and multiple linear regression.

4.3.1 Study Area

The Isle of Man (58°08’N,4°27’W) is located in the north Irish Sea, between the coasts of Ireland, Scotland, Wales and England (Figure 1). The Isle of Man’s territorial limit stretches to 12 miles offshore and the waters within this limit are shallow, mostly less than 30m deep. To the south-west of the island, depths slope to 80-90m at the 12 mile limit. The north-east coast of the island has extensive shallow sandy banks. Sediment type varies around the island, with nearshore sediments being mainly fine sand and offshore sediments divided into four categories: coarse sands and gravel, fine sand, muddy sand and mud (Barne, Robson et al. 1996, Craven, Brand et al. 2012).

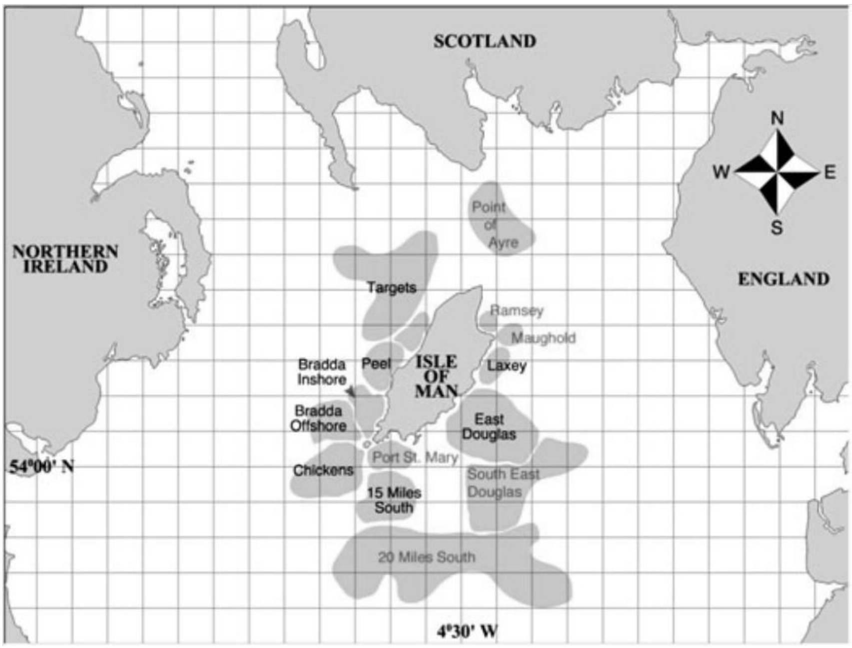


Figure 4.1. Map of the Irish Sea showing the main fishing grounds for great scallop (shaded areas). The grounds analysed in this study are labelled in bold. (Source: Beukers-Stewart *et al.*,2003.)

4.3.2 Data sources

As in the last chapter, benthic community data was obtained from catch data (which includes the target species *P. maximus* and *A. opercularis* as well as the benthic bycatch species) collected during fisheries-independent scallop surveys conducted from 1992 to 2006. Environmental data was taken from a multi-annual time series for water quality around the Isle of Man at the CYPRIS sampling site on the west coast of the Island. Data from the North Atlantic Oscillation (NAO) index was obtained from Osborn (2006) and a time series of the winter (December-March) average was used. Fishing effort data was obtained from the voluntary logbook scheme that approximately 30% of the Manx scallop fishing fleet took part in (Beukers-Stewart, Mosley et al. 2003). These data were multiplied up to the size of the total fleet using a multiplying factor (total fleet size/sample fleet size) to create an estimate of total fishing effort each year by the Manx fishing fleet. For a full description of data collection methods see Chapter 3 Methods.

4.3.3 Data Analysis

4.3.3.1 Species composition

The catch data from the queen dredges (see Chapter 3) of the bi-annual scallop surveys were separated out for each fishing ground. The queen dredges were used for this analysis because belly ring size is smaller than the great scallop dredges, therefore a greater number of benthic species were caught during the surveys. Data about fish species that were caught in the bycatch of the queen dredges were excluded from this analysis and have been investigated by Craven et al (2012). The individual species count data from each tow was calculated into a mean relative density for each sampling period (June and October) for the years 1992 to 2006, inclusive. Some grounds were not sampled at every interval in the time series. The species abundances were then calculated into proportions of the catch represented by each species, to give an overall picture of what the species composition was at each ground over the course of the time series.

Seven key species, which were dominant in the catch at most fishing grounds or showed interesting patterns over the course of the time-series, were chosen for further investigation. These species were *Aequipecten opercularis* (queen scallop), *Asterias rubens* (common starfish), *Buccinum undatum* (common whelk), *Echinus esculentus* (edible urchin), *Luidia ciliaris* (seven-armed starfish), *Neptunea antiqua* (red whelk) and *Porania pulvillus* (cushion star). The target species *P. maximus* was not included in this part of the analysis as it has been extensively studied previously (Beukers-Stewart, Mosley et al. 2003). The commercially important crab species, *Cancer pagurus*, was also excluded from this part of the analysis because it is a species that has been shown to undergo seasonal migrations on these fishing grounds (Pennington 1999, Veale, Hill et al. 2001). Relative densities of these species for each survey date and fishing ground dredged were calculated and expressed as the mean number per 100m^2.

4.3.3.2 *Effect of closed season*

The effect of the great scallop closed season (June – October, inclusive) on the density of each of the 7 species listed above was analysed using a one-way ANOVA by comparing the density of each species at each fishing ground from June (the start of the closed season) sampling with the density from October (the start of the fishing season) sampling. Data were tested for normality using Shapiro-Wilk Normality Test and tested for homogeneity of variance using Bartlett's test. Not all data were normally distributed and therefore the effect of closed season on the density of those species was tested using the non-parametric Mann-Whitney U test.

4.3.3.3 *Temporal trends in benthic species density*

The analysis on the effect of the closed season on species relative densities showed that there were no significant differences in relative species densities before and after the closed season. Therefore to allow a more continuous time series for some grounds where there were sampling gaps, mean annual relative densities were calculated for each species at each fishing ground. The temporal trends in mean annual relative density were explored using regression analysis, for each species at each fishing ground independently.

4.3.3.4 *Effect of fishing effort on species densities around the Isle of Man*

To investigate the effects of fishing on relative species density around the Isle of Man each species' density data was combined across all grounds. A number of different time lags in the fishing effort data were investigated for each species; no lag, a 1 year lag and a 2 year lag. All data were checked for normality and homogeneity of variance and it was found that the fishing effort data was not normally distributed and therefore was transformed using a square-root transformation. A series of regression analyses were then performed between square-root transformed fishing effort and each species relative density. Each model was validated to ensure no pattern in the residuals.

4.3.3.5 *Effect of fishing effort on species densities at each fishing ground*

The effect of fishing effort on the relative density of species at each site individually was then investigated. Data were checked for normality and homogeneity of variance for each analysis and fishing effort was not normal in several cases. Non-normal fishing effort data was transformed either using square-root transformation or a $\log_{10}$ transformation, depending which was most appropriate. A series of regression analyses were then performed between fishing effort and each species density at each site. Each model was validated to ensure no pattern in the residuals.

4.3.3.6 Effect of environmental variables on individual species

All environmental variables were combined into useable indices as detailed in Chapter 3. For this investigation, annual mean indices of temperature (^{o}C), chlorophyll-α concentration (μg/L), nitrate concentration (μM) and silicate concentration (μM) were used. Mean winter NAO index was also included in this analysis. To investigate the effect of these environmental variables on the density of species present a series of multiple-regression analyses were conducted. The environmental data was collected from the south-west of the Isle of Man. It is known that environmental conditions on the east coast of the Island are different from those on the west coast (Kennington, Allen et al. 1999, Veale, Hill et al. 2001, Gowen and Stewart 2005). Therefore the eastern grounds, East Douglas and Laxey, were excluded from this analysis. Gaps in the data for two other grounds also meant that they were excluded from this analysis as well. Therefore, ultimately only three grounds off the south-west of the island: Bradda Inshore, Bradda Offshore and Chickens, were found to have sufficient data for this analysis. Two common species were found across these three sites, *A. rubens* and *P. pulvillus*, that had relatively large densities and few zero values – therefore further analysis focused on these species. It should be noted that *A. opercularis* was not included in this analysis because the main grounds where this species is found on located on the eastern and southern parts of the Isle of Man (Vause, Beukers-Stewart et al. 2007). Therefore the environmental data that was used here was not directly comparable with these grounds. This is discussed in more detail in section 4.5.

Relative densities of both *A. rubens* and *P. pulvillus* showed different temporal patterns at each of the three fishing grounds. They also had different relative densities, which meant that combining the two species for an overall mean density for the south-west of the Isle of Man was not suitable. Therefore to prevent pseudo-replication in the environmental variables each species was analysed separately at each ground for patterns with the environmental variables. It was expected that there would be a lagged effect of the environmental data on the density of each species. This is because if environmental conditions were influencing species reproduction and settlement (e.g. the effect spring temperature on *Pecten maximus* recruitment (Shephard, Beukers-Stewart et al. 2010) then a certain amount of time would be required for these species to grow larger enough to be collected in the dredges. Therefore three different time lags were tested for each species at each site: no lag, a 1 year lag and a 2 year lag. Further lags were unable to be tested as each time the data was lagged some data was lost from the analysis. All data were checked for normality and homogeneity of variance and transformed where appropriate. The explanatory environmental variables were then analysed for co-linearity using

Variance Inflation Factor (VIF) analysis in the statistical programme R (R Development Core Team, 2012). No variables showed any co-linearity therefore all were included in the multiple linear regression analyses. Optimum models were selected using Stepwise Model Selection found in the statistical programme R. All final models were then validated to ensure no pattern in the residuals.

4.4 Results

4.4.1 Composition of the benthic invertebrate community

Eight fishing grounds had sufficient catch data to investigate their species composition in more detail; these grounds are highlighted in Figure 4.1. Figures 4.2 to 4.9 show the temporal patterns of the proportion of each species in the catch, with each figure representing a different fishing ground. The species composition differed between fishing grounds, although some similarities could be seen. The catch and therefore the benthic community was dominated by echinoderms and the two target scallop species, the great scallop, *P. maximus* and the queen scallop, *A. opercularis*. Bradda Inshore (Figure 4.2), Bradda Offshore (Figure 4.3), Chickens (Figure 4.4) and Peel (Figure 4.5) are grounds where *P. maximus* is predominantly fished. Figures 4.2 – 4.4 show that at the first three of these grounds *A. opercularis* became a larger component of the catch in the latter half of the time series. At Peel, however, *A. opercularis* did not appear in the catch at all. Peel fishing ground was rather impoverished in terms of the different species present as compared to the other fishing grounds and was dominated by *P. maximus* and *A. rubens* (Figure 4.5).

The main queen scallop fishing grounds are East Douglas (Figure 4.6), Laxey (Figure 4.7), South of Port St. Mary (Figure 4.8) and Targets (Figure 4.9). At East Douglas, Laxey and South of Port St. Mary (PSM), *A. opercularis* dominated the catch, in addition to *P. maximus*, *A. rubens* and *Echinus esculentus* (Figures 4.6 to 4.8). At Targets fishing ground (Figure 4.9) the catch was dominated by *E. esculentus* and *A. opercularis* in the first four years of the time-series, the middle four years were dominated by *P. maximus* and *A. rubens*, and the final four years were dominated by *A. rubens*, *A. opercularis* and *P. maximus.* Another notable difference between the two different types of ground was that *Porania pulvillus* (cushion star) was present at the scallop grounds on the south and west of the island (Figures 4.2 – 4.5) but not in large enough numbers to form a proportion of the catch shown in these charts. Likewise *Buccinum undatum* (the common whelk) and *Neptunea antiqua* (the red whelk) were only present at the queen scallop fishing grounds (Figures 6 to 9). Finally a species that did not follow the above patterns in distribution was *Luidia ciliaris* (the seven-armed starfish). *L. ciliaris* was present at Bradda Inshore, Bradda Offshore, Peel and Targets fishing grounds (Figures 4.2, 4.3, 4.5 and 4.9). These seven species mentioned above were chosen to be studied in more detail (see below).

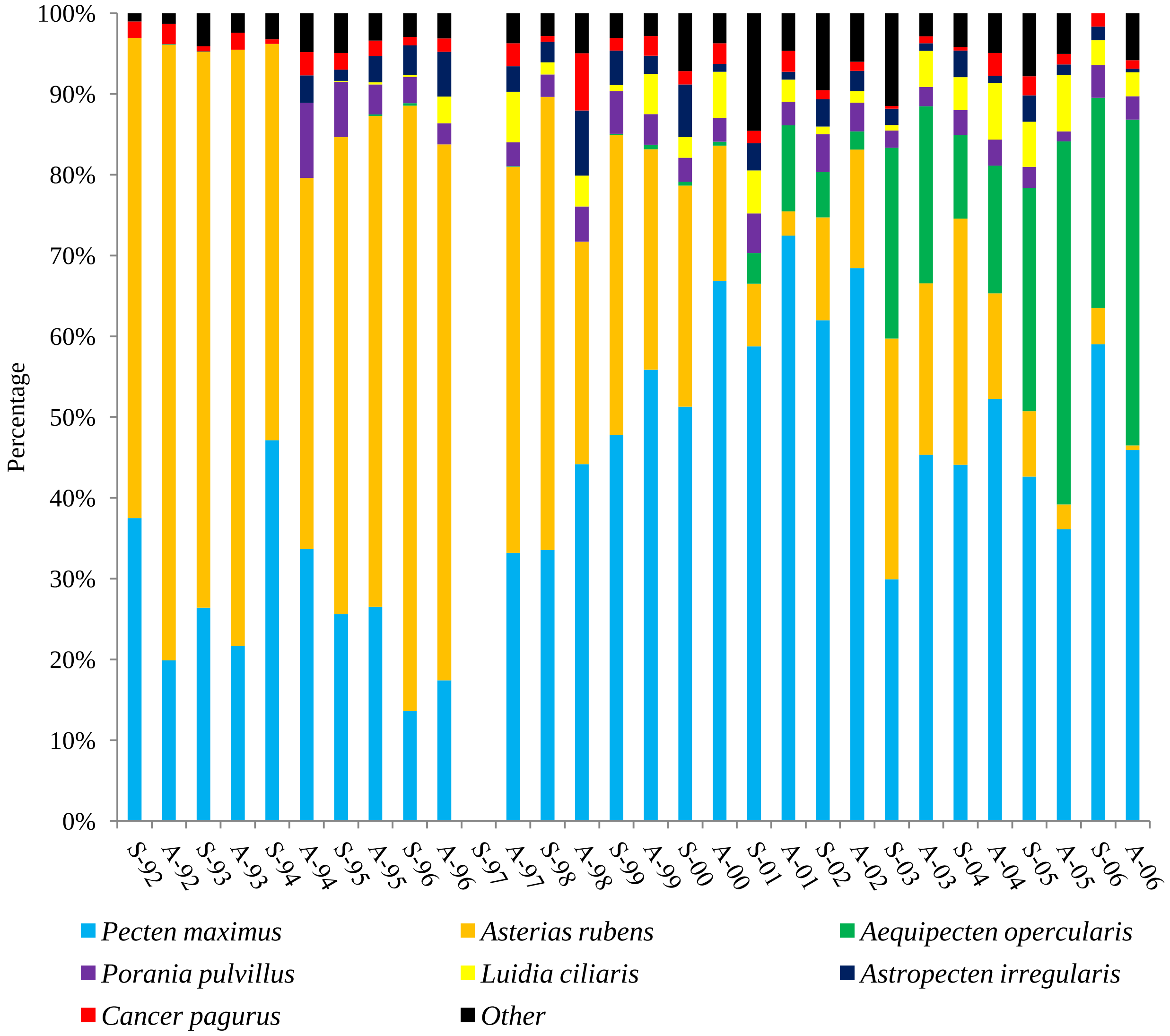


Figure 4.2 The proportion of each benthic invertebrate species present in the catch of bi-annual scallop surveys conducted at Bradda Inshore fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

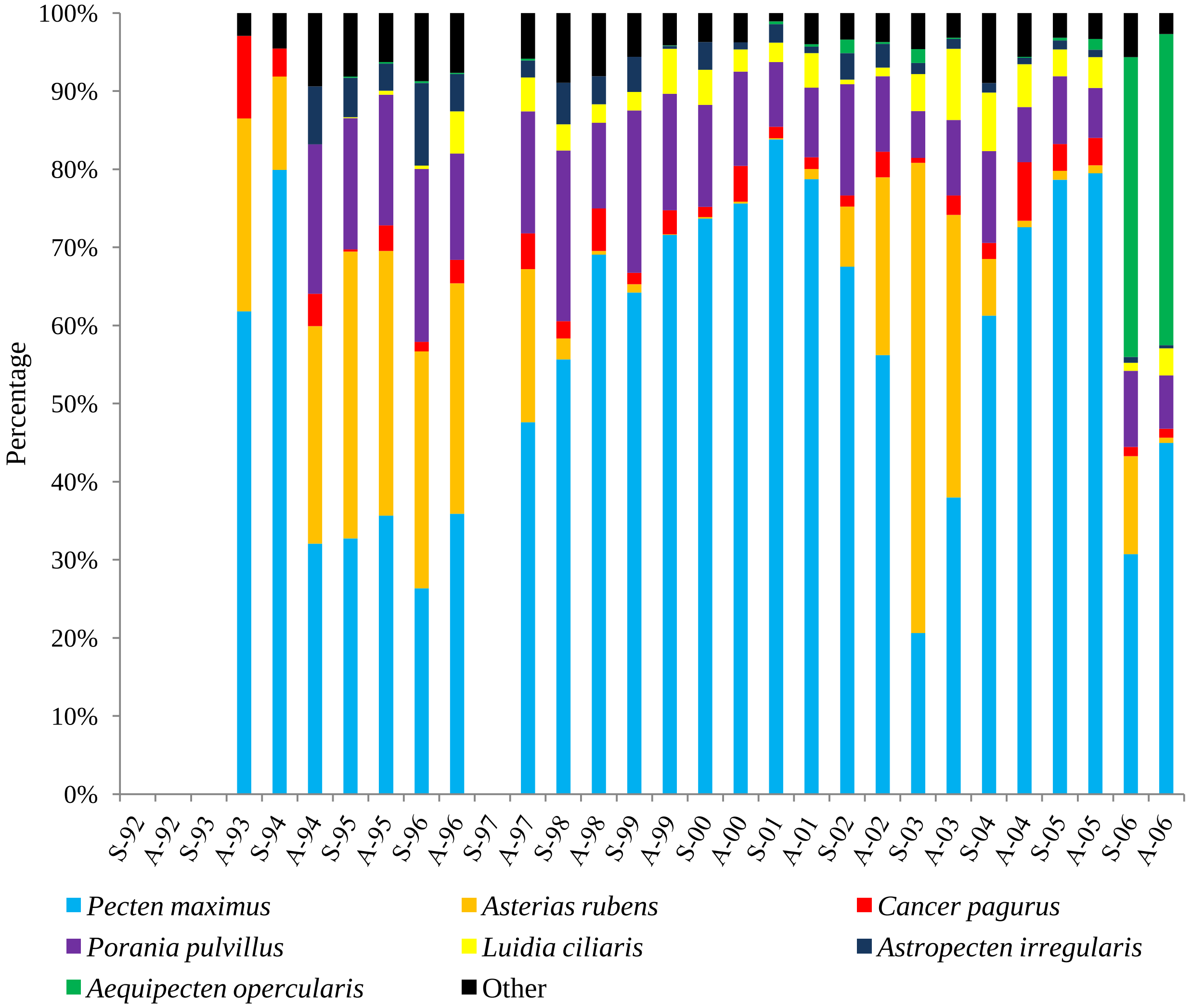


Figure 4.3 The proportion of each benthic invertebrate species present in the catch of bi-annual scallop surveys conducted at Bradda Offshore fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

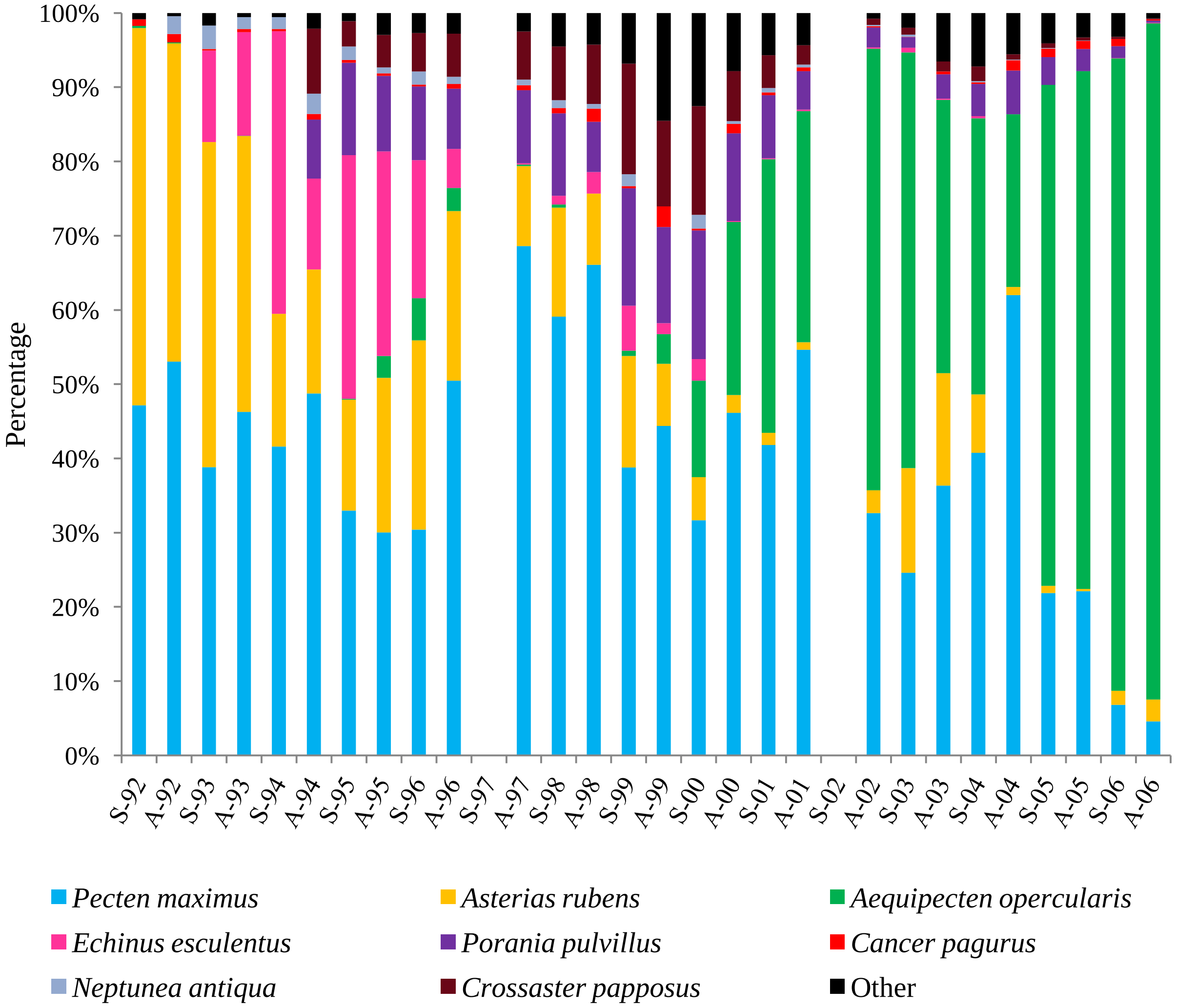


Figure 4.4 The proportion of each benthic invertebrate species present in the catch of bi-annual scallop surveys conducted at Chickens fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

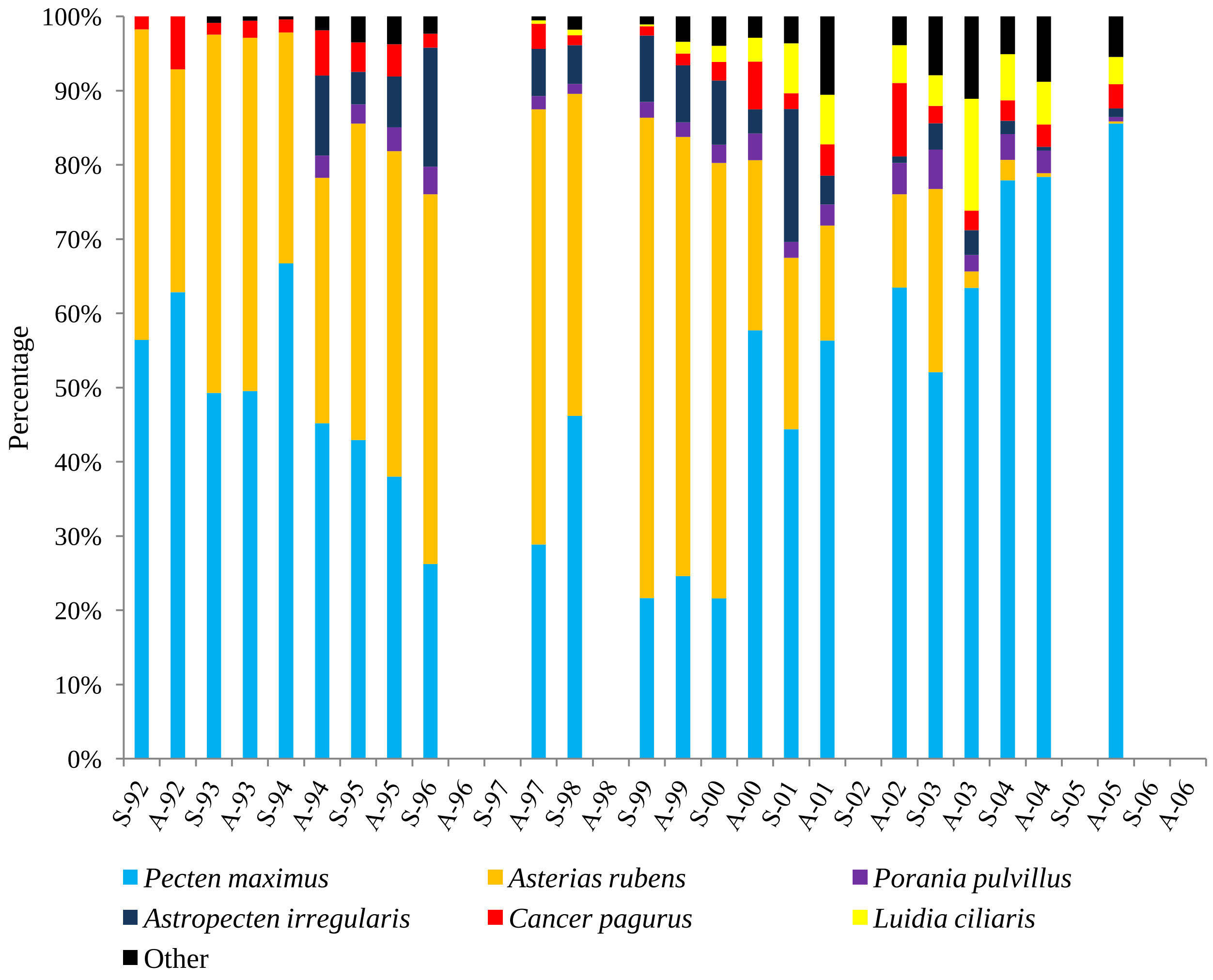


Figure 4.5 The proportion of each benthic invertebrate species present in the catch from bi-annual scallop surveys conducted at Peel fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

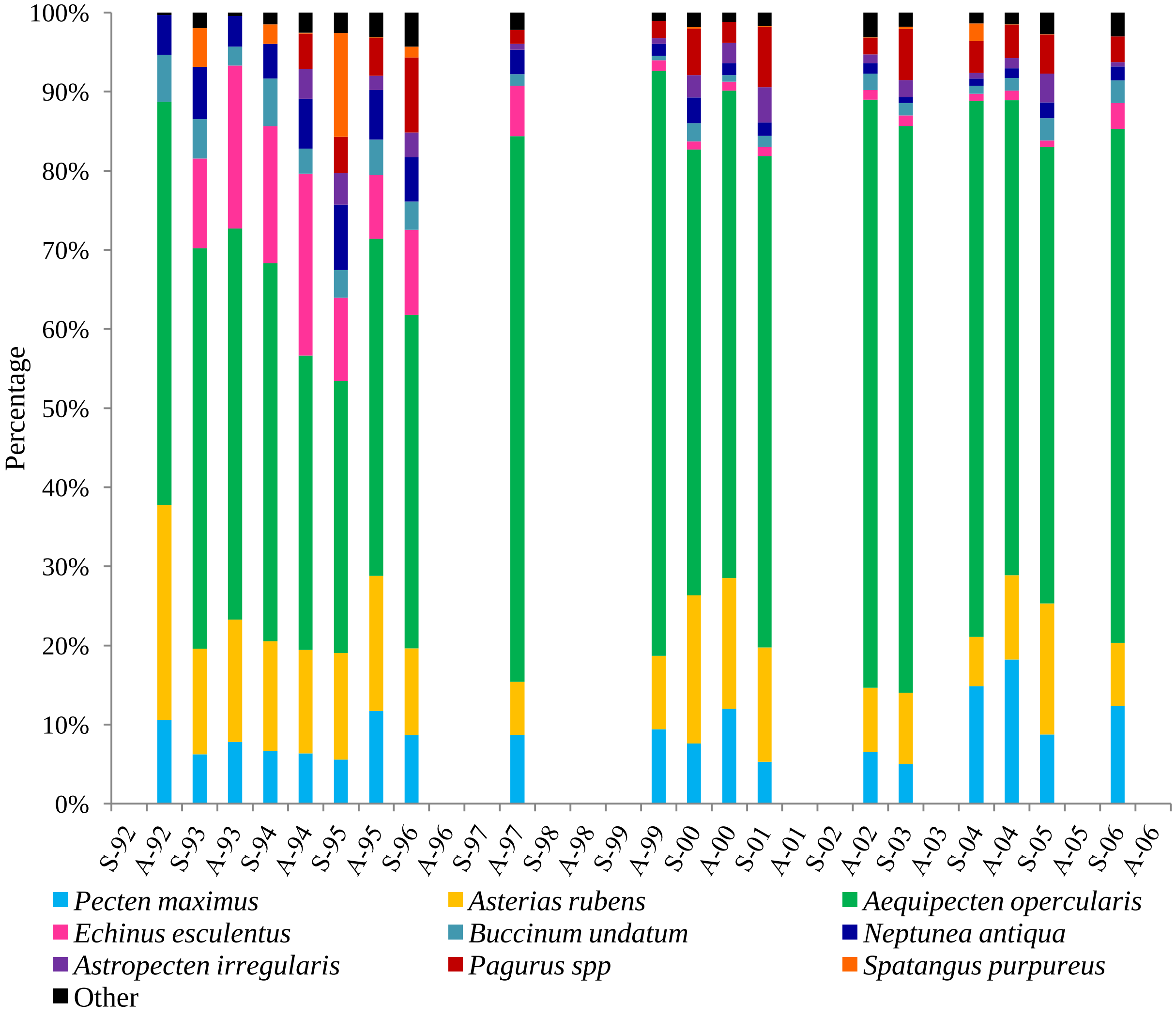


Figure 4.6 The proportion of each benthic invertebrate species present in the catch of bi-annual scallop surveys conducted at East Douglas fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

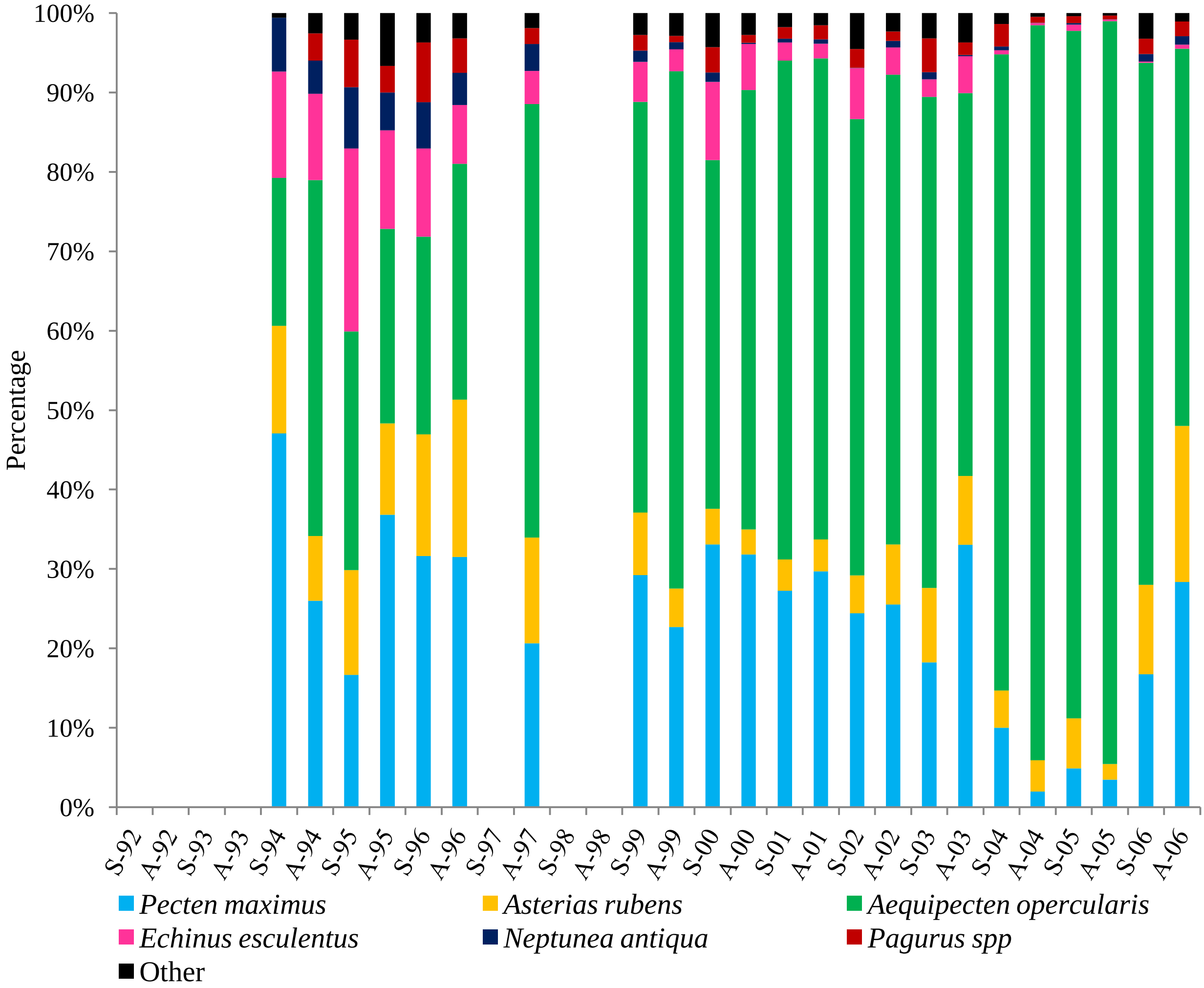


Figure 4.7 The proportion of each benthic invertebrate species present in the catch of bi-annual scallop surveys conducted at Laxey fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

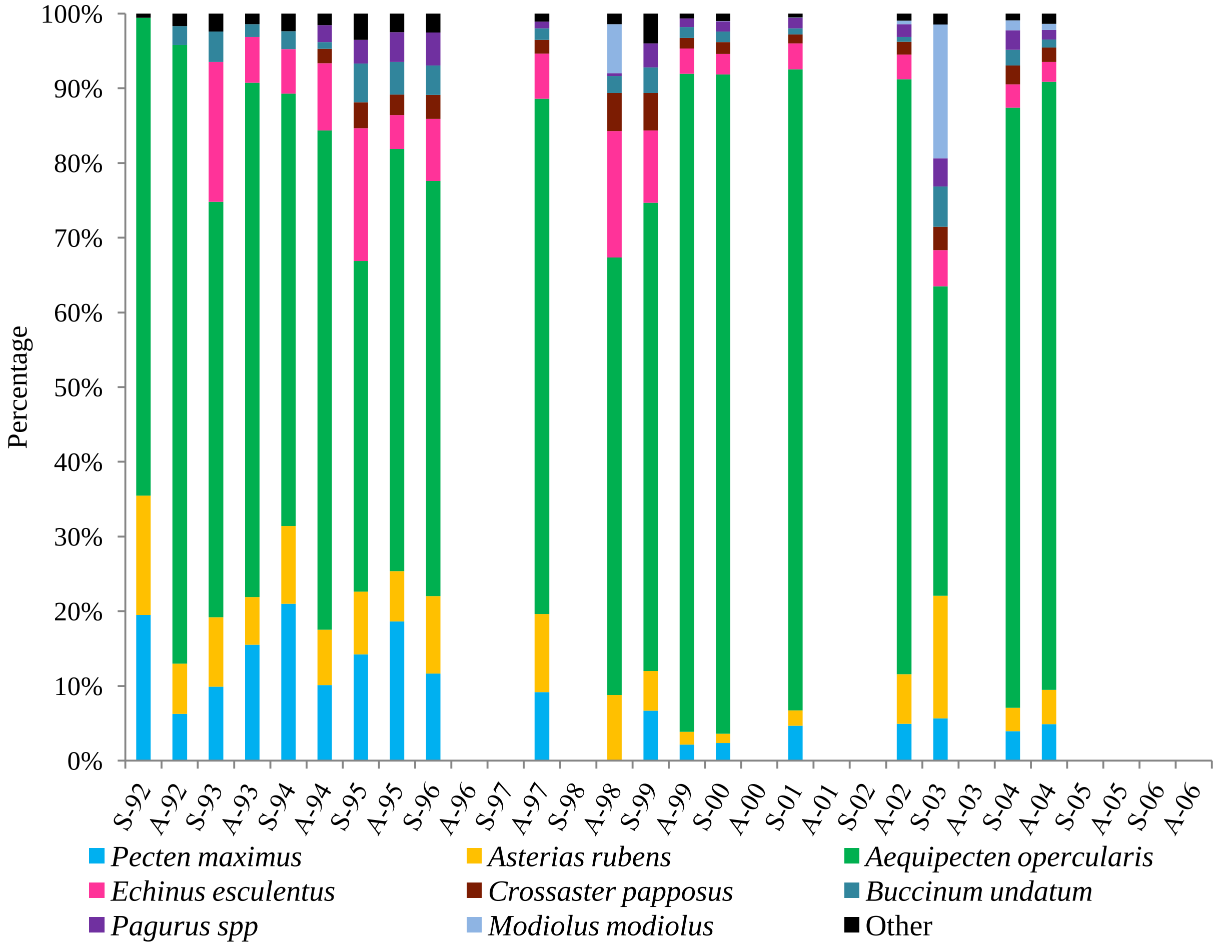


Figure 4.8 The proportion of each benthic invertebrate species present in the catch of bi-annual scallop surveys conducted at South of Port St. Mary fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

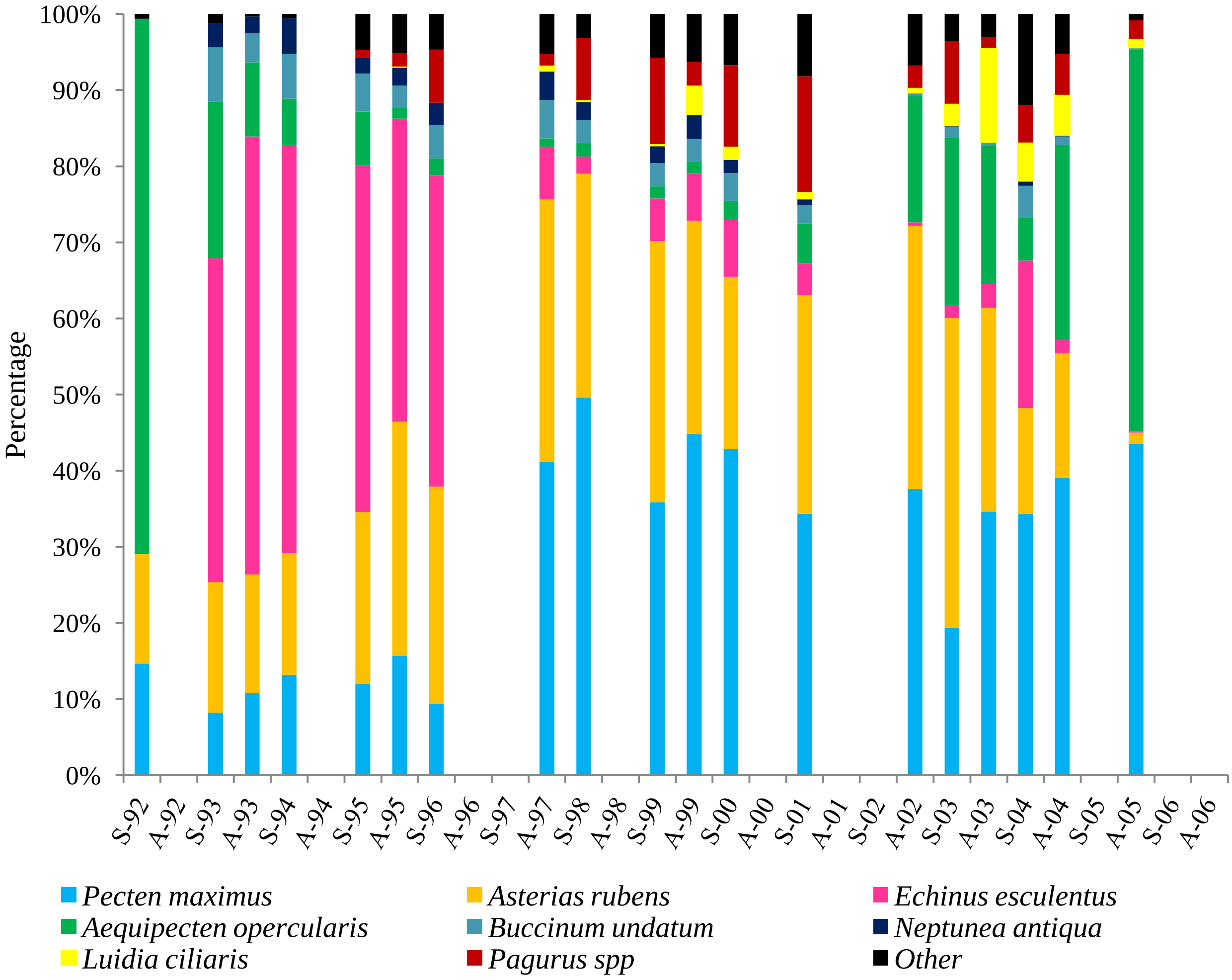


Figure 4.9 The proportion of each benthic invertebrate species present in the catch of bi-annual scallop surveys conducted at Targets fishing ground using a queen scallop dredge from 1992 to 2006. Each year was sampled twice in June (S) and October (A) and both are shown above.

4.4.2 Overall density of benthic invertebrate species

The total density of all 7 benthic invertebrate species listed above that were caught in the queen dredges during the fisheries independent surveys is shown in Figure 4.10. This figure shows that overall density of these species was less than 5 individuals per 100m^2 for the grounds Peel, Bradda Offshore and Bradda Inshore throughout the time series. The fishing ground Targets had a total density similar to these first three grounds, however fluctuations above 5 per 100m^2 were seen, with a peak of around 13 per 100m^2 in October 2005. The highest overall density was found at East Douglas, where density fluctuated between 6 and 17 per 100m^2 throughout the time series. The fishing grounds Chickens, Laxey and South PSM had total densities of around 5 per 100m^2 for the first half of the time series (1992 – 1998). However, in the latter half of the study (1999-2006) total densities peaked at each ground. At South PSM total density peaked at around 22 per 100m^2 in 2000, then density dropped to around 5 per 100m^2 in 2002, however further patterns are difficult to discern because this ground was not sampled in 2005 and 2006. At Laxey two peaks were seen, the first in the years 1999 and 2000 with a density of 20 per 100m^2, the second in 2004 and 2005 with a density of 30 per 100m^2. Chickens fishing ground showed a similar pattern as Laxey, with density peaking first in 2002 at around 20 per 100m^2 and then again in October 2006 at around 30 per 100m^2.

4.4.3 Effect of the closed season on species densities

Density of *L. ciliaris* was significantly higher in October (the start of the fishing season) than in June (the start of the closed season) at Bradda Inshore when tested with one-way ANOVA (Table 4.1, Figure 4.14). No other significant differences were observed in any of the seven species densities between June (the start of the closed season) and October (the start of the fishing season), at any of the eight fishing grounds they were found on (several species were not present at Peel and Targets) when tested with one-way ANOVA (Table 4.1). These results have been graphed for each species, separated for fishing ground (Figures 4.11 to 4.17).

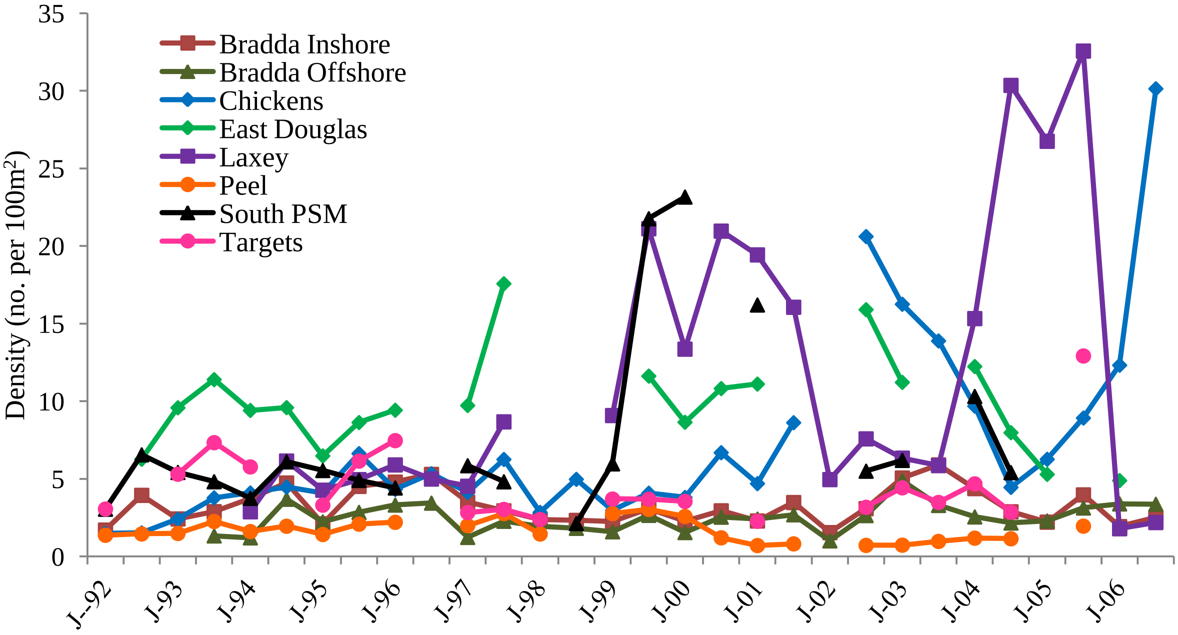


Figure 4.10 Total density (no. per 100m^2) of benthic invertebrate species from the catch of bi-annual scallop surveys across all eight fishing grounds around the Isle of Man. Grounds were sampled in June (J) and October (O) each year.

Table 4.1. Results from a series of one-way ANOVA analyses examining the difference in density (no. per 100m^2) of each species between June and October (before and after the closed season) at fishing grounds around the Isle of Man. All data were tested for normality and homogeneity of variances. *Luidia ciliaris* density was significantly different between June and October at Bradda Inshore. No other species showed a significant difference in the density found before and after the closed season.

Species	**Ground**	**df**	**SS**	**MS**	**F-ratio**	**p-Value**
Aequipecten opercularis	East Douglas	1	1.230	1.230	0.160	0.70
	Targets	1	0.013	0.013	0.075	0.79
Asterias rubens	Bradda Inshore	1	0.030	0.035	0.030	0.86
	Chickens	1	0.000	0.000	0.000	0.99
	East Douglas	1	0.200	0.200	1.660	0.23
	Laxey	1	0.006	0.006	0.052	0.82
	Peel	1	0.004	0.005	0.012	0.92
	South PSM	1	0.008	0.008	0.970	0.35
	Targets	1	0.002	0.002	0.012	0.92
Buccinum undatum	East Douglas	1	0.018	0.018	0.665	0.44
	South PSM	1	0.008	0.008	0.866	0.38
	Targets	1	0.010	0.010	0.767	0.41
Echinus esculentus	East Douglas	1	0.350	0.350	0.420	0.54
	Laxey	1	0.021	0.021	0.150	0.70
	South PSM	1	0.150	0.150	1.430	0.25
Luidia ciliaris	**Bradda Inshore**	**1**	**0.037**	**0.037**	**6.790**	**0.02**
	Bradda Offshore	1	0.011	0.011	1.776	0.20
Neptunea antiqua	East Douglas	1	0.003	0.003	0.060	0.81
	Laxey	1	0.005	0.005	0.392	0.54
Porania pulvillus	Bradda Inshore	1	0.000	0.000	0.190	0.67
	Chickens	1	0.014	0.014	0.574	0.46

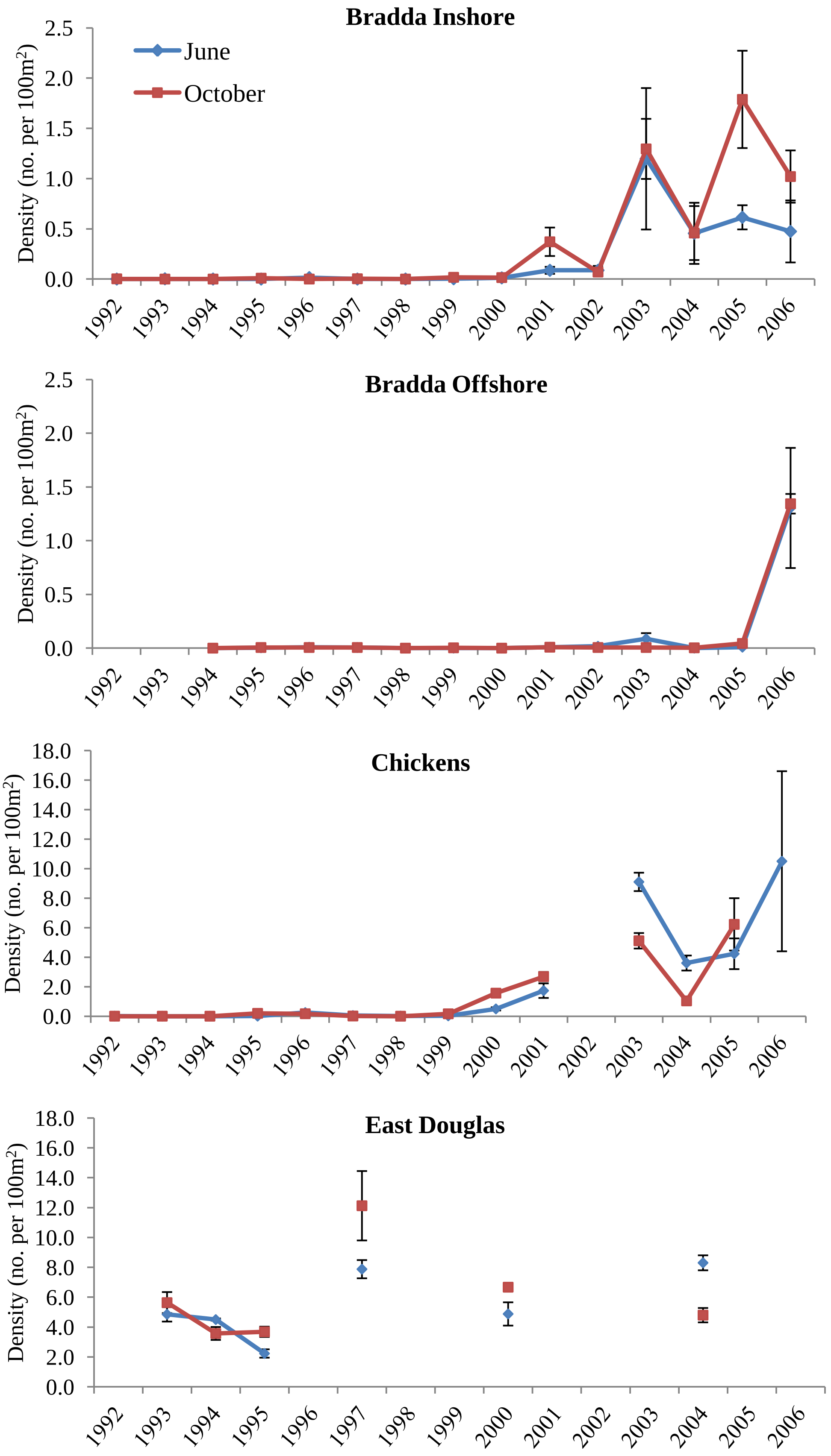


Figure 4.11a Mean density (no. per 100m^2) of *Aequipecten opercularis* at four fishing grounds around the Isle of Man in June and October from 1992 to 2006. Densities were calculated from queen dredge catch data. Note the two different scales on the y-axes of the graphs. Standard error bars are shown. No significant difference was found in the density of *A. opercularis* in June and October.

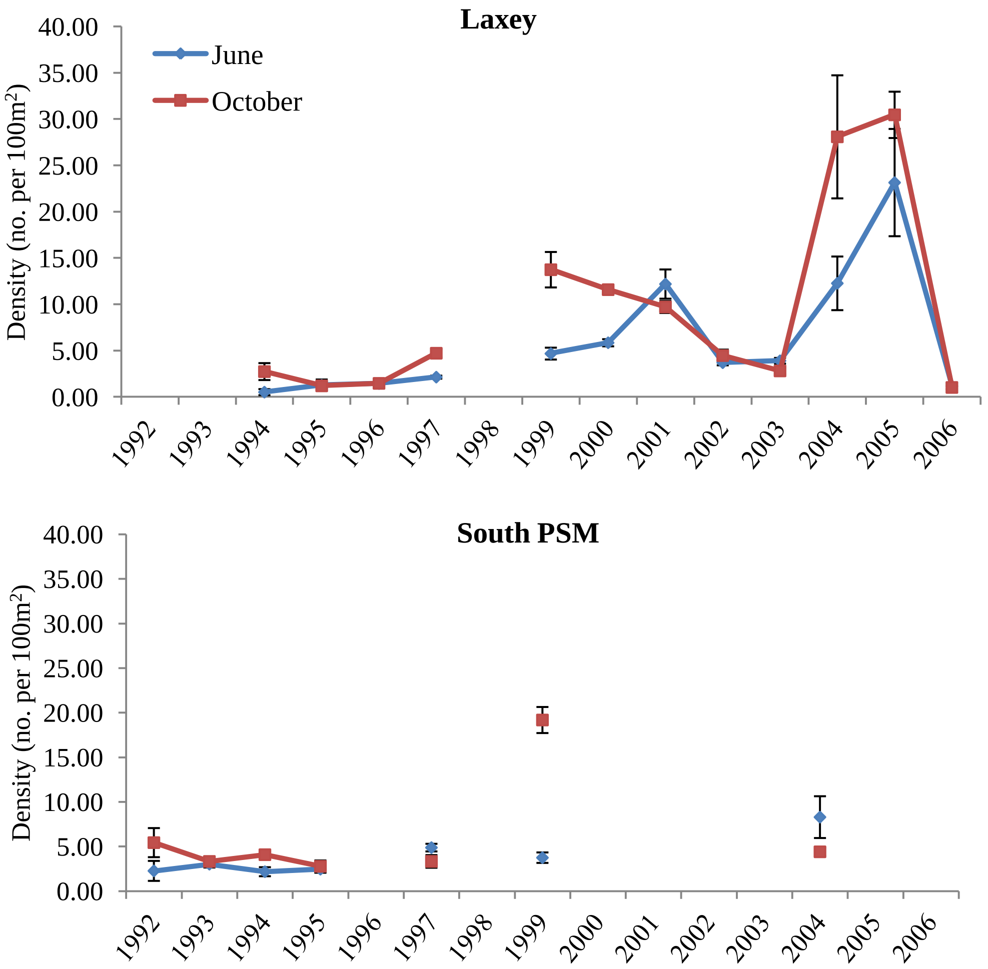


Figure 4.11b Mean density (no. per 100m^2) of *Aequipecten opercularis* at two fishing grounds around the Isle of Man in June and October from 1992 to 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown. No significant difference was found in the density of *A. opercularis* in June and October.

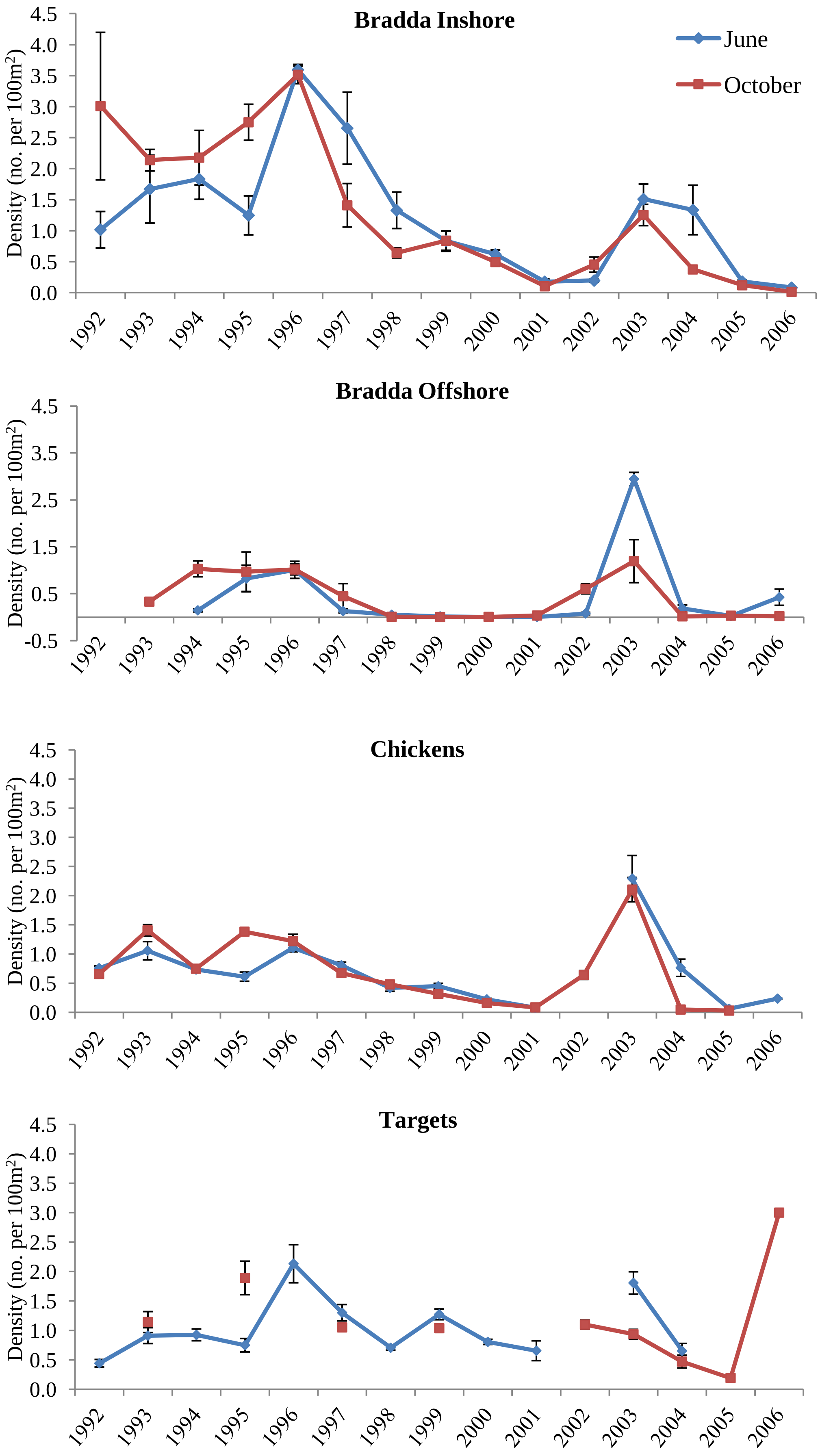


Figure 4.12a Mean density (no. per 100m^2) of *Asterias rubens* at four fishing grounds around the Isle of Man in June and October from 1992 to 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown.

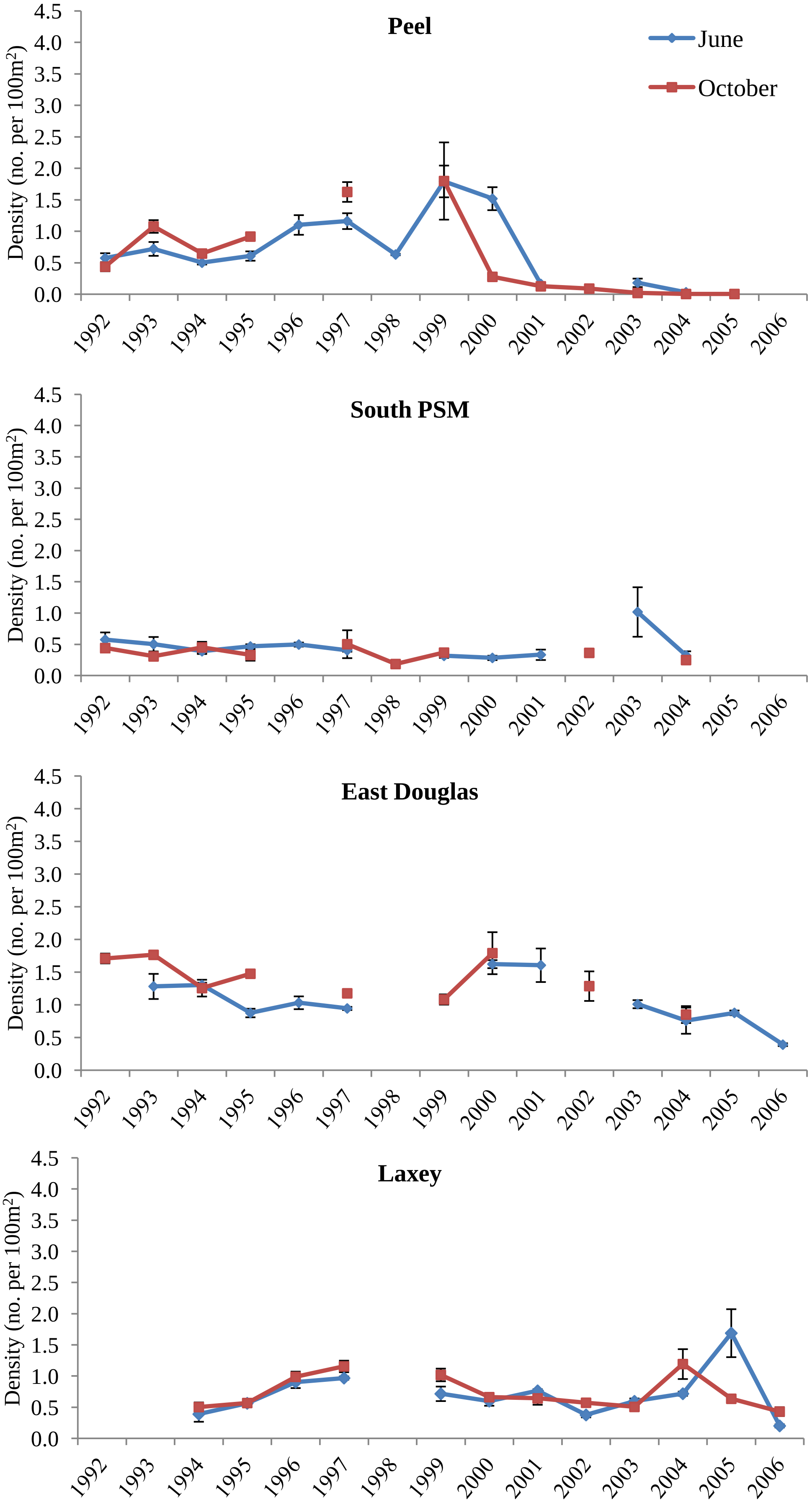


Figure 4.12b Mean density (no. per 100m^2) of *Asterias rubens* at four fishing grounds around the Isle of Man in June and October from 1992 to 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown.

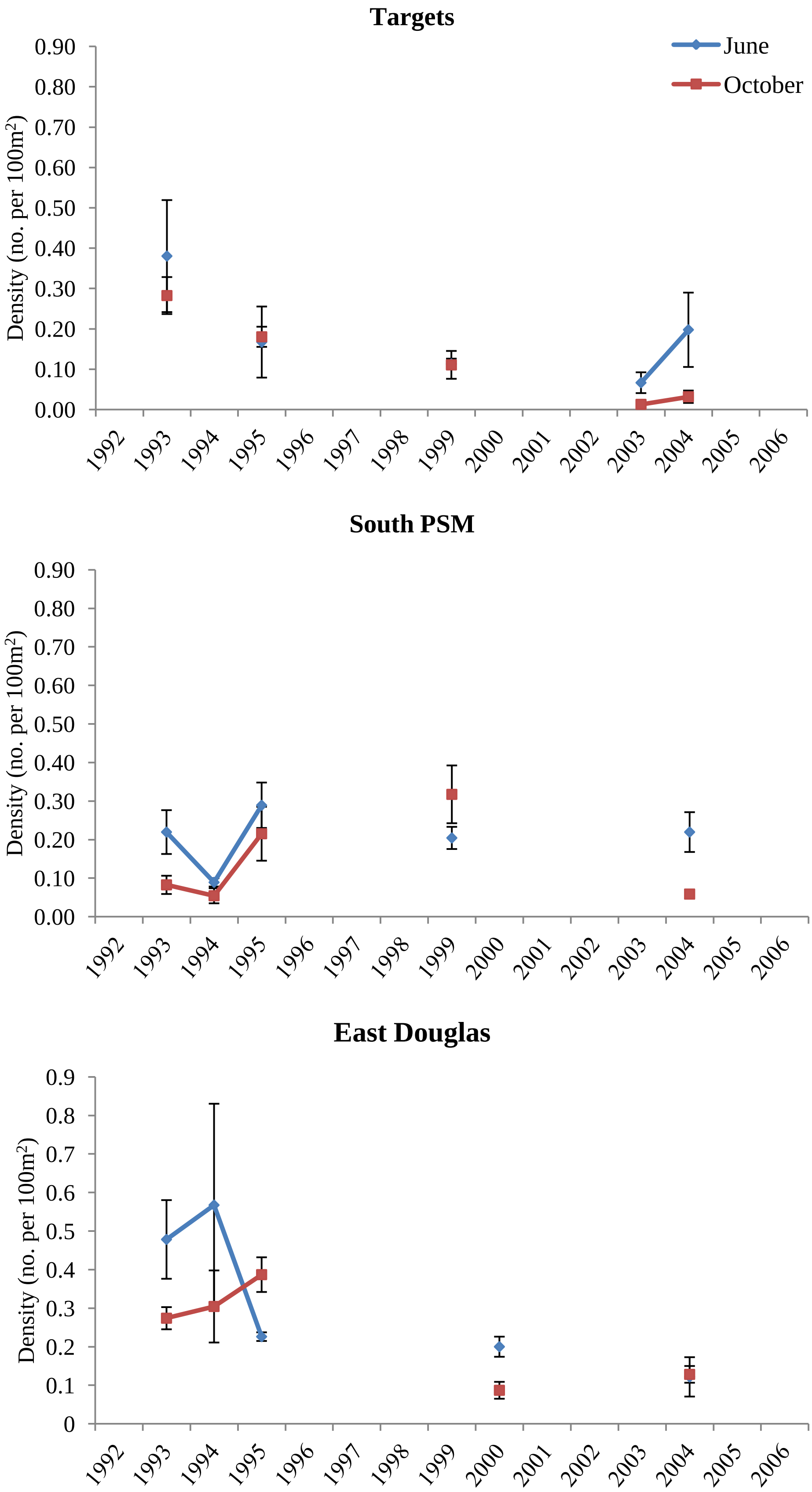


Figure 4.13 Mean densities of *Buccinum undatum* in June and October at the three fishing grounds around the Isle of Man that it was found from 1992 – 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown. No significant difference in density in June or October was found for any of the sites.

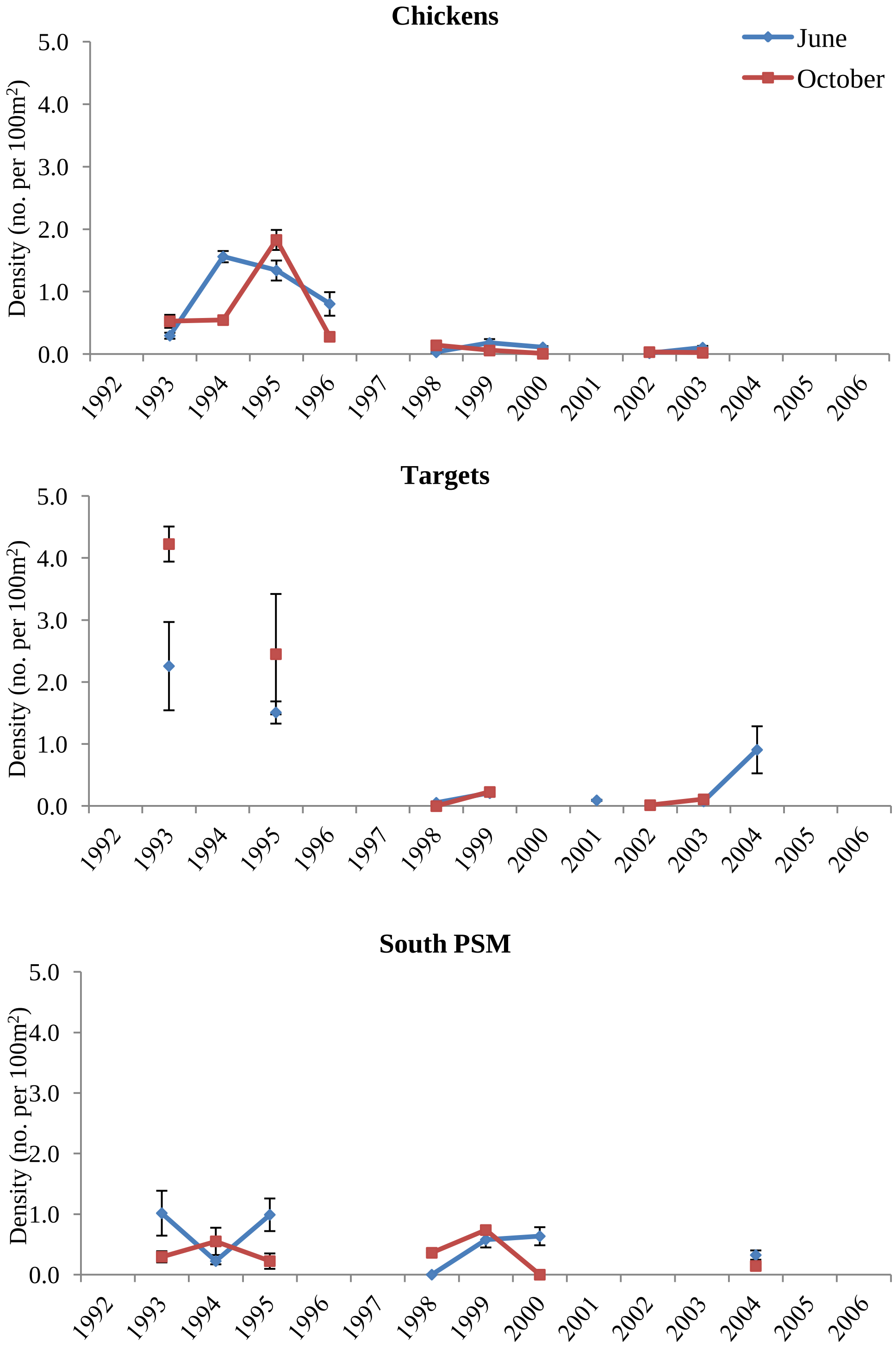


Figure 4.14a Mean density (no. per 100m^2) of *Echinus esculentus* in June and October at three fishing grounds around the Isle of Man from 1992 - 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown. There was no significant difference between the densities in June and October at any of the sites sampled.

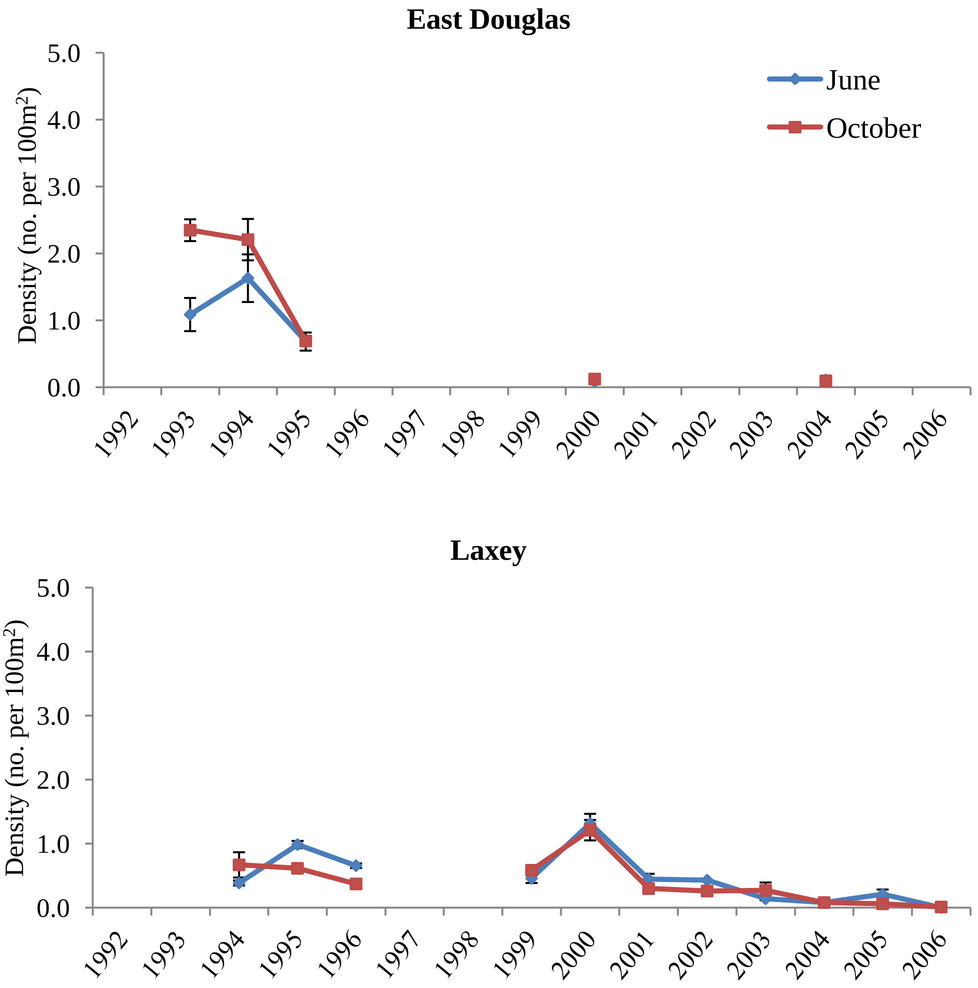


Figure 4.14b Mean density (no. per 100m^2) of *Echinus esculentus* in June and October at two fishing grounds around the Isle of Man from 1992 - 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown. There was no significant difference between the densities in June and October at either of the sites sampled.

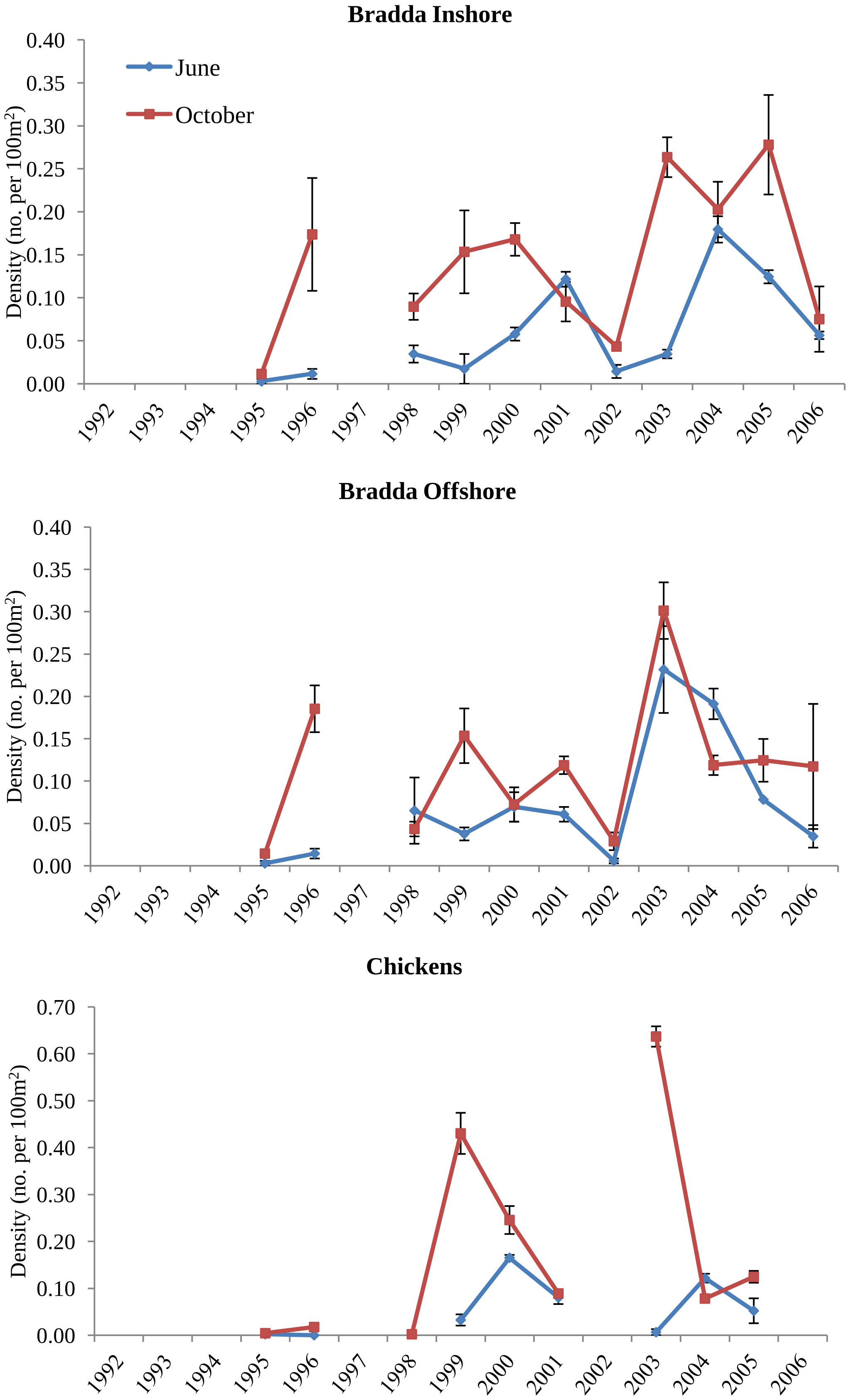
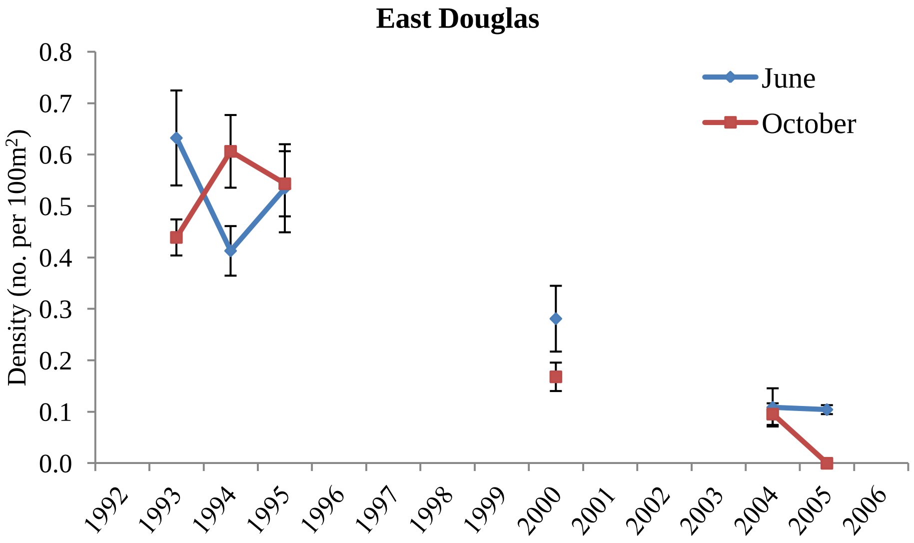


Figure 4.15 Mean density (no. per 100m^2) of *Luidia ciliaris* in June and October at the three fishing grounds around the Isle of Man where it was found, from 1992 - 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown. Note the different scale on the Chickens y-axis. Density at Bradda Inshore in October was significantly higher than density captured in June (One-way ANOVA F = 6.79, MS = 0.037, *df*= 1, p = 0.02)



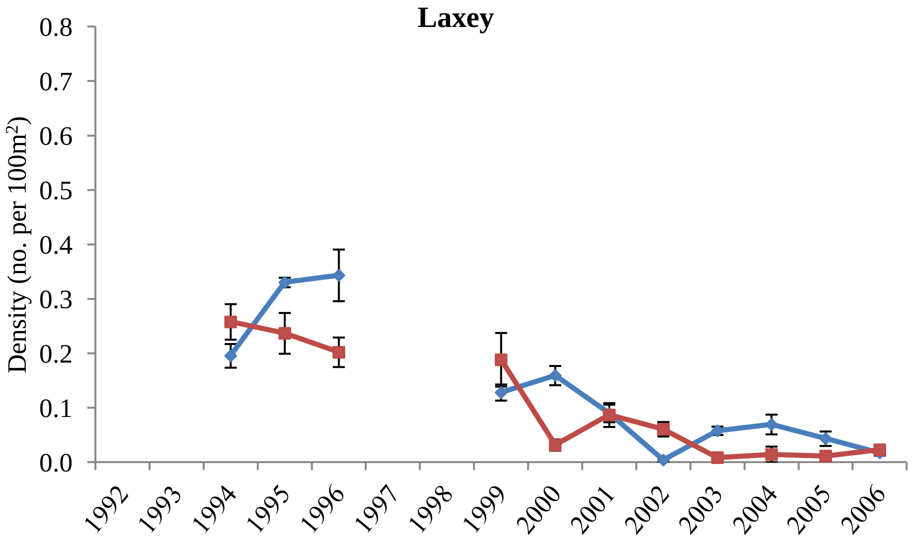


Figure 4.16 Mean density (no. per 100m^2) of *Neptunea antiqua* in June and October at the two fishing grounds around the Isle of Man where it was found from 1992 - 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown. No significant difference between density in June and density in October could be found at either site.

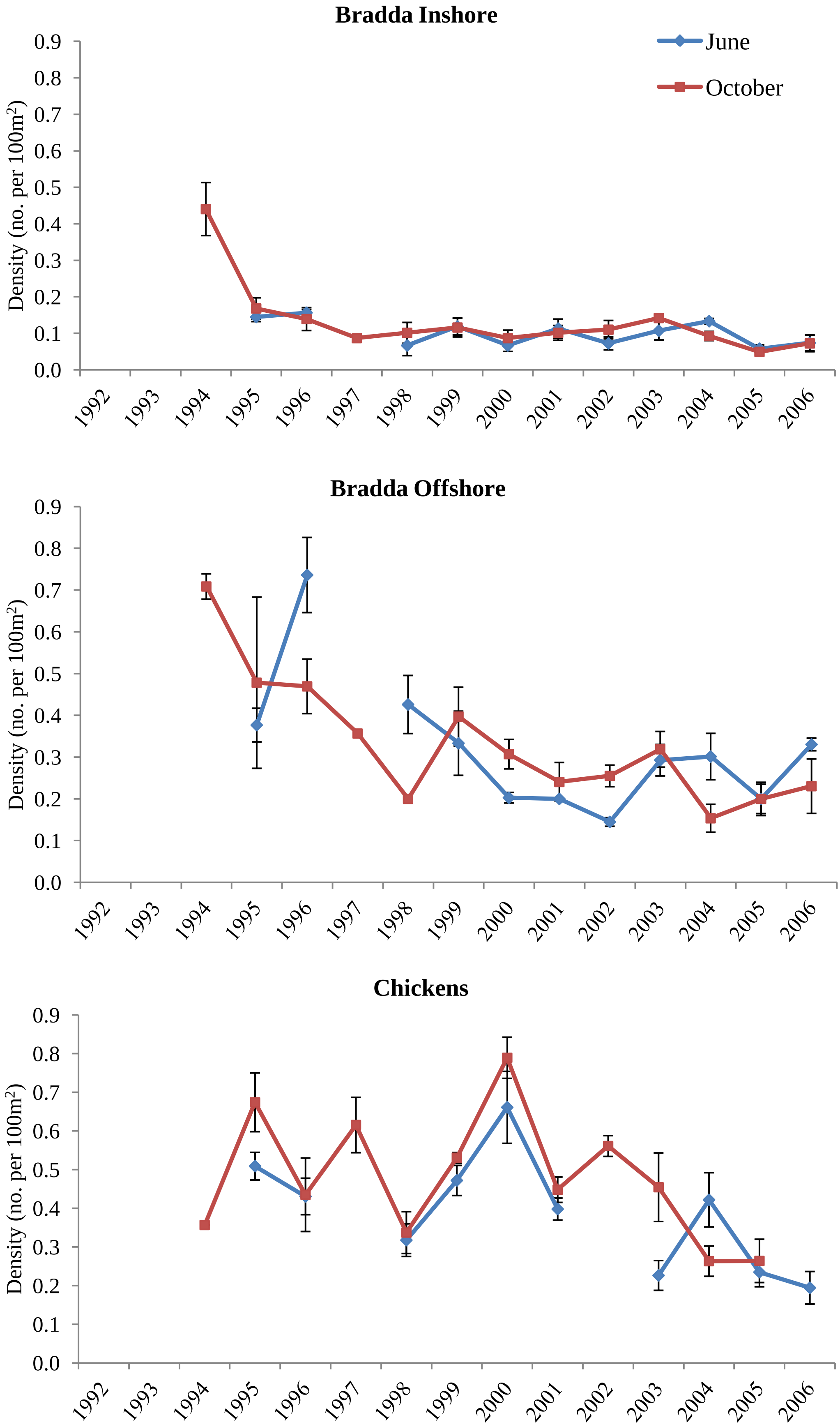


Figure 4.17 Mean density (no. per 100m^2) of *Porania pulvillus* in June and October each year at the three fishing grounds around the Isle of Man that it was found from 1992 - 2006. Densities were calculated from queen dredge catch data. Standard error bars are shown. There was no significant difference in density between June and October for any of the three grounds.

4.4.4 Temporal trends in benthic species density

The temporal trends in species density were investigated for each ground separately and are outlined below. Significant results are indicated on the relevant figures that accompany this section.

4.4.4.1 Bradda Inshore

Five of the seven chosen species were present at Bradda Inshore, four of which showed significant temporal trends (Figure 4.18). *A. rubens*, *P. pulvillus* and *E. esculentus* all showed significant decreases over the course of the time series. *L. ciliaris* showed a significant increase in density over the course of the time series. *A. opercularis* was also present, but showed no significant trend in density over the time series, although from the year 2001 there was an increase in density from less than 0.5 per 100m^2 up to 1 per 100m^2. The species with the highest density over all was *A. rubens* reaching almost 4 per 100m^2. *P. pulvillus* and *L. ciliaris* density remained less than 0.5 per 100m^2 and *E. esculentus* was even lower at less than 0.04 per 100m^2.

4.4.4.2 Bradda Offshore

All of the species, except *E. esculentus*, present at Bradda Inshore were also present at Bradda Offshore (Figure 4.19). Generally densities were the same magnitude as Bradda Inshore, apart from *P. pulvillus* which was found at densities ranging from 0.7 to 0.2 per 100m^2. *A. rubens* and *A. opercularis* showed no significant trend over time. *A. opercularis* density was generally very low (<0.01 per 100m^2) apart from the final year of the time series (2006) when density jumped to 1.32 per 100m^2. As at Bradda Inshore *P. pulvillus* showed a significant decrease in density and *L. ciliaris* showed a significant increase in density over the time series (Figure 4.18).

4.4.4.3 Chickens

At this fishing ground *A. opercularis*, *A. rubens*, *E. esculentus* and *Poranis pulvillus* were all present (Figure 4.20). *A. opercularis* was not recorded on this ground until 1999 when densities increased to a maximum density of 12.26 per 100m^2 in 2002. After this point density fluctuated, but remained greater than 2 per 100m^2. A significant positive temporal trend was seen in *A. opercularis* density at Chickens. *A. rubens* and *P. pulvillus* densities were comparable with Bradda Inshore and Bradda Offshore, but no significant temporal trends were found. *E. esculentus* density was much higher here than Bradda Inshore, up to 1.5 per 100m^2 in 1995, but this quickly declined in 1997 and remained at less than 0.2 per 100m^2 for the rest of the time series. These declines in *E. esculentus* density were significant (Figure 4.19).

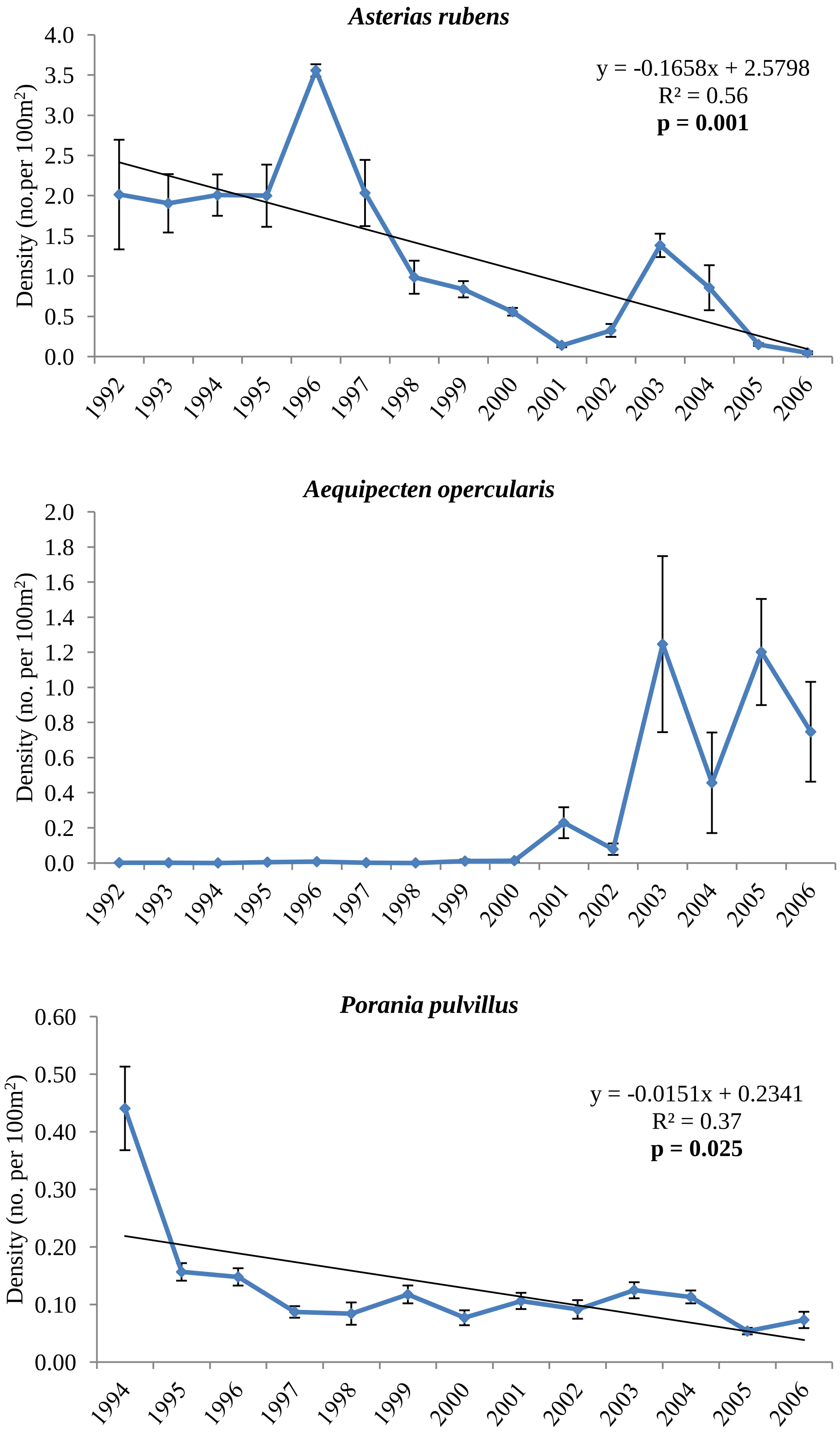
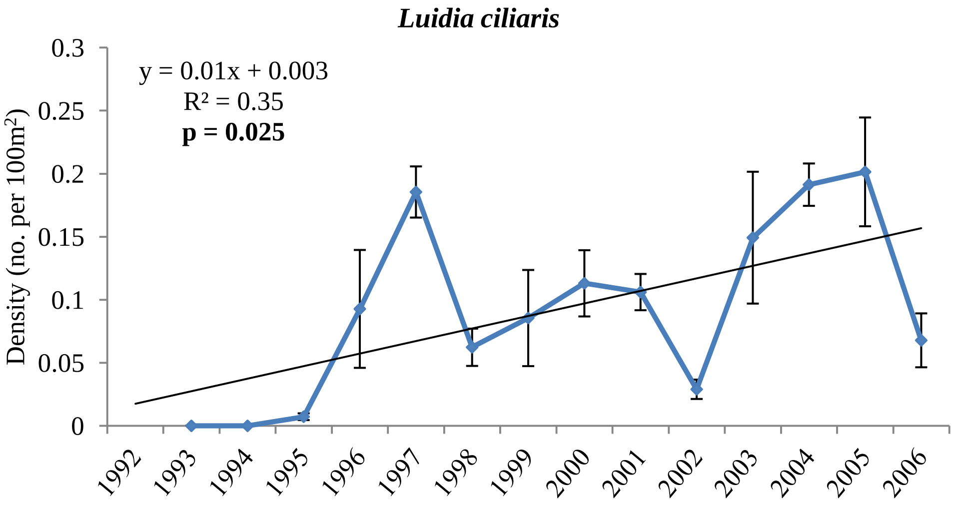


Figure 4.18a Annual mean relative densities (no. per 100m^2) of the three most common species present in catch of queen dredges in bi-annual scallop surveys at Bradda Inshore from 1992 - 2006. Significant trends and standard error bars are shown. Note the different scales of each y-axis.



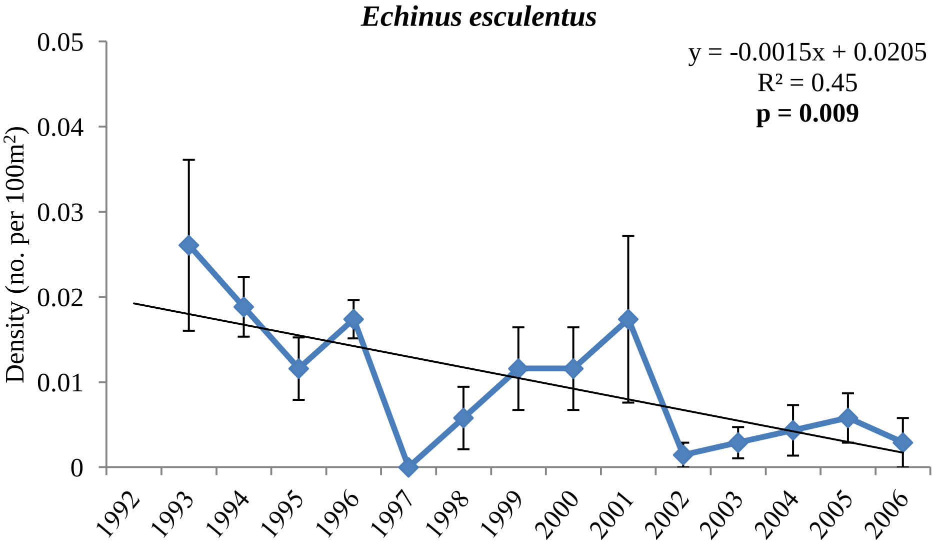


Figure 4.18b Annual mean relative densities (no. per 100m^2) of two species present in catch of queen dredges in bi-annual scallop surveys at Bradda Inshore from 1992 - 2006. Significant trends and standard error bars are shown. Note the different scales of each y-axis.

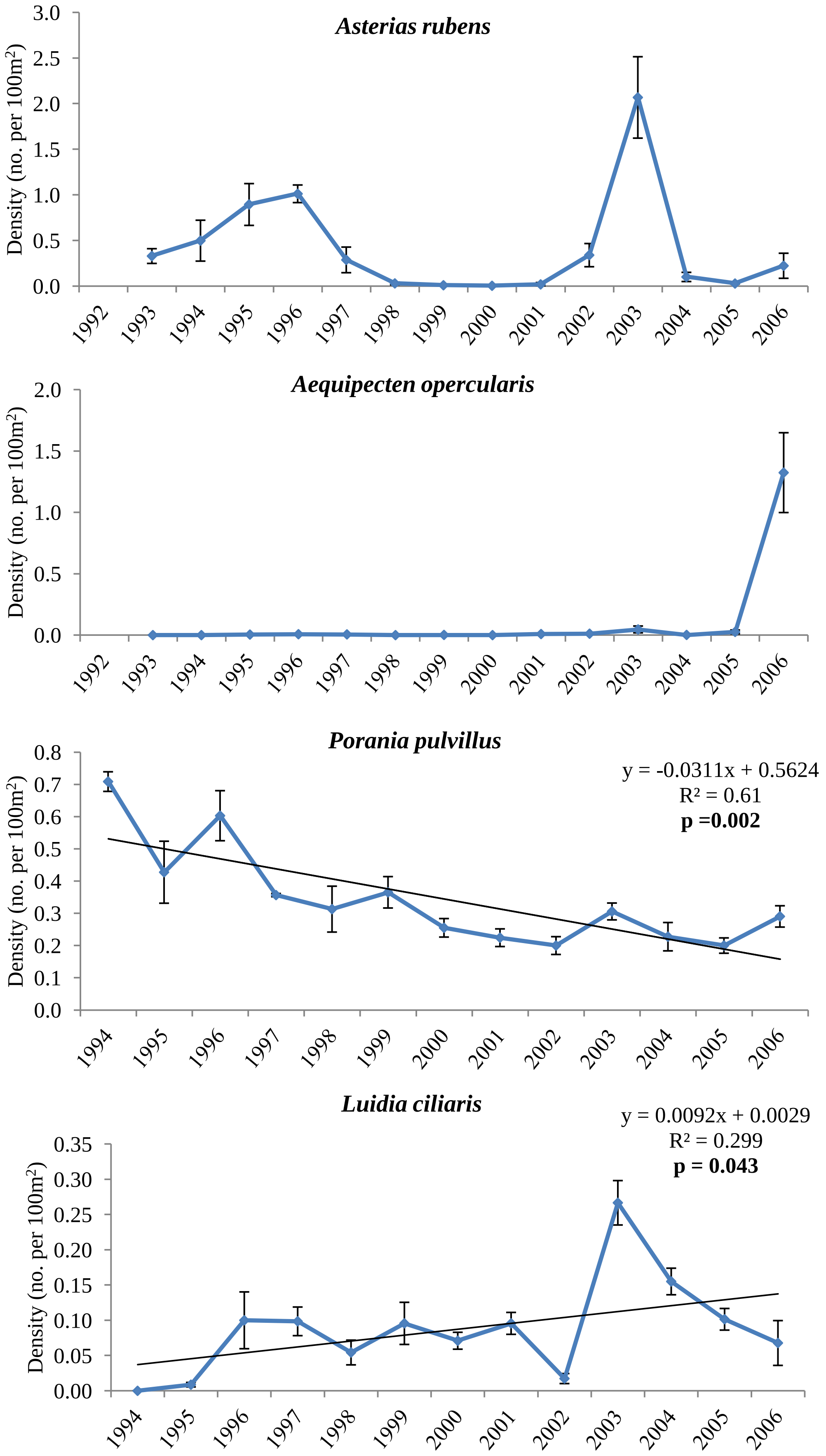


Figure 4.19 Annual mean relative densities (no. per 100m^2) of the four most common species present in catch of queen dredges in bi-annual scallop surveys at Bradda Offshore from 1992 - 2006. Significant trends and standard error bars are shown. Note the different scales of each y-axis.

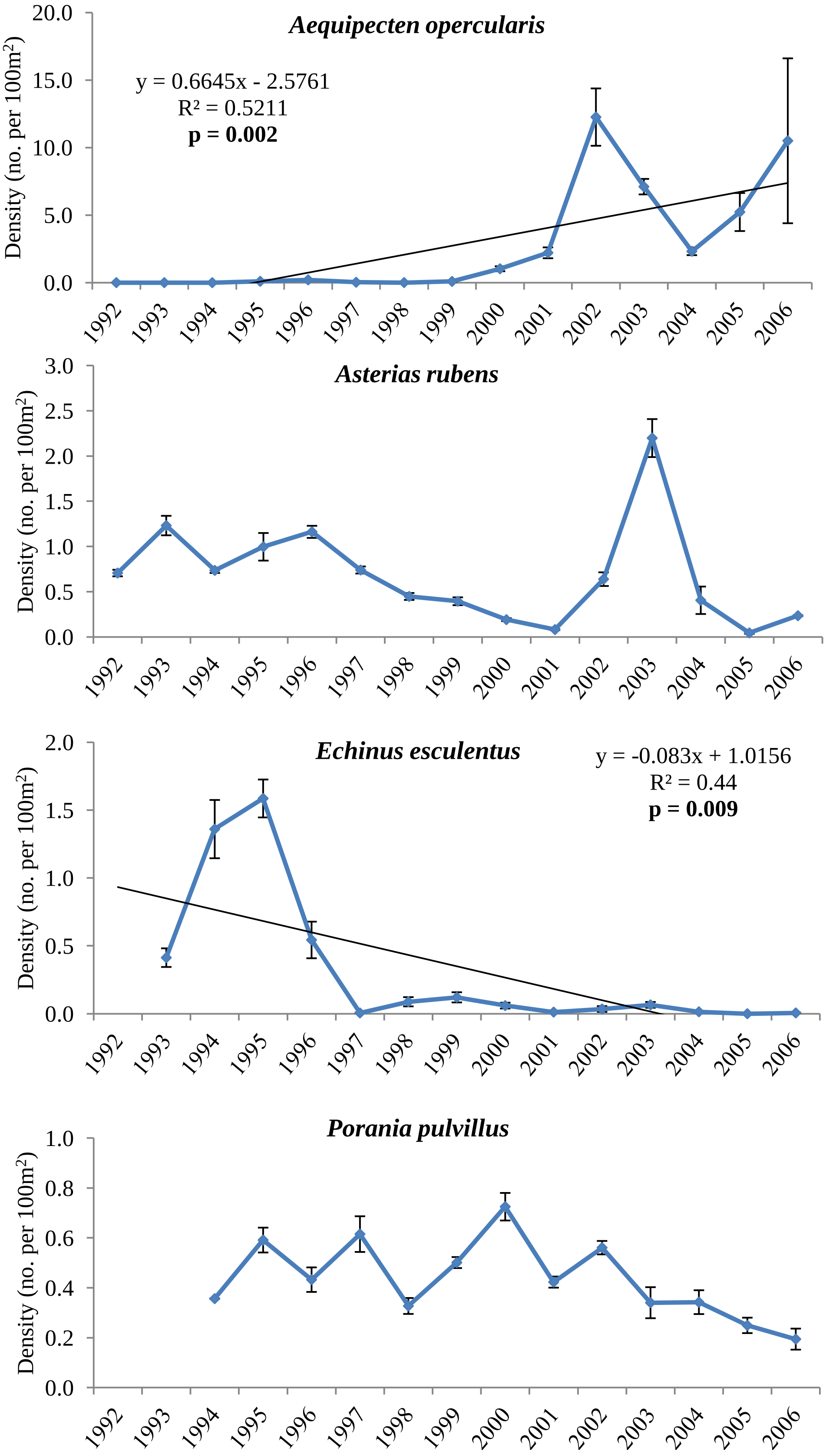


Figure 4.20 Annual mean relative densities (no. per $100m^2$) of the most common species present in catch of queen dredges in bi-annual scallop surveys at Chickens from 1992 - 2006. A significant temporal trends and standard error bars are shown. Note the different scales of each y-axis.

4.4.4.1 Peel

Only two species of the seven chosen were present at Peel fishing ground, *A. rubens* and *L. ciliaris* (Figure 4.21). No significant temporal trend was found in *A. rubens*, although density declined from a peak in 1999 of 1.8 per 100m^2 to less than 0.5 per 100m^2 for the rest of the time series. *L ciliaris* showed a significant increase in density over the time series, but overall density remained relatively low (less than 0.1 per 100m^2).

4.4.4.2 East Douglas

East Douglas had five of the seven species chosen for analysis present. *A. opercularis* had the highest density of all the species present, with between 2 and 10 per 100m^2 (Figure 4.22a). No significant temporal trend was seen in *A. opercularis* density. *E. esculentus* and *A. rubens* both had densities of around 1 to 2 per 100m^2 in the first half of the time series. Both species showed significant decreases in density over the time series (Figure 4.22a), dropping to densities of less than 0.5 per 100m^2. The two whelk species, *B. undatum* and *N. antiqua* were also present at East Douglas, and both showed significant decreases in density over the course of the time series (Figure 4.22b). Both were found at similar densities, ranging from 0.5 per 100m^2 at the beginning of the time series to less than 0.1 per 100m^2 by the end.

4.4.4.3 Laxey

The species present at Laxey were *A. opercularis*, *A. rubens*, *E. esculentus* and *N. Antiqua* (Figure 4.23). *N. antiqua* was the only species to show a significant trend over time, with density decreasing from 0.3 per 100m^2 to less than 0.1 per 100m^2 (Figure 4.23). *A. opercularis* peaked in density between 2004 and 2005 at approximately 26 per 100m^2, but by 2006 this had steeply declined to less than 5 per 100m^2. A similar pattern occurs in *A. rubens* density, however the peak is at approximately 1 per 100m^2 and this drops to 0.3 per 100m^2 over the same time period as *A. opercularis* (Figure 4.23). *E. esculentus* density fluctuates throughout the time series, with a maximum in 2000 of 1.26 per 100m^2, but no significant linear trend was found.

4.4.4.4 South Port St. Mary

There were no significant liner temporal trends in any of the species examined at the South PSM fishing ground (Figure 4.24). The species with the highest density was *A. opercularis*, which peaked at 20 per 100m^2 in 2000, but then declined steeply to around 2.5 per 100m^2 for the years 2002 to 2004. Data for the final two years of the time series at this fishing ground were missing. *A. rubens* was generally found at densities of less than 0.6 per 100m^2 apart from a peak in 2003 of 1 per 100m^2. *E.*

esculentus fluctuated around 0.5 per 100m^2 for the course of the time series. *B. undatum* appeared to oscillate from 0.3 per 100m^2 to less than 0.1 per 100m^2 every four years from 1992 to 2004 (Figure 4.24).

4.4.4.5 Targets

B. undatum was the only species of the four examined at Targets to show a significant temporal trend (Figure 4.25). Density decreased from approximately 0.3 per 100m^2 to less than 0.05 per 100m^2. *A. rubens* peaked in 1996 at 2 per 100m^2 then dropped and fluctuated around 0.6 per 100m^2 for the rest of the time series (Figure 4.25). *E. esculentus* was found at the highest density of all the fishing grounds at Targets, remaining around 3 per 100m^2 from 1993 to 1996, then dropping to almost 0 per 100m^2 for the remainder of the time series (Figure 4.25). The final species present at this ground was *A. opercularis*, which was found at very low densities from 1992 to 2004 (less than 1 per 100m^2), however, in 2005 density rose to almost 6.5 per 100m^2.

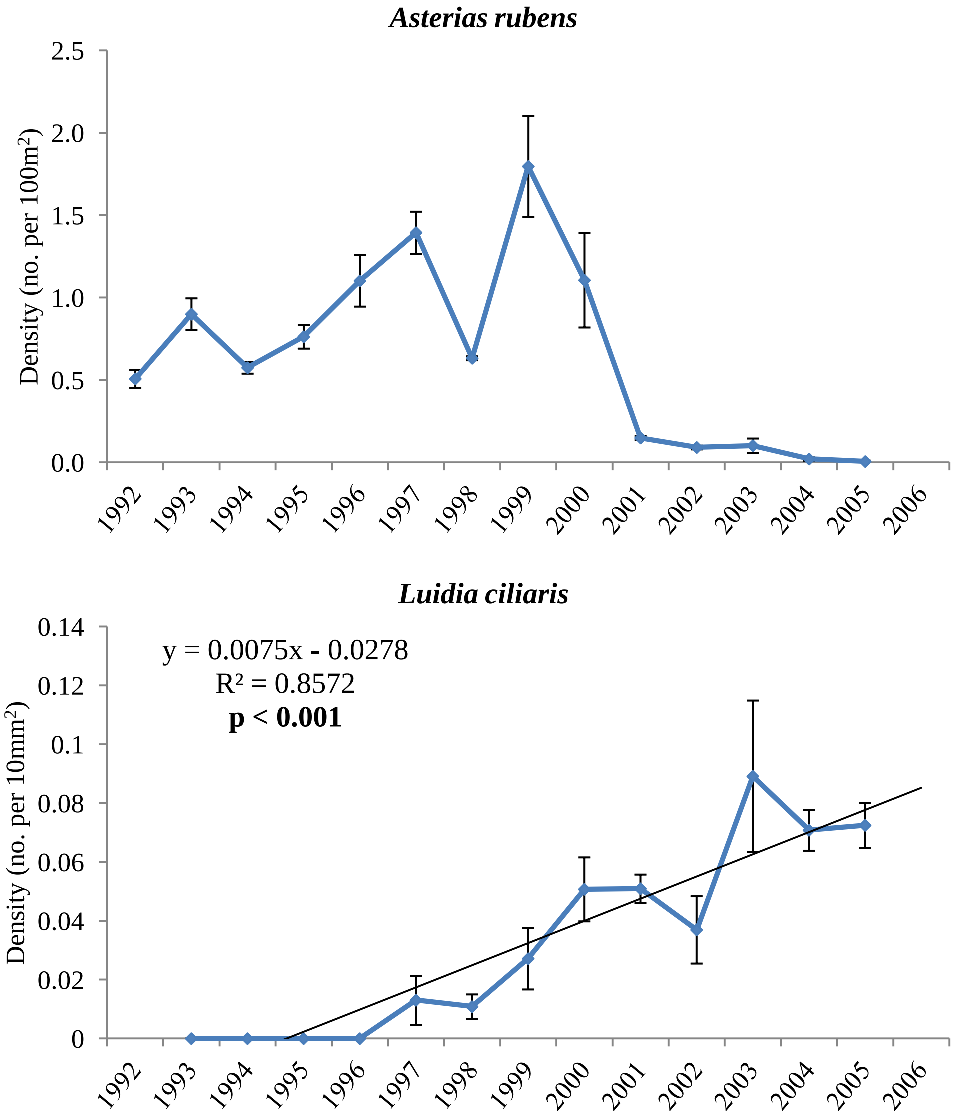


Figure 4.21 Annual mean relative densities (no. per 100m^2) of the two most common species present in the catch of queen dredges in bi-annual scallop surveys at Peel from 1992 - 2006. A significant positive temporal trend was found for *Luidia ciliaris*. Standard error bars are shown. Note the different scales of each y-axis.

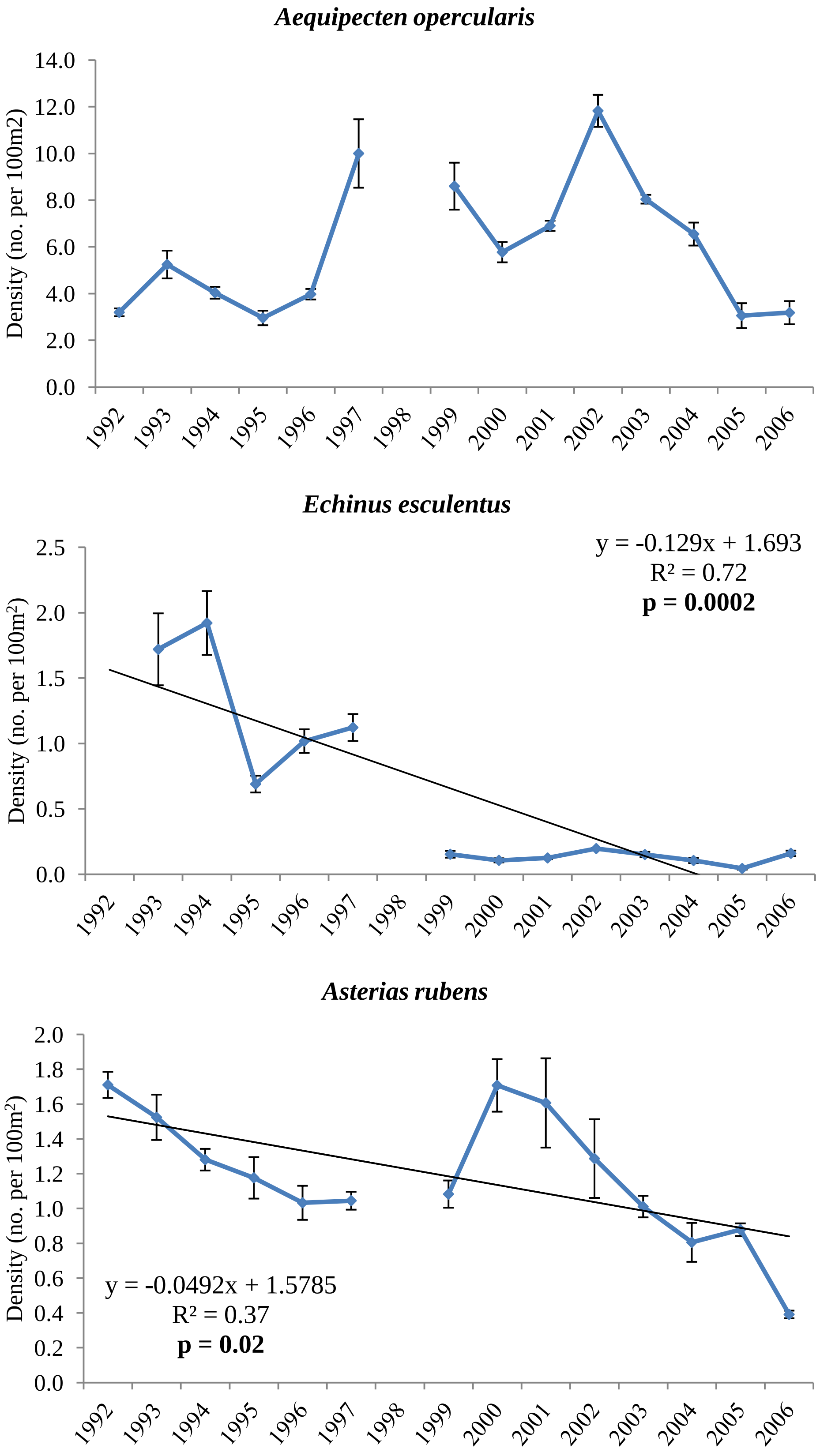
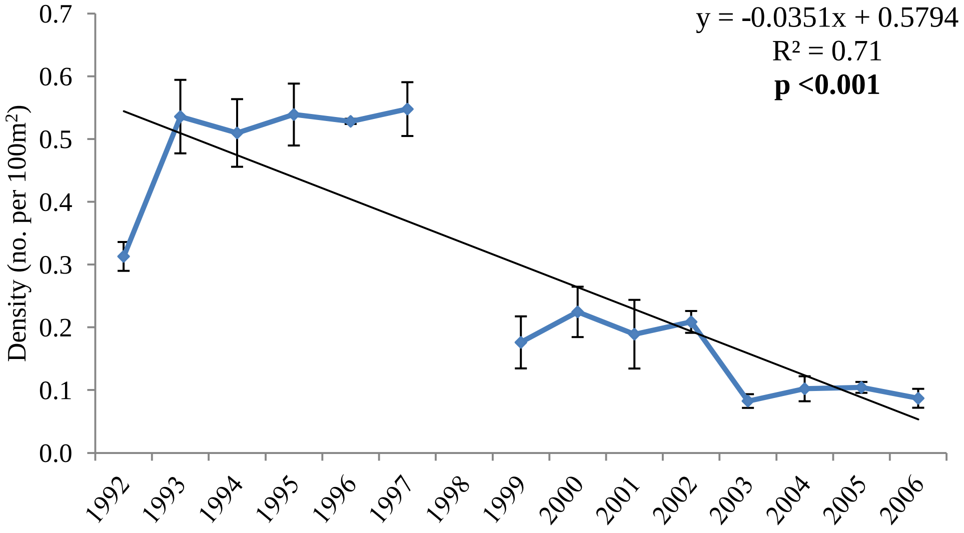


Figure 4.22a Annual mean relative densities (no. per 100m^2) of the most common species present in the catch of queen dredges in bi-annual scallop surveys at East Douglas from 1992 - 2006. Significant negative temporal trends were found for two species, *Echinus esculentus* and *Asterias rubens.* Standard error bars are shown. Note the different scales of each y-axis.

Neptunea antiqua



Buccinum undatum

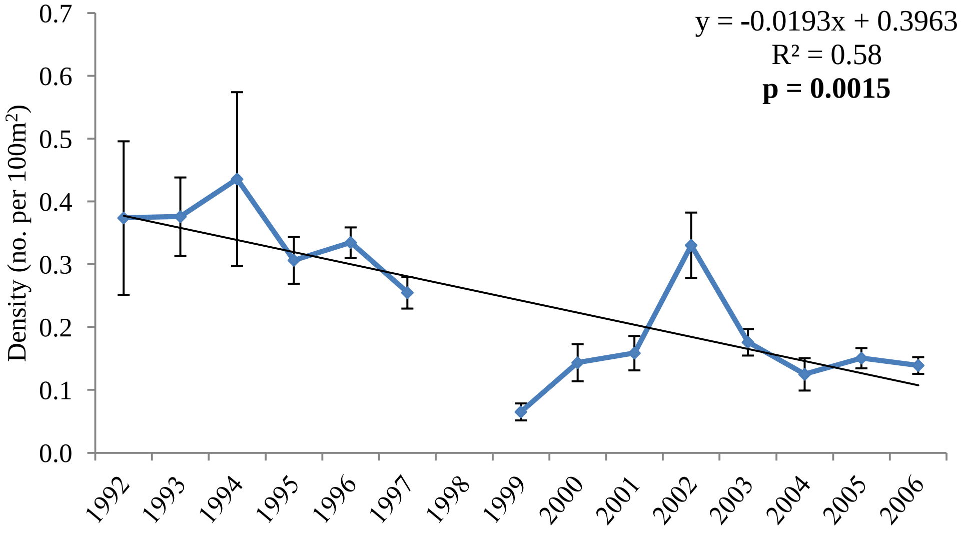


Figure 4.22b Annual mean relative densities (no. per 100m^2) of the whelks *Neptunea antiqua* and *Buccinum undatum* present in the catch of queen dredges in bi-annual scallop surveys at East Douglas from 1992 - 2006. Both species showed a significant negative temporal trend over the course of the time series. Standard error bars are shown.

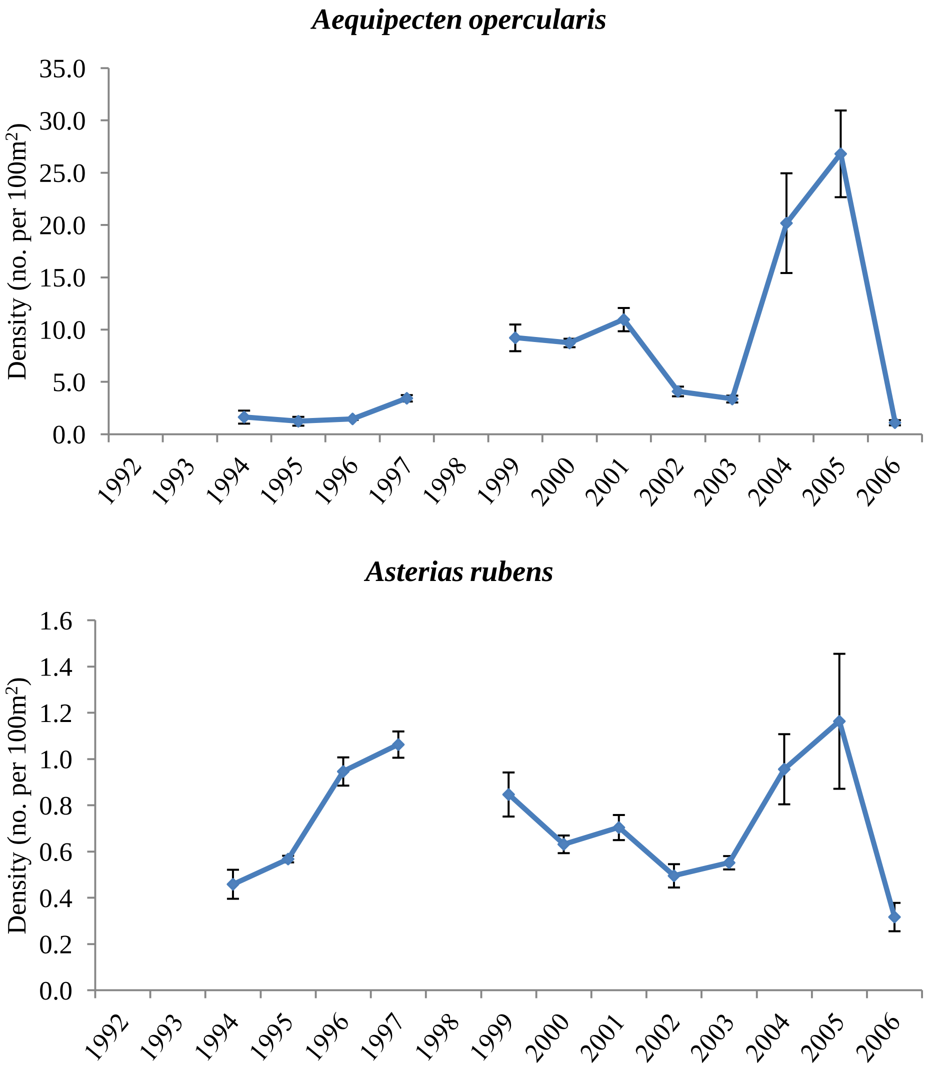


Figure 4.23a Annual mean relative densities (no. per 100m^2) of the *Aequipecten opercularis* and *Asterias rubens* from the catch of queen dredges in bi-annual scallop surveys at Laxey from 1992 - 2006. No significant temporal trends were found. Standard error bars are shown. Note the different scales of each y-axis.

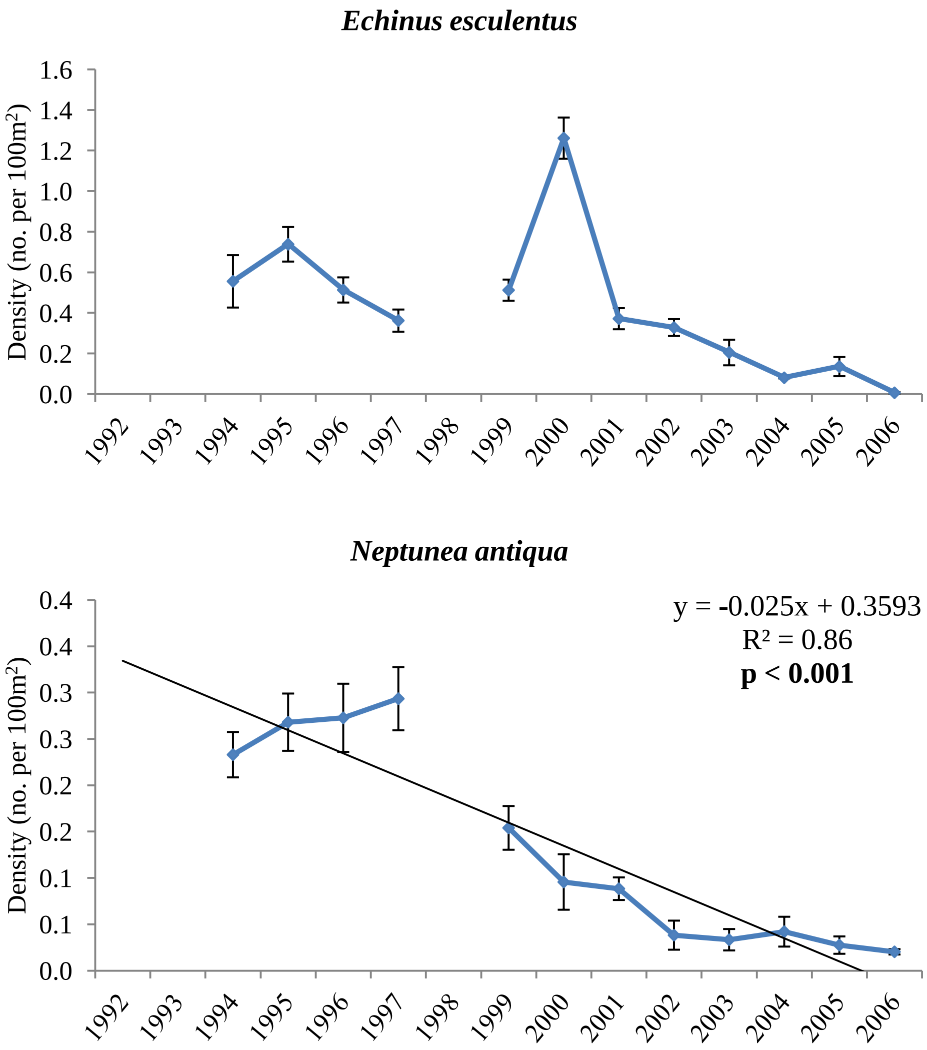


Figure 4.23b Annual mean relative densities (no. per 100m^2) of the *Echinus esculentus* and *Neptunea antiqua* from the catch of queen dredges in bi-annual scallop surveys at Laxey from 1992 - 2006. A significant decrease in *N. antiqua* density was found. Standard error bars are shown. Note the different scales of each y-axis.

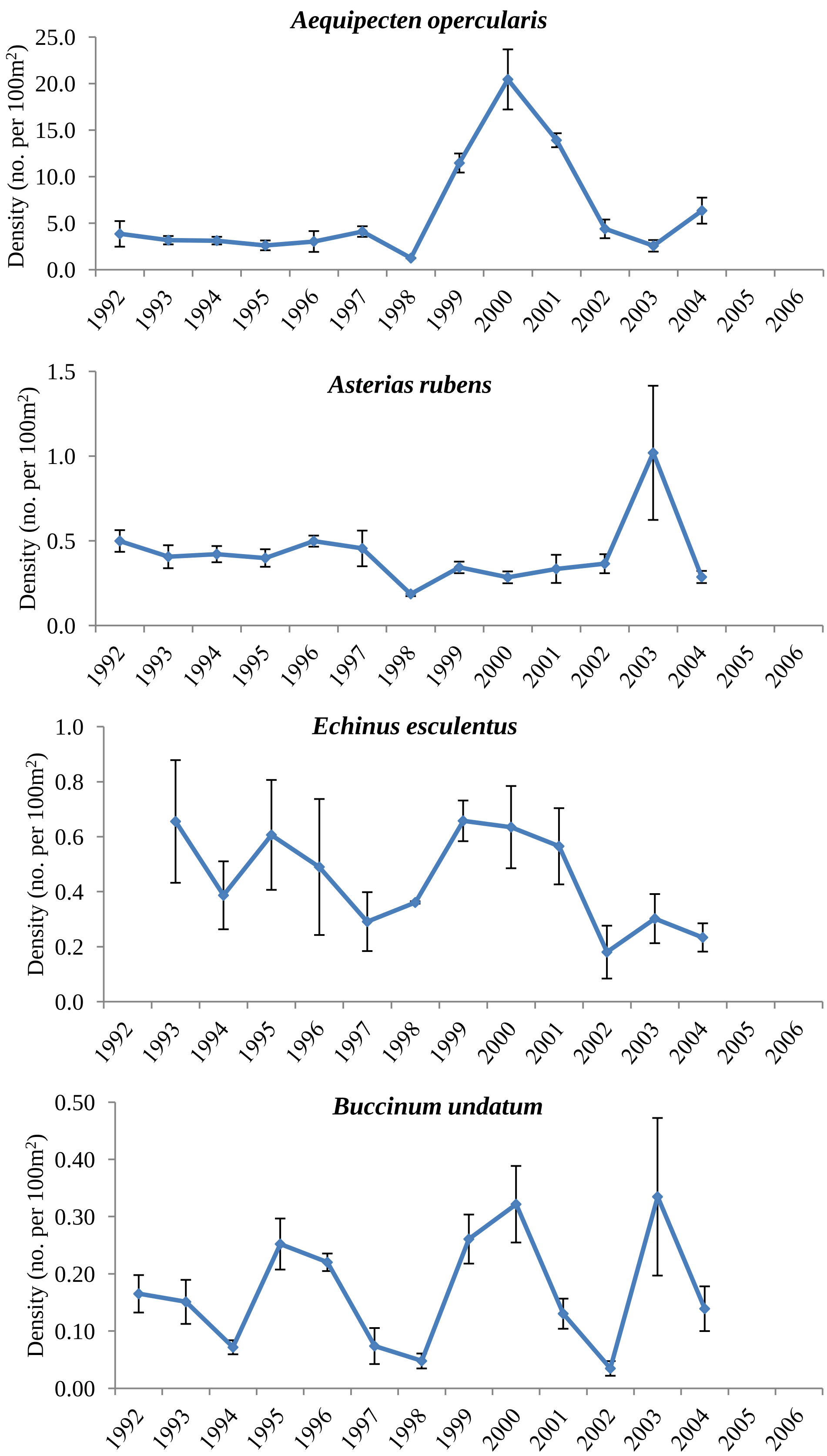


Figure 4.24 Annual mean relative densities (no. per 100m^2) of the most common species present in the catch of queen dredges in bi-annual scallop surveys at South of Port St. Mary from 1992 - 2006. No significant temporal trends were found in any of the four species studied. Standard error bars are shown. Note the different scales of each y-axis.

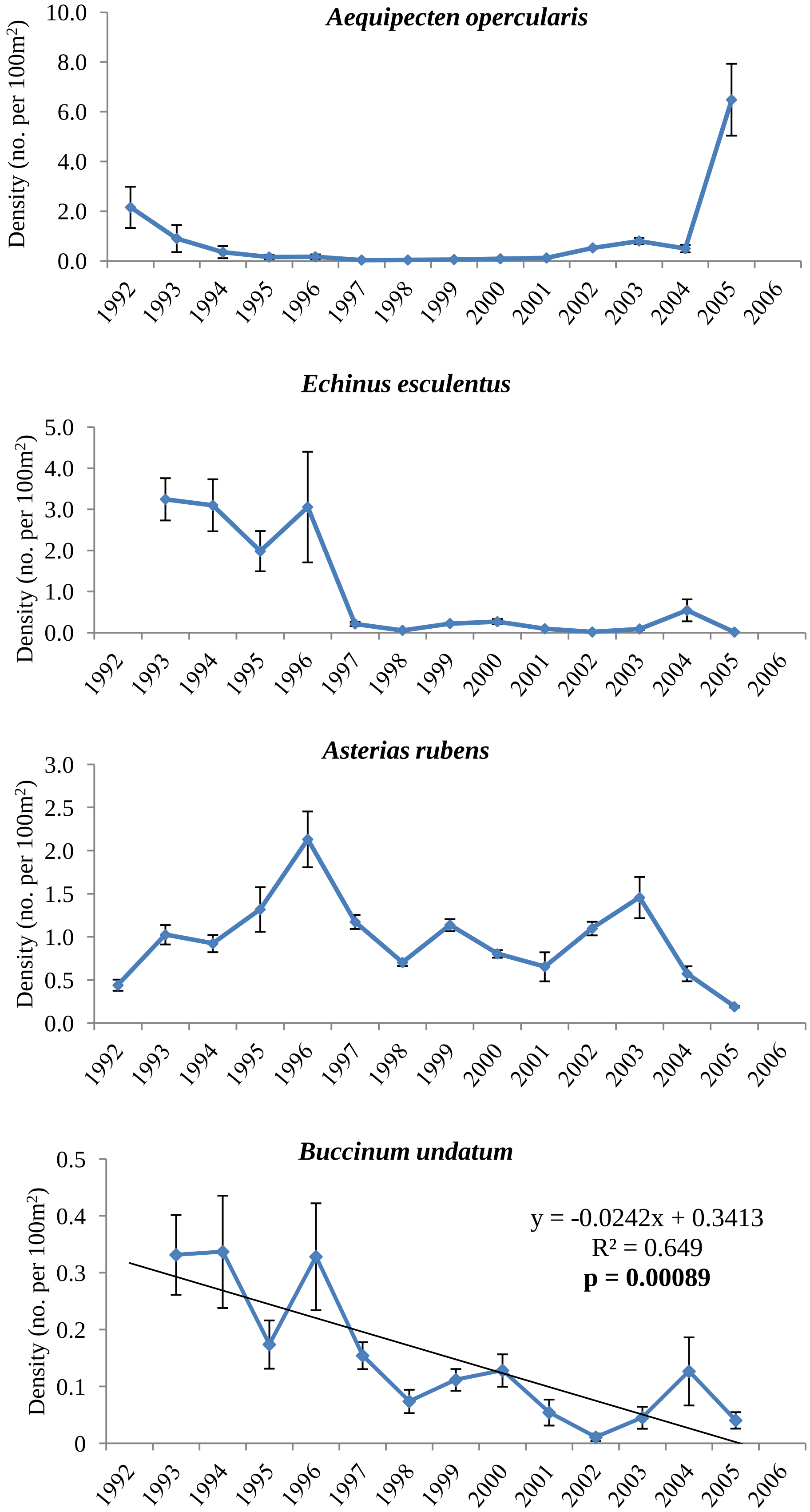


Figure 4.25 Annual mean relative densities (no. per $100m^2$) of the most common species present in the catch of queen dredges in bi-annual scallop surveys at Targets from 1992 - 2006. A significant negative temporal trend was found for *Buccinum undatum*. Standard error bars are shown Note the different scales of each y-axis.

4.4.5 The effect of fishing pressure on individual species densities

A series of linear regression analyses were performed to determine whether there was a relationship between local fishing effort and individual species density. Table 4.3 shows the results of the analyses that combined density data for each species across all of the fishing grounds where it was found. Fishing effort data were square-root transformed to ensure normality. Three different time lags in the fishing effort data were used: no lag, a 1 year lag and a 2 year lag. *E. esculentus* was the only species to show a significant relationship with square-root transformed fishing effort. At all three time lags transformed fishing effort had a significant negative relationship with *E. esculentus* density, however R^2 values were all less than or equal to 0.1 (No Lag: df = 85, F = 4.52, P = 0.04, R^2 = 0.05) (1 Year Lag: df = 89, F = 9.47, P <0.01, R^2 = 0.10) (2 Year Lag: df = 89, F = 8.43, P <0.01, R^2 = 0.09) (Table 4.2).

Table 4.2 Linear regression analysis of the effect of fishing effort on species densities on all eight grounds around the Isle of Man. Fishing effort data were square-root transformed to ensure normality and homogeneity of variance. Transformed fishing effort data were then analysed against species densities with no time lag, a 1 year time lag and a 2 year time lag.

Species	**Time Lag**	**Estimate**	***df***	**F**	**r2**	**P-value**
Aequipecten opercularis	no lag	-0.0175	88	1.80	0.02	0.18
	1 year	-0.0188	92	1.96	0.02	0.17
	2 year	-0.0051	92	0.18	0.00	0.67
Asterias rubens	no lag	0.0018	101	1.25	0.01	0.27
	1 year	0.0027	106	2.45	0.02	0.12
	2 year	0.0009	106	0.34	0.00	0.56
Buccinum undatum	no lag	-0.0006	34	1.38	0.04	0.25
	1 year	-0.0014	36	3.90	0.10	0.06
	2 year	-0.0013	36	4.22	0.11	0.47
Echinus esculentus	**no lag**	**-0.0038**	**85**	**4.52**	**0.05**	**0.04**
	1 year	**-0.0055**	**89**	**9.47**	**0.10**	**<0.01**
	2 year	**-0.0048**	**89**	**8.43**	**0.09**	**<0.01**
Luidia ciliaris	no lag	-0.0002	48	0.56	0.01	0.46
	1 year	0.0016	51	0.29	0.01	0.59
	2 year	-0.0001	51	0.18	0.00	0.68
Neptunea antiqua	no lag	-0.0007	22	0.36	0.02	0.56
	1 year	-0.0023	23	3.56	0.13	0.07
	2 year	-0.0015	23	1.92	0.08	0.18
Porania pulvillus	no lag	0.0003	35	0.12	0.00	0.74
	1 year	-0.0001	37	0.00	0.00	0.98
	2 year	-0.0005	37	0.41	0.01	0.53

Table 4.3 Linear regression analysis of the effect of fishing effort on species densities on all eight grounds around the Isle of Man. Fishing effort data were analysed against species densities with no time lag, a 1 year time lag and a 2 year time lag. To ensure normality and homogeneity of variance fishing effort data was transformed at some sites: * indicates a $\log_{10}$ transformation and ** indicates a square-root transformation. Significant relationships are highlighted in bold.

Ground	Species	Lag	*df*	F	r2	*p*
Bradda Inshore	*Aequipecten opercularis*	no lag	13	0.058	0.004	0.81
		1 year	13	0.223	0.017	0.64
		2 year	13	0.113	0.009	0.74
	Asterias rubens	no lag	13	0.005	0.000	0.94
		1 year	13	0.684	0.047	0.44
		2 year	13	0.218	0.017	0.65
	Echinus esculentus	**no lag**	**13**	**8.360**	**0.390**	**0.01**
		1 year	13	0.020	0.002	0.89
		2 year	13	0.023	0.002	0.88
	Luidia ciliaris	no lag	10	1.368	0.120	0.27
		1 year	10	3.395	0.253	0.10
		2 year	10	3.309	0.249	0.10
	Porania pulvillus	no lag	11	0.855	0.072	0.37
		1 year	11	0.487	0.042	0.50
		2 year	11	0.176	0.016	0.68
Bradda Offshore*	*Aequipecten opercularis*	no lag	11	0.453	0.040	0.52
		1 year	12	0.758	0.059	0.40
		2 year	12	0.125	0.010	0.73
	Asterias rubens	no lag	11	0.005	0.000	0.94
		1 year	12	0.583	0.046	0.46
		2 year	12	1.107	0.084	0.31
	Echinus esculentus	no lag	11	0.818	0.069	0.39
		1 year	**12**	**6.395**	**0.348**	**0.03**
		2 year	12	6.229	0.342	0.03
	Luidia ciliaris	no lag	9	0.552	0.058	0.48
		1 year	10	0.011	0.001	0.92
		2 year	10	0.089	0.009	0.77
	Porania pulvillus	no lag	10	0.029	0.003	0.87
		1 year	11	1.077	0.089	0.32
		2 year	**11**	**6.076**	**0.356**	**0.03**
Chickens	*Aequipecten opercularis*	no lag	12	0.738	0.058	0.41
		1 year	13	0.800	0.058	0.39
		2 year	13	1.014	0.072	0.33
	Asterias rubens	no lag	12	0.027	0.002	0.87
		1 year	13	0.342	0.026	0.57
		2 year	13	2.436	0.158	0.14
	Echinus esculentus	no lag	12	0.005	0.000	0.95
		1 year	13	0.560	0.041	0.47
		2 year	13	0.939	0.067	0.35
	Luidia ciliaris	no lag	9	0.251	0.027	0.63
		1 year	10	0.365	0.035	0.56
		2 year	10	0.124	0.012	0.73
	Porania pulvillus	no lag	10	3.413	0.254	0.09
		1 year	11	0.877	0.074	0.37
		2 year	11	0.302	0.027	0.59

Table 4.3 continued.

Ground	Species	Lag	*df*	F	r2	*p*
East Douglas**	*Aequipecten opercularis*	**no lag**	**11**	**15.110**	**0.579**	**<0.01**
		1 year	12	0.646	0.051	0.44
		2 year	12	0.933	0.072	0.35
	Asterias rubens	no lag	11	3.306	0.231	0.10
		1 year	12	0.307	0.025	0.59
		2 year	12	0.000	0.000	0.98
	Buccinum undatum	no lag	11	3.307	0.218	0.11
		1 year	**12**	**14.430**	**0.546**	**0.00**
		2 year	**12**	**30.370**	**0.717**	**<0.01**
	Echinus esculentus	no lag	10	0.918	0.084	0.36
		1 year	**11**	**12.810**	**0.538**	**<0.01**
		2 year	**11**	**13.580**	**0.552**	**<0.01**
	Neptunea antiqua	no lag	11	0.540	0.047	0.48
		1 year	**12**	**7.755**	**0.393**	**0.02**
		2 year	**12**	**8.026**	**0.401**	**0.02**
Laxey**	*Aequipecten opercularis*	no lag	9	0.006	0.000	0.98
		1 year	9	0.009	0.001	0.93
		2 year	9	3.061	0.254	0.11
	Asterias rubens	no lag	9	2.236	0.199	0.17
		1 year	9	0.117	0.013	0.74
		2 year	**9**	**6.501**	**0.419**	**0.03**
	Echinus esculentus	no lag	9	0.165	0.018	0.69
		1 year	9	6.236	0.409	0.34
		2 year	**9**	**5.558**	**0.382**	**0.04**
	Neptunea antiqua	no lag	9	1.502	0.143	0.25
		1 year	9	0.364	0.039	0.56
		2 year	9	0.409	0.043	0.54
Peel	*Asterias rubens*	no lag	11	0.881	0.074	0.37
		1 year	12	5.655	0.320	0.35
		2 year	12	2.414	0.168	0.15
	Luidia ciliaris	no lag	6	0.083	0.014	0.78
		1 year	7	2.763	0.283	0.14
		2 year	**7**	**13.400**	**0.657**	**0.01**
South PSM						
	Aequipecten opercularis	no lag	9	0.463	0.049	0.51
		1 year	10	0.049	0.005	0.83
		2 year	10	0.013	0.001	0.91
	Asterias rubens	no lag	9	0.392	0.042	0.55
		1 year	10	0.043	0.004	0.84
		2 year	10	0.014	0.001	0.91
	Buccinum undatum	no lag	9	1.242	0.121	0.29
		1 year	10	0.511	0.049	0.49
		2 year	10	0.128	0.013	0.73
	Echinus esculentus	no lag	8	0.412	0.049	0.54
		1 year	9	0.899	0.091	0.37
		2 year	9	2.193	0.196	0.17

Table 4.3 continued.

Ground	Species	Lag	*df*	F	r2	P-value
Targets	*Aequipecten opercularis*	no lag	11	1.243	0.102	0.29
		1 year	11	0.276	0.024	0.61
		2 year	11	1.243	0.102	0.29
	Asterias rubens	no lag	11	0.387	0.034	0.55
		1 year	11	0.039	0.004	0.85
		2 year	11	0.387	0.034	0.55
	Buccinum undatum	no lag	10	0.437	0.042	0.52
		1 year	10	0.073	0.007	0.79
		2 year	10	0.437	0.042	0.52
	Echinus esculentus	no lag	10	1.209	0.108	0.30
		1 year	10	0.861	0.079	0.38
		2 year	10	1.209	0.108	0.30
	Luidia ciliaris	no lag	6	5.817	0.492	0.05
		1 year	6	2.489	0.293	0.17
		2 year	6	5.817	0.492	0.05

4.4.6 The effect of fishing pressure on species densities at each fishing ground

Table 4.3 shows the results of the linear regression analyses that were performed individually for each fishing ground. Fishing effort data was transformed for Bradda Offshore ($\log_{10}$ transformation), East Douglas and Laxey (both square root transformed) to ensure normality. The majority of species did not show a significant relationship with fishing effort on any fishing ground (Table 4.3), those that did are explained in more detail below.

4.4.6.1 Bradda Inshore

Fishing effort data from this ground did not require transformation to ensure normality and homogeneity of variance. The only significant relationship was a negative relationship between unlagged fishing effort (metres of dredge fished per hour) and *E. esculentus* density (no. per $100m^2$) (df = 13, F = 8.36, P = 0.01, $R^2 = 0.39$) (Figure 4.26).

4.4.6.2 Bradda Offshore

Fishing effort data at Bradda Offshore was $\log_{10}$ transformed to ensure normality and homogeneity of variance. *E. esculentus* showed a significant negative relationship with transformed fishing effort at a 1 year lag (df = 12, F = 6.395, P = 0.03, $R^2 = 0.35$) and at a 2 year lag (df = 12, F = 6.23, P = 0.03, $R^2 = 0.34$) (Figure 4.27). *P. pulvillus* density also showed a significant negative relationship with transformed fishing effort lagged by 2 years (df = 11, F = 6.08, P = 0.03, $R^2 = 0.36$) (Figure 4.28).

4.4.6.3 Peel

Fishing effort data from Peel did not require transforming as it was normally distributed and had a homogeneous variance. A significant positive relationship between fishing effort lagged by 2 years and *L. ciliaris* density was found (df = 7, F = 13.4, P = 0.01, $R^2 = 0.66$) (Figure 4.29).

4.4.6.4 East Douglas

Fishing effort data was square-root transformed to ensure normality and homogeneity of variance at East Douglas. Three species showed significant negative relationships with transformed fishing effort data lagged by 1 year: *B. undatum* (df = 12, F = 14.43, $P < 0.01$, $R^2 = 0.55$), *N. antiqua* (df = 12, F = 7.76, P = 0.02, $R^2 = 0.39$) and *E. esculentus* (df = 11, F = 12.81, $P < 0.01$, $R^2 = 0.54$). The same three species also showed significant negative trends with transformed fishing effort data lagged by 2 years: *B. undatum* (df = 12, F = 30.37, $P < 0.01$, $R^2 = 0.72$), *N. antiqua* (df = 12, F = 8.026, P = 0.02, $R^2 = 0.40$) and *E. esculentus* (df = 11, F = 13.58, $P < 0.01$, $R^2 = 0.55$) (Figures 4.30 and 4.31).

4.4.6.5 Laxey

Fishing effort data from Laxey were square-root transformed to ensure normality and homogeneity of variance. *E. esculentus* had a significant negative relationship with transformed fishing effort lagged by 2 years (df = 9, F = 5.56, P = 0.04, R^2 = 0.38). *A. rubens* had a significant positive relationship with transformed fishing effort lagged by 2 years (df = 9, F = 6.50, P = 0.03, R^2 = 0.42) (Figure 4.32).

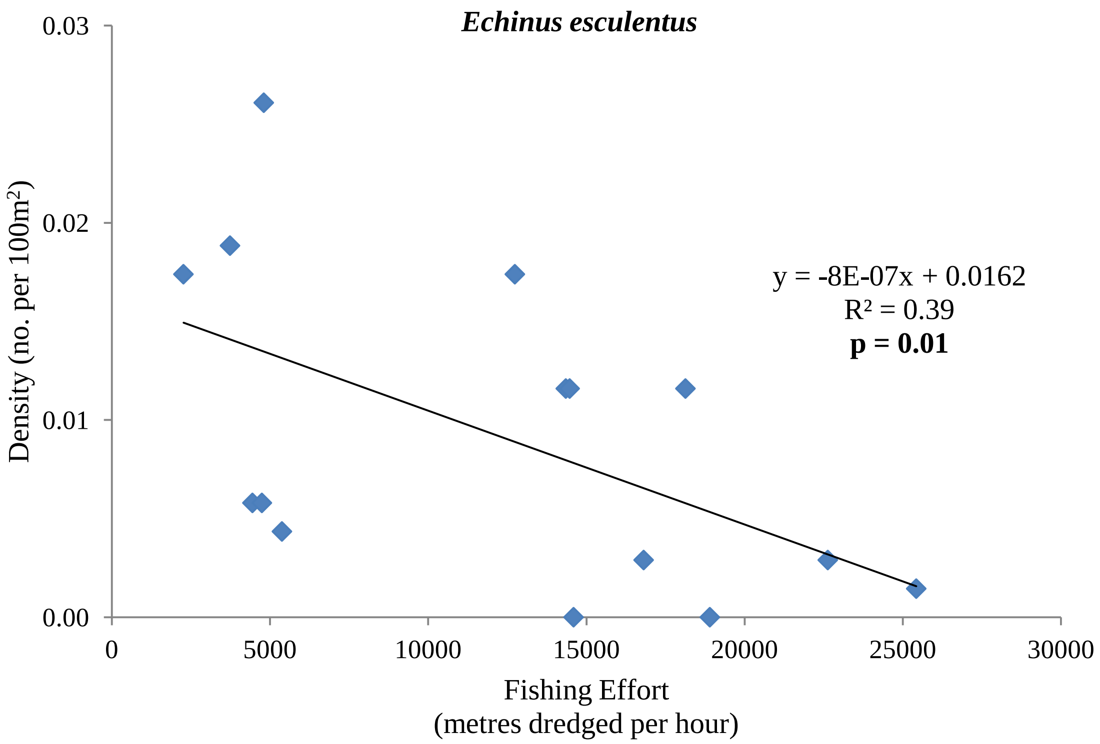


Figure 4.26 Linear regression analysis on the density of *Echinus esculentus* (no. per 100m2) and untransformed, un-lagged fishing effort (metres dredged per hour) at Bradda Inshore fishing ground. Data were collected from 1992 to 2006.

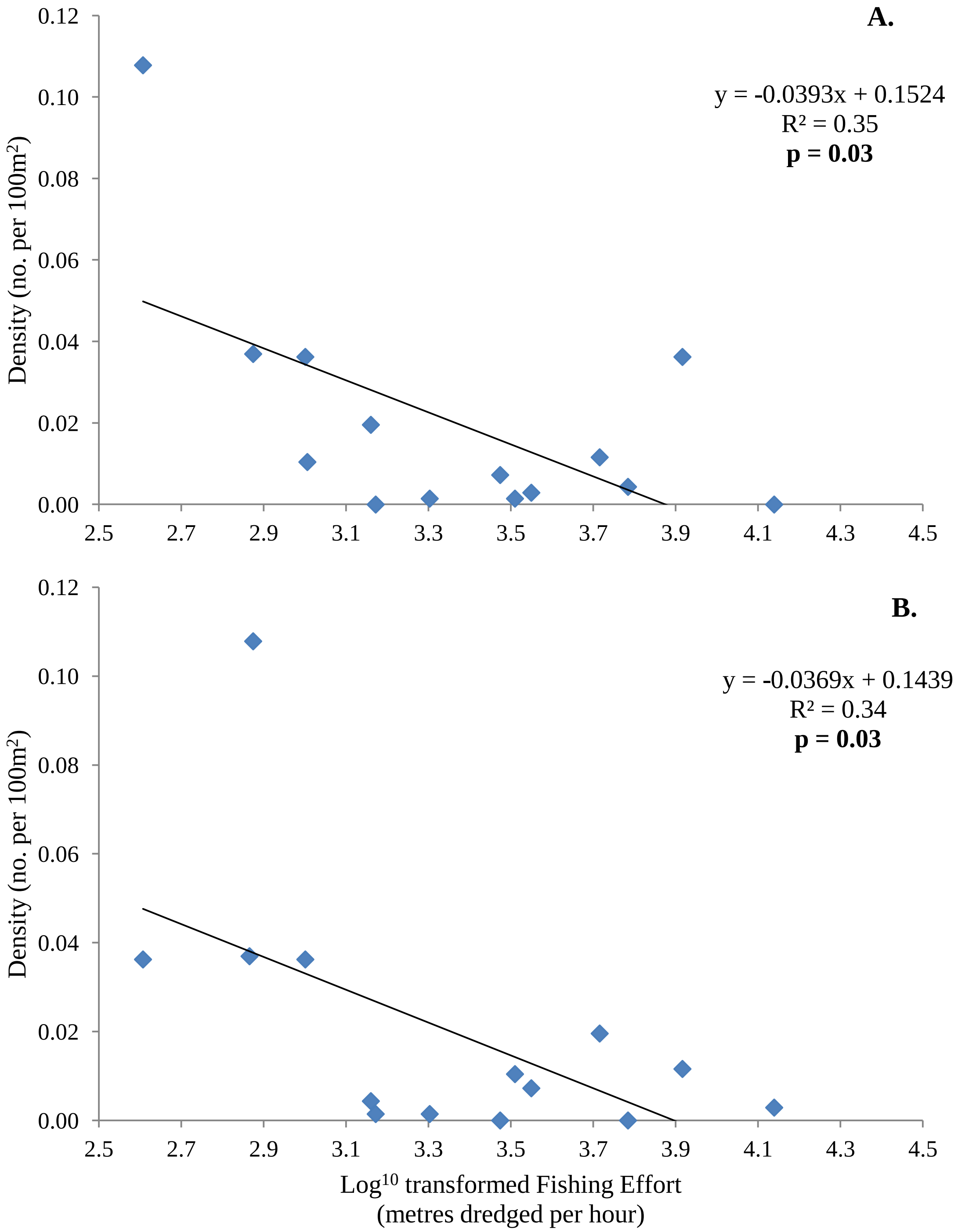


Figure 4.27 Linear regression analyses on the density of *Echinus esculentus* caught on Bradda Offshore and $\log^{10}$ transformed fishing effort lagged by (A) 1 year and (B) 2 years. Fishing effort data were transformed to ensure normality and homogeneity. Species density was calculated from queen dredge catch data obtained during the bi-annual scallop surveys conducted around the Isle of Man from 1992 – 2006 Note the truncated x-axis.

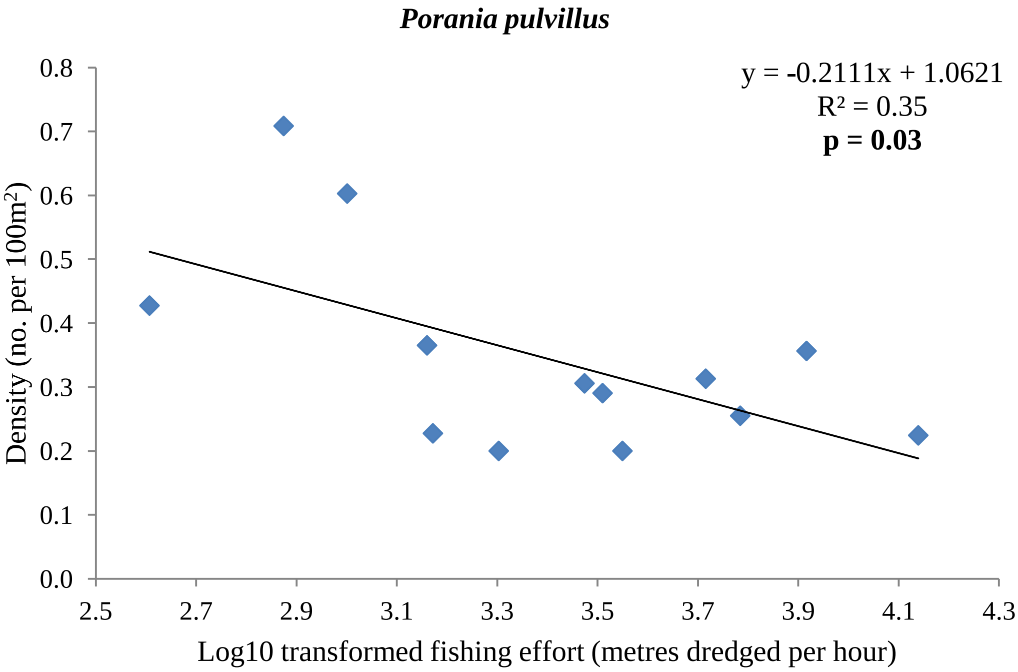


Figure 4.28 Linear regression analysis on the density of *Porania pulvillus* caught on Bradda Offshore and $\log^{10}$ transformed fishing effort lagged by 2 years. Fishing effort data were transformed to ensure normality and homogeneity. Species densities were calculated from queen dredge catch data obtained during the bi-annual scallop surveys conducted around the Isle of Man from 1992 – 2006 Note the different scale on each y-axis.

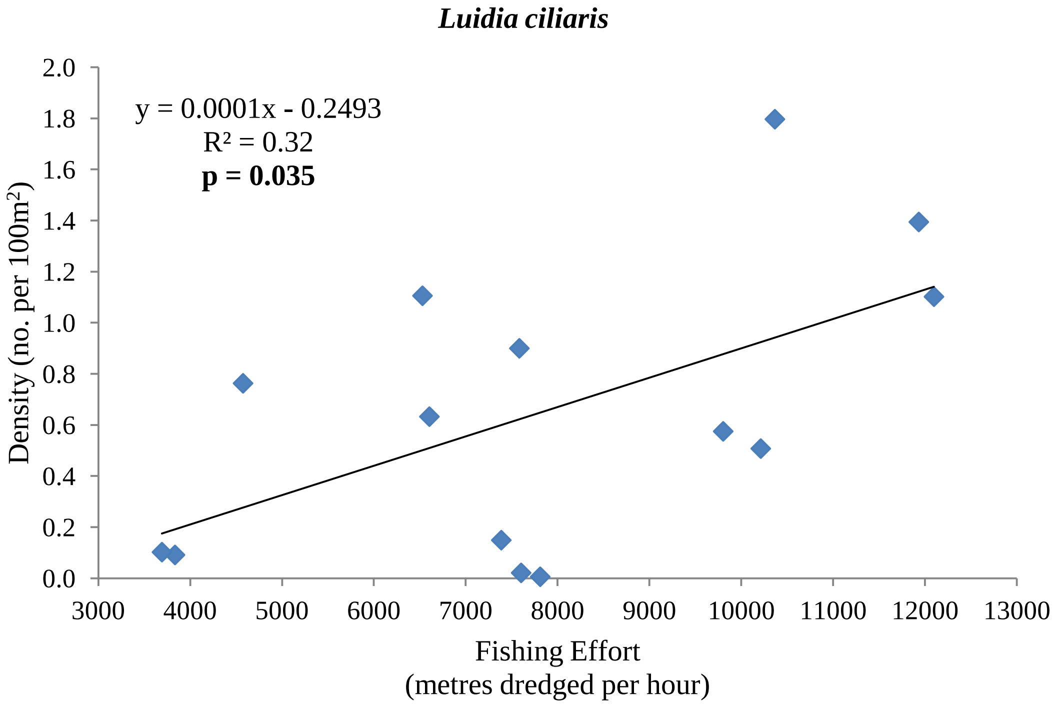


Figure 4.29 Linear regression analysis of *Luidia ciliaris* density and fishing effort lagged by 2 years at Peel fishing ground. Species densities were calculated from queen dredge catch data obtained during the bi-annual scallop surveys conducted around the Isle of Man from 1992 – 2006. Neither variable required transformation to meet normality and homogeneity of variance requirements nor were there any patterns in the residuals of this analysis. Note the truncated x-axis.

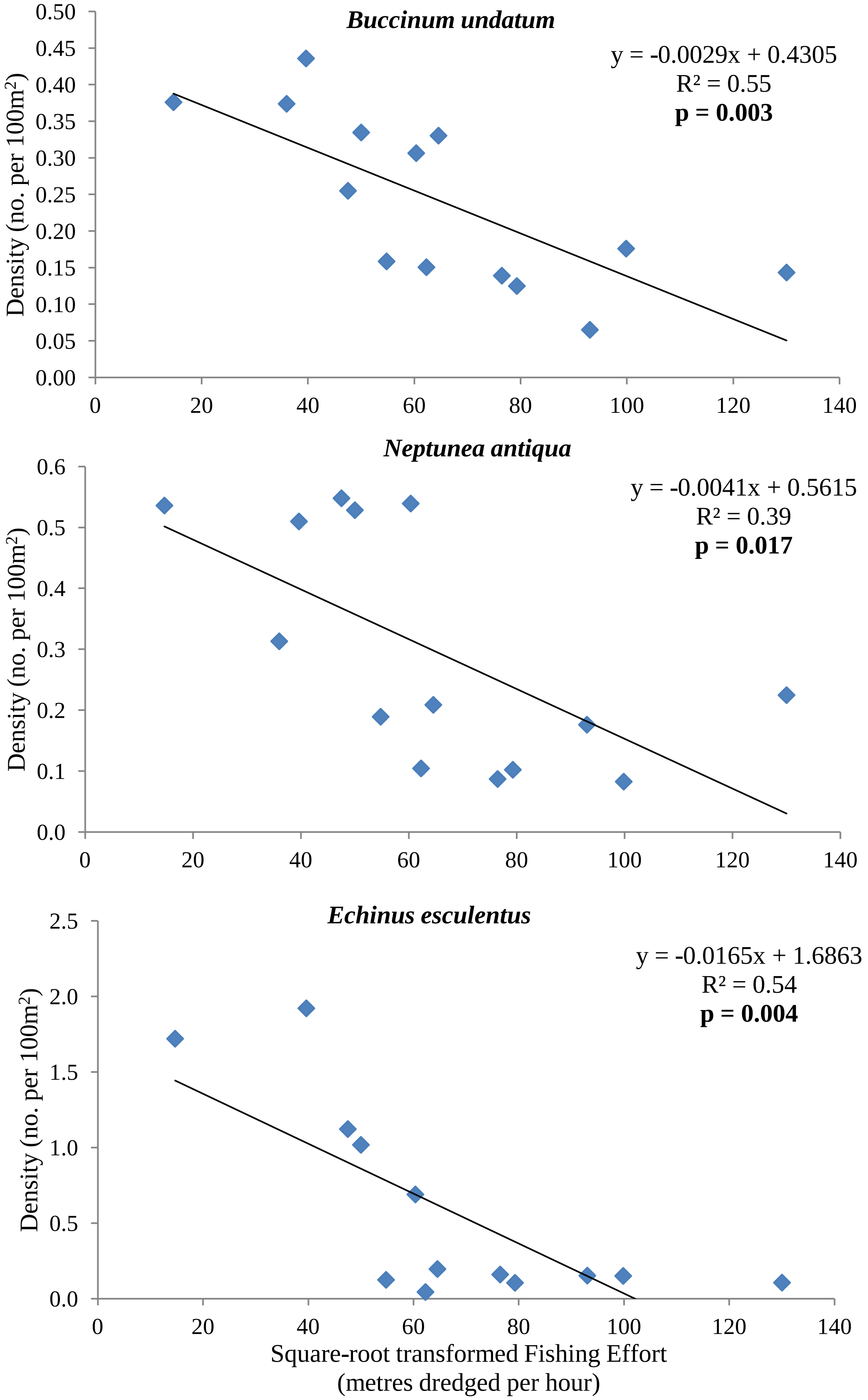


Figure 4.30 Linear regression analyses on the density of three benthic species found on East Douglas fishing ground and square-root transformed fishing effort lagged by 1 year. *Buccinum undatum*, *Neptunea antiqua* and *Echinus esculentus* densities all had significant negative linear relationships with square-root transformed fishing effort. Fishing effort data were transformed to ensure normality and homogeneity. Species densities were calculated from queen dredge catch data obtained during the bi-annual scallop surveys conducted around the Isle of Man from 1992 – 2006. Note the different scale on each y-axis.

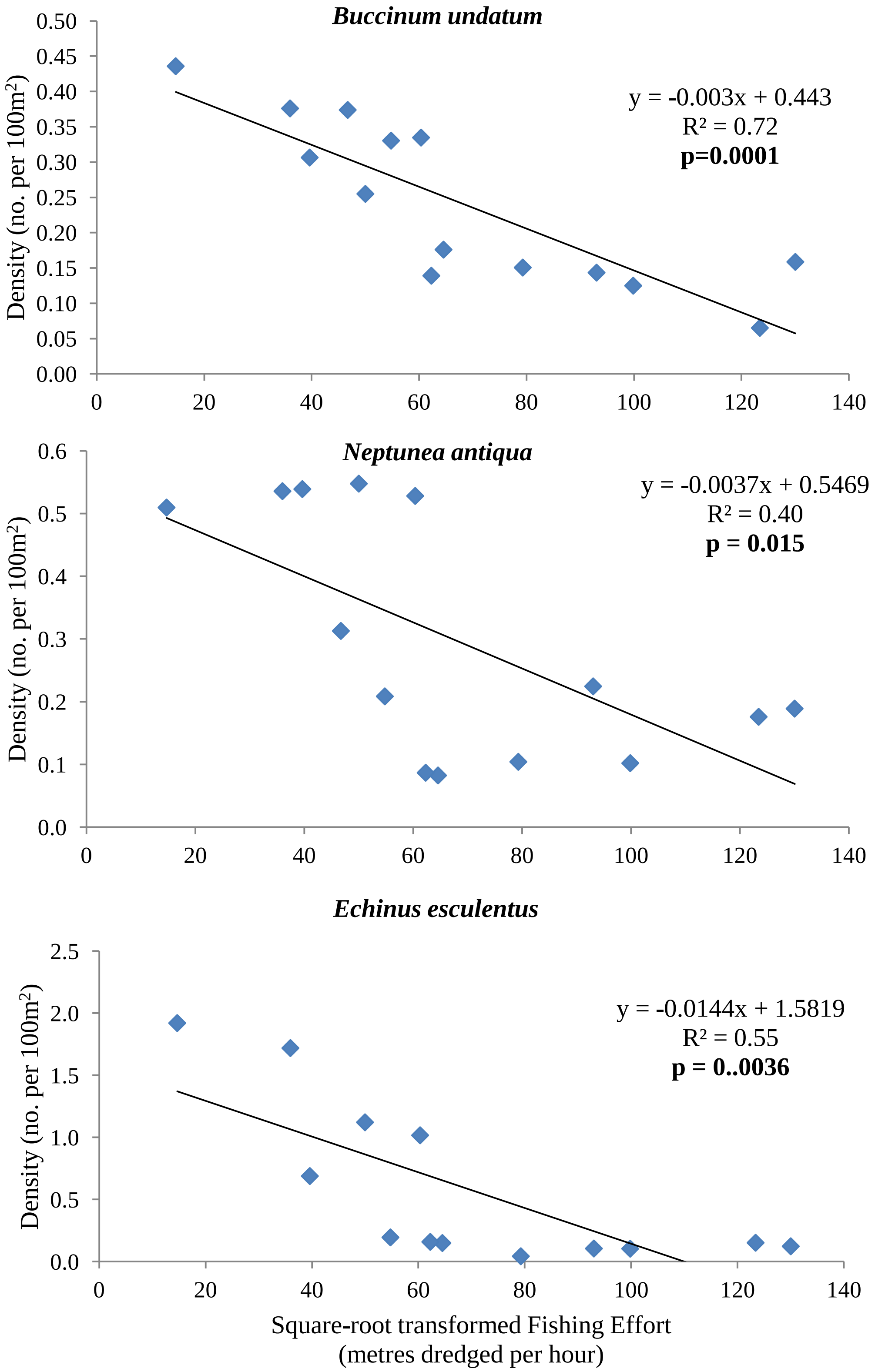
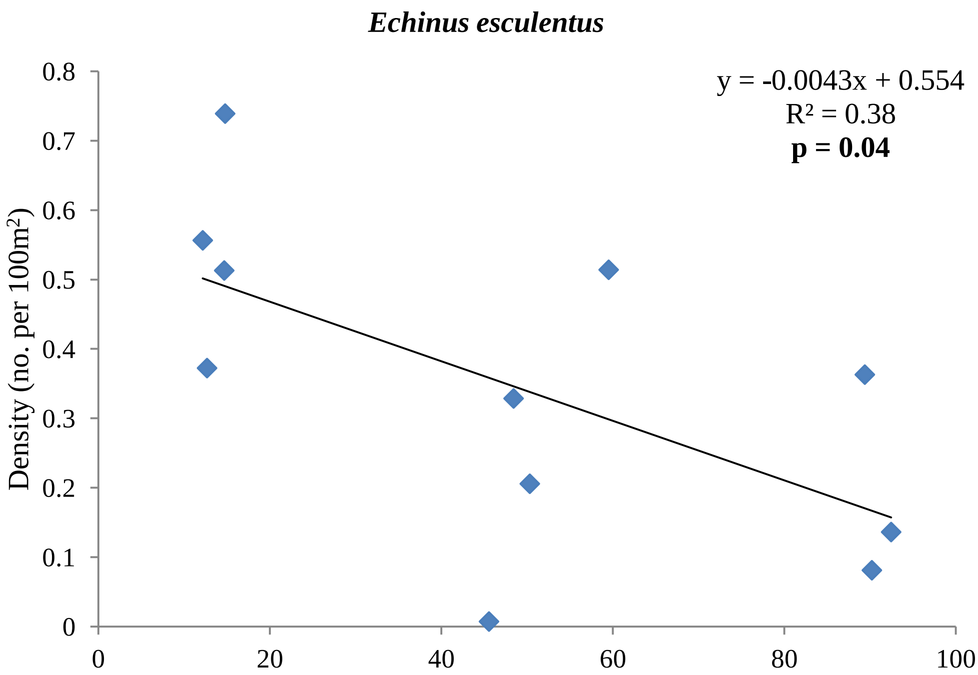


Figure 4.31 Linear regression analyses on the density of three benthic species found on East Douglas fishing ground and square-root transformed fishing effort lagged by 2 years. *Buccinum undatum*, *Neptunea antiqua* and *Echinus esculentus* densities all had significant negative linear relationships with square-root transformed fishing effort. Fishing effort data were transformed to ensure normality and homogeneity. Species densities were calculated from queen dredge catch data obtained during bi-annual scallop surveys conducted around the Isle of Man from 1992 – 2006. Note the different scale on each y-axis.


Echinus esculentus

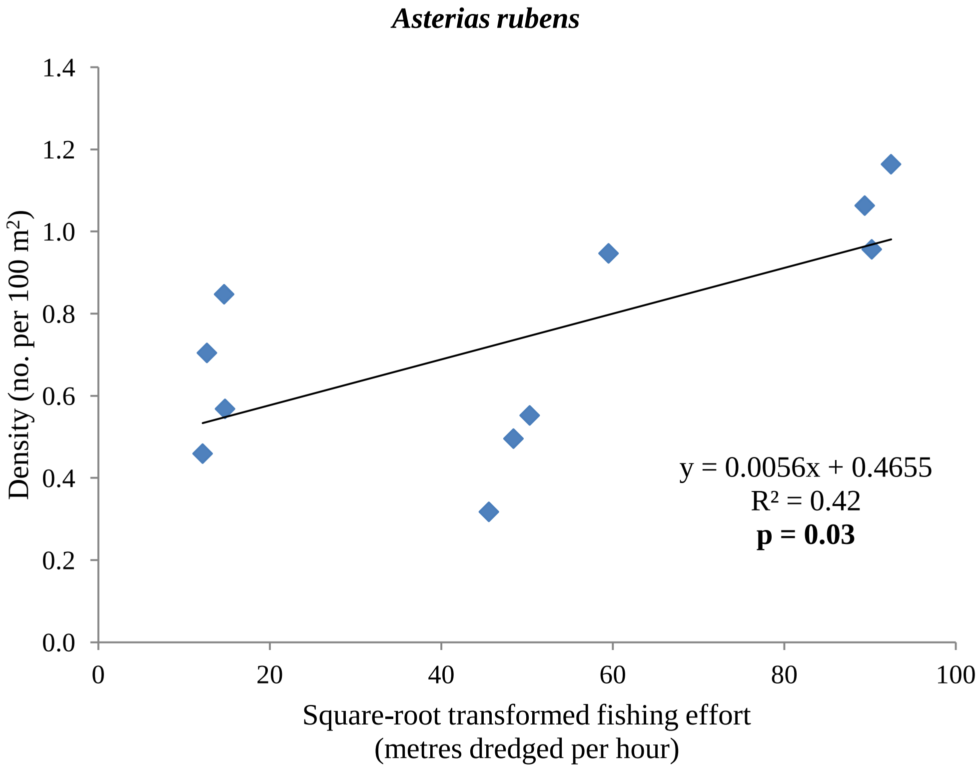

Asterias rubens

Figure 4.32 Linear regression analysis of two benthic invertebrate species density and square-root transformed fishing effort lagged by 2 years at Laxey fishing ground. *E. esculentus* has a significant negative relationship with transformed fishing effort (df = 9, F = 5.56, P = 0.04, R^2 = 0.38). *A. rubens* has a significant positive relationship with transformed fishing effort (df = 9, F = 6.5, P = 0.03, R^2 = 0.42) Species densities were calculated from queen dredge catch data obtained during the bi-annual scallop surveys conducted around the Isle of Man from 1992 – 2006. Note the different scales on the y-axes.

4.4.7 The effect of environmental variables on A. rubens density

Multiple linear regression analysis was performed on *A. rubens* density at three different fishing grounds off the south-west of the Isle of Man (Bradda Inshore, Bradda Offshore and Chickens). Data were analysed separately to prevent pseudo-replication of environmental variables (a result of including the environmental variables more than once in the same analysis). Environmental variables were lagged as was done for fishing effort data, and analyses were conducted on data with no lag, a 1 year lag and a 2 year lag. Each analysis underwent a Variance Inflation Factor (VIF) analysis prior to the multiple linear regression. In all cases no variables required removal as all VIF values were less than 3. Following multiple linear regression each model underwent an Akaike's Information Criterion (AIC) model selection procedure to create the optimum model for the data. All models were then validated to ensure no patterns in the residuals. In several instances significant relationships were found and are detailed below.

4.4.7.1 Bradda Inshore

No significant model was found when environmental variables were unlagged at Bradda Inshore. At a 1 year lag, however, model selection removed all variables apart from square-root transformed mean annual chlorophyll-α concentration (μg/L), which had a significant positive relationship with square-root transformed *A. rubens* density (df = 11, F = 48.6, $P < 0.0001$, $R^2 = 0.82$). At a two year lag, model selection left mean annual temperature as the only variable, which had a significant negative effect of square-root transformed *A. rubens* density (df = 10, F = 9.58, P = 0.01, $R^2 = 0.49$) (Figure 4.33).

4.4.7.2 Bradda Offshore

When environmental variables were unlagged at Bradda Offshore the pattern in *A. rubens* density was explained by the following model (df = 10, F = 6.68, P = 0.009, $R^2 = 0.57$) (Table 4.4).

(Equation 4.1)

Square root transformed density ~ mean annual temperature + winter NAO index + square root transformed mean annual chlorophyll-α

Table 4.4 Multiple linear regression results for square-root transformed mean annual *Asterias rubens* density (no. per $100m^2$) at Bradda Offshore from 1992 - 2006 modelled as a function of environmental variables with no time lag. Multiple $R^2 = 0.67$, Adjusted $R^2 = 0.57$, F-statistic = 6.68 on 3 and 10 *d.f.*, *P* = **0.009**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Temperature (^oC)	0.22	0.18	1.27	**0.23**
Mean Winter North Atlantic Oscillation Index	-0.12	0.07	-1.77	**0.11**
Square-root transformed mean annual Chlorophyll-α Concentration (µg/L)	2.32	0.54	4.29	**0.00**
Intercept	-4.56	2.39	-1.91	**0.09**

Multiple regression analysis with environmental variables lagged by 1 year, led to a model with just one significant variable: mean annual nitrate concentration (µM) was significantly positively correlated with square-root transformed *A. rubens* density (df = 11, F = 6.64, P = 0.03, $R^2 = 0.38$) (Figure 4.34). No significant model was found for environmental data lagged by 2 years at Bradda Offshore.

4.4.7.3 Chickens

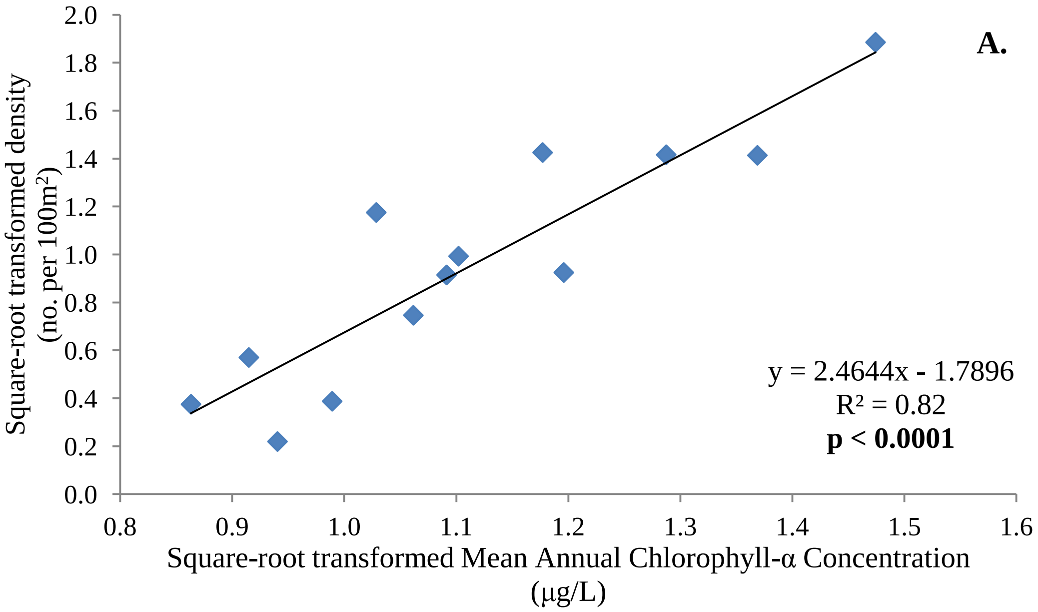
When environmental variables were unlagged the model in equation 4.2 explained the variation in square-root transformed *A. rubens* density at Chickens fishing ground (df = 10, F = 6.53, P = 0.01, $R^2 = 0.66$) (Table 4.5).

(Equation 4.2)

Square root transformed density ~ mean annual temperature + mean annual nitrate concentration + square root transformed mean annual chlorophyll-α

Table 4.5 Multiple linear regression results for square-root transformed mean annual *Asterias rubens* density (no. per $100m^2$) at Chickens from 1992 - 2006 modelled as a function of environmental variables with no time lag. Multiple $R^2 = 0.66$, Adjusted $R^2 = 0.56$, F-statistic = 6.53 on 3 and 10 *d.f.*, *P* = **0.01**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Temperature (^oC)	0.36	0.17	2.04	**0.07**
Mean Annual Nitrate Concentration (µM)	0.22	0.15	1.45	**0.18**
Square-root transformed mean annual Chlorophyll-α Concentration (µg/L)	1.75	0.46	3.82	**0.00**
Intercept	-6.11	2.58	-2.37	**0.04**



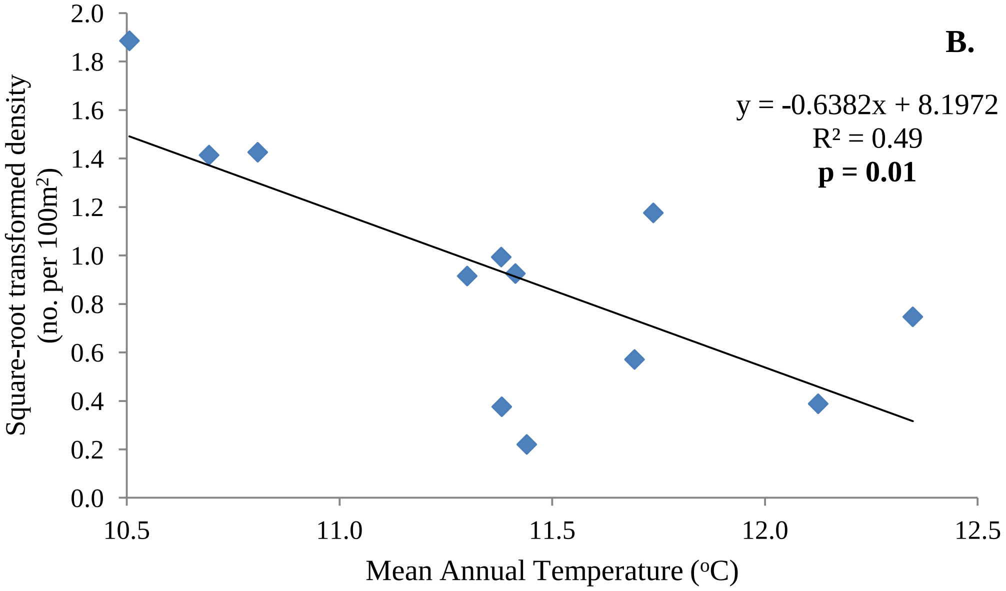


Figure 4.33 The relationship between square-root transformed *Asterias rubens* density (no. per 100m^2) at Bradda Inshore and (A.) square-root transformed mean annual chlorophyll-α concentration (µg/L) lagged by 1 year and (B.) mean annual temperature (^{o}C) lagged by 2 years. Density data were calculated from queen dredge catch data collected from 1992 – 2006, during bi-annual scallop surveys around the Isle of Man. Data were transformed to ensure normality and homogeneity of variances. Note the shortened y-axis on both graphs.

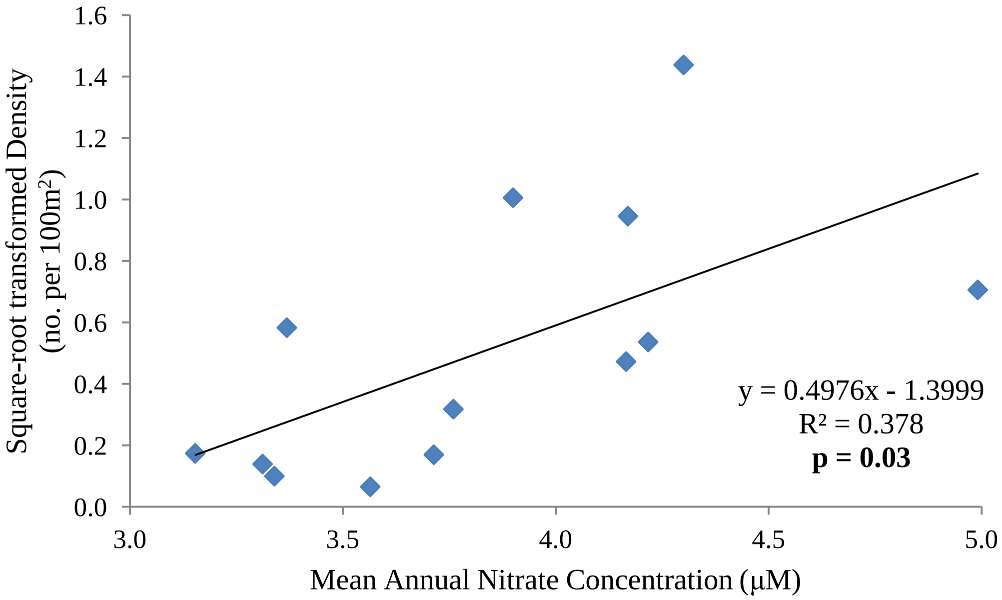


Figure 4.34 Significant positive linear relationship between square-root transformed *Asterias rubens* density (no. per 100m^2) and mean annual nitrate concentration (µM) lagged by 1 year. Density data was calculated from queen dredge catch data collected from Bradda Offshore from 1992 – 2006. Note the shortened x-axis.

4.4.8 The effect of environmental variables on P. pulvillus density

Multiple linear regression analysis was performed on *P. pulvillus* density at three different fishing grounds found on the south-west of the Isle of Man (Bradda Inshore, Bradda Offshore and Chickens). Data were analysed separately to prevent pseudo-replication of environmental variables. Environmental variables were lagged as fishing effort data and analyses were conducted on data with no lag, a 1 year lag and a 2 year lag. Each analysis underwent a Variance Inflation Factor (VIF) analysis prior to the multiple linear regression. In all cases no variables required removal all VIF were less than 3. Following multiple linear regression each model underwent an AIC model selection procedure to create the optimum model for the data. All models were then validated to ensure no patterns in the residuals. In several instances significant relationships were found and are detailed below.

4.4.8.1 Bradda Inshore

P. pulvillus densities were square- root transformed in all three time lags at Bradda Inshore. Transformed density data had a significant relationship with both mean annual temperature (^{o}C) and square-root transformed mean annual chlorophyll-α concentration (µg/L) when environmental data remained unlagged (df = 10, F = 7.85, p <0.01, R^2 = 0.61) (Table 4.6). When environmental variables were lagged by 1 year mean annual nitrate concentration (µM) and mean winter NAO index had a significant relationship with transformed *P. pulvillus* density (df = 10, F = 9.08, P < 0.01, R^2 = 0.65) (Table 4.7). When variables were lagged by 2 years, model selection removed all variables but mean annual temperature (^{o}C), which had a significant negative relationship with transformed *P. pulvillus* density (Figure 4.35A.) (df = 10, F = 9.61, P = 0.01, R^2 = 0.49).

Table 4.6 Multiple linear regression results for square-root transformed mean annual *Porania pulvillus* density (no. per 100m^2) at Bradda Inshore from 1992 - 2006 modelled as a function of environmental variables with no time lag. Multiple R^2 = 0.61, Adjusted R^2 = 0.53, F-statistic = 7.853 on 3 and 10 *d.f., P* = **0.0089**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Temperature (^{o}C)	-0.09	0.05	-1.76	**0.11**
Square-root transformed mean annual Chlorophyll-α Concentration (µg/L)	0.29	0.15	2.00	**0.01**
Intercept	1.02	0.66	1.53	**0.16**

Table 4.7 Multiple linear regression results for square-root transformed mean annual *Porania pulvillus* density (no. per 100m^2) at Bradda Inshore from 1992 - 2006 modelled as a function of environmental variables with a 1 year time lag. Multiple R^2 = 0.65, Adjusted R^2 = 0.57, F-statistic = 9.082 on 2 and 10 *d.f., P* = **0.0056**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Nitrate Concentration (µM)	0.14	0.04	3.51	**0.01**
Mean Winter North Atlantic Oscillation Index	0.04	0.02	2.36	**0.04**
Intercept	-0.21	0.15	-1.37	**0.20**

4.4.8.2 Bradda Offshore

P. pulvillus densities were square-root transformed in all three time lags at Bradda Offshore. Significant relationships between environmental variables and transformed *P. pulvillus* densities were found at all three time lags. When environmental variables were unlagged, square-root transformed mean annual chlorophyll-α concentration (µg/L) had a significant positive relationship with transformed *P. pulvillus* density (Figure 4.36) (df = 11, F = 14.35, P < 0.01 , R^2= 0.57). At a 1 year lag two variables had a significant relationship with transformed *P. pulvillus* density, mean annual nitrate concentration (µM) and square-root transformed chlorophyll-α concentration (µg/L) (Table 4.8) (df = 10, F = 14.07, P < 0.01, R^2 = 0.74). The optimum model when variables were lagged by two years was, as found at Bradda Inshore, a significant negative relationship between transformed *P. pulvillus* density and mean annual temperature (^{o}C) (Figure 4.35B) (df = 10, F = 15.38, P < 0.01, R^2 = 0.61).

Table 4.8 Multiple linear regression results for square-root transformed mean annual *Porania pulvillus* density (no. per 100m^2) at Bradda Offshore from 1992 - 2006 modelled as a function of environmental variables with a 1 year time lag. Multiple R^2 = 0.74, Adjusted R^2 = 0.69, F-statistic = 14.07 on 2 and 10 *d.f., P* = **0.0012**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Nitrate Concentration (µM)	0.08	0.04	1.99	**0.07**
Square-root transformed mean annual Chlorophyll-α Concentration (µg/L)	0.43	0.12	3.51	**0.01**
Intercept	-0.23	0.16	-1.43	**0.18**

4.4.8.3 Chickens

No significant relationships between *P. pulvillus* density and any environmental variables at any time lag were found at Chickens fishing ground.

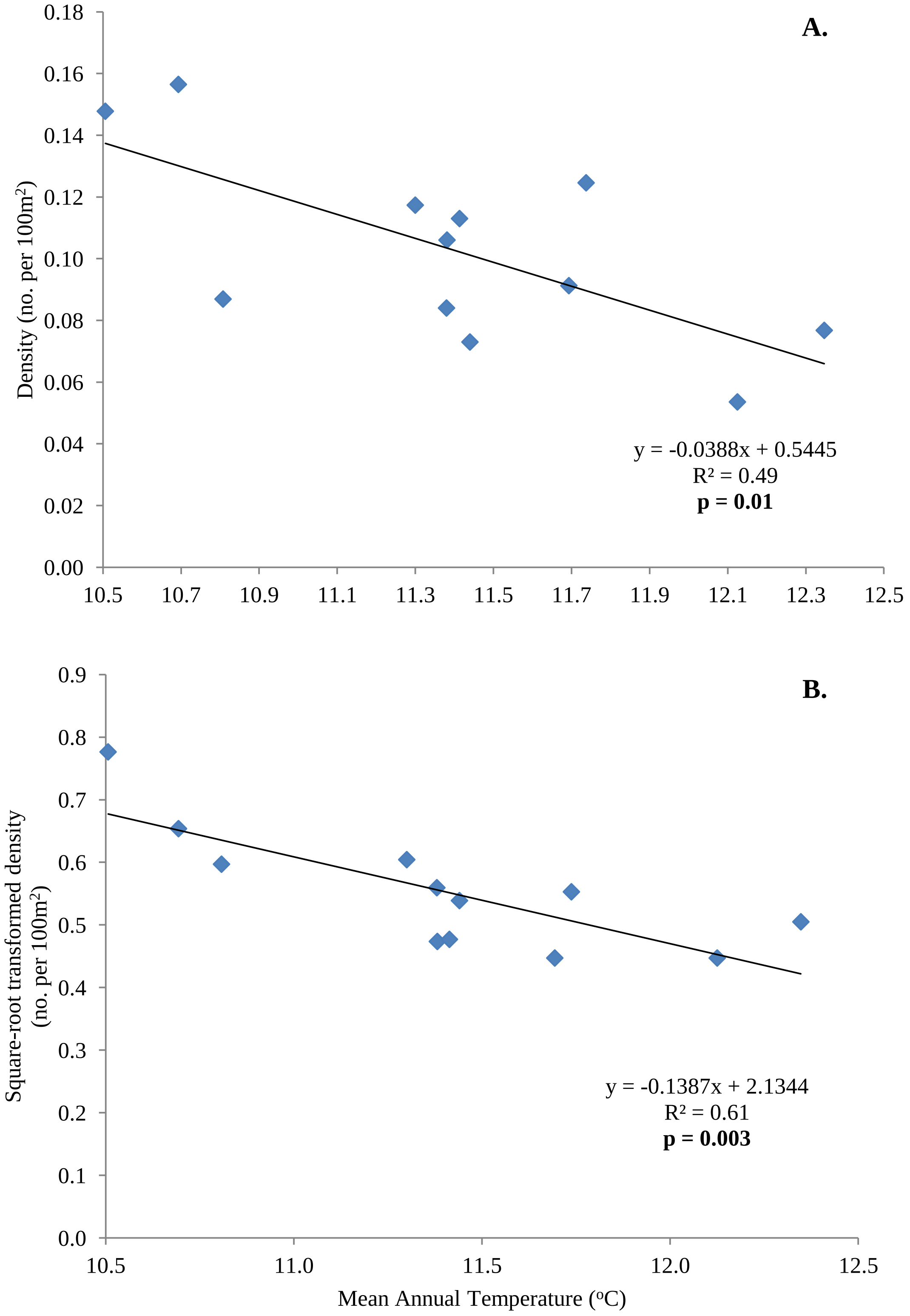


Figure 4.35 The relationship between mean annual temperature (°C) lagged by 2 years and (A.) *Porania pulvillus* density (no. per 100m^2) at Bradda Inshore and (B.) square-root transformed *Porania pulvillus* density (no. per 100m^2) at Bradda Offshore. At both sites a significant negative linear relationship was found. Density data were calculated from bycatch abundances that were collected during bi-annual scallop surveys around the Isle of Man from 1992 to 2006, inclusive. Data were transformed to ensure normality and homogeneity of variance. Note the shortened x-axis on both graphs.

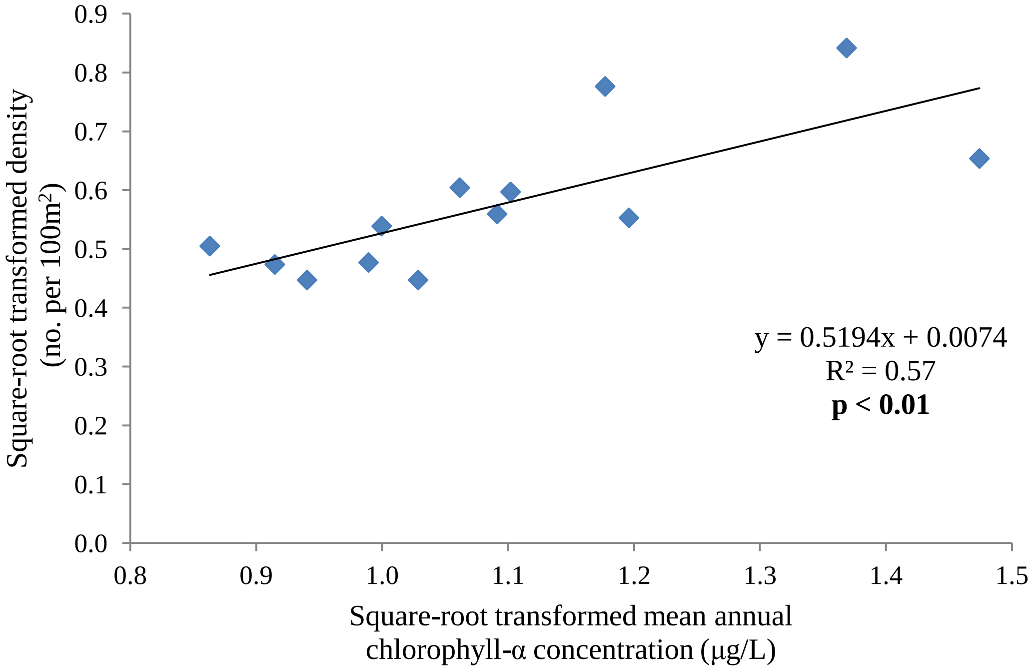


Figure 4.36 The significant positive linear relationship between transformed *Porania pulvillus* density (no. per 100m^2) and un-lagged, transformed mean annual chlorophyll-α concentration (µg/L) at Bradda Offshore. Density data was calculated from queen dredge catch data collected from Bradda Offshore from 1992 – 2006. Data were transformed to ensure normality and homogeneity of variance. Note the truncated x –axis.

4.5 Discussion

This study outlines the composition of the epibenthic invertebrates caught in queen dredges at eight different fishing grounds around the Isle of Man over the course of fourteen years. The composition of catches showed considerable spatial and temporal variation and these fluctuations have been linked in part to fishing effort and certain environmental variables. The species assemblages observed in this study broadly correspond to those that have been observed by other studies around the Isle of Man (Mackie 1990, Hill, Brand et al. 1997, Hill, Veale et al. 1999, Veale, Hill et al. 2001, Bradshaw, Veale et al. 2002) As found by Veale et al (2001) there appears to be two distinct benthic assemblages, one centred off the south-west coast of the Isle of Man, and the other on the remaining fishing grounds to the north, south and east of the island. The proportional graphs (Figures 4.2 – 4.9) show that in addition to the target species *Pecten maximus,* catches on all grounds were dominated by echinoderms and in particular *Asterias rubens*. Throughout the time series (1992 – 2006) the south-western fishing grounds, Bradda Inshore, Bradda Offshore, Peel and to a lesser extent Chickens, had similar species compositions, which were dominated by *Pecten maximus*, (the target species of the fishery) and *A. rubens*. *Porania pulvillus*, *Luidia ciliaris*, *Astropecten irregularis* and *Cancer pagurus* were also common species found at Bradda Inshore, Bradda Offshore and Peel (Figures 4.2, 4.3 and 4.5). Chickens fishing ground had a high proportion of the urchin *Echinus esculentus* present in the first half of this study (1992 – 2000). Another interesting pattern that occurred at the south western fishing grounds (apart from Peel) was an increase in the proportion of the catch containing the queen scallop, *Aequipecten opercularis,* in the latter half of the times series (2000 – 2006). At Chickens, *A. opercularis* went from not being present from 1992 to 1995, to becoming 80% of the catch in 2006. This influx of queen scallops is thought to be because of a particularly high recruitment in the latter half of the times series, which so far has not been explained (Murray and Kaiser 2012). The remaining fishing grounds (East Douglas, Laxey, South PSM and Targets) showed a notable absence of large quantities *P. pulvillus* and *L. ciliaris*. Unlike the south western grounds, these four fishing grounds had present the whelk species' *Buccinum undatum* and *Neptunea antiqua*, several members of the genus *Pagurus* (combined into the category *Pagurus spp*) and a higher proportion of *E. esculentus* (Figures 4.6 – 4.8).

The differences seen between the catch composition at each fishing ground could be caused by many different factors, including differences in substrata and hydrography (Veale, Hill et al. 2001). The sediments of the south-western grounds tend to contain more sand and less gravel than the other grounds (Holt, Fisher et al. 1990, Veale, Hill et al. 2001). Equally the environmental conditions of the water column differ on the eastern and western sides of the Isle of Man (Evans, Williams et al. 2003, Gowen and Stewart 2005). The western Irish Sea has a seasonal gyre, which may influence the retention of planktonic larvae of a number of benthic species on that side of the island (Hill, Brown et al. 1997, Veale, Hill et al. 2001). It is also likely that these observed differences in benthic invertebrate species are a result of differential exposure to fishing pressure, both directly and indirectly (Veale, Hill et al. 2001). The great scallop grounds to the south and west of the Isle of Man have been heavily exploited since 1937 and there have been observed long-term changes in both the benthic community composition and sediment size at these grounds (Brand, Allison et al. 1991, Brand 1999, Veale, Hill et al. 2001, Bradshaw, Veale et al. 2002). The species that were found at these south-western grounds in this investigation have all been found to be relatively tolerant to scallop dredging. *A. rubens* and *P. pulvillus* were both found to be relatively undamaged by scallop dredges, whether they were collected as bycatch or left in dredge track (Jenkins, Beukers-Stewart et al. 2001, Jenkins and Brand 2001). Jenkins et al (2001) also found *L. ciliari, A. irregularis* and *Crossaster papposus* suffered low levels of damage during scallop dredging. Therefore the fact that these species were dominant on the fishing grounds that have been exposed to the heaviest fishing pressure for the longest period of time fits with the theory that the benthic communities at these grounds are composed of dredge-tolerant species (Bradshaw, Veale et al. 2002).

Figure 4.10 shows overall density of all species caught in the queen dredges , the south-western grounds Peel, Bradda Inshore and Bradda Offshore had the lowest overall density of benthic invertebrates (less than 5 individuals per 100m^2). Chickens also generally had a similarly low density of overall benthic invertebrates; however the *A. opercularis* recruitment seen in the latter half of the time series seems to have led to the peaks seen in 2002 (Vause, Beukers-Stewart et al. 2007) and also 2006. Overall benthic invertebrate density was higher at the rest of grounds around the Isle of Man, with densities peaking in the latter half of the time series. These peaks were the result of large *A. opercularis* recruitment events, which are discussed in more detail below (Figure 4.10).

In total seven species were chosen to study in more detail, the choice was made based on the widespread occurrence of each species around the Isle of Man and those that were of ecological interest. The analysis of the temporal trends in each species' density showed that some species had consistent trends across the grounds they were found, for example, *L. ciliaris* density increased significantly over time at all three grounds in the south west that it was found at (Peel, Bradda Inshore and Bradda Offshore). Likewise, *N. antiqua* density significantly decreased at both Laxey and East Douglas. Whilst other species had inconsistent patterns in density over the course of the time series: *A. rubens* significantly decreased at Bradda Inshore and East Douglas, but showed no significant pattern at any other ground. *P. pulvillus* significantly decreased in density at Bradda Inshore and Bradda Offshore, but showed no significant pattern at Chickens fishing ground. *E. esculentus* density significantly decreased at Bradda Inshore, Chickens and East Douglas and showed no significant trend at South PSM, Laxey and Targets. Although at Targets *E. esculentus* was found at densities of 3 per 100m^2 from 1993 – 1996, then density dropped to less than 1 per 100m^2 for the remainder of the time series.

The temporal patterns seen in the density of species at Laxey and East Douglas go some way to explain the observed significant downward temporal trend seen in the diversity indices in Chapter 3. The reduction in diversity at Laxey seems to have been driven by the large recruitment event of *A. opercularis* seen in 2004 and 2005 (Figure 4.23). *A. opercularis* density fluctuated around 5 to 10 per 100m^2 for the majority of the time series but then in 2004 and 2005 increased to more than 20 per 100m^2. The reason for this sudden increase is thought to be because of a particularly successful recruitment event, which has yet to be explained, despite being studied in some detail (Murray and Kaiser 2012). This recruitment event meant that the community was dominated by one species, therefore reducing the diversity indices studied in the first chapter. East Douglas on the other hand, saw a significant decrease in the density of four out of the five species studied (*A. rubens, E. esculentus, N.antiqua* and *B. undatum*), with only *A. opercularis* showing no significant trend. These significant decreases seem a likely reason for the significant decrease in Simpsons' diversity index seen for this site in the last chapter. Although an analysis of effect of environmental variables on species densities could not be done for East Douglas, the effect of fishing effort was analysed and is discussed below.

4.5.1 Queen scallop recruitment events

An interesting pattern that was found across all grounds in the latter half of the time series (from 2000 onwards) was an increase in *A. opercularis* densities. Although it should be noted that the density *A. opercularis* differed greatly between grounds: at Bradda Inshore and Bradda Offshore densities remained around 1 per 100m^2, whereas density at East Douglas, Laxey and Chickens varied from 10 to 25 per 100m^2. The differences highlight which grounds are traditional queen scallop fishing grounds and which are great scallop fishing grounds. These recruitment events are not uncommon in the Isle of Man queen scallop population, where great fluctuations in population density have been found before (Vause, Beukers-Stewart et al. 2007). The location of the parent stock for each ground remains unknown and it is thought that oceanographic features play a major role in the success of the *A. opercularis* populations (Vause, Beukers-Stewart et al. 2007). Attempts have been made to use particle tracking models to identify the sources and sinks for *A. opercularis* around the Isle of Man, but no definitive conclusions have been reached (Neill and Kaiser 2008). It therefore seems that environmental conditions were favourable for the recruitment of *A. opercularis* throughout the latter part of this study. A stock assessment for *A. opercularis* was conducted after the time series of this study and found that *A. opercularis* abundance also continued to increase sharply after 2007 (Murray and Kaiser 2012).

4.5.2 Effect of fishing effort

This spatial heterogeneity of benthic invertebrate species around the Isle of Man makes predictions about the effects of anthropogenic activities difficult to make on a large scale. The fishing effort analysis done in this study shows that certain grounds were more impacted by fishing pressure than others between 1992 and 2006. The broad analysis of each species across all fishing grounds showed that *E. esculentus* was the only species to have a negative relationship with square-root transformed fishing effort. However the R^2 values were all low, indicating that fishing effort only explained 10% or less of the pattern in the data at each of the three time lags. As a relatively fragile animal this negative relationship with fishing effort confirms predictions from short term studies which have shown this species suffers relatively large amounts of damage in scallop dredges (Kaiser, Hill et al. 1996, Collie, Escanero et al. 1997, Brand 1999, Hall-Spencer and Moore 2000, Jenkins, Beukers-Stewart et al. 2001, Veale, Hill et al. 2001). The small R^2 values suggest that the impact of scallop dredging differs between fishing grounds, perhaps because of differences in substrata. Veale et al (2001) found a correlation between the volume of stones in the catch of scallop dredges and damage to *E. esculentus*. Therefore fishing grounds with a stonier substrate (those on the east coast) could possibly be causing greater damage to this sensitive species.

At East Douglas and Bradda Offshore, *E. esculentus* density had a significant negative relationship with transformed fishing effort lagged by 1 year and 2 years. The R^2 values are very similar for each time lag, suggesting that recovery from fishing impact takes more than a single year. At Laxey *E. esculentus* had a significant negative relationship with transformed fishing effort when lagged by 2 years. At Bradda Inshore, *E. esculentus* density had a significant negative relationship with unlagged fishing effort. At Chickens, Targets and South PSM there was no significant relationship between fishing effort and *E. esculentus* density. It should be noted, however, that *E. esculentus* density dropped sharply in the middle of the time series from 3 per $100m^2$ to less than 0.01 per $100m^2$, coinciding with a particularly high level of fishing effort. There is no information about the exact composition of the substrata at each ground for every year of this study, however on a broad scale Chickens, Targets and South PSM are characterised as having benthic substrates that are composed of sand and gravel (Hinz, Murray et al. 2009). The substrate at East Douglas and Laxey is primarily sand, with areas of gravel and shell (Hinz, Murray et al. 2009). Bradda Inshore and Bradda Offshore have substrates that are classified as sand or fine sand and mud (Hinz, Murray et al. 2009). Given that the results in this study do not correspond with the underlying substrate type in the way that Veale et al (2001) found, it is possible that the grounds with negative relationships between *E. esculentus* density and fishing effort in this study had a higher proportion of stones than those that showed no relationship.

The effect of fishing effort on other species' densities was also variable. *B. undatum* and *N. antiqua* showed significant negative relationships with square-root transformed fishing effort lagged by both 1 and 2 years at East Douglas. This relationship was expected for *B. undatum* because it has been found to be more vulnerable to predation following disturbance by scallop dredges (Ramsay and Kaiser 1998). *N. antiqua* is thought to be reasonably resilient to the effects of scallop dredging, therefore perhaps the relationship is due to a negative impact on the egg masses of this whelk species, known to be vulnerable to scallop dredges (Veale, Hill et al. 2001). Perhaps there is some interaction occurring with dredge fullness, a factor which is known to increase damage to *B. undatum* (Veale, Hill et al. 2001). However, the relationship between effort and whelk density was not replicated at any other site where the species were found. It is possible that the queen scallop fishery, which is predominant at this ground, could be responsible, although fishing effort did not have this effect on *N. antiqua* at Laxey. As effort of the queen dredge fishery remains unquantified in this study it is not possible to make more than general inferences about any affect it may have had on benthic species in this study.

At Peel a significant positive relationship was found between fishing effort and *L. cilaris* density, but again this relationship was not found at any of the other grounds where *L. ciliaris* was found. The results from this analysis at Peel should be treated with caution because it has subsequently come to light that there is a mis-match between where the scallop surveys were conducted and where the main fishery occurred (B. Stewart, pers. comm.). Although both activities occur within the same 5x5nm logbook square, the fishery occurred predominantly in the offshore part of this square and the surveys were conducted in the inshore part of the square. However, a possible reason for this relationship at Peel, could be predator-prey responses on a relatively species poor ground. *L. ciliaris* is a carnivore and targets, among other species, *A. rubens*, which is known to scavenge on dredge spoil after scallop dredging (Ramsay, Kaiser et al. 1998, Thrush, Hewitt et al. 1998, Bradshaw, Veale et al. 2002, Jenkins, Mullen et al. 2004). Likewise any relationship between *A. rubens* density and fishing effort at Peel, could be masked by this predator-prey interaction. *L. ciliaris* showed a significant increase in density over the course of the time series, whilst *A. rubens* showed no significant pattern. Interestingly at Laxey (a ground where *L. ciliaris* is not a large part of the community) *A. rubens* density had a significant positive relationship with square root transformed fishing effort lagged by 2 years. Although this pattern was not repeated on any of the other grounds, suggesting a less straight-forward reason, such as confounding environmental factors or predator-prey relationships, which are not investigated here.

P. pulvillus density had a significant negative relationship with transformed fishing effort lagged by 2 years at Bradda Offshore. Again this relationship was not repeated at Chickens or Bradda Inshore, however Bradda Offshore is a deeper fishing ground, and this may have played a role. In a study investigating dredging for clams, it was found that depth played a role in the impact of the dredge on benthic communities, with deeper sites taking longer to recover (Constantino, Gaspar et al. 2009). This is thought to be in part because benthic communities in deeper environments experience fewer natural disturbance events and so are less resilient to them (Constantino, Gaspar et al. 2009). This is unlikely in this study as the benthic community on Bradda Offshore has experienced scallop dredging for several decades. However, the effect of depth could mean that growth rates are slower, which would also explain longer recovery rates in deeper communities (Constantino, Gaspar et al. 2009). It is possible that additional environmental factors are confounding the responses to fishing pressure, which are discussed below.

Overall it seems that fishing effort does not have a particularly strong relationship with many of the benthic invertebrate species studied here. It is possible that this is because, as was found by Bradshaw et al (2002) the communities here are composed of species that are relatively dredge-tolerant. The only species that showed declines at more than one site was *E. esculentus*, which is a fragile-bodied organism. The rest of the species studied seem to be relatively hardy to the effect of fishing. East Douglas appears to be the ground most affected by fishing pressure, with three out of five species studied having a significant negative relationship with fishing effort. This suggests that there is a differential effect of fishing pressure between the grounds around the Isle of Man.

4.5.3 Effect of environmental variables on two benthic species

Two species were selected for an investigation into the effects of environmental variables on species density. *A. rubens* was chosen because it was a ubiquitous part of the benthic community at all grounds around the Isle of Man and also because quite a lot of published work has investigated this species. *P. pulvillus* was chosen because there are relatively few published studies investigating this species and because it was present at the three sites to be investigated at a reasonable density. The environmental data used in this study came from the CYPRIS sampling station found off the south-west of the island. This data is only comparable with grounds on the western side of the island, as environmental conditions are known to differ on the eastern side (Evans, Williams et al. 2003, Gowen and Stewart 2005). Therefore density data from Chickens, Bradda Inshore and Bradda Offshore was used in this analysis. Each ground was analysed individually for any relationships between the two chosen species and environmental variables at three different time lags.

A. rubens density showed different relationships with different environmental variables at each time lag and at each ground. At Bradda Inshore, there was no significant relationship when no time lag was applied, but a 1 year lag saw a significant positive relationship with mean annual chlorophyll-α (both were square-root transformed). When environmental variables were lagged by 2 years *A. rubens* had a significant negative relationship with mean annual temperature at Bradda Inshore. It is possible that these effects are an artefact in the data, because both mean annual temperature and mean annual chlorophyll-α concentration showed significant temporal trends over the course of this time series (Chapter 3). However, to reduce the possibility of autocorrelation in this analysis the *p*-value significance threshold was lowered from 0.05 to 0.01. The relationship with chlorophyll-α concentration had a *p*-value of <0.0001 and with temperature, a *p*-value of 0.01. Therefore even after taking autocorrelation issues into account, both of these models were significant. It should also be noted that similar relationships were not found for *A. rubens* density at Bradda Offshore or Chickens. Although both grounds did have significant models with multiple unlagged environmental variables (Table 4.4 and 4.5), the only variable to show a significant (p=0.01) relationship was chlorophyll-α, which again had a positive effect on *A. rubens* density.

The relationship between chlorophyll-α and *A.rubens* density seen in this study could be an effect seen in the larval phase of its life. *A. rubens* have a planktotrophic larval stage, present from March to April when it is herbivorous, turning carnivorous from May through to July (Barker and Nichols 1983, Villalobos, Tyler et al. 2006). A reduction in available plankton during the initial herbivorous larvae stage may be the mechanism that explains this observed relationship. However, further investigation within a laboratory would be required to confirm this. Settlement out of the plankton usually takes around 80 days and after about 2 more weeks there is a juvenile starfish, capable of feeding (Barker and Nichols 1983). Given another year to grow and *A. rubens* would begin to appear in the bycatch (Bryce Stewart, pers. comms), meaning the observed time lag of 1 year is appropriate for this potential mechanism. A similar relationship has been found for the crown-of-thorns starfish (*Acanthaster planci*) larval development, growth and survival , which increases almost ten-fold with a doubling of the concentration of some phyto-plankton species (Brodie, Fabricius et al. 2005)

The relationship between *A. rubens* density and temperature at Bradda Inshore is less clear. There is evidence that *A. rubens* are relatively hardy to temperature changes, with feeding rates increasing with temperature (Agüera, Trommelen et al. 2012). Field and laboratory experiments have suggested that optimal feeding temperature for *A. rubens* is between 10^{o}c and 13^{o}c (Hancock 1955, Agüera, Trommelen et al. 2012). The observed increase in mean annual temperature over the course of this time series did not ever go higher than 10.5^{o}C, although temperature fluctuates from 7^{o}C to 15^{o}C over the course of each year. This fluctuation is a consistent feature of the time series, therefore it is unlikely that the *A. rubens* at Bradda Inshore are exhibiting a negative effect of temperature on feeding habitats. It is possible that temperature is playing a role at some other key life history stage, such as settlement or reproduction, but the mechanism for this remains unknown and further species specific investigations are required. It is also possible that this trend is in fact an indirect negative effect of temperature brought about because of the negative correlation found between temperature and chlorophyll-α (Chapter 3).

There are few published studies on the cushion star *P.pulvillus*, and although it's known to be resilient to the effects of scallop dredging (Veale, Hill et al. 2001) there have been almost no studies looking at this species response to environmental variables. *P. pulvillus* is a detritivore and has been witnessed feeding on the octcoral *Alcyonium digitatum*, several species of ascidians and a species of brachipod in Sweden (Ericsson and Hansson 1973). *P. pulvillus* have a similar reproductive strategy to *A.rubens* and are broadcast spawners (Gemmill 1915, Bosch 1989). However this is about all that is know about this species life history, it is likely that it is predated on by *L. ciliaris* and *C. Pagurus*, both of which predate on other Asteroid species (Brun 1972, Ramsay, Kaiser et al. 1998).

In this study a significant negative relationship between *P. pulvillus* density and mean annual temperature lagged by 2 years was found at both Bradda Inshore and Bradda Offshore. This relationship was not found at Chickens, where there were no significant relationships with any environmental variables at any time lag. At a 1 year time lag Bradda Inshore and Bradda Offshore both had significant models with different variables included. Mean annual nitrate concentration was a variable in both of these models and had a positive effect on *P. pulvillus* density at both sites. However, the second variable differed, the model for Bradda Inshore incorporated winter NAO (North Atlantic Oscillation) Index, which had a significant positive effect on density. The model for Bradda Offshore incorporated chlorophyll-α concentration, which had a positive effect on density. Both models had significant p-values ($p<0.01$) and high R^2 values (0.65 for Bradda Inshore and 0.74 for Bradda Offshore), suggesting an actual trend. The reasons for these relationships remains unclear and it is possible that there is a confounding effect of fishing pressure *P. pulvillus* density, at least at Bradda Offshore, where a significant negative relationship was found.

4.5.4 Overall conclusions

This study has highlighted several key features of the benthic invertebrate community found on the fishing grounds around the Isle of Man. Firstly, scallop dredging and environmental variables are responsible for some of the fluctuations seen in this study. The picture is far from straightforward, however, with what appear to be many interactions, both between structuring variables and between species in the form of predator-prey relationships. The results of this study suggest that species composition of benthic communities and the type of substrate interact with the impacts of fishing pressure and environmental change. The benthic invertebrate communities found on the fishing grounds to the south-west of the island appeared to be composed of relatively dredge-tolerant species in comparison with the rest of the fishing grounds. This theory is backed up by the effect that increased fishing effort seemed to have at East Douglas. At the beginning of this time series, fishing effort at East Douglas had been relatively low for four years (less than 2000 metres of dredge fished per hour). Fishing effort remained at this relatively low level until the 1996-97 fishing season, when effort spiked to more than 15,000 metres dredged per hour, and remained high for the next three seasons. Four of the five species studied at East Douglas showed significant decreases in density over the course of the time series (*E. esculentus, A. rubens, B. undatum* and *N. antiqua*). Three of these species showed a significant negative relationship with fishing effort lagged by 1 and 2 years (*E. esculentus*, *B. undatum, N. antiqua*). These results seem to suggest that the eight years of relatively low fishing effort at East Douglas had allowed the benthic invertebrate community to recover somewhat from fishing effort and certain species that were not tolerant to high levels of fishing were able to increase in abundance. When fishing effort increased, these species were vulnerable and their densities dropped.

Secondly the effects of fishing pressure may be compounded by changes in environmental variables. Although environmental data for the eastern fishing grounds was unavailable, at Bradda Inshore *A. rubens* had a significant positive relationship with chlorophyll-α concentration lagged by 1 year and a significant negative relationship with mean annual temperature lagged by 2 years. The negative relationship with temperature lagged by 2 years was also seen in the density of *P.pulvillus* at both Bradda Inshore and Bradda Offshore. A relationship between temperature and *P. maximus* recruitment around the Isle of Man has been found in a previous study (Shephard, Beukers-Stewart et al. 2010), therefore it seemed likely that it would also have an effect on other members of the benthic community. Significant temporal trends in both chlorophyll-α concentration and temperature were found over the course of this time series, although they were trending in opposite directions, with temperature increasing and chlorophyll-α concentration decreasing. Organisms with planktonic larval phases, such as *A. rubens* and *P. pulvillus* could be affected by these two variables in several different ways and further investigation is required to understand fully the mechanisms involved.

This study, however, has highlighted the fact that temperature does have a relationship with two more members of the benthic community around the Isle of Man, although unlike for *P. maximus,* in a negative direction. It is possible that this negative relationship is in fact an indirect effect of the negative relationship between temperature and chlorophyll-α, which was found in Chapter 3. An inverse relationship between chlorophyll-α and temperature has been found to occur on an ocean-basin scale and appears to be controlled by basin-scale oscillations in the physical environment (Martinez, Antoine et al. 2009) In the case of the Irish Sea such oscillations would come in the form of the North Atlantic Oscillation (NAO) Index, which was not found to have a direct relationship with any variables in this study. There is, however, empirical evidence that increasing temperature would cause phytoplankton biomass to decline, because of increasing metabolic demands per unit of biomass (Brown, Gillooly et al. 2004, O'Connor, Piehler et al. 2009). The effects of temperature on phytoplankton biomass could be exasperated in a heavily impacted ecosystem. O'Connor et al (2009) suggest that if an ecosystem has been heavily impacted from other sources, for example the removal of zooplankton carnivores by overfishing, they would most likely experience a reduction in phytoplankton biomass with increasing temperature. If temperature, chlorophyll-α concentration and fishing effort are all impacting these communities it is very likely that there could be some synergistic effects, especially if each variables effects a different life history phase of a species.

Finally at all grounds where it was found, *A. opercularis* density increased towards the end of this time series, although it should be noted that the magnitude of the increase was very different at each ground. There is no obvious reason for this other than a particularly good recruitment event of a species known to vary in density (Vause, Beukers-Stewart et al. 2007). The importance of these series of recruitment events around the Isle of Man is that they highlight the need to look at both the broad-scale and species specific dynamics of an ecosystem to fully understand what is occurring. These recruitment events explain some of the observed trends in benthic diversity found in Chapter 3 that were not related to either fishing effort or environmental variables. It is possible that, like *P. maximus,* temperature may be playing a role in these recruitment events (Shephard, Beukers-Stewart et al. 2010). This again requires further study, both using long-term data sets and empirical studies of *A. opercularis*' responses to environmental variables. In this study the environmental variables were unavailable for the eastern grounds, where the major queen scallop grounds are located. However, these data have now been collected since 2006 (Kevin Kennington pers. comm.) and a longer-time series will be needed to observe long-term trends and this is an area for future study. If temperature is playing a role it could have important implications for this commercially valuable scallop species and should be factored in to the management of the fishery targeting it.

Overall this study has highlighted that even relatively species poor benthic invertebrate communities, such as those around the Isle of Man in the Irish Sea, are structured by a complex set of factors and the interactions between them. It is therefore likely that a full understanding of such constantly fluctuating ecosystems will never be reached. However, long-term datasets such as the ones used in this study can be utilized to give a better picture about the broad-scale influences of some of the important factors involved and can also be used to identify which variables seem to have the most significant influence on a community.

4.6 References

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Chapter 5

Investigating long-term recovery within a closed area and the effects of environmental variables on the benthic invertebrate community

5.1 Abstract

This final chapter investigated the dynamics of benthic invertebrate species within a closed area on the south-west coast of the Isle of Man. Previous authors have investigated the dynamics of the target species *Pecten maximus* within this closed area, and this work extends the time-series that they used. *P. maximus* has continued to increase in density within the closed area, following initial slow recovery rates. In addition to this other benthic invertebrate species have also increased in density over the course of the time series. Interestingly though the predatory starfish *Asterias rubens* actually decreased in density within the closed area, a finding which is at odds with work done elsewhere in similar habitats. A conservative analysis of the relationships between each species and environmental variables also indicates that temperature and chlorophyll-α could be important environmental variables to investigate further.

5.2 Introduction

Bottom-fishing activities have been shown to be one of the most destructive anthropogenic impacts on marine benthic communities (Dayton, Thrush et al. 1995, Jennings and Kaiser 1998, Thrush, Hewitt et al. 1998, Kaiser, Ramsay et al. 2000, Thrush and Dayton 2002, Carbines and Cole 2009). One management measure that has been utilised to counter this problem, particularly in the last two decades, is closing areas to fishing. These allow the communities present to recover from this impact (Micheli, Halpern et al. 2004, Beukers-Stewart, Vause et al. 2005). There have been many studies conducted investigating the effects of closed areas on marine communities (McClanahan and Mangi 2000, Mosquera, Cote et al. 2000, Murawski, Brown et al. 2000, Bradshaw, Veale et al. 2001, Roberts, Bohnsack et al. 2001, Halpern and Warner 2002, Gell and Roberts 2003, Halpern 2003, Micheli, Halpern et al. 2004, Beukers-Stewart, Vause et al. 2005, Stokesbury and Harris 2006, Marino, Juanes et al. 2007, Marino, Juanes et al. 2009, Howarth, Wood et al. 2011). In general these studies have shown that closed area protection leads to an increase in density, biomass and average size of organisms within the boundaries of the closed area (Halpern and Warner 2002). There is also evidence that closed area protection of marine habitats and species (both target and non-target) has helped maintain or increase biodiversity (Dayton, Sala et al. 2000, Bradshaw, Veale et al. 2001, Halpern 2003, Beukers-Stewart, Vause et al. 2005).

In addition to the benefits seen within a closed area, the protection of a complete ecosystem rather than an individual species has been shown to provide benefits back to species targeted by fisheries (Beukers-Stewart, Vause et al. 2005). Spillover of more mobile individuals from within closed areas has led to increased catches for fishers operating in surrounding areas (McClanahan and Mangi 2000, Roberts, Bohnsack et al. 2001, Gell and Roberts 2003, Beukers-Stewart, Vause et al. 2005). Furthermore, sedentary species, such as scallops, benefit from the more complex habitats within closed areas, which are important as key settlement habitats of larvae (Bradshaw, Veale et al. 2001, Beukers-Stewart, Vause et al. 2005, Stokesbury and Harris 2006, Marino, Juanes et al. 2009, Howarth, Wood et al. 2011). Populations of sedentary species that build up within closed areas also have the potential to act as reproductive reservoirs (Beukers-Stewart, Vause et al. 2005). For example broadcast spawners such as the great scallop *Pecten maximus,* rely on external fertilisation and fertilisation success is increased if adult populations are allowed to increase in density (Marelli, Arnold et al. 1999, Beukers-Stewart, Vause et al. 2005). In addition to this *P. maximus* have relatively long-lived larvae (20 – 40d) (Brand, Wilson et al. 1991, Beukers-Stewart, Vause et al. 2005), therefore there is high potential for larval export from within closed areas to fished areas (Grantham, Eckert et al. 2003, Beukers-Stewart, Vause et al. 2005).

The response of a community to the cessation of fishing activity depends on many factors, including the intensity of fishing pressure on the site prior to closure, larval supply to the area and the life history characteristics of the species present (Mosquera, Cote et al. 2000, Micheli, Halpern et al. 2004). Species are unlikely to respond in identical ways to protection, just as they respond differentially to fishing pressure (Micheli, Halpern et al. 2004). Micheli et al (2004) found that a third of all fish species studied in a meta-analysis had a negative response to protection. These were largely non-target species and when looking at all non-target fish species overall there was a lack of any response to protection (Micheli, Halpern et al. 2004). In terms of benthic species a similar disparity in the results of fishery closures have been found. For example, populations of sea scallops (*Plactopecten magellanicus*) on Georges Bank fishing grounds off the NE coast of the USA were found to be 9 to 14 times higher in closed areas than fished areas (Murawski, Brown et al. 2000). However, 3 species of scallops (*Chlamys rubida, Chlamys behringiana* and *Hinnites giganeus*) showed no difference in density between closed and fished areas even after 8 years of protection in the San Juan Islands, USA (Tuya, Soboil et al. 2000). These two studies just focus on the target species of a fishery, but in the long-term ecosystems within closed areas will likely undergo continuous change in composition over several decades following establishment (Micheli, Halpern et al. 2004). The abundance and biomass of individual species and different components of the community are also likely to vary over equally long time-frames (McClanahan and Mangi 2000, Micheli, Halpern et al. 2004).

A closed area of about 2km^2 was implemented by the Isle of Man government in 1989 on the Bradda Inshore fishing ground (Bradshaw, Veale et al. 2001, Beukers-Stewart, Vause et al. 2005). This fishing ground had been heavily fished for scallops using dredges for the 50 years prior to protection and the area around the closure continued to be heavily fished after the establishment of the closed area (Bradshaw, Veale et al. 2001). The *P. maximus* population within the closed area was slow to recover, with densities remaining low for nearly a decade, however, densities increased at an accelerated rate as protection continued (Beukers-Stewart, Vause et al. 2005). After 14 years of protection *P. maximus* densities were 7 times higher within the closed area than an adjacent fished area and more than 40% of the population was made up of individuals older than 5 years, compared to only 5% in the fished area (Beukers-Stewart, Vause et al. 2005). There is also evidence to suggest that the population of older scallops within the closed area was exporting larvae to the adjacent fishing grounds (Beukers-Stewart, Vause et al. 2004, Beukers-Stewart, Vause et al. 2005).

In addition to the target species *P. maximus*, changes in the benthic community of the closed area off the Isle of Man coast have been observed (Bradshaw, Veale et al. 2001). Experimental dredging within a portion of the closed area over the course of 5 years caused the benthic community to become more homogeneous, similar to adjacent fished areas (Bradshaw, Veale et al. 2001). Unfished areas had more abundant upright sessile species (mainly hydroids) than fished areas, which had more abundant encrusting species like bryozoans, sponges and small ascidians (Bradshaw, Veale et al. 2001). This finding has important implications in terms of suitable settlement habitat of larvae of both the target scallop species and other benthic invertebrates (Bradshaw, Veale et al. 2001, Howarth, Wood et al. 2011). In terms of more mobile benthic species, Beukers-Stewart et al (2005) found no difference in scallop predator densities between fished and closed areas in 2001 and 2002. However, in 2003 the density of the starfish *Asterias rubens* was significantly higher in the fished area than the closed area (Beukers-Stewart, Vause et al. 2005).

The previous two chapters in this study have attempted to untangle the effects of fishing effort and environmental variables on the dynamics of benthic mega-faunal species. Synergies between the effects of these variables are thought to be common (Kirby, Beaugrand et al. 2009) and the closed area off the south-west coast of the Isle of Man represents a unique opportunity to investigate how environmental variables influence the mobile mega-faunal component of the benthic community in the absence of fishing. It has been found that increasing temperature has strengthened recruitment in *P. maximus* around the Isle of Man (Shephard, Beukers-Stewart et al. 2010). The previous chapter (Chapter 4) showed significant negative relationships between temperature lagged by 2 years and the density of the starfish *A. rubens* and *Porania pulvillus* on the Bradda Inshore and Bradda Offshore fishing grounds. A significant positive relationship was also found between transformed chlorophyll-α concentration (μg/L) lagged by 1 year and *A. rubens* density at Bradda Inshore. What is interesting to note is that both of these environmental variables were shown to have significant opposing linear trends over the course of the time series (Chapter 3). Temperature showed a significant increase, whilst chlorophyll-α concentration showed a significant decrease (Chapter 3). The implications of these trends are discussed in Chapter 4, however these analyses were not done in the absence of fishing pressure and although no significant relationship with fishing effort was found for *A. rubens* and *P. pulvillus,* it is possible that fishing effort was playing an indirect role (e.g. increasing food supply or causing non-lethal damage, (Jenkins, Beukers-Stewart et al. 2001)).

This chapter aims to investigate the composition of the benthic mega-faunal community within the closed area, using data from dive surveys collected from 1989 – 2006. This work will extend the studies on the same area by Bradshaw et al. (2001) and Beukers-Stewart et al. (2005) in terms of both duration and scope. Diversity indices of this subsection of the benthic community will be calculated and temporal trends will be analysed. Comparisons between the diversity of the closed area and an adjacent fished area will be made, to determine whether the closed area has increased the diversity of megafaunal benthic invertebrates. A more in depth analysis of the closed area will then look at temporal trends in selected species' densities to discern any patterns in density from 1989 to 2006. The effect of environmental variables on both diversity and species density within the closed area will be analysed to determine whether the observed temporal trends within the closed area are related to environmental variables.

5.3 Methods

5.3.1 Study Area

This study focused on the Bradda Inshore fishing ground, located on the south-west of the Isle of Man (Figure 5.1). Bradda Inshore has been heavily fished for great scallops (*P. maximus*) since the onset of the fishery in 1937 (Brand 1999, Bradshaw, Veale et al. 2001, Beukers-Stewart, Vause et al. 2005). However, in March 1989 an exclusion zone of nearly 2km^2 was established within this fishing ground by an Isle of Man government bye-law (Beukers-Stewart, Vause et al. 2005). All commercial mobile fishing gears were banned within this area, along with taking of *P. maximus* by any means, although fishing with static gear, such as lobster and crab pots was allowed to continue (Bradshaw, Veale et al. 2001, Beukers-Stewart, Vause et al. 2005). The original purpose of the closed area was to use it as an area to research scallop cultivation and stock enhancement (Beukers-Stewart, Vause et al. 2005). This research was conducted on a small scale, deemed largely unsuccessful and not thought to have contributed significantly to scallop populations in the area (Wilson 1994, Wilson and Brand 1994, Beukers-Stewart, Vause et al. 2005). The closed area has since enabled monitoring of the benthic community and scallop population dynamics in an area of limited fishing pressure (Bradshaw, Veale et al. 2001, Beukers-Stewart, Vause et al. 2005).

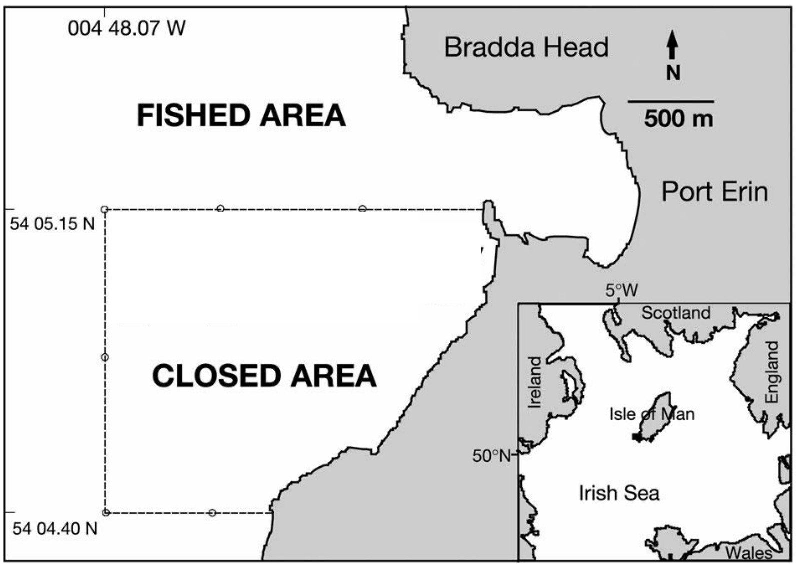


Figure 5.1. Map of the closed and fished areas sampled during this study. Inset shows the location of the Isle of Man within the British Isles.

Source: Beukers-Stewart et al (2005)

5.3.2 Dive surveys

The maximum water depth within the closed area is approximately 40m and the substrate is a mixture of mud, sand and fine gravel (Beukers-Stewart, Vause et al. 2005). This study combines previous work done by Bradshaw et al (2001) and Beukers-Stewart et al (2005) with data collected up to 2006 from dive surveys conducted by staff at the Port Erin Marine Laboratory. From 1989 to 2006 dive surveys were conducted in June of almost every year in the closed area, and then every June from 1999 to 2006. Comparable dive surveys were conducted in the fished area off Bradda Head in 1989, once every two years between 1996 and 2002 and then every year up until 2006. June was chosen for surveys because it falls within the closed season for *P. maximus* around the Isle of Man (June to October inclusive).

The dive surveys conducted prior to 2001 (Bradshaw, Veale et al. 2001) consisted of a varying number of randomly placed transects, which were 50m long by 4 m wide. Each transect was swum by a pair of divers, each diver surveying a parallel strip of 2m wide. These surveys counted an extensive range of benthic species. Dive surveys conducted between 2001 and 2006 (Beukers-Stewart, Vause et al. 2005) were modified, reducing transect width to 3m, with each diver surveying a parallel strip of 1.5m wide. Transect length also varied, from 30 to 200m, which was the result of divers swimming as far as air and decompression limits allowed (Beukers-Stewart, Vause et al. 2005). In the latter surveys divers counted all *P. maximus* observed and a range of other epibenthic species considered to be *P. maximus* predators (*Asterias rubens, Crossaster papposus, Luidia ciliaris, Marthasterias glacialis* and *Porania pulvillus*) along with several other large epibenthic species (*Cancer pagurus*, *Neptunea antiqua, Pagurus* species and spider crab species, among others). These species were chosen to replicate what was being counted in the dredge surveys (see chapters 3 and 4). Some fish species were also counted, however they are not considered in this analysis, which focuses on the epibenthic megafaunal community.

The length of the modern (2002 to 2006) dive survey transects were measured using a reel of rope carried by the divers. The reel of rope was clipped to a buoyed shot line, which marked the beginning of the survey, and released as the divers swam along. The length of the rope used was subsequently measured and this value was used to calculate area surveyed. The exception to this method was the survey conducted in 2001, in which transect length was calculated using a differential global positioning system (DGPS) as detailed in Beukers-Stewart et al (2005). Beukers-Stewart et al (2005) found there was a significant linear relationship between the distances measured by the two methods and as such used DGPS measurements when rope-based measurements were not available. Therefore in this study the DGPS transect measurements for the 2001 survey were used to calculate area sampled.

5.3.3 Environmental Data

Environmental data was taken from a multi-annual time series for water quality around the Isle of Man at the CYPRIS sampling site on the west coast of the Island (just offshore from the closed area). Data from the North Atlantic Oscillation (NAO) index was obtained from Osborn (2006) and a time series of the winter (December-March) average was used. For a full description of this data source refer to Chapter 3.

5.3.4 Data Analysis

5.3.4.1 Species Composition

All survey data were standardised to relative density measurements of number per $100m^2$ using area calculations (collected as detailed above). Post 2001 surveys focused on a fixed number of relatively larger bodied epibenthic megafauna. Reference to these fauna within this study is done using the phrase epibenthic community; however it is acknowledged that this encompasses only the selected species. Density information about these species was selected in the 1989-2000 survey data for meaningful comparisons. To give an overall picture of the species composition at both the fished and the closed area, species density data were calculated as proportions of the overall epibenthic community density each year sampled. Six species were selected from the closed area data that were dominant or of particular ecological interest for further investigation. These species were *P. maximus* (the great scallop), *Asterias rubens* (common starfish), *Cancer pagurus* (edible crab), *Luidia ciliaris* (seven-armed starfish), *Pagurus* species (hermit crabs, unable to be identified to species level) and *Porania pulvillus* (cushion star).

5.3.4.2 Diversity calculations

Relative species density data were used to calculate two diversity indices, Simpson's Diversity Index (1-D) and the Shannon Index (for the justification for selecting these two indices and calculation of these indices, see Chapter 3). These indices are only representative of the diversity of the epibenthic megafaunal community sampled, but give an indication of the dominance and evenness of species distribution at both the fished and closed area.

5.3.4.3 Comparisons between the fished and closed areas

The effect of the closed area on the diversity of the epibenthic community, total density of the epibenthic community and individual relative density of each of the six species selected was analysed using a one-way ANOVA to compare each variable between the closed area and fished area at all years where both areas were sampled. Data were tested for normality using Shapiro-Wilk Normality Test and tested for homogeneity of variances using Bartlett's test. Not all data were normally distributed, several of the species densities were non-normal and therefore the effect of the closed area on these species was tested using the non-parametric Mann-Whitney U test.

5.3.4.4 Temporal trends

Data from the fished area were not as continuous as that from the closed area and as such were unsuitable for further analysis of temporal trends. Temporal trends in the two diversity indices and relative densities were analysed using regression analysis for the closed area data only.

5.3.4.5 Effect of environmental variables on diversity and individual species

All environmental variables were combined into useable annual indices as detailed in Chapter 3. The indices run from 1993 – 2006, data prior to 1992 was collected at the CYPRIS site, however it was analysed in a different way to post-1992 data and the two sets are not wholly comparable (Evans, Williams et al. 2003). For this study, annual mean indices of temperature (^{o}C), chlorophyll-α concentration (μg/L), nitrate concentration (μM) and silicate concentration (μM) were used. Mean winter NAO index was also used in this analysis. To investigate the effects of these environmental variables on diversity and individual species density the time series for the closed area data were truncated and only data from 1993 – 2006 was included.

As in the previous two chapters, it was expected that environmental variables would have a lagged effect on the density of each species and diversity index. This is because if environmental conditions were influencing species reproduction and settlement (e.g. Shephard et al, 2010) then a certain amount of time would be required for these species to grow large enough to be visible during dive surveys. Therefore environmental variables were lagged in three different ways: no lag, a 1-year lag and a 2-year lag. Further lags were unable to be tested as each time the data was lagged some data was lost from the analysis.

Multiple linear regression analysis was used to investigate the effect of environmental variables on each response variable. All data were checked for normality and homogeneity of variance and transformations were conducted where appropriate. The explanatory environmental variables were then analysed for co-linearity using Variance Inflation Factor (VIF) analysis in the statistical program R. No variables exhibited any co-linearity and therefore all were included in the multiple regression analyses. Optimum models were selected using Stepwise Model Selection, found in the statistical program R. Following model selection all final models were re-run and any significant models were then validated to ensure that the residuals showed no patterns. To ensure that autocorrelation within the time series would not cause a Type I error, the p-value significance threshold has been increased from $p = 0.05$ to $p = 0.01$.

5.4 Results

5.4.1 Composition of the epibenthic invertebrate community

The closed area was more completely sampled than the fished area between 1989 and 2006. Figure 5.2 shows the proportional composition of the epibenthic invertebrate community at both sites. The epibenthic community was composed predominantly of asteroid echinoderms, mobile crustaceans and the great scallop, *P. maximus*, the target of the scallop fishery. In 1989 the epibenthic community in both the closed and fished areas was dominated by the common starfish, *A. rubens*, which represented about 60% of the total density at both sites. In the fished area *A. rubens* represented less than 10% of the community from 1998-2000 and 2004 – 2006, however in 2002 and 2003 it represented more than 40% of the community. In the closed area *A. rubens* became a smaller proportion of the community throughout the time series, becoming less than 10% of the community from 1998 to 2006, with the exclusion of the year 2002 when it represented 20% of the community.

Figure 5.2 illustrates that in the closed area *P. maximus* became more dominant throughout the time series. From 1989 to 1992, at the beginning of the closure, *P. maximus* represented only about 5% of the total density of the epibenthic community. *P. maximus* gradually became a greater proportion of the community, ending up representing more than 50% of the total epibenthic density from 2003 to 2006. This pattern was not repeated at such a dramatic scale in the fished area, which began with *P. maximus* as an equally small proportion of the community in 1989 as the closed area. The fished area was not adequately sampled between 1991 and 1997, however, for the latter half of the time series *P. maximus* had increased to become about 30% of the total epibenthic community.

The next most dominant species at both the fished and closed area was in fact a group of species all within the Genus *Pagurus* or hermit crabs. Figure 5.2 shows that this group of species represented only 5% of the total density at both areas in 1989, then increased to more than 20% from 1998 to 2000 and finally decreased to about 10% of the total density of epibenthic species from 2001 to 2006. The pattern was similar at both sites, however in 1998 *Pagurus* species represented just over 50% of the epibenthic community in the fished area.

The edible crab's, *C. pagurus*, proportion of the total density did not change much over the course of the times series in either the fished or closed area, remaining at about 5% of the total density. The seven armed starfish, *L. ciliaris*, showed an increase in its proportion of community density over the course of the time series in both areas from less than 1% to over 10% of the density. This increase was more noticeable at the fished area, where *L. ciliaris* represented nearly 20% of the community composition from 2004 to 2006. The pincushion starfish *P. pulvillus* became a smaller proportion of the community at both sites over the course of the time series, going from 5% to about 1%.

Fluctuations were seen in other species, but the overall pattern appeared to be that the closed area had higher epibenthic species richness than the fished area as the time series progressed. Both sites saw a reduction in *A. rubens* and an increase in *P. maximus*, which was more pronounced within the closed area.

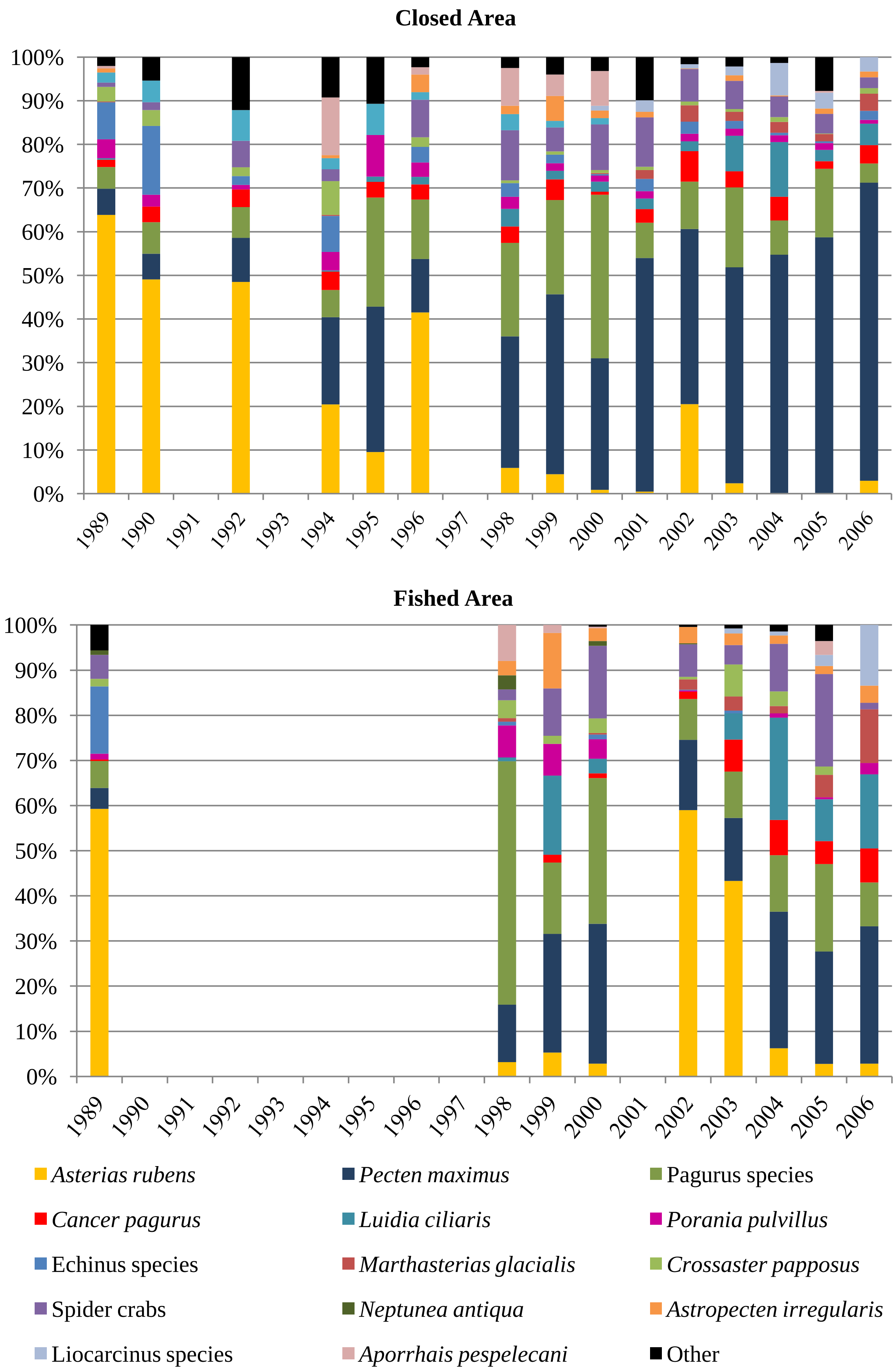


Figure 5.2. Proportional densities (mean no./ 100m^2) of the main invertebrate epibenthic species estimated by dive surveys in the closed and fished areas between 1989 and 2006.

5.4.2 Differences between the epibenthic community between closed and fished areas

Six species (*P. maximus, A. rubens*, *C. pagurus, L. ciliaris*, *P. pulvillus* and *Pagurus* species) were selected for further investigation based on their dominance within the epibenthic community at both sites and out of ecological interest. In addition to these individual species, density data for all epibenthic invertebrate species counted was used to calculate two diversity indices, Simpson's Diversity Index (1-D) and the Shannon Index. Species richness was not used as a diversity index because the diver surveys only collected data on selected species, therefore it would be artificially limited. All species densities were totalled to give a total density of epibenthic species in both areas. All of these variables were tested for normality and homogeneity of variance, those that met these requirements were tested using one-way ANOVA for differences between the fished area and the closed area (Table 5.1). Non-normal data were tested using the non-parametric Mann Whitney-U Test (Table 5.2).

There were no significant differences in Simpson's Diversity Index and the Shannon Index between the fished area and the closed area (Table 5.1 and Figure 5.3). Total density of epibenthic species was not significantly different between the fished area and closed area, although it was slightly higher within the closed area (Table 5.1 and Figure 5.4). *P. maximus* showed a significant difference in density between the fished area and closed area, with a significantly higher density in the closed area (Table 5.2 and Figure 5.5). All other species showed no significant difference in density between the fished area and closed area (Table 5.1, Table 5.2, Figure 5.5 and Figure 5.6). However, one pattern worth mentioning is that while the density of *A. rubens* was generally similar in the closed and fished areas, there was a large peak in *A. rubens* numbers in the fished area in 2002 and 2003 (up to 15 individuals / 100m^2, Figure 5.5) which was not observed in the closed area.

Table 5.1. Results from one-way ANOVA analyses examining diversity and density of epibenthic species in the closed area and fished area. All data were tested for normality and homogeneity of variance. None of the variables showed a significant difference between the closed area and fished area.

Source	**df**	**SS**	**MS**	**F**	**p**
Simpson's Diversity Index	1	0.042	0.042	3.563	0.08
Shannon Index	1	0.125	0.125	2.151	0.16
Total Density	1	97.300	97.28	0.843	0.37
Luidia ciliaris	1	0.007	0.007	0.007	0.94
Cancer pagurus	1	0.227	0.227	1.316	0.27

Table 5.2. Results from the non-parametric Mann Whitney-U tests examining the density of four epibenthic species in the closed area and fished area. All data were non-normal. Only *Pecten maximus* showed a significant difference in density between the closed area and fished area.

Species	**df**	**W**	**p**
Asterias rubens	1	35.5	0.27
Pecten maximus	1	80.0	**0.02**
Porania pulvillus	1	59.0	0.50
Pagurus species	1	56.0	0.68

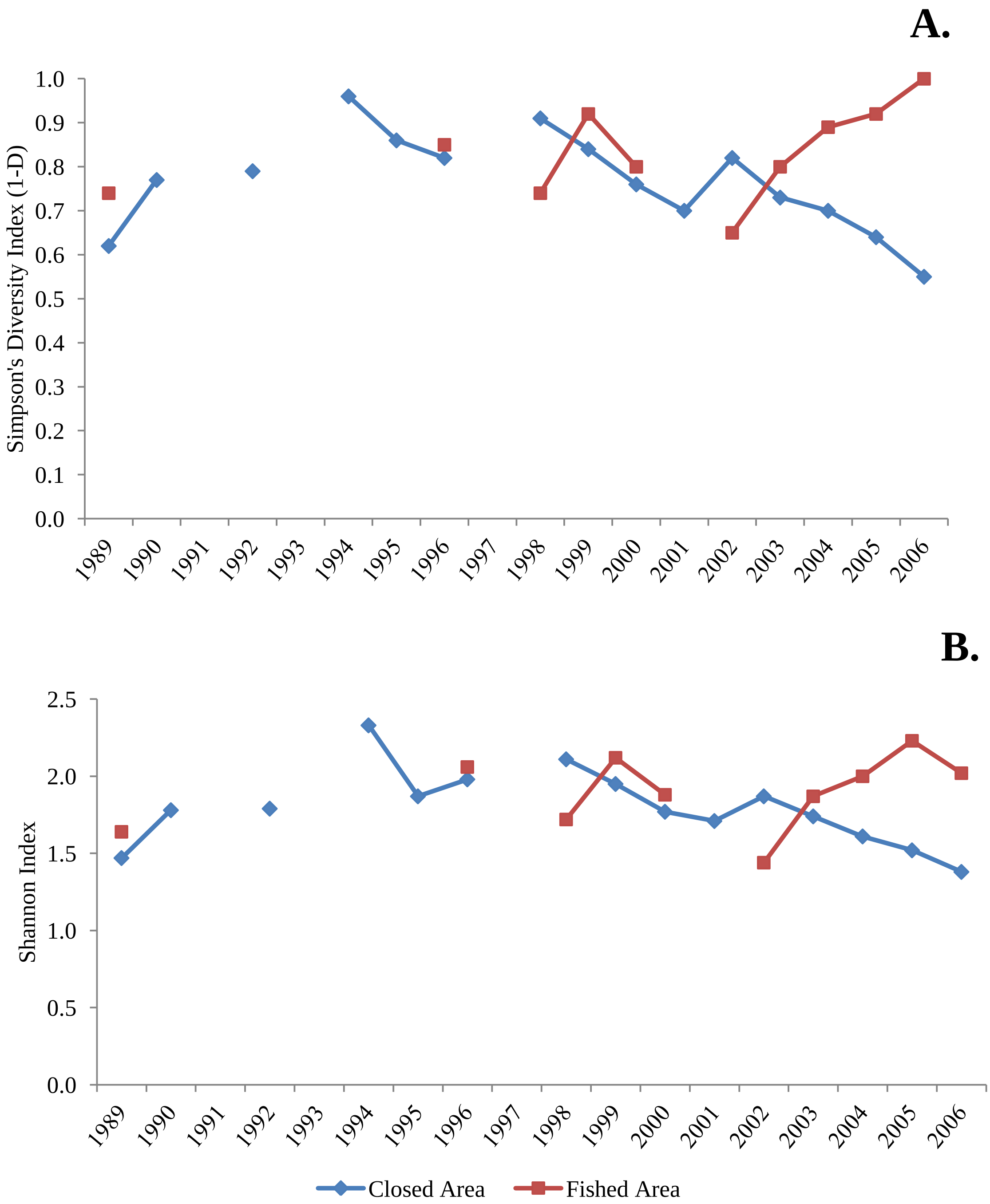


Figure 5.3. Temporal patterns in (A.) Simpson’s Diversity Index (1-D) and (B.) Shannon Index inside the closed and fished areas between 1989 and 2006. Indices calculated from species densities estimated from diver surveys.

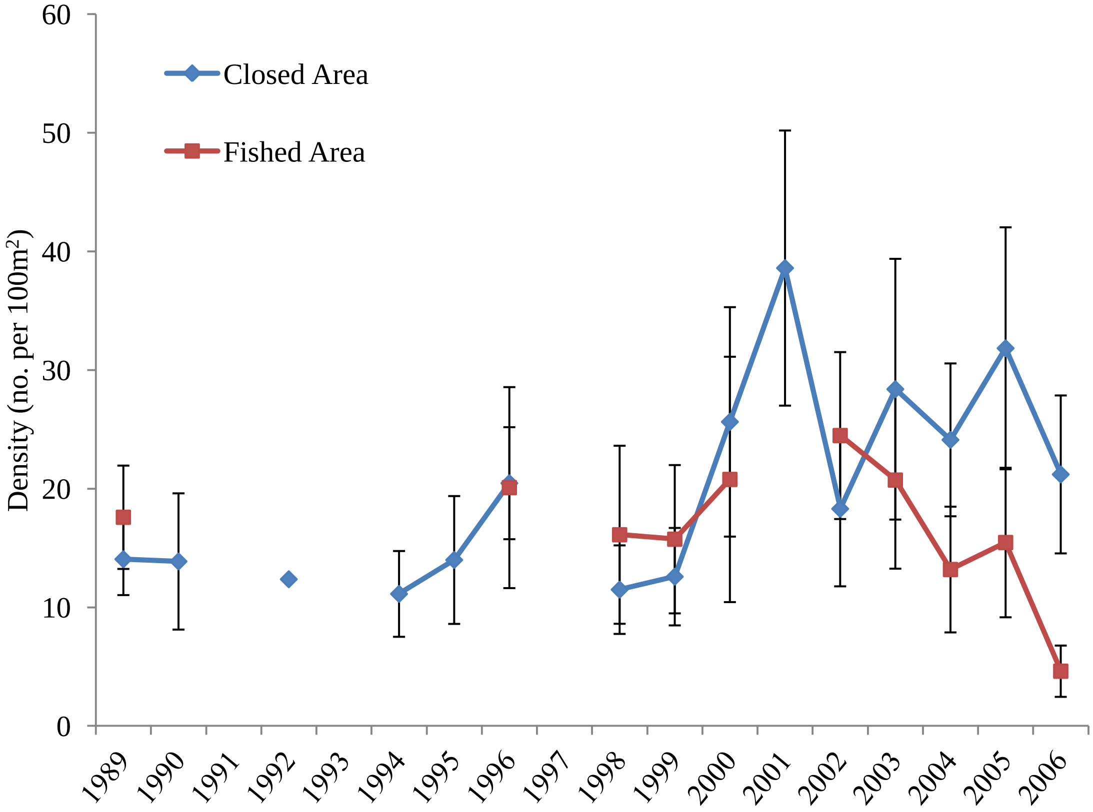
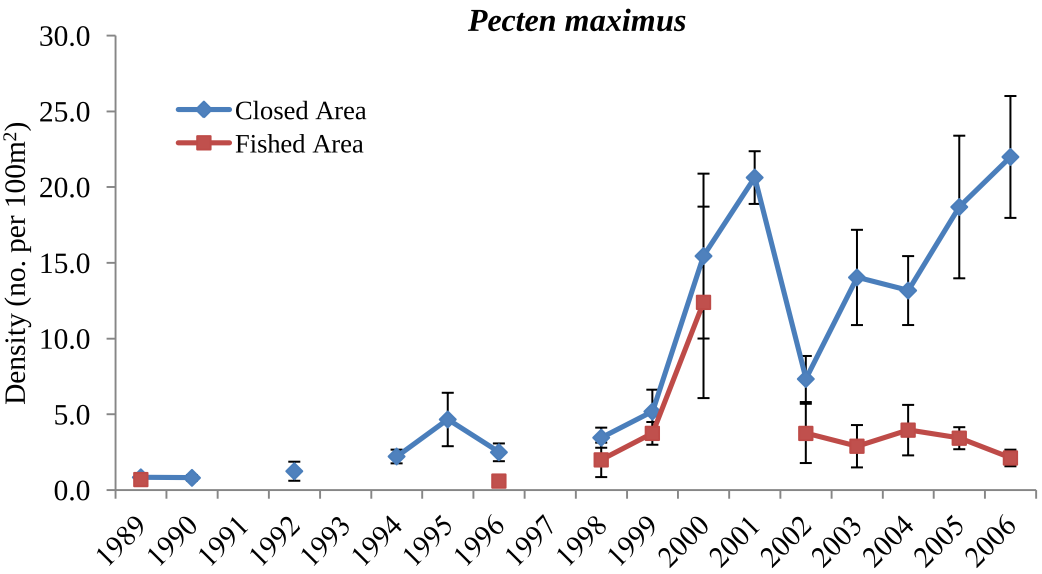
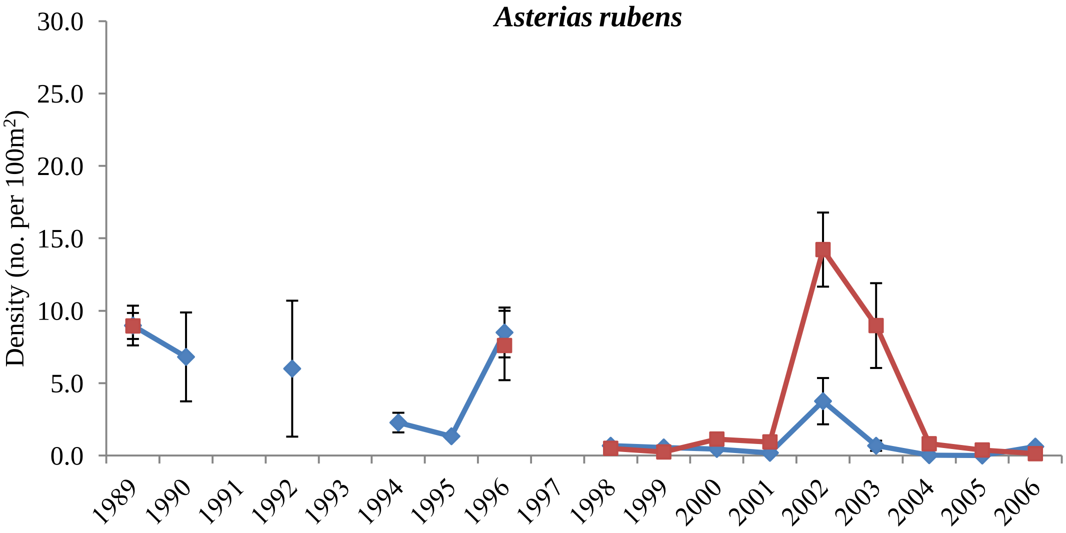


Figure 5.4. Total mean density (no./100m^2 ± SE) of the main invertebrate benthic species estimated by diver surveys in the closed and fished areas between 1989 and 2006.





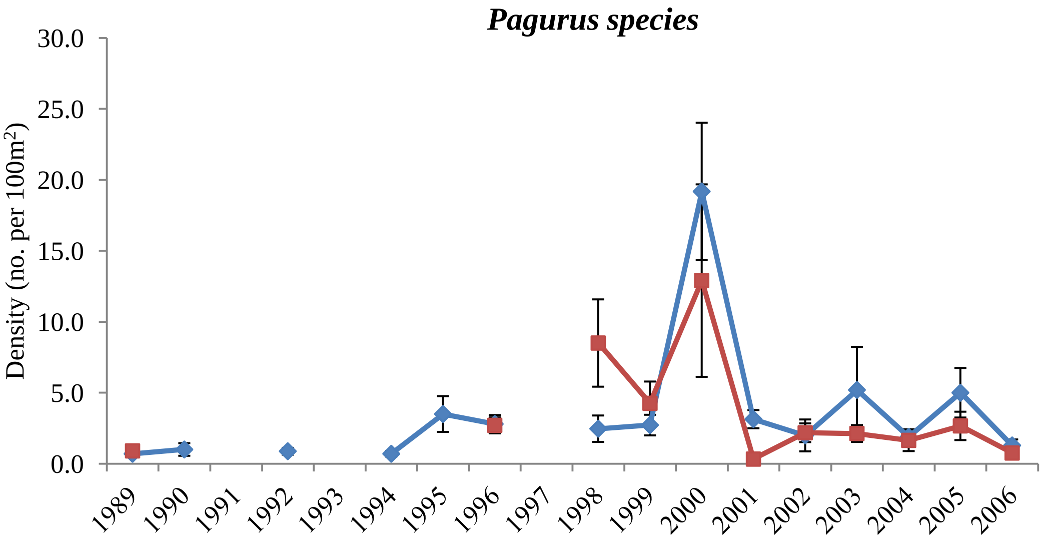
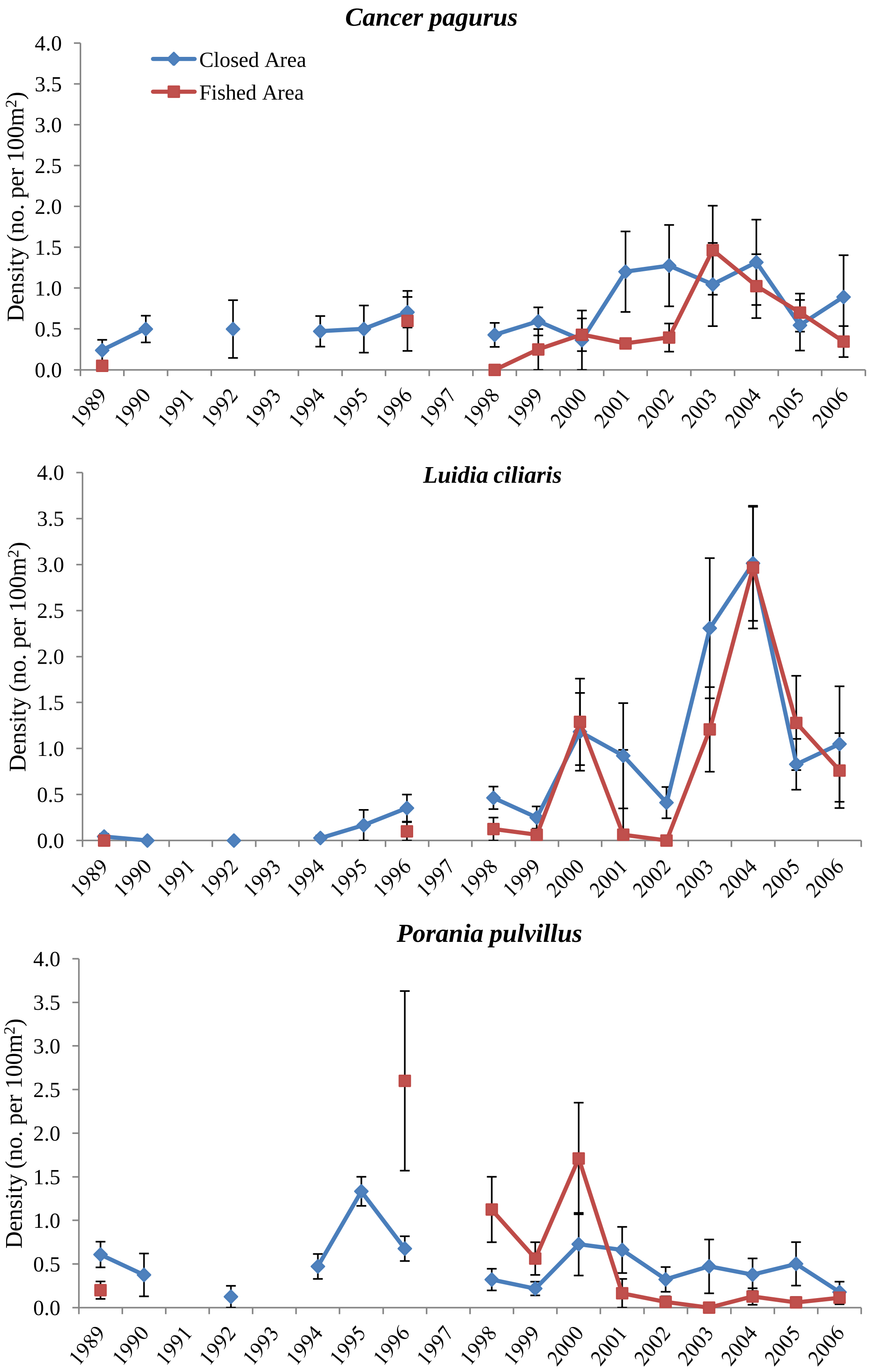


Figure 5.5. Density (mean no./100m^2 + SE) of *Pecten maximus*, *Asterias rubens* and *Pagurus species* estimated by diver surveys in the closed and fished areas between 1989 and 2003. Density of *P. maximus* was significantly higher within the closed area than the fished area (Mann Whitney-U Test: W= 80.0, *df* = 1, *p* = 0.02)


Cancer pagurus

Luidia ciliaris

Porania pulvillus

Figure 5.6. Density (mean no./100m^2 ± SE) of *Cancer pagurus*, *Luidia ciliaris* and *Porania pulvillus* estimated by diver surveys in the closed and fished areas between 1989 and 2003.

5.4.3 Temporal trends in diversity and epibenthic species density within the closed area

Both diversity indices were analysed for temporal trends and no significant trends were found with either index. There was, however a significant increase in total mean epibenthic species density within the closed area over the course of the time series (Table 5.3 and Figure 5.7). Of the six species that were selected for further analysis, four had significant temporal trends. *P. maximus, L. ciliaris* and *C. Pagurus* all showed a significant increase in density over the course of the time series (Table 5.3 and Figures 5.8, 5.9 and 5.10 respectively). *A. rubens* showed a significant decrease in density over the course of the time series (Table 5.3 and Figure 5.11).

Table 5.3. Results from temporal (1989-2006) linear regression analysis on the density of six epibenthic species densities, total epibenthic species density, Shannon Index and Simpson's Diversity Index from within the closed area. All data were tested for normality and homogeneity of variance. Significant p-values are highlighted in bold.

Source	**Estimate**	***df***	**F**	**r2**	**P-value**
Simpson's Diversity Index	-0.008	13	2.01	0.13	0.18
Shannon Index	-0.015	13	1.55	0.11	0.24
Total epibenthic species density	1.001	13	9.45	0.42	**<0.01**
Pecten maximus density	1.422	13	28.98	0.72	**<0.01**
Asterias rubens density	-0.453	13	17.44	0.57	**<0.01**
Cancer pagurus density	0.041	13	7.74	0.37	**0.02**
Luidia ciliaris density	0.109	13	11.04	0.46	**<0.01**
Porania pulvillus density	-0.011	13	0.60	0.04	0.45
Pagurus species density	0.175	13	2.54	0.16	0.14

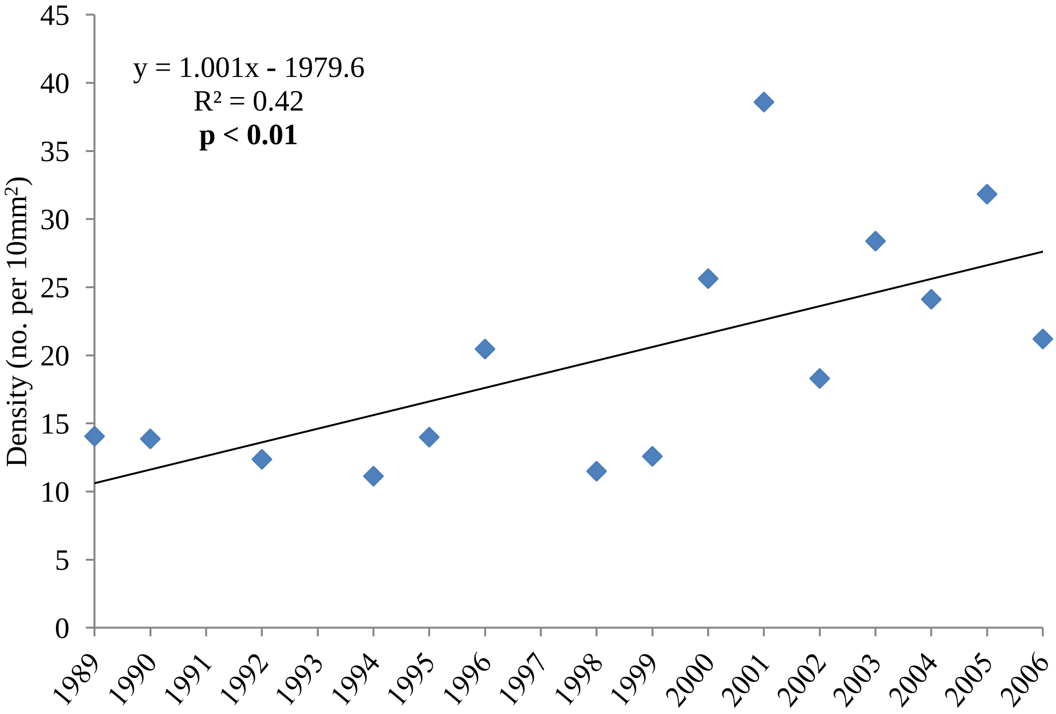


Figure 5.7. Linear regression analysis of total mean density (no./100m^2) of epibenthic invertebrate species inside the closed area from 1989 to 2006.

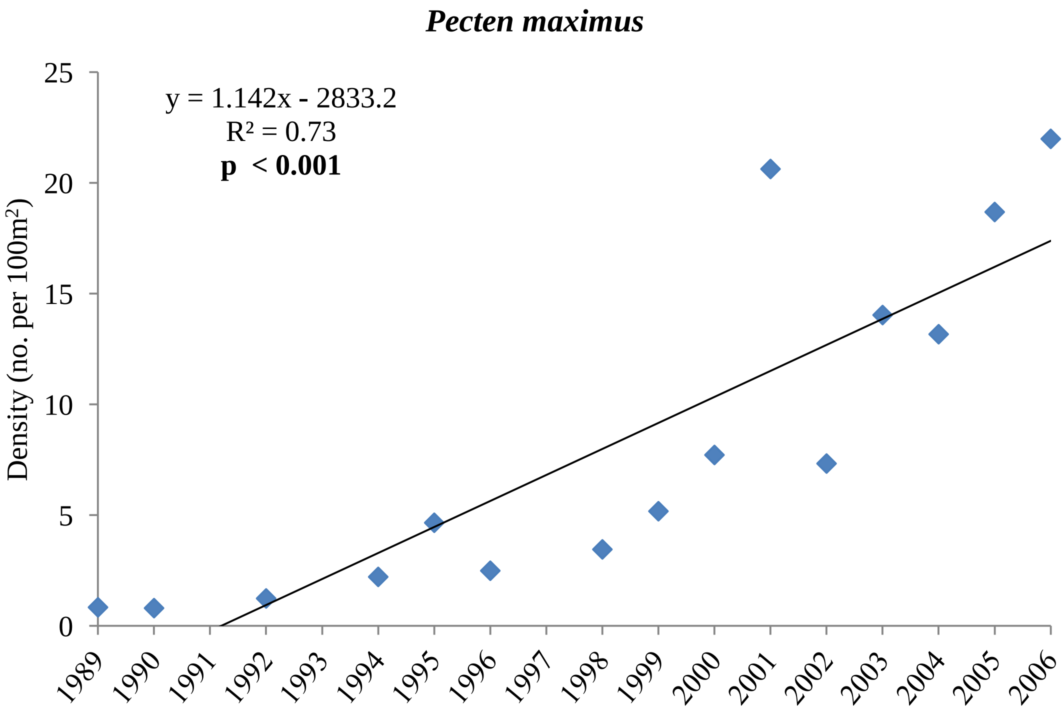


Figure 5.8. Linear regression analysis of mean density (no./100m^2) of *Pecten maximus* inside the closed area from 1989 to 2006.

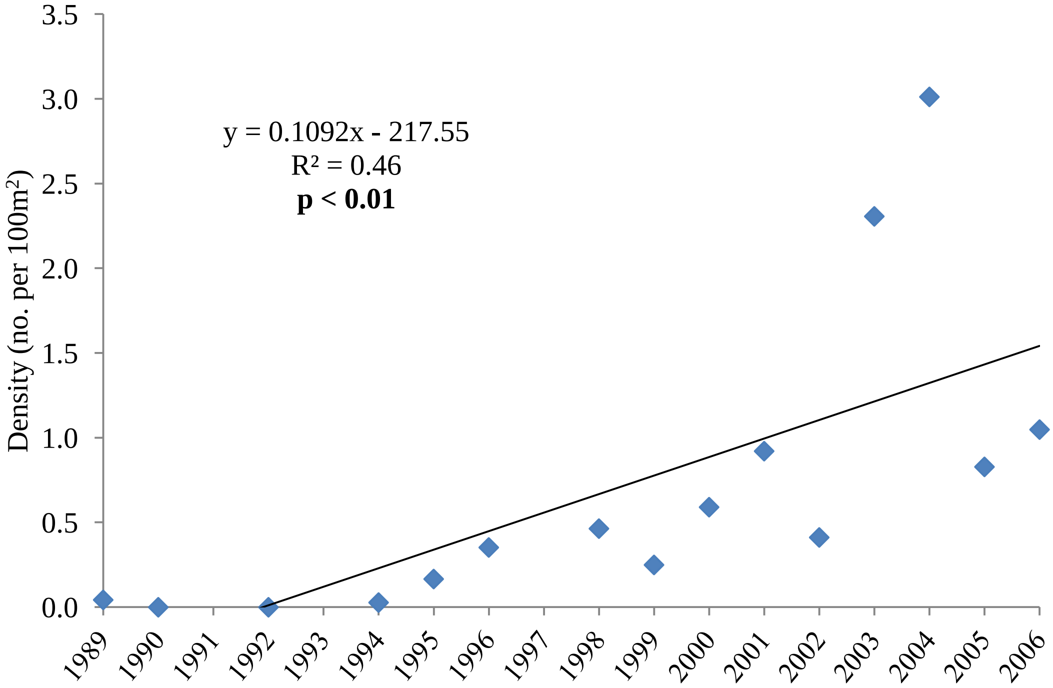


Figure 5.9. Linear regression analysis of mean density (no./100m^2) of *Luidia ciliaris* inside the closed area from 1989 to 2006.

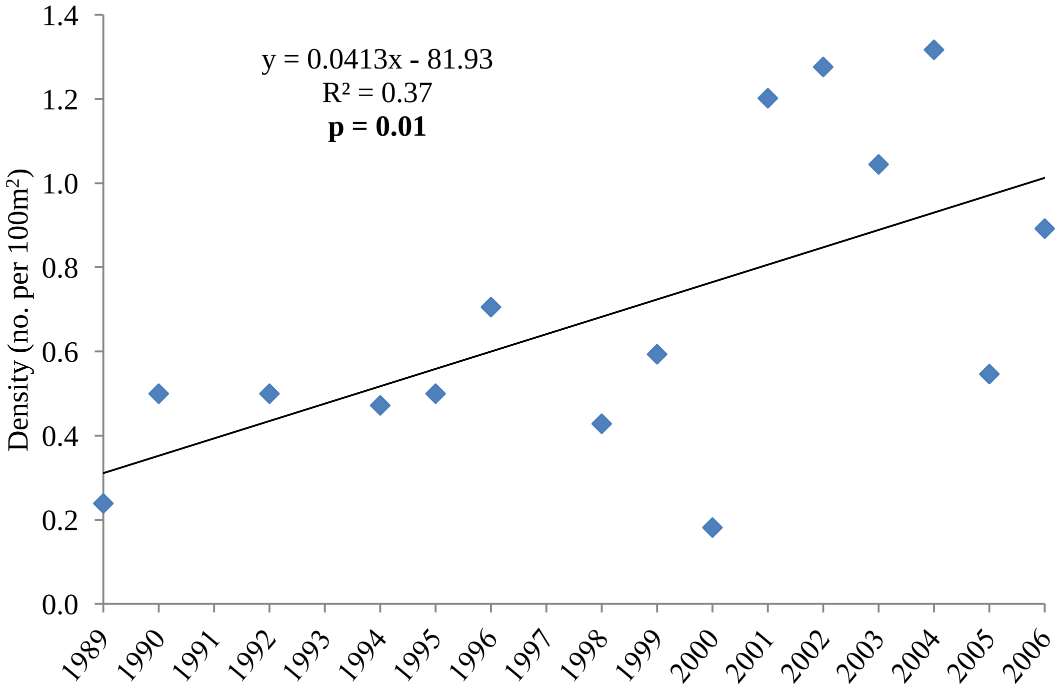


Figure 5.10. Linear regression analysis of mean density (no./100m^2) of *Cancer pagurus* inside the closed area from 1989 to 2006.

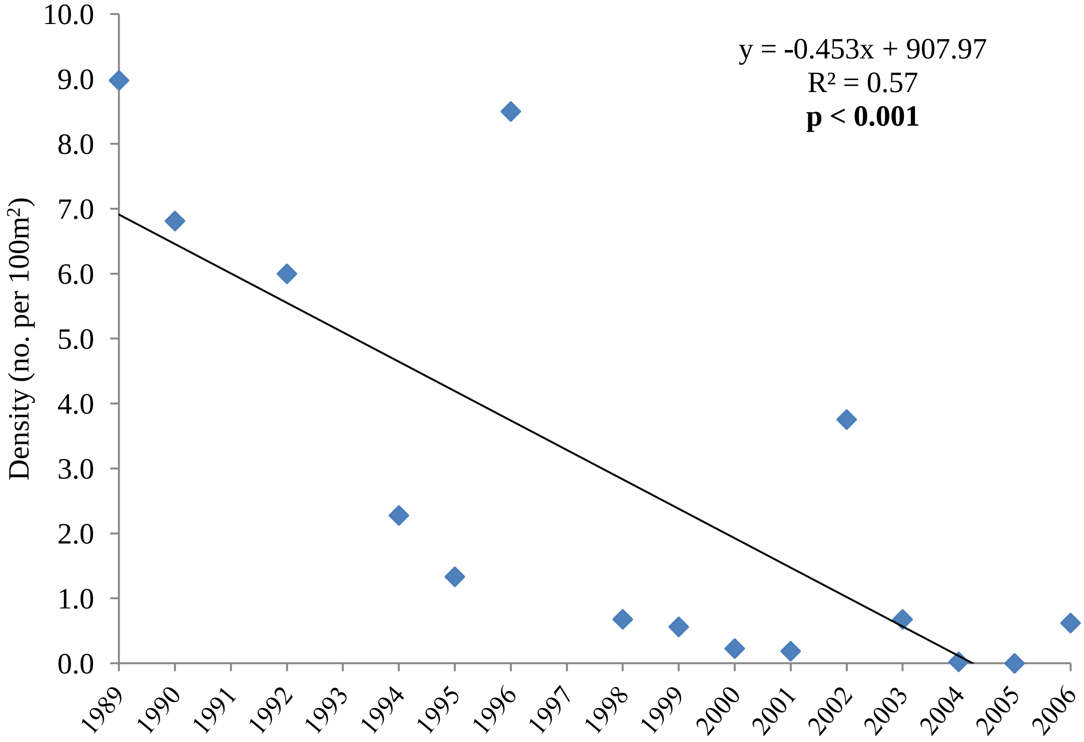


Figure 5.11. Linear regression analysis of mean density (no./100m^2) of *Asterias rubens* inside the closed area from 1989 to 2006.

5.4.4 The effect of environmental variables on diversity within the closed area

Two separate multiple linear regression analyses were performed on Simpson's and Shannon indices from within the closed area. Environmental variables were tested against diversity with three lags (un-lagged, a 1 year lag and a 2 year lag). Each analysis underwent a Variance Inflation Factor (VIF) analysis prior to the multiple linear regressions. In all three cases no variables required removal because all VIF values were less than 3. Following multiple linear regression each model underwent an AIC model selection procedure to create the optimum model for the data. All models were then validated to ensure no patterns in the residuals.

No significant relationships were found between Simpson's Diversity Index (1-D) and any of the environmental variables at any of the time lags investigated. The model selection process found a significant positive relationship between un-lagged, square-root transformed chlorophyll-α concentration (μg/L) and Shannon Index (Figure 5.12). However, no significant relationships were found with any environmental variables and Shannon Index when lagged by 1 and 2 years.

5.4.5 The effect of environmental variables on individual species' density in the closed area

a). Un-lagged environmental variables

The density of *P. maximus* was square-root transformed and showed a significant negative relationship with square-root transformed chlorophyll-α concentration (μg/L) when chlorophyll-α concentration was un-lagged (Figure 5.13). Total mean epibenthic species density showed a significant negative relationship with square-root transformed un-lagged chlorophyll-α concentration (μg/L) (Figure 5.14). Square-root transformed *C. pagurus* density also had a significant model with un-lagged environmental variables (Table 5.4).

Table 5.4. Multiple linear regression results for square-root transformed mean annual *Cancer pagurus* density (no. per $100m^2$) in the Closed Area from 1993 - 2006 modelled as a function of environmental variables with no time lag. Multiple $R^2 = 0.52$, Adjusted $R^2 = 0.42$, F-statistic = 4.96 on 2 and 9 *d.f.*, *P* = **0.04**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Silicate Concentration (μM)	0.25	0.10	2.39	**0.04**
Mean Winter North Atlantic Oscillation Index	-0.08	0.04	-1.94	0.08
Intercept	0.11	0.33	0.34	0.74

b) A 1-year lag in environmental variables

The only species to show a significant relationship with any of the environmental variables when they were lagged by 1 year, was *P. maximus.* Density of *P. maximus* had a significant negative relationship with square-root transformed chlorophyll-α concentration (μg/L) when lagged by 1 year (Figure 5.15).

c) A 2-year lag in environmental variables

No significant relationship was found between *P. maximus* density and any environmental variable when they were lagged by 2 years. However, several other species did show significant relationships with environmental variables lagged by 2 years. Tables 5.5 to 5.8 show the details of these models, only two of which had p-values less than or equal to 0.01 (the threshold artificially chosen to overcome any autocorrelation issues within the time series), these were the model for $\log_{10}$ transformed *L. ciliaris* density (Table 5.6) and *P. pulvillus* density (Table 5.8).

Table 5.5. Multiple linear regression results for mean annual *Cancer pagurus* density (no. per 100m^2) in the Closed Area from 1993 - 2006 modelled as a function of environmental variables with a 2 year time lag. Multiple R^2 = 0.69, Adjusted R^2 = 0.56, F-statistic = 5.16 on 3 and 7 *d.f.*, *P* = 0.03

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Temperature (^{o}C)	-0.42	0.19	-2.25	0.06
Mean Winter North Atlantic Oscillation Index	0.09	0.07	1.25	0.25
Mean Annual Chlorophyll-α Concentration (μg/L)	-1.07	0.29	-3.68	**0.01**
Intercept	6.85	2.35	2.91	0.02

Table 5.6. Multiple linear regression results for log$_{10}$ transformed mean annual *Luidia ciliaris* density (no. per 100m^2) in the Closed Area from 1993 - 2006 modelled as a function of environmental variables with a 2 year time lag. Multiple R^2 = 0.68, Adjusted R^2 = 0.60, F-statistic = 8.54 on 2 and 8 *d.f.*, *P* = **0.01**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Silicate Concentration (μM)	0.50	0.16	3.08	0.02
Mean Annual Chlorophyll-α Concentration (μg/L)	-0.76	0.23	-3.28	**0.01**
Intercept	-0.83	0.54	-1.54	0.16

Table 5.7. Multiple linear regression results for log$_{10}$ transformed mean annual *Pagurus* species density (no. per 100m^2) in the Closed Area from 1993 - 2006 modelled as a function of environmental variables with a 2 year time lag. Multiple R^2 = 0.54, Adjusted R^2 = 0.42, F-statistic = 4.59 on 2 and 8 *d.f.*, *P* = **0.05**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Temperature (^{o}C)	0.39	0.13	2.95	0.02
Mean Annual Chlorophyll-α Concentration (μg/L)	0.47	0.21	2.26	0.05
Intercept	-4.54	1.67	-2.72	0.03

Table 5.8. Multiple linear regression results for mean annual *Porania pulvillus* density (no. per 100m^2) in the Closed Area from 1993 - 2006 modelled as a function of environmental variables with a 2 year time lag. Multiple R^2 = 0.66, Adjusted R^2 = 0.57, F-statistic = 7.67 on 2 and 8 *d.f.*, *P* = **0.01**

Coefficients	Estimate	Std. Error	t-value	*P*-value
Mean Annual Nitrate Concentration (μM)	0.40	0.12	3.33	**0.01**
Mean Winter North Atlantic Oscillation Index	0.11	0.06	1.96	0.09
Intercept	-1.07	0.46	-2.34	0.05

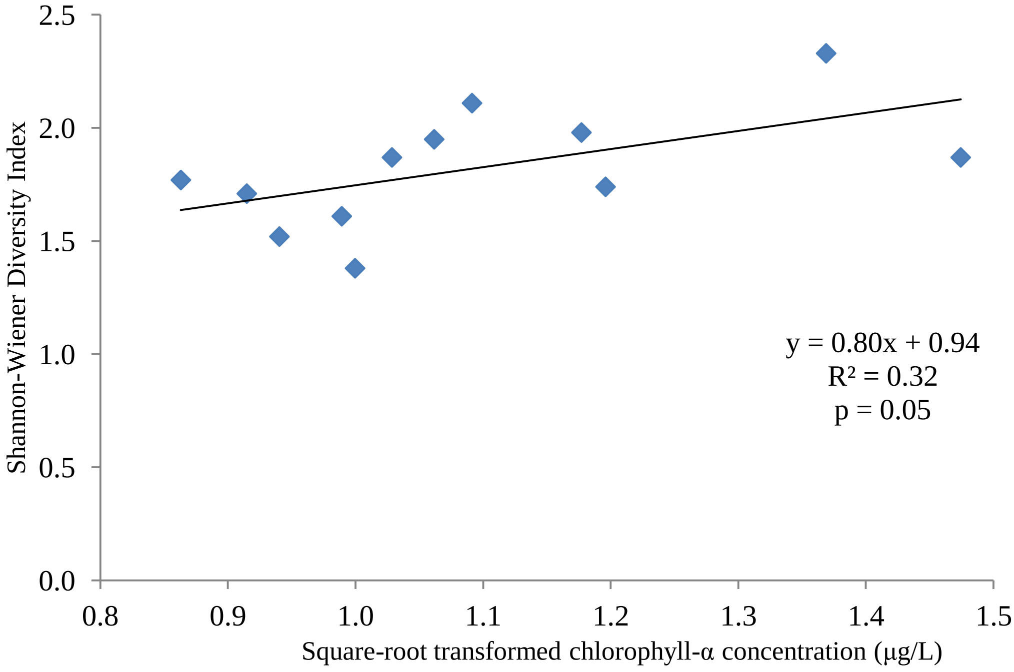


Figure 5.12. Linear regression analysis of Shannon Index and un-lagged square-root transformed chlorophyll-α concentration (µg/L) from 1993 to 2006. Shannon Index calculated from density (no. per 100m^2) estimates collected from diver surveys inside the Closed Area. Data were transformed to ensure normality and homogeneity of variance. Note the shortened x-axis.

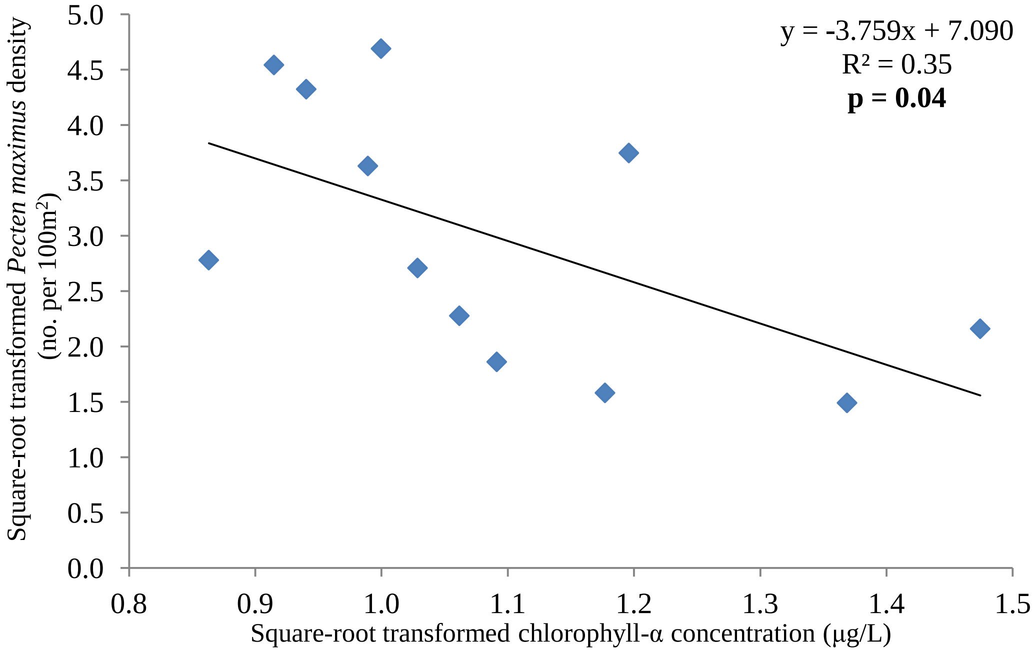


Figure 5.13. Linear regression analysis of square-root transformed *Pecten maximus* density (no. per 100m^2) and un-lagged square-root transformed chlorophyll-α concentration (µg/L) from 1993 to 2006. Densities estimated from diver surveys inside the Closed Area. Data were transformed to ensure normality and homogeneity of variance. Note the shortened x-axis.

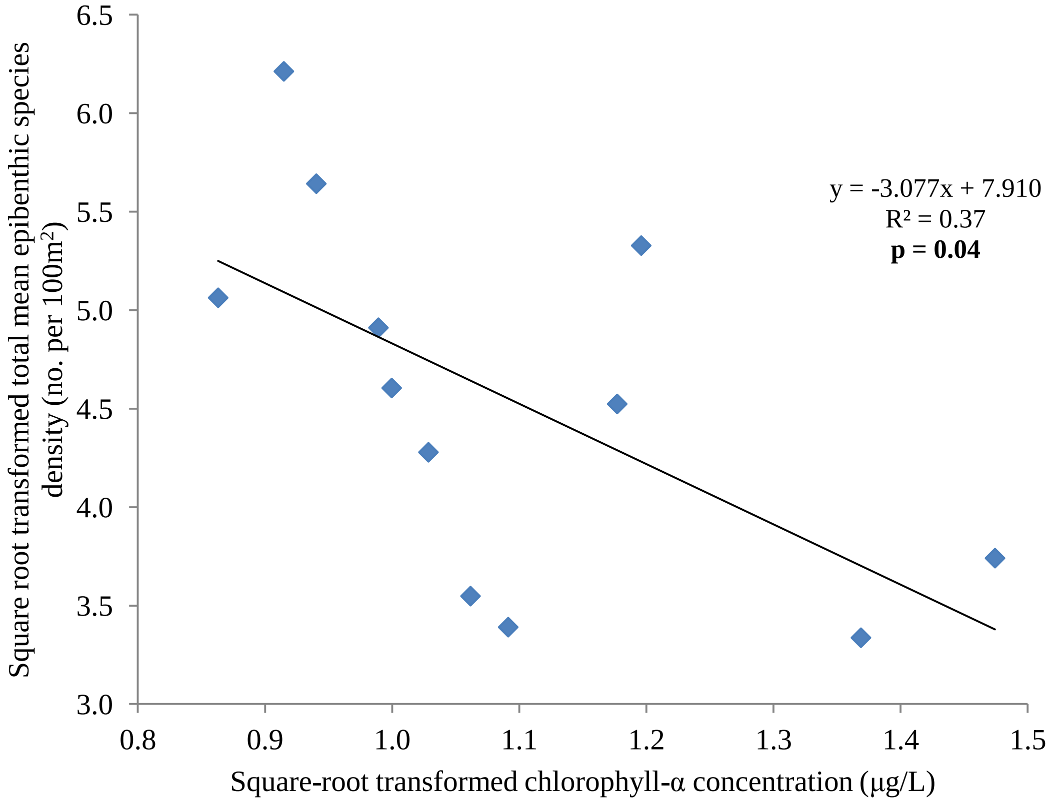


Figure 5.14. Linear regression analysis of square-root transformed total mean epibenthic species density (no. per $100m^2$) and un-lagged square-root transformed chlorophyll-α concentration (µg/L) from 1993 to 2006. Density (no. per $100m^2$) estimates were collected from diver surveys inside the Closed Area. Data were transformed to ensure normality and homogeneity of variance. Note the shortened x-axis and y-axis.

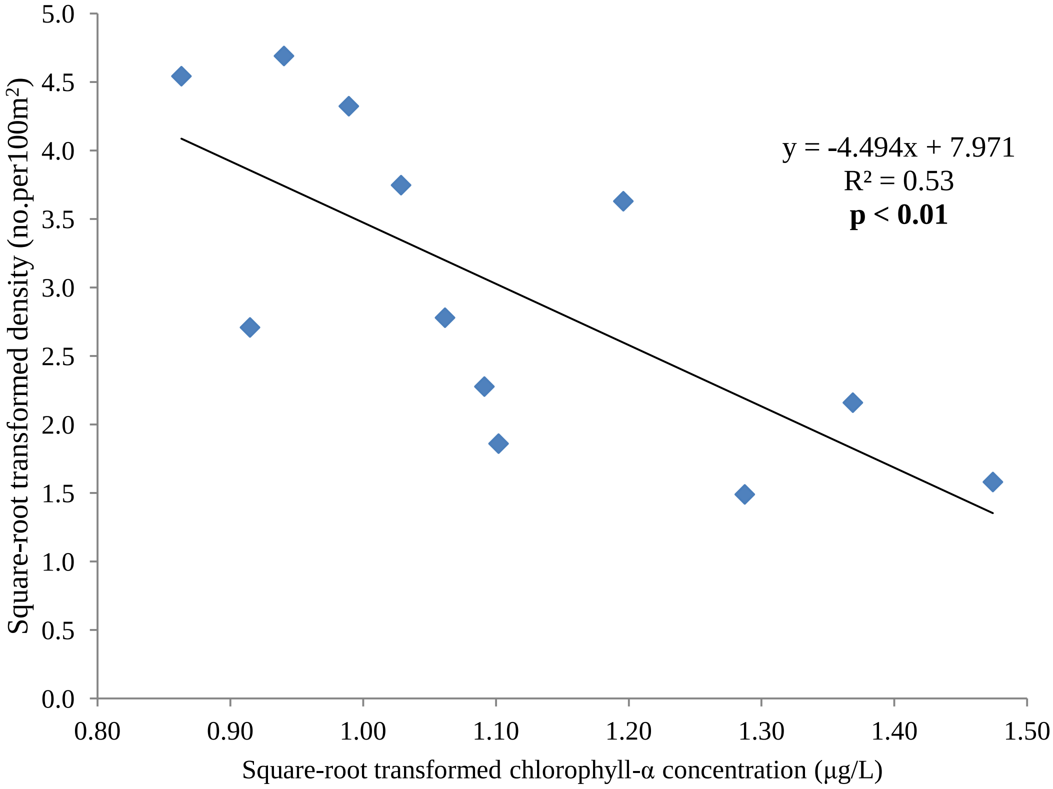


Figure 5.15. Linear regression analysis of square-root transformed *Pecten maximus* density and square-root transformed chlorophyll-α concentration (µg/L) lagged by 1 year from 1993 to 2006. *P. maximus* density (no. per 100m^2) estimated from diver surveys inside the Closed Area. Data were transformed to ensure normality and homogeneity of variance. Note the shortened x-axis.

5.5 Discussion

The use of areas closed to fishing as a management tool has received much attention in the last decade, with many benefits having been reported, including increases in target species abundance, larval export, habitat protection and recovery (Bradshaw, Veale et al. 2001, Roberts, Bohnsack et al. 2001, Gell and Roberts 2003, Beukers-Stewart, Vause et al. 2005, Stokesbury and Harris 2006, Kaiser, Blyth-Skyrme et al. 2007, Marino, Juanes et al. 2007).The closed area off the south-western coast of the Isle of Man, which was implemented in 1989, has resulted in increases in density, mean age and size of the target species *P. maximus* (Beukers-Stewart, Vause et al. 2005). The benthic community has also been found to be more heterogeneous than adjacent fished areas, with more upright sessile hydroids, important settlement habitat for *P. maximus*, within the closed area (Bradshaw, Veale et al. 2001). This study has extended the work done previously by Beukers-Stewart et al (2005) and Bradshaw et al (2001) and investigated temporal trends in diversity and individual species density over a 17 year time period (1989-2006). The results of this study can be divided into two main sections: the effect of the closed area on the benthic community, including community interactions over time, and the effect of environmental variables on the benthic community protected from fishing. I am not aware of any previous studies which have examined environmental influences in the absence of fishing. Each of these sections are discussed in turn below.

5.5.1 The effect of the closed area

Areas closed to fishing have been shown to increase and maintain biodiversity (Dayton, Sala et al. 2000, Halpern 2003), however, the diversity indices calculated for this closed area showed no significant trend over time (Figure 5.3). Both Simpson's Diversity Index and Shannon Index were higher in fished area than the closed area from 2003 to 2006, although this was not a significant difference (Table 5.1). Both diversity indices within the closed area actually declined from 2002 to 2006 (Figure 5.3). The main reason for these declines was the increased density of *P. maximus* within the closed area, which during the latter half of the time series came to dominate the benthic community (Figure 5.2 and see below for more details). In addition to this the diversity indices were calculated from a subset of benthic species, which were specifically targeted during dive surveys. Therefore they are not a true indication of total benthic community diversity, rather just highlighting the diversity of the main mega-faunal epibenthic invertebrate species. What the diversity indices do indicate though is what a dominant part of the benthic community *P. maximus* becomes in the latter half of the time series.

Over the 17 years of this study total density of the epibenthic species analysed significantly increased within the closed area (Table 5.3 and Figure 5.7). Although total density was higher inside the closed area than the fished area for the latter half of the study (Figure 5.4) this difference was not significant (Table 5.1). The data from the fished area was not sufficient to be analysed temporally, however, total density decreased from 2003 to 2006 (Figure 5.4). This trend in total density seems to have been driven by the density of *P. maximus* within the closed area, which not only significantly increased over the time series (Figure 5.8), but also became a proportionally larger part of the benthic community. Figure 5.2 shows that *P. maximus* represented only 5% of the total density of the selected benthic invertebrates within the closed area in 1989, but by 2006 it represented almost 70% (Figure 5.2). This pattern was not repeated in the fished area (Figure 5.2), although density of *P. maximus* did increase, as did the proportion of benthic species density it represented (5% in 1989 to approximately 30% in 2006). In fact *P. maximus* was the only species studied whose density was significantly higher within the closed area compared the fished area (Table 5.2).

These results demonstrate that the closed area has continued to benefit the *P. maximus* population, as was also found by Beukers-Stewart et al (2005). In 2003 scallop densities were 7 times higher in the closed area than the fished area (Beukers-Stewart, Vause et al. 2005). By 2006 scallop densities were 10 times higher within the closed area as compared to the adjacent fished area (Figure 5.5). Beukers-Stewart et al (2005) suggested that the scallop population in the fished area is not entirely independent of the population inside the closed area. There was some indirect evidence of larval export from the scallop population within the closed area to the fished area in an earlier analysis of this dataset (Beukers-Stewart, Vause et al. 2004, Beukers-Stewart, Vause et al. 2005). This study continued the dataset from 2003 to 2006 and although *P. maximus* densities continued to increase within the closed area, they remained relatively low and stable in the fished area (Figure 5.5). The reason for this difference in density between the two areas in the latter half of this study may be that fishermen increasingly targeted the scallops in the area adjacent to the closed area (B. Beukers-Stewart pers. comm.). Indeed in Chapter 3 fishing effort data for the Bradda Inshore fishing ground peaked in the 2001-2002 fishing season, which coincides with an observed drop in *P. maximus* density in the fished area in the following 2002 survey season. As reported by Beukers-Stewart et al (2005) it seems that the protected pocket of scallops within the closed area may be continuing to benefit the surrounding scallop fishery.

Statistically significant increases were also seen in seven armed starfish *Luidia ciliaris* and brown crab *Cancer pagurus* densities within the closed area (Table 5.3, Figures 5.9 and 5.10 respectively). No significant difference in the densities of these two species was found between the closed and fished areas (Table 5.1 and Figure 5.6). It should be pointed out that a pot fishery for *C. pagurus*, which is one of the few other commercially important species (Murray, Hinz et al. 2009), continued within the closed area throughout this study. Therefore the fact that the density within the closed area was not significantly different from outside the closed area is probably due to this on-going commercial fishery. In addition to this *C. pagurus* is a relatively mobile scavenger species (Bradshaw, Collins et al. 2003) and would be able to move between the closed and fished areas. Therefore it is unlikely that *C. pagurus* would benefit from closed area protection as much as other benthic species and the significant increase in density witnessed within the closed area was potentially due to environmental variables or predator-prey interactions (e.g. *C. pagurus* is a key predator of *P. maximus* - discussed in more detail below). *L. ciliaris* showed no significant relationship with fishing effort on the Bradda Inshore fishing ground, or in fact on any fishing ground where it was found (Chapter 4). Although *L. ciliaris* is quite susceptible to damage from dredging (Beukers-Stewart, Jenkins et al. 2001, Jenkins, Beukers-Stewart et al. 2001) it can also move exceptionally fast, with speeds of 3m per minute having been observed in the English Channel (Holme 1984). As a voracious predator of echinoderms and in particular *A. rubens* and several brittlestar species (Holme 1984, Guillou 1996) it is likely that *L. ciliaris* moves between the closed and fished areas, aggregating on food sources. A significant relationship between environmental variables and *L. ciliaris* density was also found and is discussed below.

The only species that was selected for further study whose density significantly decreased within the closed area over the 17 years of this study was *A. rubens* (Table 5.3, Figure 5.11). This is of particular note because *A. rubens* is the other main predator of *P. maximus* (along with *C. pagurus*) around the Isle of Man (Wilson and Brand 1994, Beukers-Stewart, Vause et al. 2005). In 1989 *A. rubens* represented around 60% of the density of benthic species studied both in fished and closed areas (Figure 5.2). In the closed area *A. rubens* proportional density decreased to less than 5% from 2003 to 2006. A similar pattern occurred in the fished area, although *A. rubens* density in 2002 and 2003 spiked back up to around 50% of the total density (Figure 5.2). In Chapter 4 Bradda Inshore was the only ground to show a significant negative temporal linear relationship in *A. rubens* density, suggesting that this difference could be linked to the closed area. This result contrasts with those found on closed areas of the Georges Bank scallop grounds, where *Asterias* species were found in higher densities within the closed areas than the fished areas, due to an apparent predator-prey aggregative response (Marino, Juanes et al. 2007). Figure 5.5 shows that *A. rubens* densities were actually generally higher in the fished area than the closed area, although this was an insignificant difference overall (Table 5.4).

There are several possible reasons for this pattern, one being a relationship with environmental variables, which was found in Chapter 4. However, *A. rubens* density in the closed area did not have a significant relationship with any of the environmental variables, at any time lag in this study. Another possibility is that *A. rubens* are highly aggregated in certain patches within the closed area and therefore diver surveys have underestimated total density. However, the data collected via experimental dredging from the Bradda Inshore fishing ground in Chapter 4 indicates that the decrease in *A. rubens* density is an actual trend, rather than a sampling artefact. A final possible explanation for this trend is a series of predator-prey relationships, which have been altered by the cessation of fishing. Both *L. ciliaris* and *C. pagurus* densities significantly increased within the closed area over the course of this study and both of these species are known to predate on *A. rubens* (Holme 1984, Guillou 1996). In addition to this the *P. maximus* population within the closed area has been shown to be dominated by older (>5 years) and larger individuals as compared to the adjacent fished area (Beukers-Stewart, Vause et al. 2005), which will have grown too large for *A. rubens* to prey on.

When *P. maximus* increased in density, as seen within this closed area, it was expected this would attract predators such as *A. rubens*. However, this study provides evidence that *A. rubens* density was actually decreasing within the closed area. In re-seeding experiments within this closed area, newly seeded scallops were heavily predated on by *A. rubens* (Wilson and Brand 1994). The results in *A. rubens* density found here are therefore unexpected. The reason for this could be that *A. rubens* are olfactory based predators (Briggs 1981) and as such are attracted to stressed prey, such as those left in the wake of dredging (Ramsay, Kaiser et al. 1998) or re-seeded (Wilson and Brand 1994). The scallops within the closed area are undisturbed and hence not producing olfactory cues for predators, therefore perhaps this is why *A. rubens* densities did not increase inside the closed area.

Heavily fished sites are often dominated by scavenging echinoderms such as *A. rubens*, which are thought to benefit from the increased food supply provided by discards from the fishery (Collie, Escanero et al. 1997, Veale, Hill et al. 2000, Bradshaw, Veale et al. 2002). Perhaps the cessation of fishing within this closed area has reduced this additional, and easily accessible food supply that helped sustain previous *A. rubens* densities. There is little direct evidence for this; however, the increase in density of *A. rubens* in 2002 does coincide with a sharp decline in *P. maxmius* density both in the fished and closed area (Figure 5.5). Beukers-Stewart et al (2005) partially attributed this drop in *P. maximus* density to a several specific illegal fishing incursions into the closed area in May 2002, just a month prior to the dive surveys of that year. Hence it is possible that these fishing incursions provided a short-term increase in food supply. Interestingly *L. ciliaris* density peaks in 2003, a year after the peak in *A. rubens* density. Although this peak is not same scale as that seen in *A. rubens* density in the fished area, it is similar in magnitude to the density of *A. rubens* within the closed area. It seems likely, therefore that a combination of increased predation, reduced incidental food supply from fishery discards and an inability to predate upon larger scallops have all contributed to a decrease in *A. rubens* density within the closed area. If this is the case, then the clear relationship between *A. rubens* density and both temperature and chlorophyll-α concentration found in Chapter 4 may be masked by these interactions within the closed area.

The two other species selected for further study (the pin cushion starfish *Porania pulvillus* and the hermit crab *Pagurus* species) showed no significant trends in density over time (Figure 5.5 and 5.6). Nor did they show a significant difference in density between the fished and closed areas (Table 5.2). However, Figure 5.6 shows that from 2001 to 2006, *P. porania* density was higher within the closed area than the fished area. *Pagurus* species density was also higher in the closed area in the latter half of the time series (Figure 5.5). The various hermit crab species grouped under *Pagurus* species have been found to be indirectly affected by fishing pressure (Kaiser, Hinz et al. 2005). Populations of hermit crabs are critically limited by the availability of suitable gastropod shells (Pechenik, Hsieh et al. 2001, Kaiser, Hinz et al. 2005). As individuals grow they utilise gastropod shells of larger species such as the whelks *Buccinum undatum* and *Neptunea antiqua* (Kaiser, Hinz et al. 2005). Fishing effort is thought to damage the gastropod shells suitable for *Pagurus* species and thereby limit population growth (Kaiser, Hinz et al. 2005). A cessation of fishing effort, such as within this closed area, would be likely to benefit *Pagurus* species. Indeed densities were higher inside the closed area as compared to the fished area, but this difference was not significant. In this instance fishing pressure or the lack of it, does not appear to be the sole factor structuring the *Pagurus* population within the closed area.

The relatively slow initial increase in *P. maximus* density within the closed area was attributed in part to illegal fishing in the first few years of establishment (Beukers-Stewart, Vause et al. 2005). The patterns in the relative densities of the species studied here (*A. rubens* being the exception) indicate similar slow increases in density in the first half of the time series (Figures 5.5 and 5.6). Initial densities of all five of the species which increased throughout the time series were low (< 1 per 100m^2). These low densities persisted until 1994, when they all began to increase, except for *A. rubens*, which decreased in density over the time series. These findings suggest that the closed area has enabled the density of at least five species of the benthic community to increase or recover. The slow rate of recovery could have also been due to the fact that prior to closure this part of Bradda Inshore fishing ground had been heavily fished for scallops for approximately 50 years (Bradshaw, Veale et al. 2001, Beukers-Stewart, Vause et al. 2005). The benthic community present within the closed area would have been adapted to high levels of disturbance (Kaiser, Ramsay et al. 2000, Bradshaw, Veale et al. 2002). Therefore ‘recovery’ of the benthic community would be expected to have taken a significant amount of time. It is unlikely that the community will remain static over time and the composition seen in this study may indeed be a transient community structure, which will continue to change (Micheli, Halpern et al. 2004). What else the closed area does provide though is an opportunity to study the effect of environmental variables on benthic species without the additional impact of fishing pressure.

5.5.2 The effect of environmental variables on benthic invertebrates

The effect of environmental variables on communities and individual species is often masked by other anthropogenic pressures such as fishing effort (Schiel, Steinbeck et al. 2004, Kirby, Beaugrand et al. 2009, Wernberg, Smale et al. 2012). An area closed to fishing presents a unique opportunity to investigate relationships between environmental variables and benthic communities. However, care must be taken, because the communities within closed areas are recovering from fishing effort, hence increases in the abundance and density of species is expected (Beukers-Stewart, Vause et al. 2005). In addition to this both temperature and chlorophyll-α concentration showed significant temporal trends over the course of this time series (Chapter 3). Therefore there is a real possibility of autocorrelation leading to a Type I error in this study. To attempt to overcome this issue a lower than usual p-value threshold of $p = 0.01$ is being utilised, even so though these results must be interpreted conservatively.

Environmental data in this study was available from 1992 to 2006 and compared with diversity and individual species' densities within the closed area over that time. Several significant ($p = 0.05$) relationships were found in this analysis (Tables 5.4 – 5.8 and Figures 5.12, 5.13 and 5.14), however, as discussed above, the significance threshold was lowered to $p = 0.01$, to overcome autocorrelation issues. At this lower p-value there were still several significant relationships between individual species densities and several environmental variables.

Square-root transformed *P. maximus* density showed a significant negative relationship with square-root transformed chlorophyll-α concentration lagged by 1 year (Figure 5.15). Interestingly in contrast to Shephard et al (2010) no relationship with temperature was found in this study. However, this is likely because this study focused on one population of scallops on the southwest of the Isle of Man, whereas Shephard et al (2010) studied the entire population of scallops from all fishing grounds and investigated the relationship between temperature and recruitment. It is also possible that the observed relationship between *P. maximus* density in the closed area and chlorophyll-α is inflated in significance because both have significant temporal trends (Chapter 3). Chlorophyll-α concentration had a significant negative temporal trend from 1993 to 2006 (Chapter 3) and *P. maximus* density has a significant positive temporal trend (Figure 5.8). However the p-value of this observed relationship was less than 0.01 and therefore even being conservative, there seems to be a relationship.

The exact physiological relationship between chlorophyll-α concentration, an indicator of phytoplankton and *P. maximus* density is unknown. *P. maximus* are filter feeders and the species composition of the phytoplankton has been found to affect growth of *P. maximus* in the Bay of Brest, France (Chauvaud, Donval et al. 2001). Information about the composition of the phytoplankton was not available in this study. It is possible that this relationship is related to the larval phase of *P. maximus*, as was suggested for the relationship between *A. rubens* and chlorophyll-α in Chapter 4. However, further investigations will be required to understand this relationship further.

Two other species showed significant (p=0.01) multi-linear relationships with environmental variables, 68% of the pattern in transformed *L. ciliaris* density was explained with a model containing mean annual silicate concentration and mean annual chlorophyll-α concentration (Table 5.6). Chlorophyll-α concentration had a negative relationship with *L.ciliaris*, whilst silicate concentration had a positive relationship. This relationship may appear complex, however a study in the north-east Irish Sea found that winter concentrations of both nitrate and silicate were closely associated with variations in the spring phytoplankton community (Kennington, Allen et al. 1999). Therefore these two variables are more than likely inter-related, although no correlation was found between them in Chapter 3. *L. ciliaris* is a secondary predator, which preys on both *A. rubens* and *P. maximus* (Guillou 1996, Beukers-Stewart, Vause et al. 2005). *P. maximus*, like *L.ciliaris,* showed a significant negative relationship with chlorophyll-α concentration. Therefore it is possible that the observed relationship between *L. ciliaris* and the two environmental variables found within the model, could be an indirect relationship linked to prey availability.

Equally, however, this relationship may be related to the larval phase of *L. ciliaris'* life history, of which very little information is available. Several studies around the world have reported changes in the composition of phytoplankton and zooplankton communities as a result of changes in environmental conditions (Hays, Richardson et al. 2005, Kirby and Beaugrand 2009, Francis, Scheuerell et al. 2012). Plankton species tend to have a tight coupling with environmental change (Hays, Richardson et al. 2005). In the Northern California Current Ecosystem a series of negative interactions (predation and competition) among zooplankton communities characterised the warm phases in climate (Francis, Scheuerell et al. 2012). A reduction in Antarctic krill has been linked to reduced food in the form of phytoplankton blooms in the summer and ice algae in the winter (Atkinson, Siegel et al. 2004, Hays, Richardson et al. 2005). In areas affected by the El Niño Southern Oscillation (ENSO), such as the Humboldt Current, warm water phases lead to reduced plankton production because of restricted nutrient upwelling (Alheit and Niquen 2004, Hays, Richardson et al. 2005).

Over the course of this environmental time series chlorophyll-α concentration significantly declined, which seems to fit with the findings of the above studies. However, the relationship between chlorophyll-α concentration and both *P. maximus* and *L.ciliaris* density is a negative one, suggesting that as chlorophyll-α decreases in concentration, the density of these two species increases. Perhaps this relationship is linked to a change in the plankton community that is only partially explained by chlorophyll-α concentration. Or perhaps in addition to environmental conditions causing reduced chlorophyll-α concentration, the recovery of both of these species (and others) within the closed area has increased the presence of their larvae within the plankton, which feed on phytoplankton. Adult *P. maximus* are also filter feeders and the increase in their density within the closed area may be contributing to the observed decreases in chlorophyll-α concentration. This is all speculation, as no direct evidence for any of these mechanisms was found, however, it seems the chlorophyll-α concentration plays a role in the life history of the benthic species studied here and in Chapter 4. It therefore appears that investigations into these relationships are required to further understand the relationships found in this study.

The final species to have a significant relationship with environmental variables was *Porania pulvillus*, which showed a significant positive relationship with both nitrate concentration and winter NAO index lagged by 2 years (Table 5.8). Interestingly this relationship was also found for this species in Chapter 4 at the Bradda Inshore fishing ground, except that environmental variables were lagged by only 1 year and *P. pulvillus* density was square-root transformed. Both models explained around 65% of the variation in *P. pulvillus* density, which indicates an actual relationship rather than an artefact in the data. The exact mechanism of both relationships is unknown and relatively little information about the biology of this starfish is known. However, the results of this investigation suggest that fishing pressure was not confounding the results of the dredge surveys in Chapter 4. These two environmental variables may explain why more dramatic increases in *P. pulvillus* density were not witnessed within the closed area. However, a more in depth analysis investigating the biology of *P. pulvillus* is required to fully understand the relationship found here.

The North Atlantic Oscillation (NAO) is the dominant mode of recurrent atmospheric variability over the North Atlantic (Hurrell 1995, Visbeck, Hurrell et al. 2001, Drinkwater, Beaugrand et al. 2010, Hurrell and Deser 2010). It influences a host of atmospheric variables such as wind speed and direction, air temperatures, heat and moisture transports and precipitation (Drinkwater, Belgrano et al. 2003, Drinkwater, Beaugrand et al. 2010). These variables in turn affect the marine environment by influencing the temperature and salinity of the water, vertical mixing and circulation patterns (Drinkwater, Belgrano et al. 2003, Drinkwater, Beaugrand et al. 2010, Hurrell and Deser 2010). Drinkwater et al (2003) review the various biological responses to fluctuations in NAO, which range from plankton to responses seen in marine mammals. It is therefore likely that *P. pulvillus* density is responding in some way to fluctuations in environmental conditions caused by the NAO. What perhaps is most surprising is that no other species had a significant (p=0.01) relationship with NAO index. Although the environmental model created for *C. pagurus* density did include a positive relationship with NAO index, the overall p-value was 0.03 and above the threshold set for this study. Like *P. pulvillus* the density of *C. pagurus* did not show a significant increase over the course of the time series (Figure 5.6). The influence of environmental variables may be part of the reason for this, particularly the influence of the NAO index.

5.5.3 Overall conclusions

The results of this study show that several benthic invertebrate species within the closed area found to the south-west of the Isle of Man have increased in density as the duration of protection increased. The most dramatic increase over time was in densities of the commercially targeted great scallop *Pecten maximus*, which came to dominate the benthic invertebrate megafaunal community. However, concurrent increases in the predatory starfish *A. rubens* (as observed on Georges Bank (Marino, Juanes et al. 2007)) were not witnessed, in fact the density of this species significantly decreased within the closed area. This in itself may have had an impact on the accelerated speed of recovery seen in *P. maximus* density witnessed from 2001 to 2006. In summary this study highlights the suitability of closed areas for protecting sessile benthic species of commercial importance such as *P. maximus.* It also suggests that the benefits of closed areas such as this can also spill over from within the closure and benefit adjacent fishing grounds.

This result is particularly significant and timely because for several years researchers, managers and conservationists around the world have been advocating increased use of protected areas for both biodiversity conservation and fisheries management (Roberts and Polunin 1993, Roberts 1997, Roberts, Bohnsack et al. 2001, Roberts, Halpern et al. 2001, Gell and Roberts 2003, Roberts, Hawkins et al. 2005, Fox, Mascia et al. 2011, O'Leary, Brown et al. 2012, Roberts 2012). Political will appears to be present, with the first network of high seas marine protected areas being implemented by OSPAR in 2010 (O'Leary, Brown et al. 2012). Also consultation has just closed in the U.K. seeking views on proposed Marine Conservation Zones around the coastline, due to be implemented later this year (2013) (although final plans for the network are yet to be decided). However, the idea of marine protected areas is often met with resistance by resource users, such as fishermen (Pita, Theodossiou et al. 2013). Therefore evidence of real benefits from a closed area such as this one in the Isle of Man can illustrate the advantages of closed area management. The Isle of Man Government is leading the way in Britain with this strategy of management, with several closed areas having been implemented in recent years (for a full review see Chapter 2).

It also appears that although environmental variables have had a significant relationship with some species within the community, they have not driven all of the trends in the density of every species within the closed area. In some cases it appears that predator-prey interactions have played a role in structuring this recovering community. It is likely that this benthic community will continue to change over the coming years and that the community witnessed here is a transient one (Micheli, Halpern et al. 2004). Therefore it is essential that monitoring continues within the closed area in a way that is comparable with the historical dataset used in this study. Long-term datasets are crucial in enabling understanding of how previously heavily fished areas recover and on the role climate change may play on species within a community (Hays, Richardson et al. 2005, Francis, Scheuerell et al. 2012)

5.6 References

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Chapter 6

General Discussion

This thesis has brought together long-term datasets of fishing effort, environmental variables and benthic species data, to give a unique perspective of the long-term trends in benthic community composition on the fishing grounds around the Isle of Man. As has been discussed in detail these fishing grounds have been exploited for more than 70 years (Bradshaw, Veale et al. 2002). The benthic invertebrate communities have been shown by other studies to have shifted in composition to communities composed of benthic invertebrate species that are relatively tolerant of fishing pressure (Bradshaw, Veale et al. 2002). However, prior to this thesis, the interaction between fishing disturbance and environmental variation in structuring these communities was unknown. Briefly summarised below are the key findings from this work.

6.1 Untangling the effects of environmental variables and fishing effort on benthic diversity.

Chapter 3 explored the temporal and spatial trends in benthic diversity, fishing effort and environmental variables. Temperature and chlorophyll-α concentration were both found to having significant temporal trends from 1992 – 2006. These two variables had a significant inverse correlation and appeared to be linked. Significant positive temporal trends in both Simpson's index and Shannon Index were found for two fishing grounds on the west coast of the Isle of Man (Bradda Inshore and Targets). In contrast, the two fishing grounds on the east of the island (East Douglas and Laxey) showed significant negative temporal trends in diversity. Analysis found a significant negative impact of fishing effort on diversity, however this relationship only explained approximately 7% of the trend in diversity. No clear relationship between the environmental variables and diversity was found. It is thought that the overall complexity of benthic community structuring and predator-prey interactions were responsible for these findings. It was also apparent that diversity indices can be lacking in terms of incorporating all aspects of community structure.

6.2 Benthic invertebrate species level responses to environmental variables and fishing effort

Chapter 4 explored the benthic invertebrate community dynamics at each fishing ground in more detail and highlighted the differences in community composition between the different fishing grounds. There were also clear differences in the responses of benthic species to fishing effort between grounds. Those benthic communities found on the fishing grounds to the south and west of the Isle of Man appear to be composed of relatively dredge-tolerant species, as few showed significant negative relationships with fishing effort. Whilst on the eastern side of the island, at East Douglas, fishing effort had a significant negative impact on most of the invertebrate species. This chapter also highlighted a clear negative relationship between temperature and the density of two echinoderms, *Asterias rubens* and *Porania pulvillus.* The exact biological mechanism for this relationship is unclear, but could potentially be affecting the larval life-history stages of these species. The results of this chapter highlighted the complex factors that interact to structure even relatively species-poor benthic communities and how potentially important interactions between species also play a role.

6.3 Investigating long-term benthic community dynamics within a closed area

This final data chapter investigated the long-term trends in benthic invertebrate species diversity and community composition in an area that has been closed to fishing since 1989. The results of this chapter concur with the findings of previous work and highlight the benefits of closed area protection not only for commercially important species, such as *Pecten maximus*, but also for the wider community. This work uncovered a reduction in *A. rubens* inside the closed area, contrary to findings in other, similar closures. The ramifications of this finding are important, because detractors of closed areas have suggested that a build up in *P. maximus* density would attract predators such as *A. rubens*, thereby reducing benefits of protection from fisheries. In addition to an explosion in the *P. maximus* population, several other benthic invertebrate species benefited from a cessation of fishing effort. Finally, the role of environmental variables was investigated and several significant relationships were found, including a positive effect of chlorophyll-α levels on diversity overall, but a negative influence on the density of certain species. However, it appeared that predator-prey interactions were also playing a role in structuring the community.

6.4 Wider implications

Although long-term studies have been conducted on the benthic communities around the Isle of Man before (Hill, Veale et al. 1999; Bradshaw, Veale et al. 2002) this is the first to attempt to incorporate both fishing effort and environmental data over a long period of time. The overall findings have highlighted a series of benthic communities that have been chronically impacted by scallop dredging yet, in their present form appear quite resilient to moderate intensity fishing. However, when fishing pressure exceeded the tolerances of benthic species, negative impacts occurred. This highlights the need for comprehensive management of all fisheries, which the Isle of Man Government has been developing for many years.

Management of fisheries is only one portion of the picture, because as the results of this thesis show, the benthic invertebrate communities found on these fishing grounds are also being structured by a complicated set of environmental variables. Even the different environmental variables are interacting with each other, to further complicate the picture. On the grounds that have been fished hardest for longest, such as Bradda Inshore, the relationships between environmental variables and invertebrates species seem to be explaining more of the variation in community composition than fishing effort. This makes management of the area particularly difficult, because not all species may respond in the same way to environmental change or even respond to the same environmental variables. For example, there have been many studies investigating the mis-match that occurs when marine plankton species use different cues for life history events (Hays, Richardson et al. 2005; Doney 2006; Kirby, Beaugrand et al. 2008; Francis, Scheuerell et al. 2012; Klauschies, Bauer et al. 2012). In addition to this already complicated picture, interactions between different species also appear to be structuring the benthic communities around the Isle of Man. These predator-prey interactions make predictions particularly difficult and it has been suggested that they may be as, if not more, important for community dynamics than individual species responses to environmental variables (Kordas, Harley et al. 2011).

There have, however, been several encouraging results found in this long-term study, particularly, from within the closed area. Areas closed to fishing have been shown to have numerous benefits, including increases in abundance, density, biomass and average size of organisms (Halpern and Warner 2002; Halpern 2003). By removing fishing pressure from an area the community can recover and they have been found to increase biodiversity (Dayton, Sala et al. 2000). In addition by protecting benthic habitats from the impacts of towed fishing gear they can recover and increase in structural complexity, which in turn provides suitable substrate for the settlement of the larvae of commercially exploited species, such as the scallops *Pecten maximus* and *Aequipecten opercularis* (Howarth, Wood et al. 2011). Within the closed area in this study, the density of several benthic invertebrate species increased over the time series. Not least *P. maximus*, which came to dominate the invertebrate community studied. This increase in *P. maximus* density and dominance within the community was primarily why diversity did not show any significant trend. However, despite this it is clear that even on a fishing ground that has been exposed to long-term fishing pressure, if an area is closed to fishing recovery of the community can take place.

Closed areas or marine protected areas (MPAs) have the potential to build up stocks of commercially important species like *P. maximus* (Beukers-Stewart, Vause et al. 2005). However, one closure on its own will do little to benefit the wider ecosystem (Roberts, Halpern et al. 2001), either around the Isle of Man or in the Irish Sea. The Isle of Man Government has in the last few years implemented several additional closed areas around the island, including a marine nature reserve (see Chapter 2 for details). The results of this work support the creation of additional reserves around the island not only as a fisheries management tool to ensure protected populations of scallops, but also as a means to allow recovery of benthic communities. The benefits of these closures should include spillover of benthic larvae into surrounding fishing grounds. This would benefit commercial interests in terms of providing resilience within scallop communities, which have notorious boom-bust cycles in recruitment (Beukers-Stewart, Vause et al. 2005). Indeed, this study adds to others illustrating the benefits that MPAs can provide in temperate waters in general, not just tropical waters as previously suggested by some authors (Fernberg, Caselle et al. 2012). These findings are particularly timely and relevant in the UK as it currently struggles to implement a network of protected areas (Marine Conservation Zones) around its coastline.

6.5 Areas for future research

A key relationship that this thesis highlighted was the inverse correlation found between temperature and chlorophyll-α (Chapter 3). As has been discussed throughout this thesis there are several potential reasons for this correlation, ranging from a regional-scale oscillation in climatic variables (Martinez, Antoine et al. 2009) to a temperature-mediated increase in heterotrophic zooplankton, which predates on phytoplankton (O'Connor, Piehler et al. 2009). However, no information about the composition of the phytoplankton was available in this study. A key area for future research therefore, is to attempt to understand the long-term trends in the plankton communities around the Isle of Man, in a similar way to work that has been done in the North Sea (Beaugrand, Brander et al. 2003; Kirby, Beaugrand et al. 2007; Kirby, Beaugrand et al. 2008). This would involve not only plankton analysis, but also an analysis of the relationships with both environmental variables and the benthic community.

Another aim of any planktonic study should also be a better understanding of the sources and sinks of benthic larvae to the fishing grounds around the Isle of Man. Although modelling work has been done (Neill and Kaiser 2008), the patterns of larval dispersal around the Isle of Man are not well understood. Not only would a better understanding of this aid management and planning for the commercial fisheries, it would also help strategically plan where to place future closed areas to maximise their benefits (Roberts, Andleman et al. 2003).

The results of this thesis highlight the importance of long-term monitoring of closed areas and a recommendation for future research is to investigate the dynamics of the newly created closed areas around the Isle of Man. Regular, robust sampling is essential to enable useful long-term investigations like this one. In addition to this, baseline data is also very important when analysing closed area trends (Roberts, Andleman et al. 2003).

Finally, one area of research which is rather broad in range, but nonetheless would be incredibly useful, is experimental studies of invertebrate species behaviours and responses to environmental fluctuations. Throughout this research it has been noticed that most recent work has take a broad-scale view of ecosystems and community dynamics. However, when looking for information about individual species behaviour, biology and dynamics there were very few modern studies. In fact for *Porania pulvillus* one paper used for background reading was almost a hundred years old. It seems almost unfashionable nowadays to focus on one or two species and study them in detail. However, this research has shown that it is often this species specific-detail that is lacking from broad-scale studies such as this one. Therefore an area for future research that would be very useful, would be to investigate the behaviour, biology and individual responses of some of the more dominant invertebrate species studied here, for which there is a paucity of recent information. In an era of increasing human populations and global environmental change, from ocean warming to acidification, improved knowledge and management of our seas is now more crucial than ever.

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