Measuring the Effects of Scotland's First Fully Protected Marine Reserve

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Abstract

In September 2008, Lamlash Bay became Scotland’s first and only fully protected marine reserve. Dive surveys conducted over a period of four years revealed the abundance of juvenile scallops to be 2-5 times greater within this marine reserve than outside. Generalised linear models showed that this greater abundance was related to a greater presence of macroalgae and hydroids growing within the boundaries of the reserve. My study also indicated that the age, size and reproductive biomass of adult king scallops were all significantly greater within the reserve. Similarly, potting surveys conducted over a two year period showed European lobsters were significantly larger and more fecund within the reserve than on neighbouring fishing grounds. However, differences between the reserve and outside were less clear after I explored benthic and fish communities within and around Lamlash Bay. Live maerl, macroalgae, sponges, hydroids, eyelash worms, feather stars, parchment worms and total epifauna were all significantly more abundant within the reserve than on neighbouring fishing grounds. In contrast, comparisons of the abundance of mobile benthic fauna and fish revealed no difference between the reserve and outside. This was likely due to the young age of the reserve (5 years) and its small size (2.67km^2), both of which are known to reduce the effects of marine reserves on mobile species. Overall, my results are consistent with the hypothesis that marine reserves can promote the density, size and age structure of commercially exploited species to return to more natural levels. My results also support that closed areas can encourage the recovery of seafloor habitats, which can increase the recruitment of scallops, cod and other commercially valuable species.

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Chapter 1. Introduction

1.1. The importance and state of the world's oceans

Earth processes and human welfare are strongly linked with the oceans. Marine ecosystems play a key role in regulating the climate and atmosphere, receiving and assimilating wastes, protecting coastlines and sequestering carbon (Covich et al. 2004; Palumbi et al. 2009). They also supply food and other resources, and provide tourism, recreational, cultural, spiritual and aesthetic benefits (Cooley et al. 2009; Barbier et al. 2011). Despite their significance, human impacts are causing an accelerating loss of populations and species in virtually every marine ecosystem on Earth (Worm et al. 2006; Valdes et al. 2009; Barbier et al. 2011). Through a combination of land conversion, overexploitation, pollution and climate change, an estimated 50% of saltmarshes, 35% of mangroves, 30% of coral reefs, and 29% of seagrasses have been lost or severely damaged worldwide since the early 1980s (Valiela et al. 2001; Kappel 2005; Orth et al. 2006; FAO 2007; Waycott et al. 2009). By impairing the ecosystem services oceans provide, a growing number of studies suggest that the declining state of the seas is responsible for a global increase in species invasions, harmful algal blooms, anoxic dead zones, fish kills, fishery and beach closures, as well as damage from flooding and storm events (Worm et al. 2006; Barbier et al. 2011; Howarth et al. 2013). These changes can negatively impact resource extraction and human welfare (Brand 2009).

In addition to the important role the oceans play in regulating Earth processes, marine ecosystems have been exploited by humans for thousands of years (Roberts 2007) and provide one of our most valuable sources of food (Ye et al. 2013). Worldwide, people obtain over 15% of their animal protein intake from fish and other seafood (Sumaila et al. 2011; FAO 2012; Ruckelshaus et al. 2013). This figure is much higher for coastal communities in developing countries, often reaching over 50% (Cooley et al. 2009; Shelton 2014). Marine resources also generate substantial levels of employment and income by supporting the fishing industry, tourism and recreational angling. The fishing industry alone generates between $80-85 billion annually and employs an estimated 43.5 million people (Ye et al. 2013; Shelton 2014), while the processing, marketing, distribution and supply businesses associated with this employs another 200 million people (Cochrane et al. 2009; Sumaila et al. 2011). However, a number of drivers threaten these livelihoods and global food security.

Recent technological advancements coupled with rising demand have caused the intensity and geographic reach of fisheries to greatly escalate over the last two centuries (Roberts 2007; Watson et al. 2013; Howarth et al. 2013). As a result, an estimated 70% of the world's fish populations are currently either fully exploited, overexploited, depleted or have collapsed entirely from overfishing (FAO 2012), and the proportion of catches originating from declining stocks is rapidly increasing (Jackson et al. 2001; Pauly et al. 2002; Worm et al. 2006; Pauly 2008; Costello et al. 2012). Some authors argue that the global decline of fish stocks is slowing and that fisheries management is showing signs of improvement (e.g. Hilborn 2007a, 2007b; Worm et al. 2009; Branch et al. 2011; Fernandes & Cook 2013). However, these improvements are localized, confined to a small number of developed countries such as the USA, Australia, New Zealand and Iceland. Fishing grounds in Europe largely remain in a state of decline (Guénette & Gascuel 2012), and it has been recently argued that unassessed fisheries, which account for more than 80% of fisheries worldwide, are in a substantially worse condition than most assessed fisheries (Costello et al. 2012). Despite global fishing effort growing 10-fold since 1950, fishery catches have not increased since the 1980s (FAO 2012; Pitcher & Cheung 2013). Our inability to increase global landings or halt their slow decline poses a serious problem for food security as the global human population is expected to increase from 7 to 9 billion by 2050, meaning the demand for seafood commodities will continue to increase (Godfray et al. 2010; Lam & Pitcher 2012; Watson et al. 2013; WorldBank 2013).

To some extent, aquaculture has allowed global seafood production to keep pace with increasing protein demand. During the last three decades, world aquaculture production has increased from 5 million to 63 million tons (FAO 2012; WorldBank 2013) and currently accounts for approximately 50% of all seafood production (FAO 2006; Jiang 2010). Unfortunately, in its current state, aquaculture is associated with a large number of negative environmental and ecological impacts including habitat loss, disease transmission, environmental contamination and genetic pollution (Davenport et al. 2003). Furthermore, much of the world's aquaculture industry relies on feeds derived from marine capture fisheries, exerting exploitation pressure on the wild fish stocks they are meant to be protecting (Naylor et al. 1998, 2000; Black 2008; Godfray et al. 2010). Until these problems are resolved, aquaculture's potential as a true sustainable alternative to capture-fisheries will not be fulfilled.

These points highlight the vital importance of the health of the oceans for human welfare. They present a clear and strong argument to better protect marine ecosystems, and to manage the resources they provide more effectively and sustainably.

1.2. The physical and ecological impacts of fishing

The poor state of many of the world's fisheries is mostly due to unsustainable levels of exploitation and the physical and ecological impacts associated with fishing gears. The principal and most direct effect of fishing is a reduction in the abundance of target species. When exploitation levels are high, the number of adults within a stock can be reduced to such low levels that it reduces both the profitability of the fishery and recruitment (i.e. the number of individuals which survive juvenile development to enter the fishery) which can lead to the sudden collapse of a stock (King 1995; Jennings et al. 2001).

High levels of fishing can also negatively impact recruitment by truncating age and size structures (Beamish et al. 2006). This can occur when larger, older individuals are preferentially targeted; as is commonly practiced since large individuals often yield the greatest economic return (Law 2000). Contributing to this, many fisheries are also regulated by minimum legal landing sizes and mesh in order to protect juveniles and allow adults the chance to spawn before they become susceptible to fishing mortality (Kaiser et al. 2005; Conover et al. 2009; Fenberg et al. 2012). Additionally, mounting evidence suggests that selective harvesting for larger individuals can promote changes in life history traits, including a shift in maturation to earlier ages and sizes (de Roos et al. 2006; Jørgensen et al. 2007). All these processes mean fewer individuals are able to reach the age and sizes they would naturally attain compared to if the population was undisturbed. The problem with this is two-fold. Not only are larger individuals economically more valuable, they also have more developed reproductive organs capable of producing substantially more eggs (Froese 2004). A decline in the abundance of larger-bodied individuals can therefore have a disproportionately high impact on reproductive output and recruitment, threatening the ability of stocks to breed at sustainable levels in the future (Roberts et al. 2005). Age truncation has also been shown to increase the variability of fisheries landings and reduce the capacity of populations to buffer environmental events (Hsieh et al. 2006).

Overexploitation of stocks can also cause the mean trophic level of the species targeted by fisheries to decline, a process known as "fishing down / through the food web" (Pauly et al. 1998, 2002; Steneck et al. 2002; Myers & Worm 2003, 2005; Essington et al. 2006; Estes et al.

2011). This occurs when stocks of large-bodied fish become overexploited, and in their place, new species are targeted (Myers & Worm 2003; Hughes et al. 2007). Generally, this has involved fishers switching from targeting large predatory finfish to smaller pelagic species and bottom-dwelling invertebrates (Pauly et al. 1998, 2002). The Northwest Atlantic, for example, was once home to some of the world’s richest fishing grounds for large predatory groundfish, particularly cod and haddock (Acheson & Steneck 1997; Jackson et al. 2001). However, over the past 30 years, fisheries within this region have experienced widespread collapse, and landings from new fisheries targeting previously unexploited species such as sea urchins (*Strongylocentrotus droebachiensis*), lobster (*Homarus americanus*), snow crab (*Chionoecetes opilio*) and shrimp (*Pandalus borealis*) have come to dominate (Worm & Myers 2003; Frank et al. 2011; Howarth et al. 2013). Likewise, the overexploitation of tuna (mainly *Thunus albacares*), hake (*Merluccius merluccius*), mackerel (*Scomber scombrus*) and anchovy (*Engraulis encrasicolus*) led to a decline in European stocks during the 1950’s and 70’s. Despite the decline, overall landings remained relatively stable as this decrease was compensated by the exploitation of new species like monkfish (*Lophius piscatorius* and *Lophius budegassa*), cephalopods and crustaceans (Guénette & Gascuel 2012). These results indicate that present rates of exploitation are unsustainable and imply major changes in the structure of marine food webs.

In addition to reducing the abundance of target species, fisheries also capture a wide variety of non-target organisms, which can include species targeted by other fisheries. For example, longlines and gillnets are well known for generating substantial levels of by-catch of fish, sharks, sea turtles, cetaceans and seabirds (e.g. Baum et al. 20003; Lewison et al. 2004). Furthermore, gillnets and longlines that become lost or abandoned are capable of generating by-catch (“ghost fishing”) for many years after their loss (Japp & Wilkinson 2007). Likewise, scallop dredges are also recognized for catching a wide variety of non-target species including fish, crustaceans, echinoderms, molluscs and cephalopods (Bradshaw et al. 2001; Craven et al. 2013). Studies in the Irish Sea, for example, report four items of by-catch for every scallop captured, and that the majority is discarded damaged, dying or dead (Beukers-Stewart et al. 2001; Jenkins et al. 2001; Hinz et al. 2012). When entire fleets are considered, the number of non-target individuals removed by scallop dredgers can be quite substantial; the dredge fleet operating in the English Channel is estimated to catch 3.3 million non-target fish per year (Enever et al. 2007). Despite this seemingly large impact, scallop dredges are considered to be relatively “clean” compared to other types of mobile fishing gears, such as beam and otter trawls (Kaiser 2007). North American shrimp trawlers, for instance, have been reported to catch up to 15 non-target organisms for every shrimp landed (Hall et al. 2000). By-catch ratios are also very high in the Scottish prawn trawl fishery, generating up to 9 kg of by-catch for every 1 kg of prawns caught (Bergmann et al. 2002a). Again, mortality rates are high and the majority of by-catch is discarded (Bergmann & Moore 2001). High levels of mortality can also occur for the non-target organisms that come into contact with fishing gears but remain on the seabed uncaptured. For example, over 75% of the benthic megafauna which encounter scallop dredges remain on the seafloor but can display even higher levels of mortality than the by-catch landed on deck due to being passed around, through or under the heavy fishing gear (Beukers-Stewart et al. 2001; Jenkins et al. 2001).

In coming into contact with the seafloor, fishing gears can generate a number of physical impacts that can further contribute to the unsustainability of fisheries. Trawl gear can be extremely heavy, requiring combinations of bobbins, rock hoppers, warps and chains to prevent the net from becoming snagged on uneven surfaces and to maximise catch rates (Japp & Wilkinson 2007). Scallop dredges, such as the Newhaven dredge, are also heavy, and are equipped with spring-loaded teeth that dig into the seabed or scrape hard substratum to rake out scallops living in or on the surface layers of sediment (Eleftheriou & Robertson 1992; Jennings et al. 2001). Such gears cause substantial physical disruption of seafloor habitats by ploughing sediments and damaging epifaunal organisms attached to the seabed, such as corals, sponges, hydroids and maerl (Dayton et al. 1995; Jennings & Kaiser 1998; Kaiser et al. 2000). However, these organisms are functionally important to marine ecosystems as they provide an element of 3-dimensional structure to otherwise featureless seafloors. In doing so, they supply important refuges for small / juvenile fish from predators and unfavourable environmental conditions (Monteiro et al. 2002; Ryer et al. 2004; Cacabelos et al. 2010), represent important feeding sites for fish and invertebrates (Bradshaw et al. 2003; Warren et al. 2010), and provide impotant substrate for the settlement of scallop spat and a range of other organisms, including the settlement of further epifauna (Beukers-Stewart & Beukers-Stewart 2009; Howarth et al. 2011). Such locations are therefore often referred to as “nursery areas” as they tend to be highly productive, support high levels of juvenile density, growth and survival, and contribute disproportionally to the production of adult recruits (Beck et al. 2001; Kamenos et al. 2004a; Gibb et al. 2007; Laurel et al. 2009). Commonly cited nursery areas include maerl beds (Kamenos et al. 2004b, 2004a; Hall-Spencer et al. 2006), seagrass beds (Warren et al. 2010) and areas of dense macrophytes / macroalgae (Christie et al. 2007; Cacabelos et al. 2010; Howarth et al. 2011), all of which have been shown to harbour high densities of commercially exploited species such as spider crabs (*Maja squinado*), juvenile cod, edible crab (*Cancer pagurus*) and edible sea urchins (*Echinus esculentus*; see previous references). In addition, many epifaunal species support unique micro-communities. For example, caprellid amphipods on hydroids, the range of invertebrates associated with kelp forests, or the diversity of organisms associated with pomatocerid tube worm heads (Kaiser et al. 1999; Airoldi et al. 2008). Consequently, the damage sustained by nursery habitats from fishing gears can have severe consequences on the recruitment of commercially important species and dramatically reduce an area's capacity to support other biodiversity (Collie et al. 1997; Bradshaw et al. 2001, 2003; Kaiser et al. 2005; Howarth et al. 2011).

In addition to damaging nursery habitats, towed fishing gears can also have a number of other physical impacts on the seabed. Overall, the general effect is that they cause homogenization of sediments and topography through penetration, mixing and flattening of sediments (Collie et al. 2000). Natural seabed features such as ripples, pits and burrows can all be eliminated by passing fishing gears. In their place, dredges and trawls can sculpt the sediment into ridges that can persist for up to three years in low wave / tide energy environments (Hall-Spencer & Moore 2000). Dredging and trawling can also move and / or remove significant quantities of stones and boulders from fishing grounds (Eleftheriou & Robertson 1992; Bradshaw et al. 2002) which has been reported to cause shifts in the particle size of surface sediments (Hall-Spencer & Moore 2000). Such changes in sediment topography can alter near bed hydrodynamics and lead to the deposition of fine sediments (Probert 1984; Dernie et al. 2003). The removal or disturbance of surface sediments can also change patterns of nutrient cycling or / and carbon flux, for example, by exposing underlying anaerobic sediments (Watling et al. 2001; Kaiser et al. 2002). Furthermore, the disturbance caused by mobile gears can also re-suspend soft sediments, nutrients, eggs, cysts and small organisms buried within the sediment (O'Neill et al. 2013). Particular concerns have been raised about this as high levels of suspended sediment can smother surrounding sessile marine life, burying important habitats such as corals and maerl, and clogging the feeding and respiratory organs of filter feeding organisms, such as mussels and scallops, thereby impacting their reproduction (Brand 2006; Dale et al. 2011; Szostek et al. 2013).

1.3. Marine reserves and marine protected areas (MPAs)

In response to the wide range of impacts fishing can have marine ecosystems, closing areas to some or all types of fishing through the implementation of marine protected areas and marine reserves is becoming an increasingly utilised management tool for the conservation of marine biodiversity, ecosystem services and fisheries resources (Roberts et al. 2005; Halpern et al.

2010). The global coverage of MPAs has increased rapidly in recent years; at an average rate of 4.6% per year since 1984 (Fox et al. 2012). The past three years alone have seen the global coverage of MPAs double, going from 1.17% in 2010, to 2.5% in 2013 (Marinesque et al. 2012; Fox et al. 2012; Ye et al. 2013). At first glance, this network looks impressive. Then again, the degree of protection afforded by MPAs can vary greatly. In fact, less than 2% of the world's oceans are within fully protected marine reserves which ban all fishing methods within their boundaries, and the majority of MPAs worldwide are poorly enforced, meaning they have little or no conservation value (Edgar et al. 2014; Halpern 2014). Hence, many argue that the protection of the oceans is still greatly lacking and that the creation of MPAs has not kept pace with human impacts (Chape et al. 2005; Wood et al. 2008; Fox et al. 2012).

The global coverage of marine protected areas (MPAs) is set to increase over the next decade following a large number of recently established policies and initiatives (Metcalfe et al. 2013). Globally agreed marine protection targets, such as the Convention on Biological Diversity's (CBD) '*Aichi Target*' are encouraging many governments to establish or expand existing MPA networks within their jurisdictions (Wood et al. 2008; CBD 2011; Harrop 2011; Wood 2011). This interest is reflected in the European Union (EU) as the Marine Strategy Frameworks Directive (MSFD), Birds and Habitats Directives, OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic), HELCOM (Helsinki Commission) and Barcelona regional seas conventions, have all initiated the process of establishing a coherent network of MPAs within European waters (Fenberg et al. 2012; Metcalfe et al. 2013). On a national level, the planned implementation of Marine Conservation Zones (MCZs; England, Wales and Northern Ireland) and Scottish MPAs (Scotland) will all lead to the creation of a network of MPAs around the United Kingdom (UK; Jones 2012; JNCC 2013). All these measures intend to achieve a variety of management goals; principally to conserve biodiversity and promote the sustainability of fisheries (Pomeroy et al. 2005; Metcalfe et al. 2013).

The growing use of MPAs as a management tool has co-occurred with a paradigm shift in fisheries management; with perspectives shifting from traditional single-species management to more holistic approaches where management priorities begin with the ecosystem rather than the target species (Pikitch et al. 2004; Zhou et al. 2010). The aim of such 'ecosystem-based fishery management' is to sustain healthy marine ecosystems and the fisheries they support by addressing some of the unintended consequences of fishing, such as the mortality of non-target organisms and the physical impacts of fishing gears (Link 2002; Zhou et al. 2010; Stokesbury et al. 2011). Theory suggests that integrating ecosystem level concerns into fishery management will result in the maintenance of more complete ecosystems, and in doing so, will generate numerous benefits that flow back to the species targeted by fisheries (Jennings & Kaiser 1998).

One way in which MPAs and marine reserves can achieve ecosystem and fishery benefits is by maintaining the integrity of benthic habitats through excluding the use of towed demersal fishing gears, such as dredges and trawls. For example, the abundance of sea fans (increase of 636%), bryozoans (increase of 385%), branched sponges (increase of 414%) and hydroids (increase of 229%) were all found to increase within an MPA compared to surrounding fishing grounds in Lyme Bay, England, after just three years of protection (Sheehan et al. 2013a,b). Such species are known to improve survivorship of juvenile fish by acting as important nursery areas (Auster et al. 1996; Bradshaw et al. 2001, 2003) and for encouraging the settlement of scallop spat (Howarth et al. 2011). In fact, the commercially valuable king scallop (*Pecten maximus*), which is the main target species of the excluded fishery, was also found to be in a state of recovery within the MPA (Sheehan et al. 2013b). Seafloor habitats can also recover through cascading ecological effects, whereby early changes trigger subsequent changes, and so on. For example, the designation of Mombasa Marine National Park in Kenya was followed by significant increases in the predators of sea urchins, which then led to reduced grazing and bioerosion of reefs, and subsequent coral recovery after 10 years of protection (McClanahan & Mangi 2000). Similarly, the establishment of two marine reserves in New Zealand led to a number of sea urchin-dominated barrens reversing back to dense kelp forest within 20 years (Shears & Babcock 2003). Evidence suggested that this was due to an increase in the density and body size of predators of sea urchins, namely snappers (*Pagrus auratus*) and rock lobsters (*Jasus edwardsii*; Langlois & Ballantine 2005).

The rising interest in MPAs is also supported by a growing number of scientific studies which indicate that closing areas to fishing can result in direct changes to fish populations within their boundaries. For instance, several meta-analyses reveal that the establishment of protected areas can lead to an increase in biomass, density and average body size of commercially targeted species (Halpern & Warner 2002; Halpern 2003; Micheli et al. 2004; Lester et al. 2009; Edgar et al. 2014). One meta-study in particular found the biomass of exploited species located within MPAs increased by an average of 166% and by 446% respectively (Lester et al. 2009). In many cases, differences in population density and biomass between protected and unprotected areas can be much greater. For example, the biomass of spiny lobsters was 25 times greater within a New Zealand marine reserve compared to previously recorded levels after 22 years of protection (Shears et al. 2006). Even greater densities of the endangered dusky grouper (*Epinephelus marginatus*) were recorded within the Cabo de Palos Marine Reserve in Spain, increasing by 40-fold after just 10 years of protection (García-Charton et al. 2008).

In allowing the abundance, biomass and body size of exploited species to return to more natural, pre-exploited levels, MPAs can generate reproductive benefits. Evidence suggests that higher levels of reproduction within MPAs can result in greater production of larvae, juveniles and adults which can then disperse ("spillover") to grounds outside the closed area where they contribute to fishery landings (McClanahan & Mangi 2000; Beukers-Stewart et al. 2005; Pelc et al. 2010; Harrison et al. 2012). This idea is supported by a number of recent molecular studies which have detected exports of fish and mollusc larvae originating from within marine reserves at distances of several kilometres away (Cudney-Bueno et al. 2009; Planes et al. 2009; Pelc et al. 2010). As a combined result of spillover and larval export, increased landings are a regularly reported phenomenon after the creation of MPAs (Roberts & Hawkins 2012). Goñi et al. (2008), for example, documented higher catch rates and profits close to the boundaries of six Mediterranean MPAs for several different fishing methods targeting a wide variety of different fish and shellfish species. Likewise, a study off the Isle of Man, found the density of king scallops to be 30 times greater within a closed area than when first protected (Beukers-Stewart et al. 2005; Beukers-Stewart & Brand 2007). The reduction in fishing mortality also allowed scallops within the MPA to reach much older and larger sizes, causing the reproductive biomass of king scallops to reach 33 times greater compared to neighbouring fishing grounds. Evidence suggests that the greater reproductive biomass within the MPA has resulted in higher rates of breeding and larval export, which has boosted populations outside the closed area and increased fishery landings (Beukers-Stewart et al. 2004, 2005; Beukers-Stewart & Brand 2007; Neill & Kaiser 2008).

Overall, the establishment of MPAs has yielded benefits, but the picture is uneven. Not all MPAs have encouraged ecosystems and fish stocks to recover. For instance, an analysis of 14 years of data from a protected area in Belize demonstrated good recovery of predatory reef fish, but only a weak response of herbivores (McClanahan et al. 2011). Correspondingly, there was little change in herbivory and coral cover as the reefs remained in an algal-dominated state. Likewise, Sciberras et al. (2013) found no difference in the abundance of scallops and epifaunal assemblages between unprotected sites and two MPAs in Wales (one closed to fishing and one open seasonally) over a period of 23 months. Whilst in the Irish Sea, stocks of

Atlantic cod have shown little or no signs of recovery despite the use of a seasonal closed area for over five years (Kelly et al. 2006).

The differing results for MPAs beg the question of why some closed areas are successful and some are not. What factors prevent or limit recovery are not always clear but are thought to include, amongst others (references below): (i) density-dependent effects (e.g. altered predator–prey ratios, recruitment failure through the Allee effect); (ii) local extinction of key functional groups; (iii) recovering functional groups not promoting return to a previous state (e.g. many reef-based herbivores do not eat late succession macroalgae and therefore do not encourage algal-dominated reefs to return to coral-dominated states) (iv) competition with/or predation by invasive species; (v) habitat alteration; (vi) life-history traits (e.g. fast-growing species such as herring are more likely to recover than long-lived species such as cod and halibut); (vii) poor enforcement and illegal harvesting; and (viii) emigration of animals outside boundaries because of continuous habitat or inadequate size of reserve (Hutchings & Reynolds 2004; Hooper et al. 2005; Hughes et al. 2005; Diaz-Pulido et al. 2009; McClanahan et al. 2011; Edgar et al. 2014).

A recent analysis by Edgar et al. (2014) found MPAs displayed a poor overall performance worldwide. However, this was due to MPAs being ineffectively designed and managed. In contrast, when MPAs were fully protected, well enforced, large (> 100 km^2), isolated by deep water or sand, and established for 10 years or more, the analysis revealed that MPAs contained, on average, twice as many large fish species, five times more large fish biomass, and fourteen times more shark biomass than fished areas. Therefore, more emphasis is clearly needed on better MPA design, management and enforcement to ensure that MPAs achieve their desired conservation and fishery goals.

Not only do some MPAs fail to generate any benefits, establishing MPAs can also displace fishing effort to surrounding areas (Bohnsack 2000; Kaiser 2005), which can cause wider environmental damage (Dinmore et al. 2003) and reduce profits through the loss of fishing grounds (Rassweiler et al. 2012). Hence, MPAs only truly yield fishery benefits when these negative effects are adequately offset by increased recruitment and landings. There are, however, a diverse range of other management tools available. Enforcing the use of fishing gears that cause less damage to habitats and select for specific species, sizes and ages is one way to reduce exploitation and damage to marine ecosystems (Pitcher and Lam 2010). For example, cod biomass in the Baltic Sea was found to triple between 2005 and 2009 after a ban on trawling led to a sudden reduction in fishing mortality (Cardinale and Svedäng 2011).

Likewise, reducing fishing effort through reductions in quotas, total allowable catch and fishing capacity have all been shown to promote recovery in a number of fish stocks (Beddington et al. 2007; Worm et al. 2009). Then again, whilst effort and gear restrictions can help restore the abundance of targeted species, they do not necessarily lead to the recovery of biodiversity and the wider ecosystem (Pitcher & Lam 2010). Overall then, it is apparent that one management tool alone is not enough to promote recovery of stocks and ecosystems. It is therefore widely agreed that a combination of managing fishing effort, fishing gears and establishing protected areas, all of which have received mutual consent from managers, fishermen and other stakeholders, is the most effective way to achieve both fisheries and conversation objectives (Hilborn 2007; Worm et al. 2009; Khan & Neis 2010).

1.4. The Firth of Clyde

The Firth of Clyde is a large inlet of sea that extends over 100 km into Scotland's west coast. The area recently gained considerable media attention after it was described as being one of the most degraded marine environments in the UK ("BBC Springwatch" 2007, "BBC Panorama" 2010; Clover & Smith 2010; Smith 2010; The Economist 2013) primarily due to over a century of intensive fisheries exploitation (Thurstan & Roberts 2010). During the 19th century and before, landings in the Clyde were spread between many different species and targeted by an artisanal fleet using sailing vessels, traps, lines and nets (Thurstan & Roberts 2010). These fisheries targeted a wide range of species including herring (*Clupea harengus*), cod, mackerel, whiting (*Merlangius merlangus*), haddock, turbot (*Psetta maxima*), skate (*Dipturus batis*) and even basking sharks (*Cetorhinus maximus*) were caught for their meat and oil (Thurstan 2007; Thurstan & Roberts 2010). Fishing effort steadily increased during the early 1900s as a greater proportion of the fleet began to take advantage of technological advancements such as beam trawls, otter trawls, Newhaven scallop dredges and steam- and diesel-powered engines. Despite, and likely because of, increasing fishing effort and two spatial closures to trawling being revoked in the late 20th century (Heath & Speirs 2011), large catches of fish were not sustained, and landings of demersal species, such as haddock and cod, declined by more than 90% during the early 1990s (Thurstan & Roberts 2010). As a result, a remarkable shift has been observed over the last two decades in the groups of species landed from the Clyde. In 1985, finfish made up more than 60% of the landings by weight and 37% by value, but by 2008, this had fallen to just 2% by weight and 0.5% by value (Howarth et al. 2013). Now, *Nephrops* prawns (*Nephrops norvegicus*) are the most valuable fishery in the Clyde, making up 84% of landings by weight and 87% by value. The remaining percentages are composed solely of other invertebrates such as king scallops, edible crabs and European lobster (*Homarus gammarus*) (Howell et al. 2006; Keltz & Bailey 2010). Since 2003, the only landings of fish in the Clyde have been as by-catch from the *Nephrops* trawl fishery (Heath & Speirs 2011).

The changes in the Firth of Clyde are problematic for a number of reasons. Firstly, the entire fishing fleet now relies on just a handful of invertebrate species. If for any reason these stocks were to suddenly collapse, the social and economic consequences would be severe as there are few species left to target (Howarth et al. 2013). Secondly, the majority of these invertebrate fisheries are targeted by vessels towing mobile gears (Murray & Cowie 2011; Dobby et al. 2012). As mentioned above, such gears are associated with high levels of by-catch, particularly of juvenile fish, which may prevent the recovery of bottom fish populations in the future (Bergmann & Moore 2001; Bergmann et al. 2002a, 2002b). Mobile fishing gears also cause substantial damage to seafloor habitats and observations suggest the health and extent of maerl, seagrass and other complex habitats have deteriorated greatly in the Clyde (Hall-Spencer & Moore 2000; Kamenos et al. 2004c; Howarth et al. 2011). The decline in seafloor habitats will likely hinder any future recovery of fish stocks as these organisms provide nursery habitats for a number of juvenile fish, scallops and other invertebrates (Bradshaw et al. 2001; Howarth et al. 2011). Furthermore, many commercially exploited fish species are known to spend significant parts of their juvenile life stage in inshore nursery habitats, migrating progressively offshore as they age and develop (Zeller & Pauly 2001; Espeland et al. 2007; Knutsen et al. 2007; Gibb et al. 2007). Interfering with this transition will therefore also contribute to the decline of commercially important fisheries further out at sea.

In response to the decline in habitats and fish stocks, residents on the Isle of Arran, the largest island in the Firth of Clyde, became increasingly concerned for their local marine environment and formed a group known as the Community of Arran Seabed Trust or “COAST” (www.arrancoast.com). In September 2008, after a decade of campaigning for better protection of their seas, COAST helped to establish Scotland’s first and only fully no-take marine reserve in Lamlash Bay, located off the south eastern shore of Arran. The no-take marine reserve prohibits all resource extraction within its 2.67 km^2 area under the Inshore Fishing (Scotland) Act of 1984. Therefore, not only is Lamlash Bay the first marine reserve in Scotland, it is also the only statutory reserve in the UK that was originally proposed by a local community which bans all extractive activities (Prior 2011). The Lamlash Bay Marine Reserve was passed by the Scottish parliament under the rationale that the reduction in fishing pressure should help regenerate the local marine environment and enhance commercial shellfish and fish populations in and around Lamlash Bay, particularly with regards to scallops. This also makes Lamlash Bay unique as the majority of MPAs in the UK were proposed either for conservation (e.g. Lundy Marine Nature reserve, Hoskin et al. 2011) or fishery purposes (e.g. closed areas off the Isle of Man, Beukers-Stewart et al. 2005), not for both.

1.5. Thesis synopsis

The global coverage of MPAs set to increase over the next decade. To help guide this change in policy and management, it is important to better understand how MPAs promote the process of recovery within marine ecosystems. As Lamlash Bay is the first and only fully protected marine reserve in Scotland, and only one of three in the UK, studying Lamlash Bay will offer a unique insight into the effects of highly protected marine reserves. This thesis can be broadly split into three sections: (i) the second chapter reviews the effects of overfishing from a global perspective in which the Firth of Clyde is a case study; (ii) the third chapter is a methodological study that aims to determine which survey techniques are the most suitable for monitoring Lamlash Bay Marine Reserve; and lastly (iii) the fourth, fifth and sixth chapters focus on the effects of the protected area.

To elaborate; in chapter two I explore the general effects of overfishing from a global perspective. The Firth of Clyde, and many over-exploited marine ecosystems worldwide, have lost their natural populations of large predatory finfish, and in their place, crustaceans and invertebrates have come to dominate. Despite the loss in biodiversity, these invertebrate species can go on to support highly lucrative fisheries, capable of generating more economic revenue than the traditional fisheries they replaced. In this chapter, I document the mechanisms underlying these changes and explore how biodiversity can influence the resilience and function of marine ecosystems in order to evaluate if our increasing reliance on invertebrate fisheries is wise.

The third chapter of this thesis homes in on Lamlash Bay Marine Reserve. In particular, it aims to test which survey methods are the best for monitoring the wide range of species that occur in Lamlash Bay. I then use the results of this study to justify the methods I employed in my following chapters.

In chapter four, I explore how Lamlash Bay Marine Reserve has affected the abundance and population dynamics of two commercially important species of scallop. This was achieved by conducting a series of quantitative diver surveys over a four-year period. These surveys investigated whether the reserve is promoting the recovery of nursery habitats and scallop recruitment. Other benefits potentially offered by the reserve were explored by testing for differences in scallop density, age structure, body size and biomass between areas situated within and outside its boundaries.

The fifth chapter investigates how Lamlash Bay Marine Reserve is influencing commercially important populations of crabs and lobster. The study involved conducting a series of pot (“creel”) and tagging surveys to test if: (1) catch rates of crab and lobster were higher within the reserve; (2) individuals were larger within the reserve; (3) there was any evidence of spillover; and (4) if the reserve was having any effect on lobster fecundity and gender ratios.

Finally, in my sixth chapter, I investigate if the protection afforded by Lamlash Bay Marine Reserve is promoting the recovery of benthic and fish populations. This was achieved by conducting a combination of diver, photo and video surveys over a four year period.

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Chapter 2. The unintended consequences of simplifying the sea: making the case for complexity

2.1. Preface

Worldwide, many over-exploited marine ecosystems have lost their natural populations of large predatory finfish and have become dominated by crustaceans and other invertebrates. Controversially, some of these simplified ecosystems have gone on to support highly successful invertebrate fisheries capable of generating more economic value than the fisheries they replaced. This is the case with the Firth of Clyde, in which the Isle of Arran sits. The Firth of Clyde used to support a large number of fisheries targeting a wide range of species, including cod, haddock and whiting. Now, after a century of intense fisheries exploitation, the only fisheries remaining are those targeting bivalve molluscs and crustaceans. However, these recently established invertebrate fisheries are proving to be highly lucrative and successful. Such systems have been therefore compared with those created by modern agriculture on land, in that existing ecosystems have been converted into those that maximize the production of target species.

In this chapter I investigate whether our increasing reliance on invertebrate fisheries is wise by drawing on a number of case studies and ecological concepts.

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I declare that the work submitted is my own. The contribution by co-authors was as follows:

Callum Roberts and Bryce Stewart: Supervision, review and editing.
Ruth Thurstan: Provided historical landings data of the Firth of Clyde

The unintended consequences of simplifying the sea: making the case for complexity

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Abstract

Many over-exploited marine ecosystems worldwide have lost their natural populations of large predatory finfish and have become dominated by crustaceans and other invertebrates. Controversially, some of these simplified ecosystems have gone on to support highly successful invertebrate fisheries capable of generating more economic value than the fisheries they replaced. Such systems have been compared with those created by modern agriculture on land, in that existing ecosystems have been converted into those that maximize the production of target species. Here, we draw on a number of concepts and case-studies to argue that this is highly risky. In many cases, the loss of large finfish has triggered dramatic ecosystem shifts to states that are both ecologically and economically undesirable, and difficult and expensive to reverse. In addition, we find that those stocks left remaining are unusually prone to collapse from disease, invasion, eutrophication and climate change. We therefore conclude that the transition from multispecies fisheries to simplified invertebrate fisheries is causing a global decline in biodiversity and is threatening global food security, rather than promoting it.

Keywords Ecosystem change, fisheries, invertebrates, phase shift, resilience, simplification

Introduction

The biodiversity of the world's oceans is changing. Human impacts are causing an accelerating loss of populations and species in virtually every marine ecosystem on the Earth (Worm et al. 2006; Valdes et al. 2009). As a result, we are seeing marine ecosystems, and the fisheries they support change on a global scale (Steneck 1998; Jackson et al. 2001; Sala and Knowlton 2006; Daskalov et al. 2007).

Fisheries that target large predatory finfish are rapidly declining (Myers and Worm 2003, 2005). To keep up with demand, fishers are increasingly targeting smaller, pelagic species and bottom-dwelling invertebrates (Pauly et al. 1998, 2002; Steneck et al. 2002; Essington et al. 2006; Estes et al. 2011). Behind these all too familiar 'fishing down' or 'through the food web' and 'boom-and-bust' cycles lies a complex interplay of ecological, economic, social and historical factors. In general, however, they share a common pattern. New fishing technologies and rising demand cause the intensity and effects of fishing to escalate over time. As a result, stocks of large-bodied fish become depleted, and in their place, new species are targeted (Worm and Myers 2003; Hughes et al. 2007). Despite offsetting fishing demand to previously little or unexploited species, the ecological functions that larger fish performed within the ecosystem (such as grazing macroalgae or feeding on benthic invertebrates) are diminished or lost (Holmlund and Hammer 1999; Worm and Duffy 2003). As a result, ecosystems become dominated by a handful of species such as prawns, lobster, macroalgae and jellyfish that used to form the diet of, or were outcompeted by, larger fish (Myers and Worm 2003) (Fig. 1). This cycle of diminishing fish stocks and offsetting fishing demand to new species may occur several times, and with this rise and fall of various species, the ecosystem may experience several different states each supporting distinct ecological communities (Steneck et al. 2004).

Paradoxically, species that come to dominate overfished, simplified ecosystems can reach high enough densities that they form a resource many times more economically valuable than those targeted before (Thurstan and Roberts 2010; Steneck et al. 2011). This may explain why calls from scientists for an ecosystem-based approach to help restore depleted fish stocks are often met with little enthusiasm, or even resistance, from fishers, managers and politicians (Steneck et al. 2011). In the short-term arena, where these players generally make their decisions, there appear to be strong economic incentives to maintain 'business as usual'. It has even been suggested that intensive fishing is a necessary process required to keep up with rising demand (Pauly et al. 2002; Hilborn 2007a; Harman 2011; Atrill and Halls 2012; Van Denderen et al. 2013). That, through overfishing, we are effectively manipulating nature in order to create simplified assemblages dominated by targeted populations, comparable to monocultures in agricultural systems. These have the advantage in that they are easier to manage, more abundant in the environment and economically more efficient than pre-existing fisheries. After all, advances in human civilization have largely been built on this approach in terrestrial environments (Foley et al. 2011).

In response to these arguments, we examine the consequences of simplified, less diverse marine ecosystems and the fisheries they support by drawing on economic and ecological perspectives, illustrated through several case-studies, and address the question of whether simplifying the seas is a sensible management strategy. Based on our findings, we then make the case that restoring the diversity of ocean ecosystems is necessary to ensure fisheries sustainability and resilience into the future.

Figure 1. The ecological effects of intensive fishing. Fishing effort increases over time (left to right). As a result, large finfish become depleted, fishers are forced to target new species, and biogenic habitat structures are damaged or lost. However, the ecological functions that larger finfish and habitat-forming organisms performed within the ecosystem become diminished or lost. Consequently, biodiversity of the system declines, and the ecosystem shifts to a new state dominated by species that were once predated by larger fish or are resilient to habitat-modifying fishing methods. These species can, however, go on to support large and lucrative fisheries.

The ecology underlying change

The number and types of species present within an ecosystem (i.e. its biodiversity) determine ecosystem function through processes such as predation, herbivory, habitat provision and mediating the cycling of energy and nutrients, which maintain ecosystems as the recognizable entities they are (Chapin et al. 2000; Loreau et al. 2001; Deutsch 2003; Worm and Duffy 2003). However, fishing can reduce the biodiversity of ecosystems by damaging habitats and lowering the abundance of target and non-target species (Auster et al. 1996; Collie et al. 1997; Pauly et al. 2002; Airoldi et al. 2008). When fishing pressure persists at too high level for too long, certain species can be driven to local extinction or at least to such low levels that any influence they have on ecosystem structure and function is essentially lost (McClanahan 1995; Sala et al. 1998). If these species played a key functional role within the ecosystem and the traits they conferred are replaced by other species, it can alter ecosystem function and result in the emergence of a new, unfamiliar ecological state (Pauly and Christensen 1995; Naeem and America 1999). It appears then that a system's biodiversity may play a key role in maintaining its stability. However, recent studies suggest the reality may be more complicated.

Marine ecosystems are complex and dynamic and are increasingly thought to be able to exist in, and shift between, several possible alternate states (Scheffer et al. 2001; Beisner et al. 2003; Deutsch 2003; Daskalov et al. 2007). An ecosystem is able to slide from one alternate state to another when external (e.g. climate change or overfishing) and/or internal perturbations (e.g. predator–prey cycles and density-dependent mortality) to the system pass a critical threshold. This causes the nature of the system to change, triggering a reorganization of its structure, altering its dynamics and bringing about a series of feedbacks that can further reinforce the change (Scheffer and Carpenter 2003) (Fig. 2). In some cases, crossing the threshold requires only a relatively small perturbation to bring about a sudden and dramatic change (Gammaitoni et al. 1998). For example, it has been reported in several lake systems that a change in phosphorus input can trigger a sudden shift from clear to turbid water, two different states capable of supporting different communities of animals and plants (Jeppesen et al. 1999; Van Nes et al. 2002; Ibelings et al. 2007). In other cases, such as the change from a grassy to a shrub-dominated rangeland (Ludwig et al. 2000), the response is more gradual. Nevertheless, once the threshold has been passed, the feedbacks are altered and the dynamics of the system shift from one state to another (Folke et al. 2004).

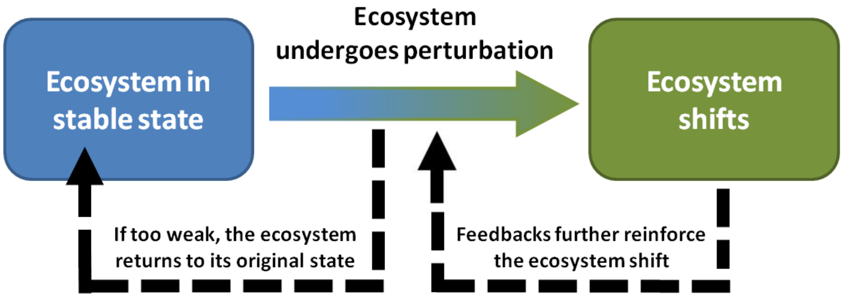

Figure 2. Theory underlying ecosystem change. An ecosystem begins as a stable, recognizable entity. However, perturbations to the system trigger an ecological reorganization. If the perturbation is weak, the system absorbs the disturbance and reverts back to its previous state. If the perturbation is strong, the system shifts to an alternative state and can trigger a number of feedbacks that further reinforce the shift and promote its stability.

The problem with simplified ecosystems

The extent to which an ecosystem can absorb natural and human disturbances without degrading or unexpectedly shifting to an alternate state is often referred to as its 'resilience' (Holling 1973; May 1977; Steneck et al. 2011). Highly resilient ecosystems can absorb perturbations and return to their previous state, whereas low-resilience systems may shift under even a relatively small disturbance. But what makes some ecosystems more resilient than others?

In theory, if species with similar functional roles are able to replace or compensate for one another, then ecosystems encompassing high species diversity will be more resilient because the likelihood of the ecosystem losing all species capable of performing a particular ecological function is low (Chapin et al. 1996; Lavorel and Garnier 2002; Hooper et al. 2005). Ecologists have therefore frequently proposed that an increase in species diversity will confer an increase in resilience by ensuring the system against loss of function (Elton 1958; Mcnaughton 1977; Tilman 1996; Yachi and Loreau 1999; Loreau et al. 2001). Despite being an area of intense debate (Chapin et al. 2000; Worm and Duffy 2003), there is growing evidence that species diversity plays a significant role in ecosystem function and resilience in several systems including kelp forests (Johnson and Mann 1988; Steneck et al. 2002, 2004; Hughes et al. 2005; Worm et al. 2006), microbial microcosms (McGrady-Steed et al. 1997; Naeem and Li 1997), grasslands (Tilman 1996; Walker et al. 1999; MacDougall et al. 2013), mycorrhizal fungi (van der Heijden et al. 1988) and marine invertebrate communities (Stachowicz et al. 2002; Levine et al. 2004). The relevance of all these to fishing is that as many heavily exploited marine ecosystems are inadvertently being transformed into simpler, managed systems, which typically contain only a few dominant species, they too are expected to have low resilience and be more susceptible to other human impacts, such as climate change, eutrophication and species invasions, and therefore more susceptible to ecological change.

The Black Sea gelatinous invasion

The overfishing of large predatory species can often open up suitable niches for other species to occupy (Worm et al. 2006; Daskalov et al. 2007; Oguz et al. 2008). Overfishing in the Black Sea, for example, has made the system more susceptible to changes in climate, hydrography, nutrient loading and invasions by both native and non-native species (Llope et al. 2011). As a result, many shallow areas have become oxygen depleted (whereas the deep Black Sea has long been anoxic), and the system has shifted from a fish-dominated community to one dominated by jellyfish and ctenophores: the most dramatic, large-scale gelatinous plankton invasion event to date (Oguz et al. 2008).

The turning point for these changes occurred in the 1960s when fishing first reached industrial levels, and stocks of pelagic predators such as bluefish (*Pomatomus saltator*, Pomatomidae) and dolphinfish (*Coryphaena hippurus*, Coryphaenidae) became severely depleted (Daskalov 2002; Sala and Knowlton 2006). As a result, predation pressure was reduced and populations of planktivorous fish expanded. This led to greater grazing pressure on zooplankton and, coupled with eutrophication, allowed the biomass of phytoplankton to increase abruptly during the early 1970s (Daskalov et al. 2007). This had further knock-on effects; phytoplankton blooms at the surface meant greater quantities of dead phytoplankton were sinking to the depths and being decomposed through bacterial action, a process that consumes oxygen. As a result, shelf waters became hypoxic, causing mass mortalities of mussels and other benthic filter feeders (Daskalov 2002; Llope et al. 2011). In turn, this led to an increase in unutilized detritus and nutrients within the system and, consequently, further oxygen depletion. In this altered ecosystem, a gelatinous invader – the comb jelly (*Mnemiopsis leidyi*, Boinopsidae) – proved highly successful, reaching biomasses of more than 2 kg m^{-2} in some cases (Shushkina and Musaeva 1983; Zaitsev and Mamaev 1997). However, cooler temperatures between 1991 and 1993 countered the invasion and allowed planktivorous fish to recover, meaning small pelagics are again controlling the food web as the main top predator of the system. Curiously, the Black Sea has shown further signs of recovery since then and appears to be linked to the collapse of the Soviet Union and the loss of state subsidies, which previously supported intensive farming practices and the application of fertilizers (Mee et al. 2005).

Hypoxia in the Baltic

The Baltic Sea is unusual in that it is essentially a large brackish lake that receives infrequent inflows of seawater from the North Sea that rapidly sink into deeper basins as they are forced underneath a less-dense layer of freshwater at the surface (Schinke and Matthäus 1998). When the period between inflows is long (known as 'stagnant periods'), continued bacterial decomposition in the depths causes natural depletion of oxygen (Hille et al. 2005). However, in recent years, overfishing, climate change and eutrophication have intensified this process, resulting in severe anoxia and ecosystem shifts at several different trophic levels and time periods.

During the early 20th century, the hunting of marine mammals resulted in the near elimination of top predators and, coupled with increasing pollution and climate change, caused the Baltic to shift from an oligotrophic to a eutrophic state (Österblom et al. 2007). In response, the system became dominated by cod (*Gadus morhua*, Gadidae), whilst deeper waters became severely hypoxic, wiping out important food chains across 100,000 km^2 of the seabed (Elmgren 1989; Folke et al. 2004). Intensive fishing then contributed to a 10-fold decline in cod biomass between 1980 and 1992 (MacKenzie et al. 1996) causing the system to shift again, but towards a community dominated by planktivorous sprat (*Sprattus sprattus*, Clupeidae) and herring (*Clupea harengus*, Clupeidae), thereby imposing major changes on zooplankton community composition (M€ollmann et al. 2008). These changes are likely being reinforced as cod eggs are not adapted for hypoxic waters, and the large populations of sprat and herring may be feeding on cod eggs and larvae and also competing with their juveniles (Koster and Möllmann 2000; Hinrichsen et al. 2002). The collapse of cod and other large predators has also led to an increase in smaller organisms, which prey upon the grazers of macroalgae (Roberts 2012). As a result, herbivory rates have declined and macroalgae have spread, further driving down oxygen levels through their decay.

Denmark and other nations bordering the Baltic have made several efforts to reduce nitrogen runoff to the Baltic Sea. As a result, nitrogen inputs have halved since the early 1980s (Conley et al. 2007), yet the ecosystem remains in a low-oxygen state (Roberts 2012). It has been proposed that severe hypoxia has eliminated the functional influence of large, deep-burrowing organisms within the sediment, hindering the recovery of the system. Normally, these organisms ingest particles of food from the water column and deposit their faeces deep into the sediment, reducing the nutrient content of the water column (Bianchi et al. 2000; Middelburg and Levin 2009; Karlson et al. 2010). However, their absence has allowed sediments to become dominated by smaller opportunistic taxa that live close to the sediment surface and release their faeces back into the open water, thereby stimulating further plankton blooms at the surface and further oxygen depletion (Hille et al. 2005; Woulds et al. 2007). Hypoxic sediments are also less able to retain phosphorous, which has triggered a large-scale relocation of phosphorous from within the sediment to the water column, again boosting plankton growth and oxygen depletion (Hille et al. 2005).

Sulphur eruptions of the Benguela upwelling system

In some ecosystems, the diversity of lower trophic levels is equally as important as top predators. A curious case-study is provided by the recent changes observed in the Benguelan upwelling system off Namibia. Here, trade winds drive intense upwelling and force cold, nutrient-rich water to the surface, stimulating large blooms of phytoplankton (Bakun 1990; Ohde et al. 2007). Like other upwelling areas (Brüchert et al. 2006), high productivity at the surface has resulted in severe hypoxia at depth and enabled high concentrations of hydrogen sulphide and methane (the waste products of microbial metabolism) to build up within the sediment (Brüchert et al. 2009). Such conditions are estimated to cover more than 50% of the Benguelan shelf (Brüchert et al. 2006) and further contribute to oxygen depletion as hydrogen sulphide reacts with oxygen as it rises to the surface, thereby stripping it from the water (Bakun and Weeks 2004; Ohde et al. 2007). Occasionally, this process is so intense that the rising gasses rush upwards in a sudden ‘eruption’ of sulphide and methane, turning the sea a bright turquoise (Fig. 3). Such effects can persist for more than 2 months and cover an area of 20,000 km^2 (Weeks et al. 2002).

This phenomenon is not new. Sulphur eruptions have been reported since the 19th century (Weeks et al. 2004; Utne-Palm et al. 2010), but observations suggest they are increasing in both frequency and intensity (Weeks et al. 2004). It has been hypothesized that the increasing eruptions are linked to overfishing of pelagic fish (Bakun and Weeks 2004). Up to a few decades ago, sardines (*Sardinops sagax*, Clupeidae) and anchovy (*Engraulis encrasicolus*, Engraulidae) shoaled off Namibia in great numbers to feed on vast quantities of plankton. These large shoals provided prey for tuna (Scombridae), swordfish (Xiphiidae) and large colonies of seabirds, sustaining one of the world’s most spectacular concentrations of marine life (Roberts 2012). In response, a large industrial sardine fishery was developed during the early 1960s, but through a combination of overfishing and environmental fluctuations, the fishery collapsed just a decade later (Cury and Shannon 2004). The large sardine stock was once estimated to exceed 10 million tons but for the past 30 years has not exceeded 1 million tons, and in some years, fluctuations have been so severe that the population has nearly vanished (Boyer 1996; Bakun and Weeks 2004). The Benguela upwelling ecosystem has therefore lost a key component that previously limited the extent of phytoplankton blooms and resulting sulphur eruptions.

Increased sulphur eruptions are a cause for concern. Hydrogen sulphide is a respiratory poison (Bagarinao 1992), and its diffusion from the sediment to the water column has been implicated in several massive kill events of fish and invertebrates. These trigger mass feedings by seabirds and large ‘walkouts’ by lobster and other edible crustaceans, which people readily collect from the shore as they try to exit the water (Weeks et al. 2002; Bakun and Weeks 2004). One event in particular killed off 80% of the hake population, leaving few individuals to sustain future catches (Bakun and Weeks 2004). Corrosive fogs of hydrogen sulphide are also released, which irritate the eyes and throats of coastal inhabitants, and are offensive in smell (Weeks et al. 2002, 2004). Climate change is predicted to further increase the frequency of sulphur eruptions (Bakun 1990), making the waters even more anoxic and less suitable to support fisheries (Bakun and Weeks 2004; Monteiro et al. 2008).

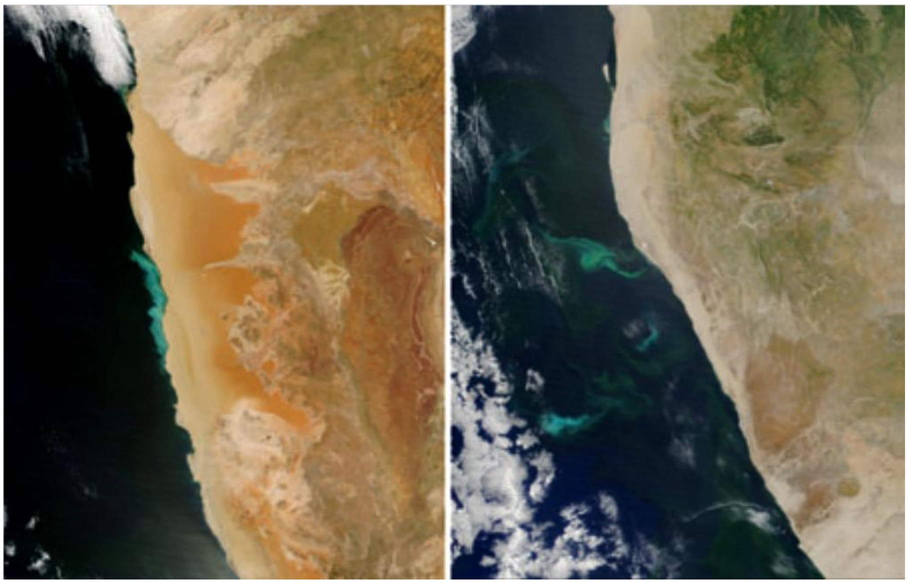

Figure 3. Sulphur eruptions observed off the coast of Namibia. Evidence suggests that this natural phenomenon may be increasing in frequency and intensity and may be linked to the overfishing of planktivorous fish. Satellite images courtesy of Jacques Descloitres and the MODIS Rapid Response Team.

Other changes linked to the decline in pelagic stocks have been observed in the Benguelan upwelling ecosystem. The loss of sardine has forced many animals of higher trophic level to switch to feeding almost exclusively on a single species of bearded goby (*Taenioides jacksoni*), making it the new predominant prey species (Utne- Palm et al. 2010). Despite the increase in predation pressure and the decline in water quality, gobies appear to be thriving as they possess an unusually high tolerance to hydrogen sulphide and low concentrations of oxygen (Boyer and Hampton 2001). In addition, prior to the period of intensive fishing, large jellyfish (e.g. Scyphozoa and Hydrozoa) were not a prominent feature of the Benguelan ecosystem, yet the abundance of jellyfish now exceeds that of fish, reaching biomasses of more than 12 million tonnes (Lynam et al. 2006). The jellyfish prove a nuisance as they disrupt fishing, spoil catches and block power station coolant intakes (Boyer and Hampton 2001). They will also likely hinder any measures to recover fish stocks as jellyfish prey upon fish eggs and larvae and are strong competitors for resources (Pauly et al. 2009).

Impacting ecosystem services

Some reports suggest that the major shifts observed in the Black Sea, Baltic and Benguela upwelling system occurred during a similar time frame (i.e. between the 1980s–1990s) and therefore likely involved a common large-scale atmospheric driver (Young 2011). However, all these systems underwent dramatic change after intensive fishing simplified their food webs and affected the ecological roles performed by various functional groups. Indeed, simplified systems are often predicted to be less capable of providing the ecological processes that maintain their stability and allow for the long-term exploitation of their resources (Peterson et al. 1998; Chapin et al. 2000). In 2006, an extensive meta-analysis conducted by Worm et al. found many cases in which loss of biodiversity impaired the filtering and detoxification functions performed by filter feeders, submerged vegetation and coastal wetlands and that these impairments were likely linked to a global increase in harmful algal blooms, fish kills, shellfish fishery and beach closures and oxygen depletion. Their study also revealed that increasing occurrences of species invasions have coincided with the loss of native biodiversity and that in the majority of cases, the invaders could not compensate functionally for the loss of native biodiversity because they comprised of other species, mostly microbes, gelatinous plankton and small invertebrate taxa. They also found that fisheries in species- poor ecosystems were more prone to collapse and less likely to recover from over-exploitation. Their study therefore supports the notion that complex, more intact marine ecosystems provide a range of ecological services, which maintain ecosystem function and support the long-term exploitation of marine resources. But when we simplify ecosystems to just a few dominant species, we trigger ecological changes that impact upon these services thereby affecting resource extraction and human welfare (Brand 2009).

From finfish to invertebrates

We have provided evidence that shifting to lower-diversity regimes can cause ecosystems to change, which can create a series of knock-on effects to ecosystem services. But what are the socioeconomic drivers that cause such adverse effects to occur? As we will now explore, the over-exploitation of finfish stocks has, in some ecosystems, resulted in unusually high densities of commercially valuable invertebrates, which can go on to support highly lucrative and successful fisheries (Caddy and Rodhouse 1998; Steneck et al. 2011). In these cases, the serial over-exploitation of fish stocks has created simplified systems – akin to agricultural monocultures – of targeted resources that are easier to manage, more abundant in the environment and economically more valuable than the finfish fisheries they replaced (Hilborn 2007a).

Prawns in the Clyde

The Firth of Clyde, a large inlet of the sea that extends over 100 km into Scotland's west coast, gained considerable media attention after it was identified as one of the most degraded marine environments in the United Kingdom (BBC Springwatch 2007; BBC Panorama 2010; Clover and Smith 2010; Smith 2010), primarily due to over a century of intensive fisheries exploitation (Thurstan and Roberts 2010). Fishing in the Clyde has origins dating back to medieval times (Tivy 1986) and, over the centuries, has supported many important fisheries targeting a wide range of species including herring, cod, mackerel, whiting (*Merlangius merlangus*, Gadidae), haddock (*Melanogrammus aeglefinus*, Gadidae), turbot (*Psetta maxima*, Scophthalmidae), skate (*Dipturus batis*, Rajidae) and even basking sharks (*Cetorhinus maximus*, Cetorhinidae) (Thurstan 2007; Thurstan and Roberts 2010). Today these fisheries no longer exist.

The Clyde follows the typical 'boom-and-bust' pattern exhibited by many of the world's overexploited fisheries. During the 19th century and before, landings were spread between many different species and targeted by an artisanal fleet using sailing vessels, traps, lines and nets (Thurstan and Roberts 2010). Fishing effort steadily increased as a greater proportion of the fleet began to take advantage of technological advancements such as beam trawls, otter trawls, Newhaven scallop dredges and steam- and diesel-powered engines. Despite, and likely because of, increasing fishing effort and two spatial closures to trawling being revoked in the late 20th century, large catches of fish were not sustained (Heath and Speirs 2011), and landings of demersal species, such as haddock and cod, declined by more than 90% (Thurstan and Roberts 2010). As a result, a remarkable shift has been observed over the last two decades in the groups of species landed from the Clyde. In 1985, finfish made up more than 60% of the landings by weight and 37% by value, but by 2008, this had fallen to just 2% by weight and 0.5% by value (Fig. 4). Now *Nephrops* prawns (*Nephrops norvegicus*, Nephropidae) are the most valuable fishery in the Clyde, making up 84% of landings by weight and 87% by value. These are targeted by around 120 vessels, of which the majority (90%) of landings are made by trawlers resident to the Clyde (Thurstan and Roberts 2010; Murray and Cowie 2011). The remaining percentages are composed solely of other invertebrates such as scallops (*Pecten maximus*, Pectinidae), crabs (*Cancer pagurus*, Cancridae) and lobster (*Homarus gammarus*, Nephropidae) (Howell et al. 2006; Keltz and Bailey 2010). Since 2003, the only landings of fish in the Clyde have been as by-catch from the *Nephrops* fishery (Heath and Speirs 2011).

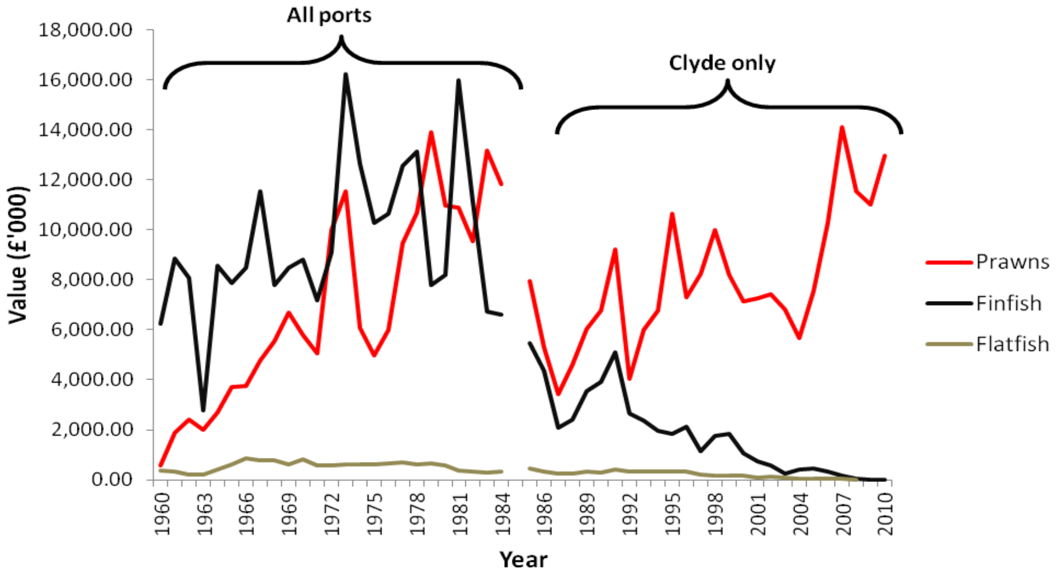

Figure 4. *Nephrops* prawns now dominate Firth of Clyde landings by value (values corrected for inflation using www. thisismoney.co.uk/historic-inflation-calculator. Data from the Scottish Government. Data pre-1985 represent all fish landed in the local ports Ayr and Campbeltown, whilst data post-1985 represent only those fish caught and landed within the Firth of Clyde.

The physical and ecological effects of overfishing in the Clyde have resulted in an altered, simplified ecosystem in which *Nephrops*, crabs, scallops and other invertebrates now thrive (Thurstan and Roberts 2010) (for contrasting views see Combes 2007). Reversing this shift will likely prove difficult as there are several ecological and social feedbacks preventing the return of the Clyde to the diverse, highly productive ecosystem it once was (Box 1).

Although a prawn-dominated state appears beneficial in a fisheries sense, there is a possibility that the *Nephrops* stock may be unusually prone to collapse. It is known that populations within low diversity ecosystems are inherently unstable, being more prone to sudden fluctuations in stock size, invasion and disease (Worm et al. 2006). In fact, there are already signs of high rates of parasitism of Clyde *Nephrops* by a microscopic dinoflagellate belonging to the genus *Haematodinium*. This parasite is also known as 'bitter crab disease', for its capacity to reduce both taste and texture of *Nephrops* and other crustaceans (Gunnarsson 2010), or as 'smoking crab disease', due to its ability to convert host's organs into its own propagules. When complete, the free-swimming stage of the parasite then erupts from every aperture and joint, giving the prawn the appearance of smoking (Roberts 2007). During seasonal peaks, *Haematodinium* prevalence has reached as high as 70% (Field et al. 1992), with infection widely believed to lead to the death of the host (Stentiford and Shields 2005; Stentiford and Neil 2011). Seasons of high infection have therefore been associated with reductions in landings per unit effort and *Nephrops* burrow density (an accepted indicator of stock density, McLay et al. 2008), as well as considerable losses to fishermen who are forced to discard high proportions of their catch that are heavily parasitized and therefore unmarketable (Field et al. 1998; Stentiford 2001; Beevers et al. 2007). Since the initial epidemic period, *Haematodinium* prevalence appears to have stabilised at levels between 20-25% in the Clyde (Beevers et al. 2012).

It has been proposed that overfishing in the Firth of Clyde may have encouraged the outbreak of *Haematodinium* through several mechanisms (Thurstan and Roberts 2010; Stentiford and Neil 2011). Parasites often modify host behaviour to increase the spread of infection. As infected prawns spend more time out of their burrows (Stentiford 2001; Stentiford and Neil 2011), there may be an increased chance of disease transmission between infected and uninfected prawns. When cod and other predatory fish were common in the Clyde, infected prawns would have been picked off quickly, limiting the spread of the parasite, but today there is little such control. Secondly, *Haematodinium* prevalence has been found to be highest at sites where Nephrops populations are made up of smaller-bodied individuals (Field et al. 1998; Stentiford 2001). Because fishing alters population size-structure, fishing could potentially increase the prevalence of the disease by creating a shift towards a higher proportion of smaller-bodied, more susceptible, individuals within the population (Stentiford and Neil 2011).

Box 1

Barriers to recovery within the Firth of Clyde

1. The decline in nursery habitat: Mobile fishing gears, like trawls and scallop dredges, alter the physical structure of the seafloor by ploughing sediments and destroying structural biological features such as maerl, seagrass and macroalgal beds (Eleftheriou and Robertson 1992; Hall-Spencer and Moore 1998; Jennings and Kaiser 1998; Kaiser et al. 2000). Such habitats often support high levels of juvenile fish density, growth and survival, and contribute disproportionally to the production of adult recruits and biodiversity in general (Beck et al. 2001; Kamenos et al. 2004a,b; Howarth et al. 2011). The decline of these ‘nursery habitats’ may hinder any future recovery of fish stocks (Bradshaw et al. 2001). In addition, many commercially exploited fish species have been shown to spend significant parts of their juvenile life stage in inshore nursery habitats, migrating progressively offshore as they age and develop (Zeller and Pauly 2001; Espeland et al. 2007; Gibb et al. 2007; Knutsen et al. 2007). Interfering with this transition will therefore also contribute to the decline of finfish fisheries further out at sea.
2. High levels of by-catch: In addition to the habitat-altering properties of trawls and dredges, the high levels of juvenile by-catch associated with their use (especially given the fine-mesh of prawn trawls) will also likely prevent the recovery of bottom fish populations. Discard ratios are very high in the Clyde *Nephrops* fishery, with 9 kg of by-catch produced for every 1 kg of *Nephrops* caught (Bergmann et al. 2002), and it is likely that the majority of these organisms die when returned to the sea (Bergmann and Moore 2001).
3. *Nephrops* are highly valuable: *Nephrops* alone generate almost as much income as all finfish combined did in the past (even when inflation is taken into account, Fig. 4). There is therefore likely to be little desire to return to a diverse mixed fishery (Steneck et al. 2011), especially given the current level of investment in the *Nephrops* fishery. Profit margins in this fishery may not be as high as they once were (Thurstan and Roberts 2010), but this single species remains the mainstay of the fishing industry in the Firth of Clyde.
4. The abundance of euphausiids and copepods: These planktonic organisms constitute important prey for juvenile cod and haddock, yet their abundance is 10–100 times lower in the Firth of Clyde than in the 1950s. However, its causes in the Clyde remain unknown, as are its consequences on the recovery of groundfish (Bailey et al. 2011).

The arguments above highlight current fishing practices in the Clyde as risky. If the Nephrops stock were to crash, the social consequences for Clyde fishermen would be dramatic as few species would be left to target. What is more, the value of trawled Nephrops has remained static since 1991, whilst the business costs of operating a vessel have steadily increased. In this market, fishers face the predicament of fishing for quantity rather than quality. Therefore, if landings were to drop, say because of disease or fishery restrictions, the trawl fleet will be highly susceptible to economic collapse (Combes 2007).

Lobster in the Northwest Atlantic

The Northwest Atlantic was once home to some of the world's richest fishing grounds for large predatory groundfish, particularly cod and haddock (Acheson and Steneck 1997; Jackson et al. 2001). However, over the past 30 years, fisheries within this region have experienced widespread collapse, and landings from fisheries targeting invertebrates such as sea urchins (*Strongylocentrotus droebachiensis*, Strongylocentrotidae), lobster (*Homarus americanus*, Nephropidae), snow crab (*Chionoecetes opilio*, Oregoniidae) and shrimp (*Pandalus borealis*, Pandalidae) have come to dominate (Worm and Myers 2003; Frank et al. 2011) (Fig. 5). In addition to growing economic dependency on newly established invertebrate fisheries, we have also seen several new ecological states emerge throughout the entire Northwest Atlantic, what may well be the largest ecological shift recorded to date as a direct consequence of overfishing.

In the Gulf of Maine, cod has been the single most valuable marine resource since the late 1880s. However, like many fisheries discussed in this study, fishing intensity and its impacts escalated over time. During the 1930s, new technologies enabled fishers to boost their catches by actively targeting spawning aggregations of coastal cod and haddock, but by 1949, these coastal stocks had become depleted (Steneck et al. 2004). Landings of cod and haddock were, however, maintained by targeting previously unexploited stocks further offshore between the 1950s and 1970s. Landings in the area then received another boost between the 1970s and 1990s due to further technological advancements and the establishment of the 200-mile exclusive economic zone. Both contributed to a temporary increase in species diversity of landings as fishers began to target new species such as monkfish (*Lophius americanus*, Lophiidae) and sea urchins. Despite the boost to landings, by 1992, stocks of predatory bottom fish experienced widespread collapse, and landings fell to just a tenth of what they had been in 1990 (Steneck and Wilson 2001, 2010).

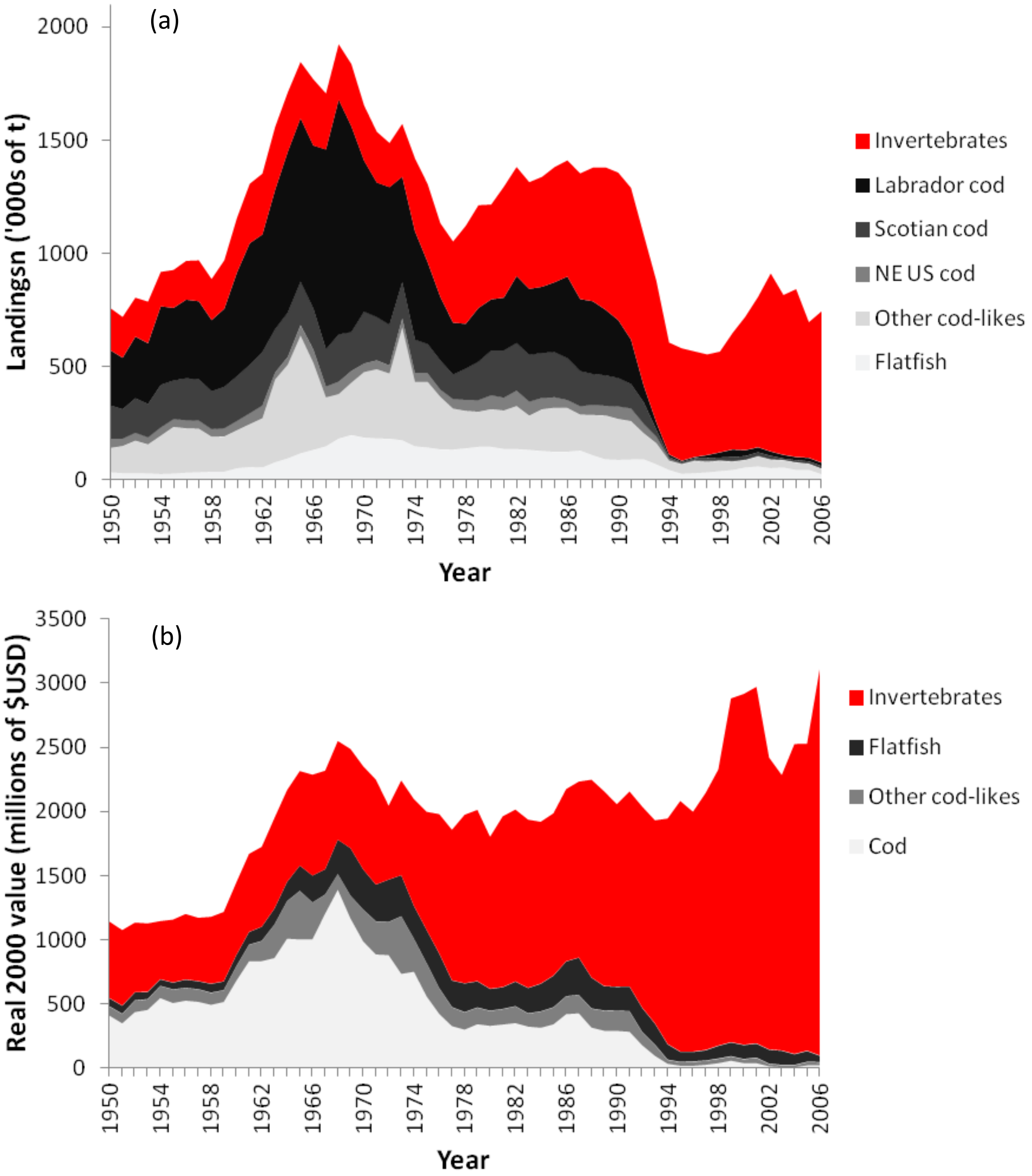

Figure 5. The rise of invertebrate fisheries in the Northwest Atlantic. Predatory groundfish fisheries have collapsed in the Northwest Atlantic triggering a dramatic shift in the value and composition of species landed. (a) Landings of several groups of species in the Northwest Atlantic between 1950 and 2006. Landings of cod split between the three large marine ecosystems. In all three regions, cod landings have almost ceased, and invertebrates now make up the majority of species landed. (b) The real 2000 adjusted value of several groups of species between 1950 and 2006. Invertebrate fisheries are now worth more than the finfish fisheries they replaced. Real 2000 value was obtained by multiplying the catch (by species) by the deflated ex-vessel price, adjusted by the Consumer Price Index. The group 'invertebrates' does not include oysters as this fishery had already boomed and collapsed by 1970. Data obtained from the Sea Around Us Project (www.seasaroundus.org).

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In contrast, since the 1950s, landings of lobster have increased dramatically to the point that their value has surpassed all other harvested stocks in Maine, representing 80% of the total value of Maine's seafood landings, thereby making it one of the most important fisheries in North America (Steneck and Wilson 2001; Steneck et al. 2011). Following this success, the number of lobster pots in Maine has increased from around 300,000 in 1930 to well more than 3 million in 2000. Now, in 2011, more than 4400 commercial fishing vessels actively fish lobsters in coastal Maine (Department of Marine Resources 2012). Despite such intensive levels of fishing, population densities of lobster remain higher in Maine than in anywhere else in the world (Steneck and Wilson 2001; Steneck et al. 2011). With no sign of landings diminishing, it is no surprise that the Maine lobster fishery is widely regarded as successful and sustainably managed (Ostrom et al. 1994; Acheson and Steneck 1997; Steneck et al. 2011). Yet, although managers and fishers have indeed contributed to this success, there is a belief that the high abundance of lobster is more a result of them becoming ecologically 'released' from their overfished predators, allowing the population to expand in size and into new, relatively unprotected habitats from which they were previously excluded (Boudreau and Worm 2010). In addition, a high proportion of the lobsters' diet now comes from herring bait used in the trap fishery (Saila et al. 2002; Grabowski et al. 2009), creating an artificial trophic link between a pelagic fish and a benthic scavenger. Meaning, undersized lobsters receive a high-energy meal every time they are caught and released, thereby enhancing their growth (Saila et al. 2002; Grabowski et al. 2009). This means that the Maine lobster fishery shares more characteristics with aquaculture and ranching (such as control of predators, provisioning of food and a greatly simplified food web) than most capture fisheries (Steneck et al. 2011).

Currently, lobsters represent more than 80% of the value of all fish and seafood landings in Maine (Steneck et al. 2011). Similar to our previous arguments, this means any future declines in lobster will have devastating social and economic consequences as we have effectively 'put all our eggs in one basket'. Furthermore, shallow ocean temperatures in the Gulf of Maine are steadily rising (Wanamaker et al. 2008), meaning lobsters may become increasingly stressed and more vulnerable to disease (Factor et al. 2006). For example, in the eastern Long Island Sound (just 200 km south of the Gulf of Maine), disease and stresses related to increases in ocean temperature have resulted in more than a 70% decline in lobster abundance after a lethal disease outbreak during the unusually warm summer of 1998 (Castro et al. 2006; Glenn and Pugh 2006). Then, in 2010, fisheries managers proposed a 5-year moratorium on lobster fishing as lobsters were experiencing recruitment failure in response to warming sea temperatures (Steneck et al. 2011), which both lowered oxygen levels and increased the incidence of disease (Castro and Angell 2000; Castro et al. 2006). Recruitment failures as a result of climate change have also been observed in rock lobster fisheries in Tasmania (Pecl et al. 2009). If a similar epidemic were to occur in Maine, the effects would be more pronounced because lobster densities are higher than those in Long Island Sound, enhancing disease transmission (Steneck et al. 2011).

Ecological shifts have not been confined to the Gulf of Maine. The eastern Scotian Shelf has experienced similar shifts driven by the collapse of the benthic predatory fish community (Frank et al. 2005). Now, in a system where cod and other predatory bottom fish used to dominate, landings of northern shrimp and snow crab have increased to such an extent that their combined economic value exceeds that of the groundfish fisheries they replaced (Worm and Duffy 2003). Furthermore, it is thought that a number of measures designed to help the recovery of benthic fish are being hindered by the dramatic rise in forage fish and macroinvertebrates (a 900 and 200% increase in biomass, respectively), which may be outcompeting their former predators (Frank et al. 2005, 2011).

As well as impacting the species composition of landings, the decline in predatory groundfish has also been observed to cause shifts in seal populations, phytoplankton community composition and the prevalence of kelp forests (Frank et al. 2005). Kelp forests, in particular, dominated coastal ecosystems of the Northwest Atlantic for more than 4000 years (Steneck 1990; Jackson et al. 2001; Steneck et al. 2002), but from the mid-1960s to 1990, the overfishing of large predators triggered a dramatic increase in the populations of sea urchins and other herbivores, leading to widespread deforestation of coastal kelp forests (Steneck et al. 2004; Boudreau and Worm 2010). Under this new regime, grazing-resistant coralline algae came to dominate the benthos (Steneck 1982; Steneck and Dethier 1994) (Fig. 6), thereby reinforcing the shift by replacing quality groundfish nursery habitat (i.e. the kelp) with new habitat suitable for sea urchin recruitment (i.e. coralline algae) (Steneck et al. 2004). This new ecological state persisted for 2–3 decades before a new fishery targeting the green sea urchin was established in 1987 (Vadas and Beal 1999). The fishery quickly depleted the sea urchin population from extensive coastal areas of Maine, allowing a return to a kelp-dominated state by the mid-1990s. This latest state looks so far to be stable, as the expansion in crustaceans appears to be preventing repopulation of sea urchins by feeding on their newly settling recruits (Steneck et al. 2004).

Figure 6. The shift from kelp forest to coralline algae**.** Between the 1960s and 1990s, coastal kelp forests in the Gulf of Maine were replaced by communities dominated by coralline algae due to intense grazing pressure from sea urchins. Picture taken in 1980 and reproduced with permission from Robert Steneck, University of Maine.

Can we 'farm' the open sea?

This study highlights several ecosystems that have undergone dramatic ecological shifts as a result of overfishing and other environmental changes. Controversially, some of these shifts have appeared to be positive from an economic perspective. Although biodiversity has been reduced, intensively fished systems can come to support important high-volume invertebrate fisheries, often capable of generating more economic value than the finfish fisheries they replaced. So the question remains is simplifying the seas a process that should welcomed, as some have argued, improving the harvesting of resources like it does in agricultural systems on land?

Modern agriculture involves converting existing ecosystems into ones that can be controlled and reducing habitat heterogeneity and biodiversity to maximize the production of a small number of target crops or animals (Kareiva et al. 2007). Reducing biodiversity simplifies management, maximizes yield and allows for faster processing through automated planting and harvesting (Hooper et al. 2005). Marine capture fisheries are also based on generating economic profit from targeted species, and as with farming, fisheries too can be more profitable when the biodiversity of their catch is low (Diamond and Beukers-Stewart 2011). This is because fisheries rarely land all the species they catch. Instead, they are often governed by species specific quotas, meaning that when a fisher's catch consists of a greater proportion of the target species, less time is spent sorting the catch and more of it can be landed, thereby generating greater profit. A simplified ecosystem should therefore provide a more predictable product, allowing fishermen to optimize their gear and techniques, and for seafood processors and retailers to streamline their supply chains. In many ways, these economic arguments are remarkably similar to those driving the dramatic expansion of the aquaculture industry which, over the past several decades, has been the fastest growing food production sector in the world (Bostock et al. 2010).

It is, however, widely recognized that monocultures are ecologically unstable. On land, crops and animals must be treated with a diverse array of chemicals (e.g. fertilizers, herbicide, pesticides, antibiotics, etc.) and biological controls (e.g. the introduction of predators and parasitoids) to maintain yields in the face of pests, weeds and diseases (Holt and Hochberg 1997; Palumbi 2001). Also, farmers often rely on a continuous supply of new crop varieties and strains as yields of successful, pest-resistant varieties are typically maintained for only 5–9 years before pests adapt to overcome them (Tilman et al. 2002). Similar methods are also used in aquaculture, but in the open sea, no such mechanisms exist for wild populations, meaning terrestrial analogies are misplaced (Roberts 2007). Maintaining low-diversity conditions in the marine environment for our long-term exploitation is therefore unlikely to be viable. Moreover, the transition from multispecies fisheries to high-volume single-species fisheries has largely been limited to crustaceans and molluscs. These organisms lay down protective shells made from carbonate, a substance predicted to become increasingly scarce in the future as a result of increasing carbon dioxide levels and consequent ocean acidification (Sabine et al. 2004; Doney et al. 2009). In fact, many experimental studies show that molluscs and crustaceans suffer exceptionally high mortality and low recruitment at acidification levels predicted to occur by the end of the century (Gazeau et al. 2007; Kurihara 2008; Watson et al. 2009), meaning shellfish fisheries all over the world are badly exposed to risk if the organisms they target cannot adapt.

Finally, the economic benefits of simplification may in reality only be short term. As we have explored, simplification can result in ecosystems shifting to new states that are entirely undesirable and result in long-term losses, such as those observed in the Black and Baltic Seas. The ecological simplifying effects of overfishing also promote a loss in ecosystem services and can result in eutrophication, harmful algal blooms and large-scale invasions, which can affect target species and human well-being.

Can ecosystem change be reversed?

In the light of the problems discussed, it is important to know whether adverse ecosystem shifts can be reversed. Studies suggest they can. Meta analyses reveal that the establishment of protected areas can restore ecosystems and biodiversity and often result in an increase in biomass, density and average body size of large predators and herbivores (Halpern and Warner 2002; Halpern 2003; Micheli et al. 2004). For example, the establishment of two marine reserves in New Zealand led to sea urchin-dominated barrens reversing back to macroalgal beds within 20 years (Shears and Babcock 2003). Evidence suggested that this was the result of an increase in the density and body size of snappers (*Pagrus auratus*, Sparidae) and rock lobsters (*Jasus edwardsii*, Palinuridae), the primary predators of sea urchins (Langlois and Ballantine 2005). Similarly, the designation of Mombasa Marine National Park in Kenya was followed by significant increases in predators of sea urchins and subsequent coral recovery after just 10 years of protection (McClanahan and Mangi 2000). Marine protected areas have also proven effective in large-scale industrial fisheries. In 1994, in the Gulf of Maine, three areas totalling 17 000 km^2 were closed to fishing gears that targeted ground- fish or were damaging to their habitats, in an emergency response to the collapse of groundfish fisheries within the region (Murawski et al. 2000). In an area known as Georges Bank, haddock and yellowtail flounder (*Limanda ferruginea*, Pleuronectidae) increased between three- and fivefold within the first 5 years of protection (Murawski et al. 2000; Stone et al. 2004) and promoted recovery of the seabed through increasing the biomass and structural complexity of bottom habitats (Hermsen et al. 2003).

Equally though, there are many examples where protected areas have not managed to restore ecosystems and fish stocks. This is particularly true when they are not enforced or complied with (Pitcher and Lam 2010), but some even fail when compliance is absolute (Frank et al. 2005). In the Northwest Atlantic, for example, most Canadian stocks of Atlantic cod showed little or no signs of recovery despite the termination of direct fishing activity for over a decade (Hutchings 2001). How much this lack of recovery is down to the effects of continued prawn and scallop dredging on cod nursery grounds is unknown, but it seems likely in view of the experience we described for the Clyde ecosystem. Returning to the George's Bank closure, although haddock stocks are improving, cod is yet to show any signs of recovery (Mayo and Col 2006; Mountain and Kane 2010). Likewise, a protected area in Belize demonstrated good recovery of predatory reef fish, but only a weak response by herbivores (McClanahan et al. 2011). Correspondingly, there was little change in total herbivory and coral cover.

There are a diverse range of other management tools available. Enforcing the use of fishing gears that cause less damage to habitats and select for specific species, sizes and ages is one way to reduce exploitation and damage to ecosystems (Pitcher and Lam 2010). For example, after the ecological shifts in the Baltic Sea described earlier in this study, cod biomass trebled between 2005 and 2009, thought to be mainly driven by a ban on trawling, which led to a sudden reduction in fishing mortality (Cardinale and Svedäng 2011). Similarly, reducing fishing effort through reductions in quotas, total allowable catch and fishing capacity have all been shown to promote recovery in a number of fish stocks (Beddington et al. 2007; Worm et al. 2009). However, whilst such approaches may help restore the abundance of targeted species, they do not necessarily lead to the recovery of biodiversity and the wider ecosystem (Pitcher and Lam 2010). In addition, any reductions made to fishing effort can cause social and economic instability as processing plant closures, unemployment and bankruptcy inevitably follow (Hilborn 2007a).

It has been heavily argued that protected areas and restrictions on fishing effort and fishing gears are not long-term solutions as they do not address the underlying causes behind overfishing (Beddington et al. 2007; Hilborn 2007a; Costello et al. 2008; Pitcher and Lam 2010). In 'open-access' systems, individuals lack secure rights to part of the quota, meaning fishermen often attempt to outcompete each other by attaining bigger vessels and better technology. Consequently, this leads to lobbying for ever larger quotas, excessive harvests and, eventually, the collapse of the stock (Costello et al. 2008). 'Dedicated access' systems, on the other hand, prevent the 'race to fish' by allocating individual rights to a quota or area to individual fishermen or communities (Hilborn 2007a). This guarantees fishers a certain proportion of the catch, thereby offering a sense of ownership, encouraging them to make more rational economic choices to manage their fishery resources more sustainably in the long term (Beddington et al. 2007; Pitcher and Lam 2010). Studies show that this approach has successfully reduced fishing effort and improved compliance and community participation in management processes (Johannes 1981; NRC 2003; Costello et al. 2008; Worm et al. 2009). In fact, greater involvement of fishermen and other stakeholders is commonly reported to result in more sustainable levels of exploitation, better distribution of power, reduced conflict and greater economic returns (Berkes 2007; Gutièrrez et al. 2007). However, there are cases where these approaches have not worked (Dulvy and Polunin 2004; Castilla et al. 2007; Chu 2008; Branch 2009), and there is little evidence for dedicated access management helping damaged ecosystems to recover (Costello et al. 2008).

Overall then, it is apparent that one management tool alone is not enough to prevent overexploitation and subsequent ecosystem change. It is therefore widely agreed that a combination of managing fishing effort, fishing gears and establishing protected areas, all of which have received mutual consent from managers, fishermen and other stakeholders, will be most effective in achieving both fisheries and conversation objectives (Hil- born 2007; Worm et al. 2009; Khan and Neis 2010).

Despite intervention, many over-exploited fish stocks and ecosystems simply never recover (Hutchings 2000, 2001; Hutchings and Reynolds 2004). What factors prevent recovery are largely unknown but are thought to include (see Hutchings and Reynolds 2004; Hooper et al. 2005; Hughes et al. 2005; Diaz-pullido et al. 2009) amongst others: (i) density-dependent effects (e.g. altered predator–prey ratios, recruitment failure through the Allee effect); (ii) local extinction of key functional groups; (iii) recovering functional groups not promoting return to a previous state (e.g. many reef-based herbivores will not eat late succession macroalgae and therefore would not encourage the reef to return to a coral-dominated state, McClanahan et al. 2011); (iv) competition with/or predation by invasive species; (v) habitat alteration; (vi) life-history traits (e.g. fast-growing species such as herring are more likely to recover than long-lived species such as cod and halibut); and (vii) the overall reduction in biodiversity in simplified ecosystems, giving fishers less opportunity to switch to alternative taxa and therefore less likely to reduce their fishing effort (Worm et al. 2006). Whatever the reason, it appears that some ecosystems are altered to such an extent that they have crossed a threshold beyond which recovery to previous conditions may be impossible. The overall message from our research is clear; it would be easier for managers to maintain ecosystems in a more natural state than to try and repair them (Schiermeier 2002; Hughes et al. 2005; Worm et al. 2009).

Conclusions and perspectives

Recent papers (e.g. Hilborn 2007a, 2007b; Worm et al. 2009; Branch et al. 2011) argue that the global decline of fish stocks is slowing and that fisheries management is improving. However, these improvements are localized, confined to countries such as the USA, Australia, New Zealand and Iceland. One report shows fishing grounds in Europe largely remain in a state of decline (Guènette and Gascuel 2012), and unassessed fisheries, which account for more than 80% of fisheries worldwide, have recently been argued to be in substantially worse condition than most assessed fisheries (Costello et al. 2012). We therefore argue that these improvements are not universal and that the perspective taken in this study better reflects the global state of fisheries and ecosystems. In addition, the above improvements come after many decades of decline, meaning it is too soon to know whether these early signs of recovery will be sustained.

Through overfishing, marine ecosystems worldwide have lost many of their natural populations of finfish, resulting in reduced biodiversity and significant ecological change. In a growing number of cases, these simplified ecosystems have come to support large invertebrate fisheries, often capable of generating more economic value than the fisheries they replaced. However, such changes are not a result of directed management, but rather a result of management failure, a failure to protect stocks of target species in the face of industry innovation and fisheries intensification.

Simplified ecosystems are only economically beneficial to one or two industry sectors and only in the short term, as low-diversity ecosystems are unstable, being more susceptible to sudden fluctuations in stock size, invasion and disease. From a wider societal perspective, ecosystem simplification makes little economic sense at all. The loss of functional groups can trigger dramatic ecosystem shifts to states that are both ecologically and economically undesirable, and often difficult and expensive to reverse. Further shifts could also leave fishers with few alternative species to turn to. In areas highly dependent on marine fisheries, this would have serious socioeconomic consequences. These changes occur because, unlike in terrestrial agricultural systems, there are no measures we can take to counter the ecological problems generated by simplification of food production systems in the open sea. All these arguments suggest that the transition from multispecies fisheries to simplified invertebrate fisheries has caused a global decline in biodiversity and ecosystem services, which is threatening global food security, rather than promoting it.

The lowered ecological and economic resilience of fisheries alone provides a strong reason for managers to avoid or reverse ecological simplification. When the wider economic costs of simplification are also taken into account (loss of ecosystem services, impacts on human well-being, etc.), it generates a compelling argument for a complete overhaul of present practice. We now need to work to implement management regimes that will promote recovery of complexity in food webs and habitats. This is why, we urgently need to shift to a management system that incorporates extensive protected areas, reduces fishing intensity, eliminates or highly constrains use of habitat destructive and unselective fishing methods, promotes recovery in the abundance and variety of target and non-target animals, and helps restore ecosystem structure and function.

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Chapter 3. Comparing the utility of SCUBA and camera surveys for monitoring a temperate marine protected area

3.1. Preface

For MPAs to be considered a successful tool in fisheries management and biodiversity conservation, it must be demonstrated that the existence of an MPA or MPA-network is responsible for generating ecological and/or fishery benefits. Monitoring programs designed to detect trends, or changes from pre-MPA conditions, are therefore essential for evaluating whether MPAs succeed in fulfilling their objectives.

In this chapter I compare a number of different survey methods to help determine which were most suitable for monitoring the abundance and size of a number of different organisms in Lamlash Bay Marine Reserve.

This chapter has been written in the style of Aquatic Conservation: Marine and Freshwater Ecosystems.

I declare that the work submitted is my own. The contribution by co-authors was as follows:

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Comparing the utility of SCUBA and camera surveys for monitoring a temperate marine protected area

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Abstract

1. Diver surveys are regularly employed in monitoring of marine protected areas, but in light of recent improvements in underwater technology, the use of photo and video surveys have increased in popularity over the past decade. These different survey methods often overlap in the types of organisms they record and it is not always clear which method should be preferred.
2. This study sought to determine which survey methods were most suitable for monitoring the abundance and size of a number of different organisms in the Lamlash Bay marine protected area in Scotland. Power analysis suggested that diver surveys were the more cost and time-effective method for estimating the density and size of scallops compared to photo methods.
3. Comparing the relative proportional cover of different epifaunal assemblages attached to seafloor generated by diver and photo surveys also revealed several differences. It was found that photo surveys detected a greater proportion of macroalgae and maerl than diver estimates, whereas diver surveys detected a greater proportion of tunicates, sponges, hydroids and bryozoans. This highlights the inherent biases created by different survey methods.
4. Diver and baited underwater video surveys differed in their ability to detect different species of crustaceans and fish. Diver surveys detected a substantially greater proportion of small, cryptic fish species and a greater proportion of smaller-bodied crustaceans. In contrast, only baited underwater video surveys were able to detect pelagic fish species such as mackerel and sand eels. These species are rarely observed by divers but in the videos were found to occur in large shoals consisting of many hundreds of individuals.
5. Based on the findings, it is argued that diver surveys should be used for the monitoring of scallop stocks within Lamlash Bay. In comparison, for the monitoring of epibenthic species, fish and crustaceans, diver surveys had no clear superiority over camera and video methods as both produced markedly different results for different types of species. Hence, our results indicate that scientists studying marine protected areas must first identify the types of species they intend to study, and from that, choose the most appropriate monitoring method.

KEY WORDS: Survey methods; Methodology; Baited remote underwater video; Diver surveys; Underwater visual census; Photoquadrat; Marine reserves; Firth of Clyde; Scallops

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Introduction

Following a large number of recently established policies and initiatives, the coverage of marine protected areas (MPAs) is set to increase dramatically over the next decade (Metcalfe *et al.*, 2013). Globally agreed marine protection targets, such as the Convention on Biological Diversity's (CBD) '*Aichi Target*' are encouraging many governments to establish or expand existing MPA networks within their jurisdictions (Wood *et al.*, 2008; CBD, 2011; Harrop, 2011; Wood, 2011). This interest is reflected in the European Union (EU) as the Marine Strategy Frameworks Directive (MSFD), Birds and Habitats Directives, OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic), HELCOM (Helsinki Commission) and Barcelona regional seas conventions, have all initiated the process of establishing a coherent network of MPAs within European waters (Fenberg *et al.*, 2012; Metcalfe *et al.*, 2013). On a national level, the planned implementation of Marine Conservation Zones (MCZs; England, Wales and Northern Ireland) and Scottish MPAs (Scotland) will all lead to the creation of a network of MPAs around the United Kingdom (UK; Jones 2012, JNCC 2013). All these measures have been agreed upon by member states to achieve a variety of management goals; principally to conserve biodiversity and promote the sustainability of fisheries (Pomeroy *et al.*, 2005; Metcalfe *et al.*, 2013).

For MPAs to be considered a successful tool in fisheries management and biodiversity protection, it must be demonstrated that the existence of an MPA or MPA-network is responsible for generating ecological and/or fishery benefits. Monitoring programs designed to detect trends, or changes from pre-MPA conditions, are therefore essential for evaluating whether MPAs succeed in fulfilling their objectives (Van Rein *et al.*, 2009; Götz *et al.*, 2013). For such studies, non-destructive and non-extractive methods are clearly preferable, particularly when working within the boundaries of MPAs. They must also be cost-effective, generating the most accurate, precise and least biased data possible, while requiring the smallest investment of money, time and sampling replicates (Legg and Nagy, 2006). The results obtained must then inform appropriate reactive management. For example, if an MPA is not contributing to the achievement of biodiversity targets, monitoring programmes can inform decisions for a change in management approach, or for a change in its geographic location or size (Gerber et al. 2005).

In the case of monitoring the ecosystem changes brought about by MPAs, collecting data that can indicate an ecosystem's environmental state or condition are generally of most interest, such as habitat heterogeneity, species diversity and abundance (Van Rein *et al.*, 2009). In comparison, the monitoring of commercially important species requires data on population structure such as body size, age, population density and reproductive output (Langlois *et al.*, 2006). Diver surveys are regularly employed to obtain these latter types of data (e.g. Beukers-Stewart et al. 2005, Harmelin-Vivien et al. 2008, Howarth et al. 2011, Horta e Costa et al. 2013). This is because diver surveys require relatively little in the way of expensive high-tech survey equipment, they are considered highly accurate (particularly when counting benthic megafauna, Beukers-Stewart et al. 2001) and offer the most flexibility by allowing divers to record other types of data *in situ* (Cole *et al.*, 2001; Langlois *et al.*, 2006). However, the total coverage offered by diver surveys is generally quite small and they are heavily constrained by environmental conditions such as depth (generally < 30m), currents, time of day and visibility (Cole *et al.*, 2001). They may also be subject to observer bias as estimates depend on diver speed and experience; meaning divers may fail to notice individuals or count them incorrectly (Assis *et al.*, 2013). Divers may also affect fish behaviour, survey time is limited, and increasing the number of survey replicates can prove time intensive and expensive (Brock, 1982; Mumby *et al.*, 1995; Harvey *et al.*, 2001; Willis, 2001).

In response to the limitations of diver surveys, and in light of recent improvements in underwater technology, the use of photo and video surveys have greatly increased in popularity over the last decade (Stokesbury and Harris 2006, Leujak and Ormond 2007, Van Rein et al. 2009). These optical systems can include diver-operated cameras (Leujak and Ormond 2007), drop-down cameras (Collins, 2002; Van Rein *et al.*, 2011), towed cameras (Morrison and Carbines, 2006; Sheehan *et al.*, 2010) and remotely operated underwater vehicles (ROVs; Neves et al. 2013). All can be used to generate videos and/or still photographic images, and as some can be operated remotely, camera surveys can therefore be conducted in depths, temperatures, weather conditions and at times (e.g. night) that would be difficult or impossible for divers to observe (Jury *et al.*, 2001; Van Rein et al. 2009). Whilst the area covered by an individual photo or video frame is small, increasing the number of frames can be conducted quickly and at little extra cost, allowing for wider coverage of MPAs to be achieved easily. Monitoring areas on a large scale can therefore prove much more efficient using remote camera methods than diver surveys, even when taking into account the costs of camera equipment and time associated with analysing images/videos (Langlois *et al.*, 2006; Assis *et al.*, 2013). In addition, observation time can be greatly increased, and their deployment results in a permanent record that can be viewed and analysed repeatedly. However, problems of the technique include the underestimating of abundance, measurements of body size can be less accurate, and they are unlikely to detect hidden or cryptic species compared to diver surveys (Smith and Tremblay, 2003).

The many pros and cons associated with diver and camera studies have stimulated much debate over which methods should be preferred (Willis and Babcock, 2000; Morrison and Carbines, 2006; Leujak and Ormond, 2007; Pelletier *et al.*, 2011). Whilst the various tools available for monitoring MPAs are relatively well documented in tropical waters (Pelletier *et al.*, 2005; Langlois *et al.*, 2006; Morrison and Carbines, 2006; Leujak and Ormond, 2007), empirical data concerning the effectiveness of different techniques in temperate and polar regions remains relatively scarce by comparison (Russ *et al.*, 2005; Götz *et al.*, 2013). Although the monitoring methods used in tropical seas can be applied in temperate and cold waters, surveying in more temperate waters does present a number of different challenges from tropical areas as the weather conditions are generally less favourable, waters are colder and less clear, and the study sites are often deeper. We therefore felt an investigation of monitoring techniques in temperate waters was warranted.

In September 2008, Scotland's first and only fully no-take MPA was established in Lamlash Bay, Isle of Arran, UK, thereby prohibiting all fishing within the MPA under the Inshore Fishing (Scotland) Act of 1984 (Axelsson *et al.*, 2009). We began monitoring the MPA in Lamlash Bay in 2010 to investigate the effects of closed area protection on scallop stocks and other organisms (see Howarth *et al*. 2011). These surveys were then repeated and expanded for the following three years by adding more sites and survey methods. However, it was found that a number of different survey methods overlapped in the types of organisms they recorded. For example, diver surveys gathered abundance data on scallops, fish and benthic megafauna, but so did the use of photoquadrats and baited underwater video cameras (BRUVs). It was therefore not clear which method should be used for which species. Hence, this study seeks to compare data generated by diver and camera surveys for a number of organisms within Lamlash Bay to determine which methods were more ideal for monitoring certain species. This was achieved by (1) comparing the precision and sampling effort offered by diver and photoquadrat surveys in quantifying the density and size of commercially important king scallops (*Pecten maximus*) and queen scallops (*Aequipecten opercularis*), (2) comparing the relative proportional cover of different epibenthic taxa estimated by diver transects and photoquadrats, and (3) comparing the proportions of a number fish and crustacean species estimated by diver and baited remote underwater video camera (BRUV) surveys.

Materials and methods

Study area

Surveys were conducted in and around Lamlash Bay on the south-eastern shore of the Isle of Arran; an island situated off the west coast of Scotland in The Firth of Clyde. Lamlash Bay MPA encompasses an area of 2.67 km^2 (Thurstan and Roberts, 2010), with water depths ranging between 0 and 29 m below chart datum, but reaching as deep as 43 and 50 m outside to the east and the west of the MPA, respectively (Admiralty Chart 1864; Baxter et al. 2008). Previous surveys (Duncan, 2003; Axelsson *et al.*, 2009) indicate a seabed of mixed sediments (i.e. mud, sand and gravel with various proportions of shell) but that the central and southern regions of the bay tend to be characterised by softer sediment, mainly muddy sand. In addition, the area has long been identified as containing important maerl beds, although recent evidence points to deterioration in their health (Howarth *et al*. 2011).

Data collection: survey design

Monitoring of Lamlash Bay began in 2010 (see Howarth *et al*. 2011). This present study is based on data collected by the 2012 surveys, the most extensive and up to date dataset at the time of writing. Thirty two sites were surveyed between July and September 2012, half of which were within the boundaries of the MPA and half outside (Fig. 1). Sites were chosen so that each site within the MPA could be paired with at least one other suitable control outside the MPA, based on similar depth and predominant substrate type. Sites were limited to areas of the seabed that were shallow enough to remain within diver no decompression limits (i.e. <30 m depth). Surveys were also conducted parallel to depth contours to ensure the depth of a single survey did not change by more than 3 m.

Data collection: survey design Diver and photo transects

Transects were surveyed along a 50 m leaded line that was laid out straight across the seabed. GPS coordinates used for surveys in 2010 and 2011 provided the start and end location of each transect. Attached to both ends of the leaded line were weighted anchors to hold the line in place, in addition to two floating buoys which reached the surface. A team of two divers then placed a 1 m^2 quadrat parallel to the transect, but at a distance of 2 m from the leaded line thereby ensuring the area about to be photographed had not just been disturbed by the laying of the line. The quadrat was divided into four 0.25 m^2 sub-quadrats and the area encompassed by each was photographed directly overhead. This process was then repeated every 5 m along the transect, giving a total of 40 images for each transect. The sub-quadrats were later combined for statistical analysis, giving a total of 10 quadrats for each transect. Although these photos were taken by divers, they are comparable to the types of images generated by remotely operated drop-down cameras, towed videos and ROVs (Morrison and Carbines, 2006; Stokesbury and Harris, 2006; Neves *et al.*, 2013).

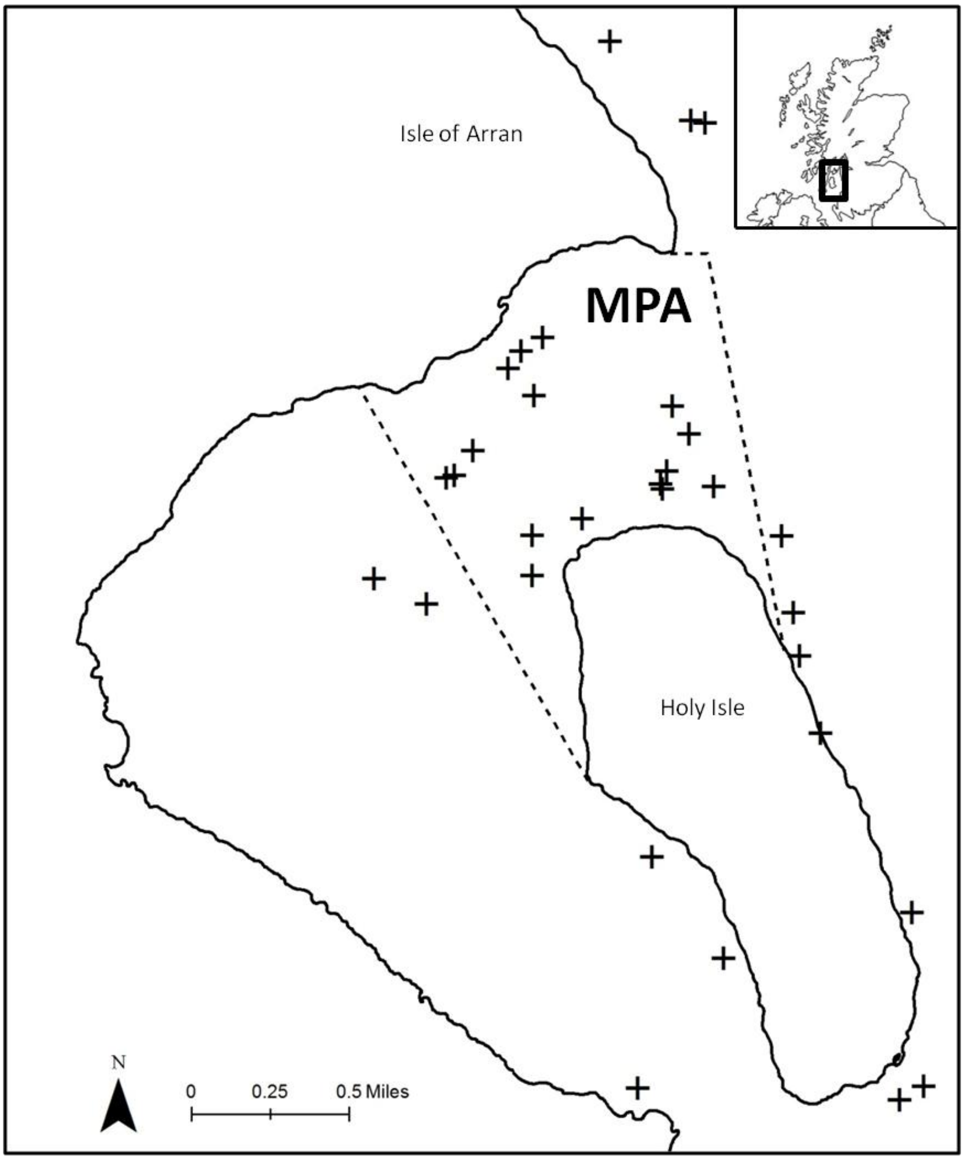

Figure 1. Site locations of the 2012 surveys. At each, a diver transect, photoquadrat and Baited Remote Underwater Video (BRUV) survey was conducted. Also displayed are the boundaries of the Lamlash Bay No-Take Marine Protected Area (MPA). The inset shows the location of the Isle of Arran off the west coast of Scotland, United Kingdom.

After a surface interval of two hours, divers returned to the transect line and made their way from one end to the other, estimating the abundance of all unattached scallops and other megafauna (e.g. fish and crustaceans) encountered within 1.5 m either side of the transect, creating a total area surveyed of 150 m^2 for each transect, the width of which was marked by a

3m long pole which the divers pushed ahead of themselves. In addition, every scallop encountered along the transect was collected and brought back to the surface to be aged and measured for shell length (Jennings *et al.*, 2001). The data generated by both divers were then pooled and adjusted to generate densities of organisms per 100 m^2. A SACFOR abundance scale (superabundant, abundant, common, frequent, occasional, rare, see Connor et al. 2004) was also used by the divers to estimate the area covered by different epibenthic taxa. These were live maerl (e.g. *Phymatolithon calcareum* and *Lithothamnion glacial*), macroalgae (e.g. *Laminaria* and *Ceramium* spp) sponges (e.g. *Pachymatisma johnstonia*), anemones (e.g. *Cerianthus lloydi*), tunicates (e.g. *Clavelina lepadiformis* and *Diazona violacea*), hydroids (e.g. *Obelia geniculata*), bryozoans (e.g. *Alcyonidium diaphanum* and *Flustra foliacea*) and soft corals (e.g. *Alcyonium digitatum*).

Still image analysis

The number of king and queen scallops within each photoquadrat was recorded and converted to density per 100 m^2. The shell length of every scallop observed was also estimated by using the length of the quadrat border as scale. Images were then analysed using the software Coral Point Count with Excel Extensions (CPCe) v 4.1 (Kohler and Gill, 2006). The quadrat border was positioned and sized manually before placing 50 stratified random points over the image. Any organism lying under a point was then identified to species level where possible. If there was no organism, the substrate type was identified instead (e.g. mud, pebble, cobble, boulder or detritus). Initial attempts used just 25 points and 40 images but the seafloor within Lamlash Bay contained such a low proportion of epibenthic fauna that the likelihood of a randomly distributed point falling upon anything other than bare substrate was too low. The number of points was therefore doubled and the number of images for each site halved. Counting the number of scallops was, however, much quicker and easier, and therefore all 40 images available for each transect were used.

Baited Remote Underwater Video (BRUV)

A BRUV was deployed at each site over the survey period between the hours of 9am-2pm. For these, a video camera was fitted to one end of a commercial lobster pot frame and a porous bait box was fitted to the other end. Rope was spliced to all four corners of the frame and joined at the centre along with three cork floats to prevent the ropes from sinking in view of the camera (Fig. 2). As baseline studies in 2010 indicated that fish abundance was relatively low in the area, 200g of coarsely cut mackerel was placed inside the bait box prior to deployment in order to attract fish from a wider area. Once recording began, a 40m long rope and surface marker buoy were attached to the central snap-shackle and the BRUV was carefully lowered to the seafloor. The system's negative buoyancy ensured the BRUV landed upright and remained in a stable position. After approximately one hour, the BRUV was hauled back to the boat, the bait replaced, and the BRUV was ready for redeployment at another site.

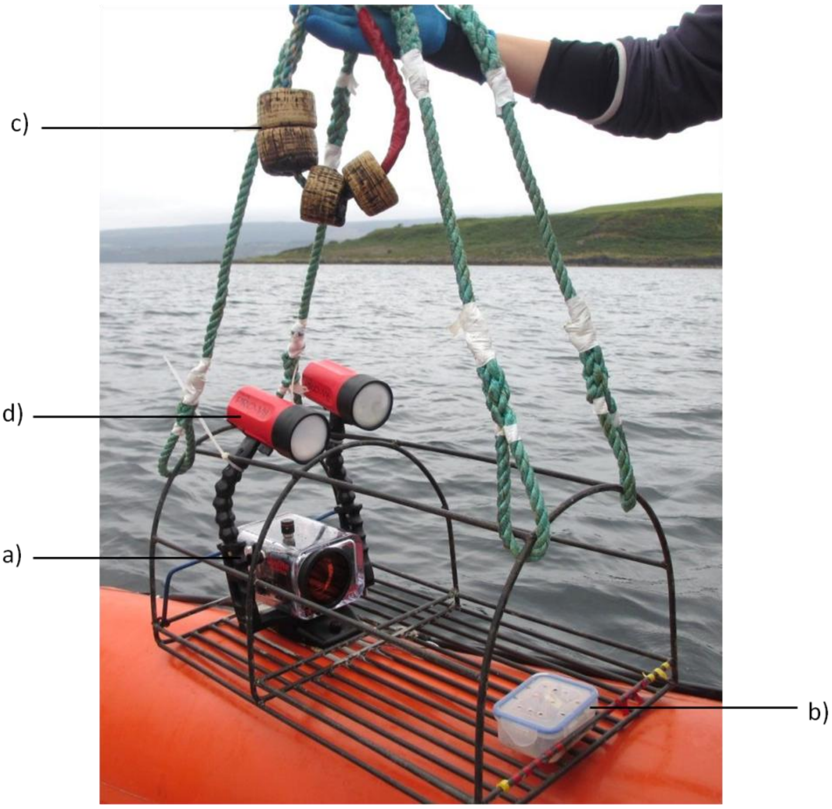

Figure 2. The Baited Underwater Video Camera (BRUV) set-up comprised of a video camera (a) mounted to a lobster pot frame in view of a porous box containing mackerel bait (b). Ropes were used to lower the system to the seafloor and cork floats (c) prevented these from descending in front of the camera. Two video lights provided lighting (d).

Video analysis

To standardise video lengths, analysis began from two minutes after the BRUV landed on the seabed and terminated 60 minutes later. For each video the following variables were recorded for all fish and crustaceans: (*i*) identity and total number of species; (*ii*) total number of families; (*iii*) time of first appearance for each species; (*iv*) maximum number of individuals of a species observed within the same frame (MaxN); and (*v*) time of MaxN. Due to the inability of an observer to recognise repeated entrances of the same individual, MaxN was used as an estimator of abundance (Cappo *et al.*, 2004). However, it must be noted that, although MaxN is commonly used to measure relative abundance, it does not reflect the detailed interactions between individuals and the bait odour plume (Stobart *et al.,* 2007, Colton and Swearer 2010) or the succession of different fish species and sizes visiting the system (Harvey *et al.,* 2012). In addition, some studies have found little correlation between abundance estimates generated by MaxN and those created from underwater visual census (Dunlop 2013).

Data analyses

Scallop density and population structure

Differences in scallop density between the MPA and outside were compared using a one-way Analysis of Variance (ANOVA) for both photoquadrat and diver methods. To compare precision between these estimates of scallop density, the co-efficient of variance (CoV) was also calculated. Using the statistical package R (www.r-project.org), a power analysis was then conducted to determine how many replicates would be required to detect a 20%, 50% and 100% difference in scallop density between the two treatments using a one-sample t-test power calculation. For this, each transect (comprising of 10 photoquadrats) was treated as an individual sample in order to calculate how many transects would need to be conducted, rather than how many individual photos. In addition, the cumulative standard deviation (SD) of scallop density were plotted against number of replicates for both diver and photoquadrat surveys to determine which generated the lowest level of error within the fewest number of replicates.

Finally, it was our intention to compare the size composition of king and queen scallops between the two treatments and methods. However, in most cases, far too few individuals ($N < 5$ per treatment i.e. MPA and outside) were detected by the camera method. Therefore, only the size composition of king scallops generated by the diver surveys and photoquadrat methods within the MPA could be explored. This was illustrated using bar charts, and tested for significance using a Kolmogorov–Smirnov (K–S) analysis.

Relative proportional cover of epibenthic taxa

SACFOR estimates of epibenthic cover were converted into percentage proportional cover in order to allow data generated by both diver and photoquadrat methods to be presented on the same chart. These data cannot be directly compared as the two methods result in entirely different types of data. Instead, our intention was solely to explore how the two methods differed in their ability to detect different epibenthic taxa. Consequently, no statistical tests were performed as it was deemed inappropriate. For the comparison, SACFOR estimates of each epibenthic taxon were converted into a numerical value ranging from 0-6, where a value of 0 indicated the absence of a taxon and 6 represented the superabundance of a taxon, as denoted by the SACFOR scale. These numerical values were then converted into percentage cover using the following equation:

$$taxon\ (\%) = \frac{SACFOR}{MaxS} \times 100$$

Where *taxon* (%) = percentage cover of a taxon category (e.g. maerl), *SACFOR* = numerical value of abundance of an epibenthic taxon derived from the SACFOR scale, *MaxS* = The maximum score possible for a transect if all taxa were superabundant (the maximum score for a taxon was 6, and as there were 8 categories, *MaxS* in this study was 48). A worked example of this process is provided in Table 1. It was then assumed that the remaining percentage represented the proportional cover of bare substrate. This was calculated using the next equation:

$$bare\ substrate\ (\%) = 100 - \sum taxon\ (\%)$$

Table 1. A worked example of how the SACFOR scale was used estimate the proportional cover by a number of different epibenthic taxa.

Taxon	SACFOR	Value	Cover (%)
Live maerl	Rare	1	2.1
Macroalgae	Super abundant	6	12.5
Sponge	Occasional	2	4.7
Anemones	Abundant	5	10.42
Soft coral	Absent	0	0
Tunicates	Common	4	8.3
Hydroids	Frequent	3	6.3
Bryozoans	Occasional	2	4.7
		Bare substrate (%)	60
		Sum	100.0

Crustacean and fish abundance

The mean number of species, individuals and Shannon's Diversity index of fish and crustaceans were calculated from the BRUV surveys and diver surveys. Any differences between the MPA and outside were then tested for significance using ANOVA and subjected to endpoint adjustment to correct for multiple testing. The false discovery rate (FDR) endpoint adjustment was used to reduce the likelihood of Type I errors.

Results

Comparisons of scallop density

Both diver and photoquadrat estimates revealed king scallop density to be higher within the MPA than outside (Fig. 3). According to diver estimates, the mean density of king scallops per 100 m^2 inside the MPA was 7.4 (SE = ±2.1, N = 16), significantly higher than 4.1 (SE = ±2.13, N= 15) for outside the MPA (ANOVA, $F_{(1, 30)} = 4.2$, $P < 0.05$). In contrast, although photoquadrats estimated a bigger difference between king scallop density in and outside the MPA; 10.6 (SE = ±7.7, N = 16) and 2.7 (SE = ±2.2, N = 16) respectively, this difference was not significant (ANOVA, $F_{(1, 30)} = 2.7$, $P > 0.05$). This was because diver estimates of king scallop density were substantially less variable (CoV = 105.6%) than those from photoquadrats (CoV = 181.7%). The density of queen scallops was slightly higher within the MPA than outside for both diver and photoquadrat estimates (Fig. 3). However, queen scallop density was comparatively much lower than king scallops and also offered substantially more variation for both photoquadrat (CoV = 203.7%) and diver estimates (CoV = 178.8%). Consequently, no significant difference between the MPA and outside was detected using either method (ANOVA, $F_{(1, 30)} = 3.3$, $P > 0.05$).

In contrast to above, when each transect was explored individually, photoquadrats underestimated the density of king and queen scallops relative to the diver surveys in almost every instance (Fig. 4). In fact, for many sites where diver estimates detected scallops, photoquadrats failed to detect any at all. King scallops generally proved difficult to identify from the photographs as they were often buried into and under the sediment (Fig. 5). This trend was also pronounced in queen scallops, which were detected at only 6 of the 31 sites by photoquadrats, compared to 21 out of 31 sites for diver estimates. However, when scallops were detected within a transect, the photoquadrat method often greatly overestimated their density. This is a consequence of the much smaller sampling area covered by the photoquadrats (40 units of 0.25 m^2 each compared to a single area of 150 m^2 for diver transects). This meant that when a scallop was detected within a photoquadrat and scaled-up to a density of individuals per 100m^2, the resulting figure was unrealistically high. To overcome this, many more photos would have to be taken per transect than the 40 used in this study. In fact, 600 images would be needed to obtain the same area sampled as the diver surveys. Based on taking 40 images per transect, power analysis suggested far fewer transects (less than 15% as many transects) would be required to detect a significant difference in king scallop density between the MPA and outside using the diver survey method compared to photoquadrats (Table 2). Similarly, plots of cumulative standard deviation indicated that diver surveys generated the lowest levels of variation within the fewest number of replicates. After three replicates, the cumulative standard deviation of diver estimates for king and queen scallop in and outside the MPA had plateaued at values ranging between 0.8 to 1 SD. By contrast, it took the photoquadrat method 6 replicates to level off and this comprised of much greater SD values, which ranged between 1 and 7.

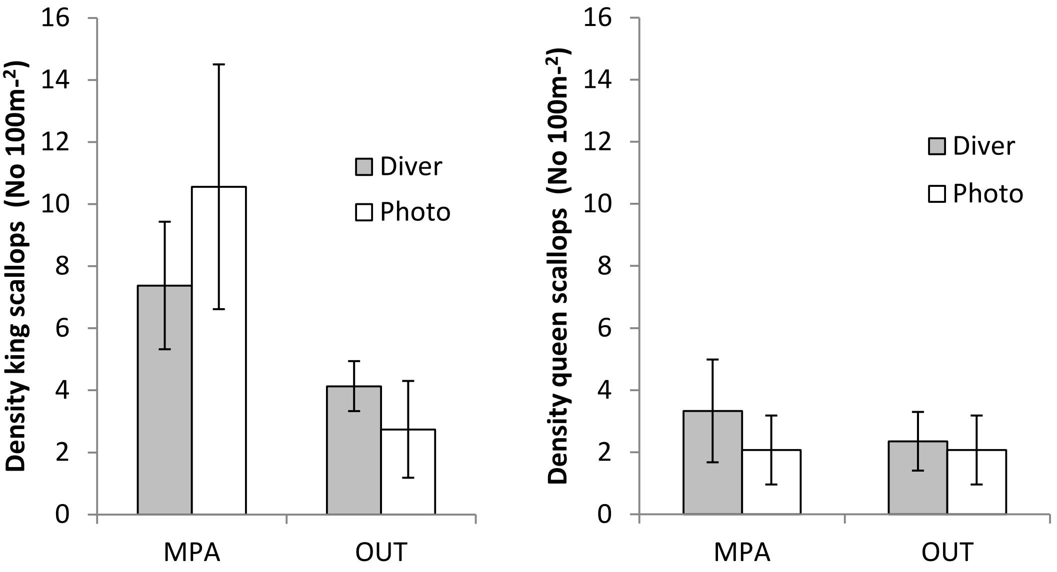

Figure 3. The density (mean no / 100 m^2) of king and queen scallops within and outside the Lamlash Bay fully protected MPA as generated by diver and photoquadrat surveys in 2012. Error bars represent ±1 SE.

Table 2. Summary of the one-sample t-test power calculations used to determine how many transects (N) would be required to detect a 20%, 50% and 100% difference in king scallop density between the MPA and outside using the two different survey methods.

	20%		**50%**		**100%**	
Method	*N*	Delta	*N*	Delta	*N*	Delta
Diver	113	0.82	19	2.1	6	4.13
Photo	954	0.55	604	1.37	40	2.74

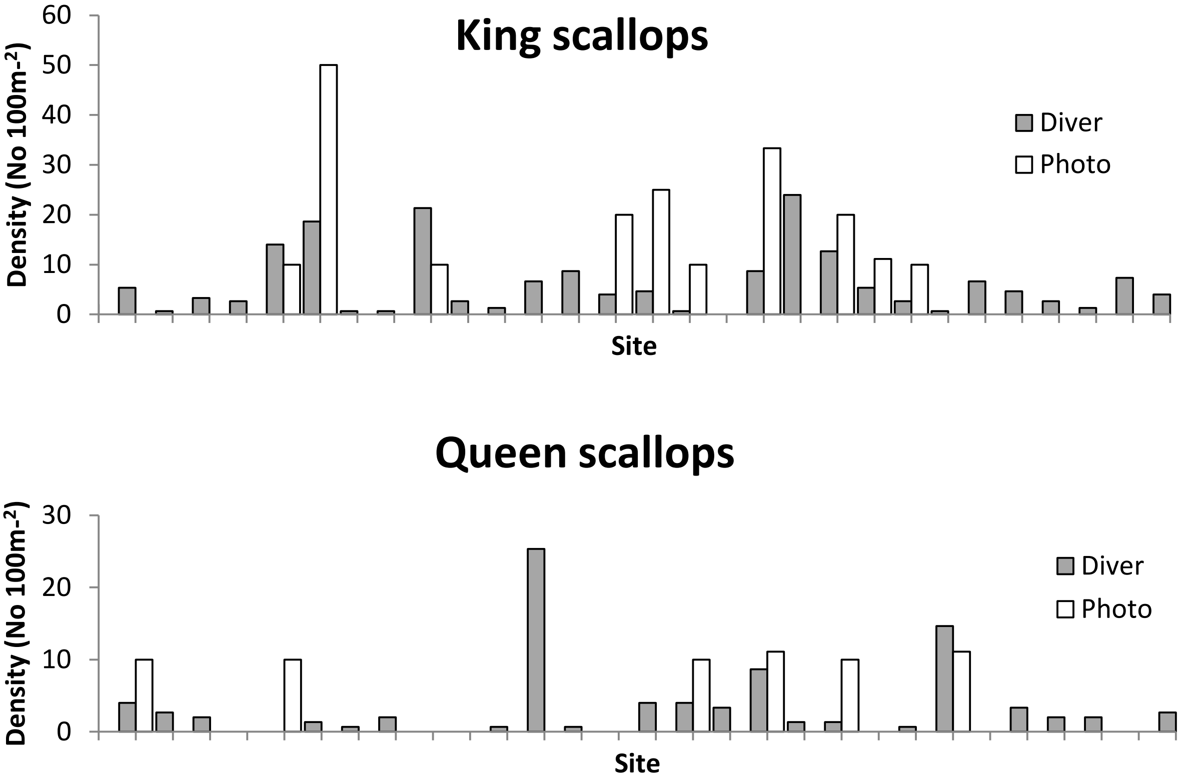

Figure 4. The density of king and queen scallops (no / 100 m^2) at every site location estimated by the two different survey methods in 2012.

Comparisons of scallop population structure

Photo and diver surveys generated a similar size structure for king scallops sampled within the MPA (Fig. 6), however, the small sample size afforded by the photoquadrat method meant that some size ranges were not represented in the photo generated data. Hence, the two size distributions were found to significantly differ (Kolmogorov–Smirnov, $Z = 1.4$, $P < 0.05$). Consequently, the photoquadrat method failed to detect a significant difference in mean king scallop size between the MPA ($\bar{x} = 115.9$, SE = ± 29.2, $N = 14$) and outside ($\bar{x} = 115$, SE = ± 13.5, $N = 4$) (ANOVA, $F_{(1, 17)} = 66.9$, $P > 0.05$), whereas diver estimates found mean king scallop size to be significantly greater within the MPA ($\bar{x} = 132.9$, SE = ± 22.8, $N = 162$) than outside ($\bar{x} = 107.3$, SE = ± 18.9, $N = 125$) (ANOVA, $F_{(1, 286)} = 0.03$, $P < 0.05$).

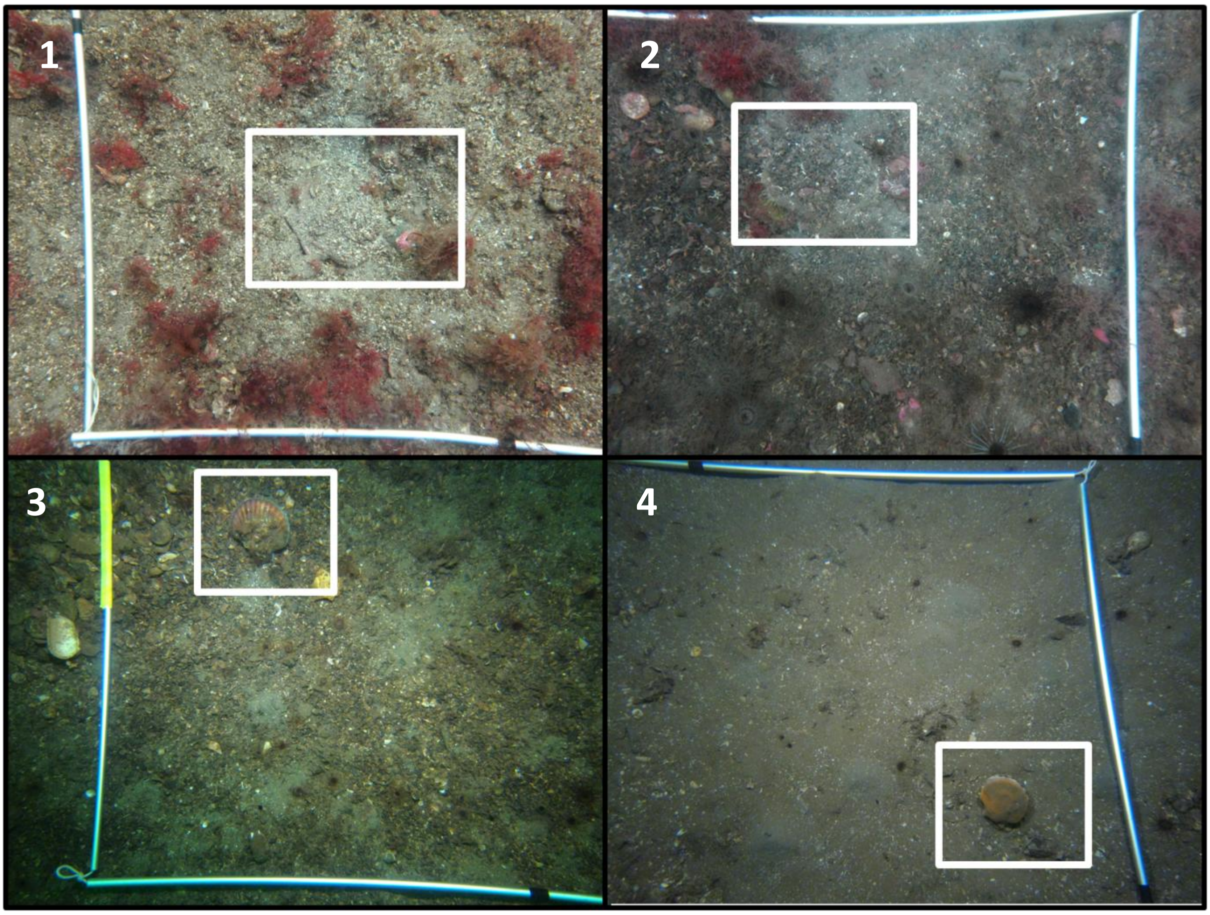

Figure 5. Examples of the images obtained from the photoquadrat surveys in 2012. King scallops often buried themselves into and under the sediment (photos 1-2) which made them harder to identify than queen scallops which tended to rest on top of the seabed (photos 3-4).

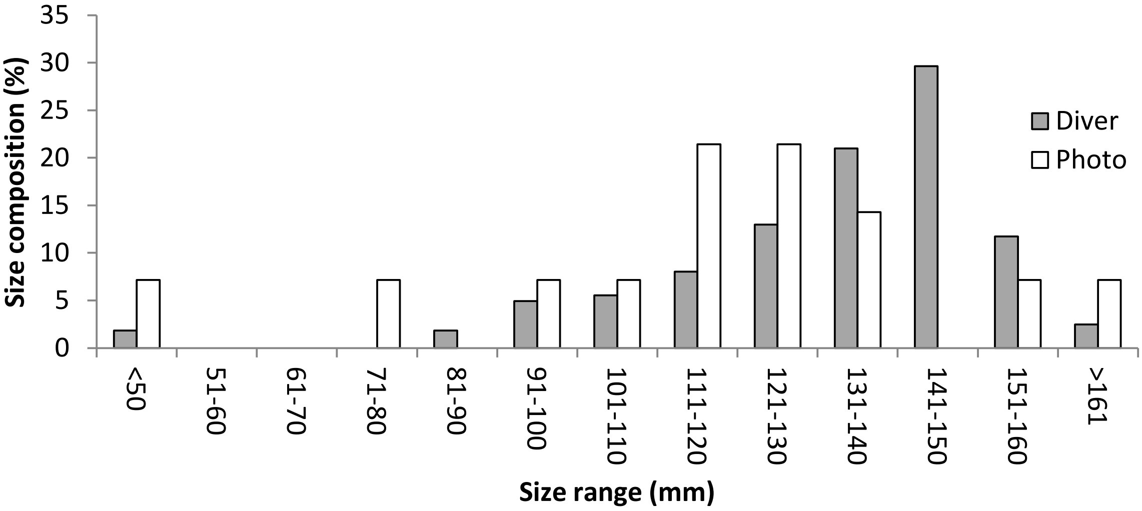

Figure 6. The size structure of king scallops within the fully protected MPA estimated from both the diver (*N* = 162 scallops) and photoquadrat methods (*N* = 14 scallops) in 2012.

Still image analysis Comparisons of proportional epibenthic cover

Comparing the relative proportional cover of epifaunal assemblages between diver and photoquadrat surveys suggested there were several differences (Fig. 7). Photoquadrats detected a greater proportion of macroalgae and maerl than diver estimates. Conversely, diver estimates detected a greater proportion of tunicates, sponges, hydroids and bryozoans. Both methods detected greater proportional cover of bare substrate outside the MPA.

Comparisons of crustacean and fish abundance and diversity

Diver and BRUV surveys detected a similar number of species, families and overall biodiversity (Table 3). Neither survey method found a significant difference in these diversity indicators between the MPA and outside (ANOVA, $F_{(1, 31)} = 6.2$, $P > 0.05$).

Both survey methods detected a similar proportion of the three commercially exploited crustaceans (Fig. 8) namely: edible crab (*Cancer pagurus*), velvet crab (*Necora* puber) and shore crab (*Carcinus maenas*). However, diver surveys detected a greater proportion of smaller-bodied species such as hermit crabs (*Pagurus* spp) and decorator crabs (*Macropodia* and *Inachus* spp), whereas BRUV surveys found a greater proportion of harbour crabs (*Liocarcinus depurator*). After end point adjustment, only the diver estimates of harbour crab abundance were significantly greater within the MPA than outside (ANOVA, $F_{(1, 29)} = 11.02$, $P < 0.05$).

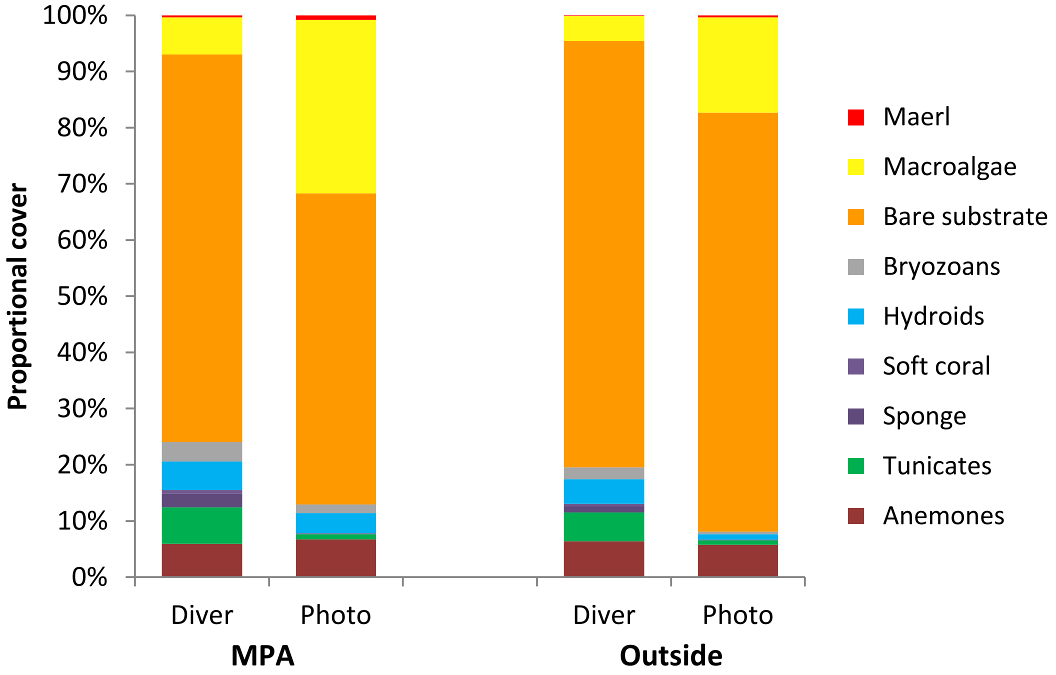

Figure 7. The percentage cover of different epifaunal assemblages within and outside the fully protected MPA detected by diver and photoquadrat surveys in 2012.

Table 3. The total number of species, families, and mean Shannon Diversity Index of fish counts generated from diver and BRUV surveys between sites in and outside the fully protected MPA in 2012.

	MPA		OUT	
Number detected	Diver	BRUV	Diver	BRUV
Species	28	27	30	31
Families	12	12	10	11
Mean diversity	1.7	1.47	1.46	1.58

In contrast to the crustaceans, there was a substantial difference in the fish species observed between the diver and BRUV surveys (Fig. 9). Only BRUVs detected pelagic species such as mackerel (Scombridae) and sand eels (Ammodytidae) while diver surveys estimated a much greater proportion of small, cryptic species such as scorpion fish (*Taurulus bubalis*), gobies (Family: Gobiidae) and blennies (Family: Blennidae). Again, after end point adjustment, only diver estimates detected significantly greater abundance within the MPA, this time just for blennies (ANOVA, $F_{(1, 29)}$ =5.49, $P < 0.05$).

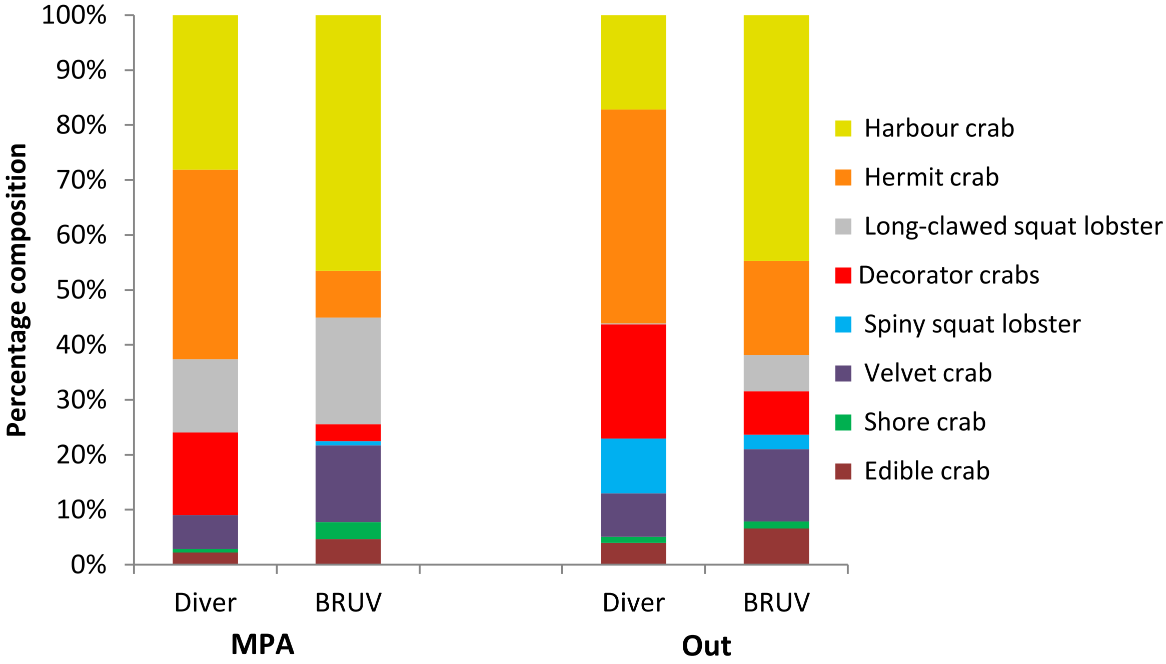

Figure 8. The percentage composition of different species of crustacean within and outside the fully protected MPA observed by diver and BRUV surveys in 2012.

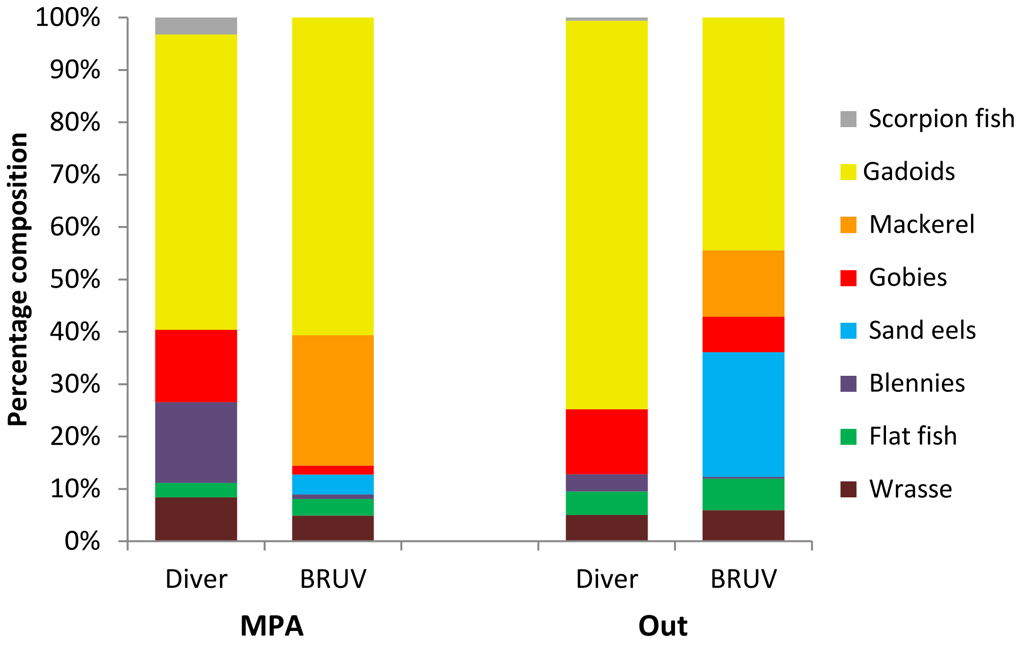

Figure 9. The percentage composition of different species of fish within and outside the fully protected MPA observed by diver and BRUV surveys in 2012.

Discussion

Camera and video surveys are regularly employed by marine and fishery scientists to study commercially important species of shellfish (e.g. Collins 2002, Stokesbury 2004, Rosenkranz and Byersdorfer 2004, Boulcott et al. 2012). However, we found this to be a less effective way of quantifying scallop density and size when compared to direct SCUBA observation. For king scallops this was partly because individuals were often buried into or under the sediment, often making them difficult to identify in a photograph. In comparison, queen scallops were underestimated because they are highly mobile (Jenkins et al. 2003) and often fled the area being photographed (pers. obs.). This meant that for many sites where divers detected scallops, photoquadrats often failed to detect any at all. There could even be further issues for those studies employing towed video systems to estimate density (as is often the case e.g. Rosenkranz and Byersdorfer 2004, Sciberras et al. 2013), as camera motion can result in even greater levels of disturbance and less clear images for analysis than what those used in this study. Paradoxically, when scallops were detected by the photoquadrat method, scallop density was often greatly over-estimated because of the much smaller sampling area covered by the photoquadrats (0.25 m^2 compared to 150 m^2 for diver transects). This meant that when a scallop was detected within a photoquadrat and scaled-up to the density of individuals per $100m^2$, the resulting figure was unrealistically high. Therefore, if camera methods were used to monitor scallop abundance in Lamlash Bay, a far greater number of images would have to be taken than what was used in this study. In fact, 600 images would be needed to obtain the same area covered by a single diver survey. In contrast, SCUBA divers were able to scan the seafloor ahead from several angles, search for hidden individuals and record any scallops (particularly queens) before they fled the transect. Diver estimates of scallop density are therefore likely to much more accurate (see also Beukers-Stewart et al. 2001). Consequently, our diver surveys provided a reliable indication of density, from which estimates generated by the photoquadrats could be compared.

If a drop-down camera was employed instead of a diver-operated camera, and if more samples covering a greater area were taken, the issues associated with the camera method would disappear. As it stands though, the number of photoquadrats in this study was too low. Photoquadrats generated greater within-sample variation and, as a result, only diver surveys were able to detect a significant difference in scallop density between the MPA and outside. Photoquadrats also failed to detect that the average king scallop size was higher within the MPA than outside, a trend found to be significant by diver surveys. Furthermore, the size structure estimated by the photoquadrat method lacked the resolution offered by diver estimates, missing several size classes and showing no clear peak in size class. As a result, the size structures estimated by the two methods were significantly different from each other, despite coming from the same sample population. Again, as the photoquadrat method afforded such a low detection rate of scallops, substantially more photoquadrats would need to be conducted than what was used in this study if they were to be used to estimating the abundance of scallops in Lamlash Bay.

Power analysis also suggested that diver surveys were the more powerful method for estimating scallop density, requiring only 19 transects to detect a 50% difference in scallop density, compared to 604 transects for the photoquadrat method. In terms of number of individual images, that would mean analysing 24,160 still images compared to the 1,240 used in this study. This suggests that diver surveys are a more time-effective, and potentially cost-effective, method for estimating scallop density, and possibly for other shellfish species. Diver surveys would also prove more capable at detecting changes over time as they were far more accurate and precise. Finally, during diver surveys there is opportunity to collect scallops for age determination. Such information cannot be obtained via remote methods, but provides an especially powerful measure of detecting demographic differences between populations (e.g. Beukers-Stewart et al. 2005).

Despite our findings, it should be recognised that in some circumstances diver surveys may be not be an option and remote camera methods must be employed. Camera surveys have been extensively used by scientists monitoring populations of the sea scallop *Placopecten magellanicus* off the east coast of North America, often working in depths over 100m (Stokesbury 2004). In cases such as these, diver surveys would be unsafe, logistically complex and expensive. Fortunately, the ecology and behaviour of sea scallops likely makes them more suitable for photographic surveys than either of the scallop species in our study. Sea scallops tend to rest on top of the sediment rather than recess into it like king scallops, but are also relatively immobile compared to queen scallops (Packer et al. 1999).

Comparing the relative proportional cover of different epifaunal assemblages attached to the seafloor, generated by diver and photoquadrat surveys, also revealed several interesting differences. For example, it was found that photoquadrats detected a greater proportion of macroalgae and maerl than diver estimates, whereas diver surveys detected a greater proportion of tunicates, sponges, hydroids and bryozoans. Why this is remains unclear, but it may be due to the different perspectives the two methods afford. For example, divers were able to view the seafloor from several angles, meaning they could observe the organisms attached to the sides and undersides of rocks and boulders; prime habitat for tunicates, sponges, hydroids and bryozoans. Photoquadrats, on the other hand, offered a strictly birds-eye view of the seabed, meaning they detected a lower proportion of these organisms, and instead, revealed a greater proportion of macroalgae and maerl. In addition, tunicates, sponges, hydroids and bryozoans are very small and were often difficult to identify in photographs, whereas divers were able to get much closer to the substrate. Nonetheless, camera methods are likely to be far more precise. This is because, due to air and decompression time constraints, the diver surveys only generated SACFOR estimates of benthic cover. Such estimates are highly subjective and can differ greatly between different scientists analysing the same transect. Although analysis of photoquadrats requires extensive training and familiarity with benthic taxa, if a quadrat was repeated and analysed by several scientists they would likely generate more consistent and quantitative data than what would be obtained from dive surveys due to computer analysis.

Diver and BRUV surveys also differed in their ability to detect different species of crustaceans and fish. Diver surveys detected a substantially greater proportion of small, cryptic, static fish species such as scorpion fish, gobies and blennies and a greater proportion of smaller-bodied crustaceans, such as hermit crabs and decorator crabs. These results were expected since, as discussed before, divers could inspect the substrate closely for small hidden species. Also, the movements of divers often disturbed cryptic species out of hiding, making them more apparent. In contrast, the BRUV offered a much narrower horizontal field of view of the substrate, thereby reducing the probability of detecting cryptic species. Hence, it is no surprise that other studies have concluded video surveys to be unsuitable for recording small, cryptic species when compared to other methods (Tessier *et al.*, 2005; Langlois *et al.*, 2010; Pelletier *et al.*, 2011). Conversely, only BRUV surveys were able to detect pelagic species like mackerel and sand eels. These species are rarely observed by divers (Kay and Dipper, 2009) but in our BRUV surveys were found to occur in large shoals consisting of many hundreds of individuals. The bait used in the BRUVs may be attracting these species to the field of view (Stewart and Beukers, 2000) and /or they may avoid SCUBA divers. Therefore, it may be best to use dive surveys to estimate the abundance of small demersal fish, and BRUV surveys to estimate the abundance of larger, more pelagic fish.

This study also highlights some of the problems scientists have in estimating fish abundance. When viewing footage generated from BRUVs, it is often not possible to recognise repeated entrances of the same individual, meaning estimators of abundance have to be used; in this case, the maximum number of fish sighted within a single field of view (MaxN). As it is unlikely that all individuals of a species will be recorded within the same frame, BRUVs can only detect a proportion of the fish that are attracted to the bait, which can make their estimates conservative (Willis and Babcock, 2000; Cappo *et al.*, 2004). Then again, when a diver observes an individual they must identify, count and record it, and in doing so, spend at least some time looking at their slate. This might allow other individuals to enter or leave the survey area without being detected by the diver. Such distractions increase the probability of counting the same fish twice or recording more species per survey. Thus, for each method the counts for each area can only be viewed as relative estimates of fish density (Willis *et al.*, 2000).

Overall, our study has revealed a number of differences between data obtained from diver and camera methods. For monitoring the density and size of king and queen scallops, and likely other similar shellfish species, diver surveys consistently outperformed the photo surveys in terms of precision and power, and are likely to be more accurate. We therefore conclude that, despite the logistical issues associated with SCUBA diving, especially in temperate/cold waters, diver surveys are likely to be the more powerful and effective tool for monitoring these types of species and should be used in monitoring the Lamlash Bay MPA. In comparison, for the monitoring of epibenthic species, fish and crustaceans, diver surveys had no clear superiority over remote methods as both produced markedly different results for different types of species. Hence, our results indicate that scientists responsible for studying MPAs must first identify the types of species they intend to study, and from that, choose the most appropriate monitoring method.

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Chapter 4. Ecosystem protection leads to increased scallop settlement within a community-led temperate marine reserve

4.1. Preface

For populations to benefit from the protection afforded by MPAs, it is necessary that a number of individuals spend a substantial part of their lives within their boundaries (Roberts et al. 2005). Thanks to their sedentary nature and fast growth, scallops should therefore be particularly responsive to closed area management. In fact, several studies have shown that marine reserves can allow scallops to build to greater population density and reach larger, older sizes, which in turn can result in greater rates of reproduction (Beukers-Stewart et al. 2005; Hart et al. 2013). In addition, reductions in fishing pressure can promote recovery of the seabed, which can further boost scallop recruitment by providing suitable substrate for the attachment of settling scallop spat (Bradhsaw et al. 2001; Howarth et al. 2011)

In this chapter I test to see if Lamlash Bay Marine Reserve is promoting the recovery of nursery habitats and scallop recruitment. Other benefits potentially offered by the reserve were explored by testing for differences in scallop density, age structure, body size and biomass between areas situated within and outside the reserve.

This chapter has been written in the style of ICES Journal of Marine Science and was submitted on 25th April 2014.

I declare that the work submitted is my own. The contribution by co-authors was as follows:

Callum Roberts, Julie Hawkins and Bryce Stewart: Supervision, review and editing.

Daniel Steadman: Assistance in the field

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Ecosystem protection leads to increased scallop settlement within a community-led temperate marine reserve

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This study investigated the effects of a fully protected marine reserve on benthic habitats and two commercially valuable species of scallop in Lamlash Bay, Isle of Arran, United Kingdom. Dive surveys showed the abundance of juvenile scallops to be significantly greater within the marine reserve than outside (two-way ANOVA, $P < 0.05$). Generalised linear models revealed this to be significantly related to the greater presence of macroalgae and hydroids growing within the boundaries of the reserve. These complex habitats appeared to have substantially increased spat settlement or survival. King scallop density declined 3-fold with increasing distance from the boundaries of the reserve (Pearson Correlation, $P < 0.05$), indicating possible evidence of spillover or reduced fishing effort directly outside and around the marine reserve. Finally, the age (ANOVA, $P < 0.05$), size (ANOVA, $P < 0.05$), and reproductive (two-way ANOVA, $P < 0.05$) and exploitable (two-way ANOVA, $P < 0.05$) biomass of king scallops were all significantly greater within the reserve. In contrast, the population dynamics of queen scallops (*Aequipecten opercularis*) fluctuated randomly over the survey period and showed little difference between the reserve and outside. Overall, this study is consistent with the hypothesis that marine reserves can encourage the recovery of seafloor habitats which can be of benefit to populations of commercially exploited species, emphasising the importance of marine reserves in ecosystem-based management of fisheries.

Keywords: Scallops, *Pecten maximus*, *Aequipecten opercularis*, Marine Protected Areas (MPAs), No-Take Zone (NTZ), Lamlash Bay, Firth of Clyde, ecosystem-based fishery management, nursery habitats

Introduction

Never before has the general public been so well informed about the current state of the world's oceans. A recent surge in environmentally focused films, documentaries and campaigns has led to much greater awareness of the methods used to harvest marine resources, and of their impacts on the marine environment (Jacquet and Pauly, 2007). In 2013, the United Kingdom (UK) based celebrity chef and environmentalist Hugh Fearnley-Whittingstall launched a television series campaigning for better protection of European waters in which the first episode showed a video of the damage to the seabed caused by a scallop dredger (www.fishfight.net). Responses from the public and media were strong (Brown, 2013; Greenpeace, 2013; Renton, 2013) with one major retailer pledging to stop selling dredge-caught scallops (Harvey, 2013), sparking rebukes from both the fishing industry and their representatives (Gray, 2013; SeaFish, 2013). Despite the media attention, fisheries for shellfish are rapidly increasing in importance in many parts of the world, as are their environmental impacts (Essington *et al.*, 2006; Estes *et al.*, 2011; Howarth *et al.*, 2013; Pauly *et al.*, 1998, 2002; Steneck *et al.*, 2002).

In the UK, landings of the king scallop (*Pecten maximus*) are growing faster than any other commercially targeted shellfish species. Generating over £66.9 million per year, king scallops represent the UK's second most valuable fishery resource, over 95% of which are caught by scallop dredgers (Keltz and Bailey, 2010; Radford, 2013). Scallop stocks located around Scotland account for over half of the UK king scallop fishery (Dobby *et al.*, 2012) but concerns have recently been made over increasing mortality, and declining recruitment and spawning stock biomass in several major Scottish stocks (Barreto and Bailey, 2013; Hall-Spencer and Moore, 2000; Hinz *et al.*, 2011; Howell *et al.*, 2006). These problems are not unique. Scallop fisheries all over the world are well known for exhibiting dramatic fluctuations in recruitment, landings and abundance (Paulet et al. 1988; Orensanz et al. 1991; Beukers-Stewart et al. 2003; Beukers-Stewart & Beukers-Stewart 2009). Such fluctuations are difficult to incorporate into fisheries management strategies and can result in their sudden and unexpected collapse (Frank & Brickman 2001; Beukers-Stewart & Beukers-Stewart 2009). Furthermore, scallop recruitment and mortality are predicted to become increasingly more erratic in the future due to ocean acidification (Gazeau *et al*. 2007, Kurihara 2008, Watson *et al*. 2009), a process which is reducing the amount of carbonate available to scallops to form their protective shells (Doney *et al.*, 2009; Sabine *et al.*, 2004). Due to anthropogenic carbon dioxide emissions, ocean acidity is currently increasing at a rate unprecedented for tens of millions of years (Doney et al. 2009). This means scallop fisheries all over the world are badly exposed to risk if the species they target cannot adapt. Stronger efforts must therefore be made to safeguard the long-term sustainability of commercially important scallop stocks whilst reducing the environmental impact of their fisheries.

Although many different management measures exist for maintaining and supporting fish stocks, it has been argued that only the establishment of Marine Protected Areas (MPAs) closed to some or all types of fishing can allow seafloor habitats to recover (Bradshaw *et al.*, 2001; Howarth *et al.*, 2011), increase the abundance and size of target species (Halpern and Warner, 2002; Halpern, 2003; Lester *et al.*, 2009), enhance local reproductive output (Gaines *et al.*, 2003; Grantham *et al.*, 2003; Roberts *et al.*, 2001) and improve the survival and growth of juveniles (Beukers-Stewart *et al.*, 2005; Myers *et al.*, 2000). All of these effects may then result in the greater production of eggs, larvae, juveniles and adults which can disperse (‘spillover’) to grounds outside the MPA and contribute to fishery landings (Harrison *et al.*, 2012; McClanahan and Mangi, 2000). Then again, establishing MPAs can displace fishing effort to surrounding areas (Bohnsack 2000; Kaiser 2005), which can cause wider environmental damage (Dinmore *et al.,* 2003) and reduce profits through the loss of fishing grounds (Rassweiler *et al.,* 2012). Hence, MPAs only truly yield benefits to fisheries when these negative effects are adequately offset by increased recruitment and landings.

For populations to benefit from the protection afforded by MPAs, it is necessary that a number of individuals spend a substantial part of their lives within their boundaries (Roberts *et al.*, 2005). Thanks to their sedentary nature and fast growth, scallops have been shown to be particularly responsive to closed area protection. In 1994, three areas totalling 17,000 km^2 were closed to fishing gears on Georges Bank in the Gulf of Maine, United States of America (USA). Ten years later, observations revealed that the reduction in fishing mortality was responsible for a 20-fold increase in scallop biomass within the closures, and increased catches in neighbouring fishing grounds (Hart *et al.*, 2013; Hart and Rago, 2006; Murawski *et al.*, 2000). The scallop fishery on Georges Bank is now the most valuable of any fishery in the USA (Lowther, 2013). On a smaller scale, after 17 years of protection a 2 km^2 closure off the Isle of Man resulted in scallop densities 30 times greater than those observed prior to protection (Beukers-Stewart and Brand, 2007; Beukers-Stewart *et al.*, 2005). The reduction in fishing mortality also allowed individuals within the closed area to reach much older and larger sizes, with exploitable and reproductive biomass of scallops being 20 and 33 times higher respectively than on adjacent fishing grounds. In addition, there is growing evidence that export of larval scallops, generated from high rates of breeding within the closed area, have boosted surrounding populations and therefore the fishery (Beukers-Stewart and Brand, 2007; Beukers-Stewart *et al.*, 2005, 2004; Neill and Kaiser, 2008).

In addition to increasing the abundance of target organisms, the exclusion of fishing from an area also eliminates the physical impacts created by mobile fishing gears such as dredges and trawls (Kaiser *et al.*, 2000, 2007). Such gears can cause substantial physical disruption of seafloor habitats by ploughing sediments and fragmenting the biogenic structure of epifaunal assemblages such as hydroids, tunicates and maerl beds (Cook *et al.,* 2013; Dayton *et al.*, 1995; Eleftheriou and Robertson, 1992; Jennings and Kaiser, 1998; Jennings *et al.*, 2001; Kaiser *et al.*, 2000). However, these organisms provide essential habitat for the settlement of scallops and a large range of other invertebrates (Bradshaw *et al.*, 2001; Kamenos *et al.*, 2004a). Consequently, such locations are often referred to as “nursery areas” as they tend to be highly productive, support high levels of juvenile density, growth and survival, and contribute disproportionally to the production of adult recruits (Beck *et al.*, 2001; Gibb *et al.*, 2007; Laurel *et al.*, 2009). The damage inflicted by fishing gears upon nursery habitats has therefore been shown to negatively impact scallop recruitment (Bradshaw *et al.*, 2002; Collie *et al.*, 1997), whilst the protection of nursery habitats has been shown to enhance scallop settlement levels (Howarth *et al.*, 2011).

The implementation of MPAs may therefore provide a “win-win” solution to safeguarding the long-term sustainability of commercially important scallop stocks. Not only can MPAs provide fisheries benefits, they also help sustain healthy marine ecosystems by addressing the physical impacts of fishing gears (Bradshaw *et al.*, 2002; Kaiser *et al.*, 2000, 2007), which can then generate numerous benefits that flow back to the species targeted by fisheries (Jennings and Kaiser, 1998; Howarth *et al.*, 2011). It is these ideas that underlie the current push towards ‘ecosystem-based fishery management’, where management priorities begin with the ecosystem, moving away from traditional single-species approaches (Pikitch *et al.*, 2004; Zhou *et al.*, 2010). However, the implementation of MPAs in Europe is still at a very early stage (Fenberg *et al.*, 2012; Metcalfe *et al.*, 2013) and their use as an ecosystem-based fishery management tool remains a highly contentious issue (Boersma and Parrish, 1999; Jones, 2007; Kaiser, 2004, 2005; Sciberras *et al.*, 2013).

MPAs can be implemented via top-down processes which are government led and enforced, or by bottom-up mechanisms, whereby local communities and stakeholders propose the establishment of an MPA and help in its management, enforcement and monitoring (Jones, 2012; Kelleher, 1999). There is growing evidence that community and stakeholder involvement in setting up and running MPAs builds greater support and reduces management costs due to lower infringements rates (Pollnac *et al.*, 2012). However, although community-led MPAs are common in tropical waters (Johannes, 2002), they are very rare in temperate areas and almost non-existent in the UK (Fenberg et al 2012). In September 2008, a fully protected marine reserve was established in Lamlash Bay, Isle of Arran, UK, prohibiting all sea fishing within the reserve under the Inshore Fishing (Scotland) Act of 1984 (Axelsson *et al.*, 2009). The Firth of Clyde, in which the Isle of Arran sits, is known to be one of the most degraded marine environments in the UK, primarily due to over a century of intensive fisheries exploitation (Howarth *et al.*, 2013; Thurstan and Roberts, 2010). The reserve was therefore passed by the Scottish parliament under the rationale that the reduction in fishing pressure should help regenerate the local marine environment and enhance commercial shellfish and fish populations in and around Lamlash Bay, particularly with regards to scallops. Lamlash Bay Marine Reserve came after a decade of campaigning by local residents for better protection of their seas (Community of Arran Seabed Trust or "COAST"; www.arrancoast.com) and is the first and only fully protected marine reserve in Scotland, and the only statutory reserve in the UK that was originally proposed by a local community which bans all extractive activities (Prior, 2011). Lamlash Bay is also unique in that the majority of MPAs in the UK were proposed either for conservation (e.g. Lundy Marine Nature reserve and Lyme Bay Marine Reserve) or fishery purposes (e.g. closed areas off the Isle of Man), not for both.

Our study therefore sought to test the hypotheses that: (1) there is a positive relationship between scallop settlement and the abundance of nursery habitat; (2) the marine reserve contains a greater abundance of these nursery habitats; and (3) that the density, age, size, biomass and growth rates of scallops are higher within the marine reserve than areas located outside its boundaries. This was achieved by conducting a series of quantitative diver surveys over a four-year study period.

Materials and methods

Study area and scallop fishery

Lamlash Bay Marine Reserve encompasses an area of 2.67 km^2 (Figure 1), with water depths ranging between 0 and 29 m below chart datum, but reaching as deep as 43 and 50 m outside to the east and the west of the reserve, respectively (Admiralty Chart 1864; Baxter *et al*. 2008). Previous surveys (Axelsson *et al.*, 2009; Duncan, 2003) indicated a seabed of mixed sediments (i.e. mud, sand and gravel with various proportions of shell) but that the central and southern regions of the bay tend to be characterised by softer sediment, mainly muddy sand. In addition, the area has long been identified as containing important maerl beds, although recent evidence points to deterioration in their health (Howarth *et al*. 2011).

The king scallop (*Pecten maximus*) fishery is the second most valuable in Scotland and has consistently ranked in the top five most valuable UK fisheries for the past 10 years (Dobby *et al.*, 2012). In contrast, landings of the comparatively smaller queen scallop (*Aequipecten opercularis*) have fluctuated greatly, meaning they tend to be fished opportunistically by fishers and are worth considerably less (Beukers-Stewart & Beukers-Stewart 2009). European Union (EU) legislation specifies a minimum landing size of 100 mm length for king scallops (Council Regulation (EC) No. 850/98). There are no size limits for queen scallops (although it is generally uneconomic to process them when smaller than 50 mm in width), and there are no limits on landings for either species. Under the Prohibition of Fishing for Scallops (Scotland) Order 2003, scallop fishing vessels are permitted to tow up to a maximum of 8 individual dredges per side in Scottish inshore waters (out to six nautical miles). The Order also prohibits the use of “French” dredges (a design incorporating water deflecting plates and rigid fixed teeth). The Firth of Clyde scallop fleet is also subject to a weekend ban (Dobby *et al.*, 2012). Unofficial observations made by the Community of Arran Seabed Trust (www.arrancoast.com) indicate fishing effort by trawlers and dredgers has been consistently low outside the boundaries of Lamlash Bay Marine Reserve in recent years, averaging at 2-4 fishing boats operating within the area per year since 2008. A small team of commercial scallop divers also operate locally within the area.

Dive surveys

We began monitoring Lamlash Bay in 2010 (see Howarth *et al*. 2011). Initially, 40 sites were surveyed, half of which were located within the reserve and the other half outside. These surveys were then repeated and expanded in 2011, 2012 and 2013 by adding more survey methods but reducing the number of study sites. Therefore we surveyed 28 sites in 2011, 31 sites in 2012, and 32 sites in 2013. Again, these sites were divided so that half fell within the boundaries of the marine reserve (Figure 1). Sites were chosen so that each one within the reserve could be paired with at least one other suitable control outside, based on similar depth and predominant substrate type (Appendix 1-4). Due to lack of data and prior knowledge of the area, the initial experimental design was relatively imbalanced. For example, 12 deep muddy sand sites were surveyed outside the reserve in 2010 compared to just 6 inside. This improved with each survey, and by 2012, our experimental design was balanced. Sites were limited to areas of the seabed that were shallow enough to remain within diver no decompression limits (i.e. <30m depth). Surveys were also conducted parallel to depth contours to ensure the depth of a single survey did not change by more than 3m.

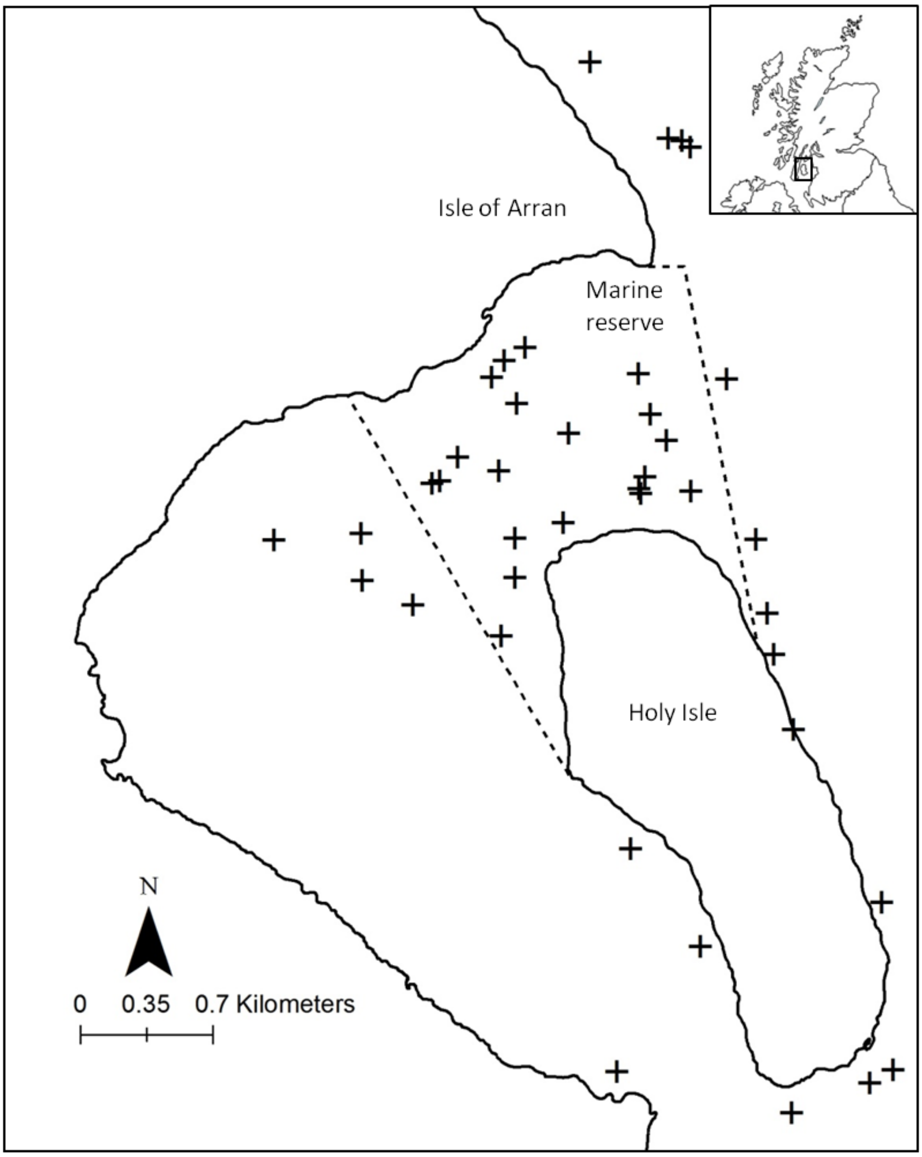

Figure 1. Site locations of dive transects for all years. Also displayed are the boundaries of the Lamlash Bay fully protected marine reserve. The inset shows the location of the Isle of Arran off the west coast of Scotland, United Kingdom.

Transects were surveyed along a 50m leaded line that was laid out straight across the seabed. GPS coordinates used for surveys in 2010 and 2011 provided the start and end location of each transect. Attached to both ends of the leaded line were weighted anchors to hold the line in place, in addition to two floating buoys which reached the surface. A team of two divers then made their way from one end of the transect to the other, recording the abundance of all adult unattached scallops and other megafauna (e.g. fish, echinoderms and crustaceans) encountered within 1.5m either side of the transect. The width of the transect was marked by a 3m long pipe that the divers pushed ahead of themselves, creating a total area surveyed of 150m^2 for each transect. To generate semi-quantitative estimates of the abundance of juvenile scallops (taken to be any scallop still attached to the substrata via byssal threads), a SACFOR abundance scale (superabundant, abundant, common, frequent, occasional, rare) was used (see Connor *et al*. 2004). Unfortunately, distinguishing between juvenile king and queen scallops whilst underwater was difficult and so these had to be grouped as one category. In addition, every adult scallop encountered along the transect was collected and brought back to the surface. These were then scrubbed with a wire brush (to help reveal their annual growth rings) and aged (Chauvaud *et al.*, 2012), measured for shell length (Jennings *et al.*, 2001), and returned to the sea.

A SACFOR abundance scale was also used by the divers to estimate the abundance of different benthic taxa. These were live maerl (e.g. *Phymatolithon calcareum* and *Lithothamnion glacial*), dead maerl, macroalgae (e.g. *Laminaria* and *Ceramium* spp) sponges (e.g. *Pachymatisma johnstonia*), anemones (e.g. *Cerianthus lloydi*), tunicates (e.g. *Clavelina lepadiformis* and *Diazona violacea*), hydroids (e.g. *Obelia geniculata*), bryozoans (e.g. *Alcyonidium diaphanum* and *Flustra foliacea*) and soft corals (e.g. *Alcyonium digitatum*). The SACFOR method was chosen to provide quick underwater estimates of benthic cover.

Laboratory analysis

Scallop dissections were conducted in the years 2010, 2011 and 2013. For these years, 60 king scallops and 60 queen scallops were retained for dissection, with half of these individuals collected from within the reserve (under a permit from Marine Scotland), and the other half from outside. As the number of scallops taken from the reserve was limited, these scallops were chosen to cover the full range of different shell lengths observed within the Lamlash Bay area. Scallops were preserved in seawater to be dissected within 24 hours of their collection. All tissues were then dissected from the samples and blotted dry. From these tissues, the wet weight of the total tissue biomass, exploitable biomass (gonad weight and adductor muscle weight combined) and reproductive biomass (gonad weight only) were obtained. The importance of recording reproductive and exploitable biomass was considered two fold. Firstly, the mass of the gonad organ is an indicator of potential reproductive output (Shephard *et al.*, 2010). Secondly, the adductor muscle is important both economically, as it partly decides the sale value of a scallop, and biologically as it forms the main mechanism of protection from predators such as the common starfish, *Asterias rubens* (Kaiser *et al.*, 2007) and is used for swimming and escaping predation (Labrecque and Guderley 2011).

Data analysis

Multivariate analyses of juvenile scallop distribution

All data were tested for normality using histograms, boxplots, QQ plots and the Shapiro–Wilk test. These basic exploratory measures were conducted within the statistical package R (www.r-project.org). The Shapiro–Wilk test was chosen as it is widely accepted to be the most suitable for small and medium-size samples (*N* up to 2000; Royston 1982, Conover 1999). For statistical analysis, the SACFOR scale used to estimate juvenile scallop abundance and benthic cover was converted into numerical categories ranging from 0 to 6, where a value of 0 would indicate the absence of a taxon and 6 would represent the superabundance of a taxon as denoted by the SACFOR scale. Whereas the counts of adult scallops collected by both divers were pooled and adjusted for each transect to generate densities of organisms per 100m^2.

The abundance of juvenile scallops was compared between the two treatments (i.e. 'reserve' and 'fishing grounds') and across the years using a two-way ANOVA, with protection and year as the two fixed factors. Levene's test for equality of variances showed that there was homogeneity of variance between the two treatments ($P > 0.05$). To determine whether environmental and ecological data recorded during diver surveys reflected the distribution and abundance of juvenile scallops, a Generalised Linear Model (GLM) was created. Predictor variables used in the GLM were treatment, depth, density of predators, and the SACFOR abundance estimates of maerl, macroalgae, sponges, hydroids, anemones, bryozoans, tunicates and soft corals. Predators of scallops were taken to be all species of starfish, although this is likely to be just a partial characterisation of the total predator assemblage for scallops. Although our monitoring program also collected higher quality data on the percentage cover of different benthic taxa through the use of photographic surveys, these surveys did not begin until 2011 and therefore could not be used in this full analysis. Before construction of a GLM, scatter plot and intercorrelation matrices (based upon Spearman's rank correlation) were created to explore basic relationships and determine whether any variables were strongly intercorrelated (i.e. $-0.7 \leq r \geq 0.7$) as such variables would not be allowed together within a GLM (Crawley, 2005). As a Kolmogorov–Smirnov (K–S) test found juvenile abundance to not significantly differ from a poisson distribution ($P > 0.05$) a GLM based upon a Poisson family error was created in R. Backward-forward stepwise reduction was then used to create a minimal adequate model. Diagnostic and Cleveland dotplots were subsequently used to explore how well the models fitted the data and to identify any extreme outliers. An Analysis of Deviance utilising Pearson's Chi-square test (χ^2) was then conducted to determine if the reduced model accounted for significantly less variance than the full model.

Density of king and queen scallops

Densities of king and queen scallops were compared between the two treatments and across the years using a two-way ANOVA as before. However, the density data did have to be square root transformed before they complied with the assumption of normality. Density data was also split between individuals of sub-legal and legal size classes. For king scallops, this was any individual greater than 100mm in length (Keltz and Bailey, 2010). For queen scallops, a size of 50mm was used as the cut-off point (see above). Differences in the density of these size classes between the two treatments were tested for significance using a Mann–Whitney–Wilcoxon test as the data no longer complied with the assumption of normality when split into different size classes.

In an attempt to investigate any spillover of scallops and / or a potential "halo effect" of reduced fishing effort close to the boundaries of the reserve, the distance of each sampling site from the boundaries of the marine reserve was calculated in the Geographical software ArcGIS 10.1. The mean density of king scallops was then calculated for all sites within the reserve, and sites 0.5 km, 1 km, 1.5 km and >2 km away from the marine reserve. This data was then plotted against distance utilising error bars of ±1 Standard Error (SE) and fitted with a polynomial trend line. This trend was tested for significance by calculating the Pearson product-moment correlation coefficient.

Population structure of king and queen scallops

Size and age distributions were compared between the two treatments for each year using a K–S two sample test. In addition, a one-way ANOVA was used to test the final difference in size and age between treatments for data collected during the last year of monitoring. Size composition data on king scallops (greater than minimum legal landing size) were then compared with government fisheries size data on king scallops caught and landed within the Firth of Clyde region in 2012 and 2013 (data provided by Shona Kinnear of Marine Scotland Science). This was done by performing two K–S tests, one to compare the size of scallops landed within the Clyde against the size of scallops sampled within the reserve, and the other to compare the size of scallops landed within the Clyde against the size of scallops sampled outside the reserve.

Fisheries statistics

The mean density per age class of king scallops combined across all years was compared between the two treatments using a line graph. A catch curve analysis was then performed by transforming the data (natural log) and fitting linear trendlines. The gradient of these trend lines then provided an indication of total mortality (*Z*). In addition, the mean length at age for both scallop species was plotted using the statistical software Simply Growth (version 1.7, http://www.pisces-conservation.com/) and fitted with two Von Bertalanffy growth curves to the separate treatments. The log-likelihood ratio test of co-incident curves (Kimura, 1980) was then used to test whether the two sampled population curves would differ from a curve created by combining the two sampled populations.

Biomass data

For the years where scallop dissections were conducted, exploitable and reproductive biomass for both species were tested for differences between the two treatments and across all years using two-way ANOVA. To investigate for any differences in the weight of gonads and adductor muscle per unit shell length between the reserve and outside, the weight of the adductor muscle and the reproductive biomass of king scallops greater than 100mm length were plotted against shell length and fitted with linear trendlines. ANCOVAs were then performed which took into account differences in body size (i.e. with shell length as the covariate). For this, a Levene's Test of Equality of Error Variances showed homogeneity of variance between the two samples ($P > 0.05$) and comparing the beta values revealed that samples had equal co-variance.

Results

Juvenile scallop abundance and the relationship with benthic habitats

The abundance of juvenile scallops was significantly greater within the marine reserve than outside for all years except 2013, when only two sites out of the 32 surveyed contained any juvenile scallops both of which were located outside the reserve (Table 1). Year, protection and the interaction between the two were all found to be significantly influencing the abundance of juvenile scallops. Overall, the abundance of juvenile scallops has fluctuated from low to high every two years (Figure 2), with 2010 and 2012 being years of high abundance, and 2011 and 2013 being years of low abundance. It should be noted that graphical representations of these differences are very conservative as they treat differences between abundance categories as proportional, whereas measures of abundance on the SACFOR scale actually differ on an exponential scale.

Table 1. Two-way ANOVA comparing juvenile scallop abundance between the marine reserve and outside across the years 2010-2013. Significant results are denoted by (*).

Test variable	SS	df	MS	*F*	*P*
Year	55.89	3	18.63	13.96	*<0.001
Protection	23.33	1	23.33	17.48	*<0.001
Year x Protection	18.57	3	6.19	4.63	*0.004
Residual	206.82	155	1.33		

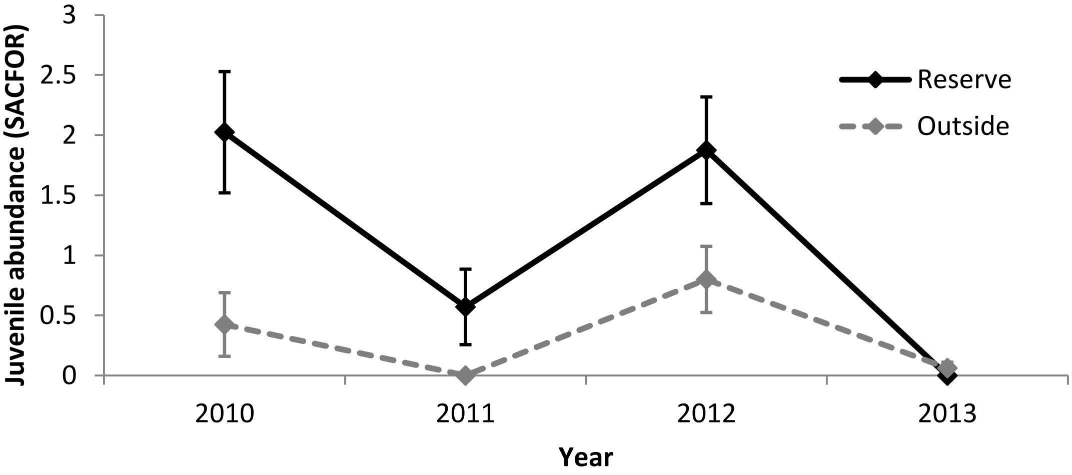

Figure 2. The mean estimated abundance (SACFOR) of juvenile scallops within and outside the fully protected marine reserve across four years. Error bars represent ±1 SE.

In 2010, we found the higher levels of juvenile scallop abundance to be associated with greater levels of macroalgae and other nursery habitats growing within the marine reserve's boundaries (see Howarth *et al.* 2011). To further explore these relationships, SACFOR estimates of benthic cover and juvenile scallop abundance were combined for the years 2010 and 2012 (i.e. years of high juvenile scallop abundance). After employing backward-forward stepwise reduction, a GLM indicated protection and the presence of macroalgae, sponges and hydroids to be significantly influencing the distribution of juvenile scallops (Table 2). This reduced model accounted for 66% of the variance in juvenile scallop abundance and did not explain significantly less variance than the full model (Pearson's Chi-squared; df = 67, $\chi^2 = 0.78$, $P > 0.05$). The relationship between juvenile scallop abundance and the presence of macroalgae was found to be positive (Figure 3a), as was their relationship with hydroids (Figure 3b). A parallel study (Howarth *et al.*, in review) revealed the percentage cover of these benthic habitats to be significantly greater within the reserve than outside, and that their abundance steadily increased over the study period. In contrast, the relationship between juvenile scallops and sponges was negative. However, as sponge abundance was very low across all sites, their relationship was comparatively unclear.

Table 2. The reduced and full models were created from a Poisson GLM to test whether environmental and ecological data reflected the distribution and abundance of juvenile scallops. Significant terms are denoted by (*).

Variables retained by reduced model			
Variable	SE	*Z*	*P*
Macroalgae	0.07	7.98	*<0.001
Hydroids	0.12	3.91	*<0.001
Sponge	0.16	-1.7	* 0.043
Protection	0.22	1.7	* 0.046
Variables removed from model			
Variable	SE	*Z*	*P*
Depth	0.04	-0.75	0.449
Dead maerl	0.06	-0.47	0.635
Live maerl	0.2	-0.8	4.432
Anemones	0.11	0.72	0.474
Soft coral	0.19	-1.78	0.076
Tunicates	0.1	-0.01	0.994
Bryzozoans	0.11	-0.41	0.68

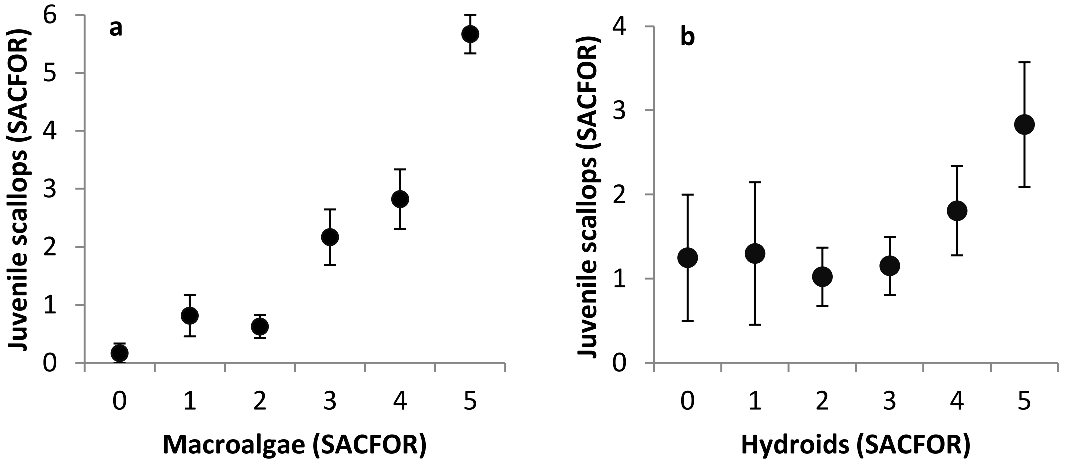

Figure 3. Mean abundance of juvenile scallops in relation to the mean abundance of macroalgae (a) and hydroids (b). These trends were highlighted as significant by a GLM. Error bars represent ±1 SE.

Comparisons of scallop density

When monitoring began in 2010, the density of king scallops was initially lower within the boundaries of the marine reserve, estimated at 6.2 individuals per 100m^2 (± 2.1 SE) within the reserve compared to a value of 7.6 (±2.3 SE) outside the reserve. However, surveys conducted over the following three years revealed that the density of king scallops had steadily increased within the reserve but decreased outside (Figure 4). Despite these apparent differences, a two-way ANOVA identified neither year nor level of protection (i.e. in or outside the reserve) as having a significant influence on king scallop density (Table 3).

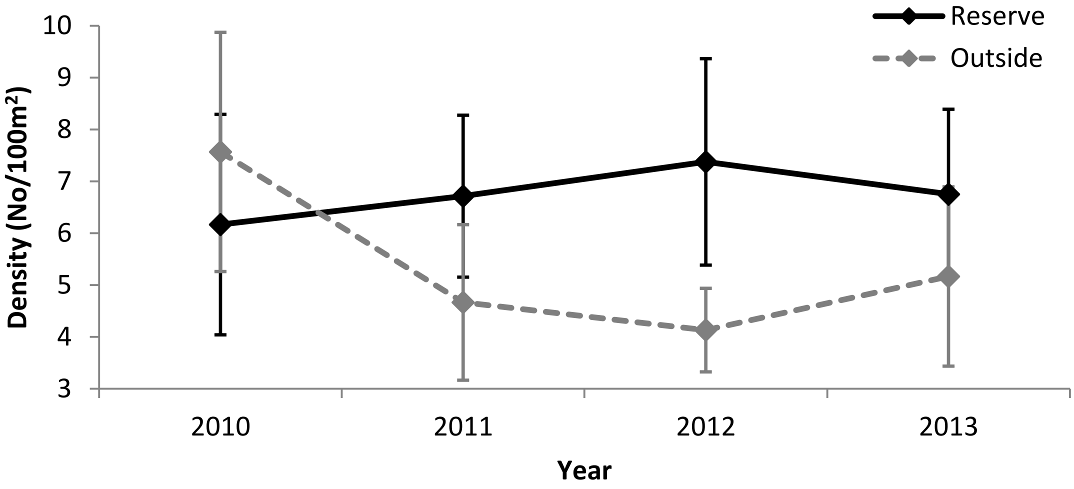

Figure 4. The density of king scallops in and outside the fully protected marine reserve across four years. Error bars represent ±1 SE.

Table 3. Two-way ANOVA comparing scallop densities (sqrt transformed) between the marine reserve and outside across the years 2010-2013. Significant results are denoted by (*).

Species	Test variable	SS	df	MS	*F*	*P*
King scallops	Year	0.14	3	0.05	0.02	0.99
	Protection	0.79	1	0.8	0.38	0.54
	Year x Protection	4.61	3	1.54	0.74	0.53
	Residual	254.3	123	2.1		
Queen scallops	Year	18.45	3	6.15	3.506	*0.01
	Protection	0.07	1	0.07	0.04	0.84
	Year x Protection	1.9	3	0.62	0.36	0.79
	Residual	215.78	123	1.75		

Compared to king scallops, queen scallop abundance fluctuated greatly over the study period (Appendix 5). In 2010, queen scallop densities did not differ between the reserve and outside, estimated at densities of 6.1 (±1.8 SE) and 6.0 (± 2.1 SE) per 100m^2 in and outside the reserve respectively. Since then, the density of queen scallops has been in decline, fluctuating from being greater within the reserve some years, to being lower within the reserve for others. For example, the density of queen scallops was 206% greater within the reserve in 2011, but fell to just 29% greater in 2012, before falling to 30% lower within the reserve than outside in 2013. In 2013, the density of queen scallops hit a low of 3 (± 0.8 SE) per 100m^2 inside the reserve and 2.3 (± 0.9 SE) outside. As a consequence of these strong yearly fluctuations, multivariate analysis found only the year to significantly affect queen scallop density (Table 3).

Differences in scallop density between the reserve and outside were more pronounced when split between sub-legal and legal size classes (Figure 5). King scallops over 100 mm in length (i.e. individuals of legal landing size) were on average 79.3% more abundant within the reserve than outside in 2013. However, this trend was not significant (Mann-Whitney: $U = 84$, $N = 32$, $P > 0.05$). Similarly, queen scallops over 50mm were 39% more abundant within the reserve than outside but was also non-significant (Mann-Whitney: $U = 71$, $N = 32$, $P > 0.05$). In contrast, smaller-bodied king scallops less than 100mm were 80% less abundant within the reserve than outside (Mann-Whitney: $U = 84$, $N = 32$, $P > 0.05$) and smaller-bodied queen scallops less than 50mm were 96% less abundant within the reserve (Mann-Whitney: $U = 118$, $N = 32$, $P > 0.05$) both of which were non-significant.

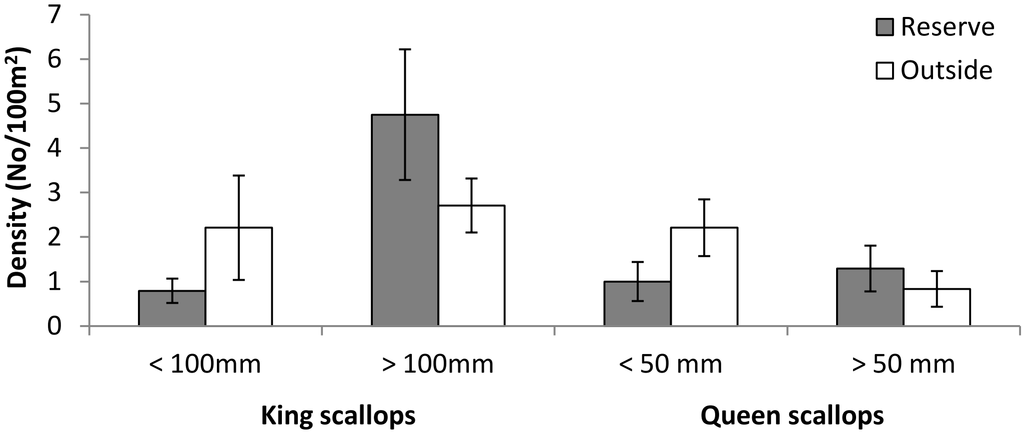

Figure 5. The density of different size classes of two scallop species sampled in 2013 within and outside a fully protected marine reserve. Error bars represent ±1 SE.

Plotting the mean density of king scallops combined for all years against distance from the boundaries of the marine reserve revealed a strong spatial interaction (Figure 6). It was found that the density of scallops significantly declined with increasing distance from the marine reserve (Pearson Correlation; $N = 91$, $R = -2.4$, $P < 0.05$). In fact, sites within or close to the marine reserve supported scallop densities three times greater than sites located over two kilometres away.

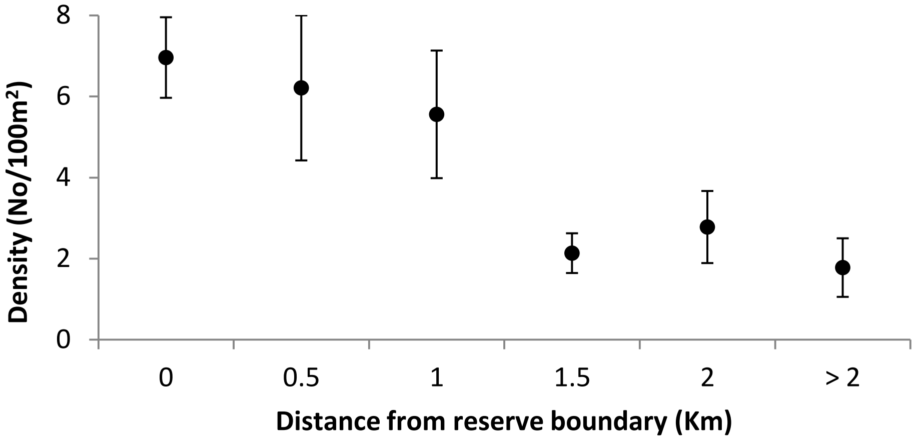

Figure 6. Mean density of king scallops for the years 2010-2013 plotted against distance from the marine reserve. A distance of 0 represents those sites located within the marine reserve. Error bars represent ±1 SE.

Comparisons of population structure

For both scallop species, the mean size and age were significantly greater within the marine reserve than outside across all years. In 2010, king scallops were on average 18mm larger (ANOVA, $F_{(1,109)} = 40.45$, $P < 0.05$) and 1.1 years older (ANOVA, $F_{(1,109)} = 42.99$, $P < 0.05$) within the reserve than outside. In 2013, the final year of monitoring, these differences had grown stronger with king scallops being on average 28mm larger (ANOVA, $F_{(1,250)} = 66.51$, $P < 0.05$) and 1.7 years older (ANOVA, $F_{(1,250)} = 47.88$, $P < 0.05$) within the reserve than outside. Queen scallops were on average 13mm larger (ANOVA, $F_{(1,108)} = 11.96$, $P < 0.05$) and 0.8 years older (ANOVA, $F_{(1,108)} = 10.88$, $P < 0.05$) within the reserve than outside in 2013.

Comparing the overall size and age distributions for both species of scallop between the two areas also revealed scallops within the marine reserve to be made up of significantly older and larger individuals (Table 4). In greater detail, the size (Figure 7) and age (Figure 8) of king scallops have been continually higher within the reserve for the past four years. In 2010, king scallops peaked at 131-140mm in length and 4 years in age within the reserve, and at 101-110mm and 2 years in age outside. The subsequent year saw this peak size class within the reserve strengthen whilst the peak age class increased to 6 years. This was then followed by the peak size class within the reserve increasing to 141-150mm in 2012 and finally becoming bi-modal in 2013. In contrast, outside the reserve scallop densities declined sharply after the first year of monitoring across all size and age classes. Subsequent years saw scallop densities outside the reserve recover slightly but remain at levels far lower than those observed in 2010. The year 2013 saw a sudden boost in recruitment of young scallops outside the reserve. However, this event was far less pronounced within the marine reserve.

Table 4. Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size and age distributions (% composition) of two commercially important species of scallop located in and outside the fully protected marine reserve.

				Size		Age	
	Year	Reserve (*N*)	Outside (*N*)	KS-Z	*P*	K-S *Z*	*P*
King scallops	2010	181	237	4.12	* <0.001	3.38	* <0.01
	2011	139	98	2.83	* <0.001	2.59	* <0.01
	2012	162	125	3.97	* <0.001	2.42	* <0.01
	2013	133	118	3.65	* <0.001	3.09	* <0.01
Queen scallops	2010	179	161	1.64	* 0.009	2.26	* <0.01
	2011	81	24	1.39	* 0.041	1.39	* 0.04
	2012	74	53	1.4	* 0.04	5.17	* <0.01
	2013	133	54	5.77	* <0.001	3.77	* <0.01

In 2010, queen scallops differed from king scallops in that their size (Figure 9) and age (Figure 10) distributions were similar. However, as observed for king scallops, queen scallop abundance suddenly declined across all age and size classes outside the reserve. Queen scallops then began to recover in 2012 and 2013 to sizes and ages slightly lower than those observed within the reserve.

Utilising government data on the size composition of king scallops caught and landed within the Firth of Clyde region revealed scallop populations in the Lamlash Bay area to be made of larger individuals compared to the Firth of Clyde region as a whole (Figure 11). When only scallops of legal landing size were considered, individuals sampled within the marine reserve were the largest in size, followed by individuals sampled directly outside it. For example, in 2012, king scallops were on average 21mm larger (± 1.77 SE) within the reserve compared to those landed from the wider Firth of Clyde, whilst scallops located directly outside the boundaries of Lamlash Bay Marine Reserve were 5mm larger (± 2.66 SE). These size distributions were found to be significantly different in both 2012 (K-S; $N = 8966$, $Z = 3.54$, $P < 0.05$) and 2013 (K-S; $N = 9241$, $Z = 3.74$, $P < 0.05$).

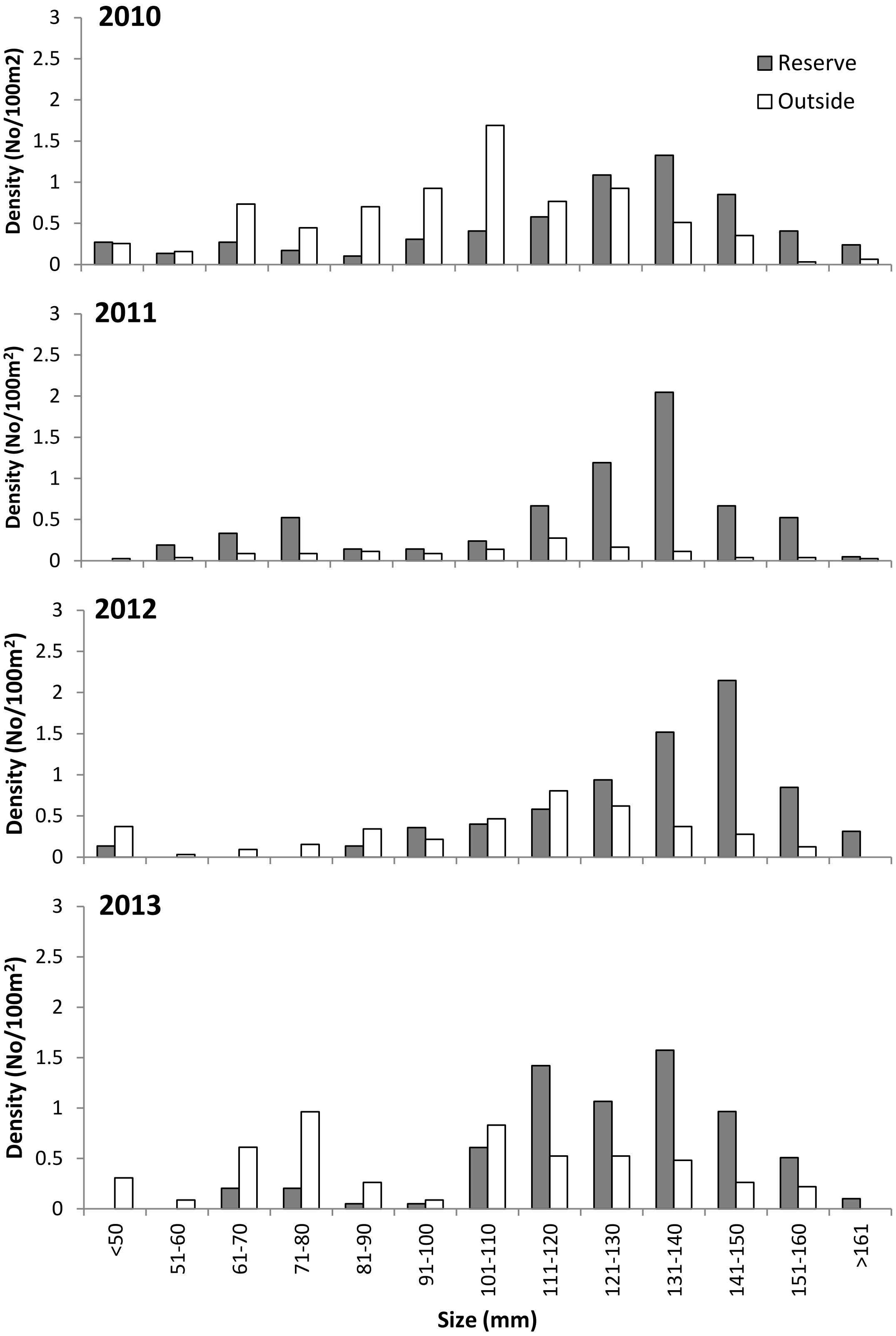

Figure 7. The size structure of king scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Table 4.

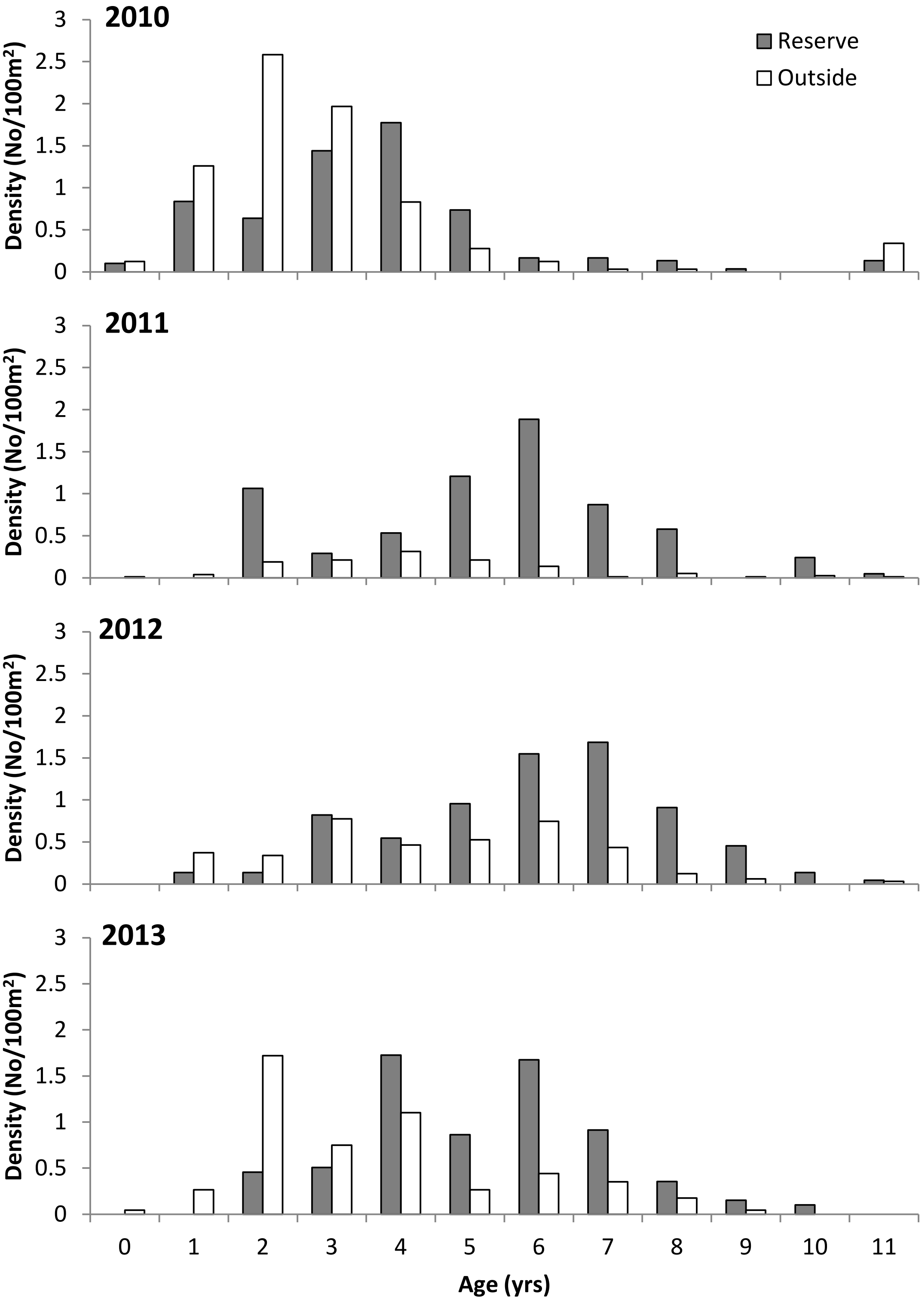

Figure 8. The age structure of king scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Table 4.

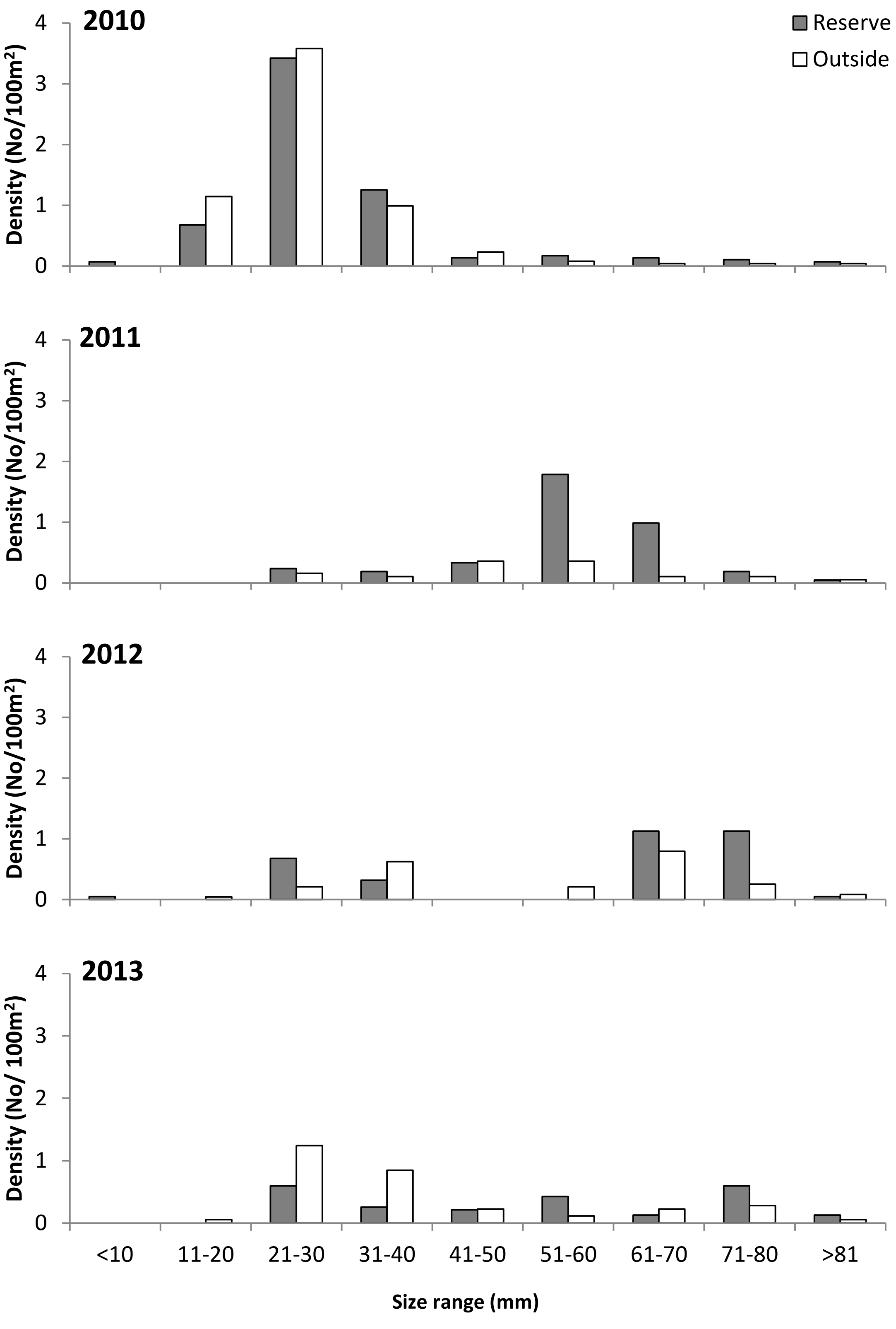

Figure 9. The size structure of queen scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Tables 4.

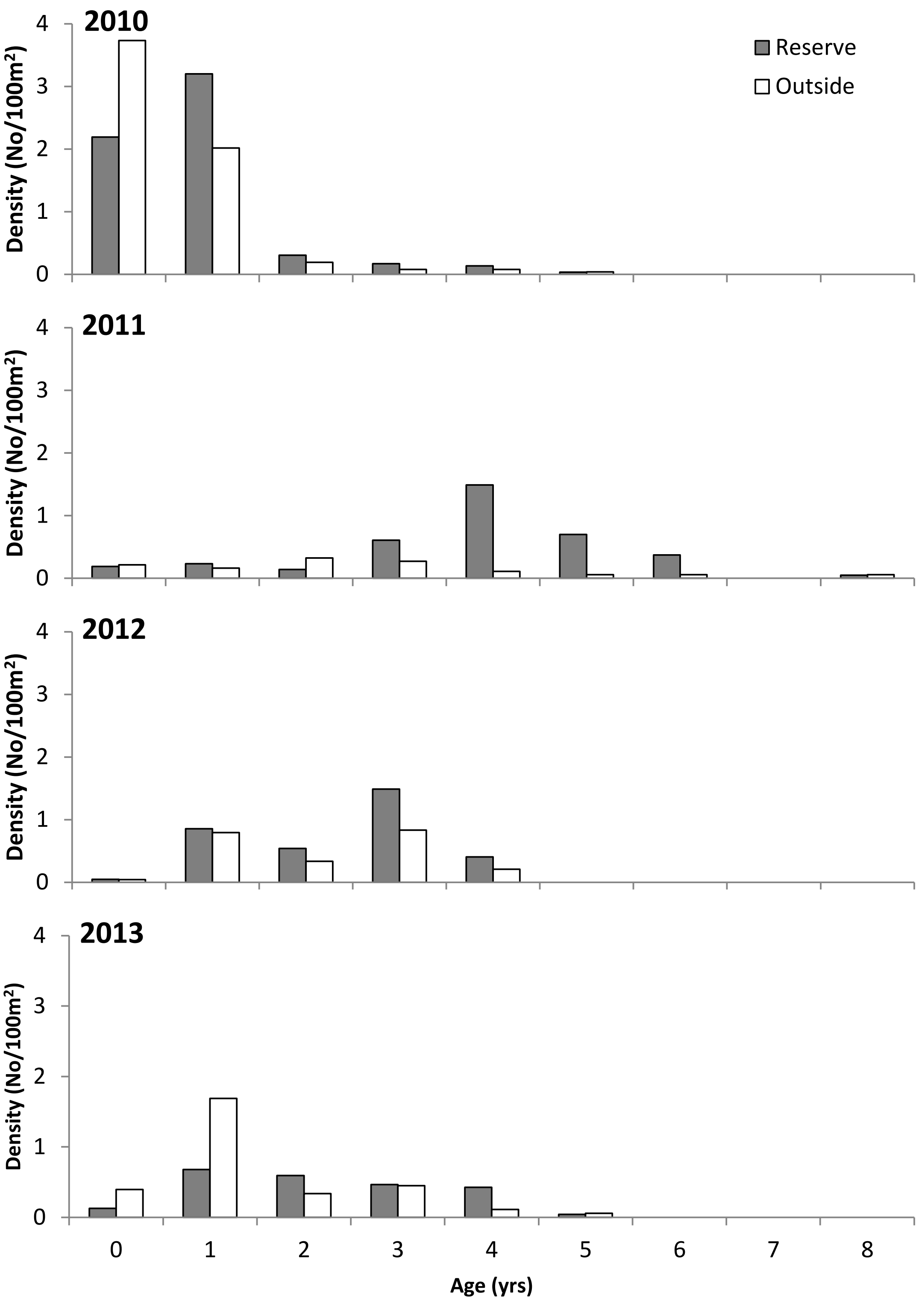

Figure 10. The age structure of queen scallops sampled within and outside the fully protected marine reserve across four years. The number (N) of individuals sampled from each population is available in Table 4.

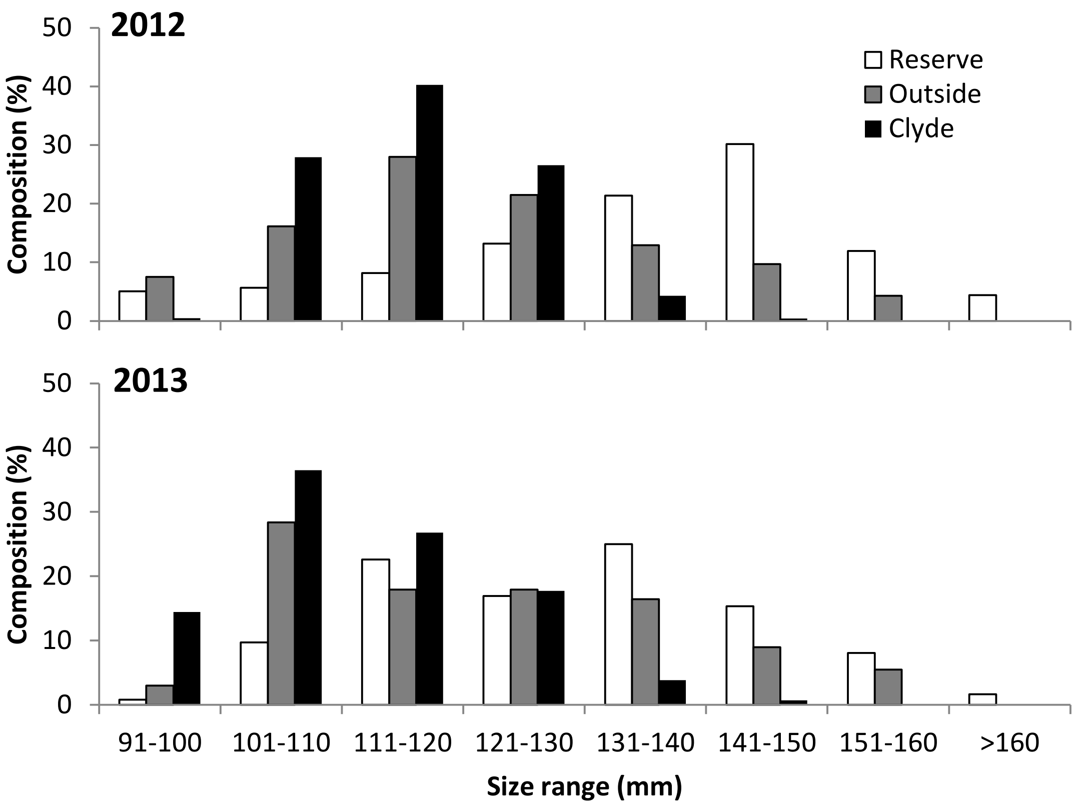

Figure 11. The size composition of king scallops above legal landing size sampled within and outside the fully protected marine reserve across two years. Also displayed is the size composition of king scallops caught and landed within the Firth of Clyde region. Data provided by Shona Kinnear of Marine Scotland - Science.

Comparisons of mortality rates

Combining the mean density-at-age data for all four years also revealed distinct differences in the population dynamics of king scallops between the two areas (Figure 12a). Catch curve analysis (Figure 12b) of these data (natural log transformed) produced linear regressions that estimated the total mortality of scallops in the fished area ($Z = 0.67$) to be 76.3% higher than in the closed area ($Z = 0.38$) (Figure 14b). As fishing mortality should not be occurring within the fully protected marine reserve, this calculation suggests the rate of natural mortality for king scallops to be 0.38.

Comparisons of growth rates

Overlaying Von Bertalanffy growth curves for king scallops within and outside the reserve across all years suggested a faster growth rate (or more accurately, rate of approach to theoretical maximum size) for scallops within the reserve ($k = 0.46$, $L_\infty = 151.01$, $T_0 = 0.13$) compared to outside ($k = 0.38$, $L_\infty = 153.18$, $T_0 = 0.13$). The Kimura likelihood ratio test of co-incident curves revealed that these two growth models were significantly different from one another (RSS_{ω}=26784.47, X_2=6.77, df =1, $P < 0.05$). In contrast, there was no difference in growth rates between in and outside the reserve for queen scallops (RSS_{ω}=10215.69, X_2=5.30, df =1, $P > 0.05$). Plotted growth curves are available in Appendix 6.

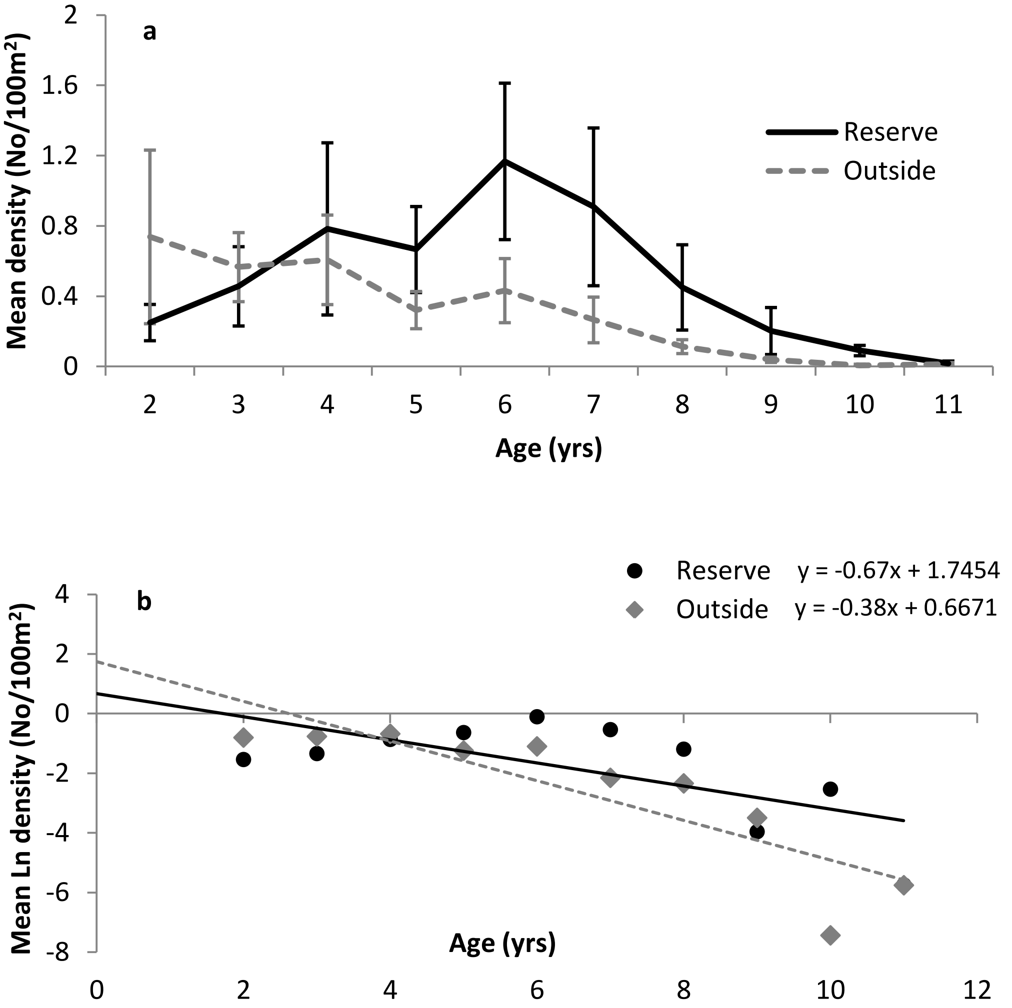

Figure 12. (a) The density per age-class of king scallops within and outside the reserve across the years 2010-2013. (b) Catch curve analysis (total mortality estimates) of king scallops within and outside the reserve across the years 2010-2013.

Comparisons of exploitable and reproductive biomass

For the years in which scallop dissections were conducted, the exploitable (Figure 13a) and reproductive (Figure 13b) biomass of king scallops were substantially greater within the reserve than outside. In 2010, the average exploitable and reproductive biomass of king scallops was 18% and 39% greater within the reserve respectively. The following years saw the biomass of king scallops increase within the reserve but remain relatively static outside. By 2013, the exploitable and reproductive biomass of king scallops within the reserve had increased to become 2 and 2.5 times more than in the fished area. Two-way ANOVA found level of protection, but neither year nor the interaction between the two, to significantly affect king scallop biomass (Table 4).

Similar to the fluctuations in queen scallop density, the exploitable and reproductive biomass of queen scallops also fluctuated greatly over time. In 2010, there was little difference in both the exploitable and reproductive biomass of queen scallops between the reserve and outside. However, in 2011, the exploitable biomass of queen scallops tripled within the reserve before returning to 2010 levels in 2013. Overall, the exploitable biomass of queen scallops was higher within the reserve across all years. In contrast, reproductive biomass was lower within the reserve across all years and also fluctuated heavily. Two-way ANOVA found level of protection, but not year nor the interaction between the two, to significantly influence the exploitable biomass of queen scallops (Table 5). In comparison, level of protection, year and the interaction between the two were all found to significantly influence the reproductive biomass of queen scallops.

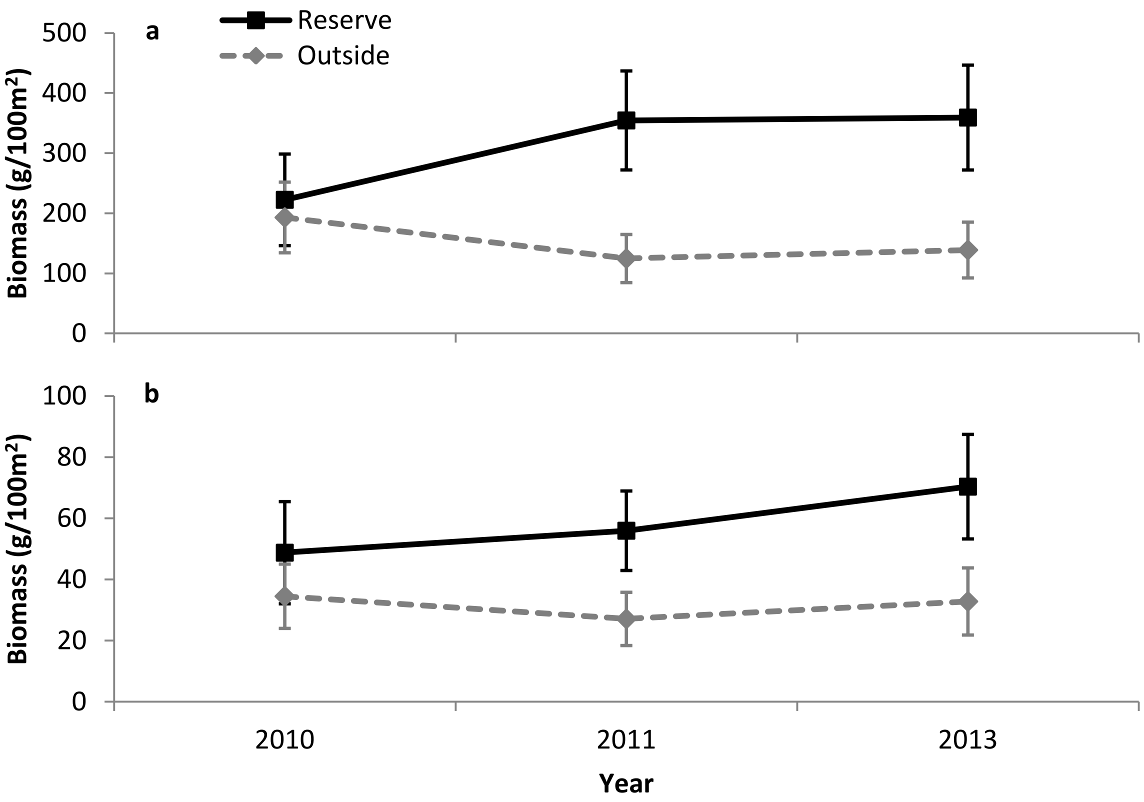

Figure 13. The mean exploitable (a) and reproductive (b) biomass of king scallops within and outside the fully protected marine reserve for the years when scallop dissections were conducted. Error bars represent ±1 SE.

Plotting the exploitable and reproductive biomass of king scallops greater than 100mm in length combined for all years against shell length revealed little difference between the reserve and outside, suggesting that the weight of gonads and adductor muscle per unit shell length were not greater within the reserve than outside. Confirming this, ANCOVAs that took into account differences in body size did not find any significant difference in the exploitable biomass (ANCOVA; $F_{(1, 180)} = 0.05$, $P > 0.05$) and reproductive biomass (ANCOVA; $F_{(1, 180)} = 0.34$, $P > 0.05$) of king scallops between the reserve and outside.

Table 5. Two-way ANOVAs comparing the exploitable and reproductive biomass of two species of scallop between the marine reserve and outside. Significant results are denoted by an (*).

Source	Test variable	SS	df	MS	*F*	*P*
King scallops (exploitable biomass)	Year	2235.37	2	1117.68	0.36	0.69
	Protection	17447.68	1	17447.68	5.61	*0.02
	Year x Protection	2613.66	2	1306.83	0.42	0.66
	Residual	8343594.12	94	78655.26		
King scallops (reproductive biomass)	Year	34078.71	2	17039.35	0.22	0.81
	Protection	625559.91	1	625559.91	7.95	*<0.01
	Year x Protection	229638.67	2	114819.33	1.46	0.24
	Residual	7393594.64	94	78655.26		
Queen scallops (exploitable biomass)	Year	1508.74	2	754.37	2.42	0.1
	Protection	1138.27	1	1138.27	3.65	*0.05
	Year x Protection	884.79	2	442.39	1.42	0.25
	Residual	29332.83	94	312.05		
Queen scallops (reproductive biomass)	Year	766.83	2	383.42	7.76	*<0.01
	Protection	298.31	1	298.31	6.04	*0.02
	Year x Protection	306.65	2	153.33	3.10	*0.05
	Residual	4645.80	94	49.42		

Discussion

This paper highlights a number of differences in the abundance, age, size and biomass of scallops between the fully protected marine reserve in Lamlash Bay and surrounding fishing grounds. However, it must be stressed that there is no data available prior to the establishment of the reserve. Ideally, a before-after control-impact (BACI) approach would have been employed, capable of definitely proving that differences between the reserve and outside were due to the protection afforded by the marine reserve (Hilborn et al. 2004; Sale et al. 2005). As this was not possible, we instead compared sites within the reserve to reference sites located outside its boundaries over a study period of four years. Several trends observed in this study showed an interaction between year and protection, meaning that the protection afforded by the marine reserve is likely to be responsible. Elsewhere, we have evidence that differences between the reserve and outside exist, but cannot conclude that protection is responsible for creating them.

Juvenile scallops were between two and five times more abundant within the marine reserve than surrounding areas, and that their increased abundance was related to a greater presence of nursery habitat growing within the boundaries of the marine reserve. That is, the distribution of juvenile scallops was strongly positively associated with the presence of macroalgae and hydroids, confirming that scallop spat settle more successfully in structurally complex habitats (Bradshaw *et al.*, 2001; Kamenos *et al.*, 2004b, 2004a; Minchin, 1992; Paul, 1981). Although data prior to the establishment of the reserve was not collected, a parallel study (Howarth *et al*., in review) found the abundance of these nursery habitats to be twice as great within the reserve than on neighbouring fishing grounds, and that the abundance of these habitats had steadily increased within the reserve over the four year study period. Theory and empirical evidence suggest that differences between MPAs and references sites should become more pronounced the longer the reserve is established (Roberts et al. 2005; Edgar et al. 2014). These results therefore provide evidence that protecting areas from fishing can allow seafloor habitats to recover, and as a result, can generate benefits that flow back to commercially important species. In the long term, these effects are highly likely to increase the numbers of juvenile scallops entering the adult stock as a greater proportion of juveniles survive to reach maturity (Beukers-Stewart *et al.*, 2003; Vause *et al.*, 2007).

Over the four year study period, we found the abundance of juvenile scallops to fluctuate greatly, alternating between high and low levels every two years. Since king and queen scallops typically undergo at least one major spawning event around spring/summer (Brand, 2006; Orensanz *et al.*, 2006), and as our dive surveys were conducted between June-September, it is unlikely that they were conducted too early in the year to detect the presence of juvenile scallops. Rather, it is more likely that the populations were exhibiting the strong natural fluctuations in recruitment typically observed in most scallop species (Paulet et al. 1988; Orensanz et al. 1991; Beukers-Stewart et al. 2003; Beukers-Stewart & Beukers-Stewart 2009). However, it is argued that by allowing populations and spawning stock biomass to recover, MPAs should offer higher and less variable catches in adjacent fishing grounds

(Bradshaw *et al.*, 2001; Roberts *et al.*, 2001, 2005). The following lines of discussion support this.

When monitoring began in 2010 it was concluded that, despite providing apparent benefits to juvenile scallops, the reserve in Lamlash Bay was yet to have a significant effect on the density of adult scallops (Howarth *et al.*, 2011). Likewise, in this extended study, neither time, nor level of protection (i.e. in or outside the reserve), nor the interaction between the two were found to be significantly influencing the density of king scallops. This result was surprising as the density of king scallops had been consistently greater within the reserve than outside for the past three years, and their density within the reserve had steadily increased over the four year study period. Nonetheless, as scallops breed by releasing both male and female gametes into the water column during synchronised spawning events (Brand, 2006), any increase in population density will likely result in a rapid increase in fertilisation success (Macleod *et al.*, 1985; Stoner and Ray-Culp, 2000; Vause *et al.*, 2007).

Despite finding no difference in the density of adult between the two treatments, we did find that scallop density significantly declined with increasing distance from the boundaries of the marine reserve. Many studies have detected similar gradients (Halpern *et al.*, 2010; Harmelin-Vivien *et al.*, 2008; Ludford *et al.*, 2012; McClanahan and Mangi, 2000) and several possibilities could explain such a trend. Environmental gradients and spatial heterogeneity of habitats are known to result in gradients of abundance (Vandeperre *et al.*, 2011) but as our survey design was balanced (i.e. we surveyed an equal number of sites of similar habitat and depth) this is unlikely. It could be that spillover of larvae and juveniles from within the reserve to outside is occurring, and that its effects diminish with increasing distance from the reserve (Kellner *et al.*, 2007). This is possible as the larvae of these two species typically spend 3–6 weeks in the water column where they can disperse over considerable distances (Brand et al. 1980; Macleod et al. 1985). Then again, it may be that fishers avoid areas immediately outside and around the marine reserve, meaning fishing pressure would consequently increase with distance from the reserve. This could be occurring as the marine reserve protects the north entrance to Lamlash Bay (see Figure 1), meaning fishers may choose to bypass the general area. Otherwise they would have to haul their fishing gears whilst they passed over the reserve, or attempt to turn around while fishing in the unprotected southern half of Lamlash Bay. As scallop densities were similar out to 1 km away from the reserve, but then suddenly dropped at 1.5 km and remained similar out to >2 km, this may be evidence of such a "halo effect” occurring. Furthermore, scallops from the wider Clyde were substantially smaller than those measured in the Lamlash Bay area, further supporting this idea.

We also found evidence that Lamlash Bay Marine Reserve was allowing the age and size structure of scallop populations within its boundaries to return to a more natural and extended state. The size and age of both scallop species were consistently greater within the reserve than surrounding areas over the study period. On average, we found king scallops to be 28mm larger and 1.7 years older within the reserve than outside. Likewise, we found queen scallops to be 13mm larger and 0.8 years older within the reserve. King scallops within Lamlash Bay Marine Reserve were also substantially larger than king scallops caught and landed by the wider Firth of Clyde scallop fishery, suggesting this was not just a localised phenomenon. The greater abundance, age and size of scallops within the reserve are consistent with the hypothesis that closing areas to fishing can protect individuals within their boundaries from fishing-induced mortality. This was confirmed by catch curve analysis, which suggested mortality was 76.3% greater outside the reserve than within its boundaries. The overall reduction in fishing pressure should mean that scallops within the marine reserve are rarely being damaged by mobile fishing gears and having to divert energy into shell repair. One study found that this allowed scallops within the boundaries of an MPA to invest a greater proportion of metabolic energy into body growth and gonad development (Kaiser *et al.*, 2007). On the contrary, we observed no difference in the weight of adductor muscle or gonads per unit shell length between Lamlash Bay Marine Reserve and fishing grounds. However, we did find that the exploitable biomass of king scallops within the reserve was twice than what was observed outside, and the reproductive biomass 2.5 times greater. As there was no significant interaction between protection and year, we could not attribute this difference to protection. Nonetheless, the greater levels of reproductive biomass within the reserve should mean the reserve is contributing disproportionally to recruitment compared to the size of area it protects by exporting large amounts of larvae to surrounding areas (Beck *et al.*, 2001; Gibb *et al.*, 2007; Harrison *et al.*, 2012; Laurel *et al.*, 2009). Furthermore, because scallops are broadcast spawners, the high densities of scallops inside the reserve would have increased the proximity of individuals to one another, which will enhance rates of fertilisation success and further add to levels of larval export (Beukers-Stewart *et al.*, 2005).

The differences between the Lamlash Bay Marine Reserve and control areas observed in this study are less pronounced than those documented in other MPAs (Beukers-Stewart *et al.*, 2005; Hart *et al.*, 2013). However, those studies were conducted over a decade after MPA implementation and in control areas subject to much greater fishing pressure. If anything, these studies suggest further improvements in scallop stocks are likely to occur within Lamlash Bay Marine Reserve in the future, since it had only been established for 2-4 years during the period of study (Roberts *et al.*, 2001, 2005). Our findings also present an interesting comparison to a recent study conducted in Wales, which found no evidence of scallop recovery within an MPA (Sciberras *et al*., 2013). This lack of response was attributed to high levels of natural disturbance. However, this study was conducted during just the first 23 months of protection and high levels of illegal fishing within the MPA have since been detected (Milford & West Wales Mercury, 2012; Misstear, 2012; Morris, 2014). In contrast, due to almost constant visual surveillance of Lamlash Bay Marine Reserve by COAST and its members, illegal fishing has been comparatively rare in Lamlash Bay (VMS data Marine Scotland 2014). It is therefore possible that the action and involvement of the local community in establishing and monitoring Lamlash Bay Marine Reserve has contributed to its success in improving scallop stocks.

In summary, we have presented several lines of evidence that suggest Scotland's first and only fully protected marine reserve is benefitting two commercially important scallop species. The growing abundance of nursery habitats within the marine reserve appears to be substantially increasing the settlement juvenile scallops, suggesting that protecting areas from fishing can generate ecological benefits that flow back to species commercially targeted by fisheries. Then again, for fisheries to truly benefit from marine reserves, it is essential that larvae, and / or juveniles and adults originating from within reserve spillover into surrounding fishing grounds where they can then contribute to landings (McClanahan and Mangi, 2000; Stelzenmüller *et al.*, 2007). However, the greater size, age and reproductive biomass observed within the reserve should translate to higher reproductive output and scallop recruitment both within the marine reserve and surrounding fishing grounds (Pelc *et al.*, 2010). Overall, our results suggest that the implementation of MPAs can be a useful tool in ecosystem-based fishery management.

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Chapter 5. Scotland's first fully protected marine reserve provides potential improvements to lobster stocks

5.1. Abstract

This study investigated the effects of the fully protected marine reserve in Lamlash Bay, Isle of Arran, United Kingdom, on commercially valuable populations of crustaceans. Potting surveys conducted over two years revealed catch per unit effort, weight per unit effort and size of lobsters to be significantly greater within the reserve than on neighbouring fishing grounds. Spatial gradients were detected in catch and weight per unit effort, suggesting that lobsters were migrating from within the reserve to surrounding fishing grounds. Preliminary tagging surveys supported this notion. Pregnant (berried) lobsters were more abundant within the reserve than outside and had greater mean potential reproductive output, which together suggested that the 2.67 km^2 marine reserve had a potential egg output equivalent to an unprotected area of 19.1 km^2. In contrast to lobsters, the catch per unit effort of crabs declined substantially over the study period in both areas. However, this may be a consequence of increased competition with lobsters. Overall, this study suggests that Lamlash Bay marine reserve is acting as a safe haven for those lobsters within its boundaries, allowing them to reach sexual maturity, greater fecundity and larger sizes.

5.2. Introduction

Scottish fisheries targeting crustaceans, such as lobster and crab, date as far back as the 12th century. These fisheries have greatly expanded and now make up the fifth most economically important fishery in Scotland (Mill et al. 2009; Barreto & Bailey 2013). However, concerns have recently been raised over declining recruitment, truncating age structures, failures in egg production and unsustainable levels of fishing mortality in several major crab and lobster stocks around Scotland (Tully et al. 2001; Mill et al. 2009; Barreto & Bailey 2013).

Although many different management measures exist for maintaining and supporting fish stocks, it has been argued that the establishment of Marine Protected Areas (MPAs) and marine reserves closed to some or all types of fishing are some of the most effective ways to reduce mortality and boost recruitment by increasing the abundance of target species, restoring and maintaining size and age structures (Halpern & Warner 2002; Halpern 2003; Lester et al. 2009), enhancing local reproductive output (Roberts et al. 2001; Gaines et al.

2003; Grantham et al. 2003) and improving the survival and growth of juveniles (Myers et al. 2000; Beukers-Stewart et al. 2005; Howarth et al. 2011). All of these effects may then result in the greater production of larvae, juveniles and adults which can disperse (“spillover”) outside the MPA and contribute to fishery landings (McClanahan & Mangi 2000; Harrison et al. 2012).

For populations to benefit from the protection afforded by MPAs, it is necessary that a number of individuals spend a substantial part of their lives within their boundaries (Roberts et al. 2005). Lobsters, crabs and other crustaceans have therefore been proposed as ideal species for closed area management thanks to their high value and relatively low mobility (Follesa et al. 2009, 2011; Moland & Olsen 2011; Moland et al. 2013a). In fact, several studies have found the abundance of lobsters to increase within MPAs 2-25 fold (Shears et al. 2006; Fenberg et al. 2012; Moland et al. 2013b) and that such increases can become evident after just 18 months of protection (Hoskin et al. 2011). Studies also report increases in mean body size (Hoskin et al. 2011; Moland et al. 2013a) and increased catches in neighbouring fishing grounds (Goñi et al. 2006, 2010; Díaz et al. 2011). Despite the potential for MPAs to provide fishery benefits, there are currently very few MPAs which currently exist in the United Kingdom (UK; Jones 2012). Of these, only three are fully protected marine reserves which ban all fishing activity within their boundaries (i.e. are “No-Take Zones” – NTZs). These are Lundy Island, in Devon; Flamborough Head, in North Yorkshire; and Lamlash Bay, in Scotland.

The Lamlash Bay NTZ was established in September 2008, prohibiting all sea fishing within its boundaries under the Inshore Fishing (Scotland) Act of 1984 (Axelsson et al. 2009). Uniquely, this fully protected marine reserve was passed by the Scottish parliament under the rationale that the reduction in fishing pressure should help regenerate both the local marine environment *and* enhance commercial shellfish and fish populations in and around Lamlash Bay. Our study therefore sought to conduct a series of crustacean surveys and tagging studies to determine if the Lamlash Bay Marine Reserve was providing benefits to commercially important populations of crabs and lobster. Specifically, these surveys were designed to test if: (1) catch rates of crab and lobster were higher within the reserve; (2) individuals were larger within the reserve; (3) there was any evidence of spillover from the reserve to fishing grounds; and (4) if there was any difference in lobster fecundity and gender ratios between the reserve and fishing grounds.

Although Lamlash Bay Marine Reserve was established in 2008, no crustacean surveys were conducted in the area prior to protection and monitoring of these populations only began in 2012 (i.e. four years after protection). A before-after control-impact (BACI) approach would have been more capable at establishing that any differences between the reserve and outside were due to protection (Hilborn et al. 2004; Sale et al. 2005). As this was not possible, I decided to monitor crustacean populations within the reserve and in several control areas located outside the reserve over a period of two years on the basis that a divergence of crustacean population characteristics over time would be indicative of an effect.

5.3. Materials and method

Study area and fisheries

I conducted this study around the southern and eastern shores of the Isle of Arran; an island situated off the west coast of Scotland within The Firth of Clyde. The Firth of Clyde is regarded as one of the most degraded marine environments in the UK, primarily due to over a century of intensive fisheries exploitation (Thurstan & Roberts, 2010; Bailey et al. 2011; Heath & Speirs, 2011; Howarth et al. 2013). The fully protected marine reserve encompasses an area of 2.67 km^2 (Thurstan & Roberts 2010) where water depths range between 0 and 29 m below chart datum, but can reach as deep as 43 and 50 m outside to the east and the west of the reserve, respectively (Admiralty Chart 1864; Baxter et al. 2008). Previous surveys (Duncan 2003; Axelsson et al. 2009; Howarth et al. 2011; SNH 2013) indicate the area to contain a mix of sediments (i.e. mud, sand, gravel and boulders with various proportions of shell) supporting a diverse range of habitats including kelp forests, seagrass and maerl beds. In addition, the area has long been identified as containing important maerl beds, although recent evidence points to deterioration in their health (Howarth et al. 2011).

Of the crab and lobster species investigated in this study, brown crab (*Cancer pagurus*) are the most important in Scotland; generating over 11,900 tonnes in landings and a first sale value of £14.2 million in 2011 (Barreto & Bailey 2013). In comparison, landings of the European lobster (*Homarus gammarus*) are much smaller but command the highest price per kilogram out of all the species landed in the UK (up to £19 per kg during seasonal highs), generating £13.1 million from just 1,200 tonnes of landings in 2011 (Mill et al. 2009; Mesquita et al. 2011). Lastly, velvet crabs (*Necora puber*) are one the smallest and recent fisheries in Scotland. Fished opportunistically by fishers, 2,600 tonnes of velvet crabs were landed in 2011 and generated £4.7 million. Despite concerns over declining recruitment and increased fishing mortality, these fisheries are regulated solely by minimum legal landing size, which is currently set at 87 mm carapace length for lobster, 130 mm carapace width for brown crab and 65 mm for velvet crab.

Sampling design

Targeted pot sampling surveys were conducted during one week in mid-July and one week in mid-August in 2012 and 2013. The catchability of crustaceans can vary heavily depending on their moult stage, reproductive condition, size, sex, seasons, habitats, water temperature and the number of crustaceans already in the trap (Jury et al. 2001; Smith and Tremblay, 2003). Hence, splitting the surveys over two months was designed to counter any shorter term fluctuations in the catchability of crustaceans.

Sampling occurred along the southern shore of the marine reserve (R1) and at near control sites (N1-N3) as displayed in Figure 1. All sites were located on shallow boulder slopes less than 10m in depth and were chosen by an experienced fisherman on the premise that he had caught lobster from those areas in the past. Near control sites were located less than 2.5 km from the boundaries of the marine reserve and were situated to the north, east and west of the reserve. Initially, it was our intention to sample along both the southern (R1) and northern (R2) shores of the marine reserve. However, SCUBA surveys (Howarth et al. 2011) indicated R2 to differ markedly from other sampling sites in that the substrate was primarily composed of sandy mud with shell. R2 was therefore excluded as a sampling site in this study.

Crustaceans were sampled using standard specification commercial shellfish pots of two side eye entrance design. Each pot was 65 mm in mesh size and measured 64 x 38 x 41 cm, with two entrances measuring 21 x 18 cm. Pots were baited with a mix of mackerel (*Scomber scombrus*) and redfish (*Sebastes* spp) and deployed in fleets of five with 20 m between each pot. Marker-buoys were attached to both ends of the fleets and pots were considered heavy enough to act as their own anchor. For each day of sampling, three fleets were deployed parallel to the shore within the reserve, and three were deployed outside. These were then left to "soak" for approximately 48 hours before being hauled and the catch sampled.

In 2012, a total of 32 fleets were deployed over the two sampling periods, half of which were inside the reserve and the other outside. In 2013, one fleet of pots intended to be placed outside the reserve was inadvertently deployed inside. Therefore 19 sites were sampled within the reserve and only 17 were sampled in the near control. Additionally, the surveys in 2013 were bolstered with some additional fishing observations made aboard two different commercial creeling vessels. These took place between July-August within the far control sites (F1-F3) 10-20km south of the marine reserve. The fishing gear used during these observations differed slightly from our pot sampling surveys in that the fleets were between 5-10 pots in length and were left to soak between 48-72 hours. While these differences have the potential to inflate measures of abundance, it has been observed that when soak times are five days or less, small variations in soak time have no significant effect on the catch rate of lobster (Bennet & Lovewell 1977; Montgomery 2005). In addition, measurements of Catch Per Unit Effort (CPUE) used in this study were based upon the average number of individuals caught per pot, largely negating the impact of varying fleet lengths. Fishing observations also differed from the pot sampling surveys in that the habitat of where these fleets were deployed was unknown.

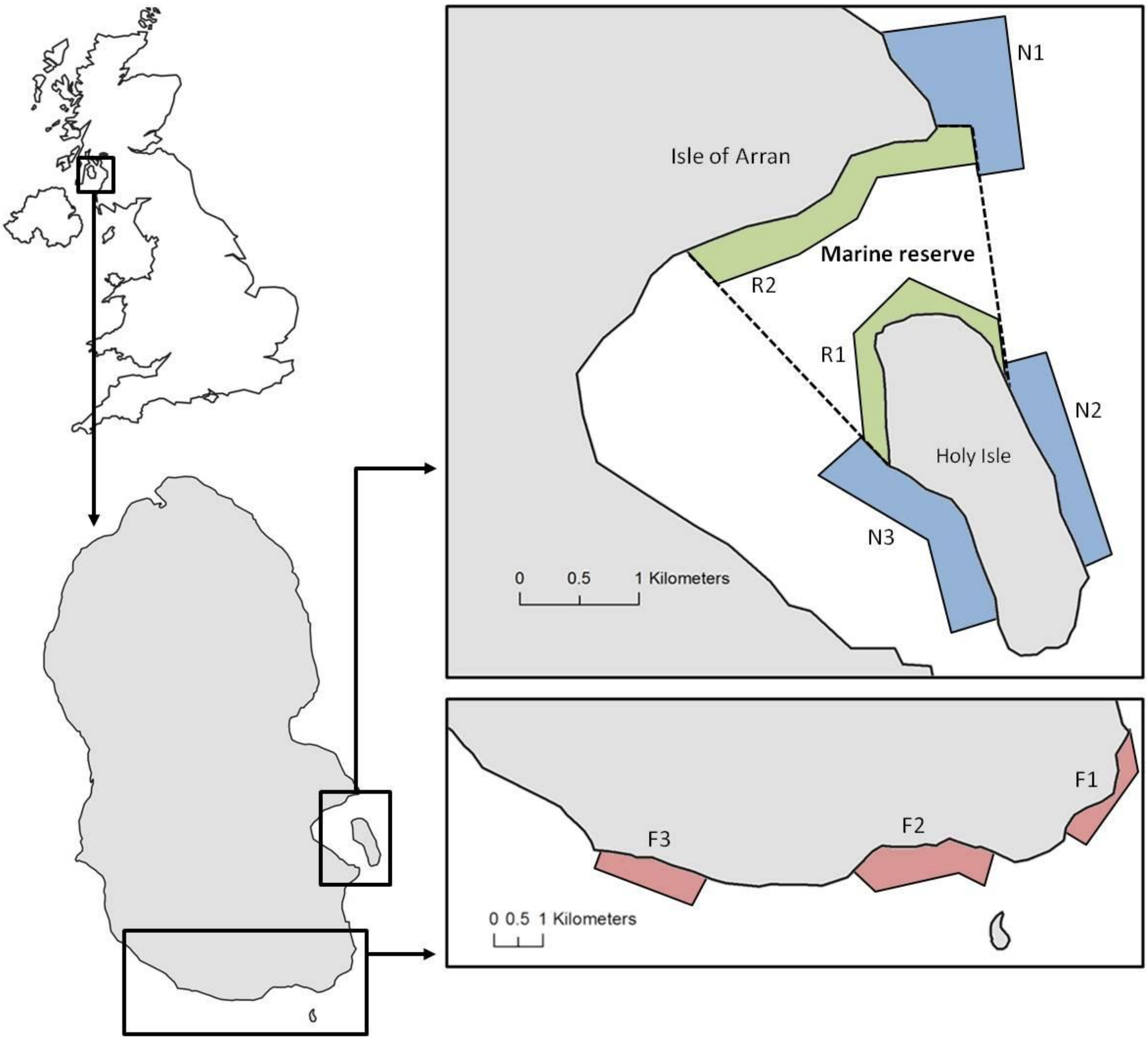

Figure 1. The locations of our pot sampling surveys. Baited shellfish pots were deployed in each area during July and August for the years 2012 and 2013. The maps on the left put these sites into geographical context within the UK and the Isle of Arran. Also displayed are the boundaries of the Lamlash Bay fully protected marine reserve.

Data collection

The abundance of all species captured per pot was recorded. All crustaceans of commercial importance were then measured (to the nearest 1mm), sexed and tagged (lobsters and brown crab only – see below) before being returned to the sea in the location where they were caught. Lobsters were measured from behind the eye stalk to the posterior edge of the carapace where the connection with the abdomen is formed. In comparison, crabs were measured at the widest point of the carapace. Signs of biological condition (e.g. berried) were recorded along with environmental conditions such as the weather, time of day, depth and location of capture, determined from a Geographical Positioning System (GPS). Again, the methodology for the additional fishing observations differed slightly. For these, the abundance of all species was recorded but only those individuals above minimum landing size were measured, sexed and inspected for biological condition.

Tagging

All lobsters (both years) and brown crabs (2012 only) caught in this study were fitted with a double T-bar anchor tag (Hallprint Pty. Ltd) measuring 55mm in length. These tags were selected for their quick application and high rate of retention during the moulting phase (González-Vicente et al. 2012). Each tag was imprinted with a unique identification number, the University of York telephone number, and coloured either green or orange depending on whether individuals were caught from within or outside the reserve respectively. Tags were inserted using a Monarch Marking 3030 tagging gun. Lobsters were tagged in their abdominal muscle immediately behind the posterior edge of the carapace, either side of the midline, in order to avoid puncturing the dorsal abdominal artery and the gut (Smith et al. 2001). Brown crabs were tagged where their fourth leg (on either side) joined the rear of the carapace.

Data analysis

Comparisons of CPUE

All analyses treated the three near control sites and three far control sites as just two independent areas (i.e. near control and far control). All variables were tested for normality using histograms, boxplots, QQ plots and the Shapiro–Wilk test. These basic exploratory measures were conducted within the statistical package R (www.r-project.org). The Shapiro–Wilk test was chosen as it is widely accepted to be the most suitable for small and medium-size samples (*N* up to 2000; Royston 1982, Conover 1999). The mean number of individuals caught per pot (calculated for each species) was used as an indicator of CPUE. This was done because the additional observations made aboard the various commercial fishing boats only recorded data at the fleet level, rather than at the level of individual pots. CPUE was calculated from the following equation:

$$\text{CPUE} = \frac{\text{Number of individuals caught in fleet}}{\text{Number of pots in fleet}}$$

The CPUE of velvet swimming crabs, brown crabs and European lobster were compared between treatments (i.e. reserve, near control and far control) for both years (where appropriate) using Mann–Whitney–Wilcoxon tests. This test was chosen as the two groups were independent and could not be transformed to a normal distribution.

The distance of each sampling location from the boundaries of the marine reserve was calculated using the spatial analysis software ArcGIS 10.1. The mean CPUE of lobsters was then calculated for all sites 0 km, 5 km, 10 km, 15 km and 20 km away from the marine reserve. Sites at a distance of 0 km were located within the marine reserve. This data was then plotted against distance utilising error bars of ±1 Standard Error (SE) and fitted with a polynomial trend line. Trends were tested for significance by calculating the Pearson product-moment correlation coefficient.

Comparisons of size and weight

The mean size of lobsters and crabs sampled in both years were compared between the reserve and near control using one-way ANOVAs. In addition, their overall size distributions were compared for both years using a Kolmogorov-Smirnov (K-S) two sample test. K-S tests were also used to compare the size distributions of lobsters (greater than minimal legal landing size) between the reserve and far control, and between the near control and far control.

The weight of lobsters was estimated by applying length-weight relationships inferred from another study conducted on lobsters off the west coast of Scotland (Leslie et al. 2006). The equation used depended on whether lobsters were male or female:

$$\text{Weight of male lobster (g)} = 0.0022 \times \text{length}^{2.7416}$$

$$\text{Weight of female lobster (g)} = 0.0016 \times \text{length}^{2.8134}$$

In order to explore the weight of lobster caught per pot, Weight Per Unit Effort (WPUE) was then calculated using the following equation:

$$\text{WPUE (g)} = \frac{\text{Total weight of lobster in fleet}}{\text{Number of pots in fleet}}$$

The WPUE of lobster was compared between the reserve and near control for both years using one-way ANOVAs. The mean WPUE of lobsters was then calculated for all sites 0 km, 0.5 km, 1 km, and 1.5 km away from the marine reserve. This data was then plotted against distance utilising error bars of ±1 Standard Error (SE) and fitted with a polynomial trend line. Trends were tested for significance by calculating the Pearson product-moment correlation coefficient. Distances greater than 1.5 km could not be used as these data were collected during the fishing observations. Fishing observations were bias in that they only measured the lengths of legally sized lobsters.

Comparisons of gender ratios and fecundity

A Pearson chi-squared (χ^2) test was used to determine if the frequency of male and female lobsters within the reserve and near controls differed from an equal 1:1 male/female ratio. The same test was then used to see if the frequency of male and female lobsters significantly differed between the reserve and near control sites for both years. Lastly, the test was utilised to determine if the frequency of berried and non-berried females differed from the reserve and near control sites. For any instances where expected values were less than five, Fisher's exact test was used instead of Pearson chi-squared to handle the low sample size (Dytham 1999).

Similar to the calculations of WPUE, fecundity-length relationships inferred by a study on European lobsters in southwest Scotland (Lizárraga-Cubedo et al. 2003) were used to estimate the potential reproductive output of each female lobster caught in this study:

$$\underset{\text{(number of eggs per female)}}{\text{Potential reproductive output}} = (1.55.4 \text{ x length}) - 10286$$

The mean potential reproductive output per female was then compared between the reserve and near control for both years using a Mann–Whitney–Wilcoxon test. Again, data collected from the fishing observations could not be used.

Investigating lobster growth and movements

Differences in size between tagging and recapture were used to investigate the growth of lobsters in and outside the reserve. The absolute minimum distance travelled by recaptured tagged lobsters was calculated in ArcGIS 10.1. Differences in the distance travelled by lobsters between the reserve and outside were tested for significance using a Mann–Whitney–Wilcoxon test. Although 55 brown crabs were tagged in 2012, none have been recaptured to date. Therefore analysis of tagged brown crabs was not possible.

5.4. Results

5.4.1. Lobster catch rates

In 2012, the mean CPUE of lobster was 1.33 (±0.16 SE) and 1.3 (±0.16 SE) in the reserve and near control respectively, and was not found to significantly differ (Mann-Whitney: U = 132, N = 32, P > 0.05). However, surveys conducted the following year saw the CPUE of lobster within the reserve increase to 1.65 (±0.11 SE) and decrease in the near control to 1.23 (±0.15 SE). This difference of 34.2% (Fig 2a) was statistically significant (Mann-Whitney: U = 100, N = 36, P < 0.05). The differences observed in 2013 became even more apparent when data were split between legal and sub-legal sized individuals. In 2013, the CPUE of legal sized lobsters was 1.11 (±0.1 SE) and 0.5 (±0.1 SE) in the reserve and near control respectively. This difference of 188.9% (Fig 2b) was also found to be significant (Mann-Whitney: U = 98, N = 36, P < 0.05). In contrast, there was no difference in the CPUE of sub-legal sized lobsters in either 2012 (Mann-Whitney: U = 130.1, N = 32, P > 0.05) or 2013 (Mann-Whitney: U = 89, N = 39, P > 0.05).

CPUE data from the far control sites suggested that the differences observed in lobster CPUE were not restricted to areas just outside the boundaries of the marine reserve. In 2013, the CPUE of legal sized lobsters was 180.5% greater within the reserve than that observed in far control sites (mean values displayed in Fig 3). This difference was found to be significant (Mann-Whitney: U = 149.5, N = 57, P < 0.05). In contrast, there was no difference in CPUE between near control and far control sites (Mann-Whitney: U = 243, N = 55, P > 0.05).

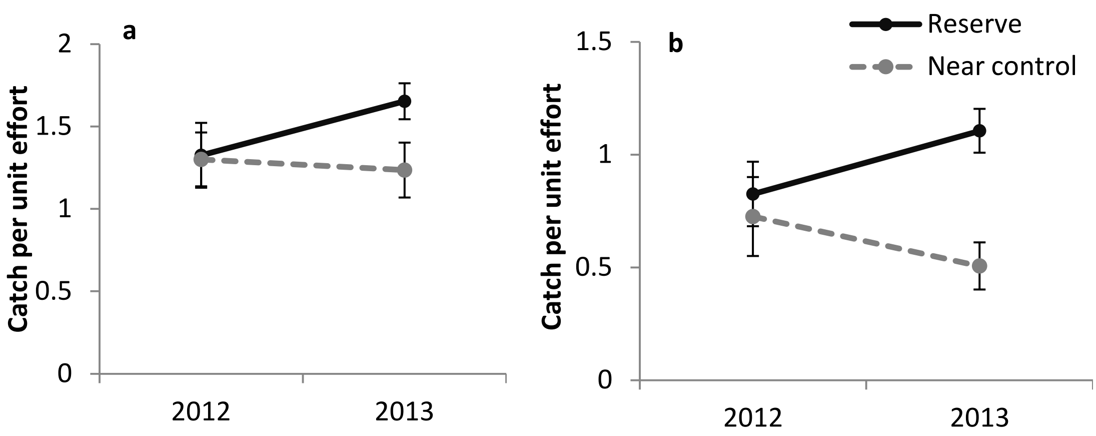

Figure 2. The mean catch per unit effort (no. lobsters / pot) of (a) all lobsters and (b) legal sized lobsters only within the fully protected marine reserve and near control across the two year study period. Error bars represent ±1 SE.

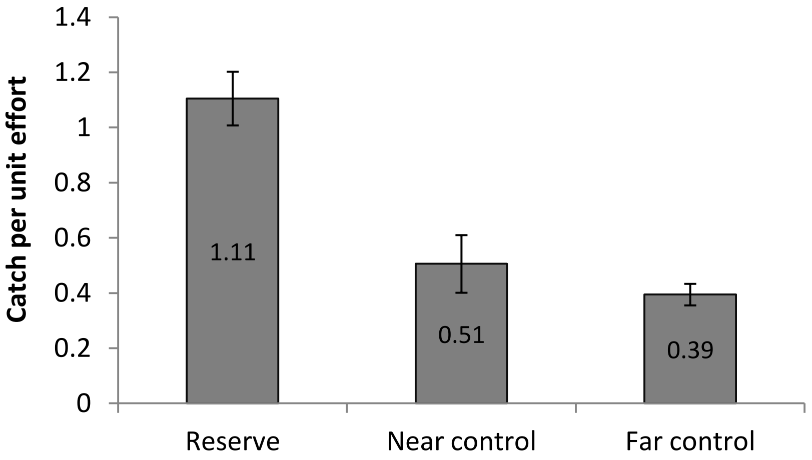

Figure 3. The mean catch per unit effort (CPUE) of legal sized lobsters in the fully protected marine reserve, and far and near controls in 2013. Error bars represent ±1 SE. Numbers within the bars represent the mean value of CPUE.

Plotting the mean CPUE of lobsters combined for both years against distance from the boundaries of the marine reserve revealed strong spatial interactions. It was found that the CPUE of lobsters declined with increasing distance from the marine reserve (Fig 4a). Sites within the marine reserve supported an average CPUE 42.1% greater than sites located at a distance of 20 km away. This negative relationship was found to be significant (Pearson Correlation; N = 125, R = -0.2, P < 0.05). Again, restricting the dataset to just lobsters of legal landing size made these trends even more pronounced (Fig 4b), with sites within the reserve supporting CPUE values 156.8% greater than sites 20 km away. This negative relationship was also found to be significant (Pearson Correlation; N = 126, R = -0.34, P < 0.05).

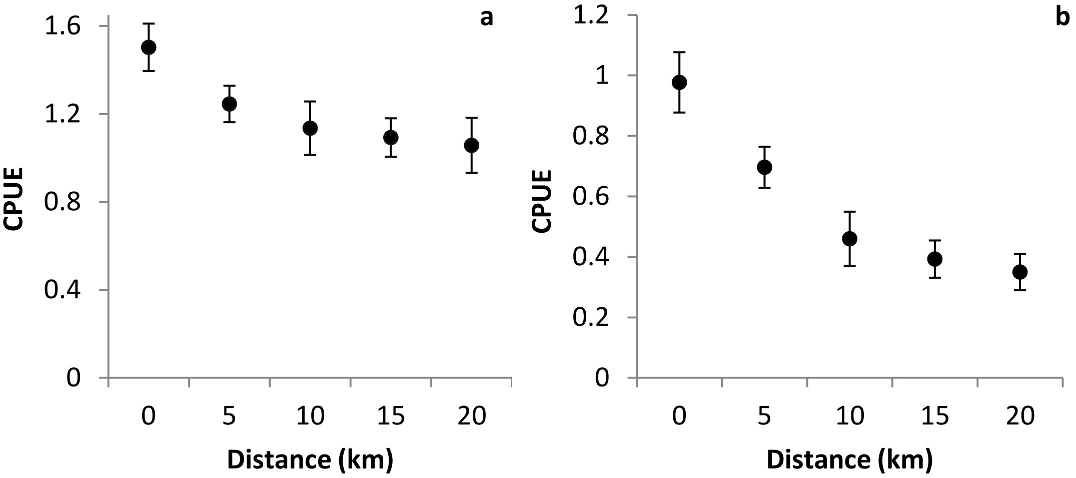

Figure 4. Mean CPUE of (a) all lobsters and (b) legal sized lobsters for the years 2012 and 2013 combined plotted against distance from the boundaries of the fully protected marine reserve. A distance of 0 represents those sites located within the marine reserve. Error bars represent ±1 SE.

5.4.2. Lobster size and weight

The mean size of lobsters was significantly greater within the marine reserve than on near control sites for both years. Lobsters were on average 5.9 mm larger in 2012 (ANOVA, $F_{(1,198)} = 9.06$, $P < 0.05$) and 7.3mm larger in 2013 (ANOVA, $F_{(1,262)} = 25.6$, $P < 0.05$). Comparing the overall size distribution for lobster between the two treatments also revealed lobster populations within the reserve to be composed of more large individuals (Fig 5). In fact, large lobsters greater than 111 mm were entirely absent from near control sites in both years. Consequently, the size distribution of lobsters within the reserve significantly differed from both control sites, whereas no difference was detected between the near and far control sites (Table 1).

In 2012, the mean WPUE did not differ between the reserve and near control (ANOVA, $F_{(1,32)} = 0.45$, $P > 0.05$). However, the following year saw WPUE increase within the reserve (mean values displayed in Fig 6) to become 45% greater within the reserve than near control sites (ANOVA, $F_{(1,36)} = 12.29$, $P < 0.05$). Similar to CPUE, it was found that WPUE significantly declined with increasing distance (Fig 7) from the boundaries of the marine reserve (Pearson Correlation; $N = 78$, $R = -0.57$, $P < 0.05$). On average, sites within the reserve provided over 250 g (± 77 SE) more lobster caught per pot than sites 1.5 km away.

Table 1. Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size distributions (% composition) of lobster populations in the fully protected marine reserve and near and far control sites. Tests involving far control sites are restricted to lobsters above minimum legal landing size. Significant terms are denoted by a (*).

Year	Test	*N*	KS-Z	*P*
2012	Near control & Reserve	108 & 90	1.57	* 0.014
2013	Near control & Reserve	157 & 105	2.12	*>0.001
2013	Near control & Far control	103 & 42	0.73	0.66
2013	Far control & Reserve	105 & 103	1.88	*>0.001

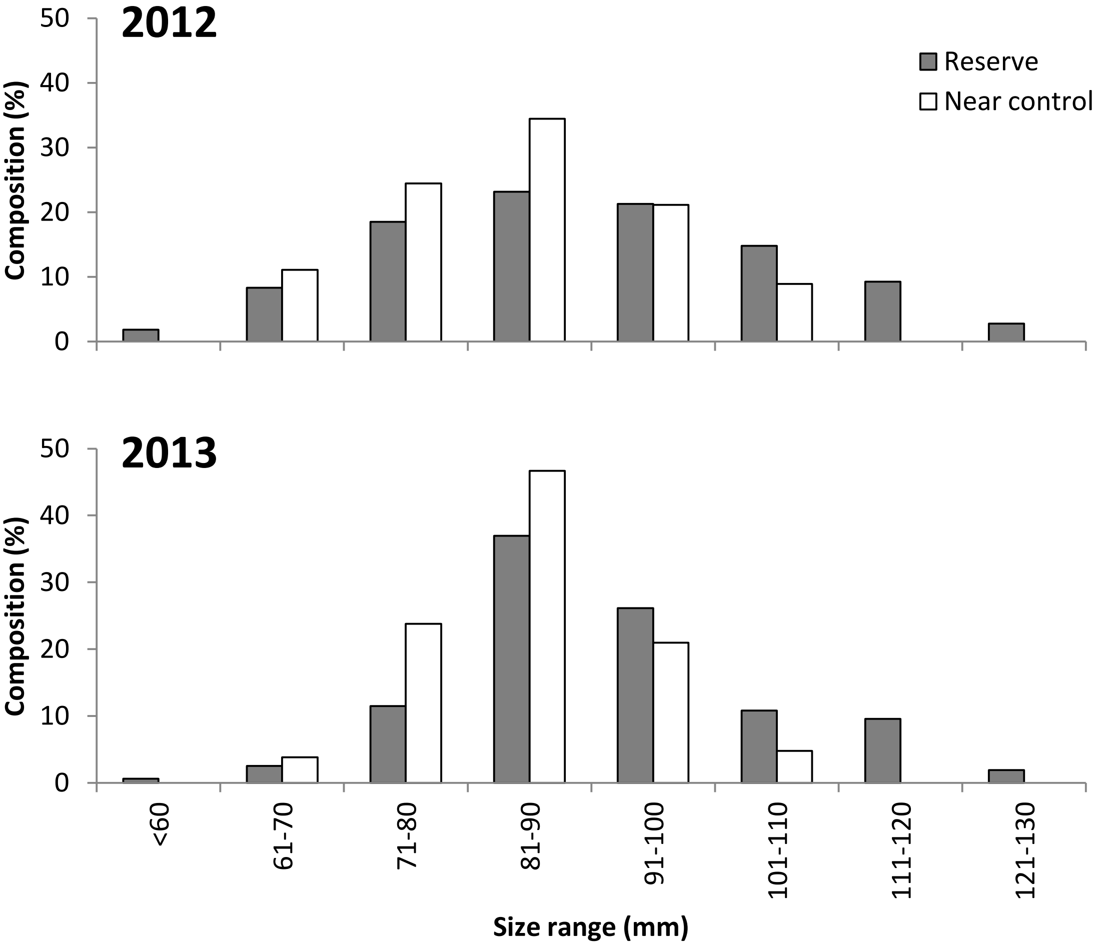

Figure 5. The size structure of lobsters sampled within the fully protected marine reserve and near control sites across the two year study period. The number (N) of individuals sampled from each population is available in Table 1.

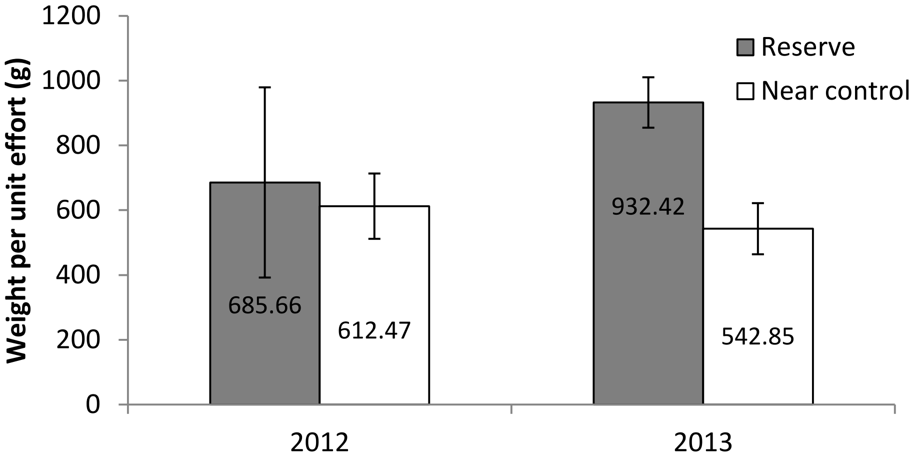

Figure 6. The mean weight per unit effort (WPUE) of lobster caught within the fully protected marine reserve and near control in 2012 and 2013. Error bars represent ±1SE. Numbers within the bars represent the mean value of WPUE.

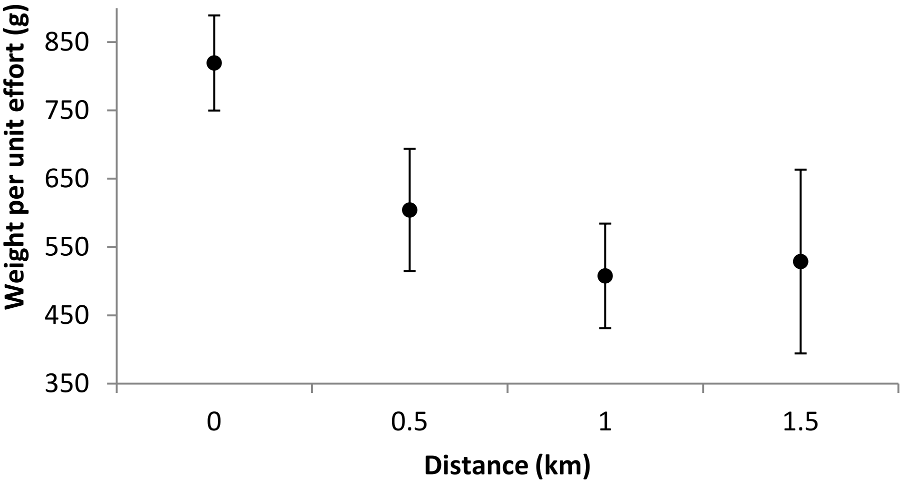

Figure 7. The mean estimated weight per unit effort (WPUE) for the years 2012 and 2013 combined, plotted against distance from the boundaries of the fully protected marine reserve. A distance of 0 represents those sites located within the marine reserve. Error bars represent ±1 SE.

5.4.3. Lobster gender ratios and fecundity

In both the reserve and near control sites across both years, the frequency of male and female lobsters significantly differed from an equal 1:1 male/female-ratio, with male lobsters being significantly more abundant than females across all groups (Table 2). Further tests revealed no significant difference in the frequency of male and female lobsters between the reserve and near control sites (Table 3). However, berried lobsters were found to be significantly more abundant within the reserve. Combining data across both years, the ratio of berried to non-berried females was 1:21 in near control sites, whereas the ratio of berried to non-berried females within the reserve 3:10. This meant the frequency of berried lobsters was 3.5 times greater within the reserve than outside in 2012, and 5.5 times greater in 2013. In addition, the mean potential reproductive output per female lobster was 27.3% (1.3 times) greater within the marine reserve than near control sites in 2013, but this was not statistically significant (Mann-Whitney: U = 149.5, N = 57, P > 0.05). Therefore, the 2.67 km^2 marine reserve had a potential egg output equivalent to an unprotected area of 19.1 km^2 (2.67 x 5.5 x 1.3).

Table 2. Outputs from Pearson chi-squared tests used to compare frequencies of male and female lobsters from an expected male/female ratio of 1:1. Significant terms denoted by a (*).

		Male		Female			
Year	Group	Observed	Expected	Observed	Expected	χ^2	*P*
2012	Reserve	62	52	42	52	3.84	*0.05
	Near control	75	53	31	53	18.64	*<0.001
2013	Reserve	26	22	18	22	1.45	*0.04
	Near control	100	78.5	57	78.5	11.77	*<0.001

Table 3. Outputs from Pearson chi-squared tests used to compare the frequency of berried and non-berried female lobsters within the fully protected marine reserve and near control sites. Significant terms are denoted by a (*). One test, denoted by a ($^+$), had expected counts less than 5 and therefore Fishers Exact test was used instead.

Year	Gender	Test	Reserve	Near control	χ2	*P*
2012	Male	Observed	75	62	2.872	0.92
		Expected	69.2	67.8		
	Female	Observed	31	42		
		Expected	36.8	36.2		
2013	Male	Observed	100	26	0.311	0.57
		Expected	98.4	27.6		
	Female	Observed	57	18		
		Expected	58.6	16.4		
2012	Non-berried	Observed	24	40	5.239	*0.03$^+$
		Expected	27.2	36.8		
	Berried	Observed	7	2		
		Expected	3.8	5.2		
2013	Non-berried	Observed	49	44	4.055	*0.04
		Expected	52.3	40.7		
	Berried	Observed	10	2		
		Expected	6.7	5.3		

5.4.4. Crustacean growth and movements

In 2012, a total of 206 lobsters were tagged, 104 from inside the reserve and 102 from the near control. In 2013, a total of 233 lobsters were tagged, 130 from the reserve and 103 from the near control. In the 12 month period following the August 2012 surveys, a total of 29 recaptures were recorded. Eleven of these recaptures were reported from local fishermen. These recaptures comprised of 27 unique individuals, representing a recapture rate of 6.12%. Only 8 lobsters had moulted and grown since tagging. These grew an average of 1.83 mm per month (±0.2 SE) and had all originated from within the reserve. Given the low numbers of moulted individuals (and that they all came from inside the reserve) it was not viable to conduct a more detailed analysis of these growth data.

Lobsters within the reserve displayed higher levels of site fidelity, moving an average distance of 0.4 km (±0.2 SE) over an approximate period of one year, compared to 1.2 km outside (±0.5 SE). However, these differences were not found to be significant (Mann-Whitney: $U = 100$, $N = 27$, $P > 0.05$). There was some evidence of spillover occurring in Lamlash Bay. Two lobsters had moved from within the reserve to the near control, representing a spillover rate of 0.85%. Conversely, two lobsters originating from the near control sites had moved into the reserve, representing a net movement rate of 0. No recaptures of brown crab were made.

5.4.5. Catch rates and size of other commercially important crustaceans

In contrast to the CPUE of lobster, the CPUE of other commercially important crustaceans declined within the reserve over the two year study period. In 2012, the mean CPUE of brown crab was 0.28 (±0.01 SE) and 0.33 (±0.01 SE) in and outside the reserve respectively. This difference was not significant (Mann-Whitney: $U = 150.5$, $N = 32$, $P > 0.05$). However, in 2013 CPUE had declined within the reserve by 49% and increased outside by 62.5%. Consequently, the CPUE of brown crab was 0.15 (±0.14 SE) and 0.53 (±0.15 SE) in and outside the reserve respectively. This difference was significant (Mann-Whitney: $U = 80.5$, $N = 36$, $P < 0.05$).

In contrast, the CPUE of velvet crabs in 2012 was 1.45 (±0.48 SE) and 0.51 (±0.14 SE) in the reserve and near control respectively, a significant difference of 200% (Mann-Whitney: $U = 58$, $N = 32$, $P < 0.05$). In 2013, CPUE declined by 87% within the reserve and increased outside by 45.1%, resulting in a CPUE of 0.22 (±0.2 SE) and 0.74 (±0.32 SE) in the reserve and near control respectively. This difference was not significant (Mann-Whitney: $U = 136$, $N = 36$, $P > 0.05$). Overall, the CPUE crabs (velvet and brown crabs) and lobsters were found to be significantly negatively correlated (Pearson Correlation; $N = 68$, $R = -0.4$, $P < 0.05$). The size distributions of velvet (Fig 8) and brown crabs (Fig 9) did not differ between the reserve and near control for all years (Table 4).

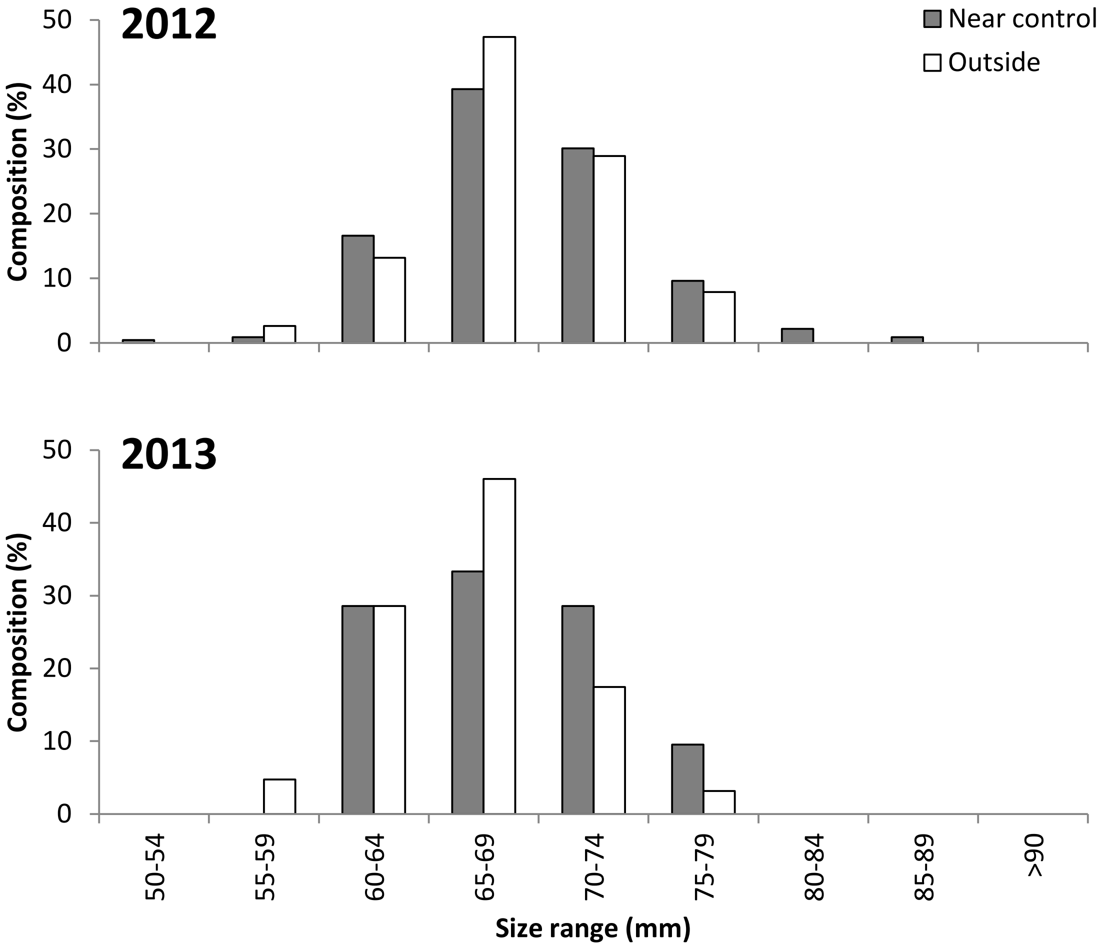

Figure 8. The size structure of velvet crabs sampled within the fully protected marine reserve and near control sites across the two year study period. The number (N) of individuals sampled from each population is available in Table 4.

Table 4. Outputs from the Kolmogorov–Smirnov (K–S) 2 sample tests used to compare the size distributions (% composition) of crab populations in the fully protected marine reserve and near control sites. Significant terms are denoted by a (*).

Year	Species	Reserve (*N*)	Near control (*N*)	KS-Z	*P*
2012	Brown crab	29	26	0.48	0.98
	Velvet crab	141	38	0.55	0.93
2013	Brown crab	14	45	0.74	0.65
	Velvet crab	21	63	1.01	0.26

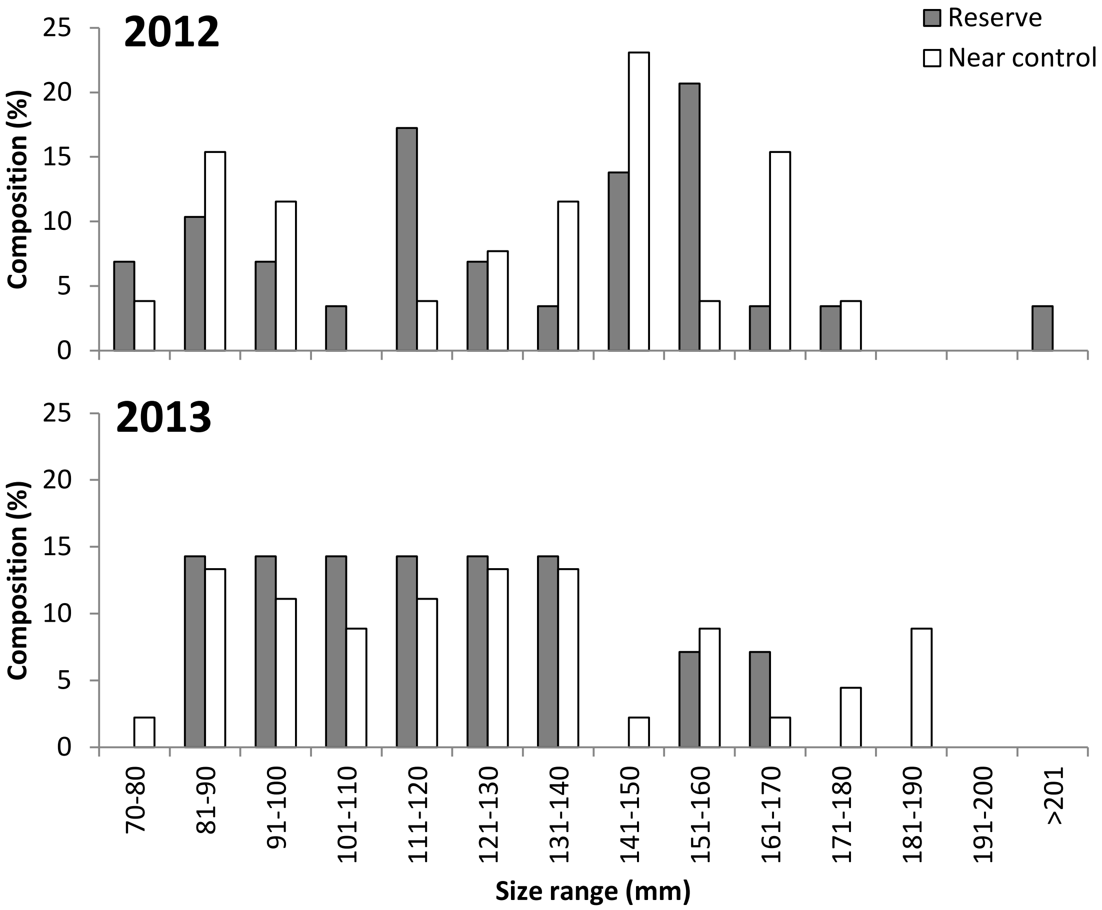

Figure 9. The size structure of brown crabs sampled within the fully protected marine reserve and near control sites across the two year study period. The number (N) of individuals sampled from each population is available in Table 4.

5.5. Discussion

This study provides evidence that, after four years of protection, Lamlash Bay Marine Reserve is potentially benefitting commercially important populations of European lobster. Lobsters were significantly larger within the reserve than on neighbouring fishing grounds during both years of study. In fact, large lobsters (> 111 mm) were entirely absent outside the reserve, meaning individuals were on average 5.9 mm larger within the reserve in 2012, and 7.3 mm larger in 2013. This trend of increased body size within Lamlash Bay reserve is consistent with other studies (Hoskin et al. 2011; Moland et al. 2013a) and supports that individuals located within the boundaries of MPAs experience increased survivorship, owing to the cessation of fishing. As egg production in lobsters is a function of population size, maturity, fecundity and body size, the greater abundance of larger-bodied lobsters within the reserve should translate to higher reproductive output and recruitment both within the reserve, and to surrounding areas (Pelc et al. 2010). Corresponding with this, size-fecundity relationships suggested that the mean potential reproductive output per female lobster (in terms of number of eggs) was 27.3% higher within the reserve than outside by 2013. I also found the frequency of berried female lobsters within the reserve to be 5.5 times greater than outside in 2013. Taking into account the greater frequency of berried lobsters and reproductive output suggested that the 2.67 km^2 marine reserve had a potential egg output equivalent to an unprotected area of 19.1 km^2. These results support the idea that MPAs can contribute disproportionally to recruitment in relation to the actual size of area they protect (Beck et al. 2001; Gibb et al. 2007; Laurel et al. 2009).

I found no difference in the sex ratios of lobster between the reserve and outside, meaning that differences in gender ratios were not likely responsible for the higher abundances of berried lobster recorded within the reserve. Therefore, it might be related to the greater abundance of large lobsters within the boundaries of the reserve. To explain, female lobsters reach sexual maturity at approximately 77 mm in size, or 4-12 years old in age (Simpson 1961; Barreto & Bailey 2013). As large-bodied adults were less abundant outside the reserve it is highly likely that sexually mature, berried female lobsters were equally less abundant. Added to this, berried female lobsters tend to exhibit less mobility and therefore lower catchability than that of unberried females (Agnalt et al. 2007) further lowering the probability of catching berried lobsters outside the reserve. Government reports indicate male and female lobsters are generally landed in equal proportions in Scotland (Mill et al. 2009) whereas I caught significantly more males than females. Again, this could be explained by the lower catchability of berried lobsters which would reduce the number of females caught both within and outside the reserve. Whatever the reason for the trend, it has been legal to land berried lobsters in the UK since 1966 (Bennet & Edwards 1981), meaning the marine reserve should act as a safe haven for those sexually mature lobsters within its boundaries allowing them to contribute to recruitment.

In addition to greater reproductive output, catch rates of lobster were 34.2% higher within the reserve than on sites located directly outside its boundaries in 2013. This difference increased to 188.9% when I considered just legal sized lobsters, reflecting the greater abundance of large lobsters within the reserve. Similar differences were observed between the reserve and control sites located 10-20 km away, suggesting these differences were not restricted to areas just outside the boundaries of the marine reserve. Greater levels of CPUE imply lobster density had increased within the reserve. However, as lobsters are solitary, territorial animals, they are known to fight each other when in close proximity (Debuse et al. 1999; Williams et al. 2006).

Therefore, an effective way for lobsters to avoid intraspecific competition would be to move outside the boundaries of the reserve where lobster densities are lower. It is therefore quite plausible that the spillover of individuals from within the reserve to neighbouring grounds is occurring. Additionally, as large lobsters were more abundant within the reserve, we can expect a greater proportion of juvenile lobsters to be displaced by territorial disputes, meaning lobster size should decrease with increasing distance from the reserve (Follesa et al. 2009). In support of these two theories, I found lobster CPUE to gradually decline with distance from the reserve, and that this declining trend was substantially stronger for legal sized lobster. In fact, the CPUE of legal sized lobster within the reserve was 156.5% greater than sample sites located 20 km away. Similarly, the weight of lobster caught (indicative of size and abundance) also significantly declined with distance from the reserve. Models and empirical evidence suggest that, as CPUE and WPUE formed gradients in the form of negatively sloping curves, these trends are likely to be evidence of spillover (Kellner et al. 2007). However, this assumes that levels of fishing mortality are consistent outside the reserve.

Data from our tagging study confirmed that spillover had occurred in Lamlash Bay, as has been observed for lobsters in several other studies of MPAs (Díaz et al. 2011; Goñi et al, 2006, 2010), but that these spillover events had been offset by lobsters migrating from outside the reserve to inside. However, our recapture rates were too low to draw any solid conclusions on spillover. Overall, a total of 441 lobsters were tagged in this study, of which only 29 were recaptured. Of these 29 lobsters, two had migrated from within the boundaries of the reserve to outside. However, two lobsters originating from outside had also migrated into the reserve, representing an overall net movement of 0. Hence, the low rates of recapture made it difficult to make any strong conclusions about spillover and movement of lobsters in Lamlash Bay. Similarly, of the 29 recaptured lobsters, only 8 had exhibited any growth, all of which were tagged and recaptured within the reserve, which made it impossible to compare growth rates between the reserve and outside.

The 34.2% difference in lobster CPUE between in and outside Lamlash Bay Marine Reserve is considerably less than those documented by other studies of MPAs. In the Lundy NTZ, which is only slightly larger than the one in Lamlash Bay, the CPUE of European lobsters was 171% higher within the reserve than control sites after just four years of protection (Hoskin et al. 2011). Likewise, several MPAs off the coast of Norway, all similar in size to the Lamlash Bay Marine Reserve, were shown to increase lobster CPUE by 245%, again after just four years of protection (Moland et al. 2013a). A limited amount of suitable lobster habitat within the

Lamlash Bay Marine Reserve may be responsible for the smaller differences in CPUE observed by this study. To explain, a pilot study was conducted on the northern shore of the reserve in 2012 and resulted in the capture of zero lobsters. SCUBA surveys (Howarth et al. 2011) revealed this area to differ from the other sampling sites used in this study, in that it was composed primarily of muddy sand and shell. As already mentioned, our pilot studies revealed that the rocky and boulder habitats preferred by lobsters (Mehrtens et al. 2005; Mill et al. 2009; Barreto & Bailey 2013) were only present along the southern shore of the reserve. In effect, this reduces the area within the reserve available for lobster habitation, thereby limiting the extent of any benefits the reserve can bestow on lobsters. The smaller area available to lobsters within the reserve is also problematic because the reserve can only protect those individuals that remain in its boundaries. Although several studies have shown that 95% of lobsters move less than 4 km in a single year (Agnalt et al. 2007; Galparsoro et al. 2009; Moland & Olsen 2011), such movements would be enough to place the lobsters outside the boundaries of Lamlash Bay Marine Reserve where they may then be captured by fishing gears. The small size of Lamlash Bay Marine reserve may also be why no tagged brown crabs were recaptured during this study period. Brown crabs are known to take extensive seasonal migrations (Barreto & Bailey 2013) and have been documented to travel over 245 km over a period of 2-4 years (Fahy & Carroll, 2009). Considering the small size of the Lamlash Bay Marine Reserve, it is likely that these species receive minimal, if any protection in the long term. Hence, marine reserves must be well designed; incorporating suitable habitat and being of adequate size to protect species of interest (see Edgar et al. 2014).

In contrast to observing greater catch rates of lobster in 2013, there was no difference between the reserve and outside in 2012. Due to the lack of data available prior to the establishment of the reserve, explaining the sudden increase in 2013 is difficult. Additional years of monitoring might reveal that lobster abundance in the area is highly variable, fluctuating naturally from year to year. Or further monitoring might reveal that lobster abundance is increasing every year, and that in 2013, the abundance of lobster within the reserve finally passed that of outside. Either way, this study is limited by only having two years of data. Our surveys should therefore be repeated for at least another two years to determine whether the trends I observed are continuing, or simply fluctuating.

Analyses of CPUE and WPUE suggest that increasing densities of lobster within the reserve may be forcing juvenile lobsters to areas outside the reserve where densities are lower. If true, the same interaction may be occurring between lobsters and crabs. During the two year study period, the abundance of legal sized lobsters increased by 188.9% within the reserve compared to outside. During the same period, the abundance of brown and velvet crab declined steeply. Aggression, predation and territorial behaviour between adult lobsters and crabs may be responsible for these contrasting trends as adult lobsters have been shown to predate on smaller crustaceans and compete aggressively with larger individuals for food (Cobb & Castro 2006; Williams et al. 2006). An alternative explanation is that the trend is an artefact of the sampling method. In locations where pots were catching increasing numbers of lobsters, fear of predation may have reduced velvet and brown crabs' willingness to enter pots and/or made them more likely to exit if already inside (Hoskin et al. 2011). Either response would result in a false appearance of declining abundance of crabs in areas with high abundance of lobsters. However, I believe this is unlikely as lobster and crabs were frequently caught in the same pot, and showed no evidence of predation between the two (although there was evidence of fighting/cannibalism between lobsters).

In summary, this study has provided several lines of evidence that the fully protected marine reserve in Lamlash Bay may be benefitting commercially important populations of European lobster. Firstly, a greater number of lobsters appear to be reaching larger sizes within the reserve, increasing their fecundity and reproductive output. I also observed that catch rates of lobster were higher within the reserve, and that catches decreased with increasing distance from its boundaries, possibly indicating spillover. However, as there are no data available prior to protection, I could not conclude that protection was responsible for these trends. Further years of monitoring will help resolve this issue. Overall, this study is consistent with the hypothesis that marine reserves can act as a safe haven for lobsters within its boundaries, allowing them to reach sexual maturity, greater fecundity and reach larger sizes.

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Chapter 6. Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve

6.1. Preface

Fishing can have a wide range of impacts on marine ecosystems. Namely, it can damage seafloor habitats and reduce the abundance of target and non-target species (Bradshaw et al. 2001; Jenkins et al. 2001). Since closing areas to fishing is the surest way of protecting marine ecosystems from the physical impacts of fishing gears, marine reserves should provide the best management tool available for encouraging the recovery of fish and benthic communities. However, the use of marine reserves as both a fisheries and conservation tool remains highly debated (Kaiser, 2004, 2005; Jones 2007; Sciberras *et al.*, 2013).

In this chapter I investigate differences in benthic and fish communities between the Lamlash Bay fully protected marine reserve and surrounding fishing grounds. This was achieved by conducting a series of quantitative diver, photo and video surveys over a four-year period.

This chapter has been written in the style of Conservation Biology.

I declare that the work submitted is my own. The contribution by co-authors was as follows:

Callum Roberts, Julie Hawkins and Bryce Stewart: Supervision, review and editing.
Lowri Evans, Sarah Pickup and Tim Cross: Assistance in the field

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Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve

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Abstract: *This study investigated the changes within a recently established, fully protected marine reserve on benthic communities and fish populations in Lamlash Bay, Isle of Arran, United Kingdom over a four year period. A combination of photo and diver surveys found live maerl, macroalgae, sponges, hydroids, feather stars and eyelash worms to be significantly more abundant within the marine reserve than on surrounding fishing grounds. Likewise, the overall composition of epifaunal communities ins and outside the reserve was significantly different. Both results are consistent with the hypothesis that protecting areas from fishing can encourage seafloor habitats to recover. In addition, the greater abundance of complex habitats within the reserve appeared to providing nursery habitat for juvenile cod and scallops. In contrast, there was little difference in the abundance of mobile benthic fauna between the reserve and outside. Similarly, the use of baited underwater video cameras revealed no difference in the abundance and size of fish between the reserve and outside. Limited recovery of these ecosystem components may be due to the relatively small size (2.67 km^2) and young age of the reserve (5 years), both of which might limit the extent of any benefits afforded to mobile fauna and fish communities. Overall, this study suggests that fully protected marine reserves can encourage seafloor habitats to recover, which in turn, can create a number of benefits that flow back to species of commercial importance. This study therefore emphasizes the important role marine reserves can play in the ecosystem-based management of fisheries.*

Keywords: Recovery, benthos, megafauna, epifauna, nursery habitat, marine protected area, ecosystem based fishery management

Introduction

A recent surge in environmentally focused films, documentaries and campaigns have caused the environmental impacts associated with exploitation of marine resources to come under close scrutiny by scientists, policy makers and the general public (Stewart 2007; Clover 2009; Psihoyos 2009; Channel 4 2010, 2013). Closing areas to some or all types of fishing through the implementation of marine protected areas (MPAs) and marine reserves is becoming a common approach to conserve marine biodiversity, ecosystem services and fisheries resources (Wood et al. 2008; CBD 2011; Harrop 2011; Wood 2011; Fenberg et al. 2012; Metcalfe et al. 2013). With the global coverage of MPAs set to increase rapidly over the next decade (CBD 2011), the growing use of MPAs as a management tool has co-occurred with a push towards "ecosystem-based fishery management"; with many scientists arguing that we need to shift away from traditional single-species management, to more holistic approaches where management priorities begin with the ecosystem rather than the target species (Pikitch et al. 2004; Zhou et al. 2010). To help guide these changes in management, it is important to better understand how MPAs promote the process of recovery within marine ecosystems (Van Rein et al. 2009; Götz et al. 2013).

Of all fishing methods, the use of mobile fishing gears such as dredges and trawls is considered to be the most damaging to marine ecosystems (Collie et al. 2000; Kaiser et al. 2006). This is because they cause substantial physical disruption of seafloor habitats by ploughing sediments and fragmenting the biogenic structure of epifaunal organisms such as hydroids, bryozoans and maerl beds (Eleftheriou & Robertson 1992; Dayton et al. 1995; Jennings & Kaiser 1998; Kaiser et al. 2000; Jennings et al. 2001). However, these organisms are functionally important to marine ecosystems as they provide an element of 3-dimensional structure to the seafloor. In doing so, they supply important refuges for small / juvenile fish from predators and unfavourable environmental conditions (Monteiro et al. 2002; Ryer et al. 2004; Cacabelos et al. 2010), represent important feeding sites for fish and invertebrates (Bradshaw et al. 2003; Warren et al. 2010) and provide essential habitat for the settlement of scallop spat and a range of other organisms, including the settlement of further epifauna (Bradshaw et al. 2001; Howarth et al. 2011). Such locations are therefore often referred to as "nursery habitats" as they tend to be highly productive, support high levels of juvenile density, growth and survival, and contribute disproportionally to the production of adult recruits (Beck et al. 2001; Gibb et al. 2007; Laurel et al. 2009). Commonly cited nursery habitats include maerl beds (Kamenos et al. 2004b, 2004a; Hall-Spencer et al. 2006), seagrass beds (Warren et al. 2010) and areas of dense macrophytes / macroalgae (Christie et al. 2007; Cacabelos et al. 2010; Howarth et al.

2011), all of which have been shown to harbour high densities of commercially exploited species such as spider crabs, *Maja squinado,* juvenile cod, *Gadus morhua*, edible crab, *Cancer pagurus*, and edible sea urchins, *Echinus esculentus* (see references above). Consequently, the damage sustained by nursery habitats from fishing gears can dramatically reduce an area's capacity to support biodiversity and negatively impact the recruitment of commercially important species (Collie et al. 1997; Bradshaw et al. 2001, 2003; Kaiser 2005).

As well as damaging seafloor habitats, mobile fishing gears often capture a wide variety of non-target organisms, which can include species targeted by other fisheries (Bradshaw et al. 2001; Craven et al. 2013). The majority are discarded damaged, dying or dead (Beukers-Stewart et al. 2001; Jenkins et al. 2001). In addition to by-catch, a large proportion of organisms are killed or damaged by passing gears but remain on the seafloor uncaptured (Jenkins et al. 2001). Both of these impacts can cause a decline in the abundance of target and non-target organisms (Currie & Parry 1996; Bradshaw et al. 2001; Lambert et al. 2011). Paradoxically, some species are attracted to areas that have been fished and consequently increase in abundance. In disturbing the sediment, damaging / killing organisms and generating by-catch / discards, the local density of scavengers and predators can increase by up to 200 times in fished areas (Veale et al. 2000; Kaiser & Hiddink 2007), elevating predation pressure (Ramsay & Kaiser 1998), particularly on injured individuals (Veale et al. 2000; Jenkins et al. 2004). However, due to the dispersion of odour plumes, resettlement of sediment and predation of damaged organisms, the high densities of scavengers gathering at fishing grounds is likely to be a relatively short-lived event. Then again, Bradshaw *et al*. (2002) found that the abundance of mobile, robust, and scavenging invertebrate species in the Irish Sea had increased over a 60 year period of increasing fishing pressure, while slow-moving or sessile, fragile taxa had decreased. Likewise, a study in the Isle of Man found the density of scavenging dog fish to substantially increase over a 14 year period, whereas the density of slow-growing yet commercially important monkfish decreased (Craven et al. 2013).

It is widely known that fishing can cause the structure and function of marine ecosystems to change. The degree of this change tends to vary with different seabed types, levels of background disturbance, local hydrography, fishing intensity and the characteristics of the ecological community (Kaiser et al. 1996; Auster et al. 1996; Bradshaw et al. 2001). In general, the majority of studies report that ecological communities in areas subject to high levels of fishing effort shift from one state to another, going from diverse communities containing fragile and slow growing organisms, to ones dominated by a handful of opportunistic, fast growing species that are comparatively much more resistant to fishing disturbance (Currie & Parry 1996; Bradshaw et al. 2001; Lambert et al. 2011; Brown 2013; Howarth et al. 2013). Since closing areas to fishing is the surest way of protecting marine ecosystems from the physical impacts of fishing gears (Beukers-Stewart et al. 2005; Roberts et al. 2005), MPAs should provide the best management tool available for encouraging their recovery. However, the implementation of MPAs is still at a very early stage in most parts of the world, including the United Kingdom (UK - Fenberg et al. 2012; Metcalfe et al. 2013) and their effectiveness as a fishery management tool is highly debated (Boersma and Parrish, 1999; Jones, 2007; Kaiser, 2004, 2005; Sciberras *et al.*, 2013). This is because establishing MPAs can displace fishing effort to surrounding areas (Bohnsack 2000; Kaiser 2005), which can cause wider environmental damage (Dinmore et al. 2003) and reduce profits through the loss of fishing grounds (Rassweiler et al. 2012). Hence, MPAs only truly yield fishery benefits when these negative effects are adequately offset by increased recruitment and landings.

In September 2008, Scotland's first fully protected marine reserve was established in Lamlash Bay, Isle of Arran, UK, prohibiting all fishing within the reserve under the Inshore Fishing (Scotland) Act of 1984 (Axelsson et al. 2009). The Firth of Clyde, in which the Isle of Arran sits, is known to be one of the most degraded marine environments in the UK, primarily due to over a century of intensive fisheries exploitation (Thurstan & Roberts 2010; Howarth et al. 2013). The marine reserve was therefore passed by Scottish parliament under the rationale that the reduction in fishing pressure should help regenerate the local marine environment and enhance commercial shellfish and fish populations. Hence, our study sought to test the hypotheses that: (1) the abundance of benthic and fish assemblages were higher within the reserve than outside; (2) fish were larger within the reserve; (3) fish assemblages were positively related to the abundance of complex habitat; and (4) complex habitats were more abundant within the reserve. This was achieved by conducting a series of quantitative diver visual, photo and video surveys within and outside the reserve over a four-year period.

Methods

Study Area

We conducted our study in and around Lamlash Bay on the south-eastern shore of the Isle of Arran, off the west coast of Scotland in The Firth of Clyde. Lamlash Bay Marine Reserve covers 2.67 km^2 (Thurstan & Roberts 2010), with water depths ranging between 0 and 29 m below chart datum, but reaching as deep as 43 and 50 m outside to the east and the west of the reserve, respectively (Admiralty Chart 1864; Baxter *et al*. 2008). Previous surveys (Duncan

2003; Axelsson et al. 2009) indicated a seabed of mixed sediments (i.e. mud, sand and gravel with various proportions of shell) but that the central and southern regions of the bay tend to be characterised by softer sediment, mainly muddy sand. In addition, the area has long been identified as containing important maerl beds, although recent evidence points to deterioration in their health (Howarth *et al*. 2011).

Unofficial observations made by the Community of Arran Seabed Trust (www.arrancoast.com) indicate fishing effort has been consistently low in unprotected parts of Lamlash Bay during recent years, averaging at 2-4 trawling / scallop vessels operating within the area per year since 2008. However, several static fishermen (i.e. employing fish pots) targeting lobster and crab routinely operate in the area, in addition to a small team of commercial scallop divers. Although these latter fishing methods cause little direct damage to the seafloor, they can alter ecosystems by removing large numbers of targeted species (Eno et al. 2001).

Data collection

Diver and Photo Transects

We began monitoring Lamlash Bay in the summer of 2010 (see Howarth *et al*. 2011; Howarth *et al*. in review). Initially 40 sites were surveyed, half within the reserve and half outside (Figure 1). These surveys were then repeated and expanded in the summers of 2011, 2012 and 2013 by adding more survey methods but reducing the number of study sites. Therefore, we surveyed 28 sites in 2011, 31 sites in 2012, and 32 sites in 2013. Again, sites were divided so that half fell within the boundaries of the marine reserve. Sites were chosen so that each one within the reserve could be paired with at least one other suitable control outside, based on similar depth and predominant substrate type (Appendix 1-4). Due to lack of data and prior knowledge of the area, the initial experimental design was relatively imbalanced. For example, 12 deep muddy sand sites were surveyed outside the reserve in 2010 compared to just 6 inside. However, this improved with every survey, and by 2012, our experimental design was balanced. Sites were limited to areas of the seabed shallow enough to remain within diver no decompression limits after a 25 minute survey (i.e. <30m depth). Surveys were also conducted parallel to depth contours to ensure the depth of a single survey did not change by more than 3m.

Transects were surveyed along a 50 m leaded line laid out straight across the seabed. Weighted anchors at each end held the line in place, in addition to two floating buoys which reached the surface. A team of two divers then made their way from one end to the other, recording the abundance of all megafauna (e.g. fish and crustaceans) encountered within 1.5 m either side of the transect, the width of which was marked by a 3m long pole which the divers pushed ahead of themselves This gave a total survey area of 150 m^2 for each dive transect. After a surface interval of approximately two hours, divers returned to the transect line and placed a 1 m^2 quadrat parallel to the transect, but at a distance of 2 m from the leaded line, thereby ensuring the area about to be photographed had not been disturbed by the line or the previous survey. The quadrat was divided into four 0.25 m^2 sub-quadrats which were photographed from directly overhead. This process was repeated every 5 m along the transect, giving a total of 40 images for each transect. Sub-quadrats were later combined for statistical analysis, giving a total of 10 quadrats for each transect.

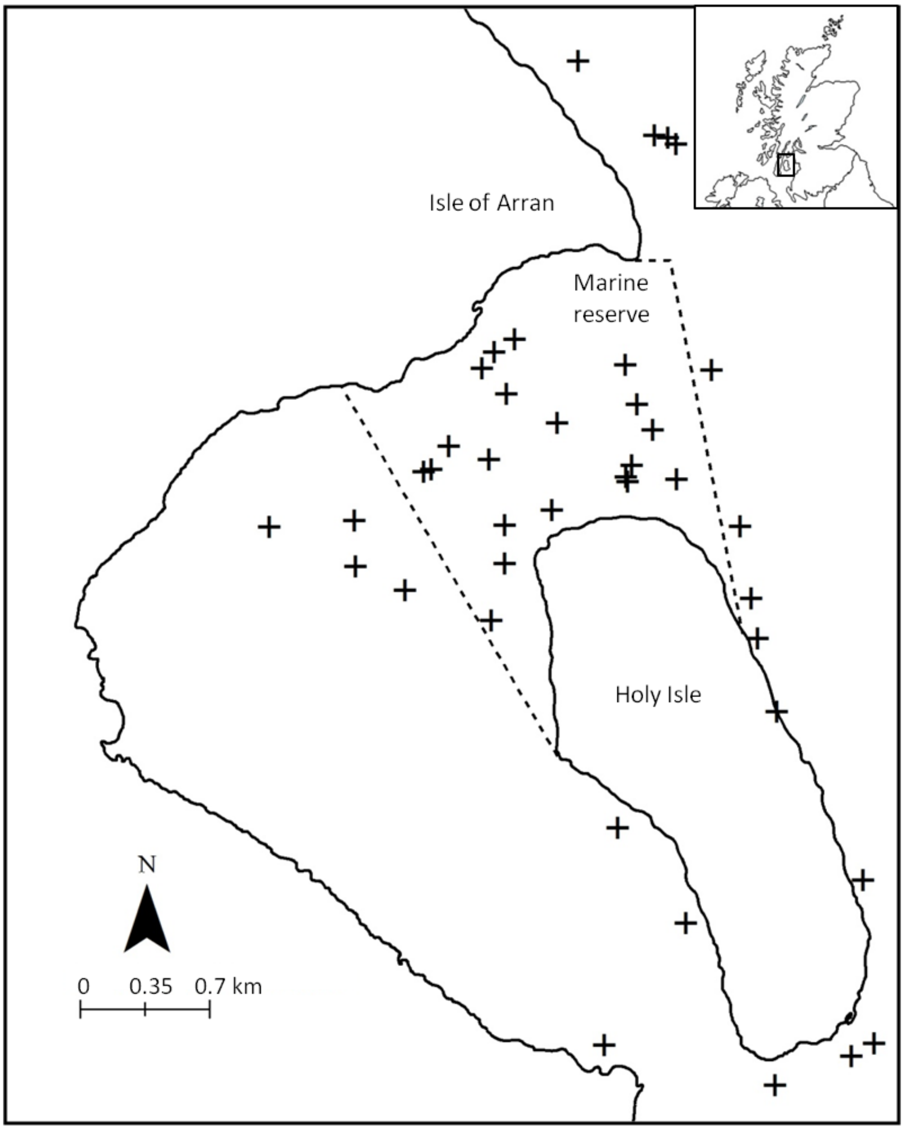

Figure 1. Site locations of dive transects for all years. Also displayed are the boundaries of the Lamlash Bay fully protected marine reserve. The inset shows the location of the Isle of Arran off the west coast of Scotland, United Kingdom.

Still Image Analysis

Photoquadrats were analysed using the software Coral Point Count with Excel Extensions (CPCe) v 4.1 (Kohler & Gill 2006). The quadrat border was positioned and sized manually before overlaying 50 stratified points (10 rows x 5 columns containing 1 point each) which were randomly generated for every image. Any organism lying under a point was then identified to species level where possible. If there was no organism, the substrate type was identified instead (i.e. mud, pebble, cobble, boulder or detritus). Initial attempts used just 25 points and 40 images but the seafloor within Lamlash Bay contained such a low proportion of benthic fauna that the likelihood of a randomly distributed point falling upon anything other than bare substrate was very low. Hence, the number of points was doubled and the number of images for each site halved.

Baited Remote Underwater Video (BRUV)

At the same time as the diver surveys, a BRUV was deployed at each site between the hours of 09.00-14.00 for the surveys conducted in 2011, 2012 and 2013. For these, a video camera was fitted to one end of a commercial lobster pot frame and a porous bait box was fitted to the other. Two video lights provided lighting. Rope was spliced to all four corners of the frame and joined at the centre along with three cork floats to prevent the ropes from sinking into view of the camera. As baseline surveys in 2010 indicated that fish abundance was relatively low, 200g of coarsely cut mackerel was placed inside the bait box prior to deployment in order to attract fish from a wider area. Once recording began, a 40m long rope and surface marker buoy were attached to the frame and the BRUV was carefully lowered to the seafloor. The system’s negative buoyancy ensured the BRUV landed upright and remained in a stable position. After approximately one hour, the BRUV was hauled back to the boat, the bait replaced, and the BRUV was ready for redeployment at another site.

Video Analysis

To standardise video lengths, analysis began from two minutes after the BRUV landed on the seabed and terminated 60 minutes later. For each video the following variables were recorded for all fish: (*i*) identity and total number of species; (*ii*) total number of families; (*iii*) time of first appearance for each species; (*iv*) maximum number of individuals for each species observed within the same frame (MaxN). Due to the inability of an observer to recognise repeated entrances of the same individual, MaxN was used as an indiciator of abundance (Cappo et al. 2004); (*v*) time of MaxN; and (*vi*) the body length (for fish) or carapace width (for crustaceans) of all individuals at MaxN that faced side-on to the camera and were aligned between the two front posts of the BRUV frame. This was estimated by using 10 mm reference markers which were painted on the front frame of the BRUV.

Data Analysis

Benthic Epifauna

Data on the percentage cover of epibenthic organisms were extracted from CPCe. These taxa included anemones (e.g. *Ceriaanthus lloydi*), soft corals (e.g. *Alcyonium digitatum*), hydroids (e.g. *Nemertesia ramosa*), sponges (e.g. *Cliona celata*), tunicates (e.g. *Corella paralellogramma*) and macroalgae (e.g. *Laminaria hyperborea*). The percentage of epifaunal taxa and bare substrate were tested for differences between treatments (i.e. in or outside the reserve) and years using simple line plots. Any trends were tested for significance with a two-way Analysis of Variance (ANOVA) using treatment and year as factors. The DIVERSE function within the software package PRIMER v6 (Clarke & Gorley 2006) was then used to generate univariate measures of biodiversity such as total number of species, total number of individuals, Pielou's evenness and Shannon's biodiversity. Again, these were plotted in line graphs and any trends were tested using two-way ANOVA (as above).

A resemblance matrix using the Bray-Curtis similarity measure (Bray & Curtis 1957) was created in PRIMER and a Permutational Multivariate Analysis of Variance (PERMANOVA+) was conducted to test for differences in epifaunal community composition. The analytical design had four factors: Year (fixed: 2011, 2012, 2013), Treatment (fixed: reserve, outside), Depth (fixed: shallow <15 m and deep >15 m), and Substrate (fixed: soft, maerl and hard). Soft substrates referred to muddy, sandy and gravelly seabeds, whilst hard substrates referred to sites containing cobbles and boulders. Each term in the analyses used 9999 permutations. Any significant multi-level interactions were further explored using PERMANOVA+ pairwise tests. PERMANOVA was considered to be an appropriate test as it is robust to datasets with many zeros, and allows the testing of interactions in complex multifactorial designs. It has significant advantages over conventional MANOVA in that it makes no assumptions about underlying data distributions and is robust to unbalanced survey designs, as is the case with this study (Anderson & Ter Braak 2003). Visualisation of the similarity matrices was achieved using non-metric Multi-Dimensional Scaling (nMDS). Additionally, a Similarity Profile (SIMPROF) routine was used to highlight if any alternative *a posteri* groups existed within the data. Finally, a Similarity of Percentages (SIMPER) was performed to determine the contribution of individual species to the average dissimilarity between treatments.

Benthic Megafauna

The total number of species, individuals, Pielou's evenness and Shannon's biodiversity of benthic megafauna observed during the diver transects were tested between treatments and years using line plots, and by using two-way ANOVAs if appropriate. In addition, the density of the 10 most abundant species was also investigated for differences between years and treatments by creating stacked bar charts and using two-way ANOVAs if appropriate. PERMANOVA+ was then used to test for differences in overall community composition using the same analytical design as before.

Fish Assemblages

The abundance of dog fish (*Scyliorhinus canicula*), gurnards (Family: Triglidae), flat fish (Family: Pleuronectidae), wrasse (Family: Labridae), gobies (Family: Gobiidae), cod and other gadoids (i.e. saithe - *Pollachius virens*, pollack - *Pollachius pollachius*, whiting - *Merlangius merlangus*, haddock - *Melanogrammus aeglefinus*, and poor cod - *Trisopterus minutus*) observed during the BRUV surveys were tested for differences between treatments and years using line graphs and two-way ANOVAs. Additionally, the total number of species, individuals, Pielou's evenness and Shannon's biodiversity were also tested in the same way. The mean size of fish were then combined across all years (due to small sample size) and plotted in bar charts. Any differences between treatments were tested for significance using one-way ANOVAs.

To determine whether environmental and ecological data affected the distribution and abundance of cod and other gadoids, negative binomial Generalised Linear Models (GLM) were created. Predictor variables used in the GLMs were treatment, depth, the abundance of crustaceans and echinoderms, and the percentage cover of bare substrate, bryozoans, soft coral, hydroids, macroalgae, sponges, tunicates, and dead and live maerl. Before construction of a GLM, scatter plot and intercorrelation matrices (based upon Spearman's rank correlation) were created to explore basic relationships and determine whether any variables were strongly intercorrelated (i.e. $-0.7 \geq r \leq 0.7$) as such variables would not be allowed together within a GLM (Crawley 2005). The percentage cover of macroalgae was found to be negatively intercorrelated with depth and the percentage cover of bare substrate. Therefore a total of four GLMs were constructed, two testing cod abundance (one including macroalgae and the other including bare substrate and depth) and two testing the abundance of other gadoids (same design as before). Backward-forward stepwise reductions were then conducted to create minimal adequate models. Diagnostic and Cleveland dotplots were then used to explore how well the models fitted the data and to identify any extreme outliers. Lastly, analyses of deviance utilising Pearson's Chi-square test (χ^2) were conducted to determine if the reduced models accounted for significantly less variance than the full models.

Results

Composition of Benthic Epifauna

A total of 77 different epibenthic species were recorded from the photoquadrat surveys. Overall, the mean number of species (Figure 2) was significantly greater within the reserve than surrounding areas (Table 1) as was the percentage cover of live maerl, sponges, hydroids, macroalgae and all epifaunal species combined. The percentage cover of these different taxa were found to be between 2 - 4 times greater within the reserve than in neighbouring fishing grounds. In many cases, their abundance within the reserve appeared to increase over the survey period but there was no significant interaction between year and protection across all taxa. In contrast to epibenthic abundance, the percentage cover of bare substrate was significantly lower within the reserve than outside. Two-way ANOVAs were not conducted for Pielou's eveness, Shannon's diversity index and the percentage cover of soft coral, anemones, bryozoans and tunicates, as line plots indicated no difference between the reserve and outside.

PERMANOVA+ analysis revealed the composition of the epibenthic community to significantly differ between treatments, depth and year (Table 2). The interaction protection x depth was also found to be significant and subsequent pairwise testing showed that differences between the reserve and outside only existed for sites located at shallow depths. Exploring these differences further, nMDS of shallow sites in 2011 revealed substantial variation in community composition between the reserve and outside (Figure 3a). Consequently, SIMPROF could not distinguish samples from within and outside the reserve ($P > 0.05$) and clustered them all together. However, nMDS of shallow sites sampled in 2013 revealed that epibenthic communities located within the reserve had become comparatively more distinguishable from communities located outside (Figure 3b). Therefore, in contrast to 2011, SIMPROF detected statistical differences between treatments ($P < 0.05$) and clearly separated sites located within the reserve from sites located outside.

SIMPER analysis also found strong differences between the reserve and outside (Table 3). Sites were characterised by a similar range of species, however sites within the reserve were characterised more strongly by bushy red seaweeds (*Heterosiphonia plumose*), kelps (*Lamanaria saccharina* and *Lamanaria hyperborea*), thin branching brown seaweeds, and upright hydroids (*Nemertesia antennia*), whereas sites outside the reserve were characterised more strongly by red algal turf and burrowing anemones (*Cerianthus lloydi*). Overall, the reserve was characterised by 10 species, whilst sites outside the reserve were characterised by just 7, suggesting sites outside the reserve were dominated by a smaller set of species.

Table 1. Two-way ANOVA comparing the total number of species and percentage cover by different epifaunal assemblages between the marine reserve and outside across the years 2011-2013. Significant results are denoted by (*).

Source	Test	SS	*df*	MS	*F*	*P*
No of species	Year	370.3	2	185.1	5.86	*0.004
	Protection	403.8	1	403.8	12.78	*0.001
	Year * Protection	60.2	2	30.1	0.95	0.39
	Residual	2558.3	81	31.5		
Total epifauna	Year	7476.9	1	7476.9	14.40	0.381
	Protection	1012.7	2	506.3	0.97	*0.002
	Year * Protection	53.4	2	26.7	0.05	0.95
	Residual	42559.6	82	519		
Bare substrate	Year	7037.5	1	7037.5	13.81	0.384
	Protection	986.6	2	493.3	0.96	*0.004
	Year * Protection	52.1	2	26.1	0.051	0.95
	Residual	41775.5	82	509.4		
Live maerl	Year	11.1	1	11.1	5.77	0.859
	Protection	0.5	2	0.2	0.15	*0.019
	Year * Protection	0.9	2	0.4	0.24	0.783
	Residual	158.6	82	1.9		
Macro algae	Year	3720.3	1	3720.3	7.9	0.852
	Protection	1507	2	75.3	0.16	*0.006
	Year * Protection	114.5	2	57.2	0.12	0.886
	Residual	38604.8	82	470.7		
Sponge	Year	0.3	1	0.3	8.7	0.148
	Protection	0.1	2	0.07	1.95	*0.004
	Year * Protection	0.07	2	0.03	0.95	0.388
	Residual	3.2	82	0.03		
Hydroids	Year	40.3	1	40.3	3.71	0.053
	Protection	66.3	2	33.1	3.05	*0.048
	Year * Protection	17.8	2	8.9	0.82	0.444
	Residual	891.8	82	10.8		

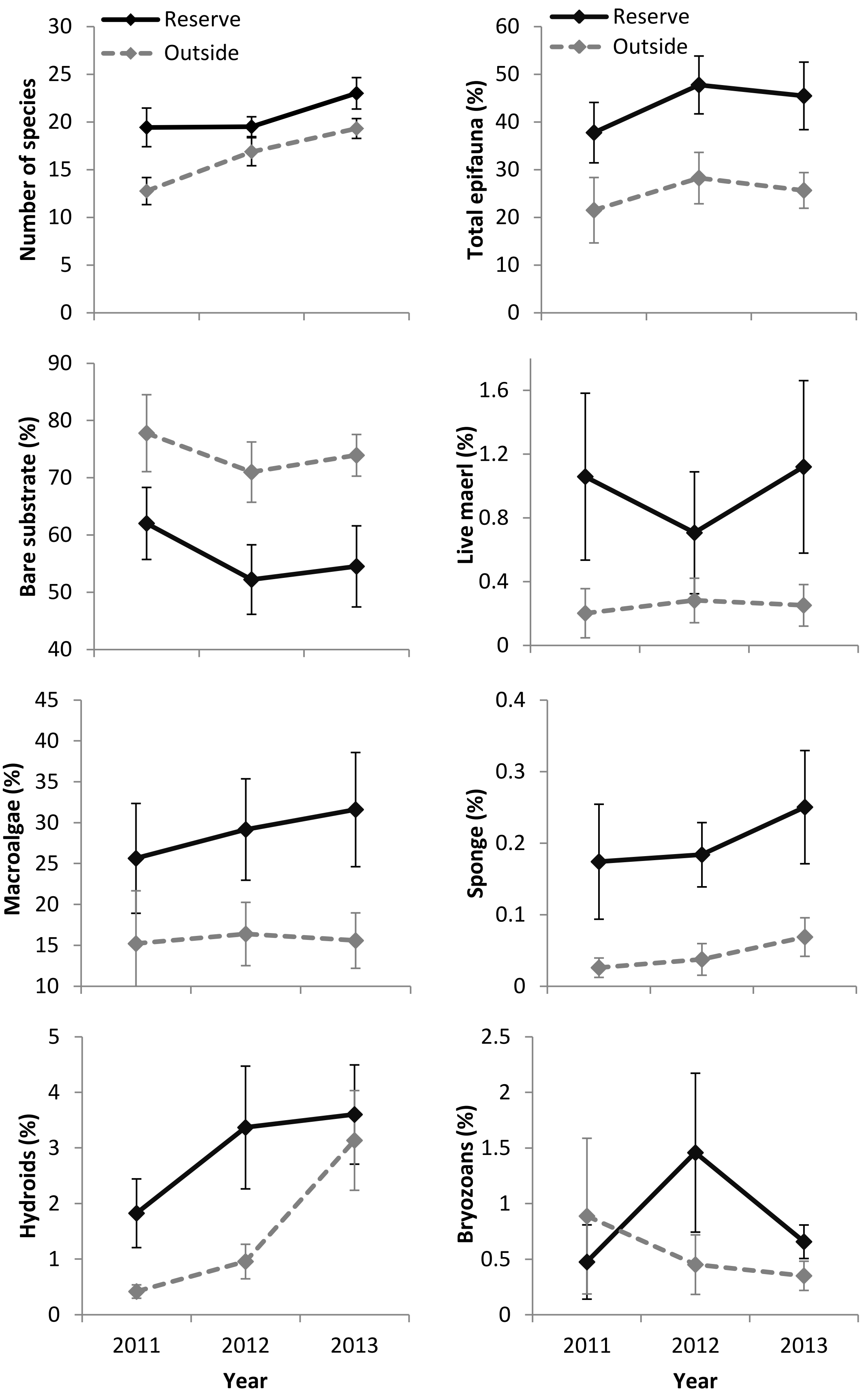

Figure 2. The total number of species and percentage cover of the seafloor by different epifaunal assemblages recorded by photoquadrat surveys across three years. Error bars represent ±1 SE.

Table 2. Results from the PERMANOVA+ analysis of epibenthic community composition. a) Main test and b) pairwise testing for the interaction Protection x Depth. Pr = level of protection, De = depth, Ye = year, Su = substrate, Out = sites outside the reserve, Res = sites within the reserve.

a)

Source	*df*	SS	MS	*F*	*P*
Pr	1	7549.2	7549.2	3.28	*0.001
De	1	26222	26222	11.4	*0.001
Ye	2	11581	5790.3	2.51	*0.002
Su	2	14321	4680.1	0.48	0.576
PrxDe	1	7826.7	7826.7	3.4	*0.002
PrxYe	2	5011.8	2505.9	1.08	0.356
PrxSu	2	4625.1	2762.6	0.99	0.45
DexYe	2	4505.1	2252.6	0.97	0.46
DexSu	2	4115.1	2992.2	0.98	0.47
YexDe	3	5175	1725.1	0.97	0.492
YexSu	6	1031	1719.4	0.96	0.562

b)

	Shallow		**Deep**	
Groups	t	*P*	t	*P*
Out, Res	2.4	*0.001	1.09	0.285

Table 3. Results from the SIMPER analysis of epibenthic communities sampled in shallow sites within and outside the marine reserve in 2013. This analysis was conducted after a PERMANOVA+ indicated an interaction between protection and depth (see Table 2).

Treatment	Taxon	Average abundance	% contribution	Cumulative %	Overall similarity
Outside	Red algal turf	5.36	30.13	30.13	34.38
	Heterosiphonia japonica	3.85	20.85	50.98	
	Cerianthus lloydi	4.43	15.45	66.44	
	Filamentous brown seaweeds	2.49	12.31	78.74	
	Laminaria saccharina	1.87	8.47	87.22	
	Laminaria hyperborea	1.04	2.68	89.89	
	Dark encrusting reds	2.07	1.92	91.81	
Reserve	*Heterosiphonia japonica*	20.1	40.43	40.43	42.26
	Filamentous brown seaweeds	7.24	16.11	56.54	
	Laminaria saccharina	6.64	8.7	65.24	
	Nemertesia antennia	7.17	5.78	71.02	
	Heterosiphonia plumosa	4.98	4.87	75.88	
	Laminaria hyperborea	3.42	3.94	79.82	
	Dark encrusting reds	1.61	3.72	83.54	
	Red algal turf	3.54	3.04	86.58	
	Thin branched browns	2.99	2.85	89.43	
	Cerianthus lloydi	3.94	2.22	91.64	

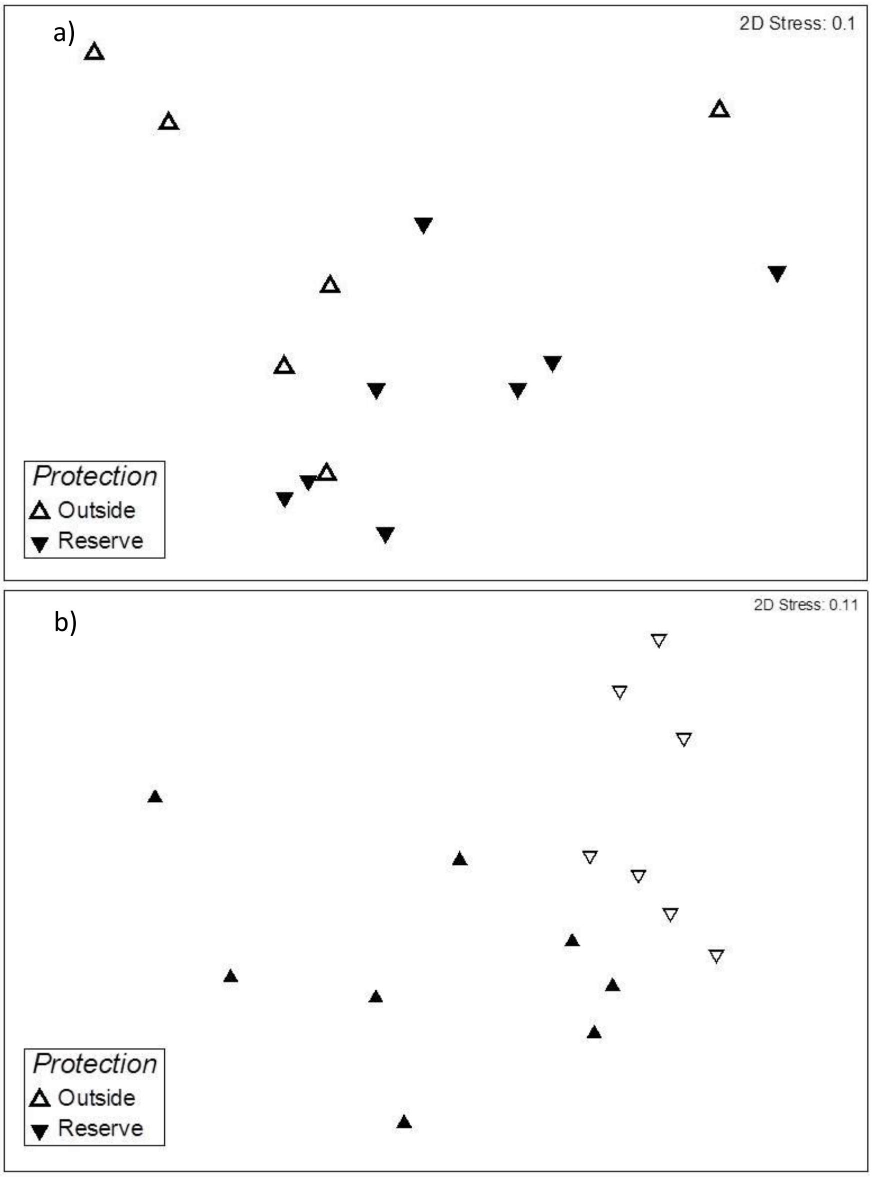

Figure 3. nMDS plots illustrating similarities in epibenthic assemblages between shallow sites (< 15 m depth) within and outside the marine reserve sampled in 2011 (a) and 2013 (b).

Composition of Benthic Megafauna

A total of 50 different benthic megafaunal species were recorded from the dive transects. Overall, the 10 most abundant species in descending order were hermit crabs (*Pagurus* spp), feather stars (Crinoidea), harbour crabs (*Liocarcinus depurator*), king scallops (*Pecten maximus*), common starfish (*Asterias rubens*), parchment worms (*Chaetopterus* spp), queen scallops (*Aequipecten opercularis*), cushion stars (*Porania pulivillus*) and decorator crabs (*Macropodia* spp). Graphs were created to see how the abundance of these taxa changed over time, however, as the population dynamics of king and queen scallops have already been explored elsewhere (see Howarth et al. In review) the abundance of spiny starfish

(*Marthasterias glacialis*) and eyelash worms (*Myxicola infundibulum*) were explored instead (i.e. the 11th and 12th most abundant species respectively).

Separating taxa into mobile and sessile groups revealed little difference in the abundance of mobile megafauna between the reserve and outside, and over time (Figure 4a). In contrast, both feather stars and eyelash worms were significantly more abundant within the reserve than outside (Table 4), and although their abundance appeared to increase over the survey period (Figure 4b), no significant interaction was found between year and protection. However, the total number of megafauna species did significantly increase during the study period and was significantly greater within the reserve than outside (Table 4). Line plots revealed little difference in the total number of individuals, evenness and biodiversity between the reserve and outside and therefore were not tested for significance using two-way ANOVA.

PERMANOVA+ analysis revealed the composition of the benthic megafauna community to significantly differ between depths, year and substrates but not between treatments (Table 5). The interaction between protection and substrate was also found to be significant, and subsequent pairwise testing revealed that differences between the reserve and outside existed for maerl, soft and hard substrates. However, further exploration of these differences using nMDS and SIMPROF did not clearly distinguish between sites located within and outside the reserve ($P > 0.05$). Although, SIMPER did suggest that maerl, soft and hard substrates within the reserve were more strongly characterised by eyelash worms and feather stars.

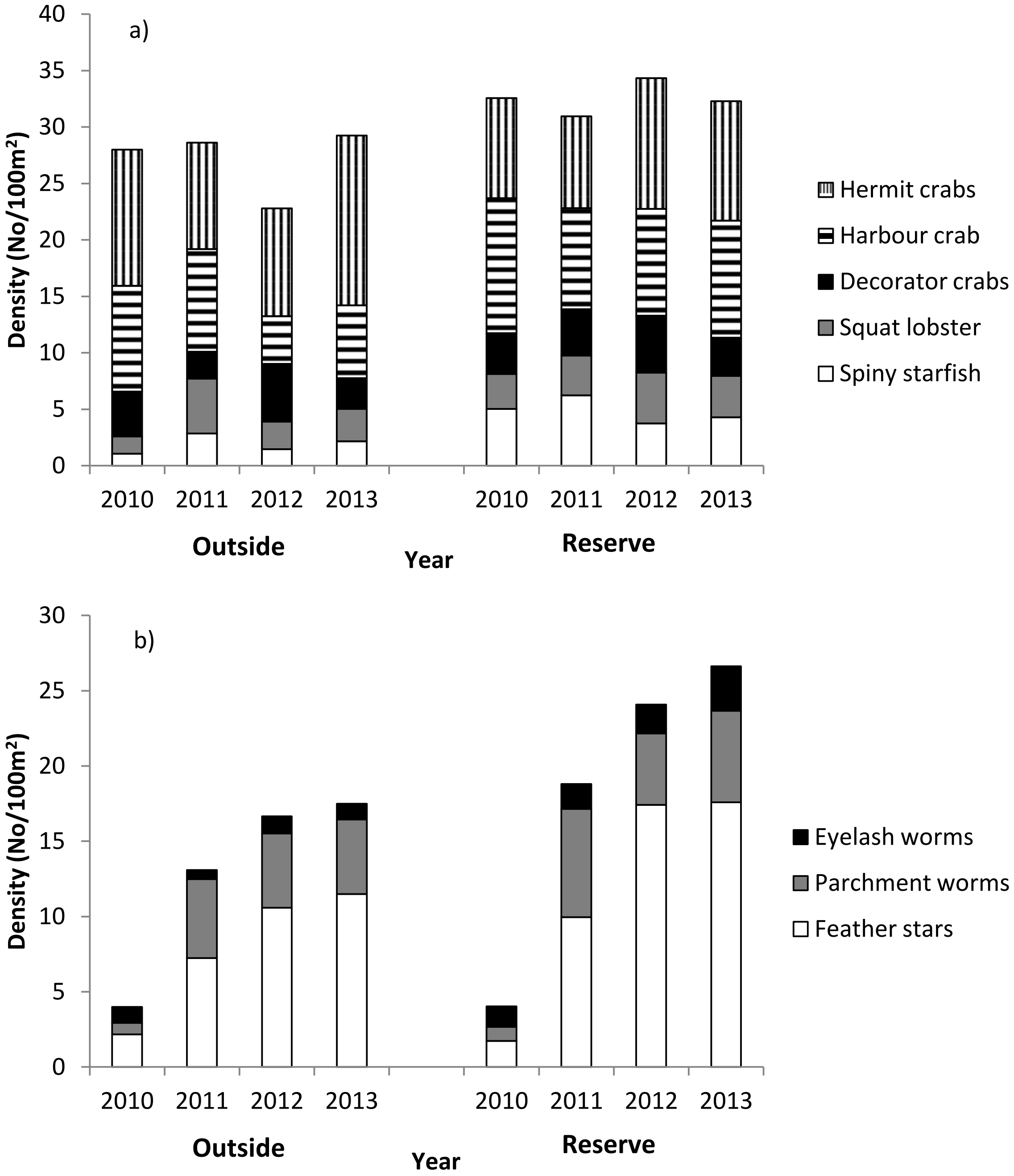

Figure 4. The density of the 10 most abundant benthic megafaunal species across the years 2010-2013 split between mobile (a) and sessile (b) species.

Table 4. Two-way ANOVA comparing the density of different benthic fauna between the marine reserve and outside across the years 2010-2013. Significant results are denoted by (*).

Source	Test	SS	*df*	MS	*F*	*P*
Feather stars	Year	711.5	1	711.5	0.60	0.103
	Protection	7498.4	3	2499.5	2.10	*0.041
	Year * Protection	525.6	3	175.2	0.15	0.931
	Residual	146213.4	123	1188.7		
Eyelash worms	Year	73.4	1	73.4	5.35	0.494
	Protection	33.0	3	11.0	0.80	*0.022
	Year * Protection	27.1	3	9.0	0.66	0.579
	Residual	1686.7	123	13.7		
Parchment worms	Year	5.1	1	5.1	0.14	*0.002
	Protection	1677.4	3	559.1	15.14	0.711
	Year * Protection	71.7	3	23.9	0.65	0.586
	Residual	4542.5	123	36.9		
No of species	Year	55.1	1	55.1	5.70	*0.018
	Protection	436.9	3	145.6	15.06	*0.001
	Year * Protection	11.2	3	3.7	0.39	0.764
	Residual	1189.2	123	9.7		

Table 5. Results from the PERMANOVA+ analysis of benthic megafaunal community composition. a) Main test and b) pairwise testing for the interaction Protection x Substrate. Pr = level of protection, De = depth, Ye = year, Su = substrate, Out = sites outside the reserve, Res = sites within the reserve.

a)

Source	*df*	SS	MS	*F*	*P*
Pr	1	1908.2	1908.2	1.07	0.382
Ye	3	13076	4358.8	2.45	*0.001
De	1	6393.1	6393.1	3.60	*0.001
Su	2	10692	5346.1	3.01	*0.001
PrxYe	3	5284.8	1761.6	0.99	0.488
PrxDe	1	1661.3	1661.3	0.94	0.503
PrxSu	2	5476.3	2738.2	1.54	*0.039
YexDe	3	5175.3	1725.1	0.97	0.492
YexSu	6	10316	1719.4	0.97	0.562
DexSu	2	5466.8	2733.4	1.54	0.054

b)

	maerl		**soft**		**hard**	
Groups	t	*P*	t	*P*	t	*P*
Out, Res	1.3	*0.08	1.5	*0.009	1.4	*0.044

Composition of Fish Assemblages

A total of 1447 individual fish were recorded from the BRUV surveys, these were from 30 different species belonging to 14 different families. Of these individuals, 803 were recorded within the reserve and 644 from outside. Despite more individuals being recorded within the reserve, neither year (Two-way ANOVA; $F_{(1,\ 82)} = 1.6$, $P > 0.05$) nor protection (Two-way ANOVA; $F_{(1,\ 82)} = 2.7$, $P > 0.05$) significantly influenced fish abundance (MaxN). As before, the total number of individuals, evenness and diversity were not tested as line plots revealed no difference between the reserve and outside. Overall, the most common species were all gadoids of which cod were the most abundant (408 observations), followed by whiting (303 observations) and haddock (163 observations). Over 98% of these gadoids were in their juvenile form. In rare cases (4 out of the 82 BRUV surveys), large pelagic shoals of mackerel and sand eels consisting of many hundreds of individuals were recorded.

Exploratory bar plots revealed no difference in the mean size of different fish taxa between sites in and outside the reserve, and therefore no statistical tests were conducted. Comparing the abundance of different taxa over time also revealed little difference between the reserve and outside (Figure 5). However, cod abundance did exponentially increase over the study period but did not significantly differ between the reserve and outside, nor was there an interaction between the two (Table 6). In contrast, the abundance of other gadoids appeared to increase outside the reserve over time and decrease inside. However, neither year, nor protection, nor the interaction between the two were significant.

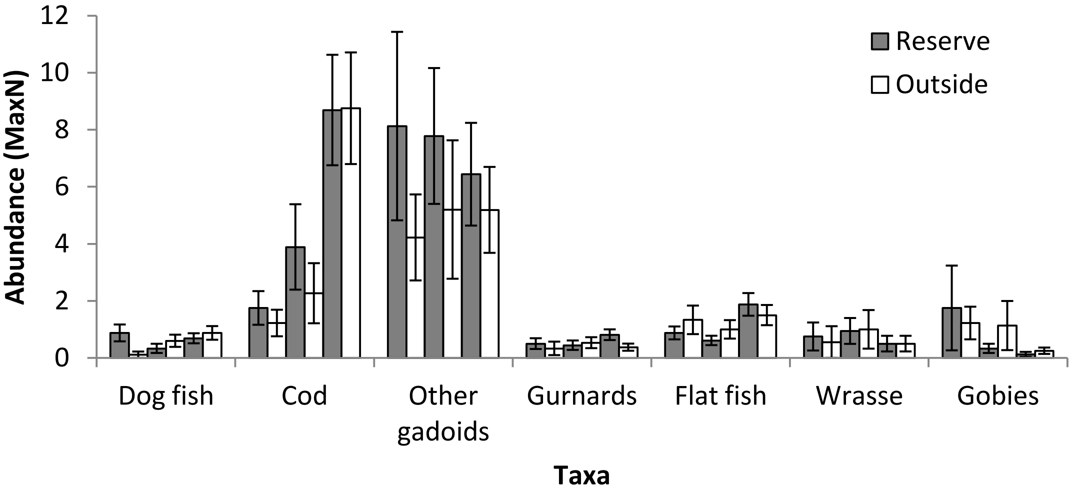

Figure 5. The abundance of a range of fish taxa within and outside the marine reserve across the years 2011-2013. For each taxa, the year increases from 2011, to 2012 and 2013 going from the left to the right.

Table 6. Two-way ANOVA comparing the abundance of cod and other gadoids between the reserve and outside over the years 2011-2013. Significant terms are denoted by (*).

Source	Test	SS	*df*	MS	*F*	*P*
Other gadoids	Year	7.4	2	3.7	0.06	0.946
	Protection	123.6	1	123.6	1.85	0.177
	Year * Protection	20.3	2	10.2	0.15	0.859
	Residual	5068.3	76	66.7		
Cod	Year	772.5	2	386.2	10.59	*0.001
	Protection	9.0	1	9.0	0.25	0.621
	Year * Protection	11.7	2	5.9	0.16	0.852
	Residual	2772.2	76	36.5		

As gadoids are of commercial importance and were the most abundant fish species recorded throughout the BRUV surveys, GLMs were constructed to determine what environmental and ecological factors were important in determining their abundance and distribution. After employing backward-forward stepwise reduction, models indicated that cod abundance was significantly positively associated with year and with the presence of macroalgae and maerl, but was negatively associated with the presence of anemones and echinoderms (Table 7). In contrast, the abundance of other gadoid species was found to be positively associated with the percentage cover of bare substrate, year, treatment and crustacean abundance, but negatively associated with the presence of sponges. A GLM including macroalgae, but excluding depth and the percentage cover of bare substrate, could not be constructed for other gadoid species as the model would not converge, likely because it had insufficient predictive power. In all cases, the reduced models did not explain significantly less variance than the full models (Pearson's Chi-squared; df = 81, $\chi^2 = 0.78$, *P* > 0.05).

Table 7. The reduced models created from a negative binomial GLM to test whether environmental and ecological data reflected the distribution and abundance of cod and other gadoid species. Significant terms are denoted by (*).

Response	Model	Deviance explained	Variable	SE	*Z*	*P*
Cod	Including macroalgae	60.43%	Year	0.24	5.63	*0.001
			Anemones	0.12	-2.29	*0.022
			Echinoderm	0.5	-2.3	*0.019
			Macroalgae	0.28	1.87	*0.041
			Maerl	0.1	2.72	*0.006
Cod	Including bare substrate and depth	71.40%	Year	0.25	5.09	*0.001
			Bare substrate	0.01	-0.48	0.632
			Treatment	0.21	0.435	0.664
			Crustacean	1.13	1.09	0.273
			Sponge	0.84	-1.6	0.11
Other gadoids	Including bare substrate and depth	68.53%	Year	0.16	4.51	*0.001
			Bare substrate	0.01	3.7	*0.001
			Treatment	0.14	2.91	*0.003
			Crustacean	0.73	3.04	*0.002
			Sponge	0.55	-3.16	*0.001

Discussion

The paper highlights a number of differences in ecological communities between the fully protected marine reserve in Lamlash Bay and surrounding fishing grounds. However, it must be stressed that there is no data available prior to the establishment of the reserve. Ideally, a before-after control-impact (BACI) approach would have been employed, capable of definitely proving that differences between the reserve and outside were due to the protection afforded by the marine reserve (Hilborn et al. 2004; Sale et al. 2005). As this was not possible, we instead compared sites within the reserve to reference sites located outside its boundaries over a study period of three to four years. As all of the trends explored in this study showed no interaction between year and protection, all we have is evidence that differences between the reserve and outside exist, but cannot conclude that protection is responsible for creating them.

Overall, we found a large number of differences between the marine reserve and outside. After four years since its establishment, live maerl (348% greater), macroalgae (100% greater), sponges (268% greater), hydroids (15-267% greater), eyelash worms (184% greater), feather stars (52% greater), parchment worms (36% greater) and total epifauna (77% greater) were all found to be significantly more abundant within the reserve than on neighbouring fishing grounds by the end of the study. Whilst the abundance of macroalgae, sponges, hydroids and eyelash worms appeared to steadily increase within the reserve over the duration of the study and remained relatively stable outside, no significant interaction was found. Likewise, nMDS plots and SIMPER analysis suggested an increasing divergence between the epifaunal community in and outside the reserve, but again no significant interaction was found.

The greater abundance of macroalgae within Lamlash Bay Marine Reserve was one of the first observations made when monitoring began in 2010 (Howarth et al. 2011). Several well-known studies have also reported differences in macroalgal abundance between reserves and reference sites (Shears & Babcock 2003; Hawkins & Roberts 2004; Langlois & Ballantine 2005). In all cases, this was due to populations of predators and herbivores recovering within the reserves, thereby altering the grazing rates on macroalgae. This study, on the other hand, did not detect any major trends in herbivore or predator abundance other than for juvenile cod, which exponentially increased in both the reserve and outside over the three year study period. However, as the diet of juvenile cod consists predominantly of copepods and other planktonic crustaceans (Demain et al. 2011) there is unlikely to be a connection. Significantly, an associated study (Howarth et al. In review) found that the greater abundance of macroalgae and hydroids growing within Lamlash Bay Marine Reserve was significantly increasing the settlement levels of juvenile scallops by providing nursery habitat. These results are consistent with the hypothesis that protection can encourage seafloor habitats to recover which can generate benefits that flow back to commercially important species. In the long term, these effects should increase the numbers of juvenile scallops entering the adult stock as a greater proportion of juveniles survive to reach maturity.

It is interesting that live maerl was over 300% more abundant within the reserve as evidence suggests that the recovery of maerl beds should take several decades, due to their extremely slow growth (Giraud & Cabioch 1976; Hall-Spencer & Moore 2000; Foster 2001; Kamenos et al. 2003Grall & Hall-Spencer 2003). As the abundance of live maerl showed no clear signs of increasing over the study period, the greater levels of maerl within the reserve may just be an artefact of maerl being more prevalent within the reserve than outside prior to its establishment. In addition, the abundance of live maerl was very low throughout both study areas, varying between 0 - 8%. These low levels of live maerl contrast greatly with earlier studies of Lamlash Bay (Kamenos et al. 2004c), which detected over 90% live maerl in some maerl beds, suggesting recent degradation in their health. Nonetheless, the reserve should act as a safe haven for any patches of live maerl remaining within the reserve and may encourage their recovery in the future.

In addition to observing differences in specific species, there were also a number of differences in the overall epifaunal community between the reserve and outside. In 2013, four years after the reserve was established, PERMANOVA+ analysis revealed strong differences in community composition between the two treatments for sites located less than 15 m in depth. Shallow sites within the reserve were more strongly characterised by a range of bushy and upright seaweeds and hydroids, whereas sites outside the reserve were more strongly characterised by red algal turf and fast-growing burrowing anemones. Sites outside the reserve are therefore likely to be providing comparatively less structural complexity and may, in turn, be providing a smaller range of ecological niches. However, despite observing broad differences in epifaunal communities, there was no difference in overall community evenness and diversity, or in the abundance of soft coral, anemones, bryozoans and tunicates.

In contrast with the epifaunal community, comparisons between the reserve and outside in the abundance of mobile benthic fauna revealed little difference. This was surprising considering the number of studies that have reported changes in the abundance of scavengers and predators, such as dog fish and star fish, in response to protection (Marino et al. 2007; Brown 2013) and differing levels of fishing disturbance (Veale et al. 2000; Bradshaw et al. 2001; Jenkins et al. 2004; Kaiser & Hiddink 2007; Craven et al. 2013). However, comparisons of the abundance of sessile fauna did reveal several differences between the reserve and outside. Both feather stars and eyelash worms were found to strongly characterise communities sampled within the marine reserve. This was because they were 52% and 184% more abundant within the reserve than outside respectively, although no significant interaction between protection and year was found. These organisms can be important to benthic diversity and commercially valuable species as they provide structural complexity to the seabed, and they can modify local hydrodynamics and influence the vertical and horizontal flux of nutrients (Auster et al. 1995; Thrush et al. 2001; Thrush & Dayton 2002).

Compared to other taxa, relatively few trends were detected in fish populations. The most common species were all gadoids, a group containing commercially important species such as cod, haddock and whiting. Over 98% of these individuals were in their juvenile form, suggesting that Lamlash Bay is providing nursery habitats to several commercially important species. This was confirmed by constructing several models, which found cod abundance to be positively associated with the presence of macroalgae, live maerl and year of study. This came as no surprise as coastal areas containing high levels of kelp, seaweeds and maerl are often reported to support large numbers of juvenile cod (Borg et al. 1997; Kamenos et al. 2004c; Gibb et al. 2007; Laurel et al. 2009; Caddy 2013). Although cod abundance appeared greater within the reserve than outside, this difference was not statistically significant. Likewise, there were no significant differences in mean fish size between inside and outside of the reserve. Nonetheless, in protecting macroalgal and maerl beds, the marine reserve should, to some degree, help boost the early survival of juvenile cod as they make the important transition from pelagic to benthic habitats (Demain et al. 2011). Cod was also found to increase exponentially over the survey period both within and outside the reserve, and is thought to be the result of exceptionally cold winter temperatures in recent years (Sophie Elliott pers. comm). In contrast to cod, models found the abundance of haddock and whiting to be positively associated with the percentage cover of bare substrate, crustacean abundance, and level of protection (likely because more gadoids were detected within the reserve). This was supported by diver observations which regularly reported high levels of whiting and haddock on deep soft / muddy sediments. Stocks of adult finfish (especially cod and other gadoids) are currently at historically low levels in the Clyde (Thurstan & Roberts 2010; Heath & Speirs 2011; McIntyre et al. 2012). Hence, an important area for future research is to establish the origin of these gadoid recruits and whether they are contributing to the recovery of stocks. Unfortunately, there are strong indications that high levels of by-catch from the Clyde *Nephrops* trawl fishery may limit the chances of these fish reaching maturity (Bergman et al. 2002).

One of the most commonly cited results of establishing MPAs and marine reserves has been an increase in fish abundance, biomass and size (Mumby et al. 1995; Hawkins & Roberts 2004; Micheli et al. 2004; Lester et al. 2009; Moland et al. 2013). However, this study found no statistical difference in fish abundance between the reserve and outside. This was likely due to the young age of the reserve (5 years) and its small size (2.67km^2), both of which are known to reduce the effects of marine reserves on mobile fish species (Halpern 2003; Molloy et al. 2009; Edgar et a. 2014). Additionally, when viewing the BRUV footage it was not possible to recognise repeated entrances of the same individual, meaning estimators of abundance had to be used; in this case, the maximum number of fish sighted within a single frame (MaxN). As it is unlikely that all individuals of a species are recorded within the same frame, BRUVs can only detect a proportion of the fish that are attracted to the bait, which can make their estimates relatively conservative (Willis & Babcock 2000; Cappo et al. 2004). This means that any differences detected between sites within and outside MPAs are also likely to be conservative.

More worryingly, recent research has shown little correlation between the abundance estimates generated by MaxN and those created from underwater visual census (Dunlop 2013). Our study also revealed no difference in fish size between the reserve and outside. Again this may be due to the age and size of the reserve, or the method we used to estimate fish size. The use of recently developed technologies, such as stereo video cameras would have generated much more accurate and precise estimates of fish size than those obtained in this study, which would reduce variation and increase the chance of detecting differences in fish size, if they exist (Harvey et al. 2001; Cappo et al. 2004; Langlois et al. 2010).

In summary, we have presented several lines of evidence that suggest Scotland's first and only fully protected marine reserve is potentially being of some benefit to ecological communities. Epifaunal assemblages, such as feather stars, eyelash worms, maerl, sponges, hydroids and macroalgae were all found to be significantly more abundant within the reserve than outside. As well as increasing the structural complexity of the seabed, the greater abundance of these habitats has substantially increased the recruitment of commercially important scallops, suggesting that protecting areas from fishing can generate ecological benefits that flow back to species commercially targeted by fisheries (see also Howarth et al. In review). In contrast, there was no difference in the abundance of mobile benthic fauna and fish populations between the reserve and outside. This may be due to the short duration of protection received to date, the small size of the reserve, and / or the methods used to estimate the abundance and size of fish. Nonetheless, it was revealed that the marine reserve contained significantly more nursery habitat for juvenile cod, which may help boost their early survival as they make the important transition from pelagic to benthic habitats. Overall, our results are consistent with the hypothesis that MPAs can encourage seafloor habitats to recover, which can provide nursery habitat for species of commercial importance.

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Chapter 7. General Discussion

7.1. Summary of thesis aims and results

In this study, I set out to measure differences between sites located within Scotland's first and only fully protected marine reserve and reference sites located outside its boundaries after having been established for four years. In particular, I aimed to investigate the population dynamics of a number of commercially important species, and the abundance of a wide range of other organisms.

In my introductory chapter, I placed my research into context by reviewing the global importance of marine ecosystems and the services they provide. This chapter highlighted the declining state of the world's oceans and detailed how marine protected areas (MPAs) and marine reserves can be used to help conserve biodiversity and fish stocks. I finished by setting out my research aims and by briefly describing the structure of the chapters that follow.

In chapter 2, I explored the general effects of overfishing from a global perspective. I reported how many over-exploited marine ecosystems, including the Firth of Clyde, have lost their natural populations of large predatory finfish, and in their place, have become dominated by crustaceans and invertebrates. Controversially, some of these simplified ecosystems have gone on to support highly successful invertebrate fisheries capable of generating more economic value than the fisheries they replaced. Such systems have therefore been compared with those created by modern agriculture on land, in that existing ecosystems have been converted into those that maximize the production of target species. By drawing on a number of ecological concepts and case-studies, I argued that this is in fact highly risky. This is because invertebrate stocks within simplified ecosystems are unusually prone to collapse from disease, invasion, eutrophication and climate change. Furthermore, the loss of large finfish has triggered many ecosystems to shift to states that are both ecologically and economically undesirable, and difficult and expensive to reverse. Hence, I concluded that the transition from multispecies fisheries to simplified invertebrate fisheries is causing a global decline in biodiversity, and is threatening global food security, rather than promoting it.

In chapter 3, I aimed to investigate which survey methods were the most ideal for monitoring the wide range of species that occur in Lamlash Bay. This was an important step as many of the survey methods used in this study overlapped in the types of species they recorded, and it was not clear which data should have been analysed in my later chapters. For example, data on the abundance of scallops was generated by both diver and photoquadrat surveys. However, by conducting a power analysis, I found that diver surveys were the more precise method for estimating the density and size of scallops. I therefore decided to analyse the data generated by diver surveys for exploring the abundance and size of scallops within Lamlash Bay. In estimating the percentage cover of epifaunal organisms on the seabed, I found that photo surveys detected a greater proportion of macroalgae and maerl than diver estimates, whereas diver surveys detected a greater proportion of tunicates, sponges, hydroids and bryozoans. Differences between survey methods were also detected in the monitoring of fish and crustacean species. Diver surveys detected a greater proportion of small, cryptic fish species and crustaceans. In contrast, only baited underwater video surveys were able to detect pelagic shoals of mackerel and sand eels. Based on these findings, I concluded that diver surveys had no clear superiority over camera and video methods in monitoring benthic and fish species as both produced markedly different results for different types of species. Hence, my study indicated that scientists studying marine protected areas must first identify the types of species they intend to study, and from that, choose the most appropriate monitoring method.

In chapter 4, I investigated the effects of the Lamlash Bay Marine Reserve on nursery habitats and commercially valuable scallops. Dive surveys conducted over a period of four years revealed the abundance of juvenile scallops to be 2-5 times greater within the marine reserve than outside. Generalised linear models showed that the greater abundance of juvenile scallops within the reserve was related to a greater presence of macroalgae and hydroids growing within its boundaries. This effect was supported by diver observations, which regularly reported high levels of scallop settlement within these complex habitats. My study also indicated that the marine reserve was having a positive effect on adult scallops. The age (1.7 years older), size (28 mm larger) and reproductive biomass (2.5 times higher) of king scallops were all significantly greater within the reserve and should translate to higher reproductive output and scallop recruitment both within the marine reserve and surrounding fishing grounds. Finally, scallop density significantly declined with increasing distance from the boundaries of the reserve, possibly indicating evidence of spillover or reduced fishing effort directly outside the reserve, a phenomenon I coin as the “halo effect”.

In chapter 5, I investigated the effects of the Lamlash Bay Marine Reserve on commercially valuable populations of lobster and crabs. Potting surveys conducted over a two year period showed European lobster were significantly larger within the reserve than on neighbouring fishing grounds. In fact, large lobsters (> 111 mm) were entirely absent outside the reserve, meaning individuals within the reserve were on average 7.3 mm larger. As egg production in lobsters is a function of population size, maturity, fecundity and body size, the greater abundance of larger-bodied lobsters within the reserve should result in higher reproductive output and recruitment both within the reserve and to surrounding areas. In support of this, size-fecundity relationships suggested the mean potential reproductive output per female lobster was 27.3% higher within the reserve than outside. In addition, the frequency of berried female lobsters was 5.5 times greater within the reserve than outside. Based on these findings, I proposed that the 2.67 km^2 marine reserve had a potential egg output equivalent to an unprotected area of 19.1 km^2; supporting the concept that MPAs can contribute disproportionally to recruitment in relation to the actual area they protect. However, as there were no data prior to protection, and as this study was based on only two years of data, I could not confidently conclude that the reserve was responsible for these differences. Further years of monitoring will resolve this issue.

Finally, in chapter 6, I explored the composition of benthic and fish communities in Lamlash Bay Marine Reserve and surrounding fishing grounds. Live maerl (348% greater), macroalgae (100% greater), sponges (268% greater), hydroids (15-267% greater), eyelash worms (184% greater), feather stars (52% greater), parchment worms (36% greater) and total epifauna (77% greater) were all found to be significantly more abundant within the reserve than neighbouring. The greater abundance of these complex habitats growing within the reserve appeared to be providing nursery habitat for juvenile cod and scallops. There were also broad differences in the overall epifaunal community. Sites within the reserve and less than 15 m in depth were more strongly characterised by a range of bushy and upright seaweeds and hydroids, whereas sites outside the reserve were more strongly characterised by red algal turf and fast-growing burrowing anemones. Sites outside the reserve are therefore likely to be providing comparatively less structural complexity and may, in turn, be providing a smaller range of ecological niches. In contrast to sessile organisms, comparisons of the abundance of mobile benthic fauna and fish revealed little difference between the reserve and outside. This was likely due to the young age of the reserve (4 years) and its small size (2.67km^2), both of which are known to reduce the effects of marine reserves on mobile species.

7.2. Future research

My research shows that a number of fishery and ecological differences exist between Scotland's first and only fully protected marine reserve and surrounding fishing grounds. This conclusion was drawn from conducting a range of field surveys over a period of four years, and by comparing sites of similar depth and substrate between the marine reserve and outside. However, as I now discuss, this study does have a number of limitations and leaves several key questions unanswered.

My research presents several lines of evidence that Lamlash Bay Marine Reserve is generating reproductive benefits by increasing the reproductive biomass of scallops and the fecundity of lobsters. In theory, this should translate to higher reproductive output and recruitment both within the marine reserve and surrounding fishing grounds (Beck et al. 2001; Gibb et al. 2007; Laurel et al. 2009). My study also revealed the abundance of lobster and scallops to decline with increasing distance from the boundaries of the reserve, and may be evidence of spillover / larval export. Whilst many studies have detected similar gradients in abundance (Harmelin-Vivien et al. 2008; Halpern et al. 2010; Ludford et al. 2012), they share a problem in that they cannot confidently conclude that such trends are a consequence of protection, and may instead be a result of differing levels of fishing activity or spatial heterogeneity in habitats. A much more suitable, although arguably more cost and time intensive, approach would be to conduct a molecular study capable of detecting larval export and spillover from within marine reserves to fishing grounds (e.g. Cudney-Bueno et al. 2009; Planes et al. 2009; Pelc et al. 2010). Such a study would be highly informative for Lamlash Bay and other marine reserves around the world.

Many studies document the phenomenon of “fishing the line”, whereby greater catches and profit near to marine reserves has resulted in fishers preferentially setting their gears close to the boundaries of marine reserves (Stelzenmüller et al. 2007; Goñi et al. 2008; Halpern et al. 2010). However, my research proposes a counter phenomenon called the “halo effect”, in which fishers may be wary of fishing near marine reserves due to potential conflict with local communities and compliance organisations, and of the logistical difficulties of having to haul up their gear to pass through reserves. It would be highly interesting and informative to analyse Vessel Monitoring System (VMS) data to investigate whether fishing vessels do avoid the fishing grounds immediately surrounding Lamlash Bay Marine Reserve, in order to test if this unexpected phenomenon is occurring.

Theory and empirical evidence suggest that differences between the reserve and outside will become more pronounced the longer the reserve is established (Roberts et al. 2005; Edgar et al. 2014). Therefore, by conducting my study over four years, I was able to observe that some of the differences I recorded between the reserve and outside became stronger over time. Hence, these trends were likely to be a response to protection. Nonetheless, this research will greatly benefit from future monitoring. This is particularly true for the crustacean surveys which were only conducted during the final two years of monitoring. The first year of these surveys found few differences in lobster populations in and outside the reserve, whilst the following year detected strong differences between the reserve and outside in lobster abundance, size and fecundity. At least one more year of study is essential in determining whether this trend continues, or is simply an artefact of natural variation.

Lastly, no blinding was used in this study, meaning the scientist in charge of analysing the videos, images and scallops knew whether samples were collected within or outside the reserve, which could have generated “confirmation bias” (Ruxton and Coldgrave 2010). This describes when scientists testing pre-existing hypotheses (e.g. the reserve is having a positive effect) search for evidence that confirm those hypotheses, rather than evidence which can disconfirm them (Jones and Sudgen 2001). If monitoring of Lamlash Bay does continue, blinding must be used to reduce these possible sources of bias.

7.4. Conclusions

Recent technological advancements coupled with rising demand have caused the intensity and geographic reach of fisheries to greatly escalate over the last two centuries (Roberts 2007; Watson et al. 2012; Howarth et al. 2013). As a result, an estimated 70% of all world fish populations are currently either fully exploited, overexploited, depleted or have collapsed entirely from overfishing (FAO 2012), and the proportion of catches originating from declining stocks is rapidly increasing (Jackson et al. 2001; Pauly et al. 2002; Worm et al. 2006; Pauly 2008). The poor state of the world’s fisheries is largely due to unsustainable levels of exploitation and the physical and ecological impacts associated with fishing gears. High levels of fishing can reduce the abundance of target species and truncate age and size structures, both of which can have severe consequences on recruitment (Jennings et al. 2001; Beamish et al. 2006). In addition, many fishing gears capture a wide variety of non-target organisms which can dramatically alter the ecological composition of benthic and fish communities (Bradshaw et al. 2001; Hinz et al. 2012). Mobile fishing gears are considered the most damaging to marine ecosystems as they plough sediments and fragment the biogenic structure of epifaunal organisms, which can negatively impact the recruitment of commercially important species and reduce an area’s capacity to support biodiversity (Collie et al. 1997; Bradshaw et al. 2001, 2003; Howarth et al. 2011).

Despite the large impacts fishing can have on the aquatic environment, my study contributes towards a rapidly growing field which argues that closing areas to some or all types of fishing through the implementation of MPAs and marine reserves can conserve biodiversity and enhance fish stocks. My research shows that Lamlash Bay Marine Reserve contains a greater abundance of juvenile scallops and lobster, and that these commercially important species are both older and larger within the reserve. These effects have resulted in greater levels of fecundity and reproductive biomass, which will likely boost reproductive output and recruitment both within the reserve and in neighbouring fishing grounds. My study also reveals that Lamlash Bay Marine Reserve contains a greater abundance of nursery habitats, which are increasing the settlement levels of commercially important scallops and providing nursery habitat for juvenile cod.

As already discussed, there are a number of limitations with this study. As there were no data available prior to the establishment of Lamlash Bay Marine Reserve, I could not conclude whether the differences I observed between the reserve and outside were due to protection. Rather, all of these differences may have existed before the reserve was created, or may be due to some other phenomenon. To help account for this I decided to compare sites within the reserve with reference sites located outside the reserve over a period of four years. Although lacking “before” data, my design still retains all the elements of a before-after control-impact (BACI) approach in that the: “before” condition is two years after protection; my “after” conditions are three and four years after protection; and my “control” and “impact” conditions refer to those sites located in and outside the reserve. The bigger problem in my study lies with there being only one marine reserve and only one control, meaning there is no true replication, meaning if I wish to interpret any differences as being due to protection the design would be pseudo-replicated (Hurlbert 1984). Such lack of replication is a common problem encountered in ecological studies (Stewart-Oaten et al. 1986), particularly those investigating MPAs (Willis et al. 2003; Claudet et al. 2006). However, this does not mean single-replication experiments have no purpose. In fact, when all the lines of evidence in this study are considered (see Appendix 6) they together provide a compelling argument that the protection afforded by Lamlash Bay Marine Reserve is generating a number of positive effects.

My research comes at a key time. Following a large number of recently established policies and initiatives, the global coverage of MPAs is set to increase over the next decade (Metcalfe *et al.*, 2013). Globally agreed marine protection targets, such as the Convention on Biological Diversity’s (CBD) ‘*Aichi Target*’ are encouraging many governments to establish or expand existing MPA networks within their jurisdictions (Wood et al. 2008; CBD 2011; Harrop 2011; Wood 2011). This interest is reflected in the European Union (EU) as the Marine Strategy Frameworks Directive (MSFD), Birds and Habitats Directives, OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic), HELCOM (Helsinki Commission) and Barcelona regional seas conventions, have all initiated the process of establishing a coherent network of MPAs within European waters (Fenberg et al. 2012; Metcalfe et al. 2013). On a national level, the planned implementation of Marine Conservation Zones (MCZs; England, Wales and Northern Ireland) and Scottish MPAs (Scotland) will all lead to the creation of a network of MPAs around the United Kingdom (UK; Jones 2012; JNCC 2013). All these measures intend to achieve a variety of management goals; principally to conserve biodiversity and promote the sustainability of fisheries (Pomeroy et al. 2005; Metcalfe et al. 2013).

Although the use of MPAs and marine reserves as management tools is receiving increasing attention, the creation of a UK and European MPA network is still at a highly vulnerable stage. Many conservation bodies and scientists are concerned that the MPA process is being changed and diluted to something far less effective than what is needed in order to maintain fish stocks and marine ecosystems in a healthy state (Chape et al. 2005; Wood et al. 2008; Monbiot 2012; Fox et al. 2012; Carrington 2013). In addition, studies into the effects of MPAs are far less common in temperate and colder waters, and are particularly limited in Europe and the UK. Consequently, some members of the fishing industry, and indeed some government managers, are sceptical about how effective marine reserves will be in UK waters (e.g. NFFO 2010). Lamlash Bay is the first and only fully protected marine reserve in Scotland, and the only statutory reserve in the UK that was originally proposed by a local community which bans all extractive activities (Prior 2011). Lamlash Bay is also unique in that the majority of MPAs in the UK were proposed either for conservation (e.g. Lundy Marine Nature reserve) or fishery purposes (e.g. closed areas off the Isle of Man), not for both. Researching the marine reserve in Lamlash Bay has therefore offered a vital insight into the benefits that highly protected marine reserves can provide. In particular, my work has highlighted that full protection and support from the local community, is likely to be highly important in maximising the effectiveness of MPAs as any illegal extraction would have further weakened the differences between Lamlash Bay Marine Reserve and surrounding fishing grounds. As my results are consistent with the hypothesis that MPAs can provide benefits to scallop and lobster populations, as well as to seafloor habitats, my research is of great interest to scientists, conservationists, managers, UK and EU administrations, and other bodies further afield.

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Appendices

Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep boulders	Out	23.1	Boulders, sand
	Out	24.5	Boulders, muddy sand
	Reserve	16.8	Boulders, sand
	Reserve	17	Boulders, muddy sand, dead maerl
	Reserve	19.1	Boulders, muddy sand
	Reserve	27	Boulders, muddy sand
	Reserve	28	Boulders, muddy sand, cobbles
Deep muddy sand	Out	16.75	Muddy sand
	Out	17.2	Muddy sand
	Out	18	Muddy sand
	Out	18	Muddy sand, dead maerl
	Out	19	Muddy sand
	Out	21	Muddy sand, pebbles, cobbles
	Out	21.9	Muddy sand
	Out	21.9	Muddy sand
	Out	22.4	Muddy sand
	Out	22.7	Muddy sand
	Out	22.7	Muddy sand
	Out	23.7	Muddy sand, pebbles, cobbles
	Reserve	18.7	Muddy sand, dead maerl
	Reserve	18.9	Muddy sand
	Reserve	19	Muddy sand, dead maerl
	Reserve	21.1	Muddy sand
	Reserve	23	Muddy sand, pebbles, cobbles
	Reserve	23.1	Muddy sand
Maerl	Out	15.1	Dead maerl, muddy sand
	Out	14.3	Dead maerl, muddy sand, pebbles
	Reserve	9.1	Dead maerl
	Reserve	10	Dead maerl
	Reserve	10.7	Dead maerl, muddy sand
	Reserve	12.5	Dead maerl, muddy sand
	Reserve	13.8	Dead maerl, sand, pebbles, boulders
Mud	Out	19	Mud
	Out	20.8	Mud
	Reserve	13.3	Mud
	Reserve	18.7	Mud
Shallow muddy sand	Out	11.8	Muddy sand
	Out	13.5	Muddy sand
	Reserve	15.5	Muddy sand, pebbles, cobbles
	Reserve	15.5	Muddy sand

Appendix 1. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2010. Sites highlighted in grey were located within the marine reserve.

Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep boulders	Out	18.5	Boulders, sandy mud, pebbles
	Reserve	17	Boulders, muddy sand, cobbles
Deep muddy sand	Out	19.3	Muddy sand
	Out	16.48	Muddy sand
	Out	17	Muddy sand, dead maerl
	Out	22.8	Muddy sand, cobbles
	Out	21.5	Muddy sand, pebbles
	Reserve	19	Muddy sand
	Reserve	17.4	Muddy sand
	Reserve	20.8	Muddy sand, cobbles
Maerl	Out	8	Dead maerl
	Out	10.7	Dead maerl
	Reserve	6.8	Dead maerl, sand
	Reserve	11.2	Dead maerl, muddy sand
	Reserve	8.45	Dead maerl, muddy sand
Mud	Out	24	Mud
	Reserve	15.6	Fine muddy sand
Shallow boulders	Out	14.35	Boulders, muddy sand, cobbles
	Out	15.4	Boulders, muddy sand, dead maerl
	Reserve	13.8	Boulders, muddy sand, pebbles
	Reserve	15.2	Boulders, dead maerl
	Reserve	10.8	Boulders, sand, dead maerl, cobbles
Shallow muddy sand	Out	11.6	Muddy sand, pebbles
	Out	15.2	Muddy sand, pebbles
	Out	15	Muddy sand, pebbles
	Reserve	11.25	Muddy sand, cobbles
	Reserve	15.2	Muddy sand, dead maerl
	Reserve	15.1	Muddy sand

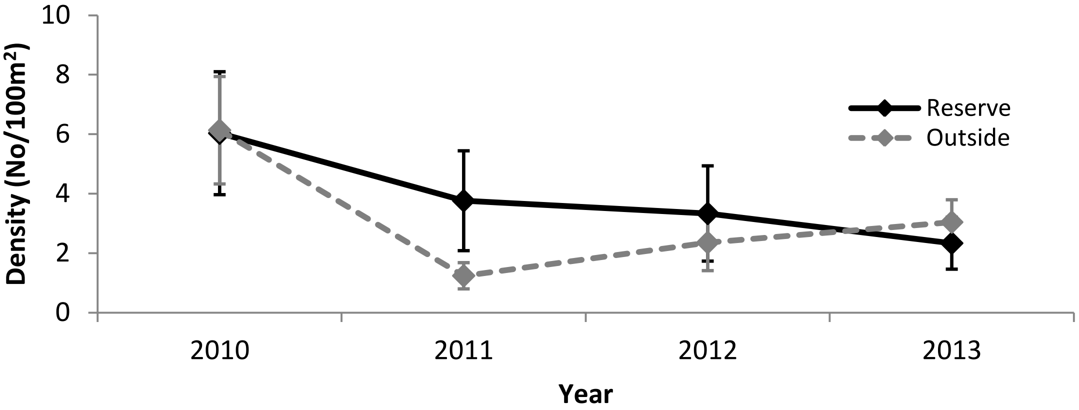
Appendix 2. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2011. Sites highlighted in grey were located within the marine reserve.

Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep boulders	Out	20	Boulders, sand
	Out	18.5	Boulders, sand, dead maerl
	Out	18.5	Boulders, sand
	Reserve	27.5	Boulders, muddy sand, dead maerl
	Reserve	20.2	Boulders, muddy sand, pebbles
	Reserve	17.35	Boulders, sandy mud
Deep muddy sand	Out	16.1	Muddy sand
	Out	23.4	Muddy sand, pebbles, cobbles
	Out	21.3	Muddy sand
	Out	24.5	Muddy sand
	Reserve	18.6	Muddy sand
	Reserve	18	Muddy sand, pebbles
	Reserve	19	Muddy sand
	Reserve	22.5	Muddy sand, pebbles, cobbles
	Reserve	21.4	Muddy sand
Maerl	Out	13.8	Dead mearl, muddy sand, boulders
	Out	12.7	Dead maerl, sand
	Out	11.5	Dead maerl
	Reserve	9.2	Dead maerl, sand
	Reserve	14.1	Dead maerl
	Reserve	10	Dead maerl, sand, pebbles
Shallow boulders	Out	14.4	Boulders, muddy sand
	Out	14.9	Boulders, muddy sand
	Reserve	11.8	Boulders, muddy sand, dead maerl
	Reserve	14.9	Boulders, muddy sand, dead maerl
Shallow muddy sand	Out	13.6	Muddy sand, pebbles
	Out	14.2	Muddy sand
	Out	12	Muddy sand, cobbles, lebbles
	Reserve	13.3	Muddy sand, pebbles
	Reserve	14	Muddy sand, dead maerl
	Reserve	15.2	Muddy sand

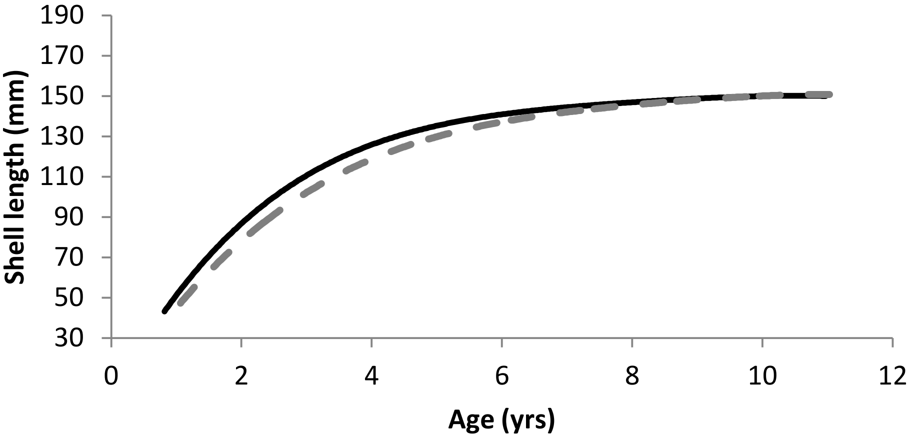
Appendix 3. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2012. Sites highlighted in grey were located within the marine reserve.

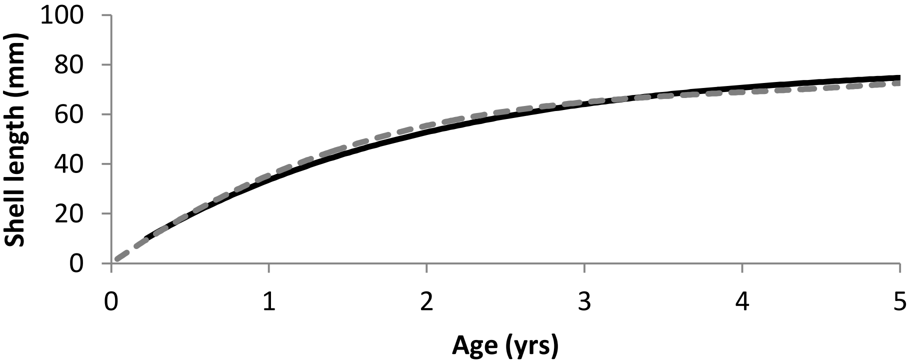
Assigned Category	Treatment	Depth BCD (m)	Substrate types
Deep Boulders	Out	22.15	Boulders, muddy sand, pebbles
	Out	20.25	Boulders, muddy sand, pebbles
	Reserve	22.65	Boulders, cobbles, muddy sand
	Reserve	27.6	Boulders, muddy sand, pebbles
Deep muddy sand	Out	16.55	Muddy sand, cobbles
	Out	18.65	Muddy sand, cobbles, dead maerl
	Out	23.35	Muddy sand
	Out	15.45	Muddy sand, pebbles
	Out	15.7	Muddy sand
	Out	20	Muddy sand
	Reserve	18.7	Muddy sand
	Reserve	18.7	Muddy sand
	Reserve	19.05	Muddy sand
	Reserve	16.2	Muddy sand
	Reserve	18.15	Muddy sand, cobbles
	Reserve	24.05	Muddy sand
Maerl	Out	10.2	Dead maerl
	Out	8.95	Dead maerl
	Reserve	8.7	Dead maerl
	Reserve	10.4	Dead maerl
Shallow muddy sand	Out	13.75	Muddy sand, dead maerl
	Out	9.8	Muddy sand, pebbles
	Out	8.9	Muddy sand
	Out	13.8	Muddy sand
	Reserve	12.75	Muddy sand, cobbles
	Reserve	12.5	Muddy sand
	Reserve	13.25	Muddy sand
	Reserve	13.85	Muddy sand
Shallow Boulders	Out	12.85	Boulders, sand
	Out	10.35	Boulders, sand
	Reserve	11.45	Boulders, sand
	Reserve	15.05	Boulders, muddy sand

Appendix 4. The depth below chart datum (BCD), substrate types, treatment and assigned category for each site surveyed in 2013. Sites highlighted in grey were located within the marine reserve.



Appendix 5. The density of queen scallops in and outside the fully protected marine reserve across four years. Error bars represent ±1 SE.





Appendix 6. Von Bertalanffy growth curves for king (top) and queen (bottom) scallops sampled between 2010-2013 from within (solid black line) and outside (dashed grey line) the fully protected marine reserve.

Hypothesis	**Variables**	**Test**	**Evidence of protection**
Juvenile scallops more abundant within reserve	SACFOR estimates of juvenile abundance, protection, year	Two-Way ANOVA	++
Juvenile scallop abundance related to benthic habitats	SACFOR estimates of juvenile abundance, benthic cover, year, protection and depth	GLM	++
Benthic habitats more abundant within reserve	Percentage cover of benthic organisms, year, protection	Two-Way ANOVA	+
Scallops more abundant within reserve	Density of king and queen scallops, year, protection	Two-Way ANOVA	-
Scallop abundance declined with distance from reserve	Density of king scallops, distance from reserve	Pearson Correlation	+
Mean size of scallops greater within reserve	Shell length of king and queen scallops, protection	ANOVA	+
Size distributions differed between reserve, outside and wider Clyde	Shell length of king and queen scallops, protection	K-S Test	+
Scallop mortality lower within the reserve	Age and density of king scallops, protection	Catch curve analysis	+
Scallop growth rates higher within reserve	Age and size of king and queen scallops, protection	Kimura likelihood ratio test	+
Exploitable and reproductive biomass of scallops higher within reserve	Exploitable and reproductive biomass, year, protection	Two-Way ANOVA	+
Lobster CPUE higher within reserve than both controls	CPUE, protection	Mann-Whitney	+
Lobster WPUE higher within reserve than both controls	WPUE, protection	ANOVA	+
Lobster CPUE and WPUE declined with increasing distance from reserve	CPUE, WPUE and distance from reserve	Pearson Correlation	+
Mean size of lobster greater within reserve	Carapace length, protection	ANOVA	+

Size distributions differed between the reserve and both controls	Carapace length, protection	K-S Test	+
Males and female lobsters not different from a 1:1 ratio	Gender frequency, protection	Pearson Chi-Squared	NA
No difference in gender ratios between reserve and outside	Gender frequency, protection	Pearson Chi-Squared	+
No difference in pregnant females frequency between reserve and outside	Pregnant female frequency, protection	Pearson Chi-Squared and Fisher's Exact	+
Lobsters spilling over into fishing grounds	GPS coordinates of recaptures	ArcGIS	-
Crab CPUE higher within reserve than both controls	Velvet and brown crab CPUE, protection	Mann-Whitney	- -
Crabs larger within reserve	Carapace length, protection	K-S Test	-
Epibenthic community composition differed between reserve and outside	Percentage cover of benthic organisms, year, protection, depth, substrate	PERMANOVA	+
Epibenthic community composition of shallow sites differed between reserve and outside	Percentage cover of benthic organisms	SIMPER	+
Benthic megafauna more abundant within reserve	Abundance of benthic organisms, protection, year	Two-Way ANOVA	+
Megafauna community composition differed between reserve and outside	Abundance of benthic organisms, year, protection, depth, substrate	PERMANOVA	-
Fish more abundant within reserve	MaxN of fish, year, protection	Two-Way ANOVA	-
Fish abundance was related to benthic habitats	MaxN of fish, year, protection, substrate, percentage cover of benthic organisms	GLM	NA

Appendix 7. Table summarising all hypotheses tested and whether tests showed evidence of an interaction between protection and year (++), of a positive difference between the reserve and outside (+), no difference between reserve and outside (-), a negative difference between reserve and outside (- -) and results that are neither positive nor negative (NA).