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Marine protected areas : efficacy, implementation and management

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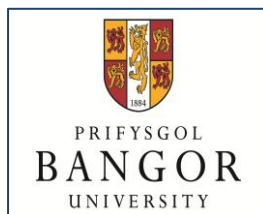*Awarding institution:*
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Marine protected areas: Efficacy, Implementation and Management

A thesis presented to Bangor University for the degree of
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by

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THESIS SUMMARY

Marine protected areas (MPAs) are increasingly viewed as an important management tool within a suite of policy alternatives to reduce, prevent and/or reverse on-going declines in marine biodiversity. The overall aim of this thesis was to test the efficacy of MPAs as a conservation measure, particularly focusing on partially protected areas which have received less attention than fully protected areas. An evidence-based approach, combining a rigorous assessment of the literature through 'systematic review' methodology, with field studies of fishing gear restriction areas in the UK was undertaken to examine the biological effects of partially protected areas on biota relative to fully protected areas and open access fished areas.

The syntheses of available evidence included in the systematic review suggested that while partially protected areas significantly enhanced density and biomass of fish relative to open access areas, fully protected areas yielded significantly higher biomass of fish within their boundaries relative to partially protected areas. The positive response to protection was primarily driven by target species. The effects of life history and ecological traits on the response of fish species to fully and partially protected areas were further examined using mixed effects modelling. Fish maximum body size, adult habitat preference and the exploitation status of the species were significantly related to the magnitude of response to full and partial protection. These results highlighted the importance of incorporating species information in the design of new MPAs, which ensures that protection is provided at spatial scales relevant to the species in need of conservation.

Fishery closed areas, where fishing with bottom-towed gear is prohibited but fishing with static gear is permitted are amongst the commonest examples of MPAs in the UK. Underwater camera surveys were conducted at Cardigan Bay Special Area of Conservation (SAC), the *Modiolus* Box within the Pen Llŷn a'r Sarnau SAC, Skomer Marine Nature Reserve and the Port Erin closed area in the Isle of Man to examine the response of epibenthic invertebrate communities to protection from bottom fishing. Benefits from protection were observed for three of these MPAs and the magnitude of response was generally higher for the target species such as scallops and for sessile, fragile taxa such as hydroids, bryozoans and sponges. Two key environmental characteristics that influenced the effect of protection were the intensity of fishing at the control unprotected areas and the level of natural disturbance from waves and tides.

Overall, the results showed that partially protected areas are a valuable spatial management tool particularly in areas where exclusion of all extractive activities is not a socio-economically and politically viable option. The findings also highlight the importance of considering the physical nature and dynamics of the environment, the nature of the species concerned and past and present level of fishing intensity throughout the designation process of MPAs, so as to avoid negative impacts on fisheries and limited conservation benefits.

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Though most people continue to perceive oceans as monochromatic, homogenous, resilient, vast - and therefore limitless - new notions about marine systems have surfaced recently. What we once thought limitless isn't; what we once thought as resilient seems less so

(Agardy, 1994)

CHAPTER 1

General introduction

Marine protected areas (MPAs) are increasingly viewed as an important management tool within a suite of policy alternatives to reduce, prevent and/or reverse on-going declines in marine biodiversity. They also promote the sustainable ecosystem-based management of fisheries and coastal resources (Agardy 1994; Pauly et al. 2002; Roberts et al. 2005; Halpern et al. 2008). A Marine Protected Area is defined by IUCN as "*any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment*". This definition covers a wide range of statutory and voluntary designations around the world. In the UK, it includes the range of designations including mSACs (marine Special Areas of Conservation), SPAs (Special Protection Areas), MNRs (Marine Nature Reserves) and MCZs (Marine Conservation Zones), but also VMCAs (Voluntary Marine Conservation Areas) and arguably a range of spatially-implemented fishing gear and effort restrictions.

This thesis examines the effectiveness of MPAs that confer full and partial protection from anthropogenic extractive activities such as fishing. Furthermore I assess the influence of the characteristics of MPAs and species-related traits on the response to protection. In the remainder of this introduction, the need for MPAs and the type of marine protection conferred by MPAs are highlighted, as well as the main goals achieved by MPA designation. The extent and distribution of MPAs worldwide and in the UK are also highlighted and the current knowledge of the ecological and fisheries effects of MPAs is reviewed. Finally the detailed objectives for each chapter of this thesis are presented.

1.1 The need for Marine Protected Areas (MPAs)

It is widely recognized that marine ecosystems worldwide are undergoing massive and acute declines in biodiversity and irreparable alterations to ecosystem functions (Boersma and Parrish 1999; Millenium Ecosystem Assessment 2005). Much of the world's oceans are affected by human influence with over a third strongly impacted by multiple anthropogenic drivers (Halpern et al. 2008). Much of this impact is aggregated in coastal regions, and overfishing and habitat degradation are amongst the most pervasive impacts (Jackson et al. 2001; Dulvy et al. 2003; Genner et al. 2010). About 75% of the global continental shelf is known to be impacted by trawling and dredging activity (Kaiser et al. 2002). Commercial fishing, in particular fishing with bottom towed gears, has been reported to reduce the numbers and size of target (Myers et al. 1996; Jennings et al. 2002; Graham et al. 2005; Scott

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et al. 2006; Barrett et al. 2007) and by-catch species (Kaiser et al. 1996; Veale et al. 2000; Jenkins et al. 2001), to reduce seabed habitat complexity and heterogeneity (Collie et al. 1997; 2000a), to cause shifts in community structure and trophic interactions (Carbines and Cole 2009; Hinz et al. 2009; Strain et al. 2012), and to alter the physical structure of the sea floor and biogeochemical processes (Schwinghamer et al. 1998; Smith et al. 2000; Jennings et al. 2005). Such impacts together with the emerging emphasis on an ecosystem-based approach to conservation and fisheries management, have led to recognition of the need for increased protection of the marine environment. As a consequence many coastal nations are currently working towards increasing the proportion of their seas covered by MPAs (Cicin-Sain and Belfiore 2005; Wood et al. 2008).

1.2   Types of marine protection

Many nations have established marine protected areas; however, these differ considerably in their extent and objectives. At one extreme, MPAs are used in a relatively small area for strict protection of biological diversity, nature-based recreation and tourism (Spalding et al. 2010). These areas are commonly known as "no-take" MPAs (or marine reserves), in which all extractive uses are prohibited. Alternatively, MPAs may be multiple use areas, whereby various human activities are permitted but regulated spatially, temporally, by species, mode of use, or by the type of users themselves (Mascia 2004). Partially protected areas, fishery reserves, fishery closures, gear restriction zones, buffer zones, national monument, marine park and marine sanctuary are all specific cases of MPAs where one or more extractive uses are forbidden, but others are allowed. MPAs often have complex governance systems. They can be managed by the state, trusts, indigenous people, local communities, companies and private owners and various combinations thereof (Spalding et al. 2010).

Many of the areas that exhibit higher levels of protection are either remote territories (e.g. Commonwealth of the Northern Mariana Islands of the USA) or are nation states with extensive EEZs (e.g. the Republic of Kiribati) or are relatively small and embedded within MPAs (Spalding et al. 2010; Claudet 2011). In heavily populated areas where anthropogenic use of the marine resources is high, MPAs tend to combine some level of protection with anthropogenic use of the area (Spalding et al. 2010).

1.3   Objectives of MPAS

Marine protected areas (MPAs) have been primarily implemented for the conservation and protection of marine habitats and species in areas that are recognized as particularly important in terms of ecological diversity. In these cases MPAs are used as a management tool to ensure the long-term viability of threatened or endangered populations and to maintain their genetic diversity, or to allow populations to recover to previous levels (Roberts et al. 2001; Willis et al. 2003; Claudet 2011). MPAs have also been used to restore damaged or overexploited areas considered to be critical for the survival of economically important species (Claudet 2011). Increasingly, the use of MPAs has been recognized as an essential fisheries management tool both by protecting the spawning stock biomass but also by acting as a source of adults and larvae which can supply surrounding fished areas (Lindeman et al. 2000; Murawski et al. 2000; Gell and Roberts 2003). In some cases, MPAs have been set up with the primary objective of reducing conflict among users with competing interests (e.g. Blyth et al. 2002), thereby improving the relationships between humans while promoting the sustainable exploitation of resources (Claudet 2011). Additionally, MPAs have been used to promote and facilitate the development of tourism through the provision of sites that fulfil aesthetic needs, and to provide undisturbed habitats and communities for education and research (Claudet 2011). In the latter case, MPAs act as ecological benchmarks against which to measure anthropogenic-induced changes (Agardy 1994).

1.4   Global extent and distribution

In 2002, the Plan of Implementation of the World Summit on Sustainable Development committed member parties to establish a comprehensive, effectively managed and ecologically representative network of MPAs by 2012 (Toropova et al. 2010). In 2006, tighter specification of targets called for at least 10% of each of the world's marine and coastal ecological regions to be effectively conserved by 2010 (Convention on Biological Diversity 2006). However, these targets were adopted without any assessment of the feasibility of the targets, and in October 2010, the 193 parties to the Convention on Biological Diversity (CBD) reaffirmed the goal of protecting and effectively managing 10% of the sea in MPAs by 2020 (Convention on Biological Diversity 2010). The spatial extent of MPAs globally has increased at a rate of 4.6% per year (1984-2006) (Wood et al. 2008) and the total ocean area protected has risen by over 150% since 2003 (Table 1.1) (Toropova et al. 2010). It is clear, however, that these CBD targets will not be met (Wood et al. 2008; Spalding et al. 2008; Spalding et al. 2010). In 2010, MPAs covered only 1.42% (5880 MPAs) of the ocean's

surface (approximately 5.1 million km^2) and 3.49% of the 200 nautical mile Exclusive Economic Zones (Spalding et al. 2010). Terrestrial protected areas, by contrast, cover more than 12% of the earth's land surface (Chape et al. 2005). The extensive global coverage of protected areas is relatively recent. Fig. 1.1 illustrates the growth of the terrestrial and marine protected areas network over time.

Table 1.1 Summary of recent growth in number and areal extent of marine protected areas globally (taken from Spalding et al. 2010).

	2003[a]		2006[b]		2008[c]		2010[d]	
Number of MPAs	4116		4435		5045		5850	
MPA area coverage statistics	million km^2	%	million km^2	%	million km^2	%	million km^2	%
Global total	1.64	0.45	2.35	0.65	2.59	0.72	4.21	1.17
Within EEZs	1.64	1.14	2.35	1.63	2.59	1.80	4.12	2.86
On continental shelf					1.20	4.09	1.27	4.32
Off-shelf					1.39	0.42	3.01	0.91

[a]Chape et al. 2003; [b]Wood et al. 2008; [c]Spalding et al. 2008; [d]Spalding et al. 2010

Although 1.42% of the world's oceans may fall within MPAs, a much smaller proportion is effectively managed. 'Paper parks' is the name given to MPAs that are mostly legislative exercises but do not provide the protection that is needed. For example, a recent global evaluation of the effectiveness of MPAs which contain areas of coral reef showed that in relation to total area of corals reefs that are within MPAs, only 6% lie in effectively managed MPAs (Burke et al. 2011). Reasons for inadequate management often include lack of management plans, limited information on natural resources, low or no enforcement and surveillance, limited human and financial resources, absence of support facilities and equipment such as boats, visitor centres, and diving equipment (Leverington et al. 2008).
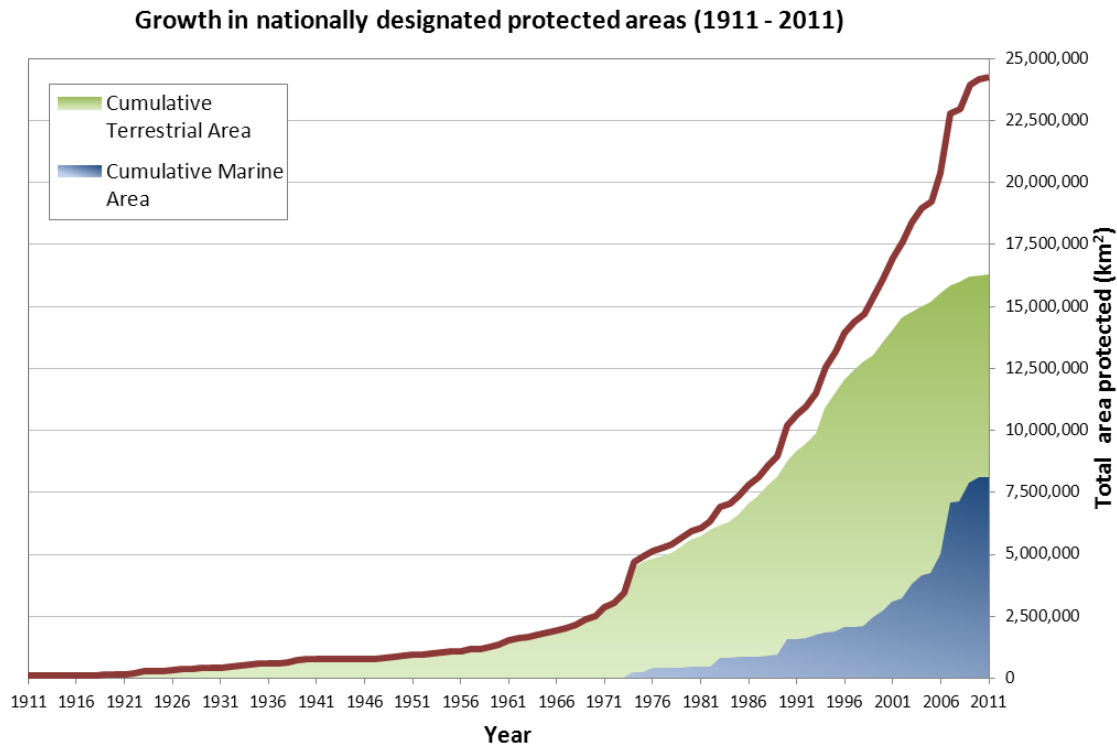
Growth in nationally designated protected areas (1911 - 2011)

Fig. 1.1 Growth of global terrestrial and marine protected areas over time. The red line indicates the cumulative growth in nationally designated protected areas for the period 1911 to 2011 (Source: IUCN and UNEP-WCMC (2012) The World Database on Protected Areas (WDPA): February 2012. Cambridge, UK: UNEP-WCMC).

The distribution of MPAs varies widely among nations, from zero to over 30% of a country's Economic Exclusion Zone (EEZ). Only 12 of 151 coastal countries exceed the 10% MPA target (Spalding et al. 2010). Most MPAs are concentrated in intertidal or near-coastal waters (Wood et al. 2008; Spalding et al. 2008; Spalding et al. 2010). On areas of continental shelf MPAs cover some 4.32% of this area, whereas protection of off-shelf areas stands at just 0.91% (Spalding et al. 2010). Rather than being ecologically representative, MPA coverage is very uneven and does not adequately represent all habitats important for conservation. Tropical coastal systems such as coral reefs, mangrove forests and seagrasses are well represented, while others such as seamounts are under-represented (Wood et al. 2008). In addition, temperate systems show particularly low coverage relative to tropical areas (Spalding et al. 2008).

The size of MPAs is highly variable, with a mean marine area of 741 km^2, but a median of only 1.6 km^2. Some 2,700 sites cover less than 1 km^2 of ocean area, which may thus not be effective at ensuring persistence of marine populations or form part of a coherent global

network. Much of the recent, rapid growth in spatial extent of MPAs has been driven by the establishment of a handful of very large (100,000 km^2) MPAs in places with sparse human populations (Spalding et al. 2010), such as Papahanaumokuakea Marine National Monument, Hawaii, 2006; Phoenix Islands Protected Area, Kiribati, 2008; and Chagos Islands Marine Reserve, British Indian Ocean Territory, 2010 (Spalding et al. 2010).

1.5 MPAs in the UK

The UK system of Marine Protected Areas is made up of Special Areas of Conservation (SACs), Special Protection Areas (SPAs), Marine Conservation Zones (MCZs), Sites of Special Scientific Interest (SSSI) and Marine Nature Reserves (MNRs), and roughly covers an area equal to 41,000 km^2, or around 4.8% of UK waters (JNCC 2012). These areas form the main components of an ecologically coherent MPA network, which the UK is committed to establish under international and regional conventions (Convention for Biological Diversity and OSPAR, respectively), European regulations (EC Habitats and Species Directive, 92/43/EEC and Marine Strategy Framework Directive) and national regulations (Marine and Coastal Access Act 2009).

SACs are sites that have been established under the EC Habitats Directive to protect habitat types and species (listed under Annexes I and II of the same directive) that are considered to be most in need of conservation at the European level. There are currently 102 SACs with marine components of which 87 are completely in inshore waters, 13 are completely in offshore waters (i.e. waters beyond 12 nautical miles) and two sites straddle inshore and offshore waters. SPAs are sites that have been established in accordance with Article 4 of the EC Birds Directive to protect rare and vulnerable birds and for regularly occurring migratory species. There are 107 SPAs with marine components, but only three of these are entirely marine (JNCC 2012). MNRs and SSSIs are established under the Wildlife and Countryside Act 1981 to protect species, habitats and geological features of national importance. Two statutory MNRs include: Skomer MNR, Pembrokeshire and Strangford Lough, Northern Ireland. Lundy Island in the Bristol Channel, a former Marine Nature Reserve, became the UK's first MCZ in January 2010. MCZs protect nationally important marine wildlife, habitats, geology and geomorphology and are established under the Marine and Coastal Access Act that came into force in 2009. In Welsh waters, the MCZs will consist of a small number of highly protected areas where no extraction, deposition or other damaging activities are allowed. In English waters, MCZs will consist of highly protected areas refered to as 'reference areas'

balanced against other areas where minimum levels of restriction on activities would be imposed to protect the features. The UK government is still in the process of establishing MCZs and along with other designations that constitute the MPA network, these will be fully implemented by 2016, in keeping with the Marine Strategy Framework Directive deadline (Jones 2012).

Within the UK SACs, many activities still occur. The aim of the SACs in the UK is not to exclude human activities, but to ensure that they are undertaken in ways that do not threaten the nature conservation interest (Stevens et al. 2006). A report produced by Client Earth and the Marine Conservation Society (2011) highlighted a number of these SACs that are undergoing degradation because of continued damaging fishing practice. Perhaps the term 'paper parks' is therefore more appropriate for some of these sites.

In addition to SACs, SPAs, MNRs and MCZs that are established primarily for the conservation and preservation of marine habitats and species, it is important to recognize that there is a range of other sites within the UK which impose, by legal or voluntary means, restrictions on human use, to effect some level of protection on the resources encompassed, and therefore fall under the definition of MPAs (Table 1.2). Examples include the Devon Inshore Potting Agreement (Blyth et al. 2004) and the range of Voluntary Marine Conservation Areas (VMCAs) around the UK coast. Some legal authority for fisheries management is devolved to regional bodies, such as the Inshore Fisheries and Conservation Authorities (previously Sea Fisheries Committees) which regulate anthropogenic activities, primarily fishing, by a combination of byelaws and regulating orders which specify spatial closures, catch limits, fishing season, vessel size, gear, and minimum landing size (e.g. http://www.devonandsevernifca.gov.uk/).

Table 1.2 UK MPA designations and IUCN protected area category equivalents.

UK MPA designation	IUCN categories	Examples
SAC, SPA	III, IV	Pen Llyn a`r Sarnau SAC Carmarthen Bay SPA
MNR/MCZ	I, III, IV, VI	I – No-take zone within Lundy Island MCZ VI – Skomer MNR
VMCA	V	Wembury VMCA
Gear-specific fisheries closures	VI	Devon Inshore Potting Agreement Irish Sea Cod Box Lyme Bay closure *Modiolus* Box in Pen Llyn a`r Sarnau SAC Port Erin scallop dredging exclusion zone, Isle of Man

IUCN Category I – Protected area managed mainly for science or wilderness protection
IUCN Category III – Protected area managed mainly for conservation of specific natural features
IUCN Category IV – Protected area managed mainly for conservation through management intervention
IUCN Category V – Protected area managed mainly for landscape/seascape conservation and recreation
IUCN Category VI – Protected area managed mainly for the sustainable use of natural ecosystems

1.6   Ecological effects of MPAs

The anticipated ecological effects of MPAs are multiple and influence populations, communities and ecosystems. Studies have demonstrated MPAs to enhance local diversity (Halpern 2003; Fraschetti et al. 2005), biomass and/or density of exploited species (Garcia-Rubies and Zabala 1990; Harmelin et al. 1995; Goni et al. 2001; Macpherson et al. 2002; Garcia-Charton et al. 2004), fecundity and reproductive output (Planes et al. 2000; Goni et al. 2003; Kaiser et al. 2007) within their boundaries compared to unprotected areas. Many of the observed direct ecological effects of no-take MPAs (marine reserves) have been synthesized in several reviews and meta-analyses (Table 1.3), but fewer attempts have been made to generalize the ecological effects of partially protected areas to date (but see Lester and Halpern 2008).

Protection influences the trophic structure of species assemblages, with abundances of top predators increasing gradually through time (Micheli et al. 2004). This suggests that MPAs may be an effective tool for rebuilding top trophic levels, typically depleted through fishing. Direct effects (i.e. benefits to species targeted by fishing) are often detectable over a

relatively short time frame (e.g. 5 years; Babcock et al. 2010), although this varies with individual and population growth rates. Indirect effects, such as those resulting from trophic interactions, tend to accrue more slowly, sometimes taking decades (Edgar et al. 2009; Babcock et al. 2010). The prevention of habitat degradation through the cessation of fishing with towed bottom fishing gear (Dayton et al. 1995; Jennings and Kaiser 1998) may provide indirect benefits to the species targeted by fisheries. For example, hydroids and bryozoans are key settlement habitats for scallop larvae but are among the first species removed by fishing disturbance (Bradshaw et al. 2003). The reduction of fishing disturbance through protected areas may also improve water quality by reducing turbidity, which has important implications for the survival and growth of filter-feeding invertebrates (Tillin et al. 2006). Finally, maintaining large enough pockets of the marine environment in a relatively undisturbed condition not only provides a safeguard for the future, but also a reference point for examining the effect of anthropogenic activities such as fishing on exploited populations and communities (Hilborn et al. 2004).

Table 1.3 Summary of results of meta-analyses evaluating the ecological effectiveness of fully protected MPAs relative to unprotected areas (adapted from Toropova et al. 2010).

Indicator	Main findings (% increase)	Region (taxon)	# of MPAs	Source
Biomass	446%	Global (for fish, invertebrates, algae)	124	Lester et al. 2009
Density	166%			
Size	28%			
Richness	21%			
Density	66%	Global (fish)	33	Molloy et al. 2009
Density	90%	Temperate (for fish, invertebrates, algae)	30	Stewart et al. 2009
Biomass	107%			
Richness	68%			
Biomass	352%	Global (for fish, invertebrates, algae)	81	Halpern 2003
Density	151%			
Size	29%			
Richness	25%			
Density	30% (28% for target species)	Global (fish)	19	Cote et al. 2001

Richness	11%			
Density	20%	Mediterranean (fish)	12	Guidetti and Sala 2007
Biomass	110%			
Density	146%	Mediterranean (fish)	12	Claudet et al. 2008
Richness	No effect			
Density	64% (150% for exploited species)	Philippines (fish)	19	Maliao et al. 2009

1.7 Fisheries effects of MPAs

MPAs provide benefits for fisheries either by providing refuge areas where heavily fished species are allowed to recover (Murawski et al. 2000; Pipitone et al. 2000; Badalamenti et al. 2008) or by acting as a source of adults, juveniles and larvae to surrounding fished areas (McClanahan and Mangi 2000; Gell and Roberts 2003; Abesamis et al. 2006; Francini-Filho and Moura 2008; Harmelin-Vivien et al. 2008). Theoretically, creation of a MPA should allow population growth through simultaneous decreases in adult mortality and increases in average female fecundity. There is a danger that intense fishing pressure may reduce stocks to densities at which little fertilization occurs, particularly for species that do not aggregate to spawn (e.g. invertebrates such as scallops). By reducing fishing mortality, MPAs can also increase fertilization success, leading to the production of better quality eggs and larvae that may additionally buffer the population against the cumulative effects of harvest pressure and environmental extremes (Carr and Reed 1993, Rowley 1994). Export of biomass may occur via two mechanisms; net emigration of juveniles and adults (spillover), which may be driven either by density-dependent or density-independent movements (Abesamis and Russ 2005), and net export of pelagic eggs and larvae (recruitment effect) (Gell and Roberts 2003). Taken together, these potential effects of MPAs act against growth overfishing (when fish are harvested at an average size that is smaller than the size that would produce the maximum yield per recruit) by providing areas in which large individuals will remain safe (Polachek 1990), as well as recruitment overfishing (a decline in the number of individuals entering the fishable population that results from depletion of the spawning biomass beyond the level where it no longer has the reproductive capacity to replenish itself) by providing a steady supply of larvae to become future fishable cohorts (Roberts and Polunin 1991).

Direct evidence of spillover showing a net emigration of exploitable individuals from MPAs to fished areas comes from tag-and-release studies, with recapture coming either from the

fishery or from experimental fishing (e.g. Rakitin and Kramer 1996; Kaunda-Arara and Rose 2004). Nevertheless, this has only been shown by a handful of studies, and mainly for lobsters and reef fish (e.g. Rowe 2001; Goni et al. 2006, 2010). The best indirect evidence of spillover comes from studies reporting declining gradients of catch per unit effort with distance from the MPA boundaries (e.g. Goni et al. 2006, 2008; Murawski et al. 2005). However, over-depletion of resources close to the MPA boundary due to relocation or concentration of fishing pressure at the boundary following the establishment of the MPA (known as "fishing the line" (Kellner et al. 2007)) may obscure this effect of protection.

Spillover has been shown over the range of 100s of metres (Goni et al. 2006; Guidetti 2006; Harmelin-Vivien et al. 2008), but can reach scales of kilometers depending on mobility of the species and habitat connectivity (Gell and Roberts 2003). The recruitment effect in contrast is expected to operate more diffusely and over broad spatial scales, generally tens of kilometers, depending on the dispersal capability of the pelagic larvae and patterns of ocean currents (Gell and Roberts 2003). Evidence that MPAs can make a significant contribution to the replenishment of fished populations through larval export is increasing (e.g. Pelc et al. 2010; Harrison et al. 2012).

1.8 Aims

The overall aim of my thesis is to test the efficacy of Marine Protected Areas as a conservation measure, particularly focussing on partially protected areas which have received less attention than fully protected areas. An evidence-based approach, combining a rigorous assessment of the literature through 'systematic review' methodology, with field studies of partially protected areas from the UK was undertaken to examine the biological effects of partially protected areas on fish and invertebrate populations relative to fully protected areas and open access fished areas.

In Chapter 2, I synthesize data on the performance of MPAs from studies that have made direct comparisons between (i) partially protected areas (PPA) and unprotected areas and (ii) partially protected areas (PPA) and no-take reserves (NTR) to examine how the level of protection inside the MPA determines benefit to fish populations. Given that species may respond differently to protection depending on the intensity of exploitation to which they are subject to outside the MPA (Williamson et al. 2004; Tetrault and Ambrose 2007; Watson et al. 2009), I examined whether the response to protection differed for whole assemblages of fish and for target and non-target fish species. Additionally, I investigated whether MPA-

related parameters such as the protection regime within the partially protected area, the duration of protection, the size of the MPA and the distance of the reference area to the MPA border influenced the magnitude of response to protection.

In Chapter 3, I retain the same datasets used in Chapter 2 and build on earlier work to examine how different traits and characteristics of fish species, including maximum body size, adult habitat type and exploitation status affect the abundance of species (density and biomass) in response to partial protection. Moreover, I analyze how the traits of species may interact with age and size of the MPA and protection regime of the partially protected area, which also affect responses to protection.

The full systematic review conducted in Chapter 2 revealed a knowledge gap on the efficacy of MPAs for invertebrate communities particularly those in soft sediments. In the rest of the thesis, field studies using underwater camera methods have been conducted at a number of bottom-gear restriction areas in the Irish Sea, concentrating on the effect of protection on large epibenthos. In Chapter 4, a seasonal and permanent spatial closure to scallop dredging within the Cardigan Bay SAC was surveyed on multiple occasions to examine differences in the abundance of target species (scallop, *Pecten maximus* and *Aequipecten opercularis*) and the macro-epifaunal benthic community structure between the two areas and to monitor recovery of the epibenthic community within the permanent closure after 23 months of no scallop dredging. In Chapter 5, the effect on the epibenthos is explored in various other case-studies that have been closed to fishing with bottom-towed gear for at least 9 years, and reasons for difference in the magnitude of 'reserve effect' among these three MPAs are discussed.

The thesis concludes with a general discussion which puts the main findings from the meta-analyses and the field surveys within the context of an evidence-based approach to conservation and highlights the implications of the findings for policy-makers and for future research on MPA efficacy. Additionally, the main gaps in knowledge identified by the literature review and the limitations of the study, particularly the field studies will be discussed.

CHAPTER 2

Evaluating the relative conservation value of fully and partially protected marine areas

This chapter has been submitted to Fish and Fisheries:

Sciberras, M., Jenkins, S.R., Kaiser, M.J., Hawkins, S.J. and Pullin, A.S. (*submitted*) Evaluating the biological effectiveness of fully and partially protected marine areas. Fish and Fisheries.

The full systematic review that includes additional analyses on invertebrate species has been accepted in Environmental Evidence and will be available online at http://www.environmentalevidence.org/:

Sciberras, M., Jenkins, S.R., Kaiser, M.J., Hawkins, S.J. and Pullin, A.S. (*in press*) Evaluating the biological effectiveness of fully and partially protected marine areas. Environmental Evidence.

2.1 ABSTRACT

The establishment of Marine Protected Areas (MPAs), particularly of no-take areas, is often viewed as a conflict between conservation and fishing. Partially protected areas (PPAs) that restrict some extractive uses are often regarded as a balance between biodiversity conservation and socio-economic viability. Few attempts have been made to generalize the ecological effects of PPAs. I synthesized the results of empirical studies that compared PPAs to (i) no-take marine reserves (NTRs) and (ii) to open access areas, to assess the potential benefits of different levels of protection for fish populations. Response to protection was examined in relation to MPA parameters and the exploitation status of fish. These syntheses suggest that while PPAs significantly enhance density and biomass of fish relative to open access areas, NTRs yielded significantly higher biomass of fish within their boundaries relative to PPAs. The positive response to protection was primarily driven by target species. There was a large degree of variability in the magnitude of response to protection, although the size of the PPA explained some of this variability. The protection regime within the PPA provided useful insights into the effectiveness of partial MPAs. In conclusion, MPAs with partial protection confer advantages, such as enhanced density and biomass of fish, compared to areas with no restrictions, although the strongest responses occurred for areas with total exclusion. Thus MPAs with a combination of protection levels are a valuable spatial management tool particularly in areas where exclusion of all activities is not a socio-economically and politically viable option.

2.2 INTRODUCTION

Much of the world's oceans are affected by human influence with over a third strongly impacted by multiple anthropogenic drivers (Halpern et al. 2008). Much of this impact is aggregated in coastal regions, and overfishing and habitat degradation are amongst the most pervasive impacts (Jackson et al. 2001; Dulvy et al. 2003; Genner et al. 2010). Such impacts have led to recognition of the need for increased protection of the marine environment, and many coastal nations have moved towards increasing the proportion of their seas encompassed by Marine Protected Areas (MPAs) (Cicin-Sain and Belfiore 2005; Wood et al. 2008).

Marine protected areas (MPAs) have been primarily advocated for the conservation and maintenance of sensitive marine habitats and associated species (Roberts et al. 2001; Willis et al. 2003). Increasingly, the use of MPAs has been recognized as an essential fisheries management tool both to limit direct effects on target species and to enhance production indirectly through, for example protection of essential fish habitat and promotion of the export of adults and larvae to adjacent areas (Lindeman et al. 2000; Murawski et al. 2000; Gell and Roberts 2003). In addition to direct protection of specific species, MPAs facilitate an ecosystem-wide approach to conservation and fisheries management, by providing broader protection to local habitats and ecosystems (Browman and Stergiou 2004; Sissenwine and Murawski 2004).

No-take marine protected areas, often called marine reserves, where all extractive uses (e.g. fishing) are prohibited, have been shown to provide a number of benefits. Such benefits include; increased biomass and density of species within (Garcia-Rubies and Zabala 1990; Garcia-Charton et al. 2004; Guidetti et al. 2005) and outside the no-take area boundary (McClanahan and Mangi 2000; Stobart et al. 2009; Goni et al. 2010), enhanced reproductive output (Planes et al. 2000; Goni et al. 2003), and re-established community and habitat structure (Castilla 1999; Shears and Babcock 2002). Despite these benefits, the prohibition of all extractive activities in certain areas can have short-term negative socio-economic impacts (Richardson et al. 2006) through the loss of or increased travelling time to fishing grounds, and decreased overall catches (Fiske 1992; Jones 2001), and may consequently be harder to implement and enforce. Partially protected marine areas with less restrictive regulations that seek a balance between the conservation of biodiversity and continued use of the area may be

a more viable management strategy. Additionally, partial fisheries closures that restrict activities such as commercial fishing with bottom-towed gear but allow others such as fishing with static gear may reduce conflict among users with competing interests (e.g. Blyth et al. 2002).

The reported effectiveness of partially protected marine areas for fisheries and ecosystem restoration is highly variable. Whereas some studies have recorded enhanced abundance and reproductive potential for exploited species (Pipitone et al. 2000; Beukers-Stewart et al. 2005) and recovery of community and habitat structure inside partially protected areas (Murawski et al. 2000), others did not detect benefits over unprotected fished areas (Piet and Rijnsdorp 1998; Denny and Babcock 2004). Very few attempts have been made to generalize the ecological effects of partially protected areas to date (but see Lester and Halpern 2008). Here, I synthesize data on the performance of marine protected areas (MPAs) from studies that have made direct comparisons between (i) partially protected areas (PPA) and unprotected areas and (ii) partially protected areas (PPA) and no-take reserves (NTR) to examine how the level of protection inside the MPA determines benefit to fish populations. Species may respond differently to protection depending on the intensity of exploitation to which they are subject to outside the MPA (Williamson et al. 2004; Tetrault and Ambrose 2007; Watson et al. 2009). Therefore, I also examined whether the response to protection differed for target and non-target fish species. Previous quantitative syntheses of fish populations in no-take marine reserves have linked the heterogeneity in response to protection among reserves to a number of MPA characteristics such as duration of protection and size of the MPA (Claudet et al. 2008; Lester et al. 2009; Maliao et al. 2009; Molloy et al. 2009; Vandeperre et al. 2011). Therefore, I investigated whether parameters such as the protection regime within the partially protected area, the age and size of the MPA and the distance of the reference area to the MPA border influenced the magnitude of response to protection. Insights into the effect of such characteristics are fundamental for the development of a more general understanding of the factors that underpin the effectiveness of a partially protected area.

2.3 METHODS

Systematic review methodology (Pullin and Stewart 2006; Higgins and Green 2008) and meta-analysis (Arnqvist and Wooster 1995; Gurevitch and Hedges 1999) were used to

examine the magnitude of the response of fish to protection inside partially protected areas relative to no-take marine areas and to fished areas (the review protocol and full systematic review are available online at www.environmentalevidence.org). The systematic review approach provides a comprehensive and robust assessment and summary of available evidence used to inform evidence-based decision making (Gates 2002; Roberts et al. 2006).

2.3.1 Data selection

Peer-reviewed scientific literature and grey literature (up until the end of February 2011) were searched to compile a database of studies that documented the biological effects of no-take marine reserves and of partially protected marine areas on fish density and biomass (refer to Table 2.1 for definitions). The search was conducted in multiple electronic databases and the internet (including organizational websites) using a range of Boolean search terms that included the terms 'Marine Protected Area', 'partially protected area', 'fishery reserve', 'marine area closure', 'gear restriction zone', 'buffer zone', 'marine sanctuary', 'marine reserve' and 'no-take area' to capture the diverse range of terminology that has been used in the literature to refer to marine protected areas. The full list of the search term combinations by source is given in Appendix 2.6.1. The bibliographies of articles included in this review and other relevant review articles were also searched.

Studies were retained if they explicitly compared (i) a no-take marine reserve (NTR) to a partially protected marine area (PPA), or (ii) a partially protected marine area (PPA) to an open access area (NP), or (iii) a combination of all the three levels of protection (NTR vs. PPA vs. NP). For studies that compared a NTR with PPA, these were included in the quantitative analysis only when the two were established at the same time or within 2 years of each other. Furthermore studies that examined any of the combinations (i) to (iii) were only included if mean, sample size values (e.g. number of transects or point counts) and an appropriate error measure (SD, SEM, variance, 95% CI) were reported for fish taxa. When several studies reported on the effects of protection for the same MPA, the most recent study was retained unless the studies measured different metrics (i.e. density, biomass) or presented data at different levels of aggregation (e.g. total or individual species mean values). Studies that presented data aggregated for several MPAs with different characteristics (e.g. Friedlander et al. 2003) were not included. A complete list of studies included in this study,

together with details of the marine protected area characteristics, the study survey design and methodology, and metrics (density, biomass) measured are given in Appendix 2.6.2.

Table 2.1 Definition and abbreviation of terms describing different levels of protection.

Abb.	Term	Definition
MPA	Marine Protected Area	Discrete geographic areas of the sea that are protected by spatially explicit restrictions designated under international, national, tribal or local laws to enhance long-term conservation of natural resources therein
NTR	No-take reserve	MPAs where all anthropogenic activities are excluded, apart from scientific research
PPA	Partially protected area	MPAs whereby regulations restrict some extractive uses but permit others
NP	Unprotected area	Areas outside the MPA that are open to fishing

2.3.2 Data handling

Whenever a study reported paired inside-outside estimates from more than one MPA, each pair was included separately in our database (e.g. Nardi et al. 2004; Walsh et al. 2004; Link et al. 2005; Friedlander et al. 2006; Tuya et al. 2006; Friedlander et al. 2010). When data were reported from two or more MPAs but one control area (e.g. LaMesa and Vacchi 1999; Miller et al. 2005; Tupper 2007; DiFranco et al. 2009; Jaworski et al. 2010), data estimates within each MPA were included separately and compared to the same control. Since the resulting density or biomass ratios for the MPAs were not independent, all analyses were repeated using average estimates for the MPAs sharing the same control and report the results only when they differ from the analyses that included them separately. When there was more than one sampling event after MPA establishment, the most recent sampling event, representing the longest duration of protection was used. This avoids analytical problems associated with temporal autocorrelation. However, when the data were collected within the same year (most frequently over different seasons) a composite effect size was used for subsequent analysis to eliminate any seasonal effects associated with the timing of sampling. Similarly, mean data presented for different depths within the same MPA were aggregated into a composite effect

size using a fixed-effect model, whereby the weight assigned to each subgroup effect size was equal to the inverse of the within-subgroup variance (Borenstein et al. 2009).

2.3.3 Data appraisal

Ecosystem processes are spatially and temporally variable at multiple scales and these variations can obscure the detection of the effects of protection (García-Charton and Pérez-Ruzafa 1999). Before-after control-impact studies that account for both spatial and temporal variability in the environment, thus allow for unambiguous inference about the effect of protection. I attempted to explore the influence of experimental design on the magnitude of the response to protection by running a sensitivity analysis using all studies and only those with BACI design. However this was not possible as the majority of studies were based on an After Control-Impact design (see Appendix 2.6.2). The variation in habitat characteristics between protected and unprotected areas is critical in making any meaningful comparisons of the protection effect (Willis et al. 2003; Anderson and Millar 2004; García-Charton et al. 2004; Claudet et al. 2011). Accordingly a sensitivity analysis was conducted parallel to the main analysis to examine the influence of including the 'habitat-confounded studies' on the overall magnitude and direction of protection effect, and report the results for the sensitivity analyses when the two differed. 'Habitat-confounded studies' refer to those studies where habitat variation in terms of features such as substratum type, substratum composition and complexity, rugosity and exposure, was reported to be significantly different for the studied locations inside and outside the MPA.

2.3.4 Meta-analysis

A weighted meta-analytical approach was used to investigate the response of fish to protection and to explicitly examine heterogeneity among MPAs. The natural logarithm transformed response ratio, Ln*RR* (Hedges et al. 1999) was used as the effect size, which is better suited than other metrics for a study of changes brought about by protection because it is designed to quantify the proportionate change that results from the intervention (Goldberg et al. 1999; Hedges et al. 1999). Ln*RR* was used instead of *RR* because it linearizes the metric so that changes in the denominator and numerator are treated equally, and yields better sampling distributions (Hedges et al. 1999). The response ratio is defined as the ratio of the mean density or biomass estimate measured inside and outside the MPA (Hedges et al. 1999):

$$LnRR = Ln\left(\frac{\overline{X}_{PPA}}{\overline{X}_{NP}}\right)$$

Effect sizes are commonly weighted to ensure a greater contribution of the most robust studies. Robustness is usually based on (inversed) sample variance (Rosenberg et al. 2000), therefore the variances associated with the response ratio (V_{LnRR}) (Hedges et al. 1999) were estimated as:

$$V_{LnRR} = \frac{SD_{PPA}^2}{n_{PPA}\left(\overline{X}_{PPA}\right)^2} + \frac{SD_{NP}^2}{n_{NP}\left(\overline{X}_{NP}\right)^2}$$

where $\overline{X}_{PPA}$ and $\overline{X}_{NP}$ are the mean density or biomass in the partially protected area (PPA) and the unprotected area (NP), SD_{PPA} and SD_{NP} are the standard deviation associated with $\overline{X}_{PPA}$ and $\overline{X}_{NP}$, n is the sample size for estimation of the mean (i.e. the number of hauls or transects or point counts sampled). Similarly, the effect size and the variance for comparison of the no-take reserves (NTR) and partially protected areas (PPA) were calculated by replacing PPA with NTR and NP with PPA in the equations above.

A weighted summary effect size ($\overline{LnRR}$) was calculated across the different MPA case studies by conducting a random effects meta-analysis using the DerSimoniam-Laird estimator method (Gurevitch and Hedges 1999; Hedges et al. 1999, Rosenberg et al. 2000):

$$\overline{LnRR} = \frac{\sum_{i=1}^{k} W_i \, LnRR_i}{\sum_{i=1}^{k} W_i}$$

where $LnRR_i$ and W_i are the effect size and weight (inverse variance) associated with each MPA included in the analysis, respectively, and k is the number of MPAs.

Positive values of the summary effect size ($\overline{LnRR}$) indicate greater density or biomass inside the partially protected area relative to the unprotected area, or inside the no-take reserve relative to the partially protected area. Negative values indicate the opposite. The summary effect size ($\overline{LnRR}$) is considered to be significantly different from zero (i.e. there is a significant either positive or negative effect of protection) when the 95% confidence interval

(CI) does not overlap zero (or 1 after back-transformation). All effect sizes reported in the text (as opposed to those shown in figures and tables) are presented back-transformed, so that they can be interpreted easily as the ratio of density or biomass inside and outside the MPA.

2.3.4.1 MPA-level analyses

To quantify the overall effect of marine protection on fish assemblage density and biomass, a meta-analysis was carried out using effect sizes calculated for MPAs that reported total mean values, or mean values for a sizeable proportion of the fish fauna surveyed (i.e. when the data were reported for 10 or more species or for more than 75% of the total catch of all fish counts). Separate meta-analyses were carried out using density and biomass estimates to quantify the effect of (i) partial protection over no protection and of (ii) full protection over partial protection in terms of each of these measures of MPA effectiveness.

Furthermore, I investigated the influence of a number of MPA characteristics on the response of the fish assemblage to protection. This analysis was only conducted for studies that compared a partially protected area to an unprotected area, as the number of studies that compared a no-take reserve to a partially protected area was too small to conduct robust analysis (biomass: $k = 6$ case-studies; density: $k = 9$ case-studies). The Q_M statistic was used to examine differences in the response to protection among categories of categorical variables and to test model fit for continuous variables (Rosenberg et al. 2000). The following variables were examined: MPA age (number of years between MPA enforcement and census); size of the PPA ($\log_{10}$ transformed); and PPA protection regime, which are described here as the combination of fishing activities prohibited and permitted inside the partially protected area. Based on the information extracted on the type of activities prohibited within the PPA (Appendix 2.6.3) partially protected areas were divided into: (i) 'indiscriminate' PPAs, if they prohibit fishing activities that are damaging to bottom habitats and non-target species (e.g. scallop dredging, bottom trawling) and (ii) 'discriminate' PPAs, if they prohibit activities which affect particular target species but not the surrounding environment (e.g. seine nets, long lines, spearfishing). 'Indiscriminate' partially protected areas may exhibit smaller responses to protection than 'discriminate' partially protected areas as habitat recovery will have to occur before some species' populations can begin to recover. Alternatively, the prohibition of fishing with highly destructive bottom towed gear in 'indiscriminate' PPAs compared to the prohibition of fishing with less environmentally

damaging gear in 'discriminate' PPAs, may lead to a stronger response to protection for 'indiscriminate' PPAs. Furthermore, based on information on the permitted activities inside the PPA (Appendix 2.6.3), 'discriminate' partially protected areas were sub-divided into those that allow some commercial and/or artisanal fishing inside the PPA, from those that allow recreational fishing or fishing for domestic purposes only. This categorisation serves as an indication of the intensity of use by the different user-groups permitted to fish inside the partially protected area. Fishing practices permitted inside 'indiscriminate' PPAs were carried out on a commercial scale. Therefore partially protected areas were categorized into three discrete groups based on their protection regime: (a) 'indiscriminate, commercial' (IdC); (b) 'discriminate, commercial' (DC); and (c) 'discriminate, recreational' (DR) (refer to Appendix 2.6.3 for full details on the 'protection regime' classification scheme).

Methodological variation among studies may have a strong impact on the results obtained. Different methods of surveying fish density and biomass were used among studies included in meta-analyses. For example fish surveys inside and outside protected areas were undertaken using underwater visual census (UVC) by belt transect, UVC by baited underwater video, or experimental fishing by trawling. These can lead to large differences in the overall area sampled. In addition the distance between protected and control sites varied to a large degree. Processes such as fish 'spillover' and increased fishing activity near the MPA border following its establishment (known as 'fishing the line' (Stobart et al. 2009) mean that variation in the distance of the control area from the MPA among studies may impact results. To account for these issues I examined (i) the relationship between effect size and the total area surveyed inside and outside the MPA and (ii) the influence of the proximity (measured as the minimum distance in km) of the unprotected area control sites (NP) to the partially protected area (PPA) border on effect size.

2.3.4.2 Species-level analyses: exploitation status

A considerable proportion of studies in the database presented mean and variance values for one or more individual species, rather than fish assemblages, and these studies were included in separate meta-analyses to determine the effect of (i) partial protection over no protection and of (ii) full protection over partial protection. Examination of effects at the species rather than assemblage level allowed assessment of how the 'exploitation status' of species, that is whether targeted or not by fisheries, determined the efficacy of protection. For these analyses

'target species' was taken to refer to those species that are primarily sought by fishermen in a particular fishery and are the subject of directed fishing effort. 'Non-target species' denoted species for which fishing gear is not specifically set, although the possibility that these species are accidentally caught as by-catch cannot be ruled out. In the analysis comparing no-take reserves to partially protected areas 'target species' were further sub-divided into those that were protected in both the no-take reserve and the partially protected area ('target-protected species', TP) and those that were protected by the no-take reserve but still permitted to be fished inside the PPA ('no-take reserve protected species', NTP).

Individual species *ln*-transformed response ratios (LnRR_i) were calculated for each MPA using species density or biomass estimates inside and outside the MPA. When a species was absent either inside or outside the MPA (i.e. the density or biomass estimate was zero), the species was removed from the analysis as it was not possible to use the natural logarithm of effect sizes involving abundance estimates of zero. Preliminary trials in which values of 0.001 and 0.0001 were added to all abundance estimates for each species resulted in an unrealistic overestimated weighted effect size for those species that were absent either inside or outside the protected area. As the effect sizes of individual species within a MPA are unlikely to be independent of each other, a single effect size measure for each 'exploitation status' category within each MPA was generated to handle non-independence of data (Raudenbush et al. 1988; Hedges et al. 2010). Individual species response ratios (LnRR_i) were therefore averaged to produce a single study-average effect size for each exploitation category (i.e LnRR_T, LnRR_{TP}, LnRR_{NTP}, LnRR_{NT}). The variance associated with the single study-average effect size was calculated using (Borenstein et al. 2009):

$$var\left(\frac{1}{m}\sum_{i=1}^{m}LnRR_i\right) = \left(\frac{1}{m}\right)^2 var\left(\sum_{i=1}^{m}LnRR_i\right)$$

$$= \left(\frac{1}{m}\right)^2 \left(\sum_{i=1}^{m} V_{LnRRi} + \sum_{i\neq j}\left(r_{ij}\sqrt{V_{LnRRi}}\sqrt{V_{LnRRj}}\right)\right)$$

where LnRR_i is the individual species' response ratio, V_{LnRRi} and V_{LnRRj} are the within-study variance for species i to j, m is the number of species within each 'exploitation status' category and r is the correlation coefficient that describes the extent to which the means of two different species co-vary.

Since the correlation coefficient among species within a study was never reported, a range of correlation coefficient values were used in the calculation (rho = 0, 0.2, 0.5, 0.8, 1) and the analyses repeated for each value of r. As the results did not differ significantly for the different values of r, data for r = 0.5 is presented. Categorical meta-analysis was conducted between 'exploitation status' categories using the Q_M statistic (Rosenberg et al. 2000) to determine whether the between-group responses were significantly different.

Finally, as for the fish assemblage analyses the influence of a number of MPA characteristics was examined on the response of target species to protection. As the overall response to protection was not significantly different between 'target-protected species' (TP) and 'no-take reserve protected species' (NTP), the effect sizes from these two sub-categories were pooled for the analysis of MPA characteristics on target species response. The sample sizes for the 'non-target' species categories were too small to allow further analysis. The variables examined for the target species data were: MPA age (years); size of the PPA (for comparison of PPA *vs.* NP), or alternatively, the size ratio of the NTR to the PPA (for comparison of NTR *vs.* PPA); PPA protection regime (for comparison of PPA *vs.* NP); and the proximity of the unprotected control sites to the PPA border (for comparison of PPA *vs.* NP), or alternatively, the distance between the borders of the no-take area and partially-protected area (for comparison of NTR *vs.* PPA). The distance of the no-take reserve to the partially-protected area was not examined for target species density as all the MPAs except for one were characterized by a zonation scheme, consisting of a no-take area and an adjacent partially protected area.

Analyses were conducted using the software package Metawin (v. 2.0: Rosenberg et al. 2000) for calculation of effect size and within-study variance and in R using the metaphor package (Viechtbauer 2010) for conducting the random-effects meta-analyses.

2.4 RESULTS

2.4.1 Comparison of partially protected *vs.* unprotected areas

2.4.1.1 Effect of protection

Overall, fish assemblage density and biomass were significantly higher inside partially protected areas (PPA) than in unprotected (NP) areas. Fish density was on average 22%

higher within PPA boundaries (sensitivity analysis: weighted summary effect size, $\overline{RR}$ = 1·22, confidence interval (CI) = 1.02 - 1.48) and biomass was 51% greater in PPA than in unprotected areas (main analysis: $\overline{RR}$ = 1·51, CI = 1.23 - 1.84) (Fig. 2.1).

Examination of individual species that have been aggregated according to their fisheries' exploitation status revealed that target fish species had significantly higher density (sensitivity analysis: $\overline{RR}$ = 1·65, CI = 1.32 – 2.03) and biomass (main analysis: $\overline{RR}$ = 1·49, CI = 1.19 – 1.88) inside partially protected areas than in unprotected areas (Fig. 2.1). In contrast no significant effect was detected for non-target species (Fig. 2.1). Despite this difference in result, a direct comparison of the magnitude of response to partial protection between the target and non-target species categories was not significant for both metrics (density (sensitivity analysis): Q_M = 1.53, df = 1, p = 0.22; biomass (main analysis): Q_M = 0.32, df = 1, p = 0.57).
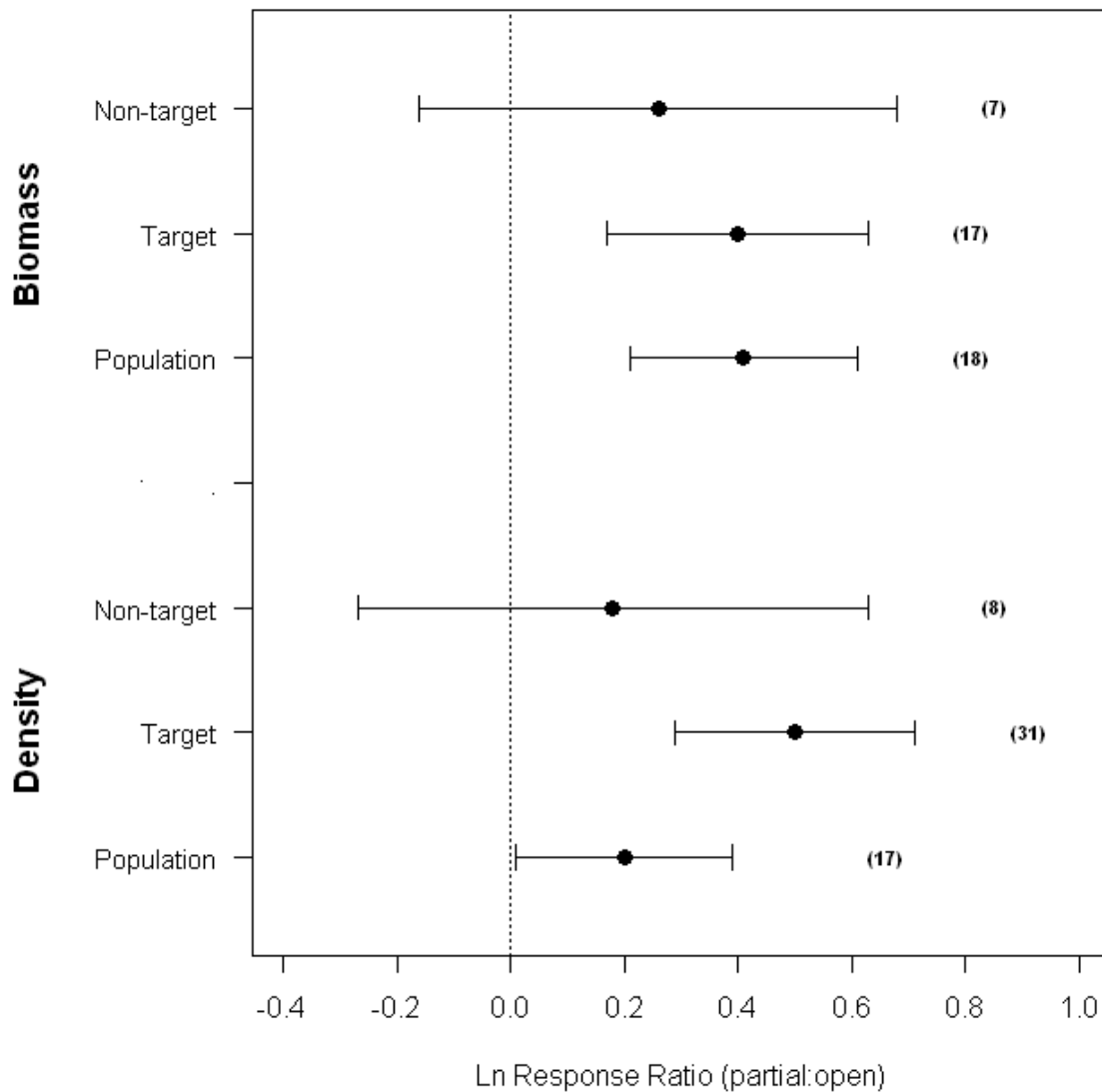
Fig. 2.1 Mean response ratios ($\overline{LnRR}$) of fish assemblage and 'exploitation status' categories using density and biomass data for partially protected areas compared to unprotected areas (partial:open). Error bars represent the 95% confidence interval. Sample size (i.e. the number of MPAs) for each ratio is shown in parentheses. The vertical dotted line at ($\overline{LnRR}$) = 0 represents equal fish density or biomass inside and outside of the MPA; ($\overline{LnRR}$) > 0 means more fish inside the MPA; ($\overline{LnRR}$) < 0 means fewer fish in the MPA.

2.4.1.2 Correlates of response to protection

Several potential effect modifiers were tested in an attempt to explain the variability in effect sizes between MPAs. To examine whether the response to protection was influenced by the type of fishing activities prohibited and permitted within the partially protected area, a categorical meta-analysis was conducted for the effect of 'protection regime' on fish

assemblage and target species. Of the six comparisons between partially protected areas and open access areas conducted for fish assemblages (three types of protection regime for each of density and biomass) only one (biomass for the 'discriminate, commercial' DC category) showed a significant difference (Fig. 2.2). Comparison of the response to partial protection among the three protection regime categories examined was not significantly different for fish assemblage density (sensitivity analysis: $Q_M = 0.63$, df = 3, p = 0.73) or biomass (sensitivity anal.: $Q_M = 2.01$, df = 3, p = 0.37). It must be emphasized however, that the results for this effect modifier on assemblage data should be interpreted with caution owing to the small number of PPA case-studies within each category, which reduced the robustness of the reported average effect size (Fig. 2.2).
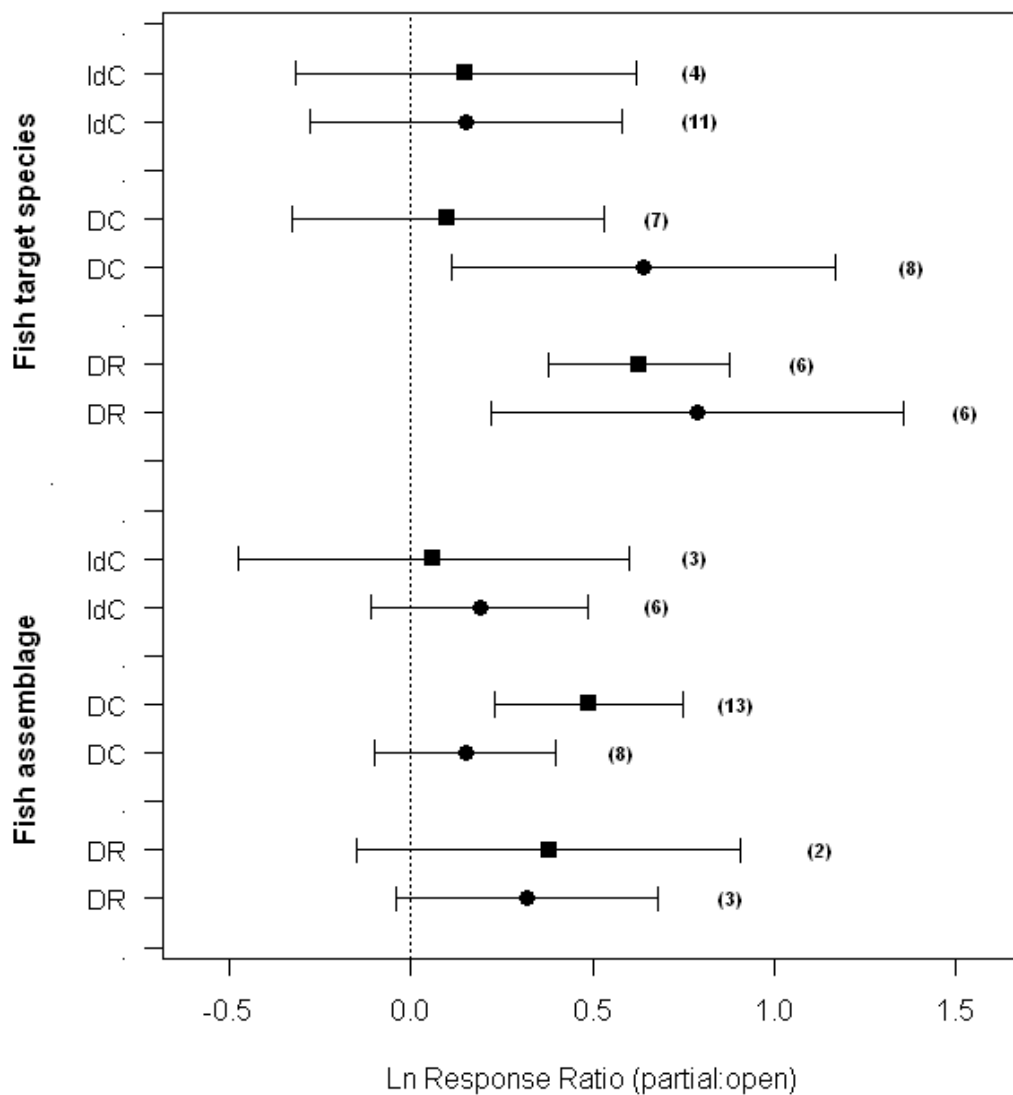
Fig. 2.2 Mean response ratio ($\overline{LnRR}$) based on density (●) and biomass (■) data in the partially protected area and the unprotected area (partial:open) for each 'protection regime' category (IdC:

Indiscriminate, commercial; DC: discriminate, commercial; DR: discriminate, recreational). Results are shown for the entire fish assemblage and for fisheries' target species only. Sample size (i.e. the number of MPAs) for each ratio is shown in parentheses. The vertical dotted line at $(\overline{LnRR}) = 0$ represents equal fish density or biomass inside and outside of the MPA; $(\overline{LnRR}) > 0$ means more fish inside the PPA; $(\overline{LnRR}) < 0$ means fewer fish in the PPA.

When the analysis was carried out on those studies that provided data for target species, density and biomass were significantly greater (on average twice as high) in the partially protected area relative to the unprotected area for PPAs that allow fishing on a recreational basis or for domestic use only (DR) (density (main analysis): $RR_{DR} = 2.20$, CI = 1.25 - 3.94; biomass (main analysis): $RR_{DR} = 1.88$, CI = 1.45 − 2.41) (Fig. 2.2). As expected, the response to protection was lowest for partially protected areas in the 'indiscriminate, commercial' category, presumably because recovery processes take longer in habitats fished by bottom towed gear prior to MPA establishment [density (main analysis): $RR_{IdC} = 1.16$, CI = 0.76 − 1.79; biomass (main analysis): $RR_{IdC} = 1.16$, CI = 0.72 − 1.86] (Fig. 2.2). Nevertheless, the magnitude of response to protection did not differ significantly among the three protection regimes for target species density ($Q_M = 3.74$, df = 3, p = 0.15) and was marginally non-significant for target species biomass ($Q_M = 5.89$, df = 3, p = 0.05).

The meta-regression analyses revealed a negative relationship between effect size and the size of the partially protected area for fish assemblage biomass (Table 2.2, Fig. 2.3). The slope suggested an average decrease in assemblage biomass, relative to unprotected areas, of 17% for every ten-fold increase in PPA size. The response to protection of target species was not related to PPA size (Table 2.3), however the plots for the log-transformed PPA size indicate that the density and biomass of the target species inside the partially protected area became comparable to or less than those from the unprotected area (i.e. effect sizes approached zero or became negative, respectively) for PPA larger than 1000km^2 (Fig. 2.4).

Whereas the effect sizes for fish assemblage density and biomass were not significantly related to duration of protection (Table 2.2), the biomass of target fish species inside the partially protected area showed a slight (~3%) but significant reduction relative to the open access area upon increasing the duration of protection (slope = -0.03, CI = -0.06 - -0.003, Table 2.3, Fig. 2.4). The response to protection for target fish density was not significantly related to MPA age (Table 2.3).

The relationship between effect size and the distance of the unprotected control area to the partially protected area border was not significant for fish assemblages or for target species (Table 2.2, 2.3). It is worth mentioning that for the majority of PPAs (15 out of 18 cases), the unprotected control area was within 1.2 km (range: 0.02 – 1.2 km) of the partially protected area boundary, and amongst these PPAs the effect size was reasonably heterogeneous ($\overline{RR}$ range: -0.5 to 2) (Fig. 2.3, 2.4). The difference in the survey methodology represented here by the total census area was not significantly related to the fish assemblage or the target species response to protection (Table 2.2).

Table 2.2 Summary of the weighted simple random effects meta-regression models for each of the four moderator variables on **fish assemblage** density and biomass effect sizes comparing partially protected areas to unprotected areas (partial:open). Results presented are for the sensitivity analysis (i.e. habitat-confounded studies were removed from the analysis).

Fish assemblage Ln Response Ratio (partial:open)

Response variable	Moderator variable	N^o of MPAs	Slope [95% CI]	p-value
Density	Age (yrs)	17	-0.004 [-0.03 → 0.01]	0.71
Density	Log(size) (km^2)	17	0.04 [-0.12 → 0.2]	0.63
Density	Log(distance) (km)	15	-0.23 [-0.65 → 0.19]	0.98
Density	Census area (m^2)	16	0.002 [-0.65 → 0.19]	0.28
Biomass	Age (yrs)	18	0.006 [-0.01 → 0.02]	0.41
Biomass	Log(size) (km^2)	18	-0.17 [-0.29 → -0.04]	**0.01**
Biomass	Log(distance) (km)	15	-0.13 [-0.31 → 0.06]	0.18
Biomass	Census area (m^2)	15	-0.24 [-0.51 → 0.03]	0.18

Table 2.3 Summary of the weighted simple random effects meta-regression models for each of the three moderator variables on **fish target species** density and biomass effect sizes comparing partially protected areas to unprotected areas (partial:open). Results presented are for the main analysis (i.e. all studies were retained from the analysis as no influence of the habitat-confounded studies was found on the overall effect of protection).

Fish target species Ln Response ratio (partial:open)

Response variable	Moderator variable	N^o of MPAs	Slope [95% CI]	p-value
Density	Age (yrs)	33	-0.1 [-0.03 → 0.02]	0.45
Density	Log(size) (km^2)	24	-0.2 [-0.44 → 0.03]	0.09
Density	Log(distance) (km)	20	0.04 [-0.02 → 0.11]	0.21
Biomass	Age (yrs)	15	-0.03 [-0.06 → -0.01]	**0.03**
Biomass	Log(size) (km^2)	17	-0.07 [-0.25 → 0.11]	0.44
Biomass	Log(distance) (km)	14	0.007 [-0.05 → 0.06]	0.81
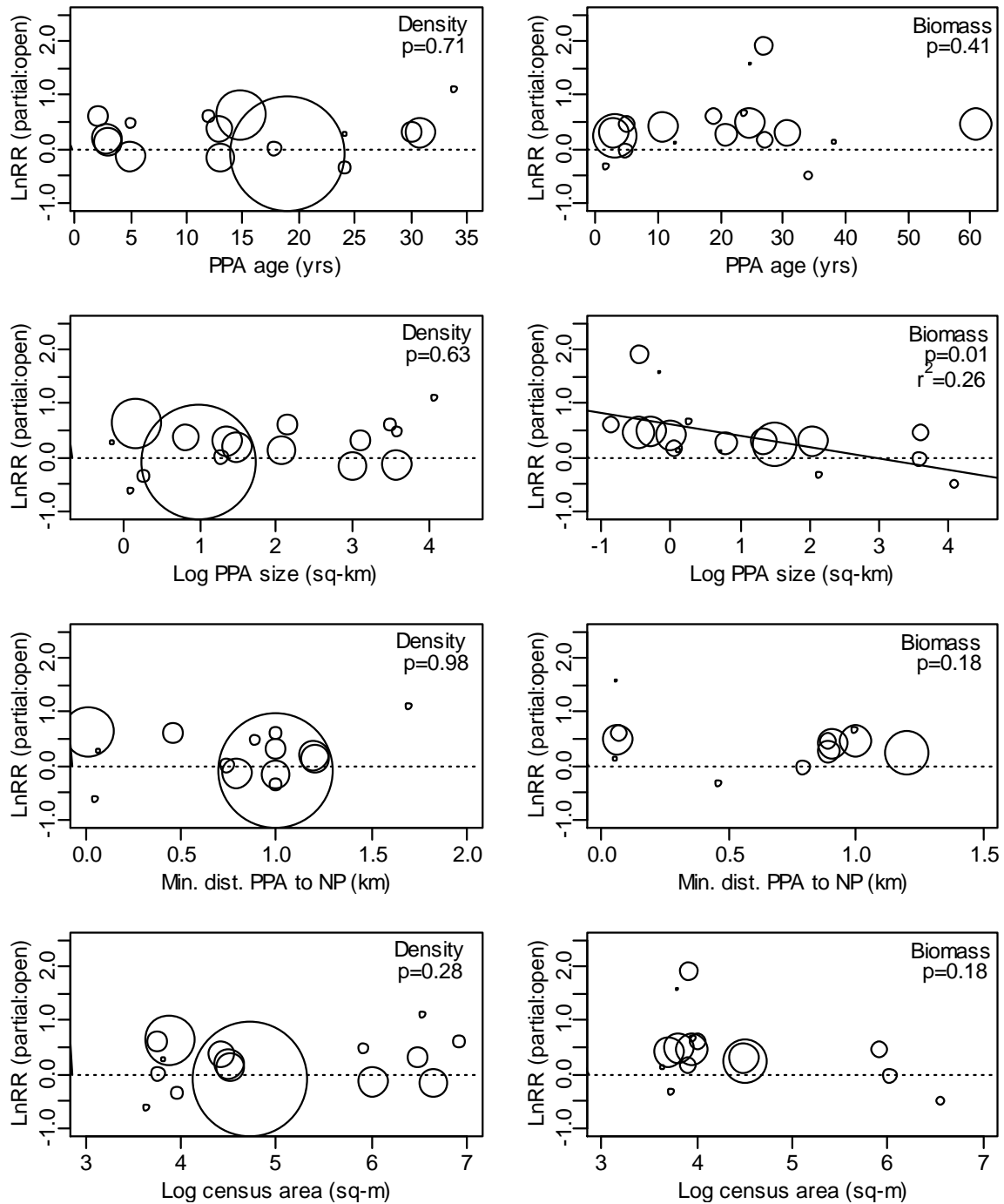
Fig. 2.3 The relationship of **fish assemblage** response to partial protection (partial:open) with MPA-related parameters (PPA age (yrs), Log PPA size (sq-km)) and survey method-related parameters (dist. PPA to NP (km), (Log census area (sq-m)) for density and biomass data. Size of the circles is proportional to the weight of the study.
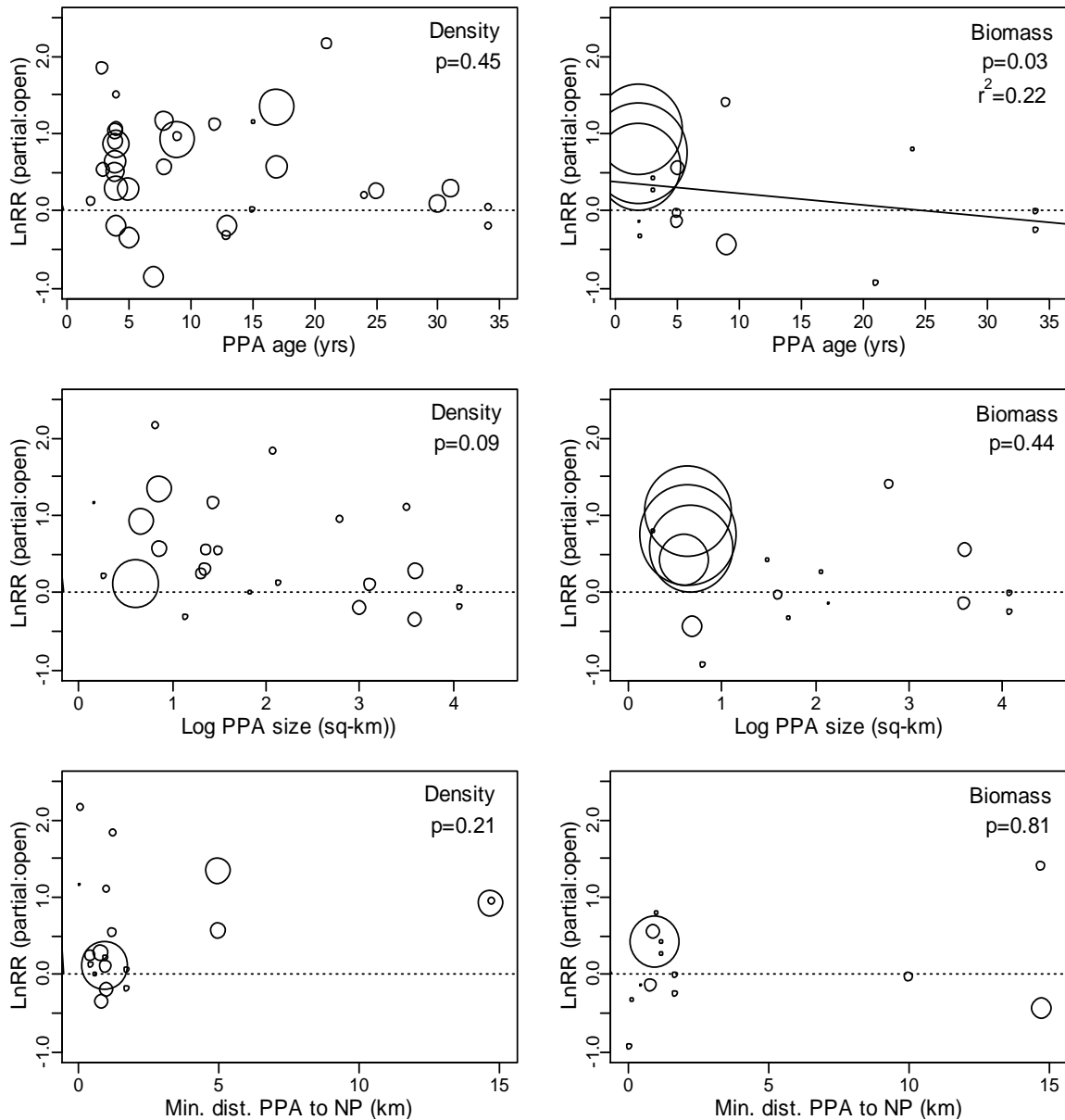
Fig. 2.4 The relationship of **target species'** response to partial protection (partial:open) with MPA-related parameters (PPA age (yrs), Log PPA size (sq-km), dist. PPA to NP (km) for density and biomass data. Size of the circles is proportional to the weight of the study.

2.4.2 Comparison of no-take reserves *vs.* partially protected areas

2.4.2.1 Effect of protection

Fish assemblage density was on average 11% higher in no-take reserves (NTRs) relative to partially protected areas (PPAs), but the difference was not significant (main analysis: $\overline{RR}$ = 1·11, CI = 0.86 - 1.43) (Fig. 2.5). In contrast, assemblage biomass was significantly higher,

with 92% more biomass in NTRs than PPAs (main analysis: $\overline{RR}$ = 1·92, CI = 1.28 - 2.89) (Fig. 2.5).

The biomass of target and non-target species was on average higher in no-take reserves than partially protected areas, but this increase was only significant for 'no-take reserve protected species' (NTP), that is for fisheries' target species that are protected inside the no-take reserve but not in the partially protected area (main analysis: RR_{TP} = 1.30, CI = 0.97 − 1.73; RR_{NTP} = 1.32, CI = 1.04 - 1.68; RR_{NT} = 1.63, CI = 0.83 − 3.22, Fig. 2.5). For density, the response to full protection was positive for the two target species categories, but negative for non-target species (Fig. 2.5). However none of the differences in number of individuals inside the NTRs compared to PPAs were significant. The magnitude of response did not differ significantly among the three 'exploitation status' categories, neither for density nor biomass (sensitivity analysis: density; Q_M = 3.01, df = 3, p = 0.22; main analysis: biomass Q_M = 0.36, df = 3, p = 0.83). It must be emphasized however, that this result should be interpreted with caution owing to the small number of MPA case-studies within each category, which reduces the robustness of the summary effect sizes (Fig. 2.5).
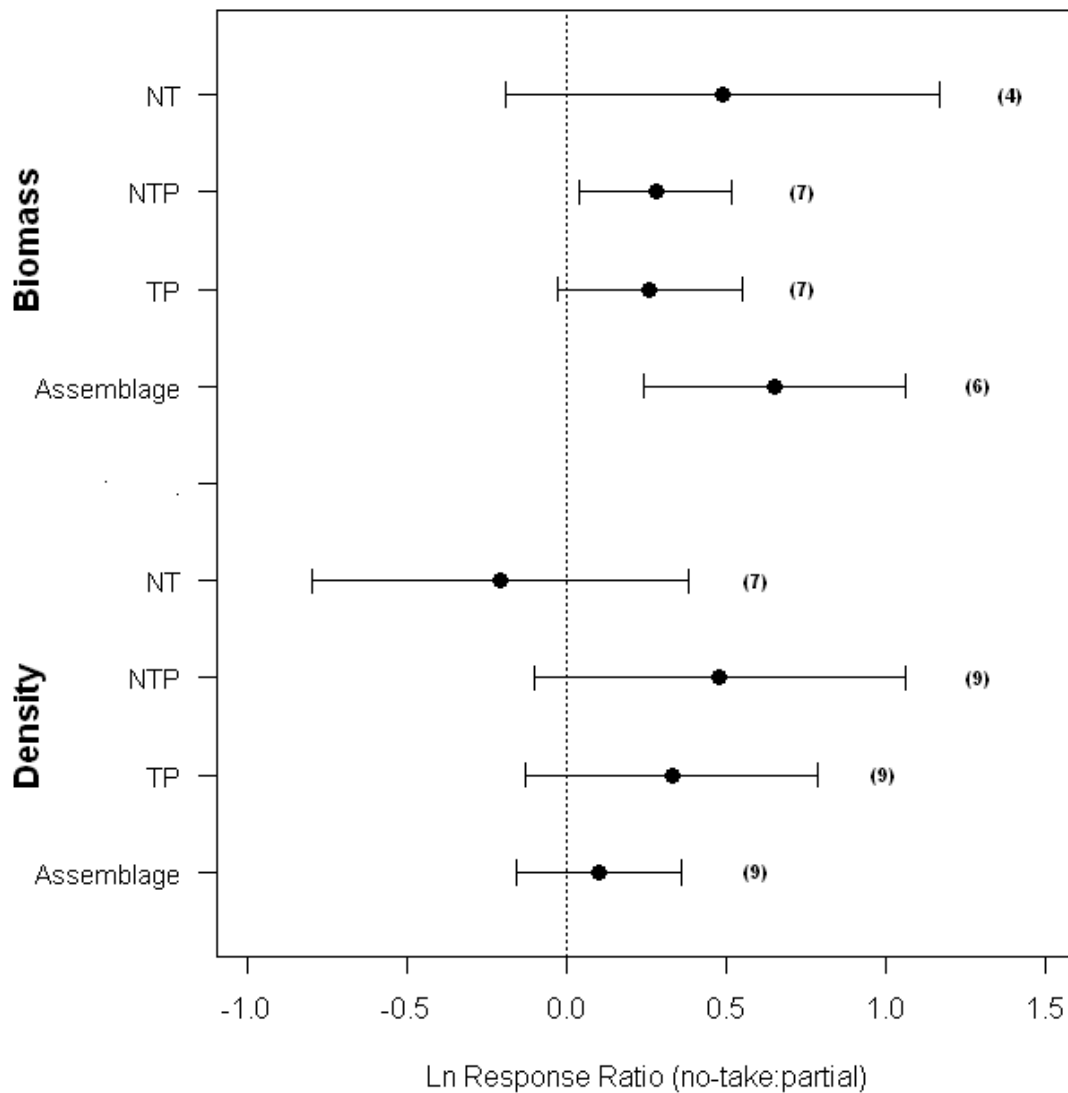
Fig. 2.5 Mean response ratios ($\overline{LnRR}$) of fish assemblage and 'exploitation status' categories using density and biomass data for no-take reserves compared to partially protected areas. Error bars represent the 95% confidence interval. NT refers to 'non-target species', TP to 'target, protected species', NTP to 'no-take reserve protected species'. Sample size (i.e. the number of MPAs) for each ratio is shown in parentheses. The vertical dotted line at ($\overline{LnRR}$) = 0 represents equal fish density or biomass inside the no-take reserve and the partially protected area; ($\overline{LnRR}$) > 0 means more fish inside the no-take reserve; ($\overline{LnRR}$) < 0 means fewer fish in the no-take reserve.

2.4.2.2 Correlates of response to protection

Duration of protection of the MPA, the size of the no-take area relative to the partially protected area (size ratio) and the distance between the no-take reserve and partially protected area did not explain a significant amount of variation in target species density or biomass effect sizes among MPAs (Table 2.4). Nonetheless, it appears that on increasing the size of

the no-take reserve relative to the partially-protected area, the density and biomass of target fish species becomes comparable between the two areas and in some MPAs the effect size goes to negative (i.e. NTR < PPA) (Fig. 2.6).

Table 2.4 Summary of the weighted simple random effects meta-regression models for each of the moderator variables on **fish target species** density and biomass effect sizes comparing no-take reserves to partially protected areas (no-take:partial). Results are for the sensitivity analysis (i.e. habitat-confounded studies were removed from the analysis).

Fish target species Ln Response ratio (no-take:partial)

Response variable	Moderator variable	N^o of MPAs	Slope [95% CI]	p-value
Density	Age (yrs)	13	0.04 [-0.03 → 0.11]	0.23
Density	Size ratio (NTR:PPA)	11	-2.33 [-5.12 → 0.45]	0.1
Biomass	Age (yrs)	10	0.02 [-0.02 → -0.06]	0.4
Biomass	Size ratio (NTR:PPA)	10	-0.37 [-0.96 → 0.21]	0.21
Biomass	Log(distance) (km)	10	-0.04 [-0.16 → 0.07]	0.47
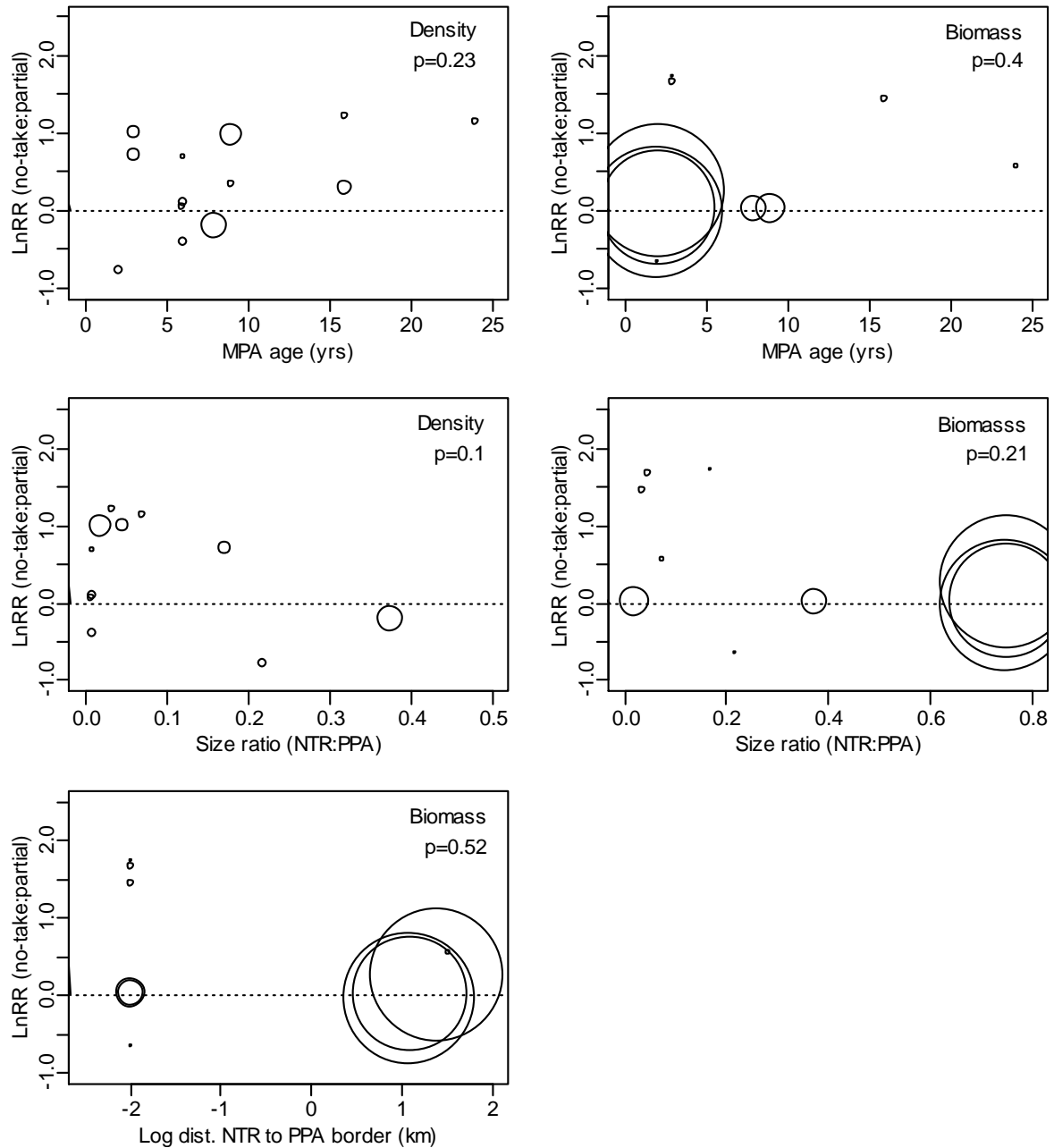
Fig. 2.6 The relationship of **target species'** response to full vs. partial protection (no-take:partial) with MPA-related parameters (PPA age (yrs), size ratio (NTR:PPA), Log dist. NTR to PPA border (km)) for density and biomass data. Size of the circles is proportional to the weight of the study.

2.5   DISCUSSION

This synthesis suggested that while partially protected areas significantly enhance the density and biomass of fish relative to open access areas, no-take reserves generally produced greater increases in fish numbers and yielded significantly higher biomass of fish within their boundaries relative to partially protected areas. The positive response to protection, whether

full or partial protection, was primarily driven by target fish species. The response for non-target species was more variable, although this was the 'exploitation status' category for which we had the least data. There was a large degree of variability in the magnitude of response to protection for all response variables. The factors determining such variation were generally unclear although the size of the MPA explained some of this variability. Examination of the protection regime within the partially protected area provided novel insights into the efficacy of partial MPAs for conservation and management.

The finding that the magnitude of protection effect is higher for no-take reserves than for partially protected areas is in agreement with the conclusion from a previous study by Lester and Halpern (2008). However, whereas this study found significantly higher response ratios (no-take:partial) for biomass ($\overline{RR} = 1.92$) than for density ($\overline{RR} = 1.11$), Lester and Halpern (2008) reported significantly higher differences between no-take reserves and partially protected areas for density ($\overline{RR} = 1.79$) but not for biomass ($\overline{RR} = 1.22$). One important difference between the two syntheses that might explain the discrepancy in findings, is that this study focussed on fish species only, whereas Lester and Halpern (2008) integrated data across broad taxonomic groups (fish, invertebrates, algae) with different life history (e.g. growth rate) and ecological characteristics (e.g. larval dispersal potential, adult mobility). For example, the sessile nature and the relative low mobility of some species (e.g. urchins, gastropods, corals, sponges) included in Lester and Halpern (2008), might have resulted in the larger differences in density that they observed between no-take reserves and partially protected areas. Furthermore, the density of individuals is also susceptible to stochastic recruitment events, such that the movement of juvenile fish across the no-take reserve boundary into the adjacent partially protected area may explain the smaller magnitude of protection effect that we observed for fish density. However, the high positive response observed in this study for fish biomass provides evidence towards the protection benefit of fully protected areas from size-selective fishing or accidental catch.

The amount of protection provided to target species will greatly influence the performance of the partially protected area relative to the no-take reserve. Lester and Halpern (2008) suggested that failure to detect significant ecological effects of partially protected areas was because most of the studies they reviewed reported data for species that were fished in both the partially protected and fished areas. I have thus kept target species that are protected only

by no-take reserves separate from those that are protected in both the no-take reserves and partially protected areas. Significantly higher biomass in the no-take reserve than in the partially protected area was observed only for target species that were protected in the no-take reserve but not in the partially protected area, suggesting that exclusion of all human-related disturbances allows more effective recovery of some previously exploited populations.

Marine protected areas (MPAs) may meet their objectives in a number of ways without necessarily excluding all extractive activities; habitat protection can be achieved by exclusion of benthic gears (e.g. Fogarty and Murawski 1998; Beukers-Stewart et al. 2005; Smith et al. 2008), avoidance of conflict can be achieved by spatial segregation of uses conflicts (e.g. Pipitone et al. 2000; Blyth et al. 2002), sustainable exploitation or recovery of over-exploited fish stocks can occur within gear-specific exclusion areas (e.g. Murawski et al. 2000; Fisher and Frank 2002). I have thus synthesized data for studies that have only examined effects of partially protected MPAs relative to open access areas to further increase our understanding of the potential value of those MPAs which strike a balance between allowing user access and achieving management and conservation measures. The majority of partially protected areas included in this study produced consistently higher density (11 out of 15 MPAs) and biomass (14 out of 17 MPAs) for fish assemblages relative to open access areas. Only a minority showed no improvement over fished areas. Almost certainly, the frequency and intensity of exploitation experienced by a species in a fishery will greatly influence the magnitude of response to protection from fishing. Indeed, the positive response to protection in partially protected areas relative to open access areas was mainly driven by species of commercial importance. This finding is in agreement with previous meta-analyses that compared fish populations in no-take marine reserves and open access areas (Mosquera et al. 2000; Micheli et al. 2004; Lester et al. 2009; Molloy et al. 2009), and hence suggests that well-managed and enforced partially protected areas with some restrictions on use are also a valuable tool to counteract the decline of target populations or to assist recovery of over-fished stocks.

In addition to the 'exploitation status' of individual fish species, 'protection regime' of the MPA, which defined the amount of protection afforded to target species by the partially protected area, was a key determinant of the magnitude of MPA efficacy. Of the three categories of protection regime, this analysis revealed that the magnitude of response to

partial protection was the largest for partially protected areas that excluded commercial fishing with mid-water gear but permitted fishing on a recreational basis. Such protection regimes typically exist in tropical and sub-tropical regions. Interestingly, such protection resulted in greater positive response than those MPAs (typically found in temperate regions) which excluded bottom-towed gear but allowed fishing with mid-water gear (e.g. nets and long-lines) or static gear (e.g. pots, traps). This is perhaps counter-intuitive given the well-recognized negative impact of towed bottom fishing gear on biota and habitat (Collie et al. 2000b; Kaiser et al. 2006; Hinz et al. 2009). However, MPAs that excluded bottom towed gear were typically established to protect large mobile demersal fish such as cod, haddock, hake and saithe (e.g. Link et al. 2005; Jaworski et al. 2010; Dimech et al. 2008), which are likely to experience less benefits from protection (e.g. compared to reef-associated species) due to their high mobility and dispersal distances. Additionally, benthopelagic species that rely on benthic invertebrates for their food might take longer to respond to protection as habitat recovery following disturbance by bottom-towed gear will have to occur before these species can begin to recover.

The relationship between the response to protection and different MPA characteristics including duration of protection, size of MPA and distance to MPA was complex and variable. Nevertheless, a number of observations are worth highlighting about the influence of MPA size on effect size. Interestingly, this study revealed a trend towards a reduction in the density and biomass difference between no-take reserves and partially protected areas for target species upon increasing the size of the no-take reserve relative to the partially protected area. The size of the no-take reserve ranged between $0.1km^2$ and $30.5km^2$ and that for partially protected areas ranged between $1.9 km^2$ and $140.1 km^2$ for case-studies comparing NTRs to PPAs. In 10 out of 11 cases the no-take reserve was less than 80% the size of the partially protected area. The larger proportion of species afforded protection upon increasing the size of the no-take reserve, should lead to greater spill-over of adult biomass in areas outside the no-take reserve. Given that in the majority of MPAs included in the dataset the no-take reserve and the partially protected area were adjacent to each other (due to zonation scheme), it is plausible to assume that some of the biomass accrued in no-take reserve ends up in the partially protected area as a result of spill-over (estimated a range of spill-over distances between 800m and 1500m (Goni et al. 2006, Harmelin-Vivien et al. 2008; Halpern et al. 2010).

Equally interesting, this study found that increasing the size of the partially protected area, in particular above 1000km^2, reduced the effectiveness of partial protection relative to no protection for fish assemblages as well as for target species. This was somewhat surprising given that previous theoretical and empirical studies have shown that larger MPAs are more effective at increasing biodiversity and density of commercial species (Hastings and Botsford 2003; Roberts et al. 2003; Claudet et al. 2008). It is not unrealistic to assume that non-compliance and infringement of regulations are more likely in large than in small MPAs (Chiappone and Sullivan-Sealey 2000). The size of the partially protected areas in the dataset comparing PPAs to Open areas ranged between 1.5 km^2 and 11980 km^2 and although a single instance of illegal fishing in a small PPA can have a more damaging effect than in a large PPA, it is more likely that the frequency of illegal fishing is higher in large PPAs. This may explain the lower effectiveness of protection that we observed for partially protected areas over 1000km^2 in size. Another possible explanation for results not conforming to expectation is the inadequacy of the sampling effort. Among the studies included in our analysis, the majority (24 out of 27) surveyed an area equivalent to less than 1% of the total area of the partially protected area. The proportion of area surveyed for MPAs larger than 20km^2 was only 0.1% of the MPA area, suggesting that the sampling effort for large MPAs may have inadequate power to detect subtle changes in density or biomass between the protected and unprotected areas.

It needs to be emphasized that the MPA-related covariates examined in this meta-analysis explained only a small proportion of the total variability ($r^2 = 0.17 - 0.26$) whenever significant relationships occurred, indicating that the heterogeneity in effect size among MPAs is also influenced by other factors not investigated in this study. These factors could be related to the biological and ecological characteristics of different species (Tuya et al. 2006; Smith et al. 2008; McLean et al. 2010) as well as to the nature of the physical environment and habitat within the MPA (Link et al. 2005; Jaworski et al. 2010). The historical levels of exploitation in the MPA and the range and relative intensity of exploitation activities in reference fished areas are two further key factors affecting MPA performance. For example, Edgar et al. (2009) found low level of change for fish between the MPA and fished areas because pre-existent fishing pressure across the region was low and historically depressed stocks only slightly. Conversely, McLean et al. (2010) found very little change between protected and unprotected populations of *Lethrinus harak* even after 15 years of protection because previously high levels of exploitation combined with low recruitment years for this

species led to large reductions in the abundance of this species across the region. In their study of the efficacy of the Invertebrate no-take reserve (PPA) at Santa Catalina Island, California, Iacchei et al. (2005) recorded a 3% increase in lobster (*Panulirus interruptus*) density in the MPA relative to a recreationally fished control area, but found a 57% increase when compared to a commercially fished area. These examples serve to show the importance of including exploitation intensity inside and outside the MPA, which remain somewhat overlooked in most studies including those reviewed in this study, for a more within-context interpretation of the efficacy of MPAs.

It is a challenge to balance the uncertainty surrounding the results of meta-analysis against their potential impact when considering management implications. Throughout the study selection process, as specified by the systematic review methodology, I have applied stringent study inclusion and quality assessment criteria in the hope of providing the best quality evidence for evaluating the efficacy of marine protected areas. I have thus excluded studies where enforcement of the MPA was described as poor or degrading during the time of survey (e.g. Acosta, 1999; Floeter et al. 2006), and have controlled for the influence of habitat confounding (as a result of habitat differences between the protected and control areas at baseline) by running a sensitivity analysis, that excluded habitat-confounding studies (e.g. Miller et al. 2005; Monaco et al. 2009), alongside the main analysis. As the primary objective of the study was to examine the effectiveness of different levels of protection in a MPA, studies that did not provide a clear description of the protection regime inside the MPA (e.g. Ohman et al. 1997; McClanahan and Muthiga 1988; Lipej et al. 2003) or that provided data from full and partial protection mixed together (e.g. sampling from within the integral reserve and the buffer zone treated together as 'protected' in the results; Garcia-Charton et al. 2004; Guidetti et al. 2005) were excluded. When comparing fully protected and partially protected MPAs, I excluded studies where the two MPAs were established more than 2 years apart (e.g. Jennings et al. 1996, Denny and Babcock 2004; McClanahan et al. 2006; Jack et al. 2009) as this difference in duration of protection is likely to confound the effect of protection from different levels of protection. I did not include *de facto* MPAs (i.e. areas around oil platforms or areas 'protected' because of their inaccessibility) (e.g. Roberts and Polunin 1992; Schroeder and Love 2002; Bergman et al. 2005), as the search terms were specific to capture 'true' MPAs (i.e. those designated under some legislation). As part of this study quality control, I have undertaken a weighted meta-analytical approach to factor in for sample size and within-study variance in the overall effect of protection, and have thus excluded studies

that did not provide sample sizes and variance measures (e.g. Ault et al. 2006). Whilst acknowledging that these strict criteria might have led to some information loss and a reduction in the pool of available studies (in particular for comparison of no-take reserves to partially protected areas), I believe that there is little benefit in including biased or confounded studies. A valid constraint that needs to be acknowledged in these analyses, however, is that density and biomass comparisons were based on single snapshot datasets after MPA establishment. Only a handful of studies included in this analysis were based on strong experimental designs such as BACI and beyond-BACI studies (Underwood 1992; Guidetti 2002) (see Appendix 2.6.2). Ecosystem processes are spatially and temporally variable at multiple scales and these variations can obscure the detection of the effects of protection (García-Charton and Pérez-Ruzafa 1999). Hence whilst acknowledging the time constraints and increased financial costs associated with BACI empirical studies, I advocate that the controversy as to whether any differences are a consequence of protection or are merely coincidental can only be satisfactorily addressed by further monitoring incorporating assessment of change from baseline conditions.

This study addressed an important question for managers and policy-makers of whether partially protected areas are an effective management option for conservation and fisheries compared to fully protected and unprotected areas. These results suggest that no-take reserves provide some benefit over less protected areas, nevertheless the significant ecological effects of partially protected areas relative to open access areas suggest that partially protected areas are a valuable spatial management tool particularly in areas where exclusion of all extractive activities is not a socio-economically and politically viable option. Change in the distribution of fishing effort could result in economically negligible net benefits (Jones 2008) or may be detrimental to habitats previously undisturbed by anthropogenic activities (Hiddink et al. 2006a). Hence, while acknowledging that MPAs are not a panacea for conservation and fisheries management, under the right conditions (that may include additional reduction of fishing effort in fishing grounds surrounding MPAs, or a network of MPAs that allow a mix of protection levels, or involvement of multiple stakeholder groups during the designation process), MPAs are valuable tools for the preservation and enhancement of fish populations.

CHAPTER 3

The influence of fish life history and ecological attributes on the efficacy of marine protected areas

3.1 ABSTRACT

The response to protection from marine protected areas may vary among species due to differences in species' ecological traits and life history characteristics. In spite of the overall positive effects of full and partial protection observed from the meta-analysis in the previous chapter, there was broad variation in the response to protection among MPAs. MPA characteristics such as age and size explained some but not all of the variation. In this study, the same datasets analyzed in Chapter 2 are used to examine the effects of life history and ecological traits on the response of fish species to fully and partially protected areas. Densities of large, slow-growing species were greater in no-take reserves than in partially protected areas. In contrast, when fish density and biomass were compared in the partially protected area and the non-protected area, the response to protection decreased on increasing maximum body size. Adult habitat preference explained some of the variation of the species' response to protection. Reef-associated species that were generally characterized by species with high site-fidelity showed the strongest benefit from full protection relative to partial protection. The response to protection in partially protected areas relative to non-protected areas was also influenced by habitat type but the effect differed among species with different exploitation level; for target species the response was highest for benthopelagic species, whereas for non-target species the response was highest for reef-associated species. Large and old no-take reserves had significantly higher numbers of target species inside the reserves relative to partially protected areas. In contrast, benefit from full protection decreased for non-target species on increasing the size and age of the no-take reserve. This study has demonstrated that the magnitude of protection effect varies with exploitation status and species-specific traits such as body size and habitat, which may interact with age and size of the MPA. These considerations need to be incorporated in the design of new MPAs to ensure that protection is provided at spatial scales relevant to species in need of conservation.

Key words: body size; exploitation level; adult habitat type; life history traits; marine protected area; partial protection; full protection; MPA design; mixed-effects modelling

3.2 INTRODUCTION

Fishing is now widely recognized as one of the most significant anthropogenic influences on marine ecosystems (Dulvy et al. 2003; Halpern et al. 2007; 2008), with direct negative impacts on the numbers, size and reproductive output of target species (Myers et al. 1996; Jennings et al. 2002; Graham et al. 2005; Scott et al. 2006; Barrett et al. 2007). The wider ecosystem effects of fishing such as changes in the functional diversity and trophic structure of biotic communities has gained increasing recognition over recent decades (Jennings et al. 1995; Greenstreet and Hall 1996; Collie et al. 2000a; Pinnegar et al. 2000; Martins et al. 2012). Marine protected areas (MPAs) have often been used as a tool to restore biodiversity (Lubchenco et al. 2003; Willis et al. 2003), but have also been employed to aid the recovery of heavily fished stocks (Garcia-Rubies and Zabala 1990; Macpherson et al. 2002; Goni et al 2008) through the provision of refuge areas from fishing and sources of larvae to exploited sink populations (Roberts and Polunin 1991; Carr and Reed 1993, Lipcius et al. 2008).

Evidence for population recovery in marine protected areas (MPAs) comes from empirical studies showing that the abundance of some species is higher in the protected than in the adjacent fished areas, or that abundance in the protected area has increased following protection (e.g. Mosquera et al. 2000; Micheli et al. 2004; Lester et al. 2009; Maliao et al. 2009; Fenberg et al. 2012). Whereas the effects of protection in no-take reserves are well documented, relatively fewer studies have attempted to generalize the ecological effects of partially protected areas with less restrictive regulations on extractive uses. In Chapter 2 I have examined the abundance of fish species in partially protected areas relative to no-take marine reserves and open access fished areas. In general positive effects on fish populations were higher in no-take marine reserves, but partially protected areas were still effective, with fish numbers and biomass on average 21% and 51% higher than that of open access areas, respectively (Chapter 2). Although these syntheses have shown an overall positive response to protection, they have also revealed broad variation, both in the direction and magnitude of the efficacy of protection among MPAs (e.g. Cote et al. 2001; Chapter 2) and among individual species responses (e.g. Mosquera et al. 2000; Micheli et al. 2004; Lester et al. 2009). The heterogeneity in the response may stem from differences in the design or age of MPAs (Micheli et al. 2004; Claudet et al. 2008; Molloy et al. 2009; Chapter 2), differences in species' ecological traits and life history characteristics (Molloy et al. 2008; Claudet et al.

2010), differences in the susceptibility of fish species to capture (Tuya et al. 2006; Valle and Bayle-Sempere 2009), or a combination of these effects.

Life history characteristics such as body size, growth rate and age at maturity that influence the rate at which a population can replace itself (Denney et al. 2002) have been shown to be important determinants of the response to exploitation (Jennings et al. 1998; Gerber et al. 2002; Reynolds et al. 2005) and recovery from fishing (Hutchings 2000; Barrett et al. 2007). For example, small or fast-growing species with early maturity have been associated with higher reproductive output and recruitment that enables them to sustain higher instantaneous mortality rates than their large or slow-growing counterparts (Denney et al. 2002). Moreover, smaller species may suffer lower fishing mortality relative to larger species because they may be less desirable and less accessible targets in size-selective fisheries (Jennings et al. 1995, 1999). Not surprisingly, therefore, fish taxa characterized by larger body sizes have been shown to respond better to protection than smaller species following the complete elimination of fishing mortality as a result of the establishment of marine reserves (Mosquera et al. 2000; Barrett et al. 2007; McClanahan and Hicks 2011). The rate of movement and migration between protected and fished areas, and the degree of association of a species with a specific habitat for food and shelter will also influence the response to protection (Jennings 2001). For example, a more rapid response to protection is expected for relatively site-attached species that spend most of their time inside the protected area (Kramer and Chapman 1999; Willis et al. 2001), or when the area of the MPA is proportional to the dispersal distances of species (Fisher and Frank 2002).

Previous quantitative syntheses of fish populations in no-take marine reserves have examined the influence of species ecological and life history characteristics on the magnitude of individual species response to protection, expressed as a ratio of abundance in the no-take marine reserve and the fished area (Micheli et al. 2004; Molloy et al. 2008; Claudet et al. 2010). Here, I retain the same sets of MPAs used in Chapter 2 and build on earlier work to examine how different species characteristics, including maximum body size, adult habitat type and exploitation status affect the abundance of species (density and biomass) in response to partial protection. The magnitude of the response to partial protection is expressed as the ratio of the mean species density and biomass: (i) in the partially protected area relative to the open access area, and (ii) in the no-take marine reserve relative to the partially protected area. Moreover, I analyze how the traits of species may interact with age and size of the MPA and

protection regime of the partially protected area, which also affect responses to protection (see Chapter 2). This understanding will help predict what species are more likely to benefit from protection within fully and partially protected marine areas on the basis of their life history characteristics.

3.3   METHODS

3.3.1 The datasets

The same datasets compiled in Chapter 2 that compared fish densities and biomass (i) in a no-take marine reserve to a partially protected marine area or (ii) in a partially protected marine area to an open access area were used for this chapter. Studies were included in the analyses if density and/or biomass estimates reported for inside and outside the MPA were available at the species level.

Ultimately four datasets were compiled: two datasets comparing density (N = 33 MPAs; 225 species) and biomass (N = 18 MPAs; 148 species) in the partially protected area and the open access area, and another two datasets comparing density (N = 12 MPAs; 115 species) and biomass (N = 10 MPAs; 42 species) in the no-take marine reserve and the partially protected area. The number of species censused per MPA ranged between 1 and 54 species. A complete list of studies included in this study, together with MPA-related and individual species characteristics are given in Appendix 3.6.1.

3.3.2 Effects of species' traits on response to protection

The primary goal was to examine the effect of fish species traits on the response of individual species to protection. Therefore, data were extracted for the following species traits from "FishBase" (available online): (i) maximum body size; (ii) growth coefficient from the von Bertalanffy growth function (K); (iii) trophic level (Troph = 1 + mean trophic level of food items); and (iv) adult habitat type (reef-associated, benthopelagic, demersal). Information on age or size at maturity, fecundity, adult and larval dispersal and other species-specific traits that are likely to influence the response of a species to protection, were available for only a small number of species and were therefore not included in these analyses. Instead, the maximum body size was used as a surrogate for some of these poorly known life history traits, since this index of body length has been shown to be negatively correlated with age at

maturity and positively correlated with reproductive output and home range size (Beverton 1963, 1987; Kramer and Chapman 1999; Jennings 2001; Denney et al. 2002). Additionally, data were extracted for the following MPA-specific variables using information from the source papers: (i) the level of exploitation of individual fish species (exploitation status: target or non-target); (ii) the duration of protection (number of years between MPA enforcement and census); (iii) the size of the no-take marine reserve and the partially protected area (km^2); and (iv) the type of protection regime inside the partially protected area (protection regime: 'discriminate, commercial' or 'discriminate, recreational' or 'indiscriminate, commercial') (refer to Appendix 2.6.3 for full details on the 'protection regime' classification scheme).

3.3.3 Statistical analysis

Linear mixed-effects models were used to assess how individual species' responses to protection were affected by the species-specific traits and the MPA characteristics described above. The growth coefficient (K) (r = -0.4, p < 0.001) and trophic level (r = 0.42, p < 0.001) were found to be significantly correlated to maximum body size, and hence were considered redundant for the analysis. The species' response to protection was expressed as the natural log of the ratio of the mean density or biomass estimate measured inside the partially protected area and in the open access, or alternatively the ratio of the mean density or biomass estimate measured inside the no-take marine reserve and in the partially protected area (Hedges et al. 1999; Osenberg et al. 1999). Positive response ratios (Ln *RR*) indicate that the species has higher abundance inside the partially protected area relative to the open access area, or inside the no-take reserve relative to the partially protected area.

The linear mixed-effects model consisted of a random effect term and a combination of several main fixed effect terms. The random effect term 'MPA ID' was included to control for non-independence of individual fish species measurements within a MPA because the response ratio of individual species within a MPA are more likely to be correlated to each other than those of species recorded from another MPA. The influence of including the random effect term was tested by comparing models constructed with no random component and with a random intercept, using the generalized linear function (gls in R) and the linear mixed-effects function (lme in R), respectively (R Development Core Team, 2004) (Zuur et al. 2009). The optimal random effects structure was determined with the likelihood ratio test

of restricted maximum likelihood (REML) estimates for each model (Zuur et al. 2009). The resulting p-values were corrected to account for the fact that this test occurred on the boundary and therefore violated the assumption that the likelihood values followed a χ^2 distribution. The log-likelihood test showed that the random effect term improved the model over the generalized least squares model with no random component, and hence the random term 'MPA ID' was included in the mixed effects model.

The fixed effects component of the model consisted of several main fixed effect terms and two-way interaction terms that examined a number of ecologically relevant hypotheses on the species' response to protection (Table 3.1). Four separate models were examined; one for each of the four datasets described above. The terms included in each of the four 'full' models are indicated by a 'Y' in Table 3.1. Some terms that included a categorical variable, for example 'adult habitat type' and 'exploitation status' in Dataset 4, were not included in the model due to inadequate number of observations within each category. These variables are indicated by a 'N' in Table 3.1. Maximum body size and size of the MPA were log-transformed prior to analysis. Selection of the final (most parsimonious) model was undertaken by using the Akaike's Information Criterion (AIC) estimated with a maximum likelihood (ML) fit to compare a sequence of nested fixed term models in which non-significant interaction and main effects were incrementally removed (Zuur et al. 2009). All statistical tests were performed at $\alpha = 0.05$ level. After completing model selection, the final model was refitted with the REML method for reporting significant relationships (Zuur et al. 2009). Model verification consisted of visually inspecting quantile-quantile plots for normality and normalized residual plots for homogeneity of variance. Plots of linear predictors against normalized residuals revealed variance to be approximately constant for all models.

3.3.4 Sensitivity analysis

A previous critical evaluation of the quality of the studies included in this chapter and in Chapter 2, identified a number of 'habitat-confounded studies', whereby features such as substratum type, substratum composition and complexity, rugosity and exposure, were reported by the study authors to be significantly different for the studied locations inside and outside the MPA. As differences in habitat characteristics between the MPA and the control areas may mask or confound the effect of protection due to the MPA itself, all analyses were

repeated with and without the 'habitat-confounded studies' to examine the influence of including them on the relationship of species traits and response ratio. The results for the sensitivity analysis (i.e. excluding the 'habitat-confounded' studies) were reported when the two differed (for model outputs from the full and sensitivity analysis see Appendix 3.6.2).

Table 3.1 Summary of the hypothesis examined under each fixed effect term of the linear mixed-effects model. The fixed effect terms included in each of the four models (one model for each dataset) are marked with a 'Y'. 'N' indicates that the term was excluded from the model due to insufficient data. Datasets 1 and 2 compare the response of species to protection inside the partially protected area (PPA) relative to the open access area (NP) in terms of density and biomass, respectively. Datasets 3 and 4 compare the response of species to protection inside the no-take reserve (NTR) relative to the partially protected area (PPA) in terms of density and biomass, respectively.

Code	Fixed effect term	Hypothesis	Datasets			
			LnRR = PPA / NP		LnRR = NTR / PPA	
			Dataset 1	*Dataset 2*	*Dataset 3*	*Dataset 4*
Main terms			Density	Biomass	Density	Biomass
H1	Maximum body size (L_{max})	Species that attain large body sizes exhibit stronger positive responses to full or partial protection	Y	Y	Y	Y
H2	Exploitation status (ES)	Response to protection for species targeted by the fishery is higher than for non-targeted species	Y	Y	Y	N
H3	Adult habitat type (Env)	The response to protection for reef-associated species is stronger than for benthopelagic and demersal species, because the former are likely to remain within the MPA due to higher site fidelity	Y	Y	Y	N
H4	Duration of protection (Age)	The response to protection increases with increasing duration of protection	Y	Y	Y	Y
H5	Partially protected area size (PPA size) No-take marine reserve size (NTR size)	The response to protection increases with increasing size of the partially protected area or the no-take marine reserve	Y	Y	Y	Y

H6	Protection regime (PR)	'Indiscriminate, commercial' partially protected areas that were fished with bottom-towed gear prior to the establishment of the MPA, will exhibit smaller responses to protection than 'discriminate, recreational' or 'discriminate, commercial' partially protected areas as habitat recovery will have to occur before some species' populations can begin to recover	Y	Y	N	N
Two-way interaction terms						
H7	L_{max} x Size	Species characterized by large body size (proxy for mobility) exhibit stronger positive responses to protection in relation to MPA size, whereas MPA size should not influence responses for smaller species	Y	Y	Y	Y
H8	L_{max} x Age	Species characterized by large body size (slow-growing, late-maturing) may exhibit strong positive responses to protection with increasing duration of protection than smaller species (fast-growing)	Y	Y	Y	Y
H9a *H9b*	ES x Size ES x Age	The response of target fish species to protection is stronger for larger and older MPAs, whereas the response for non-target species is not influenced by the size or age of the MPA	Y	Y	Y	N
H10	ES x Env	The response to protection is expected to be higher for reef-associated target species than for target benthopelagic and demersal species, because the former are likely to remain within the MPA due to higher site fidelity. No such differences among groups is expected for non-target species.	Y	Y	Y	N

H11a *H11b*	ES x PR Env x PR	Target fish species and species with high site-fidelity (such as reef-associated species) exhibit stronger response to protection inside partially protected areas that permit fishing on a recreational basis (discriminate, recreational) than those that allow fishing on a commercial basis (indiscriminate, commercial; discriminate, commercial) as fishing pressure is lower in the former.	Y	N	N	N

3.4 RESULTS

3.4.1 Effects of species' traits on the response of fish species to partial over no protection

3.4.1.1 Density (dataset 1)

The response ratios of individual species to protection exhibited broad variation, ranging from strongly negative to strongly positive in all studies comparing fish density inside and outside the partially protected area (Fig. 3.1). Nevertheless, the proportion of species showing an increase in the density inside the partially protected area relative to the open access area (i.e. positive response ratio, LnRR) (65%; 146 out of 225 species) was higher than the proportion of species showing a negative response to protection (34%; 76 out of 225 species). For a substantial proportion of species (34%; 77 out of 225 species) the density inside the partially protected area was more than double that in the fished area (i.e. LnRR > 0.69).

Species' exploitation level, adult habitat type, the protection regime and age of the partially protected area exhibited no significant relationship with the response ratios of individual species (Fig. 3.1A – D). The interaction between species' body size and the size of the partially protected area (L_{max} x PPA size) was the only term that explained a significant amount of variation in the magnitude of species response to protection (Table 3.2). The interaction term revealed two opposing trends; whereas the magnitude of response to protection increased on increasing the size of the partially protected area for small fish species, the response to protection went to negative (i.e. density in NP > PPA) for large fish species with increasing PPA size (Fig. 3.1G).

Fig. 3.1 Relationship between species' response ratio (using density data) and different species' traits and partially protected area (PPA) characteristics. Response ratio is the ln-transformed ratio of the mean species density in the PPA to that in the open access area. Adult habitat types are benthopelagic (BP), demersal (DEM), reef-associated (RA). PPA protection regime categories are 'discriminate, commercial' (DC), 'discriminate, recreational' (DDR), 'indiscriminate, commercial' (IdC). The significant interaction between fish size [Log)Max. body size)] and PPA size [Log(PPA size)] is shown in the contour plot G. The colour gradient from red to yellow indicates a gradient from negative to positive response ratios.

Table 3.2   Final model output for dataset 1, showing the species' traits and partially protected area characteristics that were significantly related to the response of fish species to protection, calculated as the ln-transformed ratio of the density estimate inside the partially protected area relative to the open access area. The structure of the final model was: Response ratio ~ log(L_{max}) x log(PPA size), random = ~1| MPA ID.

Variable	Estimate	SE	df	t-val	p-val
Intercept	0.50	0.13	178	4.10	**0.0001**
Log(PPA size)	-0.12	0.09	20	-1.25	0.22
Log(L_{max})	-0.44	0.35	178	-1.25	0.21
PPA size x L_{max}	-0.62	0.23	178	-2.66	**0.009**

3.4.1.2 Biomass (dataset 2)

In the same way as for density, a larger proportion of species achieved higher biomass inside the partially protected area than in the fished area. 56% (83 out of 148 species) showed a positive response while 42% (62 out of 148 species) showed a negative response. The proportion of species showing a positive response to partial protection was higher for density (65%) than for biomass (56%).

The magnitude of species' response ratio was not related to any of the MPA-related variables examined (Fig. 3.2A – C). In contrast, the response was negatively related to the species' maximum attainable body size, suggesting that the response to partial protection was higher for small fish species than for large species (Fig. 3.2D, Table 3.3). Furthermore, a significant amount of variation in response was explained by the interaction term 'Exploitation status x Adult habitat type' (Table 3.3). Target species that were categorized as benthopelagic showed the strongest response to protection relative to demersal or reef-associated target species (Table 3.3, Fig. 3.2E). The biomass for benthopelagic target species was on average 4 times higher in the partially protected area than in the open access area (Fig. 3.2E). Interestingly, these trends were reversed for non-target species, with reef-associated species showing stronger response to protection than either of the two other categories (Fig. 3.2E). It is worth mentioning, however, that the response of non-target species to protection exhibited broad variation, ranging from strongly negative to strongly position (length of error bars for NT species in Fig. 3.2E).

Fig. 3.2 Species' response ratio (using biomass data) in relation to different species' traits and partially protected area (PPA) characteristics. Response ratio is the ln-transformed ratio of the mean species biomass in the PPA to that in the open access area. PPA protection regime categories are 'discriminate, commercial' (DC), 'discriminate, recreational' (DDR), 'indiscriminate, commercial' (IdC). The partial residuals plot (D) shows the significant negative relationship between fish size [log(Max. body size)] and the species' response to protection. The significant interaction term between adult habitat type and the species' exploitation status is given in (E). Adult habitat types are benthopelagic (BP), demersal (DEM), reef-associated (RA). Species are grouped into target (T) and non-target (NT) species depending on their level of exploitation.

Table 3.3　Final model output for dataset 2, showing the species' traits and partially protected area characteristics that were significantly related to the response of fish species to protection, calculated as the ln-transformed ratio of the biomass estimate inside the partially protected area relative to the open access area. The structure of the final model was: Response ratio ~ $\log(L_{max})$ + Exploitation status x Adult habitat type, random = ~1| MPA ID.

Variable	Estimate	SE	df	t-val	p-val
Intercept	1.51	1.01	120	1.49	0.14
L_{max}	-1.04	0.54	120	-1.92	**0.05**
ES: target species	1.81	0.75	120	2.40	0.02
Env: demersal species	0.70	0.49	120	1.42	0.16
Env: reef-associated species	1.31	0.80	120	1.65	0.10
ES_target x Env_demersal	-2.02	0.83	120	-2.45	**0.02**
ES_target x Env_reef-associated	-2.35	1.05	120	-2.24	**0.03**

3.4.2 Effects of species' traits on the response of fish species to full over partial protection

3.4.2.1 Density (dataset 3)

The proportion of species exhibiting higher density in fully protected areas relative to partially protected areas (46%, 50 out of 108 species) was equal to the proportion of species with higher density in partially protected areas relative to fully protected areas (42%, 45 out of 108 species). For 12% of the species (13 out of 108 species), average density was similar inside the no-take marine reserve and the partially protected area (i.e. response ratio, LnRR = 0).

Maximum body size and adult habitat type explained a significant amount of variation in the response of fish species to protection, expressed as the ratio of species' density inside the no-take marine reserve relative to that in the partially protected area (Table 3.4). The response ratio was positively related to fish body size, suggesting that larger fish species benefit more from full protection relative to smaller species (Table 3.4, Fig. 3.3A). There were pronounced differences in the response to full protection among the three fish habitat categories; response was on average 1.6 and 1.9 times higher for demersal and reef-associated species relative to benthopelagic fish, respectively (Table 3.4, Fig. 3.3B). Additionally, the response was related

to the size of the no-take marine reserve and the duration of protection, and varied significantly between target and non-target species (interaction terms in Table 3.4). Whereas the response ratio (NTR : PPA) increased with the size and age of the no-take reserve for target species, the response was negatively related with these variables for non-target species (Fig. 3.3C – D, Table 3.4). This suggests that whereas large and old no-take reserves harbour higher number of individuals targeted by fishing relative to partially protected areas, a lower number of non-target species occur in large and old no-take reserves relative to partially protected areas.

Table 3.4 Final model output for dataset 3, showing the species' traits and marine protected area characteristics that were significantly related to the response of fish species to protection, calculated as the ln-transformed ratio of the density estimate inside the no-take marine reserve relative to the partially protected area. The structure of the final model was: Response ratio ~ $\log(L_{max})$ + Adult habitat type + Exploitation status x $\log$(NTR size) + Exploitation status x Age, random = ~1| MPA ID.

Variable	Slope	SE	df	t-val	p-val
Intercept	0.57	0.89	96	0.64	0.52
Age	-0.15	0.05	9	-2.92	0.02
NTR size	-1.39	0.48	9	-2.88	0.02
L_{max}	0.91	0.35	96	2.59	**0.01**
ES: target species	-2.24	0.99	96	-2.25	0.03
Env: demersal species	0.47	0.23	96	2.03	**0.05**
Env: reef-associated species	0.63	0.22	96	2.80	**0.01**
ES_target x NTR size	1.53	0.58	96	2.63	**0.01**
ES_target x Age	0.14	0.06	96	2.20	**0.03**

Fig. 3.3 Relationship between species' response to protection (using density data) and different species' traits and MPA characteristics. Response ratio is the ln-transformed ratio of the mean species density in the no-take marine reserve (NTR) to that in the partially protected area (PPA). The partial residuals plot (A) shows the significant positive relationship between fish size [log(Max. body size)] and the response to protection. (B) Mean (± SE) response ratio for each adult habitat type category; benthopelagic (BP), demersal (DEM), reef-associated (RA). Response of target and non-target species with increasing area of the NTR [log(NTR size)] (C) and duration of protection (MPA age) (D).

3.4.2.2 Biomass (dataset 4)

Fewer numbers of studies comparing the effect of full to partial protection were found from the literature search for fish biomass compared to fish density. Of the 42 species included in this analysis (dataset 4), 36% had higher average biomass inside the partially protected area relative to the no-take reserve, whereas 62% had higher biomass inside the no-take reserve.

Species' exploitation level, adult habitat type and PPA protection regime could not be examined due to the inadequate number of species within each of the categories for these

variables. Fish body size, the size of the no-take reserve and duration of protection were not significantly related to the response ratios (NTR : PPA) of individual species (Fig. 3.4).
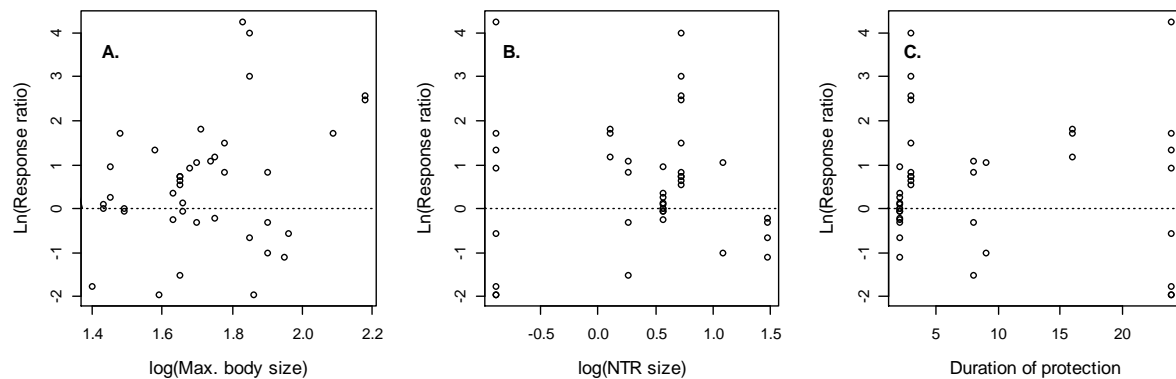
Fig. 3.4 Species' response ratio (using biomass data) in relation to different species' traits and MPA characteristics. Response ratio is the ln-transformed ratio of the mean species biomass in the no-take marine reserve (NTR) to that in the partially protected area (PPA).

3.5 DISCUSSION

A key variable known to affect both population declines and recovery from fishing is body size, either directly because large fish are generally more sought after and more accessible targets to fishing in size-selective fisheries, or through its correlation with age at maturity, growth rate and mobility (Jennings et al. 1998; Denney et al. 2002; Reynolds et al. 2005). The results of this analysis revealed complex relationships between species' maximum body size and their response to protection. Densities of large, slow-growing species were greater in no-take marine reserves than in partially protected areas, since the effect of protection increased significantly as the maximum body size of the species increased. In contrast, the response to protection decreased with species' body size when fish biomass in partially protected areas was compared to that in open access areas. The effect of partial protection (i.e. PPA *vs*. NP) in terms of fish density was rendered complicated by a significant interaction between species' body size and the size of the partially protected area.

One possible explanation for the increased response of large fish species in fully versus partially protected areas is that the majority of large species in the dataset were in fact the target of fisheries. A close examination of the body size distribution for target and non-target species in this dataset (i.e. NTR *vs*. PPA) revealed that fish species with a maximum body size equal to or greater than 50 cm were typically target species, whereas smaller species

62

were typically non-target species (Fig. 3.5A). A total prohibition on fishing activities is more likely to provide higher protection from fishing for target species than partially protected areas where some regulated fishing is allowed. Hence, this may explain why large species benefitted more from full protection. The reason as to why large species benefitted less in partially protected areas relative to open access areas is less obvious, as the body size distribution of target and non-target species for this dataset were relatively similar (Fig. 3.5B). One reason, however, may arise from the fact that large species in this dataset (i.e. PPA *vs.* NP) belonged to highly mobile families such as Squalidae, Rajidae, Gadidae, Chimaeridae and Anarchichadidae. Therefore, the shorter residency times of larger species inside the partially protected area may explain why the magnitude of protection was higher for smaller species than for large species in partially protected areas. It is intriguing that large species still benefitted less from protection than small species even as the size of the partially protected area increased (interaction term in Table 3.2). One possible explanation may be that the incidence of illegal fishing may be higher in large partially protected areas (> 1000 km^2) than in small areas, as large areas are harder to enforce and police. Given that large species have a higher probability of being caught in the fishing gear than small species the apparent benefits of protection would be higher for small species than for large species in large PPAs.
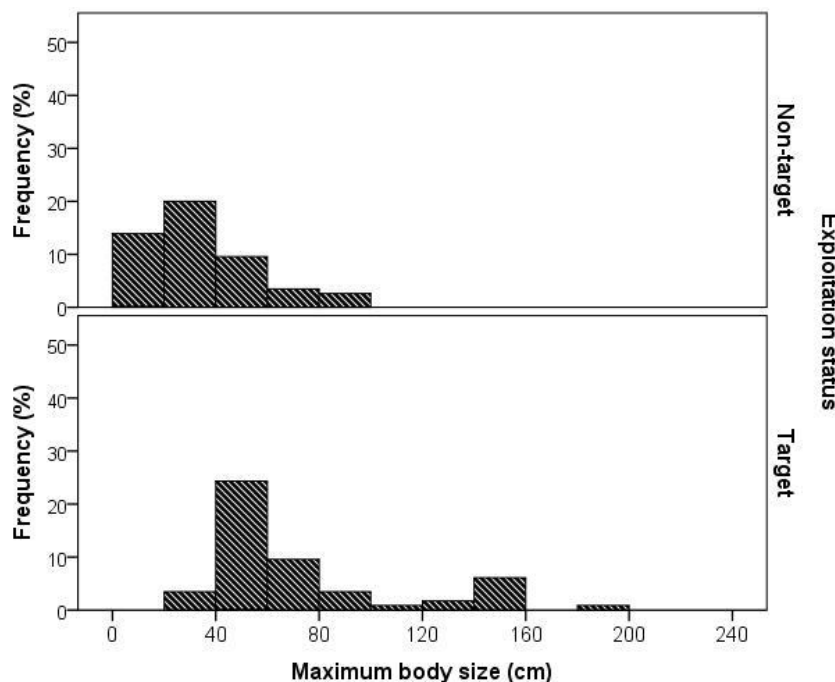
Fig. 3.5A Fish body size distribution by exploitation status for data comparing the effect of protection from no-take marine reserves relative to partially protected areas.
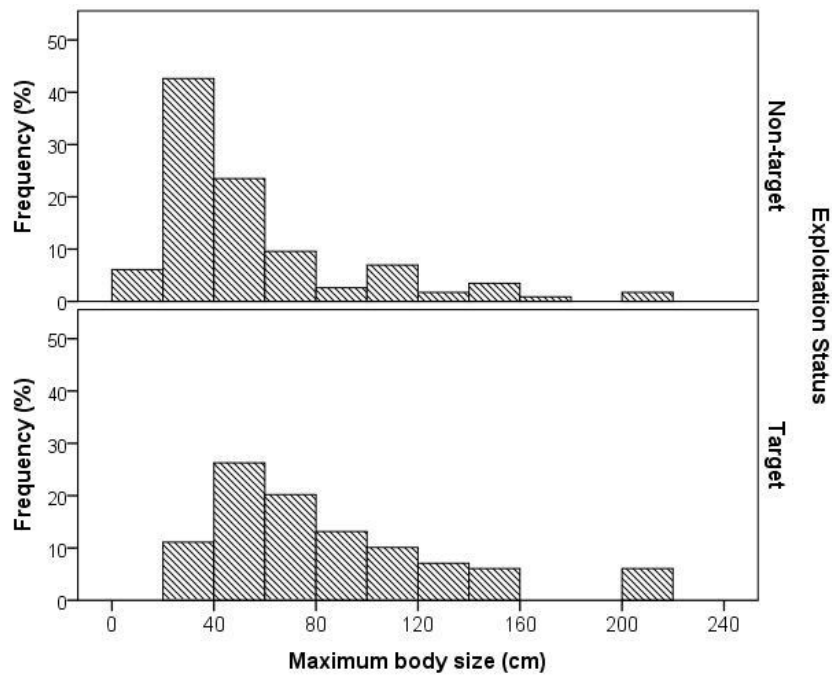
Fig. 3.5B Fish body size distribution by exploitation status for data comparing the effect of protection from partially protected areas relative to open access areas.

Another finding that stood out from this analysis is that fishes differed in their response to protection depending on their adult habitat preferences. The effectiveness of marine protected areas (MPA) ultimately depends on the tendency of at least some portion of the fish population to reside within the MPA boundaries. Typically, the benefits of marine reserves have been predicted to best serve benthic species that have a small home range and hence local residency, such as some goatfish (Meyer et al. 2000), parrotfish (Afonso et al. 2008), or kelp bass (Lowe et al. 2003). In contrast, these benefits are often limited in the case of migratory or highly mobile fishes because, unless the reserves are large enough to encompass all their habitat and migration corridors, protection within reserves will only be effective on a partial or seasonal basis (DeMartini 1993; Kaiser 2005). My results have indicated that the highest protection afforded by no-take reserves relative to partially protected areas was for reef-associated species such as grunts (Haemulidae), wrasses (Labridae), damselfish (Pomacentridae), parrotfish (Scaridae) and groupers (Serranidae). The scale of short-term home ranges of many reef fish have been typically shown to be only a few tens or hundreds of meters in length and 1 to 10 ha in size (e.g. Holland et al. 1996; Lowry and Suthers 1998; Kramer and Chapman 1999; Meyer et al. 2000; Lowe et al. 2003; Meyer and Holland 2005; Afonso et al. 2008), although some may extend up to a few hundred hectares (Chateau and

Wantiez 2008; Afonso et al. 2009). Thus, most of the reef-associated species stand a good chance of remaining inside the no-take reserve, which were about 5 km^2 in size in 60% of the cases examined (mean ± SD = 7.27 ± 9.12 km^2), and hence benefitting from full protection. In contrast, the higher mobility and home ranges displayed by some benthopelagic and demersal species makes them vulnerable to fishing when they leave the protected area. Demersal species such as flounders (Pleuronectidae), skates (Rajidae), hake (Merluccidae) and cod (Gadidae) hardly benefitted from protection, whether full protection (i.e. NTR relative to PPA) or partial protection (i.e. PPA relative to NP) was considered. Clearly, therefore, the large size and variable movement patterns among benthopelagic and demersal species makes them less likely to benefit from the higher degree of protection afforded by the no-take reserves compared to reef-associated species. Conservation of species with medium to high mobility will also require conventional management measures to control fishing effort outside the protected area.

The effect of protection may additionally be influenced by the level of association of the species with its habitat for food and shelter. For example, Hiddink et al. (2011) showed that selective benthic feeders such as plaice might not be able to compensate for the loss of particular prey types from bottom fishing. Restoration through spatial closures of previously fished populations of species with close dependence on the seabed for food will therefore depend on the severity of the damage caused by fishing to the physical and biotic environment. The majority of demersal species included in the dataset comparing partially protected areas to open access areas were from closed areas that were heavily fished by bottom-towed gear prior to the establishment of the spatial closure (67 out of 80 demersal species were found in PPAs categorized as 'indiscriminate, commercial'). Hence, it may be possible that the relatively low effect of protection observed for demersal species is due to relatively poor environmental conditions inside the MPA that would have resulted from intensive fishing activity prior to the establishment of the MPA. It was not possible to draw a clear picture of the effect of PPA protection regime for species with different habitat preference (i.e. interaction term Env x PR, Table 3.1) because of insufficient numbers of species within each category. Although species' recovery will depend on levels of previous disturbance seabed habitats within protected areas should become more suitable for demersal fish as the habitat recovers over time. Thus, it would have been intriguing to examine the trajectory of the response of species with different seabed-association to protection that is

conferred by PPAs with different protection regimes. However, there was not enough data to examine the 3-way interaction between Env x Age x PR to test this hypothesis.

Unless non-target species are killed directly via by-catch, any response of non-target species is likely to arise through indirect effects such as changes in the trophic structure of the community (Micheli and Halpern 2005; Lamb and Johnson 2010). Marine reserves have been predicted to lead to trophic cascade effects, in that protection from fishing may allow top predators to become more abundant in a reserve, which may in turn reduce the abundance of prey species (Steneck 1998). The finding from this study of lower abundance of non-target species but higher abundance of target species inside the no-take reserve relative to the partially protected area for larger and older reserves could therefore reflect potential predator-prey interactions, with the increased number of target fish preying upon non-target species. Species with trophic levels greater than 3.75 (piscivorous) were more common among the target species, whereas species with lower trophic levels (< 3) were more common among non-target species (Fig. 3.6). Because indirect effects of protection including trophic cascades lag behind direct effects of protection, such as increases in target species abundance, it is reasonable that the reductions in abundance of non-target fish in the reserves were larger for old than for young reserves.
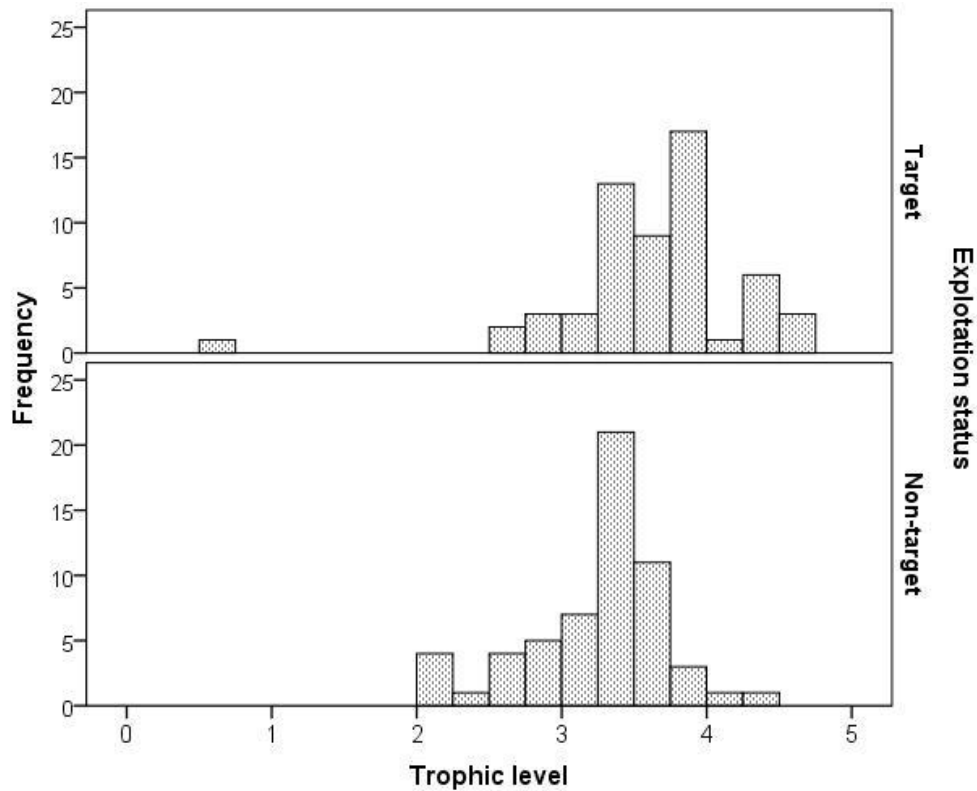
Fig. 3.6 Fish trophic level distribution by exploitation status for data comparing the effect of protection from no-take marine reserves relative to partially protected areas.

The use of marine protected areas as ecosystem-based management tool for marine conservation might lead to the perception that they should ensure protection for a wide range of species with different life history and ecological traits. This is not always the case. This study has demonstrated that the magnitude of protection effect may vary with economic value (~ exploitation status) and species-specific traits such as body size and habitat, which may interact with age and size of the MPA. Design of new MPAs and monitoring of already established ones should therefore acknowledge that the magnitude and time-frame of protection effect may vary from species to species, and that these key characteristics need to be taken into account for the evaluation of the efficacy of MPAs.

CHAPTER 4

Benthic community response to a scallop dredging closure within a dynamic seabed habitat

4.1 ABSTRACT

Fishing with bottom towed gear is widely considered an invasive form of fishing in terms of its impacts upon seabed habitats and fauna. Fishery closures or marine protected areas provide baseline conditions against which to assess the response to the removal of fishing disturbance and thus shed light on their use as fisheries management tools. We conducted repeat underwater camera surveys inside a recently established permanent scallop fishing closed area and a seasonally fished area in Cardigan Bay, UK, to test for differences in scallop abundance and epibenthic community structure and to examine recovery processes over a 23 month study period. Changes in density of scallops, diversity and community composition of epifauna were primarily driven by seasonal fluctuations; no differences were found between the permanent closed area and the seasonally fished area. Temporal changes in epibenthic community inside the permanent closed area were not related to recovery processes associated with the cessation of scallop dredging. Sediment composition and bedforms shifted between surveys, suggesting that this community is exposed to a dynamic environment. It is likely that scallop dredging at the present levels of fishing may be insufficient to induce changes sufficiently large to be detected in the presence of strong natural disturbance. We highlight the importance of considering the physical nature and dynamics of the environment and the nature of the species concerned throughout the designation process of closed areas, to avoid negative impacts on fisheries and limited conservation benefits.

4.2 INTRODUCTION

Fishing with bottom towed gears such as beam trawls and scallop dredges, impacts populations of by-catch species (Kaiser et al. 1996; Veale et al. 2000; Jenkins et al. 2001), reduce seabed habitat complexity and heterogeneity (Collie et al. 1997; 2000a), cause shifts in community structure and trophic interactions (Carbines and Cole 2009; Hinz et al. 2009; Strain et al. 2012), and alter the physical structure of the sea floor and biogeochemical processes (Schwinghamer et al. 1998; Smith et al. 2000; Jennings et al. 2005). The impacts and recovery times post fishing disturbance depend on the magnitude of the fishing disturbance relative to natural disturbance, and the nature of the habitat and species concerned (Collie et al. 2000b; Kaiser et al. 2002; Henry et al. 2006; Kaiser et al. 2006; Lambert et al. 2011). The effects of disturbance are likely to be short-lived for assemblages of biota that are subject to frequent natural perturbations, as animals that inhabit unconsolidated sediments are those with life-histories adapted to frequent disturbance by currents and re-suspension of sediment (Jones 1992; Jennings and Kaiser 1998; Collie et al. 2000b).

In recent decades, the wider recognition of the ecosystem effects of fishing activities has led to a shift in fisheries management from a single-species approach to an 'ecosystem approach', which from a fisheries management perspective is centred on an understanding of the impacts of fishing on multiple species interactions and their environment (Larkin 1996; Brodziak and Link 2002; Browman and Stergiou 2004; Pikitch et al. 2004). In the context of ecosystem-based management, properly designed marine protected areas (MPAs) and seasonal or periodic fishery closures are effective steps towards minimizing the ecosystem-wide effects of bottom fishing (Collie et al. 2000a; Kaiser 2005, Cinner et al. 2006). Failure or success of the use of MPAs or seasonal closures as fishery management tools is inextricably linked to effective fishing effort control in the surrounding waters, the participation of fishers and stakeholders, the ecology of the species concerned and the environment in which they occur (Kaiser 2005; Beddington et al. 2007; Claudet et al. 2010). Thus, for example, the resumption of fishing activity without restrictions on fishing effort after a seasonal closure or the ill-considered use of MPAs without consideration of reallocation of fishing effort may result in more damage to the marine environment than the status quo (Dinmore et al. 2003; Demestre et al. 2008).

Cardigan Bay has been an active scallop fishing ground in the UK for over 30 years, with most of the scallop dredging occurring beyond 6 nm offshore (CCW 2010, Vanstaen and Silva 2010). Until recently, the scallop fishery in Cardigan Bay has been regulated by means of minimum landing size limits, restrictions on gear size, the number of dredges and the imposition of a seasonal closure (Scallop Fishing (Wales) Order 2005). An additional measure involving the permanent closure of the fishery within an area of Cardigan Bay was introduced in March 2010 (Scallop Fishing (Wales) Order 2010). The presence of the year-round spatial closure and the seasonal closure to scallop fishing in Cardigan Bay allowed us to examine the effect of these two types of closures on the wider ecosystem effects of scallop dredging.

In many studies concerned with the impacts of towed gears on benthic assemblages, quantification of the effects of fishing has been hampered by the lack of unfished control areas (Jennings and Kaiser 1998). Hence it may be difficult to distinguish changes in benthic populations caused by natural processes in the environment from those induced by fishing disturbance. In Cardigan Bay, regulation of the scallop fishery through an area closure provided unfished controls that allowed investigation of dredging impacts against natural environmental variation.

This study sought to examine the magnitude of impact from scallop dredging on the benthic community at Cardigan Bay and to use this case-study to inform the debate about the efficacy of fisheries closed areas for fisheries management and conservation. This was achieved by (i) examining the density of target species (scallop, *Pecten maximus* and *Aequipecten opercularis*) and macro-epifaunal benthic community structure and diversity in the permanent closed area and the adjacent seasonally fished area, (ii) examining the temporal changes in the community structure and diversity after the cessation of scallop dredging within the permanent closed area, and (iii) examining the relationship between the intensity of scallop dredging and scallop density and community diversity in the seasonally fished area.

4.3   METHODS

4.3.1 Study area

The study was carried out in the Cardigan Bay Special Area of Conservation (SAC) in Cardigan Bay, Wales (Fig. 1). The SAC (960 km^2) was originally designated in 2004 to

protect populations of bottlenose dolphin, grey seal and lamprey. The area is characterized by moderate energy hydrodynamic conditions (current energy at the seabed: $0.13 - 1.16$ Nm^{-2}, wave energy at the seabed: $0.21 - 1.2$ Nm^{-2}, UKSeaMap 2010), and is exposed to prevailing south westerly and westerly gales that can develop a large uninterrupted swell. The seabed in the SAC is characterized by fields of sand ribbons that are principally oriented in a SW – NE direction parallel to the prevailing tidal current (Hinz et al. 2010a, b). The study area is composed entirely of unconsolidated sediment, with sand (< 2 mm), gravel ($2 - 4$ mm) and pebbles ($4 - 64$ mm) being the predominant sediment types (Hinz et al. 2010a, b). The western part of the study area is predominantly gravel, which becomes more sandy towards the east of the area (Hinz et al. 2010a, b). *Pecten maximus* and to a lesser extent *Aequipecten opercularis* are the main target species of the Cardigan Bay scallop fishery, which generally takes place beyond 6 nm off the coast (Walmsley and Pawson 2007). Potting for lobsters, crabs and whelks is also common, but this occurs within 6 nm off the coast (Walmsley and Pawson 2007). Until 2009, the scallop fishery for *Pecten maximus* in Wales (including in the Cardigan Bay SAC) was mainly managed through minimum landing size, restrictions on the number of dredges and a seasonal closure that ran from 1st June to 31st October for waters beyond 3 nm offshore (Table 1). Landings of scallops by the UK fleet increased by a factor of 2.6 since 1994, with the bulk of the increase occurring since 2008 (Almond and Thomas 2011). Concerns about the possible effects of increased levels of scallop fishing activity on the Cardigan Bay SAC and its' habitat features, namely cobble reefs, resulted in an extended closed season to scallop dredging (from 1st May to 31st October), coupled with a year-round prohibition of scallop dredging within 75% of the SAC (hereafter referred to as 'permanent closed area') from March 2010 onwards (Table 1, Fig. 1).

4.3.2 Data collection: Survey design

Evaluation of the spatial and temporal variation of the macro-epibenthic assemblages between the permanent closed area and the seasonally fished area was carried out over four surveys between December 2009 and April 2011 (Table 1). During each of the four sampling events, six sites were surveyed within each of the permanent closed area and the seasonally fished area (Fig 1). During the June 2010 and April 2011 surveys, an additional twelve sites were surveyed within the permanent closed area (giving a total of 18 sites) to assess community recovery following 13 and 23 months of no scallop dredging (Fig. 1, Table 1). Additionally, we surveyed a total of 12 sites in the seasonally fished area during the April

2011 survey to examine the relationship between scallop fishing intensity and univariate measures of community response to seasonal fishing (e.g. density, diversity).
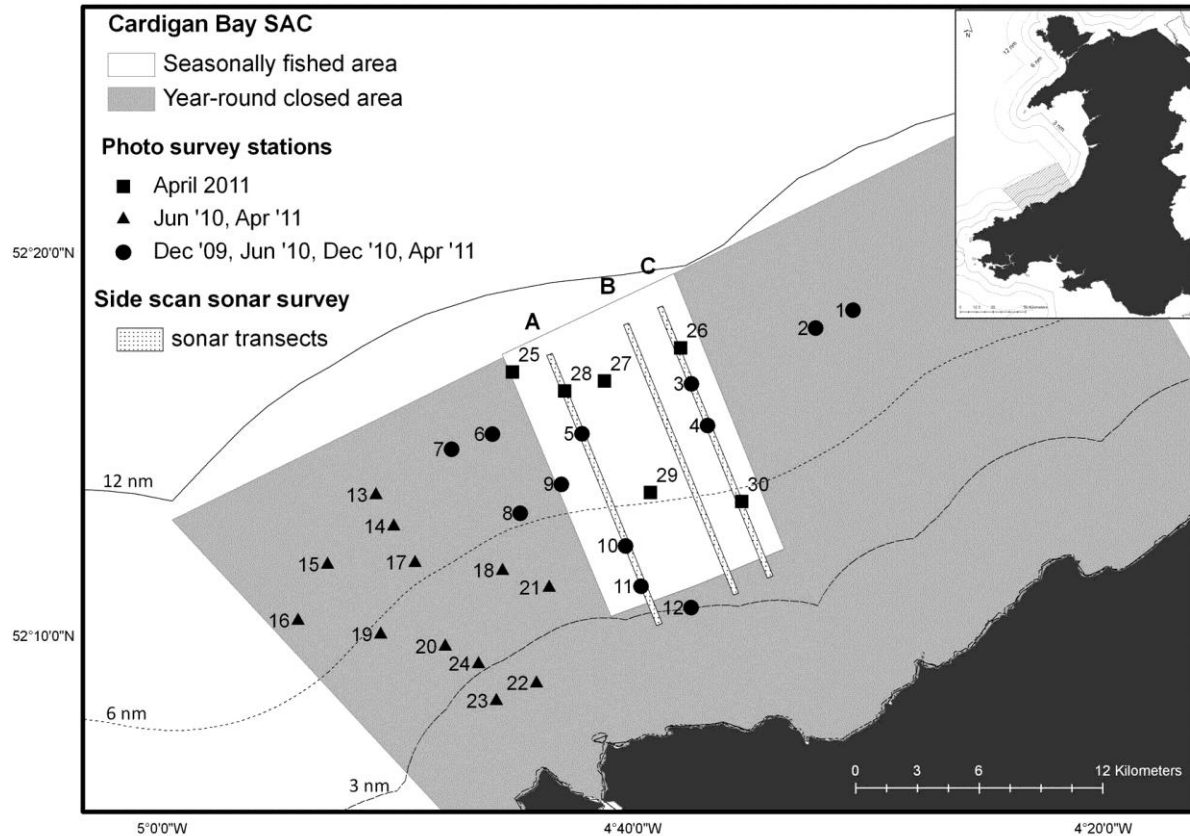
Fig. 4.1 Location of Cardigan Bay SAC along the Welsh coast (inset) and the spatial distribution of the underwater camera stations surveyed during the 4 sampling cruises (1 – 12, circles) inside the permanent closed area (grey) and the seasonally fished area (white). Stations labelled 13 – 24 (triangles) were surveyed only in June 2010 and April 2011. Stations 25 – 30 (squares) were surveyed inside the seasonally fished area in April 2011. The position of the side scan sonar transects surveyed in December 2009 and June 2010 is also shown (A – C).

Table 4.1 Legislation applicable to Welsh waters and evolution of the permanent closed area and the seasonally fished area in Cardigan Bay Special Area of Conservation (SAC). Sampling cruises are also given.

Legislation	Timeline	Cardigan Bay SAC	
(NWNW SFC Byelaw 20) and (Scallop Fishing (Wales) Order 2005)	Prior to 2009	a) Within 1.5nm of coastline - scallop dredging (SD) is prohibited all year round b) Between 1.5 - 3nm off the coastline - closed season to scallop dredging between 1 June – 31 December c) Between 3 - 12nm off the coastline - closed season to scallop dredging between 1 June – 31 October	
(Prohibition of Fishing for Scallops (Wales) Order 2009 No. 2721 (W. 232)	1 June ´09 – 28 Feb ´10	Closed season to SD in all Welsh waters extended to end of February 2010	
	$10 – 17^{th}$ Dec 2009	*Survey 1: photographic & side scan sonar*	
		Year-round closure	**Seasonally fished area**
(The Scallop Fishing (Wales) (No. 2) Order 2010 No. 269 (W. 33))	1 March – 31May ´10	Closed to SD	Open to SD
	1 June – 31 October ´10	Closed to SD	Closed to SD
	$13 – 19^{th}$ June 2010	*Survey 2: photographic & side scan sonar*	
	1 Nov ´10 – 30 April ´11	Closed to SD	Open to SD
	29th Nov – 4th Dec 2010	*Survey 3: photographic*	
	$6 – 9^{th}$ April 2011	*Survey 4: photographic*	
	1 May – 31 October ´11	Closed to SD	Closed to SD

Sites were selected based on sediment data quantified from Hamon grab samples and underwater video camera tows carried out during a habitat assessment survey in the Cardigan Bay SAC prior to the present survey (Hinz et al. 2010a, b). Sites that were predominantly composed of gravel (>50% gravel) were selected to minimize confounding factors due to differences in sediment type. At each site, images of the seabed were taken with a high resolution stills camera (Canon 400D) installed in an underwater housing and mounted on a sledge such that the objective lens pointed perpendicularly towards the seabed from a height of 60cm. The sledge was towed at a speed of approximately 1.0 knot for a period of 10 minutes, covering an average distance of 300m, as calculated from the start and end positions of each tow. Tow direction depended on the speed and direction of the tidal current. A 10-mega-pixel image covering an area of $0.13m^2$ (0.44m x 0.30m) was taken every eleven seconds.

4.3.3 Still images analysis

A minimum of forty images were analyzed per camera tow (average number of images analyzed 53 ± 10 S.D.). Epifaunal organisms were identified to the lowest taxonomic level possible and counted. Despite the high quality of the images, identification and quantification of some sessile epifauna presented a number of significant challenges. First, epifaunal annelids, in particular those belonging to the family Serpulidae, could not be quantified as it was impossible to distinguish between live and dead specimens as live tubeworms are usually retracted in their tubes. Second, the taxonomy of some species of the phylum Porifera and the classes Hydrozoa, Bryozoa and Ascidiacea could not be resolved below these taxonomic levels, as these organisms necessitated microscopic study to identify distinguishing features. In this case hydroid, poriferan and bryozoan species were recorded as 'Hydroid turf', 'Porifera indet.' and 'Bryozoan indet.', respectively.

4.3.4 Environmental data

The water depth at each site was calculated as an average of the depth at the start and end of the tow recorded by the echosounder and corrected for tidal state. Estimates of tidal-bed shear stress (Nm^{-2}) at the study sites were derived from a two-dimensional hydrographical model of the Irish Sea (see detailed description on shear stress calculations in Hiddink et al. 2006). Bed shear stress was used as a measure of natural disturbance to quantify tidally generated currents that effect sediment dynamics and hence the structure of the invertebrate community

(Hall 1994). The percentage of sand, gravel and cobbles in the sediment was considered as a factor that could affect epifaunal distributions as it is a surrogate for sediment stability. Substratum type was qualitatively identified from 40 still images selected at random from each tow. Each image was classified as predominantly sand, gravel or cobble when more than 50% of the image's surface area was covered by particles of diameters less than 2 mm, between 2 – 64 mm and between 64 – 256 mm, respectively. The percentage composition of each sediment type was then calculated for each tow.

4.3.5 Side scan sonar survey

While still images give a spatially more restricted impression of sediment types, the side scan sonar delivers spatially larger scale information on ground topography. We conducted two side scan sonar surveys concurrent to the underwater camera surveys; one in December 2009 and the other in June 2010 (Table 1). During each data collection event we surveyed the same three transects in the seasonally fished area (Fig. 1) in order to determine temporal changes in seabed morphology related to the fishing activity or to natural hydrodynamic processes. In December 2009, a sonar range of 100m (total swath width 200m and sonar frequency 325kHz) with the tow-fish altitude above the seabed kept between 5 and 10m was employed for transect A (Fig. 1). Due to equipment failure halfway through the survey, transects B and C were surveyed using a sonar range of 200m at a frequency of 100 kHz. In June 2010, all three transects were surveyed using a sonar range of 100m at a frequency of 325 kHz and tow-fish altitude above the seabed between 5 and 10m. Whenever possible, transects were run perpendicular to the coast as these gave the clearest images with the most distinct shadows.

4.3.6 Fishing intensity

Fishing intensity data for scallop dredging vessels were obtained from the European Community Satellite Vessel Monitoring System (VMS). To investigate the influence of fishing intensity on the benthic assemblage composition inside and outside the permanent closed area we generated fishing intensity data estimates for the open seasons directly before each sampling event: November 2008 to May 2009 covering the open season prior to the December 2009 survey, March to May 2010 prior to the June 2010 survey, November to December 2010 prior to the December 2010 survey and November 2010 to April 2011 prior to the April 2011 survey. Note that the December 2009 survey was carried out before the

establishment of the permanent closed area (refer to Appendix I for the spatial distribution and intensity of the scallop fishing activity in the SAC throughout our sampling period). In addition, to examine the long-term effect of fishing on species density and diversity within the seasonally fished area, we generated average fishing intensity estimates over the entire sampling period (i.e. November 2008 to April 2011) for the sites sampled during the last sampling event in April 2011.

To calculate fishing intensities from VMS data, only data records of active scallop dredgers were included in the analysis. Some records did not specify fishing gear type. However, given that the primary fishing activity beyond 3 nm in and around Cardigan Bay SAC is scallop dredging (CCW 2010, Vanstaen and Silva 2010) these records were regarded as 'scallop dredgers'. Transmitted vessel speed was used to distinguish fishing from non-fishing records (Lee et al. 2010). Calculations of fishing intensity were restricted to vessel speeds of between 1 and 4 knots. Because our sampling tows covered relatively small areas of the seabed (total tow length = ca. 0.3 km) and because VMS records are transmitted at ~ 2 hr intervals, positional records were interpolated to generate a more accurate estimate of fishing intensity at the spatial scale of our sampling sites. The inverse distance weighted interpolation method was used in ArcGIS 9.3, to interpolate positional records between two consecutive records transmitted by the same vessel using the 'heading' information for each VMS record. The modal time interval between interpolated records was 0.22 hours.

Fishing intensity was defined as the number of times an area of 0.07 km^2 was swept by scallop dredgers in one month. The area swept by each vessel was calculated as the product of the number of hours fished, average fishing speed (equal to 2.54 knots or 4.7 km/hr) and gear width. Vessels fishing between 3 and 6 nm were assumed to use 8 dredges (each with a width of 0.85 m) based on regulation, while vessels fishing beyond 6 nm were assumed to carry 16 and 14 dredges; the maximum numbers of dredges allowed beyond 6 nm to 12 nm before and after 2010, respectively (The Scallop Fishing (Wales) Order 2005, 2010). The actual fishing intensity at each site was then calculated as the sum of the area dredged from all the VMS records falling within the 0.07 km^2 area surrounding each video tow (Table 2).

Since the VMS is only mandatory for vessels over 15m (EC 2003), the activity of vessels smaller than 15m, particularly those between 8 and 15m that have been shown to operate around and beyond 6 nm offshore in Cardigan Bay (see Vanstaen and Silva 2010), was not

represented. Therefore, estimates of fishing frequency may be underestimates of the actual fishing intensity, but are still useful indicators of the relative fishing pressure at the sampled sites.

Table 4.2 Summary of fishing intensity at each sampling station, expressed as the number of times an area equivalent to 0.07km^2 around the study site was dredged per month. Bracketed values under the 'Entire sampling period' represent fishing effort as hours fished per month.

Study site	Fishing frequency (month^{-1})				
	Survey 1 (Nov '08 – May '09)	Survey 2 (Mar – May '10)	Survey 3 (Nov – Dec '10)	Survey 4 (Nov '10 – Apr '11)	Entire sampling period (Nov '08 – Apr '11)
St 1	0.2	0.0	0.0	0.0	-
St 2	0.6	0.0	0.0	0.0	-
St 3	0.3	0.1	0.3	0.1	0.1 (0.2)
St 4	0.8	0.0	2.0	0.3	0.4 (0.5)
St 5	0.4	0.1	0.7	0.3	0.3 (0.3)
St 6	0.2	0.0	0.0	0.0	-
St 7	0.1	0.0	0.0	0.0	-
St 8	0.3	0.0	0.0	0.0	-
St 9	0.3	0.0	0.0	0.0	0.1 (0.2)
St 10	0.2	0.0	0.0	0.0	0.1 (0.2)
St 11	0.1	0.0	0.0	0.1	0.03 (0.1)
St 12	0.0	0.0	0.0	0.0	-
St 25	-	-	-	-	0.1 (0.2)
St 26	-	-	-	-	0.1 (0.2)
St 27	-	-	-	-	0.1 (0.2)
St 28	-	-	-	-	0.1 (0.2)
St 29	-	-	-	-	0.1 (0.9)
St 30	-	-	-	-	0.1 (0.1)

4.3.7 Data analysis

4.3.7.1 Analysis of environmental characteristics of sampling sites

Multivariate analysis on normalized environmental data were performed using the ANOSIM routine in PRIMER v.6 to test for differences in habitat characteristics between the two management areas (permanent closed area *vs.* seasonally fished area) and among the sampling events. The following environmental variables were included: depth, percentage of sand, gravel and cobble and tidal bed shear stress.

4.3.7.2 Analysis of spatial and temporal variation of biota in Cardigan Bay SAC

Prior to analysis, the abundance and species richness data from 40 images were pooled together for each tow and expressed as the number of individuals per $1m^2$ and the number of species per tow, respectively, to facilitate comparisons between sites. The effects of the fishing closure ("Zone", 2 levels: permanent closed area, seasonally fished area) and the time of sampling event ("Time", 4 levels: Dec '09, Jun '10, Dec '10, Apr '11) were examined on the following univariate measures: total epifauna density, scallop density (*Pecten maximus*, *Aequipecten opercularis*), species richness, Shannon-Wiener diversity index and Pielou's evenness (DIVERSE routine in PRIMER-E v6) using a two-way crossed analysis of variance (ANOVA). Given the nature of the fishing closure in the seasonally fished area, it may be unreasonable to expect an effect of fishing per se (i.e. "Zone" effect alone), since the effects of fishing during the open season (November to April) may be lost when community production is at its lowest over the winter season. Rather it may be expected that an effect of fishing be reflected in a "Time × Zone" interaction where the abundance in the seasonally fished area is lower than in the permanent closed area during the open season (winter/spring), or else no different than the permanent closed area during the closed season (summer) if recovery processes are rapid enough to allow recovery of the community in the fished area to match that in the permanent closed area. The factor "Time" can be considered to gather all effects (except fishing and protection) linked to temporal variations such as recruitment, natural mortality, disease, growth, emigration and immigration. Before proceeding with the ANOVAs, the data were examined for normality using the Kolmogorov-Smirnov test and the Levene's test for homogeneity of variance. A $\log_{10}$ or square root transformation was applied to stabilize variance when necessary.

Multivariate analyses were performed on density data to detect spatial and temporal changes in the epibenthic assemblage composition, using the PRIMER-E v6 statistical package (Clarke and Gorley 2006). The similarity between each pair of samples was calculated using the Bray–Curtis similarity index, after a square root transformation of the data was performed to reduce the influence of highly dominant species. The response of the multivariate epifaunal assemblage to the 2-factor ("Zone" and "Time") sampling design was examined using PERMANOVA. Each factor in the model was tested through permutation tests based on 9999 permutations of residuals under a reduced model to obtain p-values. Canonical analysis of principal coordinates (CAP) was used to produce a constrained ordination to visualize the relationship between multivariate variation in the benthic assemblages and time of sampling event, which was the only factor that was identified as significant by PERMANOVA.

Multivariate regression analysis with the DISTLM (Distance-based linear model) routine was used to determine the independent capacities of the predictive variables (fishing intensity, percentage gravel and cobble content and tidal shear stress, time of sampling event) to explain the patterns of variability in the benthic assemblage. Sand content and depth were highly correlated to gravel content ($r = -0.95$) and tidal shear stress ($r = 0.83$), respectively, and hence were considered redundant for the analysis. Selection of variables with the highest explanatory power was performed using BEST selection and Akaike information criterion (AIC).

4.3.7.3 Analysis of temporal changes in the permanent closed area

The recovery of benthic epifauna after 13 months (June 2010) and 23 months (April 2011) of the cessation of scallop dredging within the permanent closed area was examined in terms of total density, scallop density (*Pecten maximus* and *Aequipecten opercularis*) and species richness, using one-way ANOVAs. Whole-community approaches, using total densities to detect impacts of bottom fishing, sometimes miss differential responses between individual community components. Therefore, we also decomposed the total epifaunal density data to the level of taxonomic group to examine for potential shifts in assemblage structure. A $\log_{10}$ transformation was performed when necessary to achieve homogeneity of variance. The non-parametric equivalent Kruskal Wallis test was used when assumptions of variance were not met. For the multivariate data, the ANOSIM routine was used to test for changes between the epifauna assemblages at different durations of closure. Density data were square-root

transformed and a Bray–Curtis similarity index matrix was calculated among samples. SIMPER analysis was conducted to examine the contribution to dissimilarity of individual species between different durations of closure.

4.3.7.4 Analysis of the long term effects of scallop dredging in the seasonally fished area

The relationship between cumulative fishing intensity (i.e. calculated for the period November 2008 – April 2011) and the $\log_{10}$-transformed total epifauna density and species richness at sites sampled within the seasonally fished area was analyzed using Pearson's correlation coefficient. As the variance for *Pecten maximus* and *Aequipecten opercularis* density data was still heterogeneous after transformation, the non-parametric Spearman correlation coefficient was used to examine the correlation between scallop density and fishing intensity. Since none of the correlations were significant, no further analyses were carried out.

4.4 RESULTS

4.4.1 Environmental data: video tows and side scan sonar

The environmental characteristics of the 12 stations sampled inside and outside the permanent closed area did not change significantly among the four sampling events (ANOSIM; R = -0.04, p = 0.9), nor between the two areas (ANOSIM; R = 0.06, p = 0.05). Stations within the permanent closed area were predominantly sandy interspersed with cobbles, whereas those within the seasonally fished area were on average composed of equal amounts of sand and gravel (Table 4.3). Both areas had very sparse cobbles (Table 4.3). Depth and tidal-bed shear stress did not differ significantly between the permanent closed area and the seasonally fished area (Table 4.3).

The sediment composition of the 18 stations sampled within the permanent closed area to assess recovery of the benthic community after the complete closure of the scallop fishery changed significantly between the two sampling events. In June 2010 the dominant sediment type across the study sites was gravel with some cobbles (mean ± SE: % sand = 16.7 ± 4.8; % gravel = 72.1 ± 6.8; % cobbles = 11.2 ± 4.0), whereas in April 2011 stations were on average composed of equal amounts of sand and gravel (mean ± SE: % sand = 49.7 ± 8.8; % gravel = 47.8 ± 8.6; % cobbles = 2.5 ± 1.3).

Table 4.3 Summary of the abiotic habitat characteristics (mean ± SE) at sites sampled in the permanent closed area (Closed) and in the seasonally fished area (Open).

Environmental variable	Closed	Open	Mann-Whitney test
Cobble content (%)	3.2 ± 1.3	0.8 ± 0.5	ns
Gravel content (%)	32.3 ± 5.5	50.1 ± 7.9	ns
Sand content (%)	64.5 ± 5.5	49.2 ± 7.9	ns
Bottom shear stress (N m^{-2})	0.4 ± 0.02	0.4 ± 0.01	ns
Depth (m)	30.5 ± 1.5	30.4 ± 0.9	ns

Examination of the side scan sonar records from the repeat surveys in December 2009 and June 2010 indicated temporal variation in seabed configuration. In December 2009, the bedform was characterised by numerous sand ribbons aligned parallel to the main tidal flow, with coarser gravely material in between the ribbons. Within these sand ribbons mega ripples occurred that were orientated perpendicular to the main tidal current. The repeat side scan sonar survey in June 2010 indicated a dominance of sand ribbons, but these were less extensive than in December 2009. Transect sections that overlapped significantly between the two surveys indicated temporal shifts in seabed morphology such as changes in topographic composition (Fig. 4.2) and the orientation and position of substratum features (Fig. 4.3). More examples are given in Appendix II. Interestingly, there was little evidence of scallop dredging scour marks in December 2009 compared to June 2010. At the time of the first survey the seasonally fished area had been closed to scallop dredging for a period of 6 months, whereas in June 2010 the area had only been closed for two weeks following a 3 month open period to scallop dredging. The weathering of dredge tracks may have been due to increased wave action over the winter months which, combined with the prevailing tidal currents, would serve to increase sediment transport at that time.
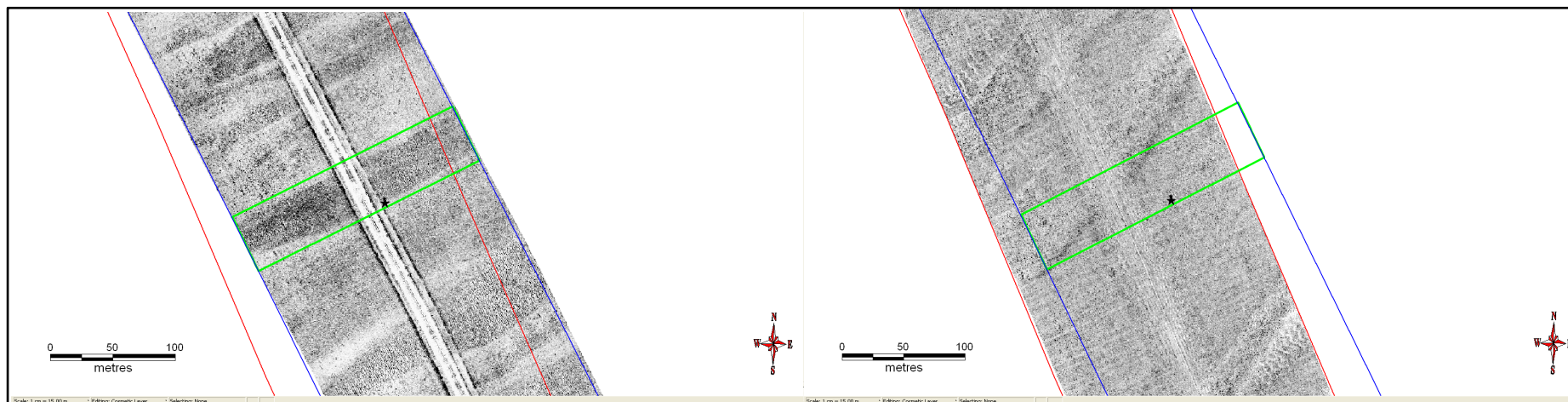
Fig. 4.2 Two sonar mosaics showing the same area of the seabed from the December 2009 survey (left) and the June 2010 survey (right) (the width of both sonar scans is 200m). The outer edges of both sonar tracks are shown to illustrate the common seabed area covered (blue: Dec '09, red: Jun '10). The asterisks show the location of a station from the photographic survey which aids correlation between the two data sets which are at the same scale and orientation. Features highlighted in green indicate a shift in seabed morphology, whereby the sand ribbons over a coarse substratum (darker shadow) seen in December 2009 were replaced by a landscape dominated by sand ripples in June 2010, and also a change in the orientation of the sand ribbons between surveys.
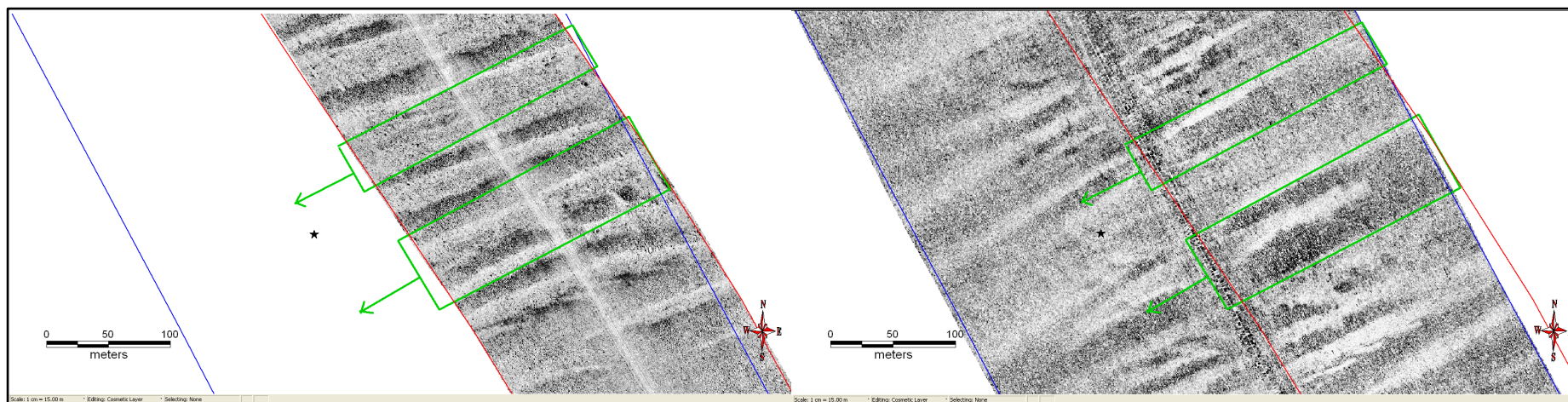
Fig. 4.3 Two sonar mosaics showing the same area of the seabed from the December 2009 survey (left) and the June 2010 survey (right) (the width of 1st sonar scan is 400m and the second scan is 200m). The outer edges of both sonar tracks are shown to illustrate the common seabed area covered (blue: Dec '09, red: Jun '10). The asterisks show the location of a station from the photographic survey which aids correlation between the two data sets which are at the same scale and orientation. Features highlighted in green indicate a change in position of the sand ribbons between surveys.

4.4.2 Identification of spatial and temporal variation of biota in Cardigan Bay SAC

A total of 100 taxa were recorded during the four surveys. On average, species richness ranged between (mean ± SE) 6.3 ± 1.3 to 29.6 ± 5.5 taxa per site (Fig. 4.4). Only 15 species contributed to more than 80% of the total density (Table 4.4). Species richness, diversity (H'), evenness (J'), total epifauna density and scallop (*Pecten maximus* and *Aequipecten opercularis*) density were similar between the permanent closed area and the seasonally fished area (Fig. 4.4, "Zone effect" in Table 4.5). Total epifauna density, species richness and diversity were consistently the lowest during the December 2009 survey and the highest in June 2010, and these temporal differences were significant ("Time effect" in Table 4.5). Furthermore, total epifauna density and species richness were on average four and two-times lower in December 2009 than in December 2010, respectively (Fig. 4.4), indicating strong interannual variability of seasons (e.g. frequency and duration of storm surges). Evenness and *A. opercularis* density did not change significantly throughout the sampling period (Table 4.5), and although mean density for *P. maximus* appeared to decrease with time (Fig. 4.4), this temporal trend was not significant (Table 4.5). The interaction term between 'management area' and 'survey time' (Time x Zone) was not significant for any of the univariate measures examined (Table 4.5), hence we did not detect effects due to dredging in the seasonally fished area or due to protection from fishing in the permanent closed area.

Table 4.4 List of macro-epibenthic taxa contributing to more than 80% of the total density at sites sampled within the permanent closed area and seasonally fished area in the Cardigan Bay Special Area of Conservation. Individual taxon contribution to overall density is given under Contr. (%).

Taxon	Taxonomic group	Contribution (%)
Hydroid turf	Hydroid	18
Ophiura albida	Ophiuroid	14.4
Ophiothrix fragilis	Ophiuroid	8.8
Cellaria sp.	Bryozoan	7.9
Epizoanthus couchii	Cnidarian	7.1
Alcyonium digitatum	Soft coral	7
Pecten maximus	Bivalve	3.2
Aequipecten opercularis	Bivalve	2.7
Nemertesia antennina	Hydroid	2.5
Cerianthus lloydii	Cnidarian	2.2

Serpula sp.	Annelid	2.2
Gibbula sp.	Gastropod	1.3
Polychaeta indet.	Annelid	1.3
Bivalvia indet.	Bivalve	1.2
Perophora listeri	Tunicate	1.1
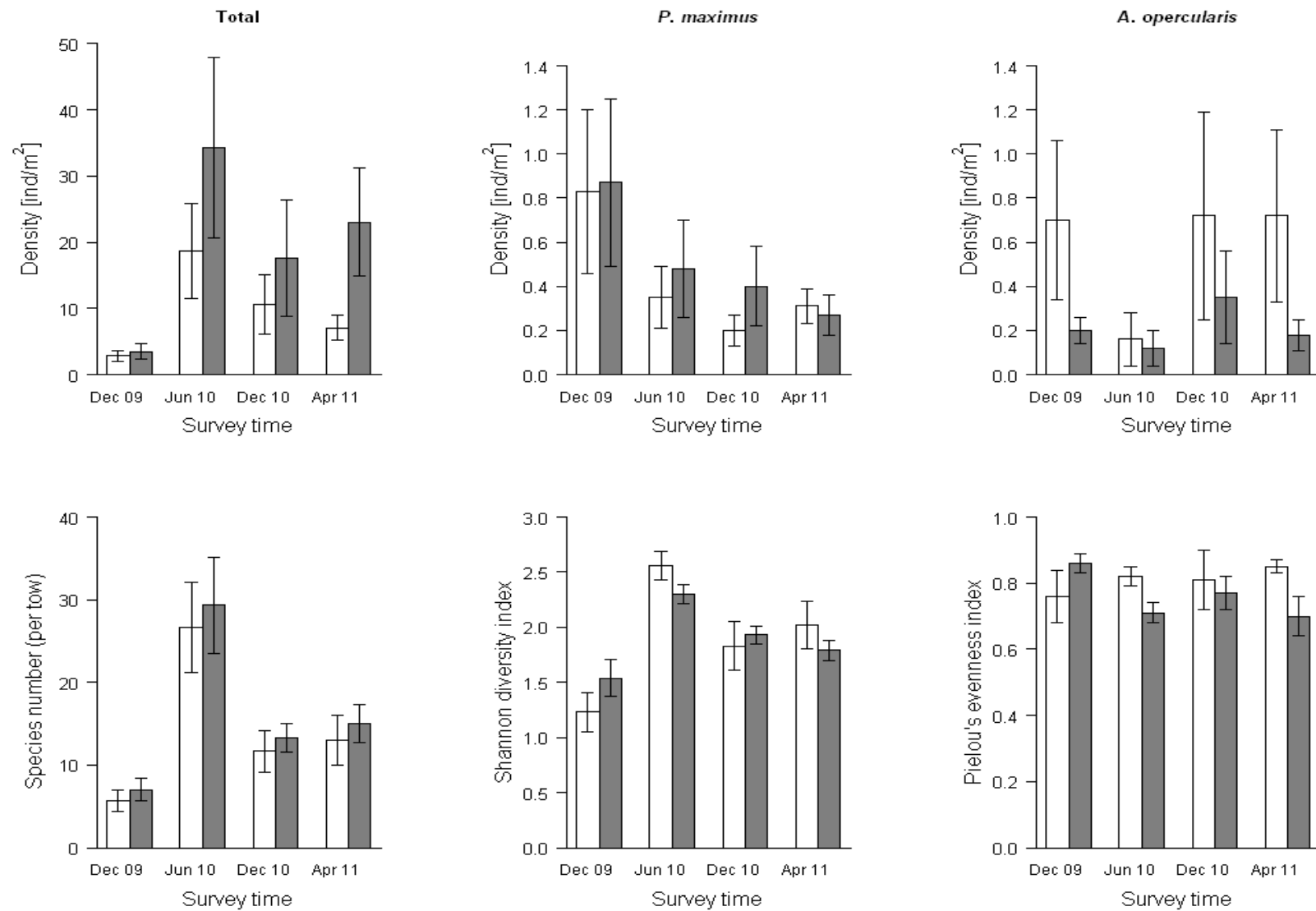
Fig. 4.4. Mean ± SE total epifauna density (ind m^{-2}), *Pecten maximus* density (indvs m^{-2}), *Aequipecten opercularis* density (ind m^{-2}), species number (species tow^{-1}), Shannon-Wiener diversity index (H') and Pielou's evenness index (J') inside the permanent closed area (shaded) and the seasonally fished area (open) during the four sampling events (Dec '09, Jun '10, Dec '10, Apr '11).

Table 4.5 Results from a 2-way crossed ANOVA for the effect of management area (Zone) and sampling event (Time) on total mean density (all taxa) and density of scallop species *Pecten maximus* and *Aequipecten opercularis* (ind m^{-2}), species richness (species tow^{-1}), Shannon-Wiener diversity index (H') and Pielou's evenness (J'). Data for total density and species richness were log-transformed, scallop densities were square-root transformed to meet homogeneity of variance.

		All taxa		*P. maximus*		*A. opercularis*	
		F	**P**	**F**	**P**	**F**	**P**
Density (# m^{-2})	Time effect	5.4	**0.003**	1.6	0.2	0.9	0.5
	Zone effect	< 0.0001	0.9	0.4	0.5	5.7	**0.02**
	Time x Zone	0.2	0.9	0.7	0.5	0.1	0.9
Species richness (S tow^{-1})	Time effect	12.4	**< 0.0001**				
	Zone effect	0.1	0.7				
	Time x Zone	0.1	0.9				
Shannon diversity (H')	Time effect	8.9	**< 0.0001**				
	Zone effect	0.6	0.4				
	Time x Zone	0.9	0.4				
Pielou's evenness (J')	Time effect	0.6	0.6				
	Zone effect	0.04	0.9				
	Time x Zone	1.8	0.2				

F: F test value of 2 factors (time and zone) ANOVA; p: probability of rejecting Ho at the 0.05 level of significance

Analogous to the results for the univariate measures, the multivariate analysis of the benthic epifaunal assemblage density identified significant differences among the four sampling events, but there was no significant zone or interaction effect (Table 4.6). The ordination plot from the canonical analysis of principal coordinates (CAP) showed clear distinctions between the assemblage sampled in December 2009 and that sampled in June 2010 (CAP1 axis in Fig. 4.5), and between the assemblage surveyed in summer (June 2010) and those sampled in winter (December 2010) and spring (April 2011) (CAP2 axis in Fig. 4.5). The size of the squared canonical correlations for each of the two axes was high; $\delta^2_1 = 0.95$ and $\delta^2_2 = 0.82$, indicating a strong association between the variation in the benthic assemblage and the time of the sampling event. Sessile emergent species such as *Nemertesia* spp., *Alcyonidium diaphanum*, *Epizoanthus couchii* and *Cerianthus lloydii* were more abundant in June 2010 than in December 2009 (Table 4.7), whereas species that typically senesce in the winter and reproduce during the summer such as *Bugula* spp. and *Clavelina lepadiformis* were more abundant in June 2010 than in December 2010 and April 2011 (Table 4.8).

Table 4.6 PERMANOVA analysis on square-root transformed epifauna density data and Bray-Curtis similarity matrix to examine the effect of management zone (Zone) and survey time (Time) using a 2-way crossed design.

PERMANOVA

Source	df	SS	MS	Pseudo-F	P(perm)
Zone effect	1	4022.8	4022.8	1.6	0.1
Time effect	3	26315	8771.8	**3.5**	**0.0001**
Zone x Time	3	4613.9	1538	0.6	0.9
Res	40	100920	2522.9		
Total	47	135870			
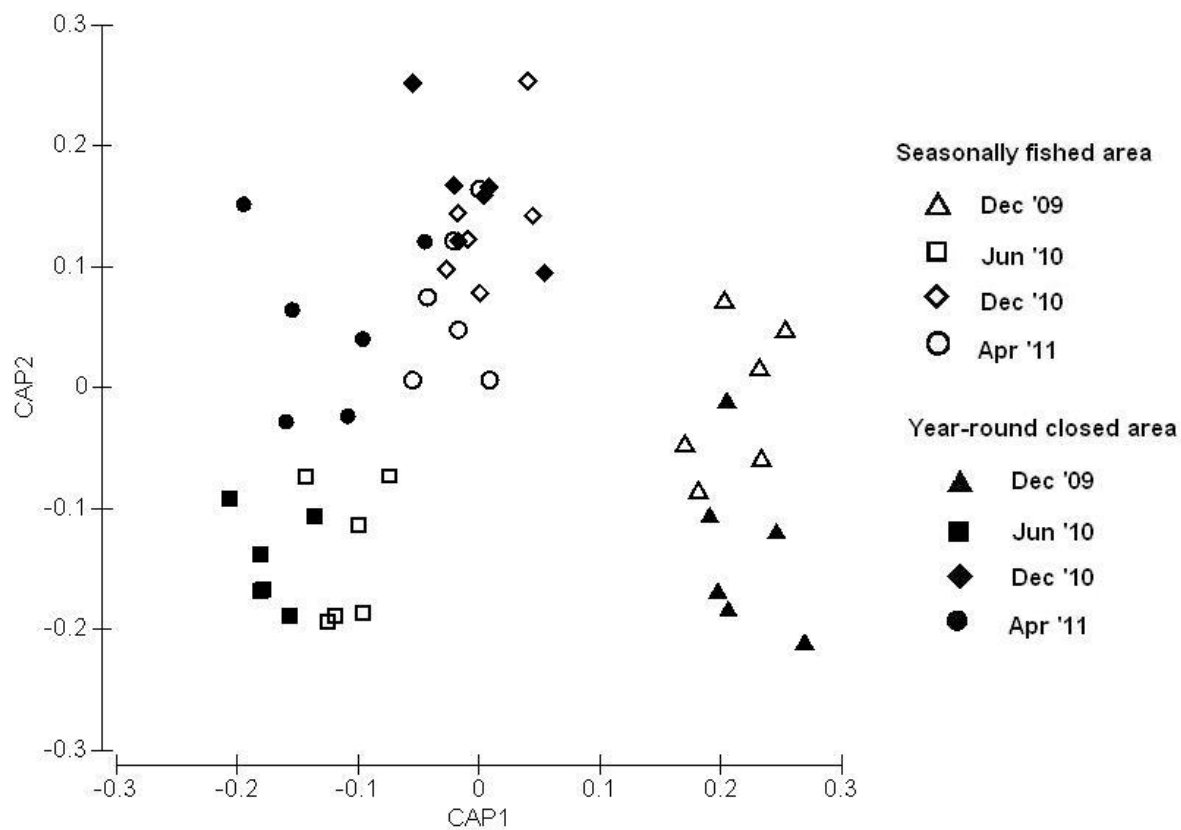
Fig. 4.5 Two-dimensional ordination plot of the first two canonical axes for CAP analysis on square-root transformed epifaunal assemblage density data.

Table 4.7 Correlation coefficients for individual species ($|r| \geq 0.4$) with the first canonical axis. A positive correlation indicates higher species density during June 2010 relative to December 2009.

Species	CAP 1: correlation coefficient	Average density (indvs m^{-2})			
		Dec 2009	June 2010	Dec 2010	April 2011
Hydroid turf	0.7	0.1	6.1	2.3	2.0
Nemertesia antennina	0.6	0.01	1.2	0.2	0.1
Alcyonidium diaphanum	0.6	0	0.6	0	0.02
Nemertesia ramosa	0.6	0	0.2	0	0.1
Cerianthus lloydii	0.5	0	0.9	0.3	0.1
Epizoanthus couchii	0.4	0	2.7	0.7	0.8

Table 4.8 Correlation coefficients for individual species ($|r| \geq 0.4$) with the second canonical axis. A positive correlation indicates higher species density during June 2010 relative to the other three sampling periods.

Species	CAP 2: correlation coefficient	Average density (indvs m^{-2})			
		Dec 2009	June 2010	Dec 2010	April 2011
Anemone indet.	0.6	0.09	0.2	0.02	0.1
Sycon spp.	0.5	0	0.3	0	0
Ebalia spp.	0.4	0.03	0.2	0.01	0.1
Alcyonidium diaphanum	0.4	0	0.6	0	0.02
Clavelina lepadiformis	0.4	0	0.1	0	0
Polymastia spp.	0.4	0	0.1	0	0
Securiflustra/Bugula sp.	0.4	0	0.1	0	0
Nemertesia antennina	0.4	0.01	1.2	0.2	0.1

Multivariate regression analysis using the DISTLM analysis indicated that total variation was best explained by gravel content, tidal shear stress and survey time (Table 4.9). However, this model only explained 34% of the total variability in the biological data. 'Survey time' explained the greatest amount of variation in the data at 19.4% and while fishing intensity explained a significant proportion of the variability in assemblage composition, it only accounted for 5% of the total variability (Table 4.9).

Table 4.9 Results of DISTLM for normalized environmental data and Bray-Curtis similarity matrix for square-root transformed epibenthic assemblage density data, using the 'BEST' selection procedure on the basis of the AIC selection criterion.

Marginal tests

Variable	SS(trace)	Pseudo-F	P	% variation explained
% cobble	4339.4	1.5	0.09	3
% gravel	5780.3	2.0	**0.02**	4
Fishing intensity	6844.6	2.4	**0.003**	5
Shear stress	14185	5.4	**0.0001**	10
Survey time	26315	3.5	**0.0001**	19.4

Overall BEST solution

AIC	R^2	Predictor variables
373.4	0.3	% gravel, shear stress, survey time

4.4.3 Temporal changes in the permanent closed area

On average total epifauna density and scallop density did not change significantly with increasing duration of protection from scallop dredging, that is after 13 months (June 2010) and 23 months (April 2011) of closure (Table 4.10). In contrast, species richness was significantly higher in June 2010 than in April 2011 (Table 4.10). When the analysis was carried out at the level of taxonomic class, we found significant differences among the two survey events for five out of the fifteen taxonomic classes and densities were lower after 23 months of closure than after 13 months (Fig. 4.6). The multivariate analysis of the benthic assemblage composition found significant differences between the two sampling events (ANOSIM on duration of closure; R = 2.6, p = 0.002), however, the species that contributed most to this difference suggest that differences are likely to be due to natural temporal fluctuations in species abundance rather than due to an increase in the density of disturbance-sensitive species (Table 4.11).

Table 4.10 Epifauna species density and species richness (mean ± SE) at the permanent closed area, following 13 months (June 2010) and 23 months (April 2011) of no scallop dredging.

Duration of closure	Total density (ind m^{-2})	Number of species (S tow^{-1})	*P. maximus* density (ind m^{-2})	*A. opercularis* density (ind m^{-2})
13 months	37.2 ± 7.4	26.9 ± 2.5	0.4 ± 0.1	0.5 ± 0.2
23 months	32.5 ± 4.7	20.3 ± 1.9	0.4 ± 0.1	0.4 ± 0.1
ANOVA-test	F = 0.28, p = 0.6	F = 4.4, p = 0.04	F = 0.01, p = 0.9	F = 0.5, p = 0.5

F: F test value of 1 factor (duration of closure) ANOVA; p: probability of rejecting Ho at the 0.05 level of significance
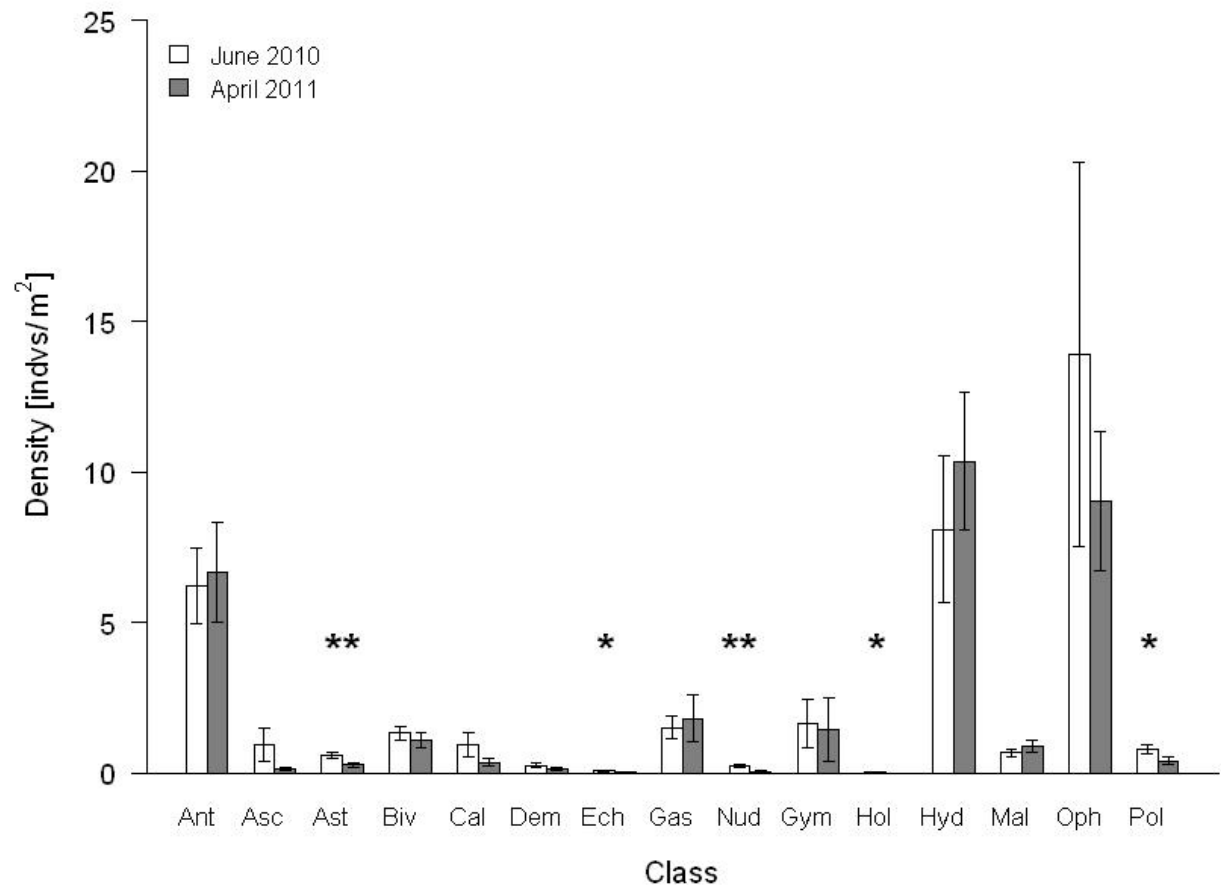
Fig. 4.6 Mean density (ind m^{-2}) by taxonomic class for survey carried out after 13 months (June 2010) and 23 months (April 2011) of closure of scallop dredging in the permanent closed area. Error bars represent standard error. Ant: Anthozoa, Asc: Ascidiacea, Ast: Asteroidea, Biv: Bivalvia, Cal: Calcarea, Dem: Demospongiae, Ech: Echinoidea, Gas: Gastropoda (snails), Nud: Nudibranchia, Gym: Gymnolaemata, Hol: Holothuroidea, Hyd: Hydrozoa, Mal: Malacostraca, Oph: Ophiuroidea, Pol:

Polychaeta. * indicate significant difference among sampling events at a 0.05 level of significance. **
indicates significant difference at a 0.01 level of significance.

Table 4.11 SIMPER analysis giving the average density (ind m^{-2}) of those species that contributed to
more than 40% of the dissimilarity between the epifauna assemblages after 13 months (June 2010)
and 23 months (April 2011) of closure. % Contrib refers to the % contribution of individual species to
the dissimilarity between the two sampling events.

Species	June 2010	April 2011	
	Avergae abundance	Average abundance	% Contribution
Ophiothrix fragilis	1.0	0.7	6.4
Ophiura albida	2.3	2.2	5.6
Hydroid turf	1.9	2.5	5.6
Epizoanthus couchii	0.6	1.3	4.9
Alcyonium digitatum	1.2	1.3	4.6
Cerianthus lloydii	0.8	0.4	3.0
Hydrallmania falcata	0.02	0.6	2.5
Nemertesia antennina	0.8	0.5	2.4
Aequipecten opercularis	0.5	0.5	2.2
Gastropod indet.	0.1	0.6	2.2
Asterias rubens	0.7	0.3	2.2

4.4.4 Effects of fishing intensity in the seasonally fished area

The effect of scallop dredging in the seasonally fished area was assessed on species data
collected within this area in April 2011. Total epifauna density, scallop density and species
richness were not significantly correlated with fishing intensity (estimated as the number of
hours fished per month for the period November 2008 to April 2011); Pearson coefficient for
(a) log-transformed total density = -0.1, p = 0.9; (b) species richness = -0.1, p = 0.7;
Spearman rho for (a) *Pecten maximus* density = 0.4, p = 0.2; (b) *Aequipecten opercularis* = -
0.1, p = 0.8.

4.5   DISCUSSION

Throughout the course of this study no differences in the abundance of scallops and the
epibenthic community composition were detected between the permanent closed area and the
seasonally fished area in Cardigan Bay Special Area of Conservation (SAC) ("Zone" effect).
Given that the open season to scallop dredging in the SAC runs from November through to

April, an effect of fishing during the open season in the seasonally fished area but not in the permanent closed area was expected. There was no interaction effect between the time of sampling event and the management zone ("Time x Zone"), thus no effect of fishing at any time throughout our 23 month sampling period was found. The lack of any clear "Zone" or interaction "Time x Zone" effect could be due to a number of reasons. One potential reason may be that seasonal fluctuations in species abundance may reduce the potential for fishing effect to be detected during the open season (November to April), which coincides with winter and spring. Species that typically senesce in winter (e.g. *Nemertesia antennina*) but reproduce and regrow in summer (e.g. *Bugula* spp., *Clavelina lepadiformis*) had the lowest densities during the winter surveys but the highest densities during the summer survey. These seasonal fluctuations are likely to reflect new growth and recruitment processes that generally occur in spring synchronised with the higher food availability from phytoplankton blooms (Winder and Cloern 2010).

Another possible explanation for the lack of fishing effect between the permanent closed area and the seasonally fished area may be the relatively high level of natural disturbance at the study area that might obscure the effect of fishing on the benthic community. Previous studies have shown that the magnitude of the effect on benthic communities from bottom-towed gears is strongly dependent on habitat type (Collie et al. 2000b; Kaiser et al. 2006); effects in high-energy environments and dynamic habitats, such as shallow sandy sediments are lower in magnitude compared to more stable habitats (Bergman and van Santbrink 2000; Hall-Spencer and Moore 2000). For example, Kaiser et al. (1998) found that beam trawling had no detectable short-term effect on epifauna communities in mobile sediment compared to more stable sediment habitats in adjacent areas. Gibbs et al. (1980) demonstrated that otter trawling on sandy, estuarine shrimp grounds in New South Wales did not cause any detectable changes in macrobenthic fauna, which they attributed to the resilience of coarser sediment fauna and pre-stressed conditions in the estuary. Stokesbury and Harris (2006) found that the effect of natural disturbance on the epibenthic community prevailed over that of fishing disturbance from the short-term scallop fishery at Georges Bank. The predominance of mobile sediment (sand and fine gravel) aligned parallel to the direction of the main tidal flow, together with the shifting bedforms observed among surveys (side scan sonar surveys) provide evidence of a naturally dynamic environment at our study area. Furthermore, the dominance of taxa such as hydroids, ophiuroids and anthozoans that are morphologically (e.g. high degree of flexibility or low-lying turf) or behaviourally (e.g. high mobility, passive suspension feeders) adapted to dynamic conditions (Labarbera 1984,

Okamura 1987, Coma et al. 1998) indicates that the benthic assemblage at Cardigan Bay is composed of species that tolerate the frequent natural perturbations from physical processes such as tidal currents and waves. The extremely low abundance and species richness that was observed at all sampling sites during the first sampling event (December 2009) is unlikely to have resulted from fishing alone, because the entire SAC had been closed to scallop dredging for six months at the time of sampling (see Table 1). Rather, it is likely that the five weeks of strong winds and heavy sea state that preceded the first survey (pers. obs.) may explain the relatively impoverished community observed in December 2009. Sessile emergent species such as *Nemertesia* spp., *Alcyonidium diaphanum* and *Cerianthus lloydii*, which are likely to experience high mortality due to displacement from the sediment or from damage due to scouring by pebbles/cobbles, had very low densities during the December 2009 survey relative to the other three surveys. Wave-induced mortality is known to impact community structure to a water depth of approximately 50m (Oliver et al. 1980; Hall 1994; Hiddink et al. 2006b; Lambert et al. 2011), and given that all our sampling sites were within 35 metres, it is possible that wave scour at the seabed may have resulted in mortality of some species. Nevertheless, the increase in abundance within a few months (i.e. the June 2010 survey) indicates substantial recovery from this natural disturbance by recolonization and re-growth of fauna. The resilience of the community following the storm event, but the lack of difference between the closed and open areas to scallop dredging suggests that the level of scallop fishing at our survey sites, estimated between 0.07 – 0.52 hours of fishing per month, may be insufficient to induce changes sufficiently large to be detected in the presence of strong background natural disturbance. This conclusion matches that of Kulbicki et al. (2007); they attributed the lack of a response to the establishment of the Abore reef MPA on fish assemblages to a relatively low fishing pressure and to natural variations that obscured changes due to fishing.

Fishing by bottom-towed gear causes shifts in benthic community composition and structure; from those dominated by slow-moving or sessile erect, filter-feeding species to highly mobile scavengers and predators or small-bodied infaunal species (Kaiser et al. 2000; Jennings et al. 2001; Hermsen et al. 2003; Carbines and Cole 2009; Strain et al. 2012). We expected that the reverse would occur in the permanent closed area after cessation of scallop dredging. There was no effect of "Duration of closure" on overall epifauna density, scallop density or species richness, thus our analysis did not reveal changes in abundance and diversity associated with recovery from fishing disturbance. The observed changes in community composition (see multivariate analysis) were mainly due to temporal patterns of natural variation associated to

processes such as recruitment, rather than shifts from robust to fragile species. One possible reason for this lack of recovery with time is that the duration of our study (~ 2 years) was not long enough to elicit a visible response in the epibenthos. The recovery of benthic communities from scallop dredging in sand habitats have been shown to occur within 39 days of disturbance, but may take up to 6 months for some taxa such as annelids and molluscs (Kaiser et al. 2006). Conversely, communities inhabiting relatively stable gravel sediments that tend to support communities with high levels of diversity and biomass, may take several years to recover (Kaiser et al. 2006). It must be acknowledged that the studies used by Kaiser et al. (2006) were experimental manipulations; hence expanding their predictions to the entire fishery comes with some difficulty as the fishery is not spatially or temporally uniform and covers a range of environmental conditions. However, given that the Cardigan Bay SAC is characterized by a highly natural dynamic environment and a predominance of sand mixed with gravel and pebble, we expected some recovery to have occurred after 23 months of closure of the fishery if scallop dredging was affecting the benthic community in the first instance. The lack of change in scallop density and community composition after almost 2 years of no fishing provides further support to the hypothesis that the highly dynamic environment is what primarily drives the community composition and structure at Cardigan Bay. Nevertheless, we recommend that further monitoring be undertaken for a better understanding of the recolonization, recovery and succession process of the epifaunal community in the permanent closed area of the SAC.

Although no effects of scallop dredging were detected on the macro-epibenthic community at the Cardigan Bay SAC, it must be recognized that scallop dredging has been a common fishing practice in Cardigan Bay (including the SAC) for over 30 years. Thus, scallop dredging may have caused previous impacts that are no longer detectable because they have become widespread and long-term. Previous studies have suggested that five to ten year periods of low-medium intensity mobile fishing can result in long-term declines in epibenthic biogenic reef forming species and their associated taxa (Bradshaw et al. 2002; Cranfield et al. 2004; Kaiser et al. 2006). In the absence of long-term environmental and biological data in the SAC, dating to before the start of scallop fishing in Cardigan Bay, it is difficult to disentangle the effects of scallop dredging from other environmental disturbances. This is not a unique problem to our study. For instance, in a well-replicated control impact study of the effect of an estuarine prawn-trawl fishery on benthic assemblages at Clarence River, Underwood (2007) found no effect of current trawling practices. The absence of data regarding long-term environmental changes caused by anthropogenic activities (including

trawling) precluded the separation of the effects of trawling from other potential confounding long-term disturbances.

In conclusion, scallop density and the epibenthic community within the seasonally fished area where scallop dredging is permitted for six months of the year were similar to those in the unfished permanent closed area. Further, the sea floor sediment composition shifted more than the epibenthic community it supported. Hence, the results suggest that the highly dynamic environment may have an effect strong enough to mask or strongly modify the effects of protection from fishing. Gauging the impact of mobile fishing gear requires an understanding of how natural disturbance affects benthic communities (Hall 1994). Unquestionably, dredges disturb the seabed. However, the seabed is also disturbed by natural physical and biological processes, and the biological communities that utilize a particular habitat will adapt to that environment (Krebs 1994). Fishers and managers of fisheries closures set a number of expectations from MPAs and unexpected results may bring around conflicts (Agardy et al. 2003). In particular, increases in diversity, density and biomass are expected outputs. These results have shown that under some circumstances permanent fishery closures may not necessarily provide detectable increases in target species and their associated communities, at least within a short period of establishment. The effect of protection from mobile fishing gear on the habitat structure and biological community must be scaled against the magnitude and frequency of seabed disturbance due to natural causes. The imposition of fisheries closed areas without due consideration of the natural environment conditions and the biology of species concerned may result in negative impacts on fisheries and limited conservation benefits.

CHAPTER 5

Evaluating effects of partial restrictions to bottom fishing on temperate epibenthic assemblages

5.1 ABSTRACT

Commercial fishing with mobile gear (e.g. otter trawls, beam trawls, scallop dredges) is among the key anthropogenic activities with significant deleterious effects on marine habitats and ecosystems. A number of areas closed to fishing with bottom-towed gear exist in UK waters with the goal of protecting biodiversity as well as conserving stocks of economically important species. Underwater camera surveys were carried out at three such fishery closed areas (Port Erin scallop dredging exclusion area, Isle of Man; Skomer Marine Nature Reserve; Modiolus Box within the Pen Llyn a'r Sarnau Special Area of Conservation) between 2009 and 2010 to examine the response of epibenthic communities to protection from bottom fishing. The effect of protection was evaluated by comparing the abundance (density and % cover) of epibenthic species including the fisheries' target species, *Aequipecten opercularis* and *Pecten maximus*, and the epibenthic community structure inside and outside each of the closed areas. *P. maximus* had consistently higher abundance inside the protected areas than in the fished areas. In contrast, *A. opercularis* was more abundant outside the closed areas. In general hydroids, bryozoans, sponges and gastropods were more abundant inside the closed areas than outside, although the magnitude of response varied among the MPAs. These differences were unlikely to be related to sediment type because there were no significant differences in sediment composition between protected and unprotected locations and habitat characteristics (sediment type and depth) were comparable among the three MPAs. Rather, the variation in 'reserve effect' among the three MPAs may be linked to differences in relative fishing effort (frequency and intensity of fishing) at the fished areas outside the MPAs. Although the results from this study should be interpreted with caution due to the lack of data from before and after the establishment of the MPAs, target species populations and epibenthic invertebrate communities showed signs of benefit due to protection from bottom fishing at the time of study, emphasizing the importance of MPAs in ecosystem-based management of fisheries.

KEYWORDS: marine protected area, fishery closure, bottom fishing, epibenthic communities, *Aequipecten opercularis*, *Pecten maximus*, underwater digital imagery

5.2   INTRODUCTION

Commercial fishing with mobile gear (e.g. otter trawls, beam trawls, scallop dredges) is among the key anthropogenic activities with significant impacts on marine ecosystems (Jennings and Kaiser 1998; Kaiser et al. 2006; Halpern et al. 2008). About 75% of the global continental shelf is known to be impacted by trawling and dredging activity (Kaiser et al. 2002). Some areas such as those in the Gulf of Maine and parts of the Irish Sea are trawled on average three times per year (Auster et al. 1996; Kaiser et al. 1996). Towed bottom-fishing gear poses a significant threat to the integrity of benthic habitats, particularly those formed by sessile emergent fauna (Collie et al. 1997; Watling and Norse 1998; Veale et al. 2000; Lambert et al. 2011). For example, these habitats act as important settlement surfaces and refuges from predation for juveniles of some commercial species (Lindholm et al. 1999; Bradshaw et al. 2003; Scharf et al. 2006; Howarth et al. 2011) and host a diverse faunal assemblage that may be important prey for some organisms (Collie et al. 2000; Thrush and Dayton 2002). Chronic fishing disturbance may be sufficient to severely reduce the complexity of such habitats by removing the fragile sessile fauna (Thrush et al. 1998; Kaiser et al. 2000; Hinz et al. 2009), thereby reducing the suitability of the area for bottom-feeders and bottom-dwelling species.

Traditionally, fisheries management has focused on the conservation and sustainability of single stocks of target species, giving little attention to the secondary impacts of fishing on marine ecosystems. However, there is now a greater appreciation of the need to take an ecosystem-based approach to fisheries management (Brodziak and Link 2002; Pikitch et al. 2004). The last decades have seen a gradual increase in the number of marine protected areas (MPAs) in coastal regions in order to preserve marine biodiversity and to promote the sustainable ecosystem-based management of coastal resources (Jamieson and Levings 2001; Gell and Roberts 2003; Abdulla et al. 2009).

Despite the increased recognition of the role of MPAs in conservation of habitat and the wider community beyond targeted species, most ecological studies on the effect of MPAs often focus on one species or group of species that are target of the fisheries (e.g. Goni et al. 2003; Beukers-Stewart et al. 2005; Claudet et al. 2006; Tuya et al. 2006; Barrett et al. 2007). Moreover, the majority of research efforts have focused on the role of MPAs in the protection of fish species, as is evidenced by the considerably large number of existing reviews and

meta-analysis on fish populations (e.g. Mosquera et al. 2000; Cote et al. 2001; Halpern 2003; Micheli et al. 2004; Guidetti and Sala 2007; Claudet et al. 2008; Lester et al. 2009; Maliao et al. 2009; Molloy et al. 2009; Vandeperre et al. 2011). Comparatively fewer studies have examined the role of MPAs for invertebrate species, and even fewer still have looked at the effect of protection on invertebrate communities as a whole; only 8 out of the 62 studies reviewed in the full systematic review conducted as part of Chapter 2 investigated the effect of protection on epifaunal and infaunal invertebrate assemblages.

In this study I focused on the overall 'reserve effect' at the community level, by testing whether the epibenthic invertebrate community inside areas closed to bottom towed fishing gear (trawls, dredges) differed from those that remained open to bottom fishing. To increase the generality of conclusions, the same general approach was taken at three different sites. Therefore, differences in community composition and structure were evaluated from benthic photographs taken between 2009 and 2010 in three MPAs in the Irish Sea that have been closed to fishing with bottom-towed gear for at least 9 years. Protection may increase both the number and abundance of species in a particular area. Hence, it was hypothesized that relative to areas open to bottom fishing, the epibenthic communities inside the closed areas would exhibit greater density of target fisheries species (*Pecten maximus* and *Aequipecten opercularis*) and of sessile emergent epifauna that would otherwise be damaged by bottom fishing. I acknowledge that evaluation of the 'reserve effect' based only on spatial comparisons after the protected area has been implemented is not an appropriate substitute for designs that include data from before and after the declaration of a MPA (Willis et al. 2003; Guidetti et al. 2005). There were, however, no prior data available for any of the three study areas. The assessment of 'reserve effect' was thus based on spatial comparisons of MPA site(s) and multiple control sites at locations of similar environmental characteristics. Evaluation of the effectiveness of MPAs plays a crucial role in their management and re-design, as well as in the designation of new ones, therefore assessment of protection in the absence of adequate temporal replication is better than no evaluation of protection at all.

5.3 METHODS

5.3.1 Study areas

Three MPAs distributed throughout the Irish Sea were surveyed between October 2009 and June 2010. Two MPAs were located along the coast of Wales, UK; one in the north, '*Modiolus* Box' on the Llyn Peninsula (hereafter *Modiolus* Box) and the other in the south of Wales, Skomer Marine Nature Reserve (hereafter Skomer MNR), about 140 km from each other (Fig. 5.1). The third MPA was located in the Isle of Man, Port Erin scallop dredging exclusion area (hereafter Port Erin closed area), about 130 km away from the *Modiolus* Box (Fig. 5.1). Port Erin closed area is the smallest (2 km^2) and the longest established (20 years at the time of the study) among the three MPAs (Table 5.1). The Port Erin closed area was primarily set up for scallop (*Pecten maximus*) stock enhancement, which is one of the major species targeted by the scallop fishery around the Isle of Man. Skomer MNR is the only statutory marine nature reserve in Wales and was established in 1990 under the Wildlife and Countryside Act 1981, mainly to conserve marine biodiversity and the seabird colonies on Skomer Island (Table 5.1). The *Modiolus* Box is by far the largest of the three MPAs and is inside the Pen Llŷn a' r Sarnau Special Area of Conservation, primarily set up to safeguard horse mussel (*Modiolus modiolus*) reefs from bottom-towed fishing gear (Table 5.1). All three MPAs may be considered as partially protected areas as they prohibit fishing with bottom towed gear including scallop dredging and beam trawling, but allow angling and fishing with static gears such as pots (Table 5.1).

The area outside Port Erin closed area is an important fishing ground for *P. maximus* around the Isle of Man (Beukers-Stewart et al. 2003) that has been fished since 1937 (Hill et al. 1999). The *P. maximus* fishery has been well regulated, with the imposition of a minimum landing size (110 mm shell length) and a summer closed season (June–October inclusive) since 1943. Furthermore, the fishery is affected by legislation limiting boat size and aggregated gear width within the Isle of Man 3-mile territorial limit (Beukers-Stewart et al. 2003). In contrast to the Isle of Man, bottom fishing outside the *Modiolus* Box and Skomer MNR is minimal (Vanstaen and Silva 2010), although fishing with static gear (e.g. pots) is more common (Vanstaen and Silva 2010). For example, potting for lobsters and crabs in and around Skomer MNR has more than tripled over the last 22 years (up until 2011) and about 75% of the reserve was potted between 2007 and 2011 (M. Burton, pers. comm., 2010).
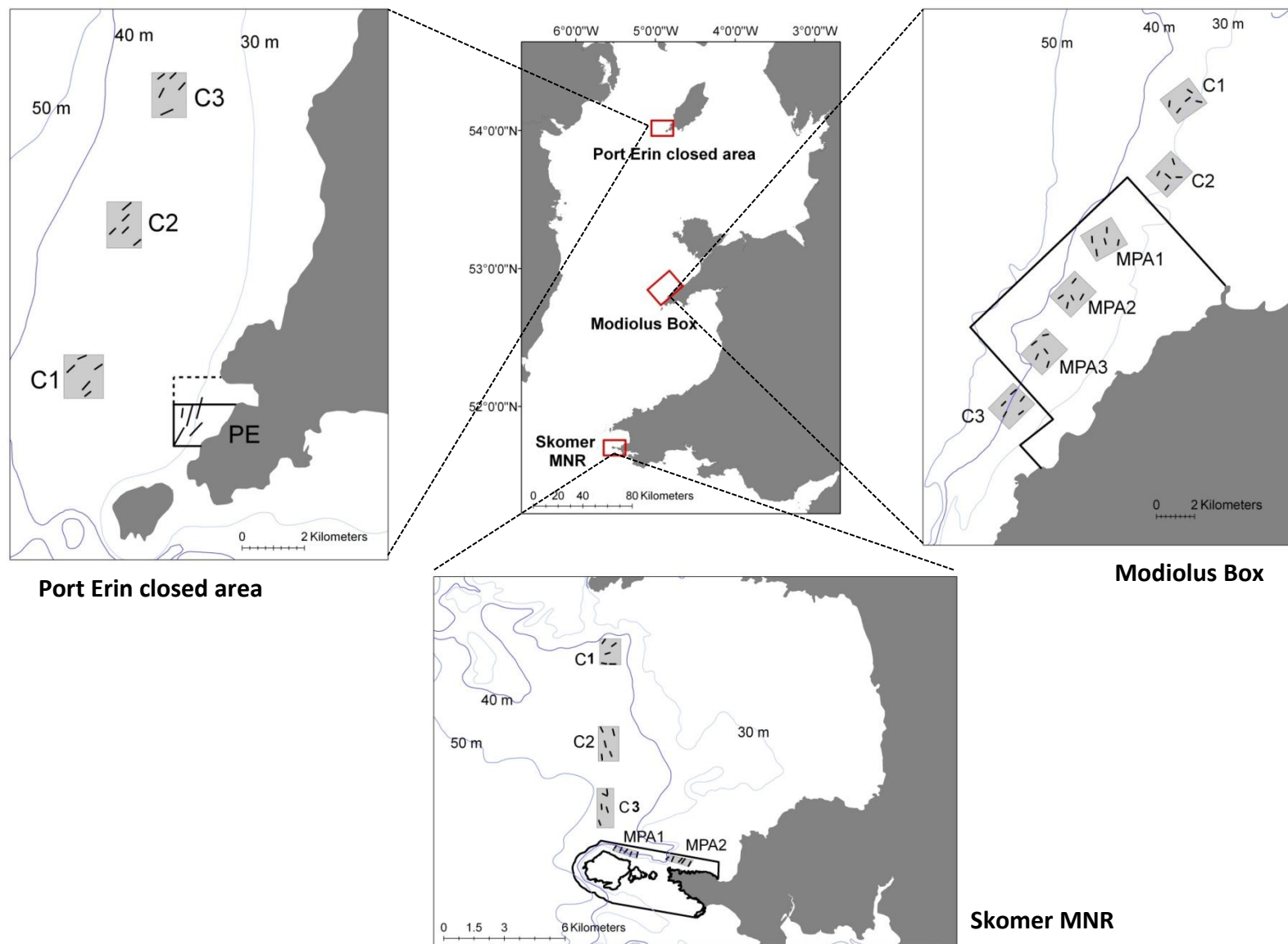
Fig. 5.1 Location of the study areas in the Irish Sea and the spatial distribution of the sites surveyed inside (labelled PE, MPA1, MPA2, MPA3) and outside (labelled C1, C2, C3) the MPA during each survey. Replicate underwater camera transects sampled at each site are indicated. Sampling was restricted to depths ranging between 30 m and 40 m.

Table 5.1 Description of the Marine Protected Areas included in the study.

MPA	Year of establish-ent	Size (km^2)	Objectives	Restricted activities	Permitted activities	Administration & enforcement
Port Erin closed area, Isle of Man	1989	2 (solid line at PE in Fig. 5.1) + 0.7 extension to the north of the area in June 2003 (dotted line at PE in Fig. 5.1)	to conserve & enhance scallop stocks to monitor recovery of benthic communities to carry out controlled experiments on the effects of scallop dredging	Fishing with bottom towed gear (dredges, bottom trawls) Collection of scallops by any method	Potting, angling	Department of Agriculture, Fisheries & Forestry (DAFF) Fisheries Division Enforcement: Good
Skomer MNR, South Wales, UK	1990	13.24	to conserve marine biodiversity to provide a 'quiet zone' around the internationally important seabird breeding colonies of the National Nature Reserve for research, monitoring and education	Fishing with dredges, beam trawls (SWSFC byelaw 27) No-take for the scallop species, *Pecten maximus* & *Aequipecten opercularis* (SWSFC byelaw 28) Restrictions on length of nets and areas for net fishing (voluntary code of practice)	Potting for lobsters and crabs	CCW MNR staff team based at Martin's Haven Enforcement: very good

'Modiolus Box' within the Pen Llŷn a' r Sarnau SAC, North Wales, UK	2000	89.06	to protect a horse mussel bed and rocky reefs from bottom towed fishing gears (trawls and dredges)	Fishing with bottom towed gear (dredges, bottom trawls) (NWNWSFC Byelaw 21)	Potting for lobsters, crabs, whelks	North Western & North Wales Sea Fisheries Committee

Enforcement: Fair, some illegal fishing is reported |

5.3.2 Data collection: survey design

Evaluation of the difference in the macro-epibenthic assemblages between the protected and unprotected areas was carried out between October 2009 and June 2010 (Table 5.2). Each study area consisted of a MPA and multiple control areas outside the MPA where fishing with bottom-towed gear is permitted to occur. Control areas with comparable environmental conditions to the MPA, primarily sediment type and depth, were identified outside each of the MPA using the local knowledge of the MPA management staff and information from bathymetric, sediment and biotope maps available from acoustic and biotic surveys for each of the study areas. In order to allow for a qualitative comparison of the epibenthic communities among the three MPAs, the sampling effort was restricted to areas composed primarily of mobile sediment (sand, gravel, pebbles) at a depth of between 30 to 40 m (Table 5.2). This meant that sampling effort at Skomer MNR was restricted to the northern side of the reserve, as the south side is dominated by rocky bottoms and boulders (M. Burton, pers. comm., 2010). Similarly, sampling in the *Modiolus* Box was restricted to areas furthest away from the coast (see Fig. 5.1), as further inshore the area is characterized by rock and boulders, kelp forests and a horse mussel reef, and depths shallower than 30 m.

One to three sampling sites were chosen randomly inside and outside the MPAs from within areas of comparable habitat (Table 5.2). Factors such as the size of the MPA, habitat heterogeneity, time and weather constraints influenced the number of sites that it was possible to sample. To avoid edge effects, sampling sites within the MPA were located at least 100 m from the boundary, and areas outside of the MPA were at least 1 km from the boundary. Each sampling site had five replicate transects, with transects at least 300 m apart. At each transect, images of the seabed were taken with a high resolution stills camera (Canon 400D) installed in an underwater housing and mounted on a sledge such that the objective lens was oriented perpendicular to the seabed at a height of 60 cm. The sledge was towed at a speed of approximately 0.5 - 1.0 knots for a period of 10 minutes, covering an average distance of 250 – 300 m, as calculated from the start and end positions of each tow. Tow direction depended on the speed and direction of the tidal current. Every eleven seconds, a 10-mega-pixel image covering an area of 0.13m^2 (0.44m x 0.30m) was taken.

Table 5.2 Summary of the survey design (number of sites sampled inside and outside each MPA during each survey) and environmental characteristics of the sites sampled at each MPA.

MPA name	Time of data collection	Spatial replication		Depth (m) mean ± SD (range)	Dominant substratum type
		Sites (in / out)	Replicates tows per site		
Port Erin closed area	7th – 10th October 2009	1 / 3	5	32.9 ± 1.22 (30.2 – 40)	Sand & shell fragments
Skomer MNR	1st – 12th May 2010	2 / 3	5	43.11 ± 5.55 (26.4 – 48.2)	Sand & pebbles
Modiolus Box	1st – 4th June 2010	3 / 3	5	35.51 ± 3.45 (29.2 – 44.4)	Sand & gravel

5.3.3 Still images analysis

Digital still images were analyzed for sediment type (20 images per transect) and organism abundance (40 images per transect). Abundance was recorded as species cover (%) for all epibenthic species including colonial, encrusting, solitary and mobile species, and as number of individuals per unit area (standardized to 1 m^2) for sessile solitary and mobile species only (i.e. all species excluding hydroids, bryozoans, sponges and colonial polychaetes). The percentage cover of benthic invertebrates was estimated using the point intercept method (Foster et al. 1991; Dethier et al. 1993). A grid of lines spaced at intervals of 5 cm was produced in Image J and superimposed on the image. The 54 intersections were used as point intercepts and % cover of organisms intercepted by a point was calculated accordingly. For organisms present in the image but not falling under a point, their percentage cover was recorded as 1 %. Despite the high quality of the images, identification and quantification of some sessile epifauna presented a number of significant challenges. First, epifaunal annelids, in particular those belonging to the family Serpulidae, could not be quantified as it was impossible to distinguish between dead specimens and live tubeworms retracted in their tubes. Second, the taxonomy of some species of the phylum Porifera and the classes Hydrozoa and Bryozoa could not be resolved below these taxonomic levels, as these organisms necessitate microscopic study to identify distinguishing features. In this case hydroid, poriferan, and bryozoan species were recorded as 'Hydroid turf', 'Porifera indet.', and 'Bryozoan indet.', respectively, and given different letters (e.g. Porifera indet. A, Porifera indet. B) to distinguish among different species.

Sediment composition at the sampling sites was also determined using the point-intercept method described above. Sediment type was divided into six categories: cobbles (64 – 256 mm), pebbles (4 – 64 mm), gravel (2 – 4 mm), sand (< 2 mm), broken shell fragments (shell) and biota (live organisms). The percentage composition of each sediment type was then calculated for each transect.

5.3.4 Data analysis

5.3.4.1 Analysis of sediment composition

Studies of assessment of the effect of protection may suffer from the possibility of bias due to differences in habitat among the MPA and control sites (Willis et al. 2003; Claudet et al. 2011). Frequency distributions of sediment type at each site were plotted and a multivariate

analysis on sediment data was performed using PERMANOVA to test for significant differences in habitat types among protected and unprotected areas.

5.3.4.2 Analysis of epibenthic species composition

Prior to analysis, the density data from 40 images were pooled for each transect and expressed as the number of individuals per $1m^2$. Percentage cover data for each individual species were averaged across 40 images and expressed as mean % cover per transect. Multivariate and univariate analyses were carried out separately for each MPA.

Multivariate analysis

The level of community similarity between protected and unprotected sites was examined using percentage cover data as these data were extracted for all species. Percentage cover data were square-root transformed to down-weight the influence of extremely abundant species and a Bray–Curtis similarity index matrix was calculated among samples. The response of the multivariate epifaunal assemblage to protection was examined using the contrast between protected and unprotected control sites (*MPA vs. Control*) in PERMANOVA. Differences among multiple control sites at each case-study and among multiple protected sites at the *Modiolus* Box were also examined using pairwise contrasts in PERMANOVA. Multidimensional scaling ordination (MDS) was used to visualize the differences in the benthic assemblages between and within-protection levels (i.e. protected vs. unprotected). Similarity percentage analysis (SIMPER) was performed to ascertain the species that contributed most to the dissimilarity between protected and unprotected areas, or among unprotected control areas.

Univariate analysis

Species were grouped into taxonomic categories to examine overall changes in the benthic community. Density and mean % cover of species belonging to the same taxonomic group were pooled together. Only those taxonomic groups that contributed to more than 5 % of the total density or percentage cover were retained for univariate statistical analysis. Furthermore, as all of the closed areas restrict fishing with bottom-towed gear primarily to limit fishing for scallops, the density of *Pecten maximus* (king scallop) and *Aequipecten opercularis* (queen scallop) was also examined between protected and unprotected areas.

Palliolum spp. was included for the analysis of the data from Port Erin closed area because it was the most common bivalve species at this study area (66% of the total bivalve density).

An asymmetric analysis of variance (ANOVA) was carried out for Port Erin closed area and for Skomer MNR, separately. Two analyses were made following the procedure described in Glasby (1997) and Underwood (1993). First, the data from all the sites (whether protected or unprotected) were analyzed in a general linear model (GLM) ANOVA, with 'site' as a fixed factor (*Step 1*). Second, the analysis was repeated using data from the unprotected sites only (*Step 2*). The detection of a significant difference between protected and unprotected areas (i.e. MPA *vs.* Fished areas) was then obtained by subtracting the sum of squares (SS) of *Step 2* from that of *Step 1*, and calculating the F-ratio and *p*-values from the resulting SS. Statistically significant differences among the fished controls (i.e. Among controls) were assessed from the analysis in *Step 2*. As the two sites surveyed inside Skomer MNR varied significantly in sediment composition, two analyses were carried out comparing each MPA site to the outside fished areas separately (i.e. MPA1 *vs.* Fished areas; MPA2 *vs.* Fished areas). A nested ANOVA was undertaken on the species data for the *Modiolus* Box. Before proceeding with the ANOVAs, the data were examined for normality using the Kolmogorov-Smirnov test and the Levene's test for homogeneity of variance. A $\log_{10}(x + 1)$ and arcsine transformation was applied to density and % cover data, respectively, to stabilize variance when necessary. Whenever transformations did not produce homogeneous variances, (GLM) ANOVA was used nevertheless after setting $\alpha = 0.01$ in order to compensate for the increased likelihood of Type I error (Underwood 1997).

In a further analysis, species were categorized into functional categories according to their physical structure and degree of adult mobility, as these features are likely to influence the vulnerability of species to bottom-towed fishing gear. The functional categories were: (a) AErFo - attached, erect or foliose (e.g. polychaetes, bryozoa, hydroids), (b) AEnTf - attached, encrusting or turf-forming (e.g. bryozoan, sponges, hydroid turf), (c) ASb - attached, soft-bodied (e.g. ascidians, sea anemones), (d) FCrNs - free-living, crawler non-shelled (e.g. decapods, asteroids, ophiuroids, nudibranchs), (e) FCrS - free-living crawler shelled (e.g. decapods, bivalves, gastropods), (f) FSw - free-living, swimmer (e.g. swimming bivalves, shrimp). Univariate analyses were carried out for each of the functional categories as described above. Furthermore, the frequency of occurrence of each of these categories was displayed.

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5.3.4.3 Comparison of the magnitude of 'reserve effect' across the 3 MPAs

To quantify the overall effect of marine protection on the epibenthic assemblages studied at the three MPAs, a meta-analysis was carried out using effect sizes calculated for taxonomic groups that contributed to more than 5% of the overall abundance at each of the MPAs. The natural logarithm transformed response ratio, Ln*RR* (Hedges et al. 1999) was used as the effect size, and is defined as the ratio of the mean abundance (density or % cover) estimate measured inside and outside the MPA. A weighted summary effect size across the different MPA case studies was then calculated for each taxonomic category by conducting a random effects meta-analysis using the DerSimoniam-Laird estimator method (Gurevitch and Hedges 1999; Hedges et al. 1999). Positive values of the summary effect size indicate greater density or % cover inside the protected area relative to unprotected areas. Effect sizes are considered to be significantly different from zero (i.e. there is a significant either positive or negative effect of protection) when the 95% confidence interval (CI) does not overlap zero.

5.4   RESULTS

5.4.1 PORT ERIN CLOSED AREA

5.4.1.1 Sediment composition

The study sites were predominantly composed of a mixture of sand and shell fragments (Fig. 5.2). The distribution of sediment types was similar across all sites; no significant differences were detected between the protected area and the control sites or among the three control unprotected sites (Table 5.3).
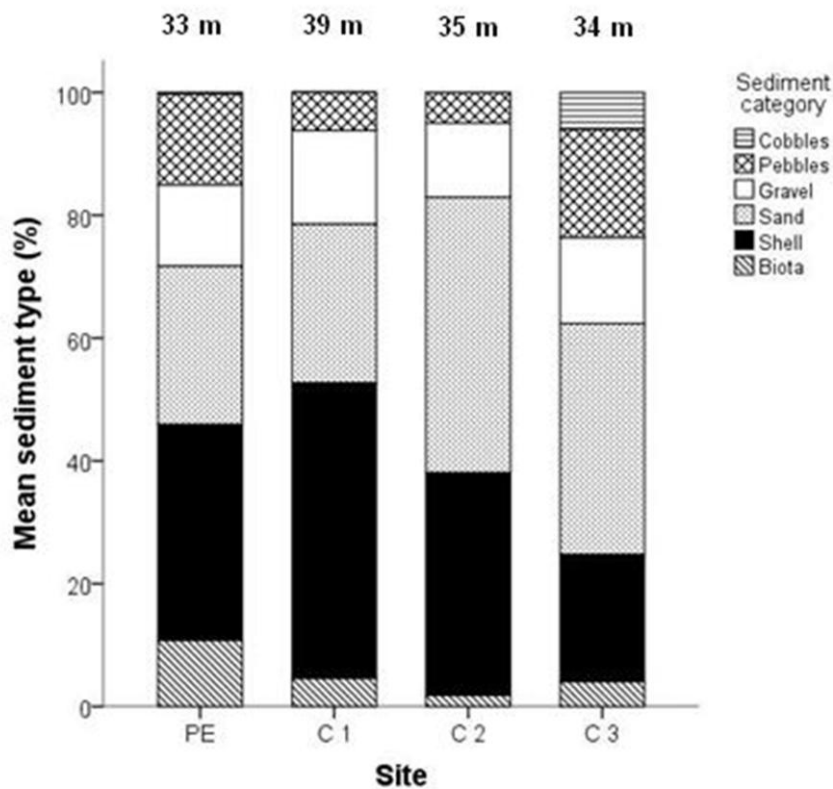
Fig. 5.2 Percentage distribution of sediment categories observed at sites surveyed inside Port Erin closed area (PE) and in the fished areas (C1, C2, C3). Mean depth (m) for each site is given above the bars.

Table 5.3 PERMANOVA analysis with contrasts on Euclidean distance matrix generated from percentage sediment data to examine differences between protected and unprotected areas and among unprotected sites at Port Erin, Isle of Man.

PERMANOVA

Source	df	SS	MS	Pseudo-F	P(perm)
Site	3	4194.6	1398.2	2.20	0.08
Contrasts					
MPA vs. Controls	1	712.34	712.34	0.94	0.38
C1 vs. C2	1	1317.7	1317.7	1.81	0.22
C1 vs. C3	1	2657.4	2657.4	2.59	0.16
C2 vs. C3	1	1248.3	1248.3	2.48	0.15
Res	16	10192	637		
Total	19	14387			

5.4.1.2 Epibenthic community analysis

Multivariate analysis of species composition detected significant differences between protected and unprotected sites, as well as significant differences among the three control sites (Table 5.4, Fig. 5.3). Contrasts among the control fished sites indicated significant differences in species composition among all three control sites (Table 5.4, Fig. 5.3). Bivalves (*Palliolum tigerinum*, *Aequipecten opercularis*), bushy / foliose bryozoans (*Crisia* spp., *Flustra foliacea*, *Cellaria* spp.) and gastropods were most abundant at C1 and least abundant at C3 (Table 5.5). Conversely, ophiuroids (*Ophiocomina nigra*, *Ophiura albida*) were more abundant in C3 than in the other control sites, and hydroids (hydroid turf, *Nemertesia antennina*) were also more abundant in C3 than C2 (Table 5.5). Interestingly, there was relatively higher variability in epibenthic community composition among the replicate tows at station C3 than at the other two control sites (C1, C2) and the protected area (PE) (Fig. 5.3).

Table 5.4 PERMANOVA analysis with contrasts on square-root transformed epifauna % cover data and Bray-Curtis similarity matrix to examine differences between protected and unprotected areas and among unprotected sites at Port Erin, Isle of Man.

PERMANOVA

Source	df	SS	MS	Pseudo-F	P(perm)
Site	3	12632	4210.8	5.94	**0.0001**
Contrasts					
MPA vs. Controls	1	5075.1	5075.1	4.83	**0.0002**
C1 vs. C2	1	3619.6	3619.6	6.49	**0.008**
C1 vs. C3	1	4382.3	4382.3	4.55	**0.01**
C2 vs. C3	1	3334.1	3334.1	3.49	**0.008**
Res	16	11341	708.83		
Total	19	23974			
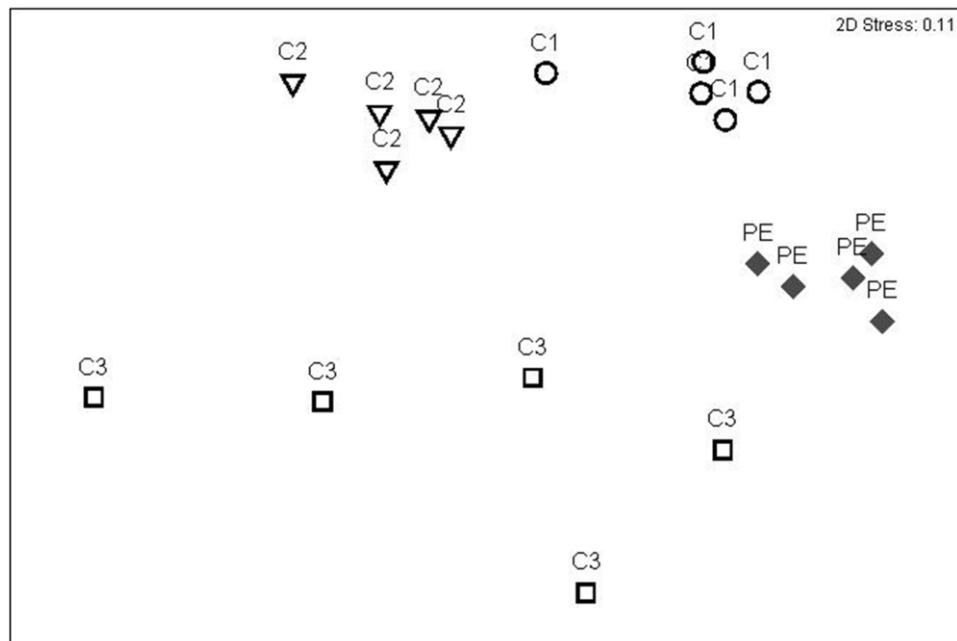
Fig. 5.3 Multidimensional scaling ordination plot of the epibenthic community data (% cover) showing the major differences between control site 3 (C3) and control sites 1 and 2 (C1, C2), but not between the protected (PE) and control (C1, C2, C3) sites.

Table 5.5 SIMPER analysis: species that contributed to more than 50% of the between-site dissimilarity.

SIMPER analysis

Groups	Average dissimilarity	Species	Average abundance in C1	Average abundance in C2	Contribution (%)
C1, C2	48.10	Hydroid turf	1.19	0.30	9.50
		Gibbula sp.	0.68	0.06	6.38
		Palliolum tigerinum	0.91	0.39	5.41
		Corella parallelogramma	1.05	0.81	4.42
		Crisia spp.	0.43	0.04	4.13
		Ascidian indet. B	0.54	0.17	3.80
		Cellaria spp.	0.40	0.72	3.43
		Ophiura albida	0.13	0.45	3.40
		Polychaete indet. A	0.44	0.13	3.28
		Flustra foliacea	0.29	0	3.04
		Nemertesia antennina	0.28	0.03	2.99
		Ascidian indet. A	0.66	0.47	2.75

Groups	Average dissimilarity	Species	Average abundance in C1	Average abundance in C3	Contribution (%)
C1, C3	56.79	*Palliolum tigerinum*	0.91	0	7.9
		Ophiocomina nigra	0	0.93	7.2
		Hydroid turf	1.19	0.52	6.5
		Aequipecten opercularis	0.69	0.06	5.7

		Species	Average abundance in C2	Average abundance in C3	Contribution (%)
		Gibbula spp.	0.68	0.23	4.4
		Corella parallelogramma	1.05	0.64	4.2
		Crisia spp.	0.43	0.08	3.3
		Ophiura albida	0.13	0.46	3.2
		Nemertesia antennina	0.28	0.3	2.8
		Flustra foliacea	0.29	0	2.5
		Abietinaria abietina	0.36	0.09	2.5
		Species	Average abundance in C2	Average abundance in C3	Contribution (%)
C2, C3	53.14	*Ophiocomina nigra*	0.14	0.93	9.2
		Aequipecten opercularis	0.54	0.06	6.0
		Palliolum tigerinum	0.39	0	4.7
		Cellaria spp.	0.72	0.4	4.4
		Ascidian indet. B	0.17	0.5	3.6
		Hydroid turf	0.3	0.52	3.6
		Corella parallelogramma	0.81	0.64	3.4
		scaphopod	0.3	0.03	3.2
		Nemertesia antennina	0.03	0.3	3.2
		Gastropod indet. A	0.3	0.06	3.1
		Ophiura albida	0.45	0.46	2.9
		Caryophyllia smithii	0	0.25	2.7

5.4.1.3 Univariate analysis

The asymmetrical ANOVA of the percentage cover data of sessile, colonial or encrusting taxa indicated that the percentage cover of all epibenthic species combined together and of polychaetes, bryozoans and hydroids was significantly higher in the Port Erin closed area relative to the fished control sites (Fig. 5.4, Appendix 5.1A). Bryozoans and hydroids were on average four and three times more abundant in the protected area (mean ± SE (%): bryozoans = 2.9 ± 0.6; hydroids = 2.8 ± 0.4) than in the fished areas (mean ± SE (%): bryozoans = 0.6 ± 0.1; hydroids = 0.8 ± 0.2), respectively (Fig. 5.4). Total epifauna cover was on average twice as high in the protected area than outside (mean ± SE (%): PE = 10.1 ± 0.2; Controls = 5.6 ± 0.9) (Fig. 5.4). The percentage cover of hydroids varied significantly among the control sites; hydroids were more abundant at C1 than at C2 and C3 and were least abundant at C2 (Fig. 5.4, Appendix 5.1A).

The asymmetrical ANOVA of the density of mobile or solitary sessile taxa indicated that the density of anthozoans, gastropods and bivalves was significantly different between the protected area and fished sites (Fig. 5.5, Appendix 5.1B). Whereas anthozoans (mean ± SE (indvs. m^{-2}): PE = 18.9 ± 10.2; Controls = 1.9 ± 0.8) and gastropods (mean ± SE (indvs. m^{-2}): PE = 6.71 ± 1.32; Controls = 3.63 ± 1.10) were significantly more abundant inside the protected area, bivalves were more abundant at the fished sites (mean ± SE (indvs. m^{-2}): PE = 1.2 ± 0.2; Controls = 9.9 ± 3.4) (Fig. 5.5, Appendix 5.1B). The high density of bivalves at the fished sites is mainly attributed to *Palliolum* spp. and *Aequipecten opercularis* whose density constituted 66 % and 26 % of the total bivalve density found at this study location, respectively. These two species were particularly abundant at C1, with average densities of 19.2 ± 4.8 indvs. m^{-2} for *Palliolum* spp. and 5.3 ± 1.3 indvs. m^{-2} for *A. opercularis* (Fig. 5.5, Appendix 5.1B). *Pecten maximus* was far less abundant than *Palliolum* spp. and *A. opercularis* and made up only 7 % of the total bivalve density. However, *P. maximus* density was on average 2.5 times higher inside the protected area than the fished sites, and this difference was significant (mean ± SE (indvs. m^{-2}): PE = 0.7 ± 0.1; Controls = 0.2 ± 0.01) (Fig. 5.5). Further to the differences in density between protected and fished sites, there were also significant differences among the control areas; C1 had significantly higher density of gastropods and bivalves (mainly *Palliolum* spp., *A. opercularis*) relative to C2 and C3 (Fig. 5.5, Appendix 5.1B).

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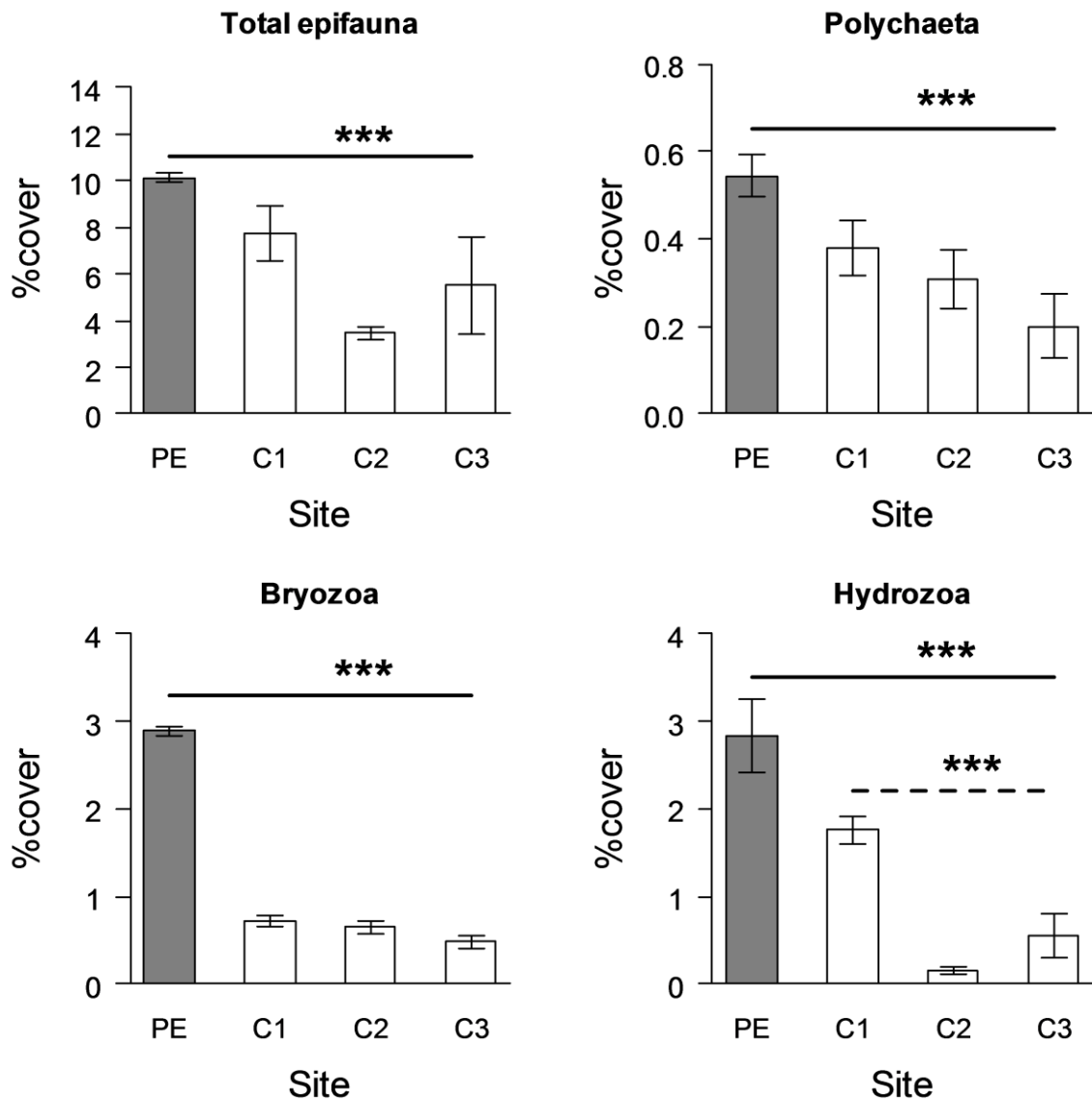
Fig. 5.4 Mean (± SE) percentage cover of all taxa (total % cover) and of colonial or encrusting taxa that differed significantly with protection level at Port Erin closed area. Black lines indicate a significant difference between protected (grey bars) and unprotected areas (white bars). A dashed line indicates a significant difference among control sites (C1, C2, C3). Statistical significance codes: '***' 0.001; '**' 0.01; '*' 0.05.
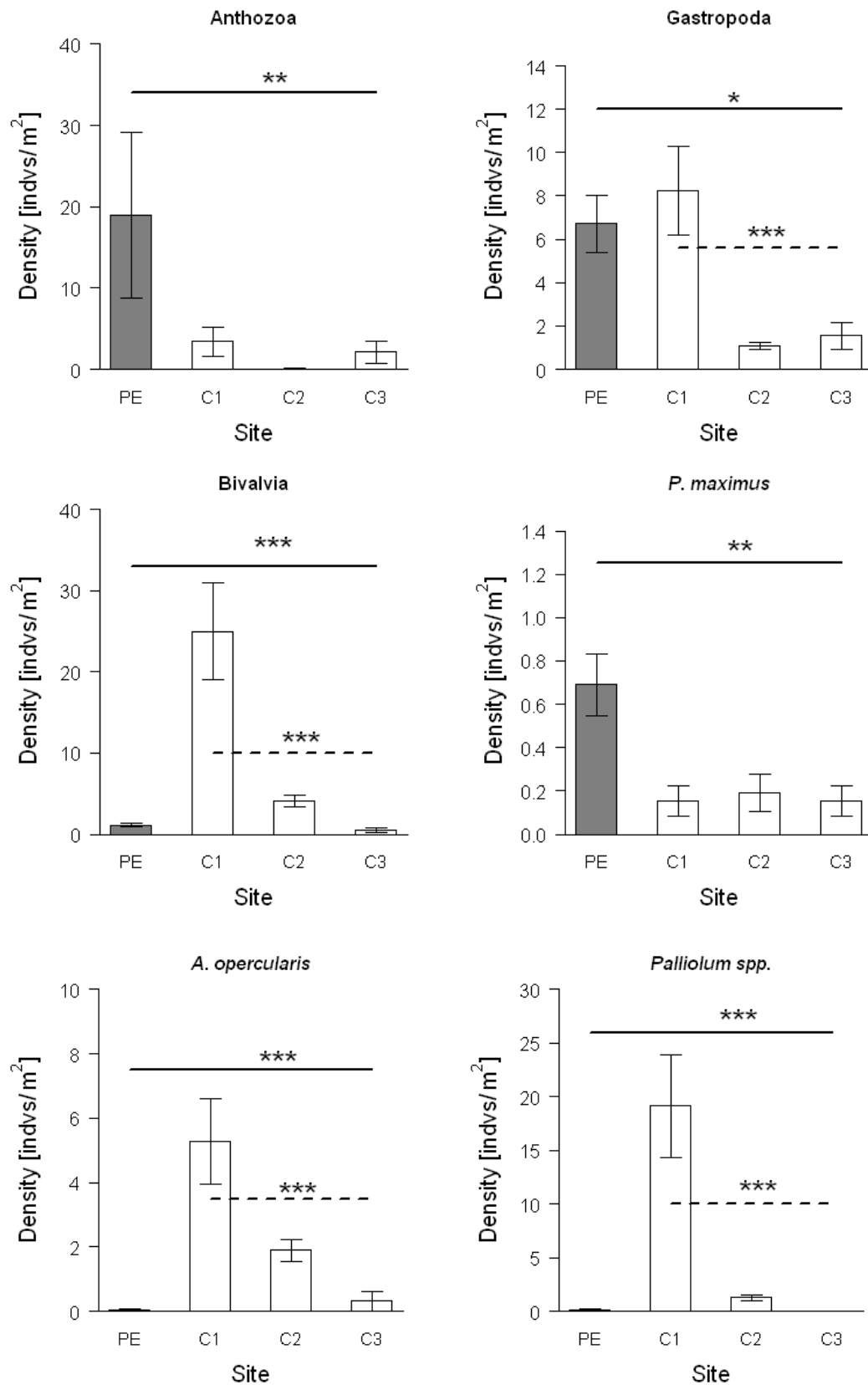
Fig 5.5 Invertebrate density (individuals m^{-2}) by site and level of protection. Data are mean $\pm$ SE) of mobile or solitary taxa and species that differed significantly with protection level at Port Erin closed area. Black lines indicate a significant difference between protected (grey bars) and unprotected areas (white bars). A dashed line indicates a significant difference among control sites (C1, C2, C3). Statistical significance codes: '***' 0.001; '**' 0.01; '*' 0.05.

5.4.1.4 Functional group analysis

'Attached, upright or foliose' species such as *Cellaria* spp., *Nemertesia antennina*, Crisia spp. and *Lanice conchilega* had a higher frequency of occurrence inside the protected area relative to the fished areas. In contrast, 'attached, soft-bodied' species mainly the ascidian *Corella paralellogramma* and 'free-living non-shelled' species such as *Ophiocomina nigra*, *Ophiura albida* and *Inachus* spp. were more common in the fished areas (Fig. 5.6). ANOVA tests using individual functional groups to assess for differences between protected and unprotected areas, revealed similar results as for the univariate analysis of taxonomic groups described above (see Appendix 5.1C).

Inside protected area   **Outside protected area**

Inside protected area: FSw, 0.07; FCrS, 15.12; AEnTf, 27.82; Asb, 4.42; FCrNs, 3.62; AErFo, 48.87

Outside protected area: FSw, 6.23; AEnTf, 14.72; FCrS, 15.69; Asb, 29.98; AErFo, 17.85; FCrNs, 16.76
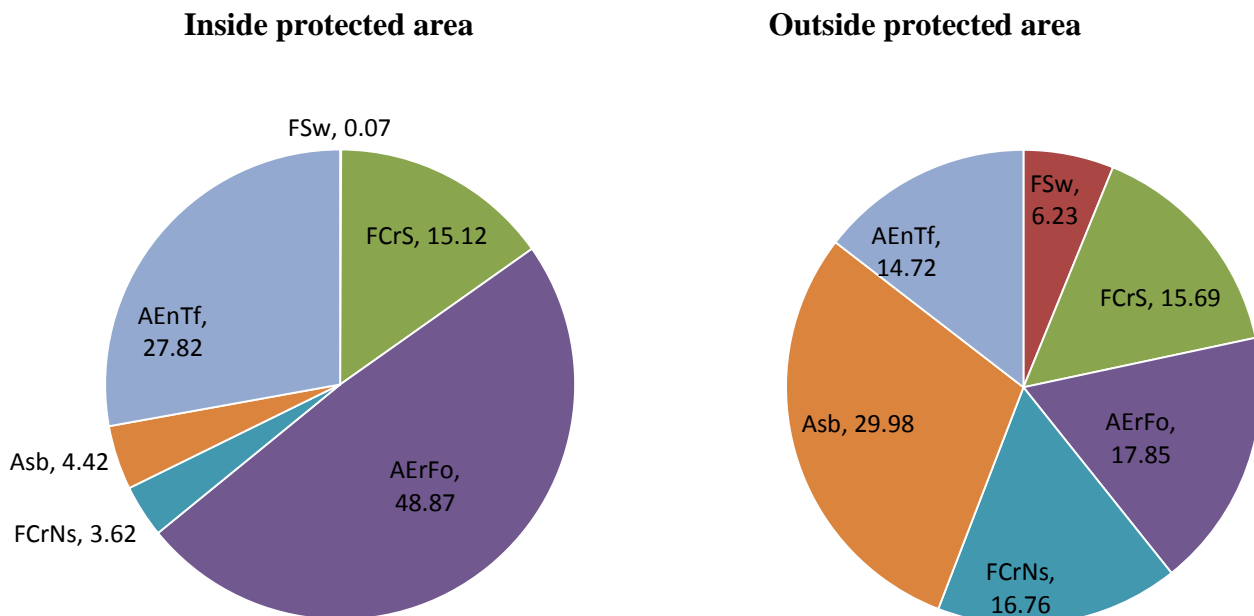
Fig. 5.6 Frequency distribution (%) of the six epibenthic species functional categories observed inside and outside Port Erin closed area. The functional categories are defined in *Methods* section.

5.4.2 SKOMER MARINE NATURE RESERVE

5.4.2.1 Sediment composition

The study sites at Skomer MNR were predominantly composed of a mixture of sand and pebbles (Fig. 5.7). Despite the best attempts at selecting study sites with comparable habitat, sediment composition was significantly different between the two sites sampled inside the MNR (Table 5.6). This difference was predominantly due to a higher composition of pebbles

at MPA1 (Fig. 5.7). Given that the differences in sediment composition may confound differences in species composition between protected and unprotected areas, separate analyses comparing the epibenthic fauna (i) at MPA1 and the control sites and (ii) at MPA2 and the control sites were carried out. The distribution of sediment types was similar between the protected area and the control sites (Table 5.6). Contrasts among the control sites found significant differences in sediment composition between C1 and C2 (Table 5.6) due to a higher proportion of biota at C1 (Fig. 5.7).
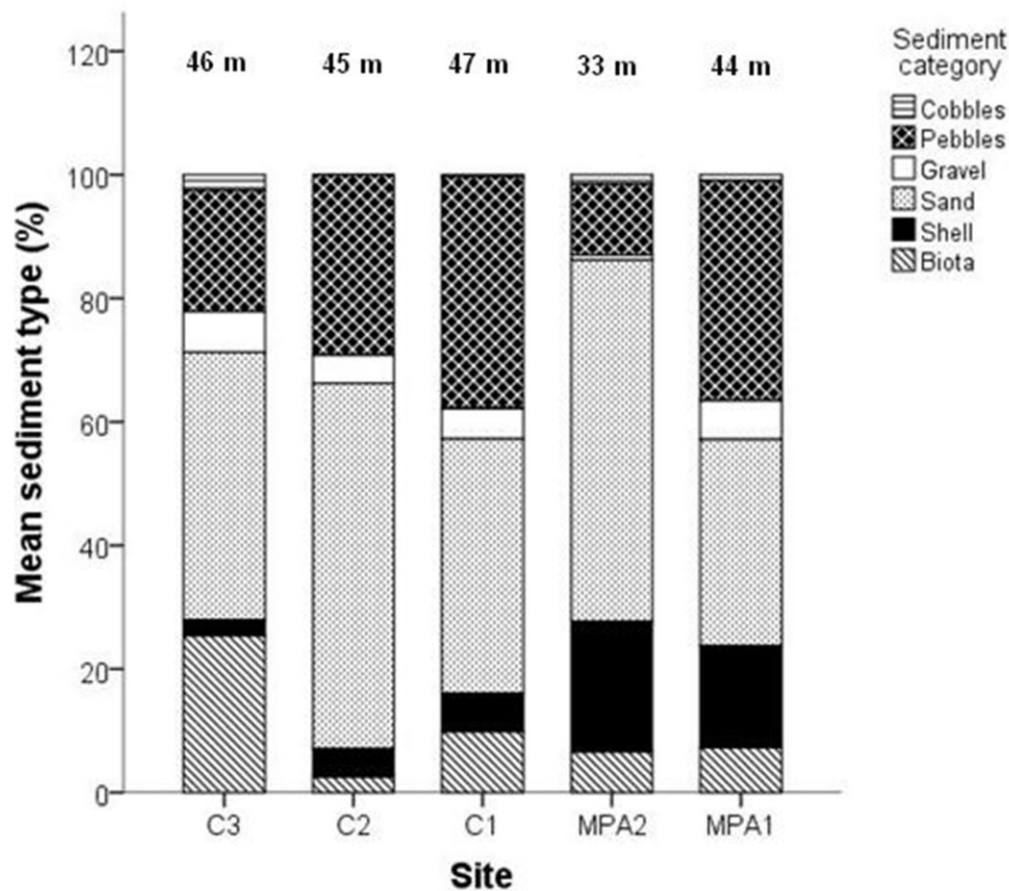
Fig. 5.7 Percentage distribution of sediment categories observed at sites surveyed inside Skomer MNR (MPA1, MPA2) and in the control sites (C1, C2, C3). Mean depth (m) for each site is given above the bars.

Table 5.6 PERMANOVA analysis with contrasts on Euclidean distance matrix generated from percentage sediment data for MPA1, MPA2, C1, C2 and C3 to examine differences between protected and unprotected areas and among unprotected sites at Skomer MNR.

PERMANOVA

Source	df	SS	MS	Pseudo-F	P(perm)
Site	4	7977.9	1994.5	4.04	**0.002**
Contrasts					
MPA vs. Controls	1	1635.6	1635.6	2.32	0.10
MPA1 vs. MPA2	1	3147.9	3147.9	7.03	**0.04**
C1 vs. C3	1	1469.8	1469.8	2.77	0.08
C1 vs. C2	1	2198.3	2198.3	4.22	**0.04**
C2 vs. C3	1	1123.5	1123.5	2.15	0.19
Res	20	9876	493.8		
Total	24	17854			

5.4.2.2 Epibenthic community analysis

Multivariate analysis of species composition found significant differences between protected and unprotected control sites, whether the control sites were compared to MPA1 (Table 5.7, Fig.5.8) or MPA2 (Table 5.8, Fig. 5.8). Significant differences were also detected among the three control sites (Table 5.7, 5.8). Hydroids (Hydroid turf, *Nemertesia antennina*) and sponges were more abundant in C1 than in C2, which had a higher percentage composition of hydroids and sponges than C3 (Table 5.9). Ophiuroids such as *Ophiura* spp. and the Sabellid worm, *Sabellaria* spp. were more abundant in C3 than in C2 (Table 5.9). There was high variability in epibenthic community composition among the replicate transects at sites C3 and C2 (Fig. 5.8). Interestingly, the difference in sediment composition between MPA1 and MPA2 was also reflected in the species composition at these two sites (Fig. 5.8). Hydroids (Hydroid turf, *N. antennina*), sponges and ascidians were more abundant at MPA1 than MPA2, whereas ophiuroids (*Ophiocomina nigra*) and polychaetes were more common at MPA2 than MPA1, presumably reflecting the coarser nature of the sediment at MPA1 (Table 5.9).

Table 5.7 PERMANOVA analysis with contrasts on square-root transformed epifauna % cover data and Bray-Curtis similarity matrix for MPA1, C1, C2 and C3 to examine differences between protected and unprotected areas and among unprotected sites at Skomer MNR.

PERMANOVA: MPA1 vs. Controls

Source	df	SS	MS	Pseudo-F	P(perm)
Site	3	19529	6509.6	6.67	**0.0001**
Contrasts					
MPA vs. Controls	1	7540.3	7540.3	4.92	**0.0006**
C1 vs. C2	1	5325.5	5325.5	4.29	**0.01**
C1 vs. C3	1	3835.7	3835.7	3.72	**0.01**
C2 vs. C3	1	8821.7	8821.7	10.71	**0.008**
Res	16	15610	975.64		
Total	19	35139			

Table 5.8 PERMANOVA analysis with contrasts on square-root transformed epifauna % cover data and Bray-Curtis similarity matrix for MPA2, C1, C2 and C3 to examine differences between protected and unprotected areas and among unprotected sites at Skomer MNR.

PERMANOVA: MPA2 vs. Controls

Source	df	SS	MS	Pseudo-F	P(perm)
Site	3	17479	5826.3	5.36	**0.0001**
Contrasts					
MPA vs. Controls	1	5490.1	5490.1	3.67	**0.003**
C1 vs. C2	1	5325.5	5325.5	4.29	**0.008**
C1 vs. C3	1	3835.7	3835.7	3.72	**0.007**
C2 vs. C3	1	8821.7	8821.7	10.71	**0.008**
Res	16	17379	1086.2		
Total	19	34857			
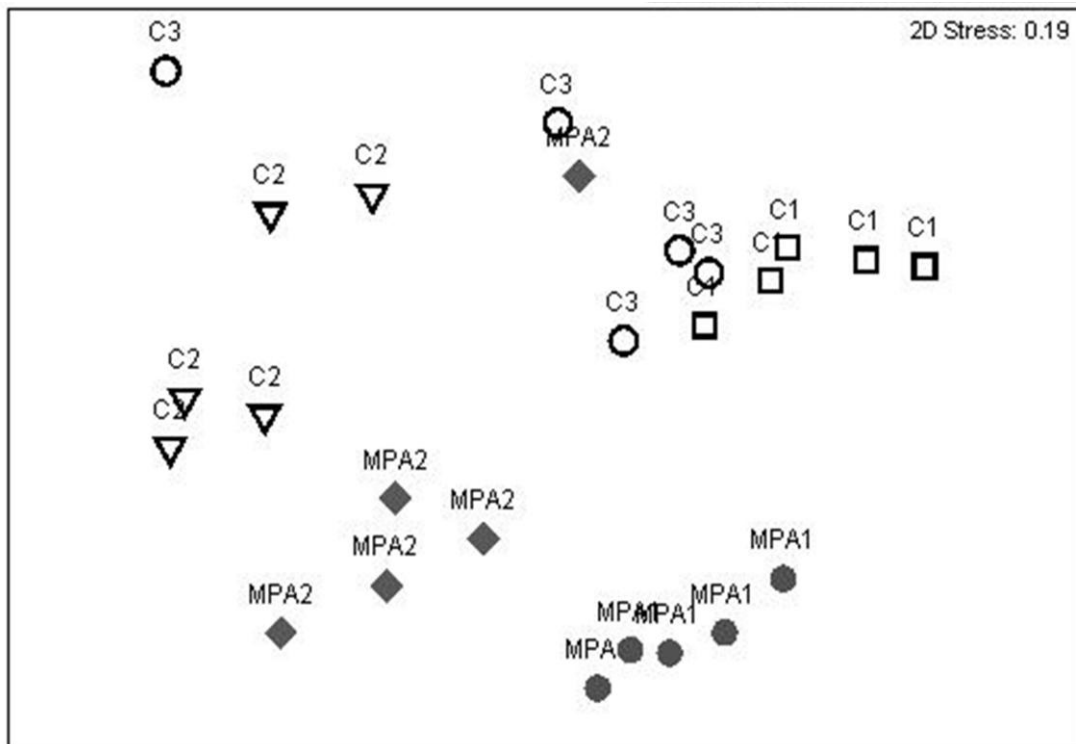
Fig. 5.8 Multidimensional scaling ordination plot of the epibenthic community data (% cover) showing the major differences between control site (C1, C2, C3) and between the two protected sites (MPA1, MPA2) but not between the protected (MPA1, MPA2) and control (C1, C2, C3) sites at Skomer MNR.

Table 5.9 SIMPER analysis species that contributed most to the between-site dissimilarity.

SIMPER analysis

Groups	Average dissimilarity	Species	Average abundance in C1	Average abundance in C3	Contribution (%)
C1, C3	69.34	Hydroid turf	4.86	2.07	13.5
		Porifera indet. C	1	0.08	4.4
		Ascidian indet. M	0.79	0	3.6
		Nemertesia antennina	0.81	0.12	3.3
		Ophiura spp.	0.25	0.78	2.8
		Porifera indet. D	0.6	0	2.8
		Porifera indet. A	0.58	0	2.7
		Porifera indet. H	0.58	0.03	2.6
		Porifera indet. T	0.54	0	2.5
		Species	Average abundance in C1	Average abundance in C2	Contribution (%)
C1, C2	54.59	Hydroid turf	4.86	2.85	12.6
		Ascidian indet. M	0.79	0	4.3
		Porifera indet. T	0.54	0	2.9
		Porifera indet. C	1	0.61	2.9
		Porifera indet. D	0.6	0.09	2.8
		Sagartia spp.	0.44	0	2.6
		Species	Average abundance in C3	Average abundance in C2	Contribution (%)
C3, C2	63.98	Hydroid turf	2.07	2.85	9.6

		Species	Average abundance in MPA2	Average abundance in MPA1	Contribution (%)
		Ophiura spp.	0.78	0	5.8
		Sabelleria spp.	0.52	0.35	3.9
		Nemertesia antennina	0.12	0.68	3.8
		Porifera indet. C	0.08	0.61	3.6
		Species	Average abundance in MPA2	Average abundance in MPA1	Contribution (%)
MPA2, MPA1	63	Hydroid turf	1.74	3.2	8.3
		Ophiocomina nigra	1.01	0.34	5.8
		Nemertesia antennina	0.31	1.24	5.3
		Polychaete indet. F	0.88	0	5.1
		Bryozoan indet. A	0.55	0	3.1
		Porifera indet. A	0.31	0.69	2.3
		Ascidian indet. G	0	0.35	1.9
		Porifera indet. D	0.34	0	1.9

5.4.2.3 Univariate analysis

The percentage cover of hydroids was significantly lower in MPA2 relative to the fished control sites (Fig. 5.9). Hydroids were on average four times more abundant at the control sites than at MPA2 (mean ± SE (indvs. m^{-2}): MPA2 = 3.3 ± 0.4; Controls = 13.3 ± 2.7). Conversely, no significant differences were found for any of the sessile colonial or encrusting taxa (i.e. porifera, hydrozoan, bryozoan, polychaeta) between MPA1 and the control sites (Appendix 5.2A). As indicated by the multivariate analysis, ANOVA also found significantly higher percentage cover of hydroids and sponges in C3 relative to C1 and C2, which contributed to the significantly higher total epifauna cover at C3 relative to the other control sites (Fig. 5.9, Appendix 5.2A).

The density of decapods, ascidians and ophiuroids differed significantly between MPA2 and fished sites (Fig. 5.10, Appendix 5.2B). Ophiuroids (mean ± SE (indvs. m^{-2}): MPA2 = 19.0 ± 8.0; Controls = 3.2 ± 1.3) were significantly more abundant at MPA2, whereas decapods and ascidians were more abundant in the fished areas (Decapod mean ± SE (indvs. m^{-2}): MPA2 = 1.7 ± 0.5; Controls = 3.5 ± 0.3) (Ascidians mean ± SE (indvs. m^{-2}): MPA2 = 1.3 ± 0.4; Controls = 11.8 ± 5.6) (Fig. 5.10).

Gastropods and bivalves were significantly more abundant at MPA1 than at the control sites, but none of the other taxa were significantly different between protected and unprotected areas (Gastropods mean ± SE (indvs. m^{-2}): MPA1 = 5.6 ± 1.5; Controls = 2.2 ± 0.9) (Bivalves mean ± SE (indvs. m^{-2}): MPA1 = 2.7 ± 0.4; Controls = 0.7 ± 0.3) (Fig. 5.10, Appendix 5.2B). The king scallop, *Pecten maximus*, and the queen scallop, *Aequipecten opercularis*, were by far the most common bivalve species found at this study area, constituting 29% and 41% of the total bivalve density, respectively. The king scallop was significantly more abundant inside Skomer MNR than at the control sites (*P. maximus* mean ± SE (indvs. m^{-2}): MPA1 = 0.8 ± 0.1; MPA2 = 0.6 ± 0.1; Controls = 0.1 ± 0.04) (Fig. 5.10). Interestingly, although queen scallop density was not significantly different inside and outside the reserve, the highest densities of *A. opercularis* occurred at C2 (mean ± SE = 1.6 ± 0.4 individuals m^{-2}) but were relatively absent at C1 and C3 (Fig. 5.10).
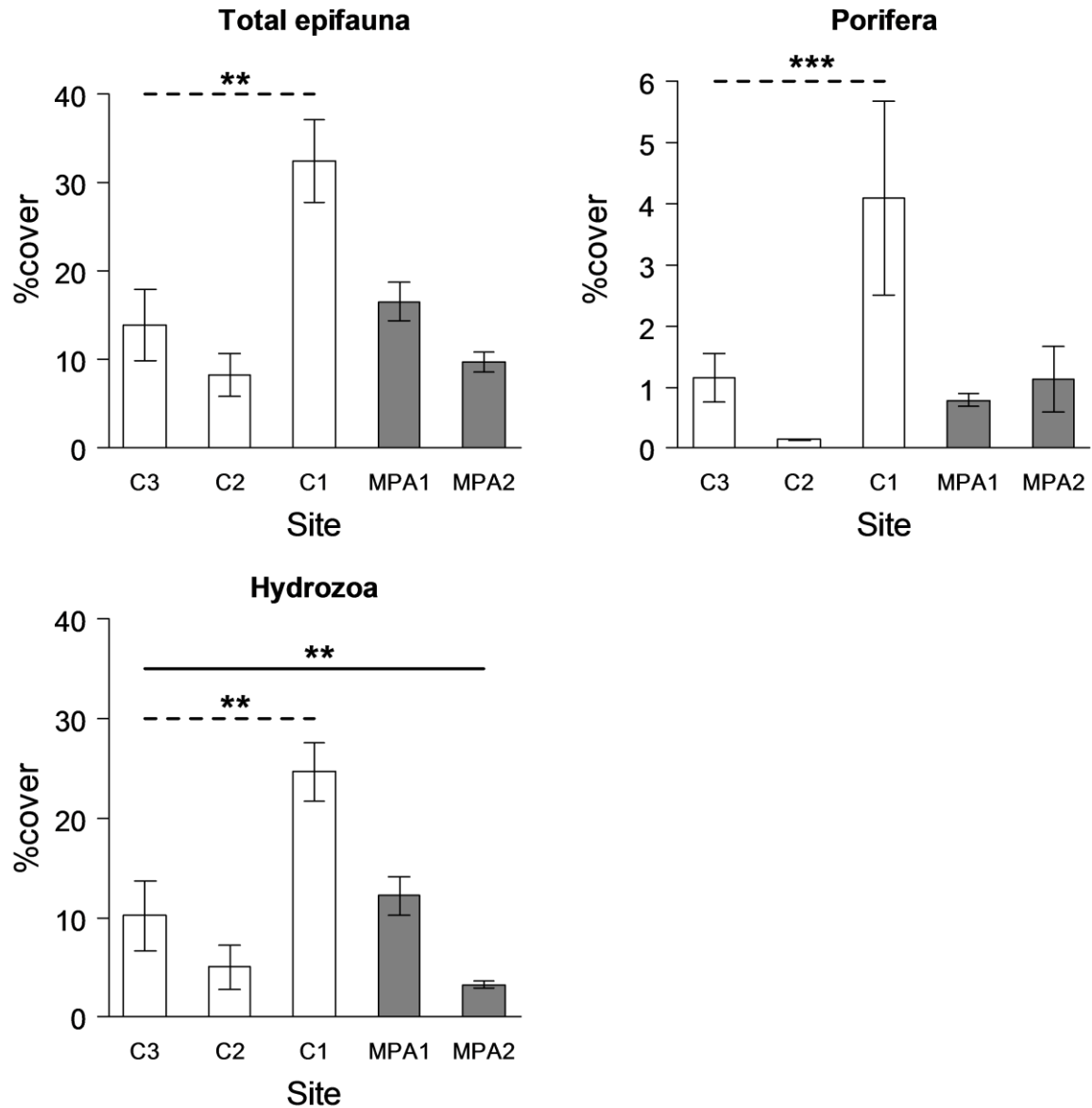
Fig. 5.9 Mean (± SE) percentage cover of all taxa (total % cover) and of colonial or encrusting taxa that differed significantly with protection level at Skomer MNR. Black lines indicate a significant difference between MPA2 and unprotected sites (white bars). A dashed line indicates a significant difference among control sites (C1, C2, C3). Statistical significance codes: '***' 0.001; '**' 0.01; '*' 0.05.
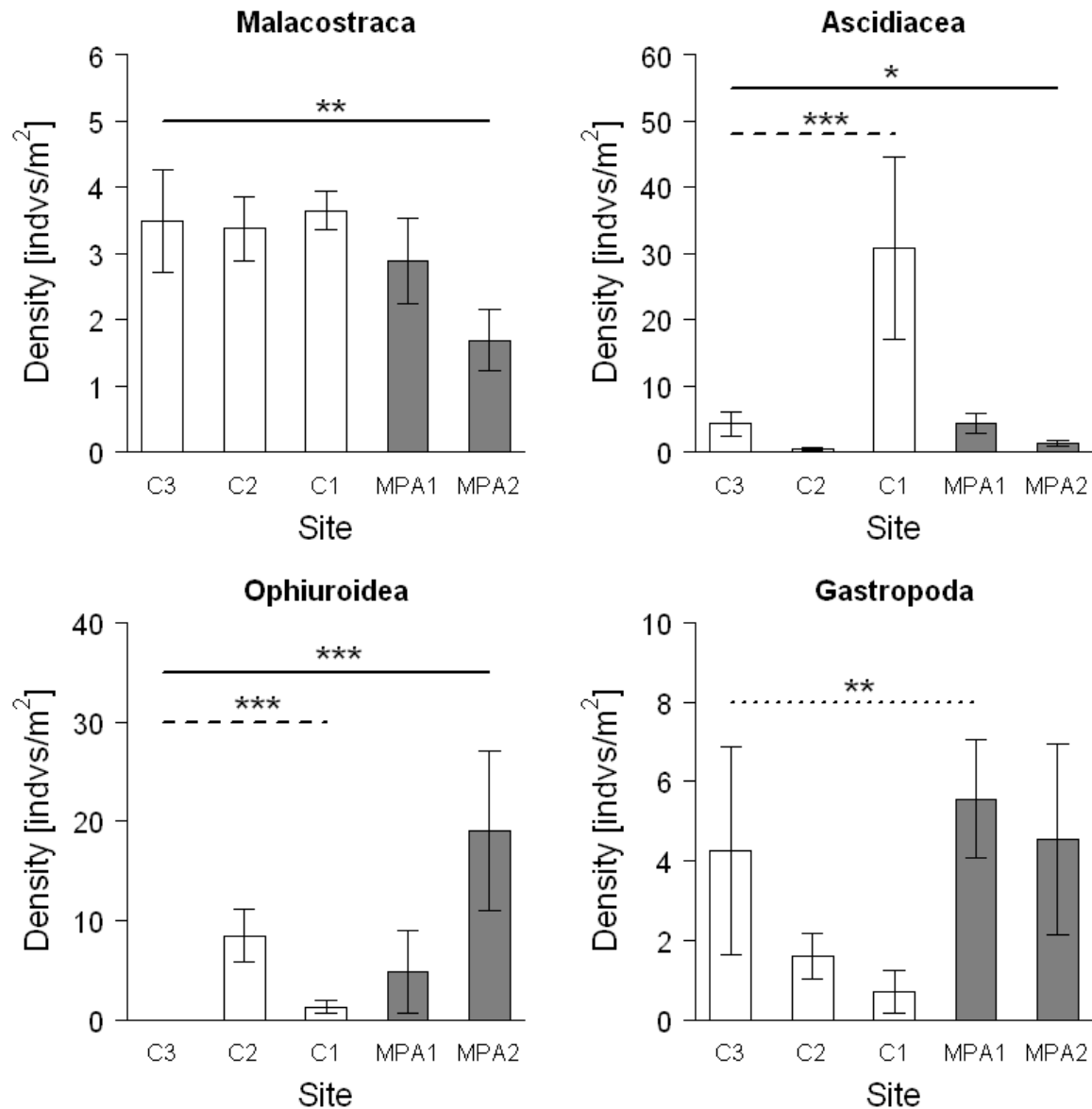
Fig. 5.10 Invertebrate density (individuals m^{-2}) by site and level of protection. Data are mean ± SE of mobile or solitary taxa and species that differed significantly with protection level at Skomer MNR. Black line indicates a significant difference between MPA2 and unprotected sites, dotted line indicates a significant difference between MPA1 and unprotected sites, a dashed line indicates a significant difference among control sites (C1, C2, C3). Statistical significance codes: '***' 0.001; '**' 0.01; '*' 0.05.
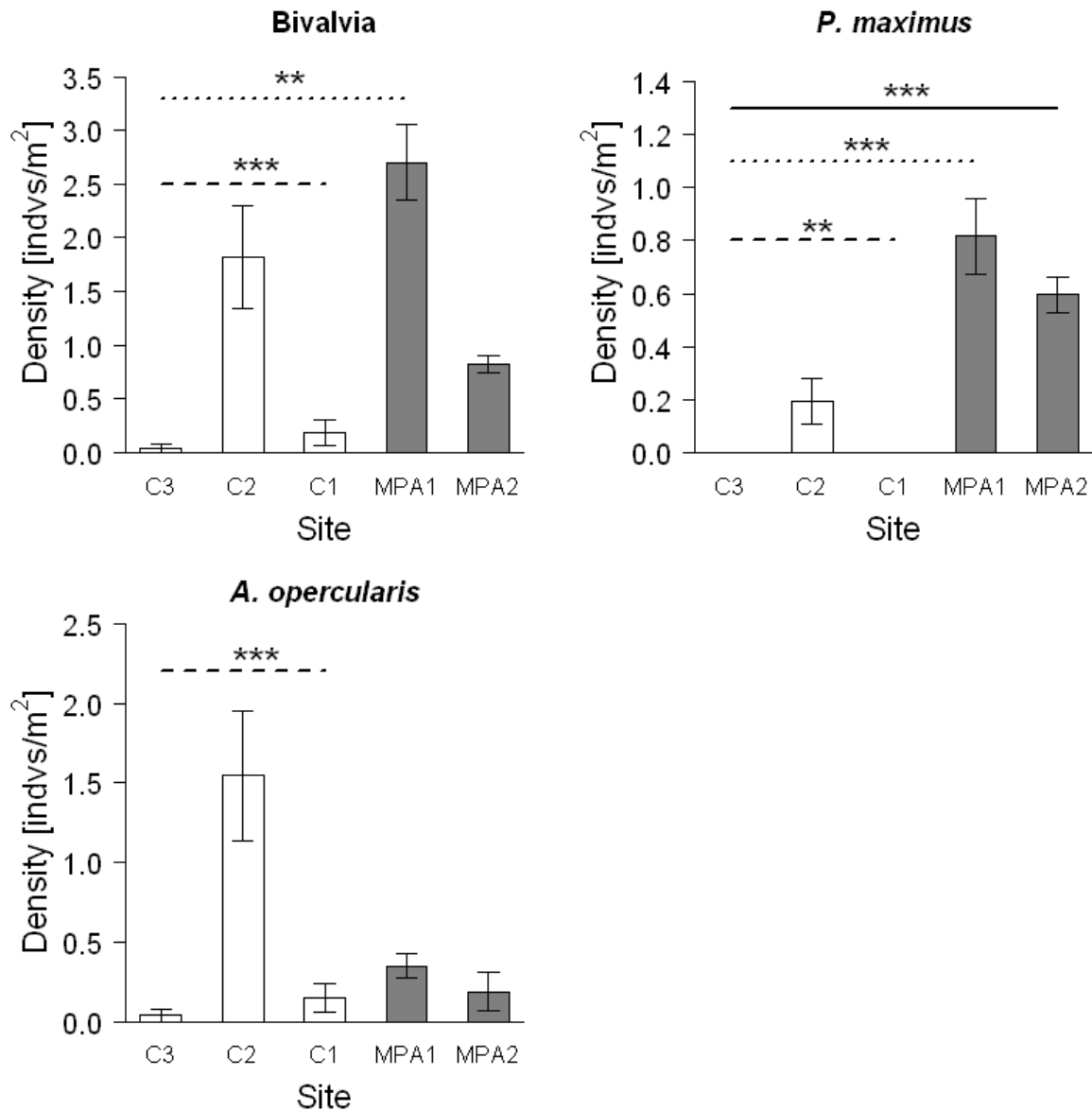
Fig. 5.10 continued.

5.4.2.4 Functional group analysis

'Attached, upright or foliose' species such as *Nemertesia antennina* and *Lanice conchilega* and 'free-living non-shelled' species such as *Ophiocomina nigra*, *Ophiura* spp., *Ophiothrix fragilis* and *Munida rugosa* had a higher frequency of occurrence inside the protected area relative to the fished areas (Fig. 5.11). 'Attached, encrusting or turf-forming' species such as hydroid turf and sponges were more common in the fished areas (Fig. 5.11). ANOVA tests using individual functional groups to assess for differences between protected and

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unprotected areas, revealed similar results as for the univariate analysis of taxonomic groups described above (see Appendix 5.2C).

Inside Skomer MNR
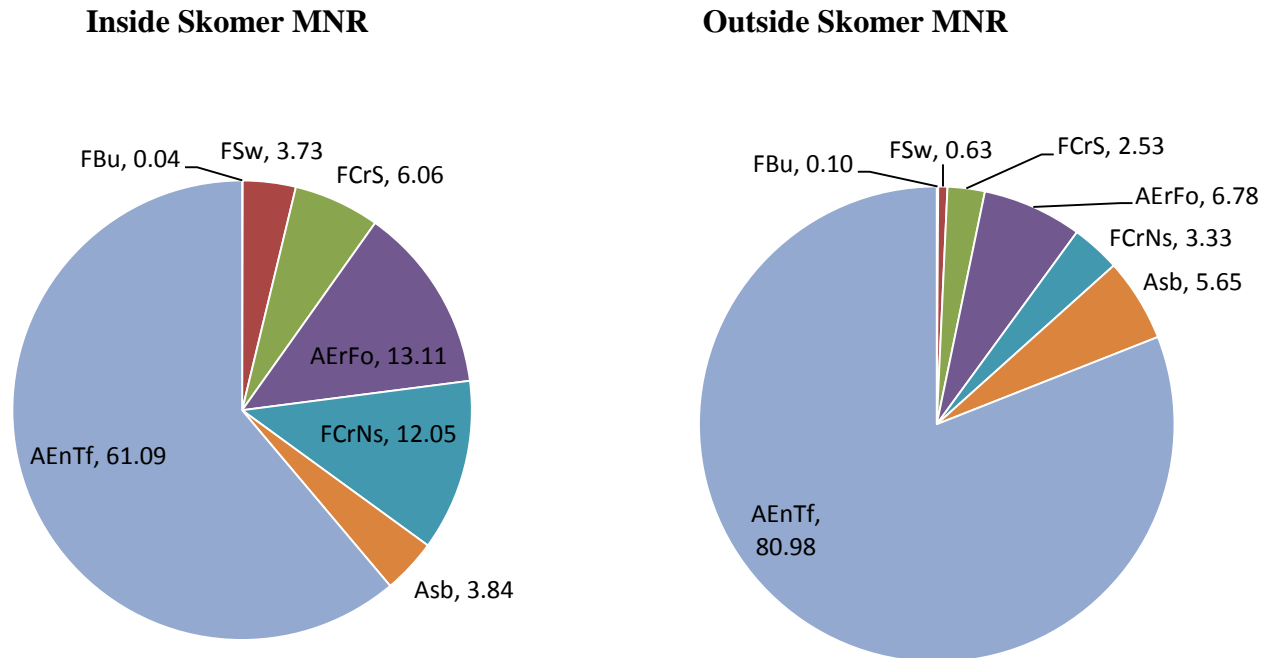
Outside Skomer MNR

Fig. 5.11 Frequency distribution (%) of the six epibenthic species functional categories observed inside and outside Skomer MNR. The functional categories are defined in *Methods* section.

5.4.3 'MODIOLUS BOX', LLYN PENINSULA

5.4.3.1 Sediment composition

From north to south of the study area there was a transition in sediment composition from sand to mostly pebbles with some sand (Fig. 5.12). Although, PERMANOVA did not detect significant differences in sediment composition between the protected sites and the control sites, significant differences were found among MPA and control sites (Table 5.10). Among the control sites, contrasts identified significant differences between C1 and C3 and between C2 and C3 (Table 5.10), as C1 and C2 had higher frequencies of sand than C3 (Fig. 5.12). Within the *Modiolus* Box, sediment composition differed significantly between MPA1 and MPA3 and between MPA2 and MPA3 (Table 5.10), as MPA3 had higher frequencies of pebbles and shell (Fig. 5.12).
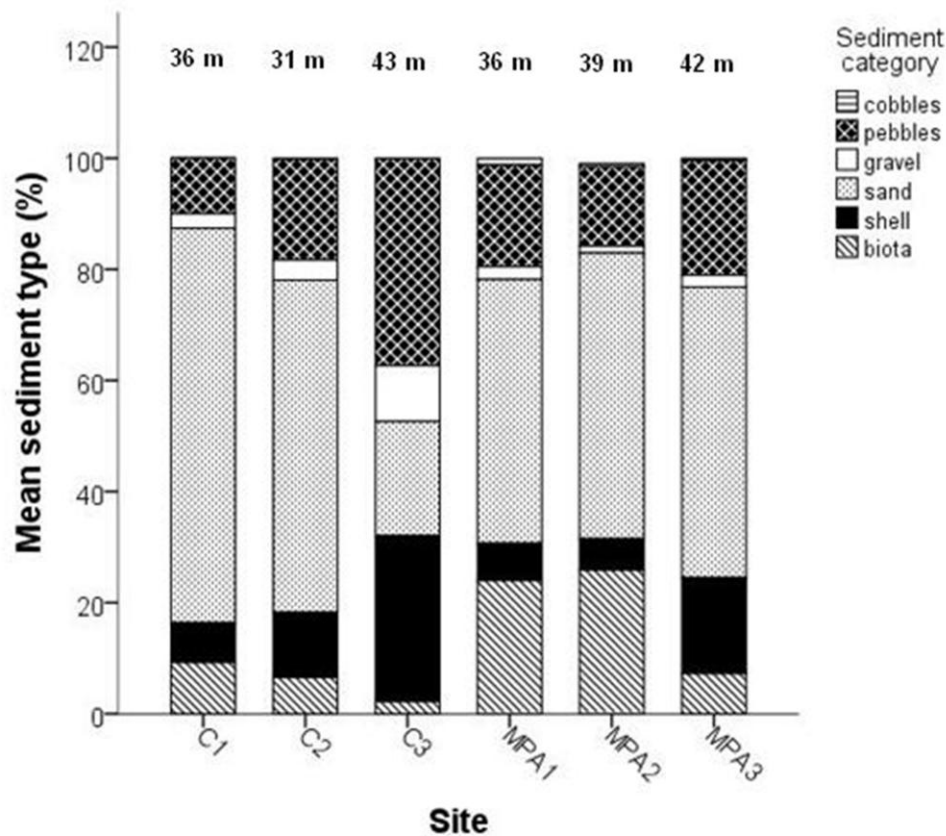
Fig. 5.12 Percentage distribution of sediment categories observed at sites surveyed inside the *Modiolus* Box (MPA1, MPA2, MPA3) and in the fished areas (C1, C2, C3). Mean depth (m) for each site is given above the bars.

Table 5.10 PERMANOVA analysis with contrasts on Euclidean distance matrix generated from percentage sediment data to examine differences between protected and unprotected areas and among MPA and among control sites at the *Modiolus* Box.

PERMANOVA

Source	df	SS	MS	Pseudo-F	P(perm)
Site	5	14161	2832.3	9.66	**0.0001**
Contrasts					
MPA vs. Controls	1	1795.6	1795.6	2.59	0.08
MPA1 vs. MPA2	1	92.66	92.66	0.26	0.77
MPA1 vs. MPA3	1	1050.3	1050.3	2.94	0.06
MPA2 vs. MPA3	1	1298.3	1298.3	4.57	**0.03**
C1 vs. C2	1	552.37	552.37	2.97	0.11
C1 vs. C3	1	9797.2	9797.2	31.17	**0.009**
C2 vs. C3	1	5757.7	5757.7	22.56	**0.007**
Res	24	7036.2	293.18		
Total	29	21198			

Analysis of biota

The differences in sediment composition among the protected sites and among the control sites were also reflected in species abundance and community composition analyses. Preliminary multivariate and univariate analyses identified significant differences in species and community composition between MPA3 and MPA1, MPA2 and between C3 and C1, C2. Therefore, as these differences in species composition are likely to be associated with differences in sediment composition rather than to the protection from fishing offered by the MPA, C3 and MPA3 were removed from the analysis of the effect of protection on the biota.

5.4.3.2 Epibenthic community analysis

Multivariate analysis of species composition found significant differences between protected and unprotected sites (Table 5.11, Fig. 5.13). Ophiuroids, hydroids, bushy / foliose bryozoans and anthozoans contributed the most to the dissimilarity between protected and unprotected sites. Species such *Ophiothrix fragilis*, *Cellaria* spp., *Flustra foliacea* and hydroid turf were more abundant inside the *Modiolus* box, whereas *Alcyonium digitatum* and *Cerianthus lloydii* had a higher percentage cover outside the protected area (Table 5.12). Additionally, significant differences in species composition were found between the two control sites (Table 5.11). Hydroid turf, *A. digitatum*, *C. lloydii* and *Flustra foliacea* were more abundant in C1 than in C2 (Table 5.12). Conversely, *O. fragilis* was more abundant in C2 than C1 and *Ensis* spp. was only found at C2 (Table 5.12). There was relatively higher variability in epibenthic community composition among the replicate transects at station C2 than at C1 and within the protected area (Fig. 5.13).

Table 5.11 PERMANOVA analysis with contrasts on square-root transformed epifauna % cover data and Bray-Curtis similarity matrix to examine differences between protected and unprotected areas and among unprotected sites at the *Modiolus* Box.

PERMANOVA

Source	df	SS	MS	Pseudo-F	P(perm)
Site	3	15030	5009.9	6.10	**0.0001**
Contrasts					
MPA vs. Controls	1	10837	10837	11.25	**0.0001**
MPA1 vs. MPA2	1	1578	1578	1.92	**0.06**
C1 vs. C2	1	2614.1	2614.1	3.18	**0.01**
Res	16	13149	821.84		
Total	19	28179			
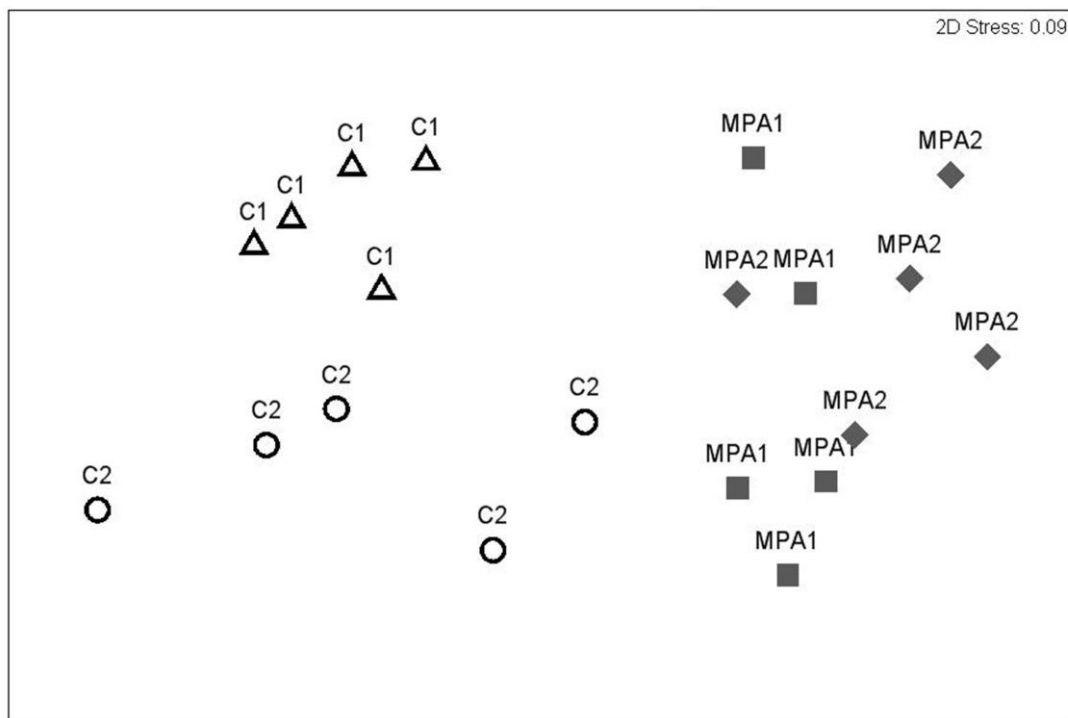
Fig. 5.13 Multidimensional scaling ordination plot of the epibenthic community data (% cover) showing the major differences between the protected (MPA1, MPA2) and control (C1, C2) sites at the *Modiolus* Box.

Table 5.12 SIMPER analysis: species that contributed to more than 50% of the between-site dissimilarity.

SIMPER analysis

Groups	Average dissimilarity	Species	Average abundance in Control	Average abund in MPA	Contribution (%)
MPA vs. Control	61.8	*Ophiothrix fragilis*	0.49	2.47	13.4
		Cellaria spp.	0.04	1.58	9.1
		Hydroid turf	2.13	3.05	6.1
		Ophiura albida	0.94	0.07	5.1
		Flustra foliacea	0.18	0.99	4.8
		Alcyonium digitatum	1.34	1.2	3.9
		Cerianthus lloydii	0.61	0.19	2.8
		Sagartia spp.	0.13	0.54	2.7
		Ascidian indet. C	0	0.39	2.3
		Species	Average abundance in C1	Average abundance in C2	Contribution (%)
C1, C2	48.1	Hydroid turf	2.49	1.77	9.0
		Alcyonium digitatum	1.65	1.04	8.6
		Ophiothrix fragilis	0	0.98	8.2
		Cerianthus lloydii	0.86	0.36	6.9
		Ophiura albida	1.11	0.77	3.8
		Ensis spp.	0	0.25	3.0
		Flustra foliacea	0.28	0.08	2.9
		Aequipecten opercularis	0.4	0.32	2.8
		Ciona intestinalis	0.14	0.29	2.7
		Pecten maximus	0	0.25	2.6

5.4.3.3 Univariate analysis

The percentage cover of all epibenthic species combined together and that of hydroids, bryozoans and sponges was significantly higher inside the *Modiolus* Box than at the fished control sites (Fig. 5.14, Appendix 5.3A). Overall biota percentage cover was on average twice as high inside the MPA compared to outside (mean ± SE (indvs. m^{-2}): MPA = 29.9 ± 3.6; Controls = 11.2 ± 1.8). Hydroids, ophiuroids and bryozoans were the most abundant taxa inside the MPA; constituting 36%, 30% and 16% of the total epifauna percentage cover inside the MPA, respectively. Hydroids and sponges were on average twice and five times more abundant in the MPA than outside, respectively (Hydroids mean ± SE (%): MPA = 9.9 ± 1.3; Controls = 4.8 ± 0.7) (Porifera mean ± SE (%): MPA = 0.4 ± 0.2; Controls = 0.1 ± 0.03). Bryozoans had significantly lower abundance at the control sites relative to inside the MPA (mean ± SE (%): MPA = 4.6 ± 1.21; Controls = 0.12 ± 0.1).

The density of decapods, ascidians and gastropods was higher inside the MPA than in the fished areas, and these differences were statistically significant (Fig. 5.15, Appendix 5.3B). The density for these taxa inside the MPA was between six and ten times higher than at unprotected sites (Malacostraca mean ± SE (indvs. m^{-2}): MPA = 2.2 ± 0.3; Controls = 0.4 ± 0.1) (Ascidiacea mean ± SE (indvs. m^{-2}): MPA = 7.4 ± 1.2; Controls = 0.8 ± 0.4) (Gastropoda mean ± SE (indvs. m^{-2}): MPA = 3.9 ± 0.6; Controls = 0.7 ± 0.2). Bivalves had significantly higher density in the fished sites, and this was mainly due to a significantly higher density of *Aequipecten opercularis* in the unprotected areas (Bivalves mean ± SE (indvs. m^{-2}): MPA = 0.4 ± 0.1; Controls = 1.1 ± 0.2) (*A. opercularis* mean ± SE (indvs. m^{-2}): MPA = 0.1 ± 0.1; Controls = 0.6 ± 0.2) (Fig. 5.15). *Pecten maximus* density was higher inside the MPA, however within-site variability at the MPA sites was considerably high and scallop density did not differ significantly between protected and unprotected areas (Fig. 5.15, Appendix 5.3B).
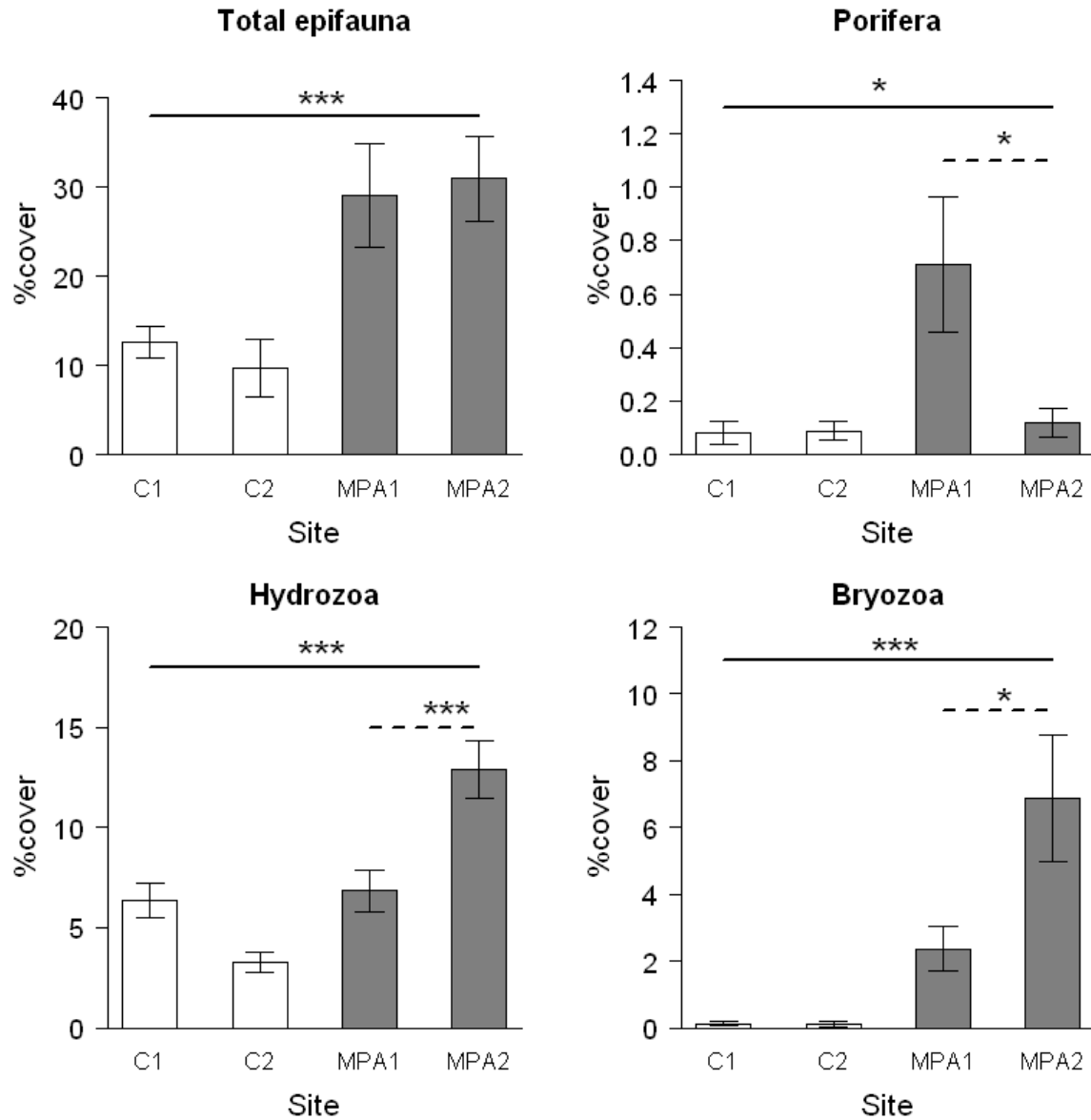
Fig. 5.14 Mean (± SE) percentage cover of all taxa (total % cover) and of colonial or encrusting taxa that differed significantly with protection level. Black lines indicate a significant difference between MPA (grey bars) and unprotected sites (white bars). A dashed line indicates a significant difference among MPA sites (MPA1, MPA2). Statistical significance codes: '***' 0.001; '**' 0.01; '*' 0.05.
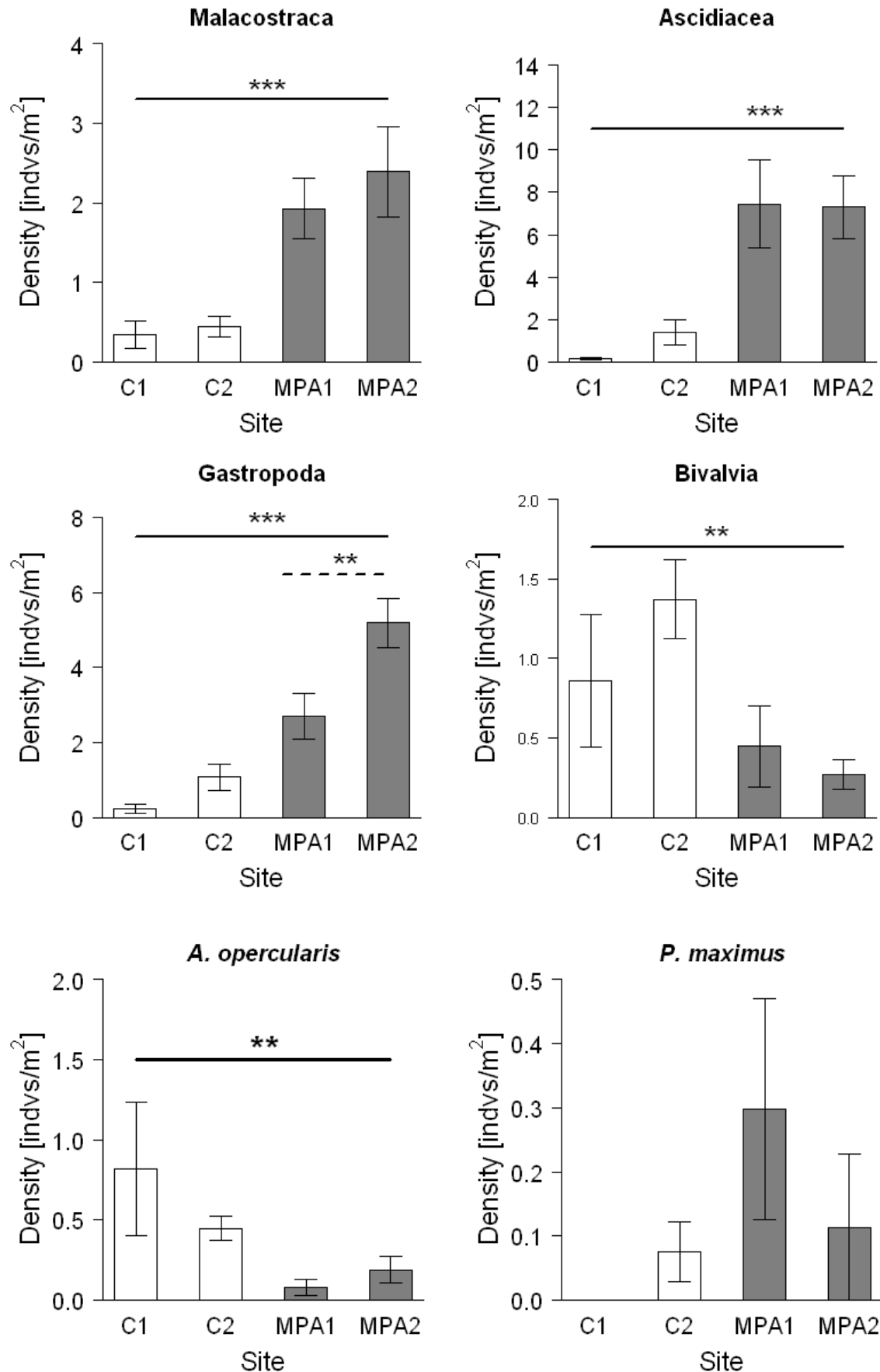
Fig 5.15 Invertebrate density (individuals m^{-2}) by site and level of protection. Data are mean ± SE of mobile or solitary taxa and species that differed significantly with protection level. Black lines indicate a significant difference between MPA (grey bards) and unprotected sites (white bars). A dashed line indicates a significant difference among MPA sites (MPA1, MPA2). Statistical significance codes: '***' 0.001; '**' 0.01; '*' 0.05.

5.4.3.4 Functional group analysis

'Attached, upright or foliose' species such as *Cellaria* spp., *Nemertesia antennina* and *Flustra foliacea* and 'free-living non-shelled' species such as *Ophiothrix fragilis* and *Ebalia* spp. had a higher frequency of occurrence inside the protected area relative to the fished areas (Fig. 5.16). 'Attached, soft-bodied' species such as *Alcyonium digitatum*, *Cerianthus lloydii* and *Ciona intestinalis* were more common in the fished areas (Fig. 5.16). ANOVA tests using individual functional groups to assess for differences between protected and unprotected areas, revealed similar results as for the univariate analysis of taxonomic groups described above (see Appendix 5.3C).

Inside Modiolus Box — FBu, 0.23; FSw, 0.55; FCrS, 2.54; AErFo, 17.32; AEnTf, 36.94; FCrNs, 31.15; Asb, 11.27

Outside Modiolus Box — FBu, 1.05; FSw, 2.13; FCrS, 4.55; AErFo, 7.30; AEnTf, 42.11; FCrNs, 18.61; Asb, 24.25
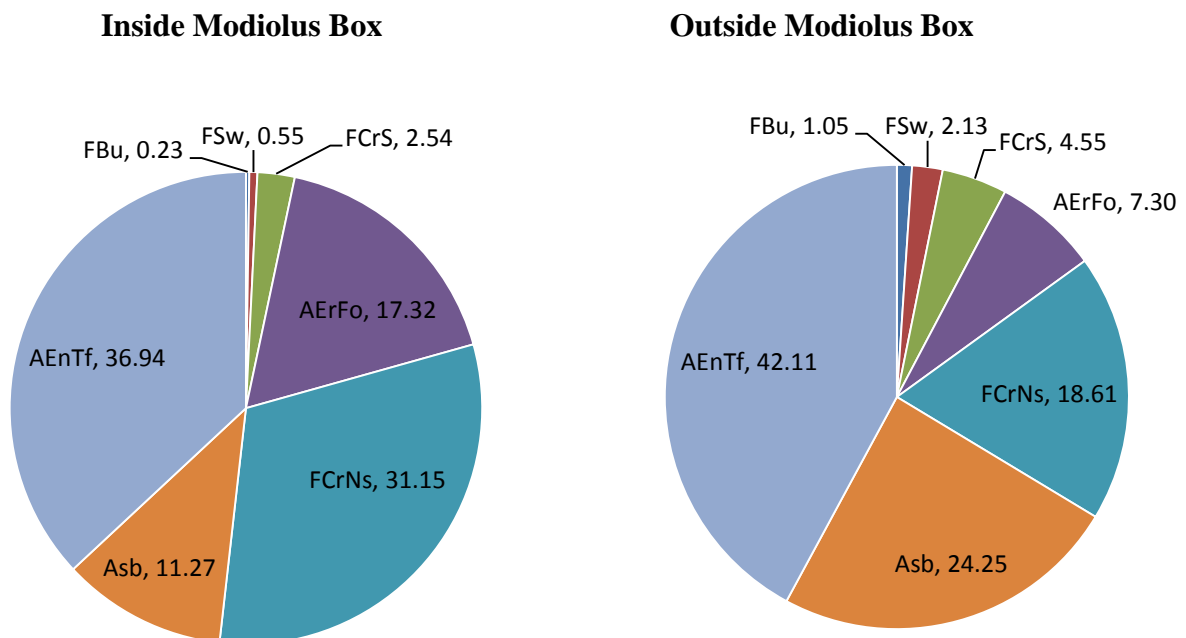
Fig. 5.16 Frequency distribution (%) of the six epibenthic species functional categories observed inside and outside Skomer MNR. The functional categories are defined in *Methods* section.

5.4.4 Comparison of the magnitude of 'reserve effect' across the 3 MPAs

On average, hydroids, bryozoans, sponges, gastropods, ascidians, ophiuroids and decapods were more abundant inside the protected areas than outside (Fig. 5.17). Overall, abundance increases ranged from 39% to 416% inside the closed areas (i.e. back-transformed Ln response ratio of abundance inside : outside ranged from 1.39 to 5.16, Fig. 5.17). However, the increase was only significant for gastropods and bryozoans, as the 95% confidence

interval around the mean response ratio did not overlap zero (Fig. 5.17). The response to protection for the other taxonomic categories was variable among the three MPA case-studies (refer to LnRR [95% CI] in Table 5.13). For example, the % cover for hydroids and sponges was higher inside the protected area relative to the fished area at Port Erin closed area and the *Modiolus* Box, but higher in the fished area at Skomer MNR (Table 5.13). *Pecten maximus* density was higher inside the protected area relative to outside at all three MPAs (Table 5.13), and density was on average 271% higher inside the closed areas than the fished areas (Fig.5.17). In contrast, *A. opercularis* was more abundant outside the closed area at all three MPAs (Table 5.13), and density was on average 12% lower inside the protected areas than the fished areas (Fig. 5.17).
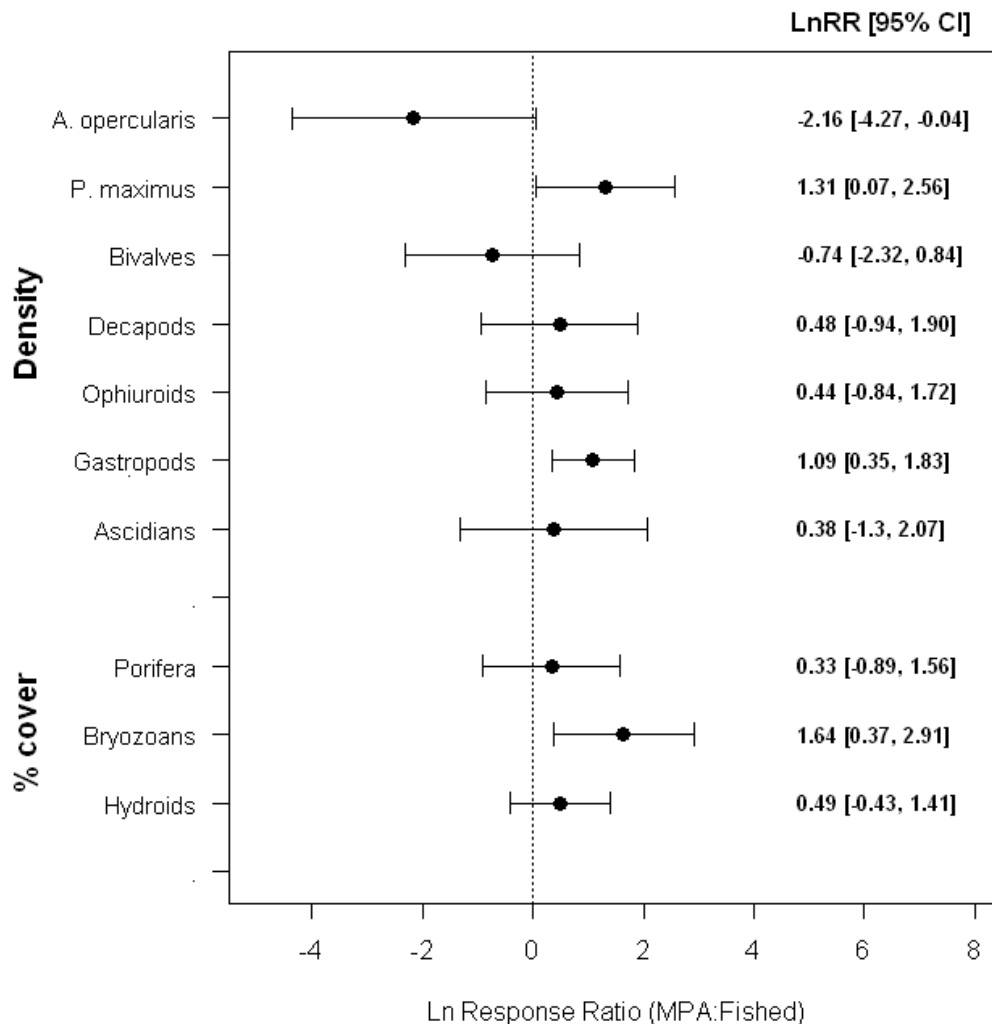
Fig. 5.17 Mean response ratios (LnRR) across the three MPA case-studies for each taxonomic category using density and % cover data inside the MPA relative to the fished area (MPA:Fished). Error bars represent the 95% confidence interval. The vertical dotted line at LnRR = 0 represents equal species density or % cover inside and outside of the MPA; LnRR > 0 means higher density or % cover inside the MPA; LnRR < 0 means lower density or % cover inside the MPA.

Table 5.13 Summary of the ANOVA tests conducted on the different taxonomic groups to test for differences between protected and unprotected areas. + indicates a significant increase (p-value < 0.05) in % cover or density in the MPA relative to outside, - indicates a significant decrease (p-value < 0.05) in % cover or density in the MPA relative to outside, ns indicates no significance (p > 0.05). The effect size (LnRR) gives the magnitude of increase or decrease of % cover or density inside the MPA relative to outside. A positive effect indicates higher density or % cover inside the MPA relative to outside. A negative effect size indicates higher density outside than inside the MPA. If the 95% confidence interval (given in brackets) overlaps 0 then the effect size is non-significant, if it does not overlap 0 then the change indicated by the effect size is significant.

	Port Erin closed area	**Skomer (MPA1) / (MPA2)**	***Modiolus* Box**	
% COVER				
Total	+ 0.60 (0.29, 0.03)	ns / ns -0.32 (-0.76, 0.05)	+ 0.99 (0.59, 0.04)	ANOVA test LnRR (95% CI)
Hydroids	+ 1.25 (0.68, 1.81)	ns / - -0.54 (-1.14, 0.06)	+ 0.72 (0.34, 1.11)	ANOVA test LnRR (95% CI)
Bryozoa	+ 1.58 (1.05, 2.10)	ns / ns 0.44 (-0.24, 1.12)	+ 3.65 (1.93, 5.36)	ANOVA test LnRR (95% CI)
Porifera	ns 0.36 (-0.94, 1.65)	ns / ns -0.62 (-1.53, 0.28)	+ 1.39 (0.24, 2.53)	ANOVA test LnRR (95% CI)
Polychaeta	+ 0.59 (0.26, 0.03)	ns / ns 0.23 (-0.85, 0.31)	ns 0 (-0.95, 0.24)	ANOVA test LnRR (95% CI)
DENSITY				
Gastropods	+ 0.61 (-0.09, 1.32)	+ / ns 0.84 (-0.15, 1.83)	+ 1.72 (1.08, 2.35)	ANOVA test LnRR (95% CI)

Decapods	ns 0.17 (-0.67, 1.01)	ns / - -0.42 (-0. 82, -0.02)	+ 1.70 (1.15, 2.26)	ANOVA test LnRR (95% CI)
Anthozoa	+ 2.32 (0.97, 0.47)	ns / ns 0.53 (-0.46, 0.25)	ns -0.21 (-1.07, 0.19)	ANOVA test LnRR (95% CI)
Ascidians	ns 0.31 (-0.20, 0.83)	ns / - -1.42 (-2.55, -0.30)	+ 2.22 (1.19, 3.25)	ANOVA test LnRR (95% CI)
Ophiuroids	ns -1.27 (-2.86, 0.32)	ns 1.30 (0.17, 2.43)	ns 0.88 (0.01, 1.75)	ANOVA test LnRR (95% CI)
Bivalves	- -2.11 (-2.86, -1.36)	- 0.95 (0.09, 1.81)	- -1.01 (-1.62, -0.41)	ANOVA test LnRR (95% CI)
Pecten maximus	+ 0.81 (0.16, 1.47)	+ 2.47 (1.26, 3.67)	ns 0.41 (-1.83, 2.64)	ANOVA test LnRR (95% CI)
Aequipecten opercularis	- -4.18 (-6.00, -2.36)	- -0.76 (-1.68, -0.16)	- -1.79 (-3.86, 0.27)	ANOVA test LnRR (95% CI)
Palliolum spp.	- -4.13 (-5.63, 0.59)			ANOVA test LnRR (95% CI)

5.5   DISCUSSION

5.5.1 Community level effects of protection

This study aimed to test for community-level differences in marine protected and unprotected areas as an attempt to quantify the effect of protection from bottom fishing on temperate epibenthic invertebrate communities. The multivariate community analysis and the univariate functional group and taxonomic category analyses revealed a number of differences between protected and fished sites at all the studied MPAs.

In order to survive disturbance from bottom-towed gear, a species must: (a) be able to avoid damage by swimming out of the way or burrowing deep into the sediment; (b) be able to physically withstand impact, either by having a robust body or protective shell, or be able to repair or regenerate damaged parts (Jennings and Kaiser 1998; Frid et al. 1999). Whilst species belonging to the 'attached and upright / foliose' category (e.g. *Cellaria* spp., *Nemertesia antennina*, *Crisia* spp., *Flustra foliacea*, *Lanice conchilega*) were generally more commonly found inside the closed areas, ascidians and species like *Alcyonium digitatum* and *Cerianthus lloydii* that were classified as 'attached, soft-bodied' organisms were more common in the unprotected fished areas. 'Free-living, crawler, non-shelled' organisms, species such as *Ophiocomina nigra* and *Ophiura albida* were more common in the fished areas outside the Port Erin closed area, whereas species such as *Ophiothrix fragilis*, *Ebalia* spp. and *Munida rugosa* were more common inside the protected area at Skomer MNR and the *Modiolus* Box. Fragile emergent epifauna that live attached to the substratum such as sponges, erect bryozoans and hydroids, are particularly adversely affected by bottom fishing (Veale et al. 2000; Bradshaw et al. 2001; Guijarro Garcia et al. 2006), which explains why these species groups were more common and abundant inside the closed areas. Perhaps not as easily explained, is the higher occurrence of fragile small tunicates (e.g. *Corella parallellogramma*) outside the closed areas. However, Bradshaw et al. (2002) observed similar patterns around the Isle of Man with much higher abundances of *Ascidiella* spp. in heavily fished areas, and suggested that their ability to regenerate new parts or to bud new individuals may enable them to withstand disturbance from dredges and bottom trawls. Brittlestars such as *Ophiocomina nigra* and *Ophiura* spp. are surface feeders (detritivores, scavengers), and hence may benefit from dredging disturbance due to increased food supply (Jenkins et al. 2004). Furthermore, brittlestars are also known to have good powers of regeneration, which would enable them to recover from non-fatal dredge damage.

Although hydroids, bryozoans, sponges, gastropods, ascidians, ophiuroids and decapods were generally more abundant inside the protected areas than outside, the magnitude of effect size was not homogeneous across all three MPA case-studies (refer to Fig. 5.17, Table 5.14). Given that sediment composition between protected and unprotected sites was not significantly different for any of the three case-studies, and that habitat characteristics (i.e. sediment type and depth) were comparable among the three case-studies, factors other than substratum type and depth may be driving the observed differences in the magnitude of the effect of protection among the three MPAs. One key characteristic that may have contributed to these differences is the frequency and intensity of fishing at the unprotected areas outside the MPA. Fishing effort with bottom-towed gear is highest outside the Port Erin closed area, is comparatively lower outside the *Modiolus* Box, and almost negligible outside Skomer MNR. For example, the fishing effort at fishing grounds around the Isle of Man, calculated from the vessel monitoring system data, was estimated to reach a maximum of 2.8 y^{-1} for the period 2007 - 2008 (Lambert et al. 2011). The fishing effort of scallop dredging vessels outside the *Modiolus* Box, calculated from boardings data from fishery patrol vessels, was estimated to range between 0 and 0.22 BPUE (boardings per patrol vessel visit) (Vanstaen and Silva 2010). Conversely, scallop dredging and trawling in the areas surrounding Skomer MNR have been virtually non-existent in the last 10 – 15 years (M. Burton, pers. comm., 2010; Vanstaen and Silva 2010). Therefore, the significantly higher effect sizes (MPA:fished) for hydroids and bryozoans at the Port Erin closed area and the *Modiolus* Box (but not at Skomer MNR) may well be due to the high bottom fishing disturbance at these areas. My findings largely concur with those of other studies. For example, Collie et al. (1997) showed that infrequently fished areas were characterized by abundant bryozoans, hydroids and worm tubes. Auster et al. (1996) reported reduced sponge cover in intensively fished areas and Hinz et al. (2011) found significantly lower occurrences and abundances of sessile emergent epifaunal species at fished sites compared to unfished sites. Relatively fewer taxa showed significant differences in abundance between protected and unprotected sites at Skomer MNR and when these occurred differences were more likely to be related to sediment composition than to fishing. For example, one of the study sites inside the reserve (MPA2) was more sandy (although not significantly so) than MPA1 or any of the control sites. The higher abundance of hydroids, decapods and ascidians at the control sites relative to MPA2 may thus be explained by these differences in sediment composition, as some of these taxa require a coarse substratum for attachment. Moreover, in the absence of anthropogenic disturbance by

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bottom towed gear, other agents of natural disturbance such as tidal currents and wave stress (see Lambert et al. 2011) may be more important in shaping the communities inside and outside Skomer MNR.

5.5.2 Effects on target species

One of the most notable results of this study was the difference in bivalve density between the closed and fished areas. Among the bivalves, *Pecten maximus* and *Aequipecten opercularis* had the highest frequency of occurrence. Interestingly, whereas *P. maximus* was more abundant inside the closed areas relative to the fished areas, *A. opercularis* was more abundant outside the closed areas. A previous study by Beukers-Stewart et al. (2005) on the king scallop population at Port Erin closed area estimated density to range between 7.91 and 20 individuals per 100 m^2 for the study period 2001 – 2003. The average density of *P. maximus* recorded in Port Erin closed area during this study was 90 individuals per 100 m^2. Although scallop density estimates from the study by Beukers-Stewart et al. (2005) and this study are not directly comparable as the former estimated density using diver surveys whereas I used underwater camera surveys, these results may suggest that *P. maximus* populations inside the closed area have continued to recover rapidly in the 6 year period after the study by Beukers-Stewart et al. (2005). It should also be noted that the survey was conducted at the end of the scallop dredging closed season, which runs between 1 June and 30 October (inclusive) in the Isle of Man territorial waters, hence differences between protected and fished areas clearly exist and are not simply an artefact of the timing of the sampling event. Given the close proximity of the closed areas and the fished sites at each of the three case-studies, it is likely that scallop populations inside and outside the closed areas are not entirely independent of each other as there is a possibility of larval export and/or dispersal of scallops from the closed area to the fished area. Therefore, the fact that *P. maximus* density is still significantly higher inside the closed areas reinforces our finding that the higher observations of scallop density are a result of protection from bottom fishing following the establishment of the closed area. Although *P. maximus* density was higher inside the *Modiolus* Box than outside this difference was not significant. Infringements of regulations and illegal fishing inside the *Modiolus* Box (pers. obs.) might have led to the smaller differences in abundance inside and outside of the MPA. It is intriguing that *A. opercularis* was higher outside the closed areas, particularly, outside Port Erin closed area where mean density was 5.2 ± 1.1 individuals m^{-2}. Reasons for the increased abundance of

this species are less clear. The fact that the queen scallop fishery operates mainly to the south and east of the Isle of Man (Vause et al. 2007) rather than west of the island where our sampling was carried out may explain the high abundance of *A. opercularis* at the fished sites. Furthermore, *A. opercularis* may be more resilient to scallop dredging than *P. maximus* due to its swimming escape mechanism which enables it to escape serious damage from scallop dredges and to its less recessed position in the sediment than *P. maximus*.

5.5.3 Conclusion

Fishers may object to the establishment of permanent marine protected areas because of increased hardships they may be faced with following the loss of fishing grounds. Assessments of the effectiveness of protection, such as this study, are therefore important for fishery managers given the current drive for using spatial restrictions on fishing effort as conservation and fishery management tools and the pressures from the fishing industry. Although I acknowledge that it is hard to ascertain that the observed differences between protected and unprotected areas were a result of a 'reserve effect' due to the lack of multiple before and after data, it is fair to conclude that at the time of study the epibenthic invertebrate species, including the main target species (*Pecten maximus*) populations showed signs of benefit from protection from closed areas to bottom-towed fishing gear. The effect was more evident in taxa abundance as well as for community structure of these assemblages. It is worth highlighting that the magnitude of the effect of protection varied among MPAs and may be linked to differences in relative fishing effort at the fished areas outside the MPA. Therefore, it is imperative that fishing intensity and frequency at the control locations is taken into consideration when evaluating the effect of protection from MPAs. Failure to do so will likely lead to unrealistic expectations regarding the extent and nature of benefits that MPAs will provide.

CHAPTER 6
General discussion

Growing evidence demonstrates the potential of well-designed and effectively implemented MPAs to conserve and restore biodiversity, fisheries and ecosystem functioning. Because there is no one size-fits-all MPA it must be recognized that different forms of MPAs are appropriate for different contexts (Agardy et al. 2011). By increasing the use of impact evaluation and adopting an explicitly adaptive approach, immediate steps can be taken to address current marine conservation challenges and to lay the foundation for more effective marine management in the future.

6.1   Evidence-based conservation

In the absence of easily accessible scientific evidence, most management decisions end up being based on anecdotal sources and personal experience (Pullin et al. 2004; Sutherland et al. 2004). A problem with using this approach is that it is difficult to determine whether the information is based upon reliable sources such as the summation of a range of well-designed studies or from less reliable sources such experience based on just one site, or simply from someone using their best guess to the best approach. In medicine and public health, the concept of 'evidence-based medicine' has been widely accepted and an industry supporting this approach has developed (Dawes 2000). Although the idea of 'evidence-based conservation' among conservation scientists and practitioners has lagged behind that in medicine, the importance of this approach for decision making on the best management practices has gained increasing recognition in recent years (Pullin and Knight 2001; Pullin and Stewart 2006).

The evidence for the direct ecological effects of fully protected marine areas (alternatively known as no-take areas, marine reserves) has been extensively reviewed and synthesized (e.g. Mosquera et al. 2000; Cote et al. 2001; Halpern 2003; Micheli et al. 2004; Guidetti and Sala 2007; Claudet et al. 2008; Garcia-Charton et al. 2008; Harmelin-Vivien et al. 2008; Lester et al. 2009; Molloy et al. 2009; Maliao et al. 2009; Stewart et al. 2009; Vandeperre et al. 2011). Conversely, the assessment of the efficacy of partially protected areas has received less attention, perhaps because factors such as the intensity and frequency of permitted extractive or destructive activities within the MPA is a source of variation that is difficult to quantify and thus control for in the analyses. In this thesis, I have undertaken the challenge of generating and assessing the evidence on the ecological effectiveness of MPAs that confer partial protection. My goal has been that the findings of my research will not only be of

relevance to the scientific community but also to a wider audience that includes MPA managers, policy-makers and conservation organizations.

6.2 Methods applied: Systematic review and meta-analysis

Within an evidence-based framework, systematic reviews present a comprehensive and objective way of collating evidence on the effectiveness of actions and then disseminating it effectively into practice and policy communities. Traditionally, reviewing of scientific evidence has been done either by narrative reviews, where results are simply described and a consensus emerges from the description, or by 'vote counting' where the number of statistically significant results for and against a hypothesis are counted. Both of these methods have potential for bias (in particular subjective bias) and may yield misleading conclusions. Systematic reviews are an improvement on these methods, in that they follow a strict methodological protocol that locates data from published and unpublished sources, critically appraise methodology and synthesize evidence usually through meta-analysis (Stewart et al. 2005). Therefore, rather than reflecting the views of authors or being based on a possibly biased selection of literature, systematic reviews provide a comprehensive assessment of the available evidence.

The advantage of meta-analysis over vote-counting is that the former moves beyond the question of statistical significance, and provides a magnitude and direction of effect (known as the effect size) (Borenstein et al. 2009). Statistical significance (i.e. p-values) is a function of the sample size and the statistical power of the study, such that two studies with the same effect size but different amount of replication might give different statistical significance. Therefore, methods such as 'vote-counting' that rely on p-values from different studies to decide if a management strategy is effective or not, might yield misleading conclusions. Although meta-analysis overcomes some of the problems with narrative reviews and vote-counting, other potential sources of bias remain. For example, poor methodology in primary studies may still render the results of a meta-analysis misleading. Publication bias in favour of significant results remains a concern (Rosenthal et al. 2001). Whilst the combination of data across numerous studies can increase the generalizability of results, the combination of studies that vary considerably in their methods of measuring variables and that vary in their environmental setting has been criticized. This criticism can be dealt with by using weighting

techniques that take into account the methodological strength of each study in the analysis and by treating these differences as moderator variables (Rosenthal et al. 2001).

6.3 Research findings: Implications for policy and conservation

In Chapter 2, I examined whether partially protected areas are an effective management option for conservation of fish populations compared to fully protected and unprotected areas. The results showed that no-take reserves generally produced greater increases in fish numbers and yielded significantly higher biomass of fish within their boundaries relative to partially protected areas. Biomass was on average twice as high in fully protected than partially protected areas. When compared to open access areas, partially protected areas yielded consistently significant increases in both density (22% increase) and biomass (51% increase) of fish inside their boundaries relative to outside. Therefore, the available evidence suggested that while no-take reserves provide some benefit over less protected areas, the significant ecological effects of partially protected areas relative to open access areas suggest that partially protected areas are a valuable spatial management tool particularly in areas where exclusion of all extractive activities is not a socio-economically and politically viable option.

The rest of this thesis provides scientific insights into the factors that shape the ecological effects of MPAs. The ecological context of MPAs — including life history traits and ecological characteristics of species (Chapter 3), habitat characteristics and the physical nature of the environment inside and outside the MPA (Chapter 4), and the level of exploitation outside the MPA (Chapter 5) — explained some of the variation in the response to protection. Species that were targeted by fisheries showed greater scope for increase inside MPAs relative to unprotected areas (Chapter 2 and 5). Large, slow-growing species received higher benefit from protection inside fully protected than in partially protected areas, although this difference might be due to the higher dispersal ability and larger home ranges of some of the species inside partially protected areas compared to those in fully protected areas (Chapter 3). In addition to MPA attributes such as the size and age of the MPA (Chapter 2 and 3), results from Chapter 4 highlighted the importance of considering the physical nature and dynamics of the environment throughout the designation process of MPAs, as these were found to influence the response to protection and the recovery of the epibenthic community following cessation of bottom fishing. The study in Chapter 5 showed a significant effect of

protection on epibenthic communities at three MPAs in UK waters, but highlighted that the magnitude of effect of protection needs to be interpreted within the context of past and present levels of exploitation inside and outside the MPA.

6.4   Research findings: *Implications for research and further work*

Lack of data is a hindrance in the development of an evidence-base regarding the effectiveness of marine protected areas. Small sample sizes result in high uncertainty about the impacts on specific taxa, in particular, invertebrates, and species groups such as non-target fish species (Chapter 2). Additionally, insufficient data were available where the effect of protection was assessed in terms of species richness and length (i.e. body size) of species. The effect of protection in soft sediment systems is under-studied relative to that in coral reefs and rocky bottoms (full systematic review from Chapter 2).

Some authors have argued that the apparent effect of protection is not due to protection *per se*, but rather due to higher-quality habitat or site-specific features in reserves before the onset of protection (Willis et al. 2003; Edgar et al. 2004). Although, I accounted for this source of confounding in Chapter 2 by examining the effect of protection after 'habitat-confounded studies' were removed from the analysis, the majority of studies generally failed to report (and/or measure) habitat covariates alongside biological data. Hence, this source of confounding could not be eliminated completely from the analyses. It is essential that future studies measure habitat covariates alongside biological data if assessment of change in a community is to be related to protection or alternatively to an intrinsic structural feature of the protected area.

One important aspect which could not be examined in Chapter 2 owing to the lack of available information was the intensity of resource exploitation inside the MPA prior to its implementation and in the surrounding waters before and during the period of protection. Data regarding the degree of enforcement and compliance inside the MPA were also hardly reported in the literature. Intense resource exploitation outside and adjacent to the MPA boundary clearly increases the likelihood of finding large effects of protection, while poaching in reserves will decrease reserve effectiveness (Samoilys et al. 2007). Spatially and temporally explicit monitoring of fishing effort would be required to provide these data.

To the best of my knowledge, the field surveys that I conducted at the Cardigan Bay SAC (Chapter 4), the *Modiolus* Box within the Pen Llyn a'r Sarnau SAC and the Skomer MNR (Chapter 5) are the first control-impact studies to assess the effect of protection on epibenthic assemblages at these sites. I recommend that further monitoring be undertaken at these sites for a better understanding of the recolonization, recovery and succession process of the epifaunal community within these MPAs. Additionally, a time series dataset will allow a much more robust evaluation of the ecological effectiveness of these MPAs.

6.5   Limitations of study

A valid constraint in Chapters 2 and 5 that needs to be acknowledged is that evaluation of the response to protection was based on single snapshot datasets after MPA establishment. For example, in the studies included in Chapter 2 only 8 out of the 63 studies included in the review used a Before-After/Control-Impact design. In Chapter 5 before data at each of the case-studies was non-existent. As a result, it is difficult to attribute definitively the differences between MPAs and adjacent controls to the establishment of the MPA itself. It is true that time constraints and increased financial costs associated with BACI empirical studies render this type of experimental design difficult in some cases, but the controversy as to whether any differences are a consequence of protection or are merely coincidental can only be satisfactorily addressed by further monitoring, incorporating assessment of change from baseline conditions. The establishment of multiple MPAs, such as those proposed in the UK provides a unique opportunity to overcome many of these deficiencies and more rigorously assess reserve effectiveness. While policy makers may be deterred by the costs of collecting the appropriate evidence to assess the performance of MPAs, the costs associated with establishing inadequate networks of MPAs could be disproportionately higher.

A problem that may affect results in Chapter 2 is non-independence of data and pooling of individual species responses for MPA-level analyses. For example, studies that have measured large numbers of species may exhibit stronger positive responses due to the higher probability of including species that benefit from protection. In Chapter 3, I used individual species response ratios to avoid bias introduced when data is pooled. Moreover, I accounted for the issue of non-independence by using mixed-effects modelling whereby the random intercept component takes into consideration that species' responses from one MPA are more likely to be related than those from another MPA.

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6.6 Concluding remarks

Marine protected areas remain a strong foundation to address ocean challenges (Agardy et al. 2011). However, they are not a panacea to the heavy pressures on the coasts and oceans. A number of shortcomings might lead to the failure of MPAs in meeting their objectives. These include: (i) a mismatch between the scale of the MPA and the home ranges of the species they were created to protect, (ii) insufficient involvement of stakeholders during the planning and failure to receive stakeholder support once established, (iii) inadequate budgeting of resources for surveillance and enforcement process, and (iv) failure to take additional management measures to account for the ecological consequences of displacing effort outside the MPA (Agardy et al. 2011). Therefore, for MPAs to achieve their objectives, they need to be designed and managed effectively, taking into consideration the socio-economic needs of their surrounding communities. They also need to be part of an effective broader framework that addresses management across all sectors. Marine spatial planning is emerging as one of the most promising tools for creating an ecosystem-based management (EBM) approach and ensuring that coasts and oceans are managed to meet current and future demands on ocean resources (Douvere 2008). It focuses on managing the multiple use of marine space, asking what activities happen where, in order to strike a balance and reduce conflicts among users and the environment.

Overall, this thesis has shown that MPAs providing full or partial protection are a valuable tool for the conservation and protection of marine species and habitats. Under the right conditions (that may include additional reduction of fishing effort in fishing grounds surrounding MPAs, or a network of MPAs that allow a mix of protection levels), MPAs are valuable tools for the preservation and enhancement of fish and invertebrate populations.

. . . To convert some of the remaining wild areas into State and National parks, however, is only part of the answer. Even public parks are not what nature created over the eons of time, working with wind and wave and sand. Somewhere we should know what was nature's way; we should know what the earth would have been had not man interfered. And so, besides public parks for recreation, we should set aside some wilderness area of seashore where the relations of sea and wind and shore - of living things and their physical world - remain as they have been over the long vistas of time in which man did not exist. For there remains, in this space-age universe, the possibility that man's way is not always best.

(Carson 1998, p. 124, taken from Pauly *et al*., 2005)

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APPENDICES

APPENDICES FOR CHAPTER 2

Appendix 2.6.1: Search terms

1.A. Electronic database searches

1.B. Website searches

1.A. Electronic database searches

Database (date searched)	Search strings
ISI Web of Knowledge (17.11.09, updated 25.02.11) **Note:** searches were conducted using the field - topic	"marine reserve*" AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) **Note**: ("marine reserve" OR "marine reserves") AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) was searched in ASFA
	marine sanctuary AND (fish OR fishes OR invertebrate*)
Science Direct (17.11.09, updated 25.02.11) **Note:** searches were conducted using the field – Abstract, title, keywords	marine AND "no take zone"
	marine AND harvest refug*
	marine AND "buffer zone"
Aquatic Science and Fisheries Abstracts (ASFA) (17.11.09, updated 25.02.11) **Note:** searches were conducted using the field – All fields (no full text) - ALL	marine AND partial* AND protect* AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity)
	marine AND closed area AND (fish OR fishes OR invertebrate*)
	marine AND area closure AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity)
	fisher* AND (reserve OR closure) AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity)
	fishing gear restriction*
	recreational fishing AND protection
	marine protected area* AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity)

Directory of Open Access Journals (17.11.09, updated 25.02.11)	marine reserve marine reserves marine sanctuary marine AND no take zone marine AND buffer zone marine AND harvest refuge marine AND harvest refugium marine AND closed area marine AND area closure fisheries AND reserve fisheries AND closure fishing gear restriction marine protected area marine protected areas
COPAC National, Academic, and Specialist Library Catalogue (18.11.09, updated 25.02.11)	marine reserve **Note:** marine reserve rather than "marine reserve" was used in COPAC, so that records with – marine nature reserve – were also included marine sanctuary marine AND no take zone marine AND buffer zone marine AND harvest refuge marine AND harvest refugium marine AND closed area marine AND area closure fisheries AND reserve

	fisheries AND closure fishing gear restriction marine protected area
CAB abstracts (18.11.09, updated 03.03.11) **Note:** searches were conducted using the field - abstract	"marine reserve" AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) marine sanctuary AND (fish OR fishes OR invertebrate* OR algae) marine AND "no take zone" marine AND harvest refug* marine AND "buffer zone" marine AND partial* AND protect* AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) marine AND "closed area" AND (fish OR fishes OR invertebrate*) marine AND area closure AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) fisher* AND (reserve OR closure) AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) fishing gear restriction recreational fishing AND protection AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) marine protected area* AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity)
Index to Theses Online (18.11.09, updated 25.02.11)	marine reserve marine sanctuary marine national park

	marine protected area

1.B. Website searches

Website	Search strings
www.googlescholar.com (25.02.11)	marine reserve marine protected area marine sanctuary marine "harvest refuge"
www.scirus.com (25.02.11)	"marine reserve" AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) marine sanctuary AND (fish OR fishes OR invertebrate*) marine AND harvest refug* marine AND "buffer zone" marine AND partial* AND protect* AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) marine AND (closed area OR area closure) AND (fish OR fishes OR invertebrate*) marine AND area closure AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) fisher* AND (reserve OR closure) AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity) recreational fishing AND protection marine protected area* AND (fish OR fishes OR invertebrate*) AND (abundance OR density OR size OR length OR biomass OR richness OR diversity)

Appendix 2.6.2A. MPA characteristics, study design and measured outcomes of partially protected areas presented in the included studies.

Table 1a. Summary of characteristics of partially protected areas included in the assessment of **partial protection over no protection** (PPA *vs* NP)

MPA name	Location	Protection regime	(Year of establishment) Year of effective protection (yrs. to survey)	MPA area (km²)	Distance range of PPA to NP (km)	Habitat
[1] Arraial de Cabo	S. America	DC	1997 (8)	0.56	0.22	firecoral colony
[2] Scandola PPA	Europe	DC	1975 (19)	9.28	1 - 20	seagrass, rocks
[3] Scandola PPA	Europe	DC	1975 (13)	5.18	10	seagrass
[4] Ahus Island TA	Asia	DR	? (60+)	0.332	1	coral reef
[5] Manele-Hulopoe MLCD	N. America	DC	1976 (27)	1.12	na	hard bottom
[5] Old-Kona Airport MLCD	N. America	DC	1992 (11)	1.06	0.91 - 2.5	hard bottom
[5] Lapakahi MLCD	N. America	DC	1979 (25)	0.54	0.07 - 0.87	hard bottom
[5] Waialea Bay MLCD	N. America	DC	1985 (19)	0.14	0.07 - 2.43	hard bottom
[5] Molokini Shoal MLCD	N. America	DC	1977 (27)	0.36	na	hard bottom
[6] Virgin Island CRNM	N. America	DC	2001 (7)	51	0.11 - 8.36	coral reef
[7] Pupukea MLCD	N. America	DC	1983 (25)	0.71	0.06 - 2	hard bottom
[7] Kealakekua Bay MLCD	N. America	DC	1969 (38)	1.24	0.05 - 1.72	hard bottom
[8] Sugar Loaf Island FCA	New Zealand	DR	1986 (17)	7.49	5	na
[8] Sugar Loaf Island PPA	New Zealand	DR	1987 (17)	7.49	5	na

[9] Mimiwhangata MP	New Zealand	DR	1984 (18)	20	0.75 - 4.58	sand, gravel, rock
[10] Tabarca Island BZ	Europe	DC	1986 (13)	6.7	na	*Posidonia oceanica*
[11] Virgin Island NP	N. America	DC	1962 (31)	22.87	na	coral reef, hard bottom, algal plain, seagrass beds
[12] Italcomis Reef MUZ	S. America	DR	2000 (5)	40	10 - 40	coral reef
[13] TMPA – PPA1	Europe	DR	(1998) 2003-4 (3)	31.13	1.2 - 7.1	rock
[13] TMPA – PPA2	Europe	DC	(1998) 2003-4 (3)	117.15	1.2 - 7.1	rock
[14] 25nm FMZ	Europe	IdC	1971 (34)	11980	1.7 - 58.3	sand, mud
[15] Northeast of Horn	Europe	IdC	1992 (12)	3113	1 - 20	na
[15] Langanesgrunn	Europe	IdC	1992 (13)	981	1 - 10	na
[15] Off Northeast coast	Europe	IdC	1970s (30)	1283	1 - 10	na
[16] Barbados MR	N. America	DR	1981 (15)	1.5	0.02 - 0.3	coral reef
[17] La Jolla ER	N. America	DC	1974 (24)	1.85	1 - 15	rocky-reef, kelp beds
[18] Virgin Island CRNM	N. America	DC	2001 (2)	51	0.11 - 8.36	coral reef
[19] Achang reef MP	Asia	DR	(1997) 2001 (2)	4.8	na	shallow reef flats
[19] Tumon Bay MP	Asia	DR	(1997) 2001 (2)	4.5	na	sand, rubble, patch reefs, seagrass beds
[20] Easter Group MPA	Australia	IdC	1994 (8)	22.29	na	coral reef, sand, rubble
[20] Wallabi Group MPA	Australia	IdC	1994 (8)	27.4	na	coral reef, sand, rubble
[21] Western Gulf of Maine CA	N. America	IdC	1998 (7)	na	na	cobble, gravel, rock,

						mud
[22] North Kohala FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Puako-'Anaeho 'Omalu FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Ka'upulehu FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Kaloka-Honokohau FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Kailua-Kona (S. Oneo Bay) FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Kailua-Kona (N. Keauhou) FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Napo' opo' o-Honaunau FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Ho'okena FRA	N. America	-	1999 (4)	na	na	coral reef
[22] Milioli'I FRA	N. America	-	1999 (4)	na	na	coral reef
[23] Cerbere-Banyuls MNR	Europe	DC	1974 (21)	6.5	0.06 – 3.47	rock, pebbles, sand
[24] Houtman-Abrolhos ROAs	Australia	IdC	1994 (15)	66.23	na	coral reef
[25] Mimiwhangata MP	New Zealand	DR	1984 (25)	20	0.4 - 4.27	sand, sand/gravel
[26] Isla La Graciosa BZ	Europe	DC	1995 (9)	609.95	14.71	rocky substrate
[26] Punta La Restiga BZ	Europe	DC	1996 (9)	4.8	14.71	rocky substrate
[27] Admiral Cockburn NPMR	N. America	DR	1992 (na)	4	0.94 - 9.62	coral reef
[28] Mtang'ata CFMZ	Africa	IdC	1996 (8)	na	20 - 200k	rock
[29] Cerbere-Banyuls MNR	Europe	DC	1974 (20+)	6.5	0.9 – 1.25	sand

[30] Jurien Bay MP	Australia	DC	2005 (2)	140.08	0.46 – 5.56	coral reef
[31] CA-I	N. America	IdC	1994 (5)	3960	0.89 - 3.97	mixed sand & gravel
[31] CA-II	N. America	IdC	1995 (5)	3880	0.8 - 2.5	sand

Table 1b. Summary of survey design & methodology and taxa & metrics measured for each partially protected area included in the assessment of partial protection over no protection (PPA *vs* NP)

MPA name	Survey design	Survey method	Total area surveyed (m^2)	Taxon; metrics	Analysis		
					Population (n)	Exploitation status (n)	
						D	B	L
[1] Arraial de Cabo	multiple control ACI	t	na	Fish: D	Y (10)			
[2] Scandola PPA	ACI (10)	t	52000	Fish: D	Y (total)			
[3] Scandola PPA	ACI	t	na	Fish: B	Y (total)			
[4] Ahus Island TA	multiple ACI	t	9000	Fish: B	Y (total)			
[5] Manele-Hulopoe MLCD	ACI	t	8500	Fish: B, SR	Y (total)			
[5] Old-Kona Airport MLCD	ACI	t	7925	Fish: B, SR	Y (total)			
[5] Lapakahi MLCD	ACI	t	5125	Fish: B, SR	Y (total)			
[5] Waialea Bay MLCD	ACI	t	6750	Fish: B, SR	Y (total)			
[5] Molokini Shoal MLCD	ACI	t	10000	Fish: B, SR	Y (total)			

[6] Virgin Island CRNM	ACI (5)	t	9000	Fish: D, B, SR	Y (total)			
[7] Pupukea MLCD	ACI (4)	t	6375	Fish: D, B, SR	Y (total)			
[7] Kealakekua Bay MLCD	ACI (4)	t	4375	Fish: D, B, SR	Y (total)			
[8] Sugar Loaf Island FCA	ACI (3)	t	13250	Fish: D, SR	Y (18)	Y (3)		
[8] Sugar Loaf Island PPA	ACI (3)	t	12875	Fish: D, SR	Y (18)	Y (3)		
[9] Mimiwhangata MP	ACI	t	6000	Fish: D	Y (31)	Y (12)		
[10] Tabarca Island BZ	ACI (6)	t	27000	Fish: D	Y (37)	Y (20)		
[11] Virgin Island NP	ACI	p	na	Fish: D, B	Y (total)	Y (10 fams)		
[12] Italcomis Reef MUZ	ACI (5)	p	26138.05	Fish: B	Y (90)		Y (13)	
[13] TMPA – PPA1	ACI (4)	t	32000	Fish: D, B, SR	Y (23)	Y (5)	Y (4)	
[13] TMPA – PPA2	ACI (4)	t	32000	Fish: D, B, SR	Y (23)	Y (5)	Y (4)	
[14] 25nm FMZ		h	3500280	Fish: D, B	Y (101)	Y (62)	Y (61)	
[15] Northeast of Horn	ACI	h	8284552	Fish: D, L	Y (21)	Y (8)		Y (8)
[15] Langanesgrunn	ACI	h	4418428	Fish: D, L	Y (21)	Y (5)		Y (5)
[15] Off Northeast coast	ACI	h	2982439	Fish: D, L	Y (21)	Y (5)		Y (5)
[16] Barbados MR	ACI	t	8000	Fish: D, L	Y (26)	Y (26)		Y (26)
[17] La Jolla ER	ACI (2)	t	9240	Fish: D, B, L	Y (12)	Y (9)	Y (8)	Y (9)
[18] Virgin Island CRNM	ACI (3)	t	11900	Fish: B			Y (16)	
[19] Achang reef MP	ACI (8)	t	16000	Fish: B			Y (5)	

[19] Tumon Bay MP	ACI (8)	t	16000	Fish: B			Y (5)	
[20] Easter Group MPA	BACI (B: 1, A: 2)	t	12000	Fish: D		Y (2)		
[20] Wallabi Group MPA	BACI (B: 1, A: 2)	t	12000	Fish: D		Y (2)		
[21] Western Gulf of Maine CA	ACI (2)	h	11520	Fish: D		Y (1)		
[22] North Kohala FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Puako-'Anaeho 'Omalu FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Ka'upulehu FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Kaloka-Honokohau FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Kailua-Kona (S. Oneo Bay) FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Kailua-Kona (N. Keauhou) FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Napo' opo' o-Honaunau FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Ho'okena FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[22] Milioli'I FRA	BACI (B: 6, A: 28)	t	800 survey^{-1}	Fish: D		Y (1)		
[23] Cerbere-Banyuls MNR	ACI	t	na	Fish: D, L		Y (2)		Y (2)
[24] Houtman-Abrolhos ROAs	multiple ACI (5)	p (BUV)	na	Fish: D, L		Y (1)		Y (1)
[25] Mimiwhangata MP	ACI	p (BUV)	na	Fish: D, L		Y (1)		Y (1)
[26] Isla La Graciosa BZ	ACI (2)	t	6000	Fish: D, B		Y (4)	Y (4)	
[26] Punta La Restiga BZ	ACI (2)	t	6000	Fish: D, B		Y (3)	Y (2)	
[27] Admiral Cockburn NPMR	ACI	t	8000	Fish: D, B, L		Y (3)	Y (3)	Y (3)

[28] Mtang'ata CFMZ	ACI (2)	Inv: p (quadrat) Fish: t	11000	Fish: B Inv: B	Y (total)			
[29] Cerbere-Banyuls MNR	ACI (2)	h	na	Fish: B Inv: B			Y (3) Y (2)	
[30] Jurien Bay MP	multiple ACI (8)	t	5600	Fish: D, B,SR Inv: D, SR	Y (21) Y (7)	Y (11)	Y (4)	
[31] CA-I	ACI	Fish: h Inv: p (grab)	832104	Fish: D, B, L Inv: B	Y (13) Y (10)	Y (13)	Y (13) Y (10)	Y (11)
[31] CA-II	ACI	Fish: h Inv: p (grab)	1069848	Fish: D, B, L Inv: B, SR	Y (15) Y (10)	Y (15)	Y (14) Y (10)	Y (11)

Appendix 2.6.2B. MPA characteristics, study design and measured outcomes of no-take marine reserves presented in the included studies.

Table 2a. Summary of characteristics of **no-take reserves and partially protected areas** included in the assessment of full protection over partial protection (NTR *vs* PPA)

NTR name	PPA name	Location	(Year of establishment) Year of effective protection (yrs. to survey)	NTR area (km^2)	PPA area (km^2)	Distance range of NTR to PPA (km)	Habitat
[2] Scandola IR	Scandola PPA	Europe	1975 (19)	na	na	adjacent	seagrass, rocks
[3] Scandola IR	Scandola PPA	Europe	1975 (13)	na	na	adjacent	seagrass

[32] Giannutri Island HPA	Giannutri Island LPA	Europe	(1989) 1996 (9)	4.4	na	adjacent	rock
[33] Ustica Island IR	Ustica Island GR	Europe	(1986) 1991 (6)	0.6	80	adjacent	rock
[33] Ustica Island IR	Ustica Island PR	Europe	(1986) 1991 (6)	0.6	79.01	adjacent	rock
[34] Mayor Island NTMR	Mayor Island RFA	New Zealand	1993 (11)	10.31	30.93	adjacent	reef, sand
[12] Italcomis Reef NTZ	Italcomis Reef MUZ	S. America	2001 (4) 2000 (5)	10	40	adjacent	coral reef
[13] Tavolara IR	Tavolara PR	Europe	(1997) 2003-4 (3)	5.29	31.13	adjacent	rock
[13] Tavolara IR	Tavolara GR	Europe	(1997) 2003-4 (3)	5.29	117.15	adjacent	rock
[17] Laguna - Heisler ER	La Jolla ER	N. America	1974 (24)	0.13	1.85	32	rocky-reef, kelp beds
[19] Piti MP	Achang MP	Asia	(1997) 2001 (2)	3.6	4.8	24	shallow reef flats
[19] Piti MP	Tumon Bay MP	Asia	(1997) 2001 (2)	3.6	4.5	12	sand, rubble, patch reefs, seagrass beds
[26] Isla La Graciosa IR	Isla La Graciosa BZ	Europe	1995 (9)	12.5	609.95	adjacent	rock
[26] Punta La Restiga IR	Punta La Restiga BZ	Europe	1996 (8)	1.8	4.8	adjacent	rock
[35] Kingston Reefs MS	Rottnest Island reserve	Australia	1988 (16)	1.26	38	adjacent	reef
[36] Maud SZ	recreational zone	Australia	1991 (9) 1989 (11)	na	na	11	coral lagoon
[36] Osprey SZ	recreational zone	Australia	1991 (9) 1989 (11)	na	na	6	coral lagoon
[36] Mandu SZ	recreational zone	Australia	1991 (9) 1989 (11)	na	na	9	coral lagoon
[37] Kisite MNP	Mpunguti MNR	Africa	(1978) 1989 (3)	28	11	adjacent	coral reef
[38] Giannutri Is zone 1	Giannutri Is zone 2	Europe	(1990) 1996 (4)	4.4	na	adjacent	rock, sand

[38] Capraia Is zone 1	Capraia Is zone 2	Europe	(1989) 1996 (4)	5.4	na	adjacent	seagrass meadow
[39] Long-Island MR	Charlotte Sound	New Zealand	1993 (16)	6.19	na	adjacent	cobble & small boulders
[30] Jurien Bay SZ	Jurien Bay RZ	Australia	2005 (2)	30.49	140.08	adjacent	reef

Table 2b. Summary of survey design & methodology and taxa & metrics measured for each no-take reserve and partially protected area included in the assessment of full protection over partial protection (NTR *vs* PPA)

NTR name	PPA name	Survey design	Survey method	Taxon; metrics	Analysis		
					Population (n)	Exploitation status (n)	
						D	B	L
[2] Scandola IR	Scandola PPA	ACI	t	Fish: D	Y (total)			
[3] Scandola IR	Scandola PPA	ACI (10)	p (stationary UVC)	Fish: B	Y (total)			
[32] Giannutri Island HPA	Giannutri Island LPA	ACI (4)	p (area search)	Fish: D	Y (56)	Y (47)		
[33] Ustica Island IR	Ustica Island GR	ACI (10)	t	Fish: D, SR	Y (total)	Y (15)		
[33] Ustica Island IR	Ustica Island PR	ACI (10)	t	Fish: D, SR	Y (total)	Y (15)		
[34] Mayor Island NTMR	Mayor Island RFA	ACI	p (BUV)	Fish: D, SR	Y (total)	Y (6)		
[12] Italcomis Reef NTZ	Italcomis Reef MUZ	ACI (5)	p (stationary UVC)	Fish: B	Y (total)		Y (4)	
[13] Tavolara IR	Tavolara PR	ACI (4)	t	Fish: D, B, SR	Y (total)	Y (5)	Y (5)	
[13] Tavolara IR	Tavolara GR	ACI (4)	t	Fish: D, B, SR	Y (total)	Y (5)	Y (5)	

[17] Laguna - Heisler ER	La Jolla ER	ACI (2)	t	Fish: D, B, L	Y (total)	Y (12)	Y (12)	Y (12)
[19] Piti MP	Achang MP	ACI (8)	t	Fish: B			Y (5)	
[19] Piti MP	Tumon Bay MP	ACI (8)	t	Fish: B			Y (5)	
[26] Isla La Graciosa IR	Isla La Graciosa BZ	ACI (2)	t	Fish: D, B		Y (4)	Y (4)	
[26] Punta La Restiga IR	Punta La Restiga BZ	ACI (2)	t	Fish: D, B		Y (4)	Y (4)	
[35] Kingston Reefs MS	Rottnest Island reserve	ACI (2)	p (baited BUV)	Fish: D, B, L		Y (4)	Y (3)	Y (3)
[36] Maud SZ	recreational zone	ACI (2)	p (BUV)	Fish: D, B, L		Y (5)	Y (1)	Y (1)
[36] Osprey SZ	recreational zone	ACI (2)	p (BUV)	Fish: D, B, L		Y (1)	Y (1)	Y (1)
[36] Mandu SZ	recreational zone	ACI (2)	p (BUV)	Fish: D, B, L		Y (5)	Y (1)	Y (1)
[37] Kisite MNP	Mpunguti MNR	ACI	t	Fish: D Inv: D	Y (total)	Y (41) Y (3)		
[38] Giannutri Is zone 1	Giannutri Is zone 2	ACI (3)	Fish (stationary count) Inv (quadrat)	Fish: D, SR Inv: SR	Y (total)			
[38] Capraia Is zone 1	Capraia Is zone 2	ACI (3)	Fish (stationary count) Inv (quadrat)	Fish: D, SR Inv: D, SR	Y (total)	Y (2)		
[39] Long-Island MR	Charlotte Sound	BACI (x/x) & ACI (x)	Fish: t Inv: p (quadrat)	Fish: D, L Inv: D, L		Y (7) Y (3)		Y (3) Y (3)
[30] Jurien Bay SZ	Jurien Bay RZ	multiple ACI (8)	t	Fish: D, B, SR Inv: D, L, SR	Y (21)	Y (12) Y (5)	Y (5)	Y (1)

Table 2c. Studies not included in the meta-analysis due to different years of establishment of the no-take reserve and the partially protected area.

NTR name	(Year of NTR establishment) Year of effective protection	PPA name	Year of PPA protection	Age diff (NTR – PPA) (yrs)
[9] Poor Knights Island MR	1998	Mimiwhangata MP	1984	+14
[40] Oculina Experimental CA	1994	Oculina Habitat APC	1984 expanded in 2000	+10 / -6
[28] Kisite MNP & GRZ	1978	Mtang'ata CFMZ	1996	-18
[25] Poor Knights MR	1998	Mimiwhangata MP	1984	+14
[17] Catalina MLR	1988	La Jolla ER	1974	+14
[17] Natural Area	1971	La Jolla ER	1974	-3

Appendix 2.6.3: MPA 'protection regime' categories

Several characteristics of the MPA that may potentially influence the magnitude of response to protection include (i) the type of the restricted and permitted activities within the partially protected area and (ii) the scale of the permitted activities, whether commercial or recreational, within the partially protected area. Collectively, we refer to these characteristics as 'protection regime' of the partially protected area.

Approach

Information about the 'protection regime' for each MPA was extracted from the studies. When this was lacking or unclear the first authors were contacted, and in the event of no reply additional publications and web resources were consulted. A detailed description of the 'protection regime' for each MPA is given in Table 2 and Table 3. We then applied the questions in Table 1, once using the data on the type of restricted activities and once using the data on the type and scale of the permitted activities inside the partially protected area, to categorize the partially protected areas by their 'protection regime'. When more than one fishing activity was restricted and/or permitted within the MPA, the answer to the questions was based on the activity with the potentially most negative impact on biota and their surrounding environment. The two binary datasets were examined in PRIMER v. 6 using CLUSTER analysis to identify categories based on 'protection regime'. CLUSTER analysis was used to minimize bias through subjective judgment.

Table 1. Questions applied to categorize the partially protected areas by their 'protection regime'

	Question re fishing activity	**Answer**	
Q1.	Is it destructive or damaging to bottom habitats?	Yes (1)	No (0)
Q2.	Does it target particular species or group of species?	Yes (1)	No (0)
Q3.	Is it a selective fishing practice in terms of size of individuals?	Yes (1)	No (0)
Q4.	Is it likely to impact non-target species through by-catch?	Yes (1)	No (0)
Q5.	Is the activity carried out for subsistence or leisure/recreation purposes?	Subsistence (1)	Recreation (0)
Q6.	Is subsistence fishing carried out on a commercial scale or on a local/domestic scale?	Commercial (1)	Domestic (0)

Outcome

The CLUSTER analysis divided the partially protected areas into two main groups based on the **activities restricted** within their boundaries:

(a) those that restrict activities that damage bottom habitats and have high incidence of impacting non-target species, referred to hereafter as **'Indiscriminate'**

(b) those that restrict activities that only effect particular target species but not the surrounding environment, referred to hereafter as **'Discriminate'**

Based on the activities **permitted** inside the partially protected area, the CLUSTER analysis divided the partially protected areas into four groups:

(a) those that allow recreational fishing using size-selective methods, referred to hereafter as **'recreational, selective'**

(b) those that allow subsistence fishing on a personal-use (domestic) scale using size-selective methods, referred to hereafter as **'domestic, selective'**

(c) those that allow subsistence fishing on a commercial scale using size-selective methods, referred to hereafter as **'commercial, selective'**

(d) those that allow subsistence fishing on a commercial scale using methods that are non-selective in terms of size of individuals, referred to hereafter as **'commercial, non-selective'**

The partially protected areas in our dataset fell within six of the 'protection regime' categories identified by CLUSTER analysis. However, since there were not enough partially protected areas for statistical analysis of all the six 'protection regime' categories some categories were grouped together as follows:

'Indiscriminate; commercial, selective'
'Indiscriminate; commercial, non-selective' } 'Indiscriminate; commercial' = IdC

'Discriminate; commercial, selective'
'Discriminate; commercial, non-selective' } 'Discriminate; commercial' = DC

'Discriminate; recreational, selective'
'Discriminate; domestic, selective' } 'Discriminate; recreational' = DR

Table 2. Description of the fishing activities that are restricted within the partially protected areas included in our dataset. The response to the questions in Table 1 is given under the headings Q1 to Q6 for each MPA. In the event of more than one fishing activity being restricted inside the MPA, we based answers to Q1 to Q6 on the activity marked in bold. The resulting category identified by CLUSTER analysis is given under 'Category'.

PPA name	Restricted activities	Q1	Q2	Q3	Q4	Q5	Q6	Category
[1] Arraial de Cabo	na	No indication of the type fishing gear restricted						
[2] [3] Scandola PPA	Amateur fishing, **spearfishing**, SCUBA diving	0	1	1	0	0	na	Discriminate
[4] Ahus Island TA	**Spear and net fishing**	0	1	1	0	1	1	Discriminate
[5] Manele-Hulopoe MLCD	**Spearfishing**, trap and **net fishing** in 50% MLCD	0	1	1	0	1	0	Discriminate
[5] Old-Kona Airport MLCD	na	No indication of the type fishing gear restricted						
[5] Lapakahi MLCD	na	No indication of the type fishing gear restricted						
[5] Waialea Bay MLCD	na	No indication of the type fishing gear restricted						
[5] Molokini Shoal MLCD	na	No indication of the type fishing gear restricted						
[6] [18] Virgin Island CRNM	extractive uses, anchoring	0	1	0	0	1	1	Discriminate
[7] Pupukea MLCD	na	No indication of the type fishing gear restricted						
[7] Kealakekua Bay MLCD	na	No indication of the type fishing gear restricted						
[8] Sugar Loaf Island FCA	Commercial fishing, recreational set **netting**, longlining	0	1	0	0	1	1	Discriminate
[8] Sugar Loaf Island PPA	Commercial & recreational fishing, anchoring by commercial vessels, mining & drilling	0	1	0	0	1	1	Discriminate
[9] [25] Mimiwhangata MP	Commercial fishing, **nets & long-lines**	0	1	0	0	1	1	Discriminate

[10] Tabarca Island BZ	Recreational fishing, anchoring. Professional fishing (with traditional gears) is regulated	0	1	0	0	1	1	Discriminate
[11] Virgin Island NP	Spearfishing, commercial fishing using **cast nets** with mesh > 2.5cm or over 6.1m in length	0	1	0	0	1	1	Discriminate
[12] Italcomis Reef MUZ	Fishing for aquarium species, drive nets	0	1	0	0	1	1	Discriminate
[13] TMPA – PPA1	Spearfishing	0	1	1	0	0	na	Discriminate
[13] TMPA – PPA2	Spearfishing	0	1	1	0	0	na	Discriminate
[14] 25nm FMZ	**Trawling** within 3nm from coast, and in specified areas beyond 3nm	1	1	1	1	1	1	Indiscriminate
[15] Northeast of Horn	Closed to **trawling** since 1992 and fishing with longline in 1993	1	1	1	1	1	1	Indiscriminate
[15] Langanesgrunn	Closed to **trawling** since 1992 and fishing with longline in 1994	1	1	1	1	1	1	Indiscriminate
[15] Off Northeast coast	Closed to **trawling** since 1970s and to longline since 1993	1	1	1	1	1	1	Indiscriminate
[16] Barbados MR	**Spearfishing**, hook-and-line fishing, cast **netting**, trapping	0	1	1	1	1	1	Discriminate
[17] La Jolla ER	na	No indication of the type fishing gear restricted						
[19] Achang reef MP	Extraction of adult fish, or the use of any fishing gear up to a depth of over 600ft	No indication of the type fishing gear restricted						
[19] Tumon Bay MP	na	No indication of the type fishing gear restricted						
[20] Easter Group MPA	Hook-and-line, any form of netting, **trawling for scallops/prawns**, trolling with rods and lures for species such as coral trout, spearfishing	1	1	1	1	1	1	Indiscriminate
[20] Wallabi Group MPA	Hook-and-line, any form of netting,	1	1	1	1	1	1	Indiscriminate

	trawling for scallops/prawns, trolling with rods and lures for species such as coral trout, spearfishing							
[21] Western Gulf of Maine CA	**Mobile bottom gear**, gill netting	1	1	0	1	1	1	Indiscriminate
[22] North Kohala FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Puako-'Anaeho 'Omalu FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Ka'upulehu FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Kaloka-Honokohau FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Kailua-Kona (S. Oneo Bay) FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Kailua-Kona (N. Keauhou) FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Napo' opo' o-Honaunau FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Ho'okena FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[22] Milioli'I FRA	Fishing for aquarium species	No indication of the type fishing gear restricted						
[23] [29] Cerbere-Banyuls MNR	Spearfishing	0	1	1	0	0	na	Discriminate
[24] Houtman-Abrolhos ROAs	Fishing for scalefish species	1	1	1	1	1	1	Indiscriminate
[26] Isla La Graciosa BZ	**Traps**, underwater fishing	0	1	1	0	1	1	Discriminate
[26] Punta La Restiga BZ	**Traps**, underwater fishing	0	1	1	0	1	1	Discriminate
[27] Admiral Cockburn NPMR	Commercial fishing	No indication of the type fishing gear restricted						
[28] Mtang'ata CFMZ	**Dynamite & poison fishing**, beach seining, dragging of nets	1	1	1	1	1	1	Indiscriminate

[30] Jurien Bay MP	Finfish fishing using **lines & nets**	0	1	0	0	1	1	Discriminate
[31] CA-I	**Trawls**, gill nets, **scallop dredge** (no bottom tending gear allowed)	1	1	1	1	1	1	Indiscriminate
[31] CA-II	**Trawls**, gill nets, **scallop dredge** (no bottom tending gear allowed)	1	1	1	1	1	1	Indiscriminate
[32] [38] Giannutri Island LPA	Commercial fishing, **spearfishing**	0	1	1	0	0	na	Discriminate
[33] Ustica Island GR	**Trawling**, spearfishing, sea urchin harvesting	1	1	1	1	1	1	Indiscriminate
[33] Ustica Island PR	**Trawlin**g, purse seining	1	1	1	1	1	1	Indiscriminate
[34] Mayor Island RFA	Commercial fishing, recreational fishing with set nets (including **gill nets) and long lines**	0	1	0	0	1	1	Discriminate
[35] Rottnest Island reserve	**Commercial lobster fishing** within 1600m from shore, recreational sport fishing within 800m from shore, spearfishing	0	1	1	0	1	1	Discriminate
[36] recreational zone	Commercial fishing (beach netting & spearing not allowed except in some areas)	0	1	1	0	1	1	Discriminate
[37] Mpunguti MNR	Spearfishing, **poison fishing**, aquarium fishing	1	1	1	1	1	0	Indiscriminate
[38] Capraia Is zone 2	Spearfishing	0	1	1	0	0	na	Discriminate
[39] Charlotte Sound	Commercial fishing for blue cod	No indication of the type fishing gear restricted						

Table 3. Description of the fishing activities permitted within the partially protected areas included in our dataset. The response to the questions in Table 1 is given under the headings Q1 to Q6 for each MPA. In the event of more than one fishing activity being restricted inside the MPA, we based answers to Q1 to Q6 on the activity marked in bold. The resulting category identified by CLUSTER analysis is given under 'Category'.

PPA name	Permitted activities	Q1	Q2	Q3	Q4	Q5	Q6	Category
[1] Arraial de Cabo	Fishing using traditional techniques	0	1	0	0	1	1	Commercial
[2] [3] Scandola PPA	Professional fishing using small boats with low engine power & traditional fishing methods	0	1	0	0	1	1	Commercial
[4] Ahus Island TA	Line fishing, limited harvesting of invertebrates allowed 3 times a year	0	1	0	0	1	0	Domestic
[5] Manele-Hulopoe MLCD	Hook & line (shore), **thrownet** allowed in all of the MLCD	0	1	0	0	1	1	Commercial
[5] Old-Kona Airport MLCD	**Thrownet** & pole-and-line (shore), sea urchin collecting from June to October	0	1	0	0	1	1	Commercial
[5] Lapakahi MLCD	Hook & line, **thrownet**, liftnet for opelu in 90% of MLCD	0	1	0	0	1	1	Commercial
[5] Waialea Bay MLCD	Netting	0	1	0	0	1	1	Commercial
[5] Molokini Shoal MLCD	Trolling in 60% of MLCD	0	1	1	0	1	1	Commercial
[6] [18] Virgin Island CRNM	Fishing for blue runner (Caranx crysos) by hand line and of baitfish using a **castnet**	0	1	1	0	1	1	Commercial
[7] Pupukea MLCD	**pole-and-line** (shore) and harvest of seaweed	0	1	1	0	1	1	Commercial
[7] Kealakekua Bay MLCD	hook-and-line, **throw net,** harvest of seaweed & crustaceans in 60% of MLCD	0	1	0	0	1	1	Commercial

[8] Sugar Loaf Island FCA	Fishing for kahawai (Arripis trutta) and kingfish Seriola lalandi) for bait, either through trolling or **spearfishing**. Recreational fishing, diving and potting for rock lobster	0	1	1	0	0	na	Domestic/recreational
[8] Sugar Loaf Island PPA	Trolling & **spearfishing** for kingfish (Seriola lalandi) and kahawi (Arripis frutta)	0	1	1	0	1	0	Domestic/recreational
[9] [25] Mimiwhangata MP	Recreational fishing with unweighted, single-hook lines, trolling, **spearfishing**	0	1	1	0	0	na	Recreational
[10] Tabarca Island BZ	Troll lines, 10 **trap nets** to catch Atherinidae fish from Oct-Dec, sport fishing by rod, controlled diving	0	1	0	0	1	1	Commercial
[11] Virgin Island NP	Fishing including with traps	0	1	1	0	1	1	Commercial
[12] Italcomis Reef MUZ	Hand lines, **spears & various types of nets** are allowed by local community only	0	1	0	0	1	0	Domestic
[13] TMPA – PPA1	Professional & regulated recreational fishing	0	1	1	0	0	na	Recreational
[13] TMPA – PPA2	Fishing with **trammel/gillnets**, longlines by local fishermen	0	1	0	0	1	1	Commercial
[14] 25nm FMZ	artisinal fishing, **restricted trawling** in specified areas, lampuki fishing using Fish Aggregating Device, Lampara using a small scale pelagic purse seine that targets bodue & mackerel, fishing for tuna, swordfish & highly migratory fish	1	1	0	1	1	1	Commercial
[15] Northeast of Horn	na but assuming that use of fishing gear that does not make contact with	0	1	1	0	1	1	Commercial

	the seafloor is allowed							
[15] Langanesgrunn	na but assuming that use of fishing gear that does not make contact with the seafloor is allowed	0	1	1	0	1	1	Commercial
[15] Off Northeast coast	na but assuming that use of fishing gear that does not make contact with the seafloor is allowed	0	1	1	0	1	1	Commercial
[16] Barbados MR	Fishing with cast netting for clupeids	0	1	0	0	1	0	Domestic
[17] La Jolla ER	Commercial bait fishing for squid by hand-held scoop net	0	1	1	0	1	1	Commercial
[19] Achang reef MP	Seasonal fishing for Siganus & Mulloidichthys using **cast nets** and hook-and-line	0	1	0	0	1	0	Domestic
[19] Tumon Bay MP	Traditional fishing with hook-and-line or **cast net** from the shore is allowed for 4 types of fish: Acanthurus triostegus, Siganus spp. Caranx xpp, Mullidae	0	1	1	0	1	0	Domestic
[20] Easter Group MPA	Potting for rock lobster	0	1	1	0	1	1	Commercial
[20] Wallabi Group MPA	Potting for rock lobster	0	1	1	0	1	1	Commercial
[21] Western Gulf of Maine CA	**Shrimp trawls**, lobster traps, mid-water trawls, research bottom trawling, recreational fishing	1	1	0	1	1	1	Commercial
[22] North Kohala FRA	na	No indication of the type fishing activities permitted						
[22] Puako-'Anaeho 'Omalu FRA	na	No indication of the type fishing activities permitted						
[22] Ka'upulehu FRA	na	No indication of the type fishing activities permitted						

[22] Kaloka-Honokohau FRA	na	No indication of the type fishing activities permitted						
[22] Kailua-Kona (S. Oneo Bay) FRA	na	No indication of the type fishing activities permitted						
[22] Kailua-Kona (N. Keauhou) FRA	na	No indication of the type fishing activities permitted						
[22] Napo' opo' o-Honaunau FRA	na	No indication of the type fishing activities permitted						
[22] Ho'okena FRA	na	No indication of the type fishing activities permitted						
[22] Milioli'I FRA	na	No indication of the type fishing activities permitted						
[23] [29] Cerbere-Banyuls MNR	Commercial, recreational fishing, regulated SCUBA diving	0	1	0	0	1	1	Commercial
[24] Houtman-Abrolhos ROAs	Commercial fishing for rock lobster	0	1	1	0	1	1	Commercial
[26] Isla La Graciosa BZ	Hook and traditional fishing gear for (i) salema (Sarpa salpa), (ii) migratory pelagic species (tunids), (iii) guelds (minnows, "gueldera") and morays (net drum). **Traps and pots** for crustaceans. Sport fishing using spinning tackle, hook-and-line	0	1	1	0	1	1	Commercial
[26] Punta La Restiga BZ	Hook and traditional fishing gear for (i) salema (Sarpa salpa), (ii) migratory pelagic species (tunids), (iii) guelds (minnows, "gueldera") and morays (net drum). **Traps and pots** for crustaceans. Sport fishing using spinning tackle, hook-and-line	0	1	1	0	1	1	Commercial
[27] Admiral Cockburn NPMR	Recreational hook-and-line fishing	0	1	1	0	0	na	Recreational

[28] Mtang'ata CFMZ	na							
[30] Jurien Bay MP	Line fishing, **netting,** rock lobster & abalone fishing	0	1	1	0	1	1	Commercial
[31] CA-I	Any and all surface activities	0	1	1	0	1	1	Commercial
[31] CA-II	Any and all surface activities (hook-and-line, **midwater trawl**)	0	1	1	0	1	1	Commercial
[32] [38] Giannutri Island LPA	SCUBA diving, recreational fishing with longlines, **gill nets**, traps	0	1	0	0	1	1	Commercial
[33] Ustica Island GR	SCUBA diving, **artisinal fishing** (limited to local boats), recreational fishing (limited to anglers)	0	1	0	0	1	1	Commercial
[33] Ustica Island PR	**Spearfishing**, sea urchin harvesting	0	1	1	0	0	na	Recreational
[34] Mayor Island RFA	Recreational fishing	0	1	0	0	0	na	Recreational
[35] Rottnest Island reserve	Recreational fishing, **potting,** SCUBA diving	0	1	1	0	1	1	Commercial
[36] recreational zone	Recreational fishing	0	1	0	0	0	na	Recreational
[37] Mpunguti MNR	Artisinal fishing using basket traps and **gill netting**	0	1	0	0	1	1	Commercial
[38] Capraia Is zone 2	Recreational fishing including angling, long lining, **gill netting, traps**	0	1	0	0	1	1	Commercial
[39] Charlotte Sound	Recreational fishing	0	1	0	0	0	na	Recreational

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APPENDICES FOR CHAPTER 3

Appendix 3.6.1 List of the species recorded from the studies and their exploitation status (NT = non-target species, T = target species, NA = data not available) and ecological categories (Adult habitat type: RA = reef-associated, DM = demersal, BP = bentho-pelagic). L_{max} is the maximum body size recorded for the species. The column 'Dataset' indicates in which of the 4 datasets the species was included in.

Family	Species	L_{max} (cm)	Exploitation Status	Adult habitat type	Dataset
Acanthuridae	*Acanthurus bahianus*	38.1	NT	RA	1
	Acanthurus coerulens	39	NT	RA	1
	Acanthurus triostegus	27	T	RA	2, 4
	Naso lituratus	46	T	RA	2, 4
	Zebrasoma flavescens	20	T	RA	1
Anarhichadidae	*Anarhichas lupus*	150	T	DM	1
Apogonidae	*Apogon imberbis*	15	NT	RA	3
Argentinidae	*Argentina sphyraena*	35	NT	DM	1, 2
Blenniidae	*Blennius ocellaris*	20	NT	DM	1, 2
	Parablennius gattorugine	30	NT	DM	3
	Parablennius rouxi	8	NT	DM	3
	Parablennius zvonimiri	7	NT	DM	3
Callionymidae	*Synchiropus phaeton*	18	NT	DM	1, 2
Caproidae	*Capros aper*	30	NT	DM	1, 2
Carangidae	*Caranx ruber*	59	NT	RA	1
	Seriola dumerilii	190	T	RA	3
Carangidae	*Trachurus picturatus*	60	NT	BP	2
Centracanthidae	*Spicara maena*	25	NT	DM	3
	Spicara smaris	20	NT	DM	1, 3
Centriscidae	*Macrorhamphosus scolopax*	20	NT	DM	1, 2
Centrophoridae	*Centrophorus granulosus*	160	NT	DM	1, 2
Cepolidae	*Cepola macrophtalma*	80	NT	DM	1, 2
Chaetodontidae	*Chaetodon striatus*	16	NT	RA	1
Cheilodactylidae	*Cheilodactylus spectabilis*	100	NT	DM	1
	Nemadactylus macropterus	70	NT	DM	3
Chimaeridae	*Chimaera monstrosa*	150	NT	DM	1, 2
Chlorophthalmidae	*Chlorophthalmus agassizi*	40	NT	DM	1, 2
Citharidae	*Citharus linguatula*	30	NT	DM	1, 2
Congridae	*Conger conger*	300	NT	DM	1, 2

Cottidae	*Myoxocephalus octodecemspinosus*	46	T	DM	1, 2
Embiotocidae	*Embiotoca jacksoni*	39	NT	DM	1, 2, 3, 4
Epigonidae	*Epigonus telescopus*	75	NT	DM	1, 2
Etmopteridae	*Etmopterus spinax*	60	NT	DM	1, 2
Gadidae	*Gadus morhua*	200	T	BP	1, 2
	Melanogrammus aeglefinus	112	T	DM	1, 2
	Pollachius virens	130	T	DM	1
	Trisopterus esmarkii	35	T	BP	1
	Trisopterus minutus capelanus	40	NT	BP	1, 2
Glaucosomatidae	*Glaucosoma hebracium*	122	T	RA	1, 3, 4
Gobiidae	*Gobius auratus*	10	NT	DM	3
	Gobius bucchichi	10	NT	DM	3
	Gobius vittatus	5.8	NT	DM	3
Haemulidae	*Anisotremus virginicus*	40.6	T	RA	2
	Haemulon album	79	T	RA	1, 2
	Haemulon aurolineatum	25	NA	RA	1, 2
	Haemulon carbonarium	36	NT	RA	1
	Haemulon chrysargyreum	23	NT	RA	1
	Haemulon flavolineatum	30	NT	RA	1, 2
	Haemulon plumierii	53	T	RA	2
	Haemulon sciurus	46	T	RA	2
Hemitripteridae	*Hemitripterus americanus*	64	T	DM	1, 2
Hexanchidae	*Heptranchias perlo*	137	NT	DM	1, 2
Holocentridae	*Holocentrus rufus*	35	NT	RA	1
	Myripristis jacobus	25	NT	RA	1
Kyphosidae	*Girella nigricans*	66	NT	BP	1, 3
	Girella tricuspidate	71	NT	BP	1
	Kyphosus cornelii	70	NT	RA	1, 2, 3, 4
	Kyphosus sectatrix	76	T	RA	1
	Kyphosus sydneyanus	80	NT	DM	1, 2, 3, 4
	Medialuna californiensis	48	NT	DM	1, 2, 3, 4
	Scorpis lineolatus	30	NT	RA	1
Labridae	*Austrolabrus maculatus*	12.6	NT	RA	1, 3
	Bodianus rufus	40	NT	RA	1

	Bodianus unimaculatus	45	NT	RA	1, 3
	Choeroden rubescens	90	T	RA	1, 2, 3, 4
	Coris auricularis	40	NT	RA	1, 3
	Coris julis	30	NT	RA	1, 3
	Coris sandageri	25	NT	RA	1
	Halichoeres poeyi	20	NA	RA	1
	Halichoeres semicinctus	38	NT	RA	1, 2, 3, 4
	Labrus merula	45	NT	RA	1, 3
	Labrus mixtus	40	NT	RA	3
	Labrus viridis	47	NT	RA	1, 3
	Lachnolaimus maximus	91	T	RA	1, 2
	Notolabrus celidotus	23.9	NT	RA	1, 3
	Notolabrus fucicola	38	NT	RA	1, 3
	Notolabrus parilus	NA	NT	RA	1, 3
	Oxyjulis californica	25	NT	DM	1, 2, 3, 4
	Pictilabrus laticlavius	23	NT	RA	3
	Pseudolabrus miles	27.2	NT	RA	1, 3
	Semicossyphus pulcher	91	T	RA	1, 2, 3, 4
	Symphodus cinereus	16	NT	DM	3
	Symphodus doderleini	10	NT	DM	3
	Symphodus mediterraneus	18	NT	DM	3
	Symphodus melanocercus	14	NT	RA	3
	Symphodus ocellatus	12	NT	RA	1, 3
	Symphodus roissali	17	NT	RA	1, 3
	Symphodus rostratus	13	NT	RA	1, 3
	Symphodus tinca	44	NT	RA	1, 3
	Tautogolabrus adspersus	38	NT	RA	1, 2
	Thalassoma lunare	45	NT	RA	1, 3
	Thalassoma lutescens	30	NT	RA	1
	Thalassoma pavo	25	NT	RA	1, 3
Labrisomidae	*Labrisomus nuchipinnis*	23	NA	RA	1
Latridae	*Latridopsis ciliaris*	80	NT	DM	3
Lethrinidae	*Lethrinus harak*	50	T	RA	2
	Lethrinus miniatus	90	T	RA	1
Lophiidae	*Lophius americanus*	120	T	DM	1
	Lophius budegassa	100	T	DM	1, 2

	Lophius piscatorius	200	T	DM	1, 2
Lotidae	*Molva dipterygia*	155	NT	DM	1, 2
Lutjanidae	*Lutjanus apodus*	67.2	T	RA	2
	Lutjanus jocu	128	T	RA	2
	Lutjanus mahogani	48	T	RA	1
	Ocyurus chrysurus	86.3	T	RA	2
Macrouridae	*Caelorhynchus caelorhynchus*	48	NT	BP	1, 2
	Hymenocephalus italicus	25	NT	BP	1, 2
Merlucciidae	*Merluccius bilinearis*	76	T	DM	1, 2
	Merluccius merluccius	140	T	DM	1, 2
Monacanthidae	*Cantherhines pullus*	20	NT	RA	1
	Meuschenia hippocrepis	51	NT	DM	3, 4
	Parika scaber	31	NT	DM	1, 3
	Stephanolepis hispidus	27.5	NA	RA	1
Moronidae	*Dicentrarchus labrax*	103	T	DM	1
Mullidae	*Mulloidichthys flavolineatus*	43	T	RA	2, 4
	Mulloihchthys martinicus	39.4	NT	RA	1
	Mullus barbatus	33.2	T	DM	1, 2, 3
	Mullus surmuletus	40	T	DM	1, 2, 3
	Upeneichthys lineatus	40	NT	DM	1
Muraenidae	*Gymnothorax prasinus*	91.5	NT	RA	3
	Muraena helena	150	T	RA	3
Myliobatidae	*Amblyraja (Raja) radiata*	105	T	DM	1
Odacidae	*Odax pullus*	40	NT	DM	1, 3
Ostraciidae	*Lactophrys triqueter*	47	NT	RA	1
Paralichthyidae	*Hippoglossina tetrophthalma*	36	NT	DM	1, 2
	Peristedion cataphractum	40	NT	DM	1, 2
Phycidae	*Phycis blennoides*	110	NT	BP	1, 2
	Urophycis chuss	66	T	DM	1, 2
Pinguipedidae	*Parapercis colias*	45	T	DM	1, 3
Pleuronectidae	*Hippoglossoides platessoides*	82.6	T	DM	1, 2
	Limanda ferruginea	64	T	DM	1, 2
	Pseudopleuronectes americanus	64	T	DM	1, 2
Pomacanthidae	*Holocanthus tricolor*	35	NT	RA	1
Pomacentridae	*Abudefduf saxatilis*	22.9	NT	RA	1
	Chromis chromis	25	NT	RA	1, 3

	Chromis multilineata	20	NA	RA	1
	Hypsypops rubicundus	30	NT	RA	1, 2, 3, 4
	Microspathodon chrysurus	21	NT	RA	1
	Parma alboscapularis	22	NT	RA	1
	Parma mccullochi	20	NT	RA	1, 3
	Stegastes fuscus	12.6	NA	DM	1
	Stegastes pictus	7.5	NA	DM	1
Rajidae	*Dipturus laevis*	152	NT	DM	1, 2
	Leucoraja erinacea	54	T	DM	1, 2
	Leucoraja ocellata	110	T	DM	1, 2
	Raja circularis	120	NT	DM	1, 2
	Raja clavata	105	NT	DM	1, 2
	Raja miraletus	63	NT	DM	1, 2
	Raja oxyrinchus	150	NT	DM	1, 2
Scaridae	*S. rubripinne*	47.8	NT	RA	1
	Scarus iserti	35	T	RA	1, 2
	Scarus taeniopterus	35	T	RA	1, 2
	Scarus trispinosus	35.5	T	RA	2
	Scarus vetula	61	T	RA	1, 2
	Sparisoma aurofrenatum	28	NT	RA	1, 2
	Sparisoma chrysopterum	46	T	RA	2
	Sparisoma cretense	50	T	RA	1, 2, 3, 4
	Sparisoma viride	64	T	RA	1, 2
Sciaenidae	*Sciaena umbra*	70	T	DM	1, 3, 4
Scophthalmidae	*Lepidorhombus boscii*	40	NT	DM	1, 2
	Lepidorhombus whiffjagonis	60	NT	DM	1, 2
	Scophthalmus aquosus	45.7	T	DM	1, 2
Scorpaenidae	*Scorpaena elongata*	50	NT	DM	1, 2
	Scorpaena scrofa	50	NT	DM	1, 2, 3
Scyliorhinidae	*Galeus melastomus*	75	NT	DM	1, 2
Scyliorhinidae	*Scyliorhinus canicula*	100	NT	DM	1, 2
Sebastidae	*Helicolenus dactylopterus dactylopterus*	45	T	DM	1, 2
Serranidae	*Anthias anthias*	27	NT	RA	3
	Cephalopholis cruentata	42.6	T	RA	2
	Cephalopholis fulva	41	T	RA	2
	Epinephelides armatus	56	T	RA	1, 2, 3,

					4
	Epinephelus costae	140	T	DM	3
	Epinephelus cruentatus	42.6	T	RA	1
	Epinephelus fulvus	41	T	RA	1
	Epinephelus marginatus	150	T	RA	1, 2, 3, 4
	Epinephelus merra	31	T	RA	2, 4
	Epinephelus striatus	122	T	RA	1, 2
	Mycteroperca boncai	150	T	RA	2
	Mycteroperca fusca	80	T	DM	1, 2, 3, 4
	Paralabrax clathratus	72	T	BP	1, 2, 3, 4
	Paralabrax nebulifer	67	T	RA	1, 2, 3
	Plectropomus leopardus	120	T	RA	1
	Serranus cabrilla	40	NT	RA	1, 2, 3
	Serranus hepatus	25	NT	DM	1, 2
	Serranus scriba	36	NT	DM	1, 3
Siganidae	*Siganus spinus*	28	T	RA	2, 4
Soleidae	*Microchirus ocellatus*	20	T	DM	1, 2
Sparidae	*Boops boops*	36	NT	DM	1, 2, 3
	Dentex dentex	100	T	BP	3
	Dentex macrophthalmus	65	NT	BP	1, 2
	Diplodus annularis	24	T	BP	1, 3
	Diplodus argenteus	37.8	NA	RA	1
	Diplodus cervinus cervinus	55	T	RA	1, 2, 3, 4
	Diplodus puntazzo	60	T	BP	1, 2, 3, 4
	Diplodus sargus	45	T	DM	1, 2, 3, 4
	Diplodus sargus cadenati	45	T	RA	1, 2, 3, 4
	Diplodus vulgaris	45	T	BP	1, 2, 3, 4
	Oblada melanura	34	NT	BP	1, 3
	Pagellus acarne	36	NT	BP	2
	Pagellus erythrinus	60	NT	BP	1, 2, 3
	Pagrus auratus	130	T	RA	1, 3
	Pagrus pagrus	91	T	RA	1
	Sarpa salpa	51	NT	BP	1, 3
	Sparus aurata	70	T	DM	1, 2, 4
	Spondyliosoma	60	T	BP	3

	cantharus				
Squalidae	*Squalus blainvillei*	100	NT	DM	1, 2
Tetraodontidae	*Sphoeroides pachygaster*	40.5	NT	BP	1, 2
Trachichthyidae	*Hoplostethus mediterraneus*	42	NT	BP	1, 2
Trachinidae	*Trachinus draco*	53	NT	DM	1, 2
Triakidae	*Mustelus mustelus*	200	NT	DM	1, 2
Trichiuridae	*Lepidopus caudatus*	210	NT	BP	1, 2
Triglidae	*Aspitrigla cuculus*	50	NT	DM	1, 2
	Lepidotrigla cavillone	20	NT	DM	1, 2
	Trigla lyra	60	NT	DM	1, 2
Tripterygiidae	*Tripterygion delaisi*	8.9	NT	DM	3
	Tripterygion tripteronotus	8	NT	DM	3
Uranoscopidae	*Uranoscopus scaber*	40	NT	DM	1, 2
Zeidae	*Zeus faber*	90	NT	BP	1, 2
Zoarcidae	*Zoarces americanus*	110	NT	DM	1, 2

Appendix 3.6.2 Mixed-effects analyses using (i) all the studies (Full analysis) and (ii) excluding those studies with a reported significant difference in habitat characteristics between the protected and the control area (Sensitivity analysis).

A. Dataset 1: Evaluating the effect of partially protected areas relative to open access areas using density estimates for fish species

Full analysis: The structure of the final model was: Response ratio ~ $\log(L_{max})$ x $\log$(PPA size), random = ~1| MPA ID.

Variable	Estimate	SE	df	t-val	p-val
Intercept	0.50	0.13	178	4.10	**0.0001**
Log(PPA size)	-0.12	0.09	20	-1.25	0.22
Log(L_{max})	-0.44	0.35	178	-1.25	0.21
PPA size x L_{max}	-0.62	0.23	178	-2.66	**0.009**

Sensitivity analysis: The structure of the final model was: Response ratio ~ $\log(L_{max})$ x $\log$(PPA size), random = ~1| MPA ID.

Variable	Estimate	SE	df	t-val	p-val
Intercept	0.45	0.13	174	3.61	**0.0004**
Log(PPA size)	-0.10	0.09	18	-1.05	0.31
Log(L_{max})	-0.29	0.35	174	-0.83	0.41
PPA size x L_{max}	-0.53	0.24	174	-2.23	**0.03**

B. Dataset 2: Evaluating the effect of partially protected areas relative to open access areas using biomass estimates for fish species

Full analysis: The structure of the final model was: Response ratio ~ Exploitation status x Adult habitat type, random = ~1| MPA ID.

Variable	Estimate	SE	df	t-val	p-val
Intercept	-0.27	0.44	120	-0.61	0.54
ES: target species	1.67	0.75	120	2.23	**0.03**
Env: demersal species	0.60	0.48	120	1.25	0.21
Env: reef-associated species	1.40	0.79	120	1.76	0.08
ES_target x Env_demersal	-1.94	0.82	120	-2.36	**0.02**

ES_target x Env_reef-associated	-2.67	1.03	120	-2.59	**0.02**

Sensitivity analysis: The structure of the final model was: Response ratio ~ log(L_{max}) + Exploitation status x Adult habitat type, random = ~1| MPA ID.

Variable	Estimate	SE	df	t-val	p-val
Intercept	1.51	1.01	102	1.49	0.14
L_{max}	-1.04	0.54	102	-1.92	**0.05**
ES: target species	1.81	0.75	102	2.40	0.02
Env: demersal species	0.70	0.49	102	1.42	0.16
Env: reef-associated species	1.31	0.80	102	1.65	0.10
ES_target x Env_demersal	-2.02	0.83	102	-2.45	**0.02**
ES_target x Env_reef-associated	-2.35	1.05	102	-2.24	**0.03**

C. Dataset 3: Evaluating the effect of no-take reserves relative to partially protected areas using density estimates for fish species

Full analysis: The structure of the final model was: Response ratio ~ log(L_{max}) + Adult habitat type + Exploitation status x log(NTR size) + Exploitation status x Age, random = ~1| MPA ID.

Variable	Slope	SE	df	t-val	p-val
Intercept	0.57	0.89	96	0.64	0.52
Age	-0.15	0.05	9	-2.92	0.02
NTR size	-1.39	0.48	9	-2.88	0.02
L_{max}	0.91	0.35	96	2.59	**0.01**
ES: target species	-2.24	0.99	96	-2.25	0.03
Env: demersal species	0.47	0.23	96	2.03	**0.05**
Env: reef-associated species	0.63	0.22	96	2.80	**0.01**
ES_target x NTR size	1.53	0.58	96	2.63	**0.01**
ES_target x Age	0.14	0.06	96	2.20	**0.03**

Sensitivity analysis: The structure of the final model was: Response ratio ~ $\log(L_{max})$ + Adult habitat type + Exploitation status x log(NTR size) + Exploitation status x Age, random = ~1| MPA ID.

Variable	Slope	SE	df	t-val	p-val
Intercept	0.92	1.01	91	0.91	0.36
Age	-0.16	0.06	8	-2.68	0.03
NTR size	-1.48	0.58	8	-2.58	0.03
L_{max}	0.78	0.35	91	2.25	**0.03**
ES: target species	-2.44	1.13	91	-2.15	0.03
Env: demersal species	0.48	0.23	91	2.13	**0.04**
Env: reef-associated species	0.64	0.22	91	2.96	**0.004**
ES_target x NTR size	1.65	0.67	91	2.45	**0.02**
ES_target x Age	0.16	0.07	91	2.21	**0.03**

D. Dataset 4: Evaluating the effect of no-take reserves relative to partially protected areas using biomass estimates for fish species

There were no 'habitat-confounded' studies, therefore only the full analysis was carried out on this dataset.

APPENDICES FOR CHAPTER 4

Appendix 4.6.1. Spatial distribution and frequency of scallop dredging throughout sampling period (December 2009 – April 2011)

The spatial distribution and frequency of scallop dredging activity over the Cardigan Bay fishing ground was derived using the VMS data provided by the Marine Management Organization for the periods; November 2008 to May 2009 that covers the open fishing season prior to our December 2009 survey, March to May 2010 prior to our June 2010 survey, November to December 2010 prior to December 2010 survey and November 2010 to April 2011 prior to our April 2011 survey. We defined **fishing frequency as the number of hours an area of 1 km^2 was fished in 1 month**. The sum of the number of hours fished (calculated as the time interval between two consecutive records) in each 1 km^2 cell was calculated in ArcGIS 9.3, giving a relative estimate of fishing frequency per month during the open scallop dredging seasons. Fishing frequency ranged from 0 to 30 hours km^{-2} month^{-1} for the 2 month open season between November and December 2010, and from 0 to 15 hours km^{-2} month^{-1} for the other open seasons. The change in the spatial distribution of fishing activity is notable for the open season before and those after 2009 (i.e. before and after the establishment of a permanent closed area for scallop dredging in 75% of the SAC); all the offshore sampling stations in our study (i.e. those beyond 3 nm) were dredged at some point.

Fishing frequency for the scallop dredging open season November 2008 to May 2009
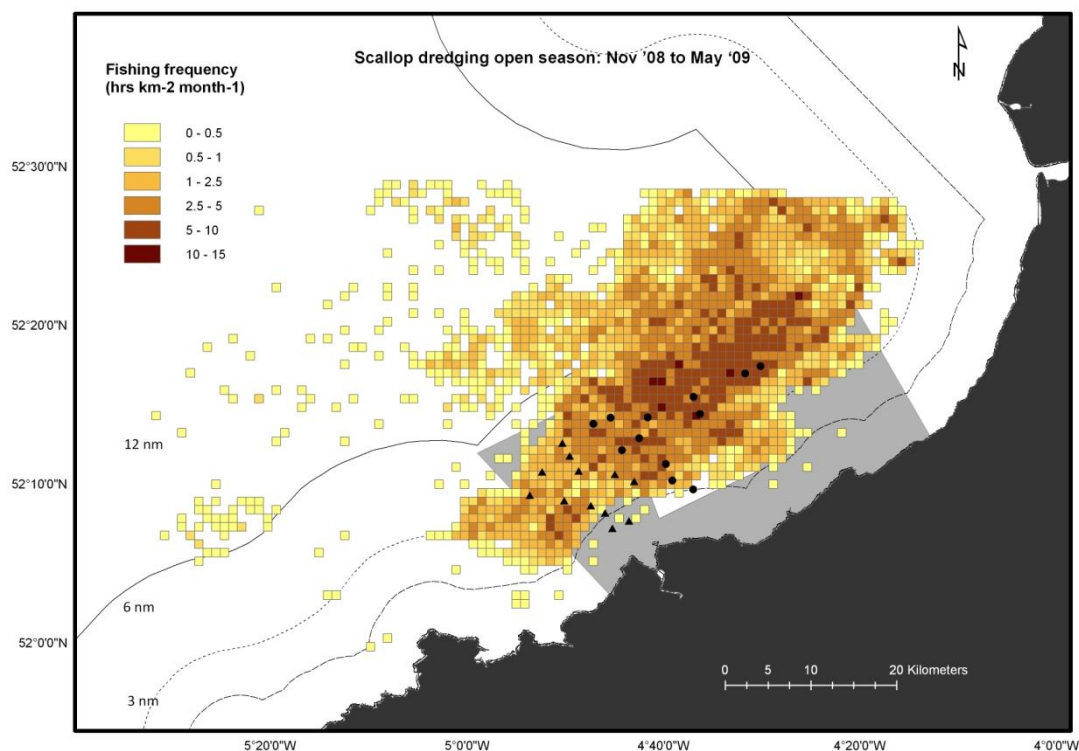
Fishing frequency for the scallop dredging open season March to May 2010
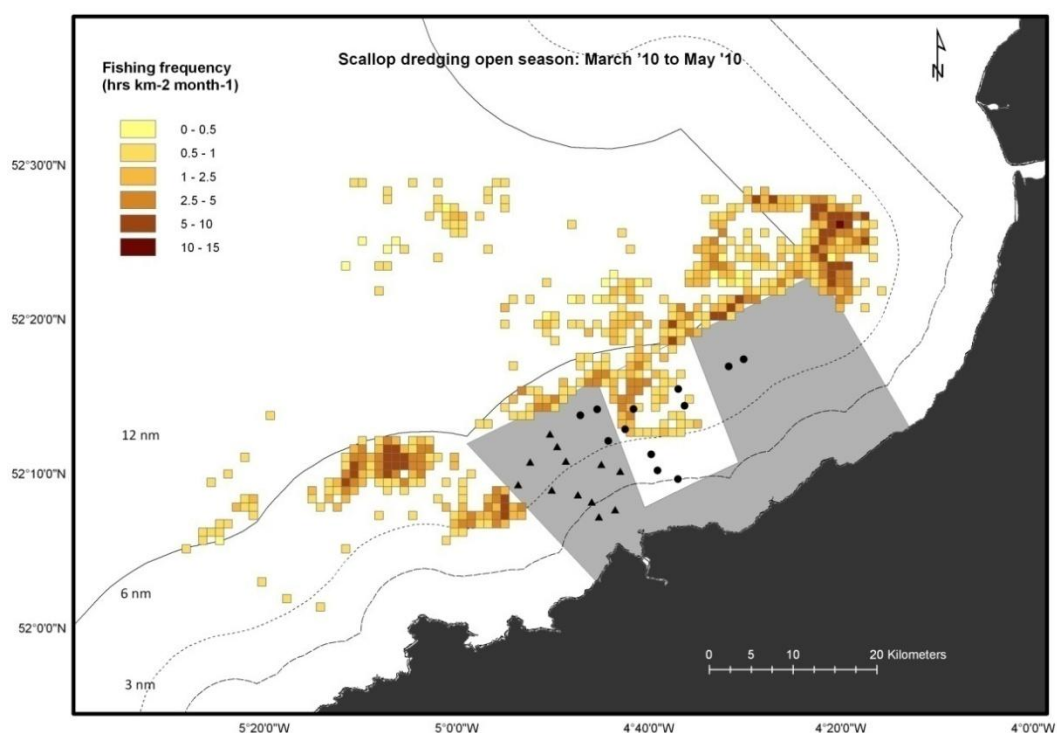
Fishing frequency for the scallop dredging open season November to December 2010
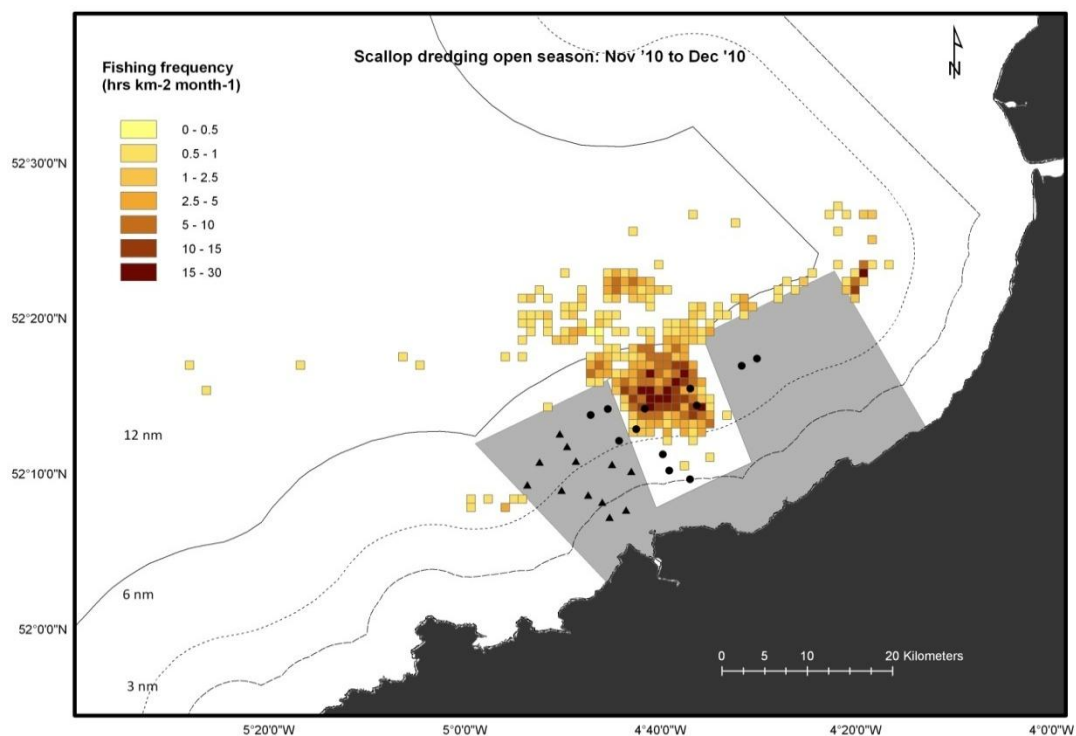
Fishing frequency for the scallop dredging open season November 2010 to April 2011
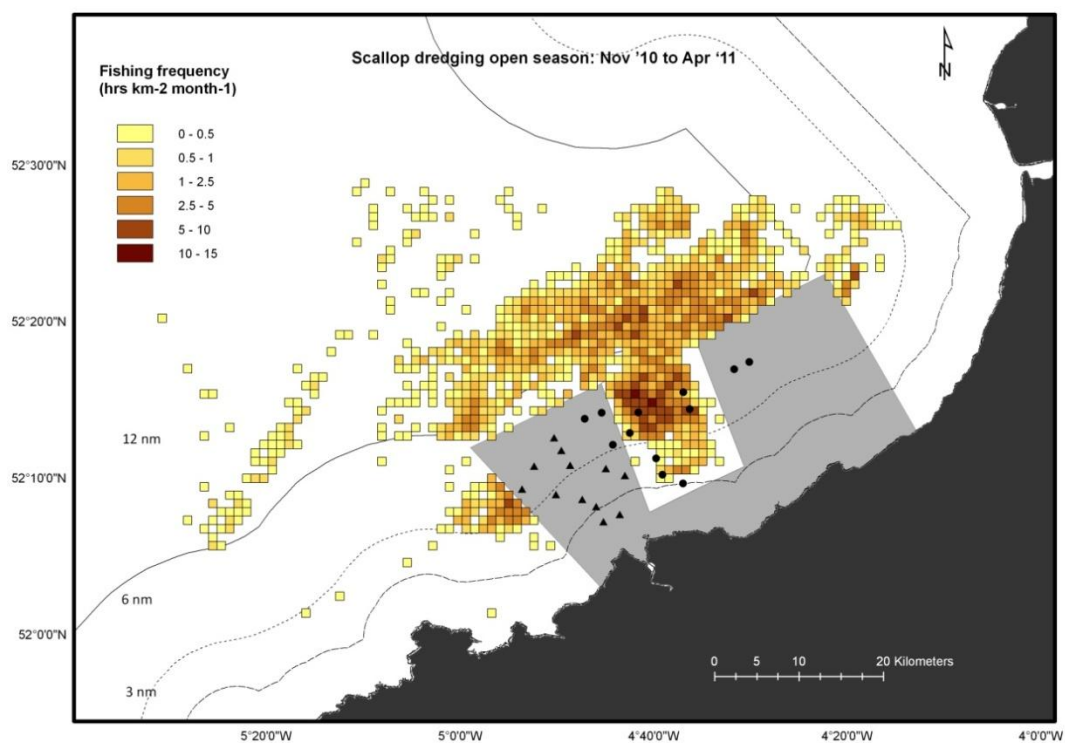
Appendix 4.6.2. Additional side scan sonar data

Side scan sonar mosaics showing the same area of the seabed from the December 2009 survey (left) and the June 2010 survey (right). The outer edges of both sonar tracks are shown to illustrate the common seabed area covered (blue: Dec '09, red: Jun '10). The asterisks show the location of a station from the photographic survey which aids correlation between the two data sets which are at the same scale and orientation. Features highlighting changes in seabed morphology between surveys are marked in green.
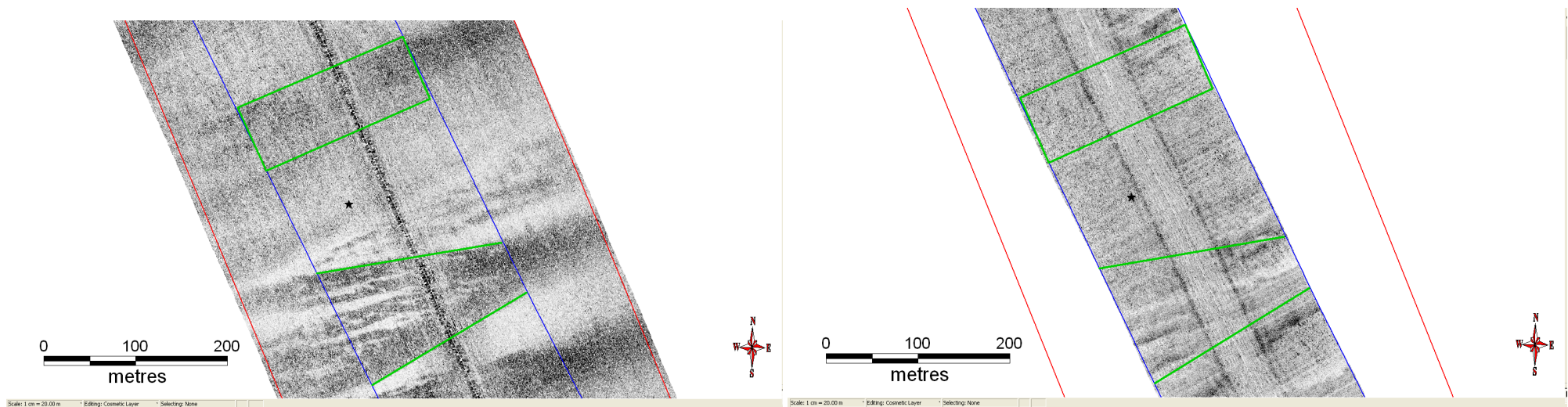
Plate I. A sand ribbon dominated environment characterized by coarser sediment in the December 2009 survey, which changes into a finer sediment environment in the June 2010 survey.
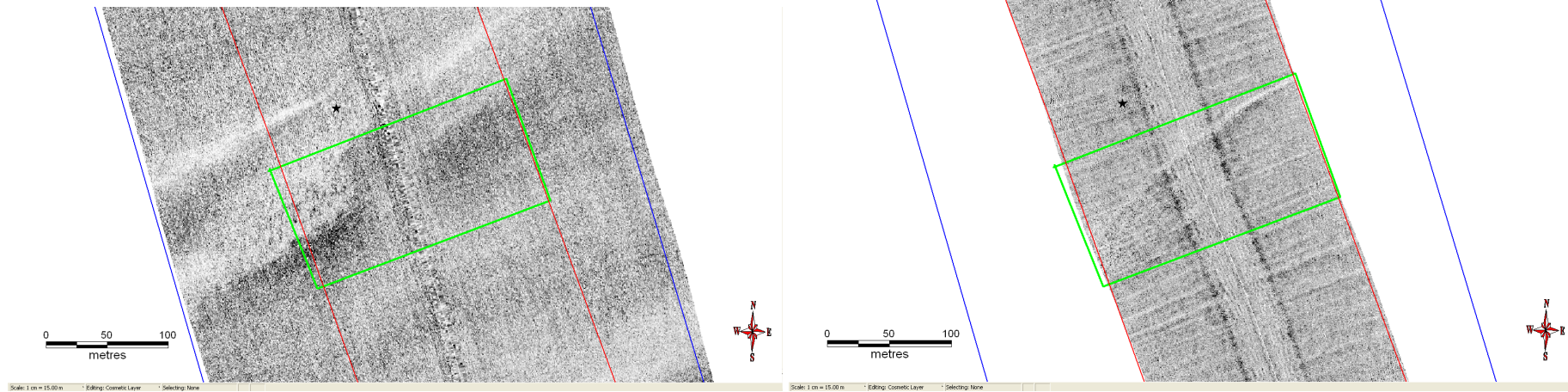
Plate II. Area characterized by large sand ribbons in the December 2009 survey which appear to change into smaller and more closely spaced sand ribbons in the June 2010 survey.
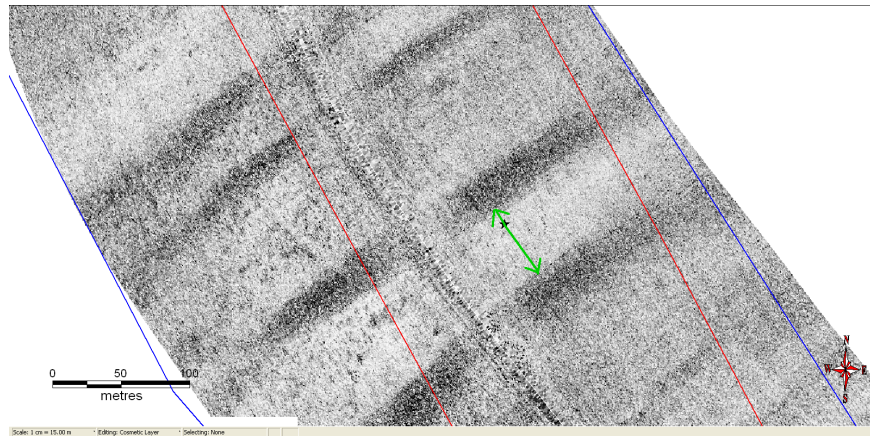
Plate III. In both surveys the environment is characterized by sand ribbons covering coarser substrate. However, as indicated by the arrows the position of the ribbons changed between the 2 surveys.

APPENDICES FOR CHAPTER 5

Appendix 5.1: Port Erin closed area

A. Asymmetric ANOVA using percentage cover data for sessile colonial or encrusting taxonomic groups that contributed to more than 5% of the overall percentage cover at Port Erin closed area case-study. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) Total epifauna % cover (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	123.31	3	41.11	5.62	0.01
PE vs. control contrast	78.48	1		10.73	< 0.001
Among controls contrast	44.84	2	22.42	2.31	0.14

(ii) Polychaeta (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.31	3	0.10	5.12	0.01
PE vs. control contrast	0.23	1		11.40	< 0.001
Among controls contrast	0.08	2	0.04	1.74	0.22

(iii) Hydrozoa (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	177.25	3	59.08	24.18	< 0.001
PE vs. control contrast	98.05	1		40.12	< 0.001
Among controls contrast	79.20	2	39.60	16.59	< 0.001

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	5.46	< 0.001
C1 vs. C3	3.93	0.004
C2 vs. C3	-1.53	0.30

(iv) Bryozoa (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	105.23	3	35.08	15.48	< 0.001
PE vs. control contrast	102.13	1		45.08	< 0.001
Among controls contrast	3.10	2	1.55	1.20	0.33

B. Asymmetric ANOVA using density data (indvs. m^{-2}) for sessile solitary and mobile taxonomic groups that contributed to more than 5% of the overall percentage cover at Port Erin closed area case-study. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) Anthozoa (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	2.30	3	0.77	4.03	0.03
PE vs. control contrast	1.70	1		8.94	0.01
Among controls contrast	0.60	2	0.30	2.78	0.10

(ii) Ascidiacea (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	1551.68	3	517.23	1.02	0.41
PE vs. control contrast	371.56	1		0.73	0.41
Among controls contrast	1180.12	2	590.06	0.90	0.43

(iii) Bivalvia (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	4.12	3	1.37	29.13	< 0.001
PE vs. control contrast	0.59	1		12.47	< 0.001
Among controls contrast	3.53	2	1.77	29.25	< 0.001

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	0.64	0.004
C1 vs. C3	1.19	< 0.001
C2 vs. C3	0.55	0.01

(iv) Gastropoda (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	196.98	3	65.66	8.29	< 0.001
PE vs. control contrast	35.45	1		4.47	0.05
Among controls contrast	161.53	2	80.77	10.52	< 0.001

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	7.19	0.004
C1 vs. C3	6.71	0.006
C2 vs. C3	-0.48	0.96

(v) Ophiuroidea (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.95	3	0.32	3.14	0.05
PE vs. control contrast	0.05	1		0.53	0.48
Among controls contrast	0.90	2	0.45	3.70	0.06

(vi) *Pecten maximus* (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.19	3	0.40	3.04	0.06
PE vs. control contrast	1.15	1		8.78	0.01
Among controls contrast	0.04	2	0.02	0.20	0.82

(vii) *Aequipecten opercularis* (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.961	3	.654	33.659	< 0.001
PE vs. control contrast	0.70	1		35.82	< 0.001
Among controls contrast	1.265	2	.633	24.747	< 0.001

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	0.23	0.1
C1 vs. C3	0.70	< 0.001
C2 vs. C3	0.47	0.002

(viii) *Palliolum* spp. (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	4.66	3	1.55	34.15	< 0.001
PE vs. control contrast	0.84	1		18.39	< 0.001
Among controls contrast	3.83	2	1.91	32.20	< 0.001

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	0.86	< 0.001
C1 vs. C3	1.20	< 0.001
C2 vs. C3	0.34	0.11

C. Asymmetric ANOVA using percentage cover data for different functional groups at Port Erin closed area case-study. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) FCrNs - free-living, crawler non-shelled (e.g. decapods, asteroids, ophiuroids, nudibranchs) (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	16.59	3	5.53	1.58	0.23
PE vs. control contrast	1.48	1		0.42	0.53
Among controls contrast	15.11	2	7.56	1.63	0.24

(ii) FCrS - free-living crawler shelled (e.g. decapods, bivalves, gastropods) (Arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	64.74	3	21.58	14.06	< 0.001
PE vs. control contrast	0.00	1		0.00	0.97
Among controls contrast	64.74	2	32.37	17.57	< 0.001

(iii) ASb - attached, soft-bodied (e.g. ascidians, sea anemones) (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	4.62	3	1.54	1.67	0.21
PE vs. control contrast	1.05	1		1.14	0.30
Among controls contrast	3.57	2	1.78	1.50	0.26

(iv) AEnTf - attached, encrusting or turf-forming (e.g. bryozoan, sponges, hydroid turf) (Arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	114.21	3	38.07	12.38	< 0.001
PE vs. control contrast	58.25	1		18.94	< 0.001
Among controls contrast	55.96	2	27.98	10.84	0.002

(v) **AErFo - attached, erect or foliose (e.g. polychaetes, bryozoa, hydroids) (Arcsine transformation)**

Source of variation	SS	df	MS	F	p-value
Station	140.78	3	46.93	18.07	< 0.001
PE vs. control contrast	131.22	1		50.52	< 0.001
Among controls contrast	9.56	2	4.78	2.79	0.10

(vi) **FSw - free-living, swimmer (e.g. bivalve, shrimp)**

Source of variation	SS	df	MS	F	p-value
Station	0.71	3	0.24	5.83	0.01
PE vs. control contrast	0.25	1		6.32	0.02
Among controls contrast	0.45	2	0.23	5.74	0.02

Appendix 5.2: Skomer Marine Nature Reserve

A. Asymmetric ANOVA using percentage cover data for sessile colonial or encrusting taxonomic groups that contributed to more than 5% of the overall percentage cover at Skomer Marine Nature Reserve. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) **Total epifauna % cover (arcsine transformation)**

Source of variation	SS	df	MS	F	p-value
Station	0.92	3	0.31	5.57	0.01
MPA1 vs. control contrast	0.02	1		0.28	0.61
Among controls contrast	0.91	2	0.45	6.63	0.01
Station	0.98	3	0.33	6.02	0.01
MPA2 vs. control contrast	0.08	1		1.43	0.25
Among controls contrast	0.91	2	0.45	6.63	0.01

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	0.58	0.01
C1 vs. C3	0.44	0.05

C2 vs. C3	-0.14	0.68

(ii)   Polychaeta (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.11	3	0.04	1.73	0.20
MPA1 vs. control contrast	0.06	1		2.92	0.11
Among controls contrast	0.05	2	0.02	0.87	0.44
Station	0.14	3	0.05	1.29	0.31
MPA2 vs. control contrast	0.09	1		2.49	0.13
Among controls contrast	0.05	2	0.02	0.87	0.44

(iii) Bryozoa (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.11	3	0.04	0.67	0.58
MPA1 vs. control contrast	0.00	1		0.08	0.78
Among controls contrast	0.10	2	0.05	1.18	0.34
Station	0.12	3	0.04	1.09	0.38
MPA2 vs. control contrast	0.01	1		0.31	0.59
Among controls contrast	0.10	2	0.05	1.18	0.34

(iv) Hydrozoa (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.32	3	0.44	6.37	0.00
MPA1 vs. control contrast	0.03	1		0.50	0.49
Among controls contrast	1.29	2	0.64	7.58	0.01
Station	1.85	3	0.62	9.37	0.00
MPA2 vs. control contrast	0.56	1		8.51	0.01
Among controls contrast	1.29	2	0.64	7.58	0.01

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	0.70	0.006
C1 vs. C3	0.47	0.06
C2 vs. C3	-0.23	0.44

(v) Porifera (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.89	3	0.30	11.14	0.00
MPA1 vs. control contrast	0.03	1		0.95	0.34
Among controls contrast	0.86	2	0.43	12.64	0.00
Station	0.87	3	0.29	8.03	0.00
MPA2 vs. control contrast	0.01	1		0.22	0.65
Among controls contrast	0.86	2	0.43	12.64	0.00

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	0.58	0.001
C1 vs. C3	0.34	0.03
C2 vs. C3	-0.24	0.13

B. Asymmetric ANOVA using density data (indvs. m^{-2}) for sessile solitary and mobile taxonomic groups that contributed to more than 5% of the overall percentage cover at Skomer Marine Nature Reserve. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) Anthozoa (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.45	3	0.48	3.91	0.03
MPA1 vs. control contrast	0.49	1		3.96	0.06
Among controls contrast	0.96	2	0.48	5.35	0.02
Station	0.98	3	0.33	3.71	0.03

	SS	df	MS	F	p-value
MPA2 vs. control contrast	0.02	1		0.25	0.63
Among controls contrast	0.96	2	0.48	5.35	0.02

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	0.52	0.04
C1 vs. C3	0.55	0.03
C2 vs. C3	0.03	0.99

(ii) Malacostraca (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.61	3	0.54	0.32	0.81
MPA1 vs. control contrast	1.42	1		0.84	0.37
Among controls contrast	0.19	2	0.09	0.06	0.94
Station	12.56	3	4.19	2.91	0.07
MPA2 vs. control contrast	12.37	1		8.60	0.01
Among controls contrast	0.19	2	0.09	0.06	0.94

(iii) Ascidiacea (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	3.55	3	1.18	9.95	0.00
MPA1 vs. control contrast	0.01	1		0.10	0.75
Among controls contrast	3.54	2	1.77	15.45	0.00
Station	4.00	3	1.33	14.40	0.00
MPA2 vs. control contrast	0.46	1		4.99	0.04
Among controls contrast	3.54	2	1.77	15.45	0.00

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	1.18	< 0.001
C1 vs. C3	0.71	0.02
C2 vs. C3	-0.47	0.11

(iv) Ophiuroidea (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	2.10	3	0.70	5.72	0.01
MPA1 vs. control contrast	0.00	1		0.00	0.99
Among controls contrast	2.10	2	1.05	19.08	0.00
Station	4.32	3	1.44	18.12	0.00
MPA2 vs. control contrast	2.22	1		27.94	0.00
Among controls contrast	2.10	2	1.05	19.08	0.00

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	-0.61	0.004
C1 vs. C3	0.28	0.18
C2 vs. C3	0.89	< 0.001

(v) Gastropoda (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.04	3	0.35	4.75	0.01
MPA1 vs. control contrast	0.65	1		8.92	0.01
Among controls contrast	0.39	2	0.19	2.26	0.15
Station	0.54	3	0.18	1.57	0.24
MPA2 vs. control contrast	0.15	1		1.29	0.27
Among controls contrast	0.39	2	0.19	2.26	0.15

(vi) Bivalvia (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.08	3	0.36	28.11	0.00
MPA1 vs. control contrast	0.58	1		45.49	0.00
Among controls contrast	0.50	2	0.25	17.54	0.00
Station	0.52	3	0.17	15.85	0.00
MPA2 vs. control contrast	0.03	1		2.60	0.13

Among controls contrast	0.50	2	0.25	17.54	0.00

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	-0.36	0.001
C1 vs. C3	0.05	0.79
C2 vs. C3	0.41	< 0.001

(vii) *Pecten maximus* (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	2.24	3	0.75	21.57	0.00
MPA1 vs. control contrast	2.12	1		61.09	0.00
Among controls contrast	0.13	2	0.06	5.19	0.02
Station	1.18	3	0.39	26.80	0.00
MPA2 vs. control contrast	1.06	1		71.88	0.00
Among controls contrast	0.13	2	0.06	5.19	0.02

Tukey HSD posthoc test	Mean difference	p-value
C1 vs. C2	-0.19	0.04
C1 vs. C3	0	1.00
C2 vs. C3	0.19	0.04

(viii) *Aequipecten opercularis* (log(x+1) transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.41	3	0.14	13.59	0.00
MPA1 vs. control contrast	0.00	1		0.21	0.66
Among controls contrast	0.40	2	0.20	16.33	0.00
Station	0.43	3	0.14	12.40	0.00
MPA2 vs. control contrast	0.03	1		2.26	0.15
Among controls contrast	0.40	2	0.20	16.33	0.00

Tukey HSD posthoc test	Mean difference	p-value

C1 vs. C2	-0.33	0.002
C1 vs. C3	0.04	0.84
C2 vs. C3	0.37	0.001

C. Asymmetric ANOVA using percentage cover data for different functional groups at Skomer Marine Nature Reserve. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) FCrNs - free-living, crawler non-shelled (e.g. decapods, asteroids, ophiuroids, nudibranchs) (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.08	3	0.03	1.49	0.25
MPA1 vs. control contrast	0.00	1		0.28	0.61
Among controls contrast	0.07	2	0.04	5.79	0.02
Station	0.32	3	0.11	5.16	0.01
MPA2 vs. control contrast	0.25	1		11.89	< 0.001
Among controls contrast	0.07	2	0.04	5.79	0.02

(ii) FCrS - free-living crawler shelled (e.g. decapods, bivalves, gastropods) (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	2.05	3	0.69	2.43	0.10
MPA1 vs. control contrast	1.20	1		4.27	0.06
Among controls contrast	0.85	2	0.43	1.52	0.26
Station	0.89	3	0.30	1.15	0.36
MPA2 vs. control contrast	0.04	1		0.16	0.70
Among controls contrast	0.85	2	0.43	1.52	0.26

(iii) ASb - attached, soft-bodied (e.g. ascidians, sea anemones) (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.37	3	0.12	9.02	0.001
MPA1 vs. control contrast	0.01	1		0.77	0.39
Among controls contrast	0.36	2	0.18	10.78	0.002
Station	0.42	3	0.14	10.43	< 0.001
MPA2 vs. control contrast	0.06	1		4.50	0.05
Among controls contrast	0.36	2	0.18	10.78	0.002

(iv) AEnTf - attached, encrusting or turf-forming (e.g. bryozoan, sponges, hydroid turf) (Arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.43	3	0.48	6.63	0.004
MPA1 vs. control contrast	0.00	1		0.06	0.81
Among controls contrast	1.43	2	0.71	8.38	0.005
Station	1.80	3	0.60	8.85	0.001
MPA2 vs. control contrast	0.38	1		5.54	0.03
Among controls contrast	1.43	2	0.71	8.38	0.005

(v) AErFo - attached, erect or foliose (e.g. polychaetes, bryozoa, hydroids) (no transformation)

Source of variation	SS	df	MS	F	p-value
Station	1.15	3	0.38	0.48	0.70
MPA1 vs. control contrast	1.01	1		1.27	0.28
Among controls contrast	0.14	2	0.07	0.07	0.94
Station	0.97	3	0.32	0.27	0.85
MPA2 vs. control contrast	0.83	1		0.70	0.42
Among controls contrast	0.14	2	0.07	0.07	0.94

(vi) FSw - free-living, swimmer (e.g. bivalve, shrimp) (arcsine transformation)

Source of variation	SS	df	MS	F	p-value
Station	0.12	3	0.04	46.31	< 0.001
MPA1 vs. control contrast	0.09	1		102.22	< 0.001
Among controls contrast	0.03	2	0.02	20.55	< 0.001
Station	0.07	3	0.02	14.39	< 0.001
MPA2 vs. control contrast	0.04	1		24.49	< 0.001
Among controls contrast	0.03	2	0.02	20.55	< 0.001

Appendix 5.3: *Modiolus* **Box, Llyn Peninsula**

A. Nested ANOVA using percentage cover data for sessile colonial or encrusting taxonomic groups that contributed to more than 5% of the overall percentage cover at the *Modiolus* Box, Llyn Peninsula. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) Total epifauna % cover (arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	962.3	962.3	22.19	< 0.001
Station(Protection)	2	32.6	16.3	0.38	0.69
Residuals	16	693.8	43.4		

(ii) Polychaeta (arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	0.01	0.01	0.02	0.90
Station(Protection)	2	2.47	1.23	2.41	0.12
Residuals	16	8.18	0.51		

(iii) Bryozoa (arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	489.8	489.8	46.71	< 0.001

Station(Protection)	2	92.1	46.1	4.39	0.03
Residuals	16	167.8	10.5		

(iv) Hydrozoa (arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	156.3	156.3	26.36	< 0.001
Station(Protection)	2	131.37	65.68	11.07	< 0.001
Residuals	16	94.89	5.93		

(v) Porifera (arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	14.10	14.10	7.27	0.02
Station(Protection)	2	20.09	10.05	5.19	0.02
Residuals	16	31	1.94		

B. Nested ANOVA using density data (indvs. m^{-2}) for sessile solitary and mobile taxonomic groups that contributed to more than 5% of the overall percentage cover at the *Modiolus* Box, Llyn Peninsula. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i)　Anthozoa (log(x+1) transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	0.03	0.03	0.29	0.60
Station(Protection)	2	0.41	0.21	2.35	0.13
Residuals	15	1.32	0.09		

(ii) Ascidiacea (log(x+1) transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	2.05	2.05	46.02	< 0.001
Station(Protection)	2	0.27	0.14	3.09	0.08

Residuals	15	0.67	0.04		

(iii) Malacostraca (log(x+1) transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	0.61	0.61	37.93	< 0.001
Station(Protection)	2	0.01	0.004	0.26	0.77
Residuals	15	0.24	0.02		

(iv) Asteroidea (no transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	0.21	0.21	2.73	0.12
Station(Protection)	2	0.50	0.25	3.28	0.07
Residuals	15	1.16	0.08		

(v) Ophiuroidea (log(x+1) transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	0.01	0.01	0.03	0.86
Station(Protection)	2	0.30	0.15	0.37	0.69
Residuals	15	6.19	0.41		

(vi) Bivalvia (log(x+1) transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	0.15	0.15	7.16	0.02
Station(Protection)	2	0.05	0.02	1.14	0.35
Residuals	15	0.32	0.02		

(vii) Gastropoda (no transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	51.23	51.23	41.64	< 0.001

Station(Protection)	2	17.67	8.84	7.18	0.01
Residuals	15	18.46	1.23		

(viii) *Aequipecten opercularis* (log(x+1) transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	0.11	0.11	9.13	0.01
Station(Protection)	2	0.01	0.004	0.38	0.69
Residuals	15	0.18	0.01		

(ix) *Pecten maximus* (log(x+1) transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	< 0.001	< 0.001	0.04	0.85
Station(Protection)	2	0.01	0.003	1.37	0.29
Residuals	15	0.04	0.002		

C. Asymmetric ANOVA using percentage cover data for different functional groups at the *Modiolus* Box, Llyn Peninsula. Results from Tukey HSD multiple comparison test are given when the term 'Among controls contrast' indicated significant differences.

(i) FCrNs - free-living, crawler non-shelled (e.g. decapods, asteroids, ophiuroids, nudibranchs) (no transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	321.8	321.8	3.69	0.07
Station(Protection)	2	106.7	53.4	0.61	0.55
Residuals	15	1396.9	87.3		

(ii) FCrS - free-living crawler shelled (e.g. decapods, bivalves, gastropods) (Arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	24.73	24.73	30.84	< 0.001

Station(Protection)	2	7.53	3.77	4.70	0.02
Residuals	15	12.83	0.80		

(iii)   ASb - attached, soft-bodied (e.g. ascidians, sea anemones) (no transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	6.41	6.41	0.76	0.40
Station(Protection)	2	54.21	27.10	3.21	0.07
Residuals	15	135.31	8.46		

(iv)   AEnTf - attached, encrusting or turf-forming (e.g. bryozoan, sponges, hydroid turf) (Arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	175.11	175.11	32.08	< 0.001
Station(Protection)	2	114.89	57.44	10.52	0.001
Residuals	15	87.33	5.46		

(v)   AErFo - attached, erect or foliose (e.g. polychaetes, bryozoa, hydroids) (Arcsine transformation)

Source of variation	df	SS	MS	F	p-value
Protection	1	429.9	429.9	41.4	< 0.001
Station(Protection)	2	82.3	41.1	3.96	0.04
Residuals	15	166.2	10.4		

(vi)   FSw - free-living, swimmer (e.g. bivalve, shrimp)

Source of variation	df	SS	MS	F	p-value
Protection	1	2.77	2.77	0.88	0.36
Station(Protection)	2	0.72	0.36	0.11	0.89
Residuals	15	50.59	3.16		