



Taxonomic and functional recovery of epifauna after the permanent closure of an area of the Cardigan Bay Special Area of Conservation (SAC), Wales, to a scallop dredge fishery.



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Abstract

In 2009 75% of the area of Cardigan Bay Special Area of Conservation (SAC) was closed to scallop dredging due to concerns over the rapid growth of the scallop fishery and the destructive potential of this fishing practice. The remaining 25% of the SAC remained seasonally open. Previous studies undertaken over a 22 month period since the introduction of the closed area have not detected signs of recovery in the SAC. However, it has been suggested that more time may be required for signs of recovery to become apparent. This study builds on that of Sciberras et al. (2013), extending the time since the introduction of the closed area to 40 months. An analysis of functional traits, which provide information on the vulnerability or robustness of epifaunal communities, is also included for the first time. Hypotheses which predict that the closed area benefits taxonomic and functional measures of the epifaunal community are tested. Sampling was conducted using a towed camera sledge which took photographs of the seabed, from which epifauna were identified. “Fuzzy-coding” was used to quantify the association of epifaunal communities with a selection of functional traits. Analysis using statistical methods such as PERMANOVA and CAP found there to be no significant effect of the closed area on taxonomic or functional measures of the epifaunal communities. This result was attributed to relatively high levels of background disturbance in the SAC caused by mobile sand wave seabed features, and the ability of epifaunal communities in the SAC to recover quickly through the recruitment of organisms with traits such as broadcast spawning and dispersal by planktonic larvae. When benthic communities have rapid recovery rates, permanent spatial closures to fisheries (for conservation or fisheries management) may not be necessary when less strict seasonal closures could provide adequate protection.

Table of contents

Table of contents.....	4
1 Introduction.....	1
1.1 Impact of bottom fishing on the seabed	1
1.2 Mechanisms of recovery	2
1.3 Variation in response to and recovery from fishing disturbance	3
1.4 Marine protected areas	5
1.5 Background of the Cardigan Bay Special Area of Conservation.....	5
2 Methods.....	7
2.1 Study site	7
2.2 Sampling design	8
2.3 Image analysis	12
2.3.1 Seabed habitat type	12
2.3.2 Density of epifaunal species	12
2.4 Functional traits and fuzzy coding	12
2.5 Statistical analysis	15
2.5.1 Multivariate analysis of spatial and temporal change in the SAC.....	15
2.5.1.1 Habitat type.....	15
2.5.1.2 Community composition.....	16
2.5.2 Univariate analysis of spatial and temporal change in the SAC.....	16
3 Results.....	17
3.1 Spatial patterns in habitat type	17
3.2 Spatial and temporal trends in multivariate and univariate measures of epifauna.....	17
3.2.1 (H1) Spatial and temporal patterns in taxonomic community composition.....	17
3.2.2 (H2) Spatial and temporal patterns in functional community composition.....	21
3.2.3 (H3) Spatial and temporal trends in univariate species community metrics	25
3.2.4 (H4) Spatial and temporal trends in fishing sensitive traits.....	28

3.2.5 (H5) Spatial and temporal trends in the diversity of functional traits	36
4 Discussion	37
5 Acknowledgments.....	42
6 References.....	42
7 Appendix 1: R scripts.....	46
7.1 Multivariate analysis of taxonomic composition	46
7.2 Multivariate analysis of functional composition.....	52
7.3 Univariate analysis of taxonomic measures	61
7.4 Univariate analysis of fishing sensitive trait modalities.....	65
7.5 Univariate analysis of trait diversity	71

List of figures

- Figure 1. An example of a scallop dredge viewed from above (top) and from the front (bottom). Key components of the dredge are labelled (after O'Neill et al. 2013).2
- Figure 2. Map showing the location of the Cardigan Bay Special Area of Conservation (SAC) and ICES rectangle 33E5 in Wales (top left). Also shown are maps of the location of sampling stations (in both the open and closed areas) in each of the five surveys undertaken between December 2009 and October 2012. 10
- Figure 3. Ordination plot showing the first two canonical axes for the canonical analysis of principle coordinates (CAP) on square-root transformed epifaunal species density data and Bray-Curtis dissimilarity..... 19
- Figure 4. Biplot showing individual species with an absolute Pearson correlation of $|r| \geq 0.30$ between species and canonical axes on at least one of the first two canonical axes. Abbreviated species names are; *Cellepora pumicosa*, *Epizoanthus couchii*, *Tubularia indivisa*, *Cerianthus lloydii*, *Mesacmaea mitchellii*, *Ophiura albida*, *Nemertesia ramose*, *Alcyonium digitatum*, *Hydrallmania falcate*, and *Nemertesia antennina*.....20
- Figure 5. Ordination plot showing the first two canonical axes for the canonical analysis of principle coordinates (CAP) on square-root transformed density weighted trait modality value data and Bray-Curtis dissimilarity.22
- Figure 6. Biplots showing position of all Pearson correlations between modality and station scores on the first two canonical axes. For ease of interpretation each plot represents the modalities of one functional trait. For modalities represented by numbers see Table 3.24
- Figure 7. Changes in univariate measures of the epifaunal community, in the open and closed areas of the SAC, with time (in months) since the permanently closed area was introduced. Mean \pm standard deviation of square root transformed data for, A: total epifaunal density (individuals m^{-2}), B: species richness (number of species per camera tow), C: Shannon-Weiner diversity index (H'), and D: Pielou's evenness index (J'). Note that points have been separated slightly along the x-axis for ease of interpretation.28

Figure 8. Changes in density weighted fishing sensitive trait modalities, in the open and closed areas of the SAC, with time (in months) since the permanently closed area was introduced. Each plot is labelled with the traits modalities it displays. Points are mean \pm standard deviation of square-root transformed data. Note that points have been separated slightly along the x-axis for ease of interpretation (figure continues on following page).....34

Figure 9. Changes in Shannon diversity (H') of density weighted trait modalities, in the open and closed areas of the SAC, with time (in months) since the permanently closed area was introduced. Points are mean \pm standard deviation of square-root transformed data. Note that points have been separated slightly along the x-axis for ease of interpretation.....37

List of tables

Table 1. Fishing effort, catch, and value of king scallops in the ICES rectangle 33E5 from 2000-2011. Data is from log books and includes vessels under 15 m in length and was provided by the marine management organisation.8

Table 2. Legislation applicable to Welsh waters and evolution of the permanently closed area and the seasonally open area in Cardigan Bay Special Area of Conservation (SAC). Sampling surveys (and the time since the introduction of the permanently closed area, to the nearest month) are also given in italics (after Sciberras et al. 2013) 11

Table 3. Functional traits, their modalities and the modality codes used in this study. Traits predicted to be sensitive to the impacts of fishing are underlined (table continues on following page) (after Lambert 2011).....13

Table 4. Results of one-way permutational multivariate ANOVA (PERMANOVA) for the effect of zone on habitat type. The level of statistical significance is indicated as; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$ 17

Table 5. Results of two-way crossed permutational multivariate ANOVA (PERMANOVA) for the effect of zone, time (survey occasion), and their interaction on epifaunal community composition. The test was conducted on square-root transformed species density data and

Bray-Curtis dissimilarity matrix. The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$18

Table 6. Results of two-way crossed permutational multivariate ANOVA (PERMANOVA) for the effect of Zone, Time (survey occasion), and their interaction on functional composition of epifaunal communities. Test was conducted on square-root transformed species density data and Bray-Curtis dissimilarity matrix. The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$21

Table 7. Taxa accounting for over 80% of the total epifaunal density, in both the open and closed area of the SAC, over all five survey occasions. Percentage contribution of each taxa is also displayed.25

Table 8. Results of two-way crossed ANOVA for the effect of zone, time (survey occasion), and their interaction on the total density of epifauna (ind. m^{-2}), species richness (species tow^{-1}), Shannon-Wiener diversity (H'), and Pielou's evenness (J'). All data was square-root transformed. Information displayed for degrees of freedom (df), sum of squares (SS), mean square (MS), F -statistic (F), and P -value (P). The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$27

Table 9. Traits and modalities accounting for over 80% of the total trait modality density, in both the open and closed area of the SAC, over all five survey occasions. Percentage contribution of each modality is also displayed.29

Table 10. Results of two-way crossed ANOVA for the effect of zone, time (survey occasion), and their interaction on the selected fishing sensitive trait modalities. All data was square-root transformed. Information displayed for degrees of freedom (df), sum of squares (SS), mean square (MS), F -statistic (F), and P -value (P). The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$ (table continues on following page).31

Table 11. Results of two-way crossed ANOVA for the effect of zone, time (survey occasion), and their interaction on Shannon diversity (H') of trait modalities. All data was square-root

transformed. Information displayed for degrees of freedom (df), sum of squares (SS), mean square (MS), *F*-statistic (*F*), and P-value (P). The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$36

1 Introduction

1.1 Impact of bottom fishing on the seabed

Bottom-trawling, using gears such as benthic otter trawls, beam trawls and scallop dredges, is thought to be one of the greatest causes of disturbance to marine benthic communities. Aside from effects on target species, bottom-trawling is known to have a number of impacts on the wider environment, affecting both biological and physical components (Kaiser et al. 2000).

Bottom-trawling can damage biological components of the benthos through the direct removal, burial and crushing of organisms, all of which can lead to mortality (Jenkins et al. 2001, Kaiser et al. 2002, Lambert et al. 2011). Non-biological components of seabed habitats can also be impacted by bottom trawling. Trawls and dredges that are in contact with the seabed will leave tracks in the sediment, which can be seen on side scan sonar records (Hinz et al. 2010b, Kaiser et al. 2002). The depth of these tracks will depend on the gear used and the sediment composition, with depth of tracks increasing with increased weight of gear and decreased grain size. The otter boards of an otter trawl may create furrows in the seabed 1-4 cm deep. On a large scale, such as that of a whole fishery, this can smooth over terrain and also removes emergent epifauna, which can be an important group of organisms for increasing habitat complexity. Habitat complexity has been shown to positively influence biodiversity (see Lambert et al. 2012 and references therein). Although on a finer scale, tracks left by trawling may increase the roughness of the seabed (Kaiser et al. 2002). Trawling can also act to resuspend sediment which settles in the surrounding area. The resulting settlement of sediment has the potential to interfere with feeding as well as the settlement of larval stages of benthic organisms (Kaiser et al. 2002, O'Neill et al. 2013).

Scallop dredging is regarded to have a particularly high detrimental impact on the seabed (Collie et al. 2000, Kaiser 2006). The design of dredges varies but typically consists of a bar of teeth to rake through the sediment and dislodge buried scallops, which are then captured in a net held open by a rigged frame. Undersize scallops may escape through metal belly rings. These have the advantage to prevent abrasive damage to the nets but the disadvantage of having a significant impact by being dragged over the seabed (Fig. 1). The Scallop Fishing (Wales) (No. 2) Order (2010) (available at www.legislation.gov.uk/wsi/2010/269/contents/made¹) specifies that, in Welsh waters, a

¹ accessed 18/09/2013).

scallop dredge may have up to eight, 110 mm long teeth per bar and weigh up to 150 kg. The number of dredges a vessel can tow is restricted depending on the distance from shore (a maximum of 14 may be towed at a distance over 6 nautical miles from shore) but is also restricted physically by the size of a fishing vessel. Larger, more powerful vessels are capable of towing more dredges.

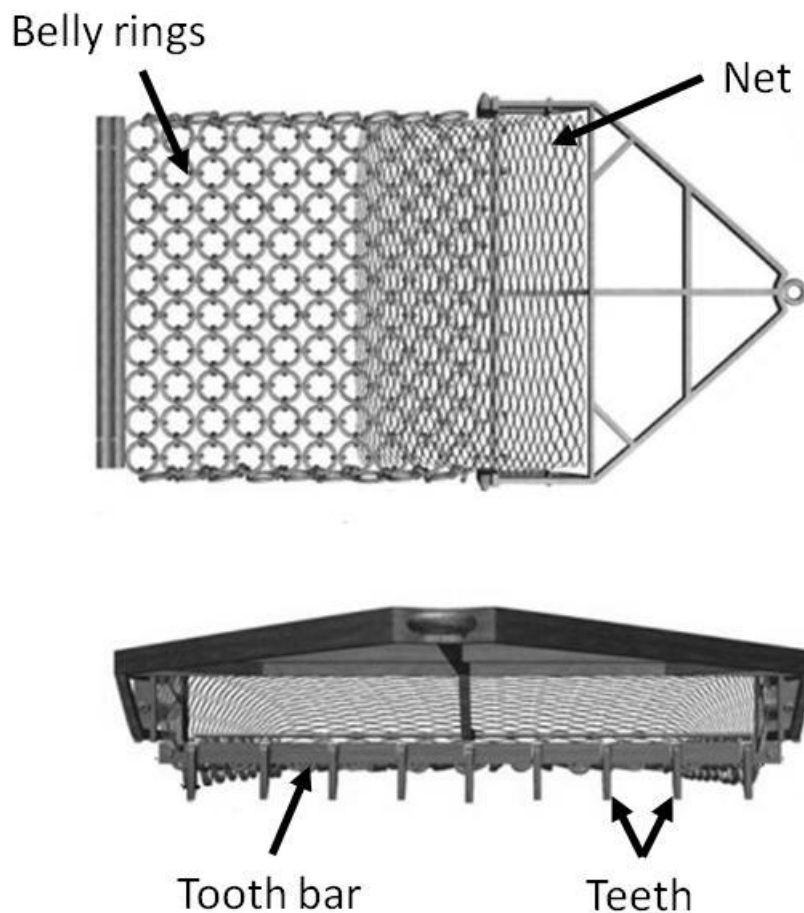


Figure 1. An example of a scallop dredge viewed from above (top) and from the front (bottom). Key components of the dredge are labelled (after O'Neill et al. 2013).

1.2 Mechanisms of recovery

Seabed habitats can recover between fishing events. Recovery to a “pristine state” requires both the physical and biological components of the habitat and associated community to be restored. The biological components of an area can recover from disturbance by three means: immigration from adjacent areas, growth and recruitment (Hinz et al. 2009). If disturbance is

isolated to a small patch then mobile fauna can quickly recolonise the disturbed area. When a large area is disturbed, as is often the case with a fishery, it will be more difficult for immigration through movement of adults, and there will be a greater reliance on larvae transported over large distances by currents for recovery. As a result recovery will typically be expected to take longer when the scale of disturbance is larger (Kaiser et al. 2002; Blyth et al. 2004; Hinz et al. 2009). Physical marks of tracks left by trawls in the substratum can recover by erosion and sedimentation processes caused by currents and waves (Dernie et al. 2003; Hinz et al. 2010b). Different sedimentary habitats will therefore have different recovery rates, with unstable sandy habitats expected to recover quicker than more stable habitats, such as cohesive mud (Dernie et al. 2003, Kaiser et al. 2006).

1.3 Variation in response to and recovery from fishing disturbance

Benthic species provide valuable ecosystem services through their various ecological functions. Those functions depend on a range of functional traits. Feeding type, for instance, has traditionally been used as a functional trait, in part due to being relatively easy to predict from mouth parts of poorly described species (Bremner et al. 2003). Through their respective function, different feeding types (or modalities) will affect the ecosystem in different ways (e.g. affecting localised water current or nutrient cycling). Each species has got a specific set of ecological functional traits and modalities, including traits such as food type and mobility for instance. There is a growing body of evidence showing that some of these ecological functional traits and modalities may, at least partly, determine the vulnerability and resilience of benthic communities to fishing impacts. Furthermore, species are also characterised by life history traits which relates to the ecological functions of the organisms, such as lifespan, reproduction method and body size, which again may act to determine the level of damage caused by fishing and the potential for recovery of a community (Bremner et al. 2003, Tillin et al. 2006, Strain et al. 2012). Henceforth, both ecological functional traits and life history traits are referred to functional traits, with functional trait modalities referring to the different categories within a trait. For instance, scavenger is a modality of the feeding type trait.

Different functional trait modalities can have a disposition to be more or less adversely affected by disturbance events, both natural and anthropogenic. With regards to epifauna, species that are upright, not flexible and attached to the seabed are typically most sensitive to the initial impacts of bottom trawling as these traits make a species likely to be broken, removed and killed by a passing trawl. By their nature, passive filter feeding species, which

require feeding apparatus that reach up into the water column, often display some, if not all, of these traits. Conversely, encrusting, highly flexible, or unattached species are more likely to survive being trawled, as they are less likely to have body parts broken off (Bremner et al. 2003, Tillin et al. 2006, Strain et al. 2012).

Functional traits can also influence the recovery rate of a species. Species which grow to a large size, are long lived, have a low fecundity, have restricted dispersal range of offspring and little to no mobility are likely to recover slowly after disturbance. These characteristics hinder recovery as species which display them are likely to produce only few offspring and grow slowly. Limited mobility and dispersal range of offspring will reduce their ability to recolonise disturbed areas. Conversely, broadcast spawning species that produce planktonic larvae are often the first to recolonise a disturbed area and begin recovery (Kaiser et al. 2002, Bremner et al. 2003, Blyth et al. 2004, Tillin et al. 2006, Strain et al. 2012).

The impacts of bottom-trawling may also affect different species in different ways through the interactions between species and their environment. Opportunistic, scavenging species may benefit from increased availability of food left after trawling (in the form of dead or dying organisms exposed by the trawl) (Ramsay et al. 1998). Removal of predatory fish or crustaceans by fishing can result in reduced predation and increased abundance of their prey species (Lilly et al. 2000). Changes in the availability of habitats may also benefit some species whilst hindering others (Bradshaw et al. 2002).

The above impacts of towed fishing gear can lead to changes in community composition (Bremner et al. 2003, Strain et al. 2012) and reduction in the density and diversity of benthic fauna (Thrush et al. 1998, Hiddink et al. 2006, Hinz et al. 2009). Community composition is traditionally viewed as the variety of species that make up a community (taxonomic composition). An alternative view, which is being used more frequently in studies of marine communities, is that of the variety of functional traits that make up a community (functional composition) (Bremner et al. 2003, Tillin et al. 2006). As bottom-trawling has the potential to affect species displaying different functional trait modalities in different ways, it also has the potential to alter the taxonomic and functional composition of a community (Tillin et al. 2006).

1.4 Marine protected areas

The term Marine Protected Area (MPA) is broad and may refer to any spatial restriction on activities that could damage the marine environment. MPAs that restrict the use of bottom fishing gears or other fishing methods can be used to achieve conservation or fisheries management goals (Halpern & Warner 2002, Halpern 2003, Kaiser 2005, Murawski et al. 2005).

The use of MPAs as a management tool has increased rapidly over the last 20 years in many areas of the world (Pita et al. 2011). In the UK and in Europe, the use of MPAs has been promoted by legislation such as the European Union Habitats Directive. The habitats directive requires member countries to protect biodiversity as well as populations of species and habitats which have been listed as conservation priorities using Special Areas of Conservation (SAC). The preferred design of those MPAs depends on the management objectives (Auster & Shackell 2000, Hastings & Botsford et al. 2003).

By removing anthropogenic impacts such as fishing, MPAs have often proven successful in increasing the total density, biomass, diversity, and size of organisms in closed areas compared to open areas (or after closure compared to before closure). However, in some cases, MPAs have had no effect or even negative effects on the above measures of communities (Halpern 2003). With the increasing use of MPAs, it is important to understand what makes an MPA successful but it is equally important to identify why some MPAs are unsuccessful in achieving their goals. Improper use of MPAs can not only have an impact on the environment itself (Dinmore et al. 2003) but it can also damage their perception by the public and stakeholders (Agardy et al. 2003). Failure to obtain stakeholder support can have major consequences, as it has recently halted the development of Marine Conservation Zones in Welsh coastal waters.

1.5 Background of the Cardigan Bay Special Area of Conservation

The Cardigan Bay SAC, Wales, has an area which has been permanently closed to scallop dredging since 2009. This study aims to investigate the recovery of epifaunal communities in the permanently closed area of the SAC (for more details on the study site see section 2.1). A previous study with a similar aim (Sciberras et al. 2013) was unable to identify any signs of recovery in the taxonomic community composition of the SAC over a period of 22 months since the introduction of the closed area. This result was attributed to the unstable seabed

habitat present in Cardigan Bay. However, it was also noted that 22 months may be a relatively short time scale for recovery to be expected (Sciberras et al. 2013). Here the methods of Sciberras et al. (2013) are expanded on to see if an increased length of time since the closure of the SAC has lead to signs of recovery.

While Sciberras et al. (2013) focused primarily on the recovery of species, here I further analysed recovery in terms of functional traits, as it may be able to detect changes that are not apparent from the taxonomic analysis. In order to study recovery of the taxonomic and functional components of the epifaunal communities in the closed area of Cardigan Bay SAC, the following five hypotheses have been developed:

H1: The TAXONOMIC COMPOSITION of the epifaunal community will become increasingly different between the open and closed areas of the Cardigan Bay SAC with time, since the introduction of the permanently closed area to the scallop fishery.

H2: The FUNCTIONAL COMPOSITION of epifaunal community will become increasingly different between the open and closed areas of the Cardigan Bay SAC with time, since the introduction of the permanently closed area to the scallop fishery.

H3: There will be an increase in the DENSITY AND DIVERSITY OF EPIFAUNA in the closed area with time since its permanent closure. Also, this increase will be proportionately greater than any increase observed in the open area.

H4: There will be an increase in the DENSITY OF FUNCTIONAL TRAIT MODALITIES SENSITIVE TO FISHING IMPACTS in the closed area with time since its permanent closure. Also, this increase will be proportionately greater than any increase observed in the open area.

H5: There will be an increase in the DIVERSITY OF FUNCTIONAL TRAIT MODALITIES in the closed area with time since its permanent closure. Also, this increase will be proportionately greater than any increase observed in the open area.

2 Methods

2.1 Study site

The Cardigan Bay SAC is located in the Irish Sea, on the west coast of Wales, within the International Council for Exploration of the Seas (ICES) rectangle 33E5 (Fig. 2). The 960 km² SAC was designated in 2004 in order to protect species (specifically bottlenose dolphins, *Tursiops truncatus*) and habitats (specifically permanently submerged sandbanks and cobble reefs) listed under the European Union's Habitats Directive, although subsequent surveys have found low and variable occurrence of cobble reefs. The area also supports a scallop dredging fishery, predominantly targeting king scallops (*Pecten maximus*) and to a lesser extent queen scallops (*Aequipecten opercularis*) (Hinz et al. 2010a). The physical characteristics of the SAC have previously been described in detail by Sciberras et al. (2013). The SACs orientation, facing south west and the prevailing wind, exposes the shallow seabed to large uninterrupted swells. Tidal currents in the SAC create a seabed characterised by mobile sand waves. The sediment structure of the seabed is a mixture of sand (<2 mm), gravel (2-4 mm), and pebbles (4-64 mm) (Hinz et al. 2010a, Hinz et al. 2010b, Sciberras et al. 2013).

Prior to 2009, the scallop dredging fishery was only restricted spatially according to distance from shore. However, the king scallop fishery in Cardigan Bay underwent marked growth during 2007 and 2008, with notable increases in effort, catch, and value of the fishery (Table 1). A sudden increase in fishing effort, from 989-2328 days at sea per year spent in ICES rectangle 33E5 between 2007 and 2008, raised concerns over the affect the fishery was having on the seabed. Due to the risk of scallop dredging to negatively impacting the seabed, the entire SAC was closed to the scallop fishery in June 2009 (Table 2) (Sciberras et al. 2013).

As the SAC contained some of the main scallop grounds in Cardigan Bay and was an important area for the industry (Hinz et al. 2010a), a 240 km² area was reopened to the fishery on a seasonal basis in June 2009, while the remaining 720 km² of the SAC remained permanently closed (Table 2, Fig. 2).

It is assumed that no fishing has taken place in the closed area since 1st June 2009. The open area of the SAC is one of the most productive scallop grounds in ICES 33E5 and it is likely

that the majority of fishing effort spent in ICES 33E5 since 1st March 2010 was done in the open area (Gwladys Lambert pers. com.).

Table 1. Fishing effort, catch, and value of king scallops in the ICES rectangle 33E5 from 2000-2011. Data is from log books and includes vessels under 15 m in length and was provided by the marine management organisation.

Year	Effort (days at sea)	Catch (kg)	Value (£)
2000	390	297,471	430,333
2001	309	124,761	239,237
2002	254	102,911	182,026
2003	331	250,887	398,415
2004	649	641,180	997,968
2005	330	245,180	467,675
2006	453	430,469	750,393
2007	989	1,134,880	1,831,140
2008	2328	3,808,789	6,390,265
2009	1756	2,073,068	3,691,184
2010	1287	1,658,637	2,908,301
2011	1257	1,936,454	3,733,939

2.2 Sampling design

Sampling was undertaken over five surveys (Fig. 2, Table 2) which will be referred to as December 2009, June 2010, April 2011, and October 2012. These sampling occasions were distributed throughout the year to help distinguish seasonal effects. Sampling effort was spread across both the open and closed areas of the SAC. Because the funding and time allocated to the surveys and their objectives varied between years, the number and location of

stations varied accordingly. A maximum of 53 stations were sampled in December 2009 and a minimum of 12 stations in June 2010. Some stations were also revisited in later surveys.

Epifaunal abundance was recorded from photographic images of the seabed. Images were obtained by towing a camera (Canon 400D) mounted on a sledge behind the RV Prince Madog. The sledge was towed at approximately 1 knot for 20 minutes at each station, with a photograph taken every 11 seconds. The camera was mounted so as to be above the seabed taking a picture directly downwards and each image captured an area of 0.135 m^2 (when the sledge was on a flat surface).

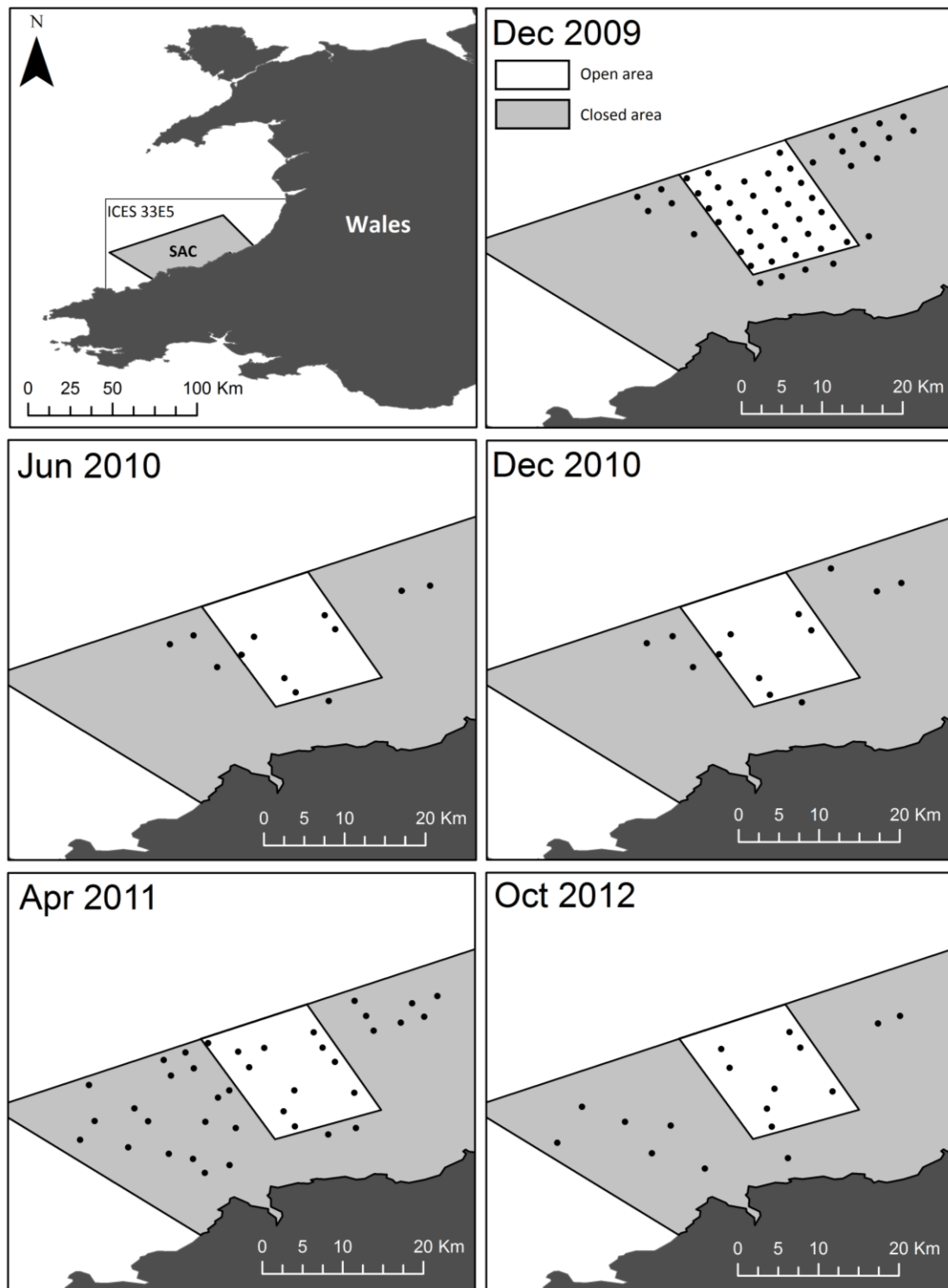


Figure 2. Map showing the location of the Cardigan Bay Special Area of Conservation (SAC) and ICES rectangle 33E5 in Wales (top left). Also shown are maps of the location of sampling stations (in both the open and closed areas) in each of the five surveys undertaken between December 2009 and October 2012.

Table 2. Legislation applicable to Welsh waters and evolution of the permanently closed area and the seasonally open area in Cardigan Bay Special Area of Conservation (SAC). Sampling surveys (and the time since the introduction of the permanently closed area, to the nearest month) are also given in italics (after Sciberras et al. 2013)

Legislation	Time period	Cardigan Bay SAC	
North Western and North Wales Sea Fisheries Committee Byelaw 20 and Scallop Fishing (Wales) Order 2005	Prior to 2009	(1) Within 1.5 nautical (n) miles of coastline: Scallop dredging (SD) is prohibited all year round (2) Between 1.5 and 3 n miles off the coastline: Closed season to SD between 1 Jun and 31 Dec (3) Between 3 and 12 n miles off the coastline: Closed season to SD between 1 Jun and 31 Oct	
	1 Jun 2009-28 Feb 2010	Closed season to SD in all Welsh waters extended to end of Feb 2010	
	<i>10-17 Dec 2009</i>	<i>Dec 2009 Survey (6 months)</i>	
		Permanently closed area	Seasonally open area
Scallop Fishing (Wales) (No.2) Order 2010 No. 269 (W. 33)	1 Mar-31 May 2010	Closed to SD	Open to SD
	1 Jun-31 Oct 2010	Closed to SD	Closed to SD
	<i>13-19 Jun 2010</i>	<i>Jun 2010 Survey (12 months)</i>	
	1 Nov 2010-30 Apr 2011	Closed to SD	Open to SD
	<i>29 Nov-4 Dec 2010</i>	<i>Dec 2010 Survey (18 months)</i>	
	<i>6-9 Apr 2011</i>	<i>Apr 2011 Survey (22 months)</i>	
	1 May-31 Oct 2011	Closed to SD	Closed to SD
	1 Nov 2011-30 Apr 2012	Closed to SD	Open to SD
	1 May-31 Oct 2012	Closed to SD	Closed to SD
	<i>3-10 Oct 2012</i>	<i>Oct 2012 Survey (40 months)</i>	

2.3 Image analysis

Firstly, images which were out of focus, obscured by turbid water, or otherwise unsuitable for analysis were removed. For the October 2012 survey 20 images were randomly subsampled from each station however, some surveys had a much higher subsample (up to 75 images in some cases). The number of images subsampled varied between samples due to different time constraints for the analysis and different numbers of volunteers available to help with the analysis. There was also a problem with availability of data for some of the surveys (i.e. only data on the density of species per station was available for the December 2009 survey). This has resulted in a bias when calculating species richness and diversity as more of the rare species are likely to have been identified in stations with a larger subsample. However, no bias was introduced between survey stations for the October 2012 survey.

2.3.1 Seabed habitat type

In order to identify if the open and closed areas were comparable, seabed habitat was characterised from the still images at each station into one of five types. These habitat types were assumed to be representative of the habitats found in the SAC based on personal assessment of over 500 images from the SAC, and were defined as follows: sand-mud, sand-gravel-shell, gravel-pebble, and mixed (sand-cobbles-gravel).

2.3.2 Density of epifaunal species

Images were then analysed with individual epifaunal organisms counted and identified to the lowest possible taxonomic level. Some organisms were excluded from the analysis due to inadequacies in this method's ability to estimate their density. This included highly mobile organisms (such as fish) which may avoid the camera sledge, and tube dwelling worms visible (such as *Pomatoceros* and Serpulidae species) for which it was difficult to tell if the individual was alive or dead unless feeding apparatus were visible. In order to standardise observations between stations and surveys, densities of different species at each station were calculated as the number of individuals per m².

2.4 Functional traits and fuzzy coding

Information on functional traits was collected from the Biological Traits Information Catalogue (BIOTIC, www.marlin.ac.uk/biotic/), Tillin et al. 2006, Bremner et al. 2003 and from information provided by Gwladys Lambert. Forty modalities were chosen, belonging to

eleven different functional traits. These traits were chosen in order to represent the feeding, morphological, behavioural and life history function of a species (Table 3). A species may use a range of different modalities for any one trait, for example the brittlestar, *Ophiura albida*, can be a suspension feeder or a deposit feeder depending on environmental conditions (www.marlin.ac.uk/biotic/). To include the variety of traits and modalities a species might employ “fuzzy-coding” was used. Fuzzy-coding involves assigning the proportional use of a modality for each trait. Using the above example, the feeding habit of *O. albida* can be described using fuzzy-coding as; deposit-detritus = 0.5, filter-suspension = 0.5, opportunistic-scavenger = 0, predator = 0, and grazer = 0. Note that some studies calculate a percentage from a scale of affiliation to a modality (e.g. Bremner et al. 2003, Tillin et al. 2006), however, this step was skipped in this case allowing for less rigid adjustment of percentages when seen appropriate. Values were assigned to modalities based on Bremner et al. 2003, Tillin et al. 2006, BIOTIC and Gwladys Lambert’s database (unpublished). Some species had little available information on their functional traits. In these cases, information from a higher taxonomic level was used in the interest of obtaining a complete dataset. Density weighted value of each trait modality at each station were calculated by multiplying species density by the proportions assigned to fuzzy-coded trait modalities. For instance, taking the example of *O. albida*, if its density was 10 ind/100m² at station 1, then station 1 had 5 ind/100m² of deposit-detritus feeders and 5 ind/100m² of filter-suspension feeders. All the densities of other species which were deposit-detritus feeders and filter-suspension feeders at station 1 could thereby be combined and a final density estimate of deposit-detritus feeders and filter-suspension feeders at station 1 could be estimated.

Table 3. Functional traits, their modalities and the modality codes used in this study. Traits predicted to be sensitive to the impacts of fishing are underlined (table continues on following page) (after Lambert 2011).

Trait	Modality	No.
Size	Small (<2 cm)	1
	Small-medium (3-10 cm)	2
	Medium (11-20 cm)	3
	<u>Medium-large (21-50 cm)</u>	4

	<u>Large (>50 cm)</u>	5
Lifespan	<2 years	1
	2-5 years	2
	<u>>5 years</u>	3
Reproductive method	Asexual	1
	Broadcast spawner	2
	Sexual-planktonic larvae	3
	<u>Sexual-mini adult</u>	4

Table 3 (continued). Functional traits, their modalities and the modality codes used in this study. Traits predicted to be sensitive to the impacts of fishing are underlined (after Lambert 2011).

Trait	Modality	No.
Mobility	<u>None</u>	1
	<u>Low</u>	2
	Medium	3
	High	4
Attachment	None	1
	<u>Temporary</u>	2
	<u>Permanent</u>	3
Movement	<u>Sessile</u>	1
	Swim	2
	Crawl	3
	Burrow	4
Body flexibility	>45°	1
	10-45°	2
	<u><10°</u>	3
Body form	Flat	1
	Mound	2
	<u>Upright</u>	3

Feeding Habit	Deposit-detritus	1
	<u>Filter-suspension</u>	2
	Opportunistic-scavenger	3
	Predator	4
	Grazer	5
Sexual differentiation	<u>Gonochoristic</u>	1
	Synchronous	2
	hermaphrodite	3
	Sequential hermaphrodite	
Sociability	Solitary	1
	Gregarious	2
	<u>Colonial</u>	3

2.5 Statistical analysis

All statistical analysis was undertaken using the R statistical software (R core team 2013). The scripts developed for statistical analysis are included with annotations in appendix 1 (section 7).

2.5.1 Multivariate analysis of spatial and temporal change in the SAC

2.5.1.1 Habitat type

Survey stations that were revisited in multiple surveys and had the same habitat type on more than one occasion were removed to avoid pseudoreplication. Transformations were not required for the categorical habitat type data and Euclidean distance was used to form a resemblance matrix.

As seabed habitat can influence community composition, it is important to make sure substratum type is similar between the open and closed areas. This was tested using a Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001). PERMANOVA, using 9999 random permutations of the data, was applied to the resemblance matrix of habitat type to investigate if habitat type was significantly different between zones during any of the five surveys. If there is no statistically significant difference in habitat type between zones, then confidence that habitat will not be responsible for driving any differences in epifaunal communities will be increased.

2.5.1.2 Community composition

In order to remove the very rare species from the species density and functional traits data only species in the top 95% of cumulative density were selected from each station. Despite this, the raw data for species density and for functional trait density was skewed by the absence of certain species at some stations. Therefore the data was square-root transformed to down weight the influence of highly abundant species. Once transformed, a resemblance matrix was created using Bray-Curtis dissimilarity for species and density weighted trait modalities.

This analysis aimed at addressing hypotheses H1 and H2. The objective was to identify whether there was a significant difference in community composition between the open and closed areas (i.e. spatial difference) and between the surveys (i.e. change in time), and, most importantly, if the community composition had evolved differently in the two zones (closed vs. open) since 2009. This was achieved by using a two-way crossed PERMANOVA (9999 permutations). PERMANOVA was applied independently to the resemblance matrices of species density and trait modalities, using the factors zone (open or closed), time (with each of the five surveys as a level), and their interaction. A significant effect of the interaction is required to provide evidence for recovery in the closed area.

In order to visualise the distribution of the different surveys and zones in a multivariate space, a Canonical Analysis of Principal Coordinates (CAP) was used to produce ordination plots for the species and functional trait composition data. To identify the species and trait modalities which were influencing the similarity or dissimilarity between surveys and zones, a Pearson correlation between individual species (or modalities) and canonical axes was performed. Pearson correlation coefficients lie between -1 and 1, the further the value of a correlation coefficient is from 0 the stronger the influence of the species or modality on the distribution of surveyed stations in multidimensional space. Arbitrary correlation coefficient were selected as cut-offs to display only species (or modalities) exerting the strongest influence on changes in community composition (Anderson & Willis 2003)

2.5.2 Univariate analysis of spatial and temporal change in the SAC

The species density data was broken down into univariate measures of community structure to identify trends in the data (hypothesis H3). These measures were total epifaunal density, species richness, Shannon diversity, and Pielou's evenness. For the trait modality density data, Shannon diversity and change in fishing sensitive trait modality densities were analysed (H5

and H4 respectively). Fishing sensitive trait modalities were those predicted to be negatively affected by trawling (underlined in Table 3). After being square-root transformed to normalise the data, these metrics were analysed using a two-way crossed ANOVA. The intention of this test was to identify any effect of zone, time and their interaction on the univariate metrics. As with the above described PERMANOVA, a significant effect of the interaction will be required to provide evidence of recovery. Where significant effects of any factor were found a post hoc Tukey HSD test was performed to identify between which levels the difference laid.

3 Results

3.1 Spatial patterns in habitat type

Statistical analysis revealed that there was no significant effect of zone on habitat (Table 4). Having the same habitat type in both zones increases the likelihood that any observed difference in species composition and densities between zones is a result of fishing disturbance.

<p>Table 4. Results of one-way permutational multivariate ANOVA (PERMANOVA) for the effect of zone on habitat type. The level of statistical significance is indicated as; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$.</p>
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Source	df	SS	MS	Pseudo- <i>F</i>	P (perm)
Zone	1	0.348	0.34803	0.47352	0.7075
Residual	87	63.944	0.73499		
Total	88	64.292			

3.2 Spatial and temporal trends in multivariate and univariate measures of epifauna

3.2.1 (H1) Spatial and temporal patterns in taxonomic community composition

For the multivariate species composition data, a significant difference was found between surveys and between zones, however there was no interaction (Table 5). The ordination plot of the CAP analysis shows the differences between the five surveys (Fig. 3). The December 2009 stations separate from those of the other surveys along the first canonical axis (Axis 1).

The October 2012 stations separate away from the three surveys between June 2010 and April 2011 along the second canonical axis (Axis 2). The June 2010 stations also separate out from the stations of October 2012, and December 2010, along the second canonical axis (Fig. 3). As there was a significant effect of zone on community composition one-way PERMANOVAs were used to identify which surveys were responsible for differences in zone. There were two surveys that had statistically significant differences in community composition according to zone. These were December 2009 (PERMANOVA: pseudo- $F_{1,53} = 1.7605$, $P_{\text{perm}} = 0.0467$) and April 2011 (PERMANOVA: pseudo- $F_{1,36} = 2.0768$, $P_{\text{perm}} = 0.021$). It is important to note that stations separated out further along canonical axes according to their survey as opposed to within the survey they belong to. This indicates that there is generally a greater difference between surveys than within surveys (regardless of the zone stations belong to) (Fig. 3).

Table 5. Results of two-way crossed permutational multivariate ANOVA (PERMANOVA) for the effect of zone, time (survey occasion), and their interaction on epifaunal community composition. The test was conducted on square-root transformed species density data and Bray-Curtis dissimilarity matrix. The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$.

Source	df	SS	MS	Pseudo- F	P (perm)	
Zone	1	1.272	1.27222	4.4138	0.0002	***
Time	4	6.620	1.65506	5.7420	0.0001	***
Zone x Time	4	1.059	0.26473	0.9185	0.6521	
Residual	125	36.030	0.28824			
Total	134	44.981				

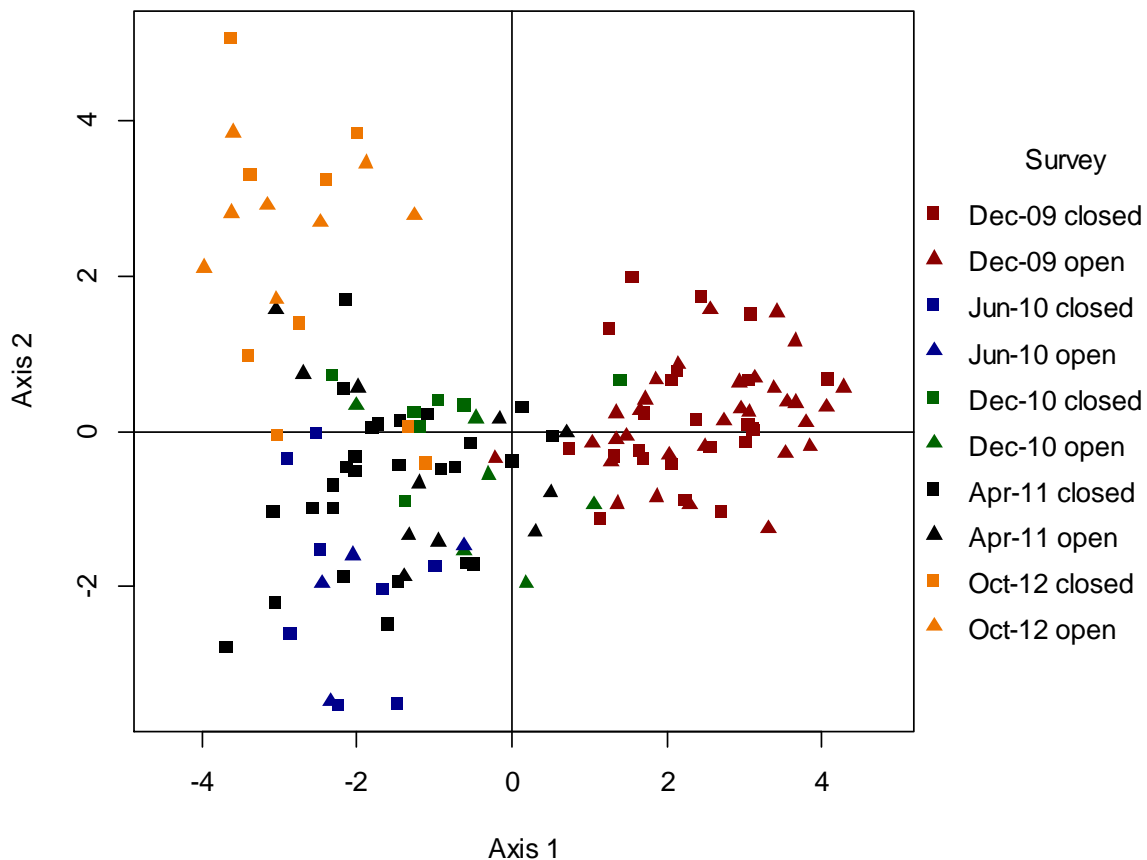


Figure 3. Ordination plot showing the first two canonical axes for the canonical analysis of principle coordinates (CAP) on square-root transformed epifaunal species density data and Bray-Curtis dissimilarity.

The species responsible for changes along the axes were identified from the Pearson correlation coefficient between each species and station on the first and second CAP axes. Species with the strongest influence on changes in the community composition (defined arbitrarily as those with absolute Pearson correlation of $|r| \geq 0.30$ between species and station scores on the first two canonical axes) are used to create a biplot (Fig. 4) which can be compared with Fig. 3. It can be seen that 18 taxa exceeded this threshold on at least one of the two axes (Fig. 4). Of these 18 taxa hydroid turf, *Epizoanthus couchii*, and *Ophiura albida* had a particularly strong influence on the change in community composition (all obtaining a Pearson correlation of $|r| \geq 0.50$) between December 2009 and October 2012 along the first canonical axis. The density of these three taxa, mentioned above, was relatively greater in the four surveys conducted after December 2009 compared to the December 2009 survey, however this trend is true for all 18 species included in Fig. 4.

Along the second canonical axis *Nassarius* sp., bivalve sp., *Cellepora pumicosa*, and *Epizoanthus couchii* had a particularly strong influence on the change in community composition (all obtaining a Pearson correlation of $|r| \geq 0.35$) between June 2010 and October 2012. The October 2012 survey was characterised by relatively high densities of *Nassarius* sp., *Cellepora pumicosa*, and *Epizoanthus couchii* compared to other surveys. The June 2010 survey was characterised by relatively high densities of bivalve sp. compared to the other surveys.

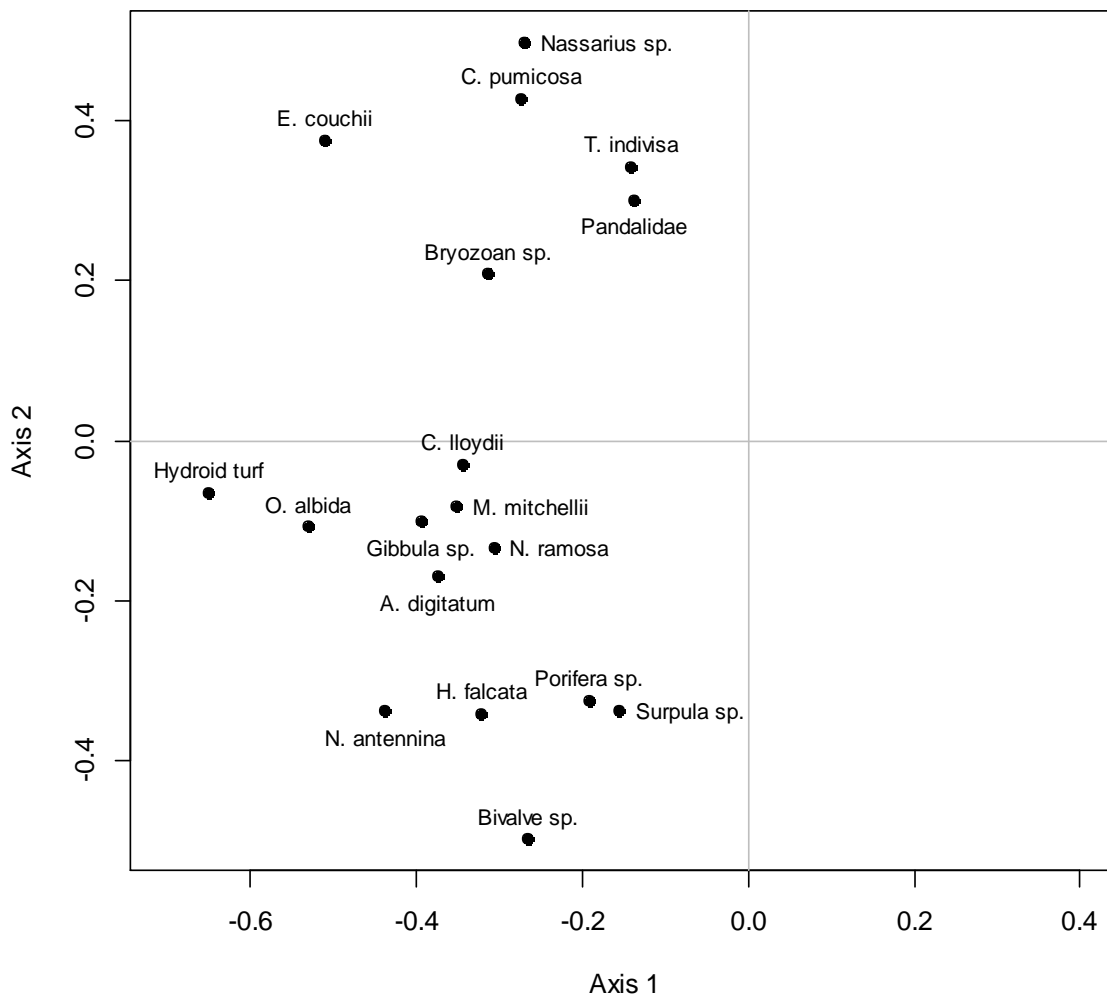


Figure 4. Biplot showing individual species with an absolute Pearson correlation of $|r| \geq 0.30$ between species and canonical axes on at least one of the first two canonical axes. Abbreviated species names are; *Cellepora pumicosa*, *Epizoanthus couchii*, *Tubularia indivisa*, *Cerianthus lloydii*, *Mesacmaea mitchellii*, *Ophiura albida*, *Nemertesia ramosa*, *Alcyonium digitatum*, *Hydrallmania falcata*, and *Nemertesia antennina*.

3.2.2 (H2) Spatial and temporal patterns in functional community composition

A significant difference in functional community composition was identified between surveys and between zones, however there was no significant effect of the interaction (Table 6). The ordination plot for the CAP analysis shows how much or how little stations resembled each other in terms of their density weighted trait modality composition (Fig. 5). In a similar fashion to the CAP analysis of species composition (Fig. 3), along the first canonical axis stations from the December 2009 and October 2012 surveys separate out from each other. Although none of the surveys appear to separate from one another along the second canonical axis, within the October 2012 survey a small group of five stations (three from the open and two from the closed area) are clearly distinct from the other stations (Fig. 5). One-way PERMANOVAs investigating the effect of zone in each survey suggest that the April 2011 survey is responsible for the effect of zone, identified in the two-way ANOVA, as this was the only survey to obtain a marginally significant result (PERMANOVA: pseudo- $F_{1,36} = 2.5425$, $P_{\text{perm}} = 0.0783$).

Table 6. Results of two-way crossed permutational multivariate ANOVA (PERMANOVA) for the effect of Zone, Time (survey occasion), and their interaction on functional composition of epifaunal communities. Test was conducted on square-root transformed species density data and Bray-Curtis dissimilarity matrix. The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$.

Source	df	SS	MS	Pseudo- F	P (perm)	
Zone	1	0.4667	0.46669	5.1293	0.0055	**
Time	4	3.2208	0.80520	8.8499	0.0001	***
Zone x Time	4	0.2098	0.05246	0.5766	0.8752	
Residual	125	11.3731	0.09098			
Total	134	15.2704				

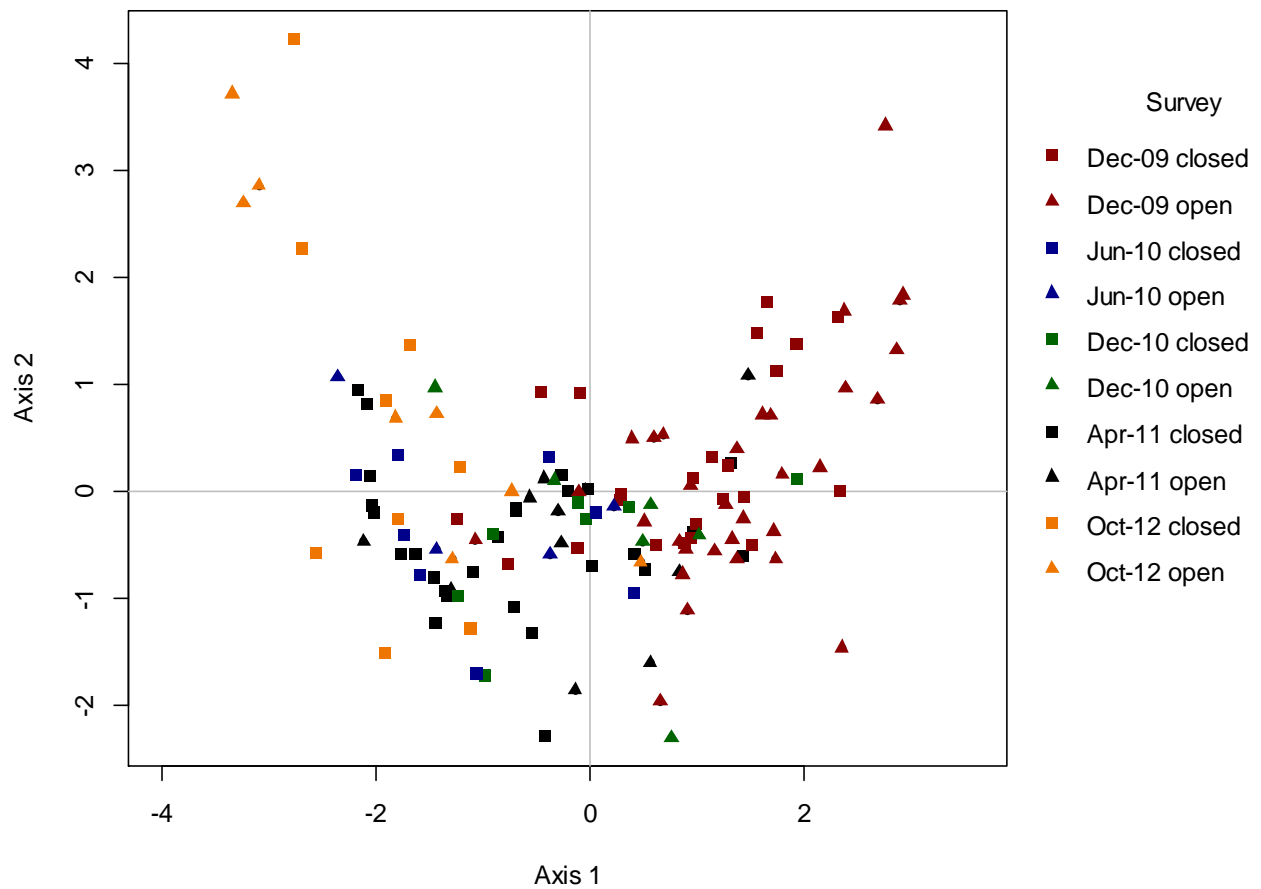


Figure 5. Ordination plot showing the first two canonical axes for the canonical analysis of principle coordinates (CAP) on square-root transformed density weighted trait modality value data and Bray-Curtis dissimilarity.

The Pearson correlation coefficients for all the modalities of each trait are shown in (Fig. 6). It can be seen that almost all trait modalities, excluding movement by swimming (Fig. 6F), increased in density weighted value since the December 2009 survey. The traits (and modalities) which most strongly influenced change along the first canonical axis (obtaining a Pearson correlation of $|r| \geq 0.60$) were: size (small and small-medium), lifespan (< 2 years and 2-5 years), reproductive method (asexual, broadcast spawned, and sexual-planktonic larvae), mobility (none), attachment (temporary and permanent), movement (sessile and burrower), body flexibility ($>45^\circ$), body form (mound and upright), feeding habit (filter feeder, opportunist-scavenger, predator), sexual differentiation (gonochoristic), and sociability (colonial).

Along the second canonical axis the traits (and modalities) with the strongest influence on change in composition (obtaining a Pearson correlation of $|r| \geq 0.30$) were; size (small and medium), lifespan (>5 years), mobility (medium), attachment (none and temporary), body flexibility (10-45°), body form (flat and mound), feeding habit (deposit-detritus, opportunist-scavenger, predator). The subgroup of stations from the October 2012 survey were distinguished from the rest of the stations in that survey by relatively high density weighted values of small size, temporary attachment, mound body form, opportunistic-scavengers or predatory feeding habits (Fig. 5, Fig. 6).

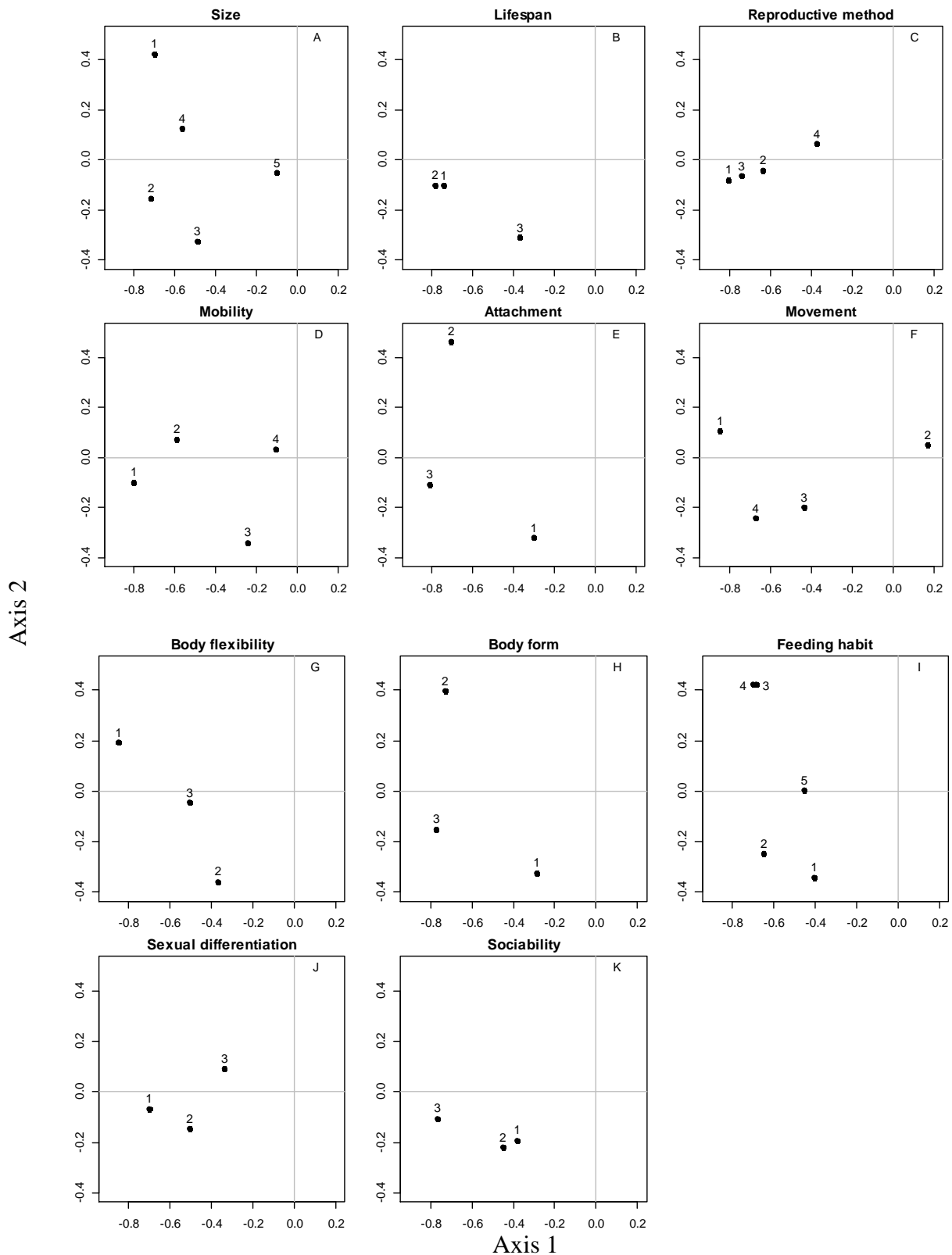


Figure 6. Biplots showing position of all Pearson correlations between modality and station scores on the first two canonical axes. For ease of interpretation each plot represents the modalities of one functional trait. For modalities represented by numbers see Table 3.

3.2.3 (H3) Spatial and temporal trends in univariate species community metrics

In total, 140 different taxa were identified in the Cardigan Bay SAC over the five survey occasions. Of these 140 species only 10 accounted for the top 80% (the cut-off of 80% was chosen so as to display the dominant species in the epifaunal community) the total density of epifauna (Table 7). Over the duration of the study period, the epifaunal community of the SAC was predominately hydroid turf, the anemone *Epizoanthus couchii*, and Ophiuroids.

Table 7. Taxa accounting for over 80% of the total epifaunal density, in both the open and closed area of the SAC, over all five survey occasions. Percentage contribution of each taxa is also displayed.

Species	Taxonomic group	Contribution (%)
Hydroid turf	Hydroid	19.2
<i>Epizoanthus couchii</i>	Cnidarian	17.0
<i>Ophiothrix fragilis</i>	Ophiuroid	14.1
<i>Ophiura albida</i>	Ophiuroid	12.5
<i>Alcyonium digitatum</i>	Soft Coral	5.6
<i>Cellaria</i> sp.	Bryozoan	3.4
<i>Pecten maximus</i>	Bivalve	2.4
<i>Cerianthus lloydii</i>	Cnidarian	2.1
<i>Aequipecten opercularis</i>	Bivalve	2.0
<i>Nemertesia antennina</i>	Hydroid	1.6

The total density of epifauna, species richness, Shannon diversity, and Pielou's evenness were all found to change significantly with time since the closure of the SAC. Total epifaunal density was the only measurement where an effect of zone was identified (Table 8, Fig. 7). The mean value of epifaunal density was higher in the closed area. However, there is a trend of increasing mean epifaunal density with time since introduction of the closed area in both zones. High variance around these means should also be taken into account (Fig. 7A). A Tukey HSD test (all Tukey HSD tests use an alpha level of $P < 0.05$) revealed the low densities in December 2009 (6 months after the introduction of the permanently closed area)

and relatively high densities in October 2012 (40 months after the introduction of the permanently closed area) were responsible for the statistically significant differences in time.

For species richness and Shannon diversity, Tukey HSD tests identified differences between December 2009 and June 2010 (12 months after the introduction of the permanently closed area) as driving the statistical difference in time. For both these measures, December 2009 had the lowest mean value (Fig. 7B,C).

A reversal of the above trends was seen for Pielou's evenness index, mean values of which generally decreased with time (Fig. 7D). Again a Tukey HSD test revealed differences between December 2009 and October 2012 were driving the significant difference in time however, December 2009 had relatively high levels of evenness compared to October 2012. It is important to note that the major differences in univariate measures of the epifaunal community were found between winter and summer survey occasions.

Table 8. Results of two-way crossed ANOVA for the effect of zone, time (survey occasion), and their interaction on the total density of epifauna (ind. m⁻²), species richness (species tow⁻¹), Shannon-Wiener diversity (H'), and Pielou's evenness (J'). All data was square-root transformed. Information displayed for degrees of freedom (df), sum of squares (SS), mean square (MS), F -statistic (F), and P -value (P). The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$.

	df	SS	MS	F	P	
Total epifaunal density						
Zone	1	20.3	20.29	5.217	0.024	*
Time	4	189.2	47.31	12.164	<0.001	***
Zone x Time	4	16.8	4.21	1.083	0.368	
Residual	125	486.2	3.89			
Species richness						
Zone	1	0.16	0.159	0.267	0.606	
Time	4	54.01	13.501	22.625	<0.001	***
Zone x Time	4	2.44	0.609	1.021	0.399	
Residual	129	76.98	0.597			
Shannon diversity						
Zone	1	0.244	0.2443	2.380	0.125	
Time	4	4.061	1.0153	9.892	<0.001	***
Zone x Time	4	0.741	0.1852	1.804	0.132	
Residual	129	13.240	0.1026			
Pielou's evenness						
Zone	1	0.0140	0.01400	2.763	0.0991	
Time	4	0.1308	0.03271	6.455	<0.001	***
Zone x Time	4	0.0163	0.00409	0.806	0.5234	
Residual	120	0.6081	0.00507			

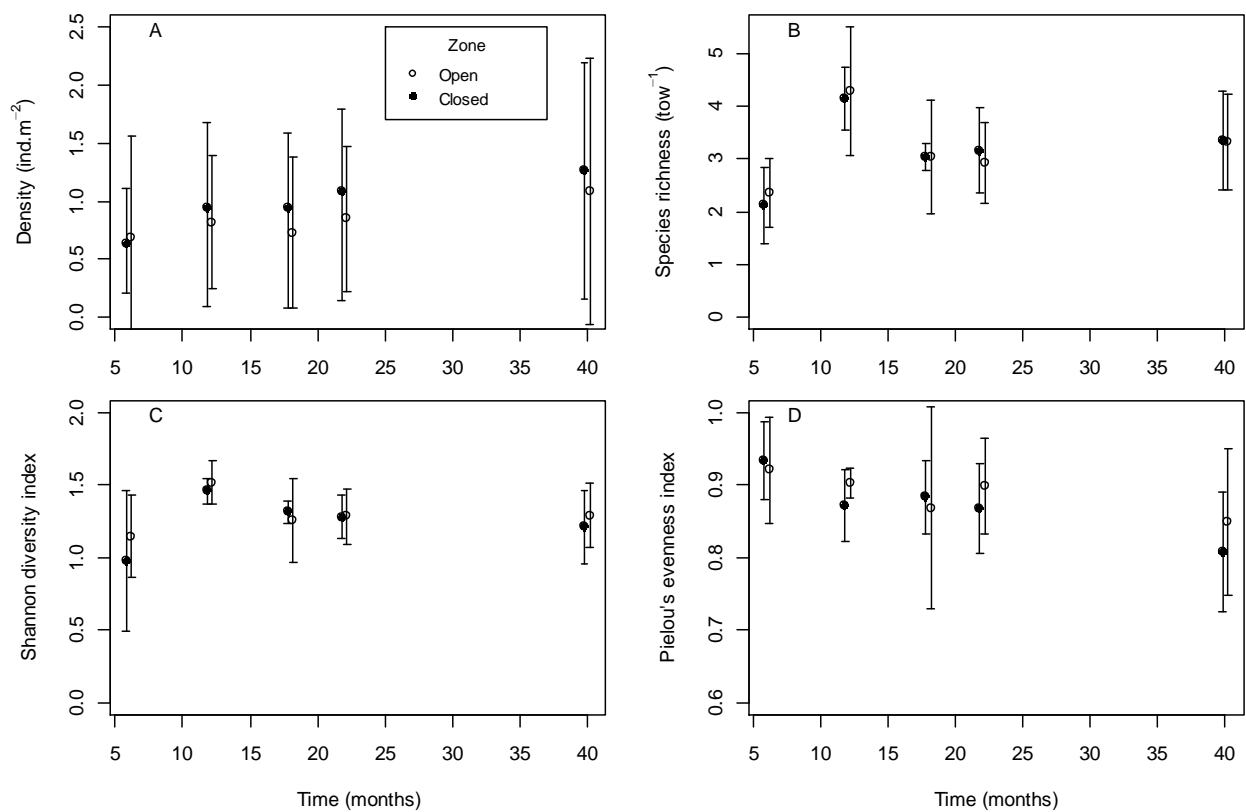


Figure 7. Changes in univariate measures of the epifaunal community, in the open and closed areas of the SAC, with time (in months) since the permanently closed area was introduced. Mean \pm standard deviation of square root transformed data for, A: total epifaunal density (individuals m^{-2}), B: species richness (number of species per camera tow), C: Shannon-Weiner diversity index (H'), and D: Pielou's evenness index (J'). Note that points have been separated slightly along the x-axis for ease of interpretation.

3.2.4 (H4) Spatial and temporal trends in fishing sensitive traits

Of the 40 modalities used in the analysis of function, 19 were found to account for the top 80% of trait modality densities over all five surveys (Table 9). All 11 traits used in this study

were represented by at least one modality in the top 80% of trait modality densities. The list of trait modalities in Table 8 consists of both fishing sensitive and robust modalities.

Table 9. Traits and modalities accounting for over 80% of the total trait modality density, in both the open and closed area of the SAC, over all five survey occasions. Percentage contribution of each modality is also displayed.

Trait	Modality	Contribution (%)
Sexual differentiation	Gonochoristic	6.6
Reproductive method	Broadcast spawning	6.3
Feeding habit	Filter feeder	5.9
Movement	Sessile	5.3
Sociability	Colonial	5.1
Body flexibility	>45°	4.6
Attachment	Permanent	3.9
Mobility	Low	3.8
Size	Medium (11-20 cm)	3.8
Attachment	None	3.6
Lifespan	>5 years	3.5
Body form	Upright	3.4
Body form	Flat	3.2
Size	Small-medium (3-10 cm)	3.2
Movement	Crawl	3.1
Body flexibility	10-45°	3.0
Body form	Mound	2.7
Sociability	Gregarious	2.4
Life span	<2 years	2.3

For nearly all the fishing sensitive trait modalities, there was a significant effect of time. The only exception being the reproductive method of sexual reproduction to produce offspring which are miniature adults (Table 10, Fig. 8). Note that large size (>50 cm) has not been included due to absence of this trait from most surveys.

Of the trait modalities with significant effect of time, the difference between surveys was always caused, at least in part, by low densities of a specific modality in December 2009, as revealed by Tukey HSD tests. There was also an influence of high densities of modalities in the summer surveys (Jun 10 and October 2012) for all trait modalities with a significant effect of time except >5 year lifespan (where the differences lay between December 2009 and April 2011).

There was also a significant zone effect for some trait modalities including no mobility, permanent attachment, sessile movement, upright body form, filter-suspension feeding habit, and colonial sociability (Table 10). All of these trait modalities had greater mean values in the closed area compared to the open area for surveys 12-40 months (June 2010-October 2012) after the SAC was closed to fishing (Fig. 8D,G,H,J,K,M). Despite this, proportional changes in density weighted fishing sensitive trait modalities in the open and closed area lead to no significant effect of the time x zone interaction for any of the fishing sensitive trait modalities (Table 10, Fig. 8).

Table 10. Results of two-way crossed ANOVA for the effect of zone, time (survey occasion), and their interaction on the selected fishing sensitive trait modalities. All data was square-root transformed. Information displayed for degrees of freedom (df), sum of squares (SS), mean square (MS), F-statistic (F), and P-value (P). The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$ (table continues on following page).

Trait	Modality	<i>F</i>	<i>P</i>	
Size	Medium-large			
	Zone	2.176	0.143	
	Time	10.539	<0.001	***
	Zone x Time	0.705	0.590	
Lifespan	>5 years			
	Zone	1.426	0.2346	
	Time	3.067	0.0189	*
	Zone x Time	1.232	0.3007	
Reproductive method	Sexual - mini adults			
	Zone	0.006	0.936	
	Time	1.058	0.380	
	Zone x Time	0.324	0.861	
Mobility	None			
	Zone	18.282	<0.001	***
	Time	15.930	<0.001	***
	Zone x Time	1.125	0.348	
	Low			

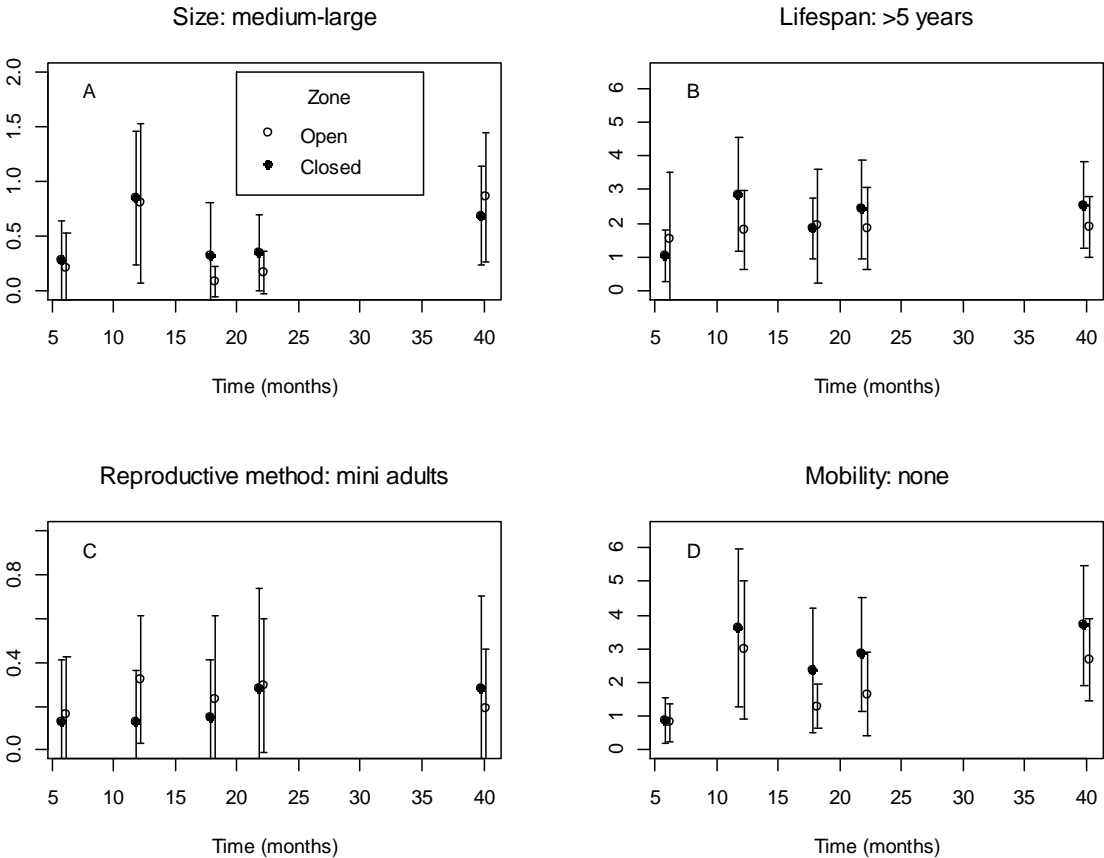
Attachment	Temporary	Zone	1.112	0.294	
		Time	8.277	<0.001	***
		Zone x Time	0.417	0.796	
	Temporary	Zone	2.245	0.137	
		Time	14.005	<0.001	***
		Zone x Time	0.313	0.869	

Table 10 (continued). Results of two-way crossed ANOVA for the effect of zone, time (survey occasion), and their interaction on the selected fishing sensitive trait modalities. All data was square-root transformed. The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$.

Trait	Modality		<i>F</i>	<i>P</i>	
Attachment	Permanent				
		Zone	18.701	<0.001	***
		Time	16.808	<0.001	***
		Zone x Time	1.041	0.389	
Movement	Sessile				
		Zone	13.807	<0.001	***
		Time	19.690	<0.001	***
		Zone x Time	0.829	0.509117	
Body flexibility	<10°				
		Zone	1.001	0.319098	
		Time	5.851	<0.001	***
		Zone x Time	1.168	0.328393	
Body form	Upright				
		Zone	20.637	<0.001	***
		Time	14.724	<0.001	***
		Zone x Time	1.316	0.268	

Feeding habit	Filter-suspension			
		Zone	8.217	0.00487 **
		Time	9.108	<0.001 ***
		Zone x Time	1.558	0.18976
Sexual differentiation	Gonochoristic			
		Zone	4.939	0.028
		Time	12.948	<0.001 ***
		Zone x Time	0.756	0.556
Sociability	Colonial			
		Zone	15.323	<0.001 ***
		Time	22.076	<0.001 ***
		Zone x Time	0.791	0.533092

Density of trait modality (trait modality m⁻²)



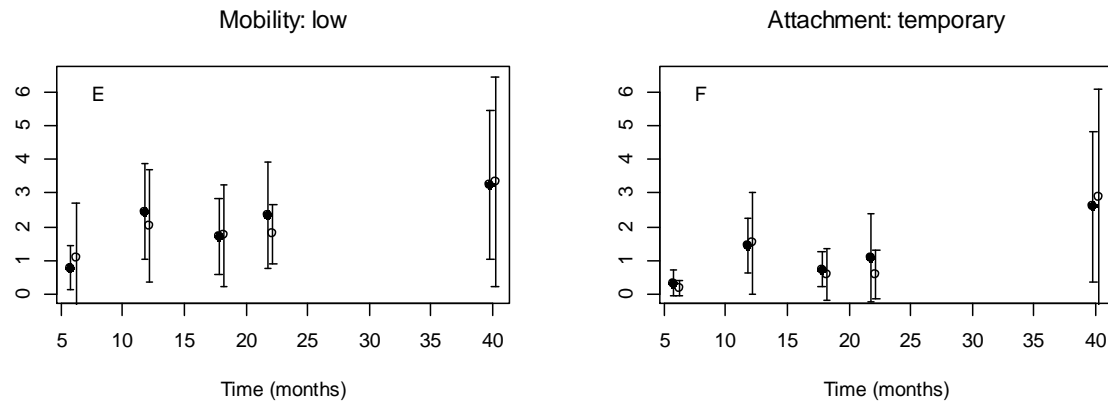


Figure 8. Changes in density weighted fishing sensitive trait modalities, in the open and closed areas of the SAC, with time (in months) since the permanently closed area was introduced. Each plot is labelled with the traits modalities it displays. Points are mean \pm standard deviation of square-root transformed data. Note that points have been separated slightly along the x-axis for ease of interpretation (figure continues on following page).

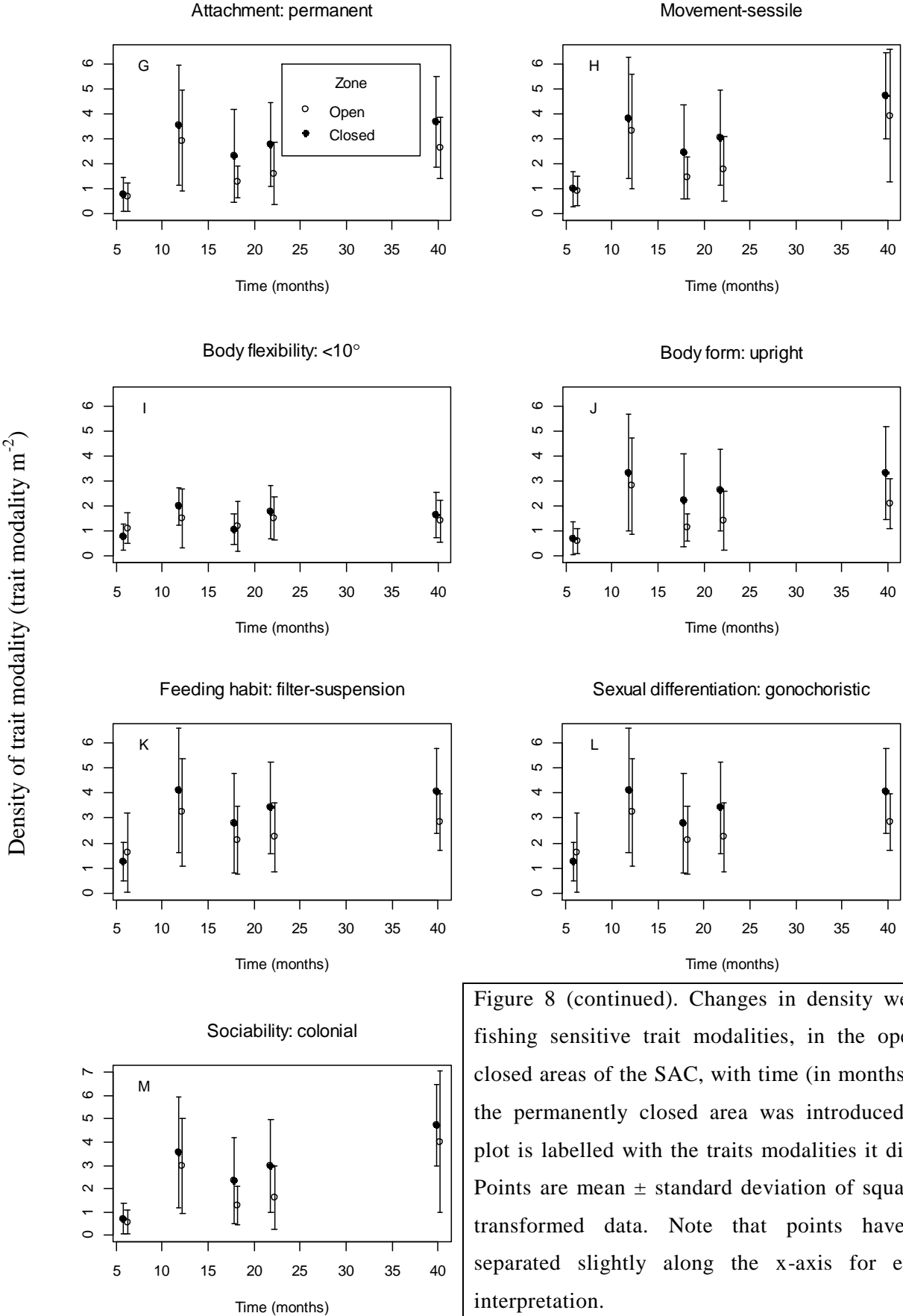


Figure 8 (continued). Changes in density weighted fishing sensitive trait modalities, in the open and closed areas of the SAC, with time (in months) since the permanently closed area was introduced. Each plot is labelled with the traits modalities it displays. Points are mean \pm standard deviation of square-root transformed data. Note that points have been separated slightly along the x-axis for ease of interpretation.

3.2.5 (H5) Spatial and temporal trends in the diversity of functional traits

The diversity of functional traits was also found to change over time but there was no significant effect of zone or the interaction (Table 11, Fig. 9). The change in time was driven by low mean diversity in December 2009 compared to June 10 as revealed by a Tukey HSD test. However, it is evident that deviation around mean values is high (Fig. 9) and any significant results should be interpreted with caution.

Table 11. Results of two-way crossed ANOVA for the effect of zone, time (survey occasion), and their interaction on Shannon diversity (H') of trait modalities. All data was square-root transformed. Information displayed for degrees of freedom (df), sum of squares (SS), mean square (MS), F -statistic (F), and P-value (P). The level of statistical significance is also indicated; $P < 0.05 = *$, $P < 0.01 = **$, and $P < 0.001 = ***$.

Source	df	SS	MS	F	P
Zone	1	0.0083	0.00832	3.787	0.0519
Time	4	0.2619	0.06548	29.810	<0.001 ***
Zone x Time	4	0.0063	0.00158	0.721	0.5774
Residual	1230	2.7017	0.00220		

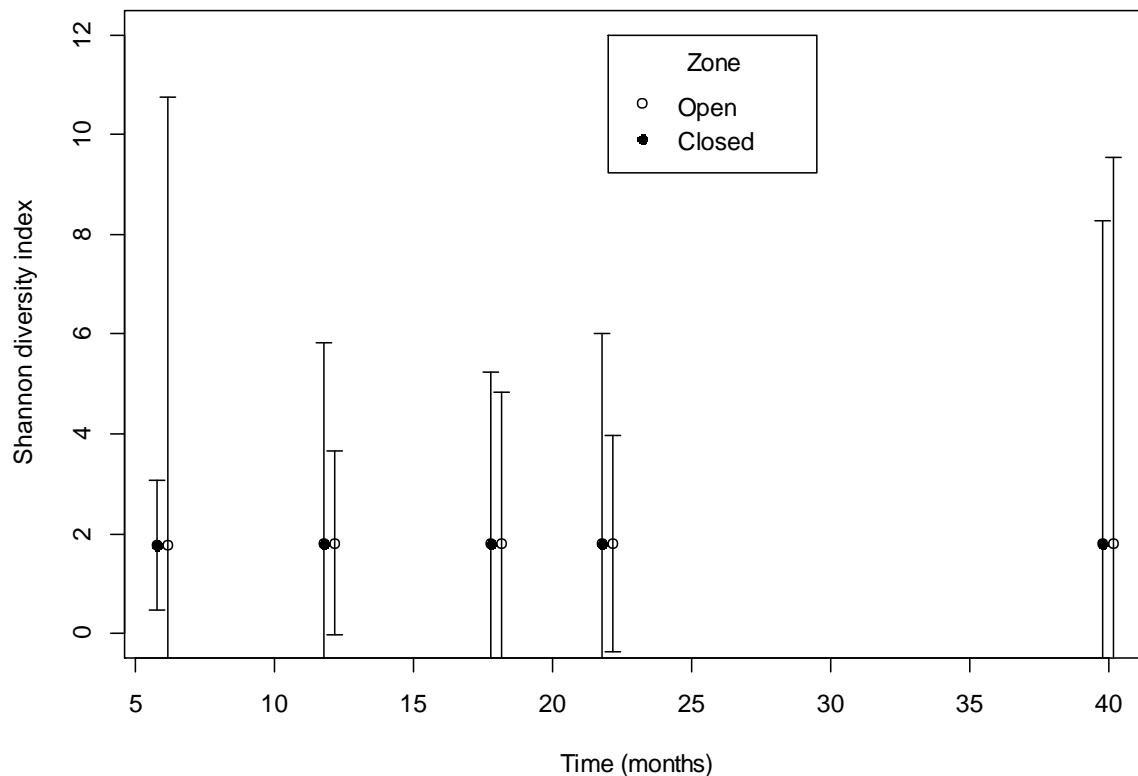


Figure 9. Changes in Shannon diversity (H') of density weighted trait modalities, in the open and closed areas of the SAC, with time (in months) since the permanently closed area was introduced. Points are mean \pm standard deviation of square-root transformed data. Note that points have been separated slightly along the x-axis for ease of interpretation.

4 Discussion

Although this study identified changes in both taxonomic and functional community composition through time and between zones, these changes were similar in both the open and closed areas of the Cardigan Bay SAC (Fig 3 & Fig 5). This suggests that fishing is not responsible for these changes. If it were responsible, different trends would have been observed in the two zones. The surveys where there was a significant difference in taxonomic composition between zones were identified as December 2009 and April 2011. For functional composition, the April 2011 survey was identified as responsible for the significant difference between zones.

In the December 2009 and April 2011 surveys there was more sampling in the closed area towards the east of the SAC (Fig. 2). Seabed sediment composition can have strong influences on community composition. With large cobbles or rocks providing surfaces for epifauna to colonise, while fine, cohesive, mud sediments enable infauna to create stable burrows (Thrush et al. 2003). The eastern side of the SAC is known to have had different sedimentary composition to the open area and western side of the SAC, with a greater proportion of sand (Hinz et al. 2010a). Although this study did not identify a significant difference between zones (Table 4), habitat type was classified into broad categories which may not have been able to detect more subtle changes in sedimentary habitats. It is recommended that a detailed analysis of seabed habitats be conducted in future studies. If this is not achievable, as accurate description of sediment type can be difficult to obtain from still images of the seabed, then it is recommended that sampling be confined to the western portion of the closed area, and the open area of the SAC as these regions have been seen to be more closely similar in their sediment composition (Hinz et al. 2010a).

Similar spatial and temporal trends were observed for the univariate measures of the taxonomic and functional community. Total epifaunal density, species richness, diversity, and evenness for the taxonomic analysis and fishing sensitive traits and diversity of trait modalities for the functional analysis. Most of these measures of the epifaunal community varied in time (apart from the fishing sensitive trait modality of sexual reproduction to produce offspring which are miniature adults, for which there was no significant effect of time or zone). However, trends in the open and closed area were once again similar. It should be noted that some bias was introduced in the methodology used to measure species richness and diversity as a different number of images were used in different surveys. Despite this, the results obtained for the period between December 2009 and April 2011 are similar to the results obtained by Sciberras et al. (2013) and for the October 2012 survey 20 images were randomly selected from all stations. Therefore, although caution is advised when interpreting differences between October 2012 and the four other surveys, no bias has been introduced between the two zones in the October 2012 survey.

The temporal variation in community composition is likely influenced by seasonal changes in water temperature and productivity. Spring and summer blooms in phytoplankton can increase the availability of food for filter feeding organisms, providing energy for growth and reproduction (Bavestrello et al. 2006). In winter months, natural disturbance events such as

waves created by storms can disturb the seabed and alter community composition (Posey et al. 1996). The study site is known to be dominated by hydroids (Table .7), and many temperate or boreal hydroid species display seasonal cycles in abundance, with a spring and summer growth season and winter dormancy or regression (Coma et al. 2000, Bavestrello et al. 2006).

As no significant interaction of time and zone was identified in this study, it appears that the scallop fishery has not had observable negative impacts on the taxonomic or functional communities in the closed area of the SAC. This is a similar result to that obtained by Sciberras et al. (2013) for taxonomic composition, even after an additional 18 months since the permanently closed area was introduced. The reasons for this lack of response to the permanently closed area have previously been attributed to the mobile sand wave habitat present in Cardigan Bay (Sciberras et al. 2013). The sand waves, which are moved by waves and tidal currents, make for an unstable constantly shifting seabed. This can result in rapid infilling of trawl tracks, which has been shown to take approximately three weeks in Cardigan Bay, but may also regularly uncover then recover underlying cobble and rock habitats (Hinz et al. 2010a, Hinz et al. 2010b). The regular disturbance of epifauna living on these rocks and cobbles could be analogous to the disturbance caused by scallop dredging, in that epifauna will be required to find new substrate to colonise after disturbance events. As a result the epifauna in Cardigan Bay SAC could be tolerant of scallop fishing as they are adapted to frequent disturbance events (Sciberras et al. 2013).

From the information obtained on the epifaunal community present in Cardigan Bay SAC it seems likely that recovery would be rapid. The December 2009 survey can be identified as being dissimilar from the four other surveys in terms of its taxonomic (Fig. 3) and functional (Fig. 5) community composition. This has previously been attributed to rough weather shortly before the survey (Sciberras et al. 2013). The differences in taxonomic composition between December 2009 and the other four surveys was shown to be driven by the increase in density of a number of epifaunal species, including a number of taxa which were hydroids (*Hydrallmania falcata*, *Nemertesia antennina*, *Nemertesia ramosa*, and hydroid turf) (Fig. 4), this is in agreement with the findings of Sciberras et al. (2013). Additionally this study has identified that difference in functional composition between December 2009 and the other four surveys was driven by increased densities of a number of trait modalities (both sensitive and robust to the impacts of fishing). The most consistent pattern however, is that of an

increased density of organisms which are relatively small in size (< 2 cm and 3-10 cm), short lived (< 2 years and 2-5 years), sessile, attached to the seabed and reproduce by broadcast spawning and/or have planktonic larvae. This supports the idea that the epifaunal community in Cardigan Bay are adapted to the unstable environmental sedimentary habitat and are able to recover quickly due to a short life cycle and large dispersal range. As there are signs of disturbance and subsequent recovery from the winter storms in December 2009, but no signs of disturbance or recovery from the scallop fishery, this study provides more evidence that the impacts of the scallop fishery at its current level of effort are within the range that can be tolerated by epifaunal communities in the Cardigan Bay SAC.

It may still be possible however, that 40 months is not an adequate period of time for signs of recovery to emerge. There has been a scallop fishery in Cardigan Bay for over 30 years (Sciberras et al. 2013), although the number of boats and equipment used will have changed. Over long periods of time fisheries can cause more long lasting damage to seabed habitats. The process of “cleaning” a fishing ground involves removing large structures like rocks which have the potential to damage fishing gear or catch if they are caught in a trawl. Cleaning of fishing grounds is known to have occurred in the Isle of Man scallop fishery and may have happened in Cardigan Bay as well. The removal of rocks reduces habitat complexity and may be one factor that has resulted in long term changes in community composition in the Irish Sea. These long term changes are characterised as an increase in mobile, robust, scavenging taxa and decrease in sessile, fragile taxa over the last 60 years (Bradshaw et al. 2002).

Studies that have investigated recovery of seabed communities after disturbance from bottom trawling fisheries have identified quite different recovery times from one another. Strain et al. (2012) found that a scallop fishery operating in Strangford Loch had altered the functional and taxonomic composition of benthic communities. Divers assessed the presence and absence of benthic fauna at designated sites before and after the 10 year operation of the scallop trawl fishery and it was concluded that fishing may have played a role in observed changes in community composition. Before the scallop fishery developed, the loch was characterised by sessile filter feeders which can attach themselves to the seafloor (such as the bivalves; *A. opercularis*, *Modiolus modiolus*, and *Chlamys vira*) and permanently attached upright filter feeders (such as the ascidian *Ascidella aspersa*, and the anthozoan, *Alcyonium digitatum*). 12 years after the period of trawling had ended the Loch was still characterised by

mobile predators and scavengers (such as: the asteroids, *Asterias rubens*, *Crossaster papposus*, *Henricia oculata*; and the decapods, *Cancer pagurus*, and *Necora puber*) (Strain et al. 2012).

Strangford Loch however, is a very different habitat to that found in Cardigan Bay, as it is sheltered from waves with low levels of background disturbance (Strain et al. 2012). The example of the Inshore Potters Agreement (IPA) on the Devon coast is more comparable to the Cardigan Bay SAC as it also consists of a moderately exposed stretch of coastline with predominantly sand and gravel substrate. The IPA is a network of zones with different gear restrictions, including areas where bottom trawling is not permitted (Blythe et al. 2004). Although complete recovery to a “pristine state” was not identified Blythe et al. (2004) found there to be signs of recovery, in the form of significantly greater species richness and biomass in areas closed to bottom trawling compared to those that remained open, after just two years. As there are still no signs of recovery after over three years of closure to the fishery in Cardigan Bay SAC it seems increasingly likely that the closed area of the SAC is not influencing the epifaunal communities it contains.

To conclude, the increase in time from 22 to 40 months since the permanent closure of an area of the Cardigan Bay SAC to a scallop dredge fishery has not revealed signs that epifaunal communities are benefiting from the fisheries exclusion. Patterns in taxonomic composition of epifaunal communities, total epifaunal density, species richness, diversity, and evenness remain consistent with those identified by Sciberras et al. (2013). These patterns are of similar changes through time in both the open and the closed area of the SAC. This study has identified similar patterns in the ecological function of the epifaunal community, density of fishing sensitive traits, and diversity of traits. The failure of the Cardigan Bay SAC to promote recovery of epifaunal communities has been attributed to high levels of background disturbance, in the form of a benthic habitat characterised by mobile sand waves. Epifauna in the Cardigan Bay SAC may be adapted to rapidly colonise disturbed areas through broadcast spawning and settlement of planktonic larvae.

Although there may still be a possibility of recovery from more long term damage caused by scallop fishing in Cardigan Bay, there is an increasing body of evidence (Hinz et al. 2010a, Hinz et al. 2010b, Sciberras et al. 2013) to suggest that epifaunal communities in the SAC are able to tolerate disturbance caused by the scallop fishery at its current level of effort. It is suggested that monitoring of epifauna continues but infaunal communities should also be

taken into account as they to have the potential to be impacted by bottom trawling (Kaiser et al. 2006).

Marine protected areas can be effective tools for conservation and for fisheries management. However, if they are implemented poorly they can have negligible or even negative effects on the environment they are designed to protect (Halpern 2003, Dinmore et al. 2003). Failure of MPAs can also result in a loss of support from stakeholder groups. This can in turn threaten future development of MPAs (Agardy et al. 2003).

The case of the Cardigan Bay SAC highlights the importance of taking into consideration the seabed habitat and the resilience of benthic communities to anthropogenic disturbance when designating MPAs for fisheries and conservation use. In cases where recovery rates are naturally high less strict restrictions on fishing effort, such as seasonal closures, may be more appropriate for achieving management goals (Agardy et al. 2003, Kaiser 2005).

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7 Appendix 1: R scripts

Examples of the scripts that I developed in the R statistical software (R core team 2013) to run the statistical tests described in the methods section of this report (section 2.5) are presented below with annotations.

7.1 Multivariate analysis of taxonomic composition

#~~~ in this script the data is prepared for the application of PERMANOVA and CAP

requires two sets of data, a community matrix and a table of predictor variables (Zone and Survey)

Load the libraries

library(vegan)

library(Hmisc)

library(labdsv)

library(BiodiversityR)

Read the dataset

setwd("") # insert ("working directory")

dat <- read.table("combined surveys.txt", sep="\t", header=T) # insert ("data")

dat[1,] # view first row of data

```
## Select the data that is needed
```

```
dat1 <- dat[,c(1:5)]
```

```
dat1<-subset(dat1,Survey!="Jun-12")
```

```
## form community matrix
```

```
dat1 <- aggregate(dat1$Density, by=list(dat1$Survey, dat1$Zone, dat1$Station.tow, dat1$Species), sum)
```

```
names(dat1) <- c("Survey", "Zone", "Station.tow", "Species", "Density")
```

```
community.mat <- reshape(dat1, v.names=c("Density"), timevar="Species",  
idvar=c("Survey","Zone","Station.tow"), direction="wide")
```

```
community.mat[is.na(community.mat)] <- 0 # make "NA"s = 0
```

```
rownames(community.mat) <-
```

```
paste(as.character(community.mat$Survey),as.character(community.mat$Station.tow),sep=".")
```

```
community.mat <- community.mat[,-c(1:4)] # remove columns with no species density data (information is  
retained in rownames)
```

```
community.mat<-community.mat[rownames(community.mat) %nin% c("Dec-09.5","Dec-09.61","Dec-  
09.62","Dec-09.73"),]# remove these stations as they have 0 species (the function %nin% is from the  
Hmisc library)
```

```
community.mat[1,]
```

```
## square root transform the community matrix
```

```
community.mat <- sqrt(community.mat)
```

```
## form table of predictor variables
```

```
pred.var <- dat1[,c(1:3)]#factors; survey, zone, and station
```



```

pred.var <- unique(pred.var)# removes duplicate combinations of values for survey, station, and zone.

rownames(pred.var) <- paste(as.character(pred.var$Survey),as.character(pred.var$Station.tow),sep=".")

pred.var <- pred.var[rownames(pred.var) %nin% c("Dec-09.5","Dec-09.61","Dec-09.62","Dec-09.73"),]

## put rownames for both matrices in alphabetical order

pred.var <- pred.var[order(rownames(pred.var)),]

community.mat<-community.mat[order(rownames(community.mat)),]

## perform PERMANOVA using the function adonis() from the vegan library

adonis(community.mat~pred.var$Zone*pred.var$Survey, permutations=9999, method="bray")

#~~~~~

## CAP analysis

ord.mod <- CAPdiscrim(community.mat~Survey, data=pred.var, dist="bray",axes=2,m=0)

ord.mod

# plot ordination

windows()

plot1 <- ordiplot(ord.mod,type="n")

plot2 <- as.data.frame(plot1$sites)

plot2$symbol <- c(rep(16,38),rep(17,55),rep(18,13),rep(15,12),rep(8,17))

plot2$colour <- 153

points(plot2$LD1,plot2$LD2, col=plot2$colour, pch=plot2$symbol)

```

```

legend("topright",c("Dec-09","Jun-10","Dec-10","Apr-11","Oct-12"),
pch=c(17,15,18,16,8),title="Survey")

## CAP analysis survey and zone

pred.var2 <- pred.var

pred.var2$Survey.Zone <- paste(as.character(pred.var2$Survey),as.character(pred.var2$Zone),sep=".")

rownames(pred.var2) <-
paste(as.character(pred.var2$Survey),as.character(pred.var2$Station.tow),sep=".")

pred.var2$rownm <- paste(as.character(pred.var2$Survey),as.character(pred.var2$Station.tow),sep=".")

ord.mod2 <- CAPdiscrim(community.mat~Survey, data = pred.var2, dist="bray",axes=2,m=0)

ord.mod2

## plot ordination with formatting of plots appearance

windows()

par(mar=c(4,4,2,9))

plot3 <- ordiplot(ord.mod2,type="n", xlab="Axis 1",ylab="Axis 2")

abline(h=0, col="gray")

abline(v=0, col="gray")

plot4 <- as.data.frame(plot3$sites)

plot4$rownm <- rownames(plot4)

plot5 <- merge(plot4, pred.var2, by=c("rownm"), all=T)

plot5 <- plot5[,c(1:3,7)]

plot6 <- plot5[order(plot5$Survey.Zone, decreasing=F),]

plot6$symbol <-
c(rep(15,27),rep(17,11),rep(15,23),rep(17,32),rep(15,7),rep(17,6),rep(15,8),rep(17,4),rep(15,9),rep(17,8))

```

```

#plot6$symbol <-
c(rep(1,27),rep(16,11),rep(2,23),rep(17,32),rep(5,7),rep(18,6),rep(22,8),rep(15,4),rep(3,9),rep(8,8))

plot6$colour <-
c(rep("black",27),rep("black",11),rep("darkred",23),rep("darkred",32),rep("darkgreen",7),rep("darkgreen",
6),rep("darkblue",8),rep("darkblue",4),rep("darkorange2",9),rep("darkorange2",8))

#plot6$colour <- "red"

points(plot6$LD1,plot6$LD2, col=plot6$colour, pch=plot6$symbol)

par(xpd=T)

legend(5,4,c("Dec-09 closed","Dec-09 open",
"Jun-10 closed",
"Jun-10 open",
"Dec-10 closed",
"Dec-10 open",
"Apr-11 closed",
"Apr-11 open",
"Oct-12 closed",
"Oct-12 open"),
pch=c(15,17,15,17,15,17,15,17,15,17),
col=c("darkred","darkred","darkblue","darkblue","darkgreen","darkgreen","black","black","darkorange2",
"darkorange2"),
title="Survey", bty="n")

## Create a species biplot

ord.mod4 <- add.spec.scores(ord.mod2,community.mat,method="cor.scores")

labels_sp <- substr(rownames(ord.mod4$scproj), 9,30)

```

```

axis1<-ord.mod4$proj

axis1<-as.data.frame(axis1)

X<-subset(axis1,LD1 < -0.3 | LD1 > 0.3)

Y<-subset(axis1,LD2 < -0.3 | LD2 > 0.3)

Z<-rbind(X,Y)

Z$species<-rownames(Z)

Z<-subset(Z, species %nin% c("Density.Nemertesia antenninal","Density.Hydrallmania
falcata1","Density.Epizoanthus couchii1"))

Z$sp<-c("A. digitatum","Bryozoan sp.,"C. lloydii","E. couchii", "Gibbula sp.,"H. falcata","Hydroid
turf","M. mitchellii","N. antennina","N. ramosa","O. albida","Bivalve sp.,"C. pumicosa","Nassarius
sp.,"Pandalidae","Porifera sp.,"Surpula sp.,"T. indivisa")

labels_sp <- Z$sp

windows()

par(mar=c(5,4,1,1))

plot(Z$LD1,Z$LD2, type="p",pch=19,xlim=c(-0.7,0.4), xlab="Axis 1", ylab="Axis 2")

abline(h=0,col="gray")

abline(v=0,col="gray")

text(Z$LD1[c(8,10,17,14)],Z$LD2[c(8,10,17,14)], labels_sp[c(8,10,17,14)], cex=0.8, pos=4)

text(Z$LD1[c(1,5,9,15)],Z$LD2[c(1,5,9,15)], labels_sp[c(1,5,9,15)], cex=0.8, pos=1)

text(Z$LD1[-c(1,5,9,15,8,10,17,14)],Z$LD2[-c(1,5,9,15,8,10,17,14)], labels_sp[-c(1,5,9,15,8,10,17,14)],
cex=0.8, pos=3)

```

7.2 Multivariate analysis of functional composition

#~~~ in this script the data is prepared for the application of PERMANOVA and CAP to the functional trait modalities density data.

```
## Load the libraries
```

```
library(vegan)
```

```
library(Hmisc)
```

```
library(labdsv)
```

```
library(BiodiversityR)
```

```
## Read the dataset
```

```
setwd("") # insert ("working directory")
```

```
dat <- read.table("combined surveys.txt", sep="\t", header=T) # insert ("data")
```

```
dat[1,]
```

```
## select data required
```

```
dat1 <- dat[,-c(6)]
```

```
dat1 <- subset(dat1,Survey!="Jun-12")
```

```
dat1 <- dat1[,-40]
```

```
## create community matrix with trait densities instead of species
```

```
dat1[,c(6:41)]<-dat1$Density*dat1[,c(6:41)]#multiply fuzzy coded traits by density
```

```
community.mat <- dat1
```

```
require(reshape2)
```

```

df_melt <- melt(community.mat, id = c("Survey", "Zone", "Station.tow", "Species", "Density"))

community.mat <- dcast(df_melt, Survey + Zone + Station.tow ~ variable, sum, na.rm=T)

rownames(community.mat) <-
paste(as.character(community.mat$Survey),as.character(community.mat$Station.tow),sep=".")

community.mat<-community.mat[rownames(community.mat) %nin% c("Dec-09.5","Dec-09.61","Dec-
09.62","Dec-09.73"),]

community.mat1<-community.mat[,-c(1:3)]

## square-root transform the community matrix

community.mat1 <- sqrt(community.mat1)

## form table of predictor variables

pred.var <- community.mat[,c(1:3)]

pred.var <- unique(pred.var)# removes duplicate combinations of values for survey, station, and zone.

rownames(pred.var) <- paste(as.character(pred.var$Survey),as.character(pred.var$Station.tow),sep=".")

pred.var<-pred.var[rownames(pred.var) %nin% c("Dec-09.5","Dec-09.61","Dec-09.62","Dec-09.73"),]

## put rownames for both matrices in alphabetical order

pred.var <- pred.var[order(rownames(pred.var)),]

community.mat1<-community.mat1[order(rownames(community.mat1)),]

## perform PERMANOVA using the function adonis() from the vegan library

adonis(community.mat1~pred.var$Zone*pred.var$Survey, permutations=9999, method="bray")

##~~~~~

```

```
## CAP
```

```
community.mat1<-community.mat1[,-35]
```

```
## CAP analysis using function CAPdiscrim()
```

```
ord.mod <- CAPdiscrim(community.mat1~Survey, data=pred.var, dist="bray",axes=2,m=0)
```

```
ord.mod
```

```
windows()
```

```
plot1 <- ordiplot(ord.mod)
```

```
plot2 <- as.data.frame(plot1$sites)
```

```
plot2$symbol <- c(rep(16,38),rep(17,55),rep(18,13),rep(15,12),rep(8,17))
```

```
plot2$colour <- 153
```

```
points(plot2$LD1,plot2$LD2, col=plot2$colour, pch=plot2$symbol)
```

```
legend("topright",c("Dec-09","Jun-10","Dec-10","Apr-11","Oct-12"),  
pch=c(17,15,18,16,8),title="Survey")
```

```
## CAP analysis survey and zone
```

```
pred.var2 <- pred.var
```

```
pred.var2$Survey.Zone <- paste(as.character(pred.var2$Survey),as.character(pred.var2$Zone),sep=".")
```

```
rownames(pred.var2) <-
```

```
paste(as.character(pred.var2$Survey),as.character(pred.var2$Station.tow),sep=".")
```

```
pred.var2$rownm <- paste(as.character(pred.var2$Survey),as.character(pred.var2$Station.tow),sep=".")
```

```

ord.mod2 <- CAPdiscrim(community.mat1~Survey, data = pred.var2, dist="bray",axes=2,m=0)

ord.mod2

windows()

par(mar=c(4,4,2,9))

plot3 <- ordiplot(ord.mod2,xlab="Axis 1",ylab="Axis 2")

abline(h=0, col="gray")

abline(v=0, col="gray")

plot4 <- as.data.frame(plot3$sites)

plot4$rownm <- rownames(plot4)

plot5 <- merge(plot4, pred.var2, by=c("rownm"), all=T)

plot5 <- plot5[,c(1:3,7)]

plot6 <- plot5[order(plot5$Survey.Zone, decreasing=F),]

plot6$symbol <-
c(rep(15,27),rep(17,11),rep(15,23),rep(17,32),rep(15,7),rep(17,6),rep(15,8),rep(17,4),rep(15,9),rep(17,8))

#plot6$symbol <-
c(rep(1,27),rep(16,11),rep(2,23),rep(17,32),rep(5,7),rep(18,6),rep(22,8),rep(15,4),rep(3,9),rep(8,8))

plot6$colour <-
c(rep("black",27),rep("black",11),rep("darkred",23),rep("darkred",32),rep("darkgreen",7),rep("darkgreen",
6),rep("darkblue",8),rep("darkblue",4),rep("darkorange2",9),rep("darkorange2",8))

#plot6$colour <- "red"

points(plot6$LD1,plot6$LD2, col=plot6$colour, pch=plot6$symbol)

par(xpd=T)

legend(4,4,c("Dec-09 closed","Dec-09 open",
"Jun-10 closed",
"Jun-10 open",

```



```

"Dec-10 closed",

"Dec-10 open",

"Apr-11 closed",

"Apr-11 open",

"Oct-12 closed",

"Oct-12 open"),

pch=c(15,17,15,17,15,17,15,17,15,17),

col=c("darkred","darkred","darkblue","darkblue","darkgreen","darkgreen","black","black","darkorange2",
"darkorange2"),

title="Survey", bty="n")

## Create biplot for each functional trait

ord.mod4 <- add.spec.scores(ord.mod2,community.mat1)

windows()

plot(ord.mod4$scproj[,1],ord.mod4$scproj[,2],type="n")

abline(h=0,col="gray")

abline(v=0,col="gray")

text(ord.mod4$scproj[,1],ord.mod4$scproj[,2], rownames(ord.mod4$scproj), cex=0.5,col="black")

###

```

```

axes<-ord.mod4$cproj

axes<-as.data.frame(axes)

axes<-subset(axes,LD1!="NA")

axes$Num<-
c("1","2","3","4","5","1","2","3","1","2","3","4","1","2","3","4","1","2","3","1","2","3","4","1","2","3","1",
,"2","3","1","2","3","4","5","1","2","3","1","2","3")

### Size

Size<-axes[c(1:5),]

windows()

plot(Size$LD1,Size$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis 1",ylab="Axis 2")

abline(h=0,col="gray")

abline(v=0,col="gray")

text(Size$LD1,Size$LD2, rownames(Size), cex=1)

### Lifespan

Lifespan<-axes[c(6:8),]

windows()

plot(Lifespan$LD1,Lifespan$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis 1",ylab="Axis
2")

abline(h=0,col="gray")

abline(v=0,col="gray")

```

```
text(Lifespan$LD1,Lifespan$LD2, rownames(Lifespan), cex=1)
```

```
### Reproduction
```

```
Reproduction<-axes[c(9:12),]
```

```
windows()
```

```
plot(Reproduction$LD1,Reproduction$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis  
1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(Reproduction$LD1,Reproduction$LD2, rownames(Reproduction), cex=1)
```

```
### Mobility
```

```
Mobility<-axes[c(13:16),]
```

```
windows()
```

```
plot(Mobility$LD1,Mobility$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis 1",ylab="Axis  
2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(Mobility$LD1,Mobility$LD2, rownames(Mobility), cex=1)
```

```
### Attachment
```

```
Attachment<-axes[c(17:19),]
```

```
windows()
```

```
plot(Attachment$LD1,Attachment$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis  
1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(Attachment$LD1,Attachment$LD2, rownames(Attachment), cex=1)
```

```
### Movement
```

```
Movement<-axes[c(20:23),]
```

```
windows()
```

```
plot(Movement$LD1,Movement$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis  
1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(Movement$LD1,Movement$LD2, rownames(Movement), cex=1)
```

```
###Body Flexability
```

```
Flexability<-axes[c(24:26),]
```

```
windows()
```

```
plot(Flexability$LD1,Flexability$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis  
1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(Flexability$LD1,Flexability$LD2, rownames(Flexability), cex=1)
```

```
###Body Form
```

```
BodyForm<-axes[c(27:29),]
```

```
windows()
```

```
plot(BodyForm$LD1,BodyForm$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis 1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(BodyForm$LD1,BodyForm$LD2, rownames(BodyForm), cex=1)
```

```
###Feeding habit
```

```
Feeding<-axes[c(30:34),]
```

```
windows()
```

```
plot(Feeding$LD1,Feeding$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis 1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(Feeding$LD1,Feeding$LD2, rownames(Feeding), cex=1)
```

```
###Sexual differentiation
```

```
SexualDifferentiation<-axes[c(35:37),]
```

```
windows()
```

```
plot(SexualDifferentiation$LD1,SexualDifferentiation$LD2,ylim=c(-0.4,0.5),xlim=c(-0.9,0.2),type="n",xlab="Axis 1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(SexualDifferentiation$LD1,SexualDifferentiation$LD2, rownames(SexualDifferentiation), cex=1)
```

```
###Sociability
```

```
Sociability<-axes[c(38:40),]
```

```
windows()
```

```
plot(Sociability$LD1,Sociability$LD2,xlim=c(-0.9,0.2),ylim=c(-0.4,0.5),type="n",xlab="Axis  
1",ylab="Axis 2")
```

```
abline(h=0,col="gray")
```

```
abline(v=0,col="gray")
```

```
text(Sociability$LD1,Sociability$LD2, rownames(Sociability), cex=1)
```

7.3 Univariate analysis of taxonomic measures

```
### spatial and temporal change in CB SAC ###
```

```
###          UNIVARIATE          ###
```

#~~in this session we prepared the data and tested hypothesies that; total density, spp. richness, diversity, and evenness are significantly different between zone, survey, and an interaction. Post hoc tests are also included

```
# Load the libraries
```

```
library(car)
```

```
library(vegan)
```

```
library(stats)
```

```
# Read the dataset
```

```
setwd("")
```

```
dat <- read.table("combined surveys.txt", sep="\t", header=T)
```

```
dat[1,]
```

```

dat1 <- dat[,c(1:5)]# contains columns; survey, zone, station, species

dat1<-subset(dat1,Survey!="Jun-12")

summary(dat1)

# create matrix in long format with density summed for each species at each tow in each zone on each
survey (removes any dupliates)

dat1 <- aggregate(dat1$Density, by=list(dat1$Survey, dat1$Zone, dat1$Station.tow, dat1$Species), sum)

names(dat1) <- c("Survey", "Zone", "Station.tow", "Species", "Density")#name the columns


##### total density #####

# Calculate total density per station (as aposed to per species above)

dat2 <- aggregate(dat1$Density, by=list(dat1$Survey, dat1$Zone, dat1$Station.tow), sum)

names(dat2) <- c("Survey", "Zone", "Station.tow", "Density")

summary(dat2)


mod.totden <- aov(sqrt(dat2$Density) ~ dat2$Zone*dat2$Survey) #make sure to include transformation if
it was used to meet assumptions

summary(mod.totden)


TukeyHSD(mod2)


##### Species richness #####

dat1$ones <- 1 #a collumn of 1s is added to the table

dat3 <- aggregate(dat1$ones, by=list(dat1$Survey, dat1$Zone, dat1$Station.tow), sum)#sum all 1s per
station to identify the number of sp./station

```

```
names(dat3) <- c("Survey", "Zone", "Station.tow", "sp.rich")#name each column
```

```
sp.rich<-subset(dat3,Survey!="Jun-12")
```

```
mod.sp.rich <- aov(sqrt(sp.rich$sp.rich) ~ sp.rich$Zone*sp.rich$Survey) #make sure to include
transformation if it was used to meet assumptions
```

```
summary(mod.sp.rich)
```

```
TukeyHSD(mod.sp.rich)
```

```
##### Diversity #####
```

```
# Change dataset into community matrix.
```

```
#reshape() so there are columns of density for each species, and stations are rows (maintaining the
information for their survey and zone
```

```
community.mat <- reshape(dat1, v.names=c("Density"), timevar="Species",
idvar=c("Survey","Zone","Station.tow"), direction="wide")
```

```
community.mat[1,]
```

```
community.mat[is.na(community.mat)] <- 0 # make "NA"s = 0
```

```
# add rownames, survey and station.
```

```
##### THIS STOPS VALUES BEING ASIGNED TO THE WRONG STATION/SURVEY###
```

```
rownames(community.mat)
```

```
paste(as.character(community.mat$Survey),as.character(community.mat$Station.tow),sep=".")
```

```
<-
```



```

#Shannon diversity

#apply to species densitys only so exclude survey, zone, station,ones, and density

div <- diversity(community.mat[,-c(1,2,3,4,5)], index = "shannon", MARGIN = 1, base = exp(1))

#now we need to match up the diversity metrics with the correct stations

#prepare a diversity table with 1 column (diversity) and rownames (which are survey and station)

div1 <- as.data.frame(cbind(rowname=rownames(div), div))

div1$rownm <- rownames(div1)# add a column which is the same as the rownames

# make a matrix with columns; survey, zone, station, density

dat2$rownm <- paste(as.character(dat2$Survey),as.character(dat2$Station.tow),sep=".")

#as both matrices have the same column "rowname" they can be merged together

#if two data frames have the same column, merge lines up these columns

div2 <- merge(dat2, div1, by=c("rownm"), all=T)

div2<-subset(div2,Survey!="Jun-12")

mod.div <- aov(sqrt(div2$div) ~ div2$Zone*div2$Survey) #make sure to include transformation if it was
used to meet assumptions

summary(mod.div)

TukeyHSD(mod.div)

#####Pielou's test for evenness

```

```
dat3$rownm <- paste(as.character(dat3$Survey),as.character(dat3$Station.tow),sep=".")
```

```
div2 <- merge(div2, dat3[,-c(1:3)], by=c("rownm"), all=T)
```

```
div2$J <- (div2$div/(log(div2$sp.rich)))
```

```
mod.J<-aov(sqrt(div2$J)~div2$Zone*div2$Survey)
```

```
summary(mod.J)
```

```
TukeyHSD(mod.J)
```

7.4 Univariate analysis of fishing sensitive trait modalities

##~ identify spatial and temporal change in trait modalities predicted to be fishing sensitive using two-way ANOVA and Tukey HSD tests.

```
## Read the dataset
```

```
setwd("")
```

```
dat <- read.table("combined surveys.txt", sep="\t", header=T)
```

```
## Select data
```

```
dat1 <- dat[,-c(6)]
```

```
dat1 <- subset(dat1,Survey!="Jun-12")
```

```
## calculate trait densities
```

```
dat1[,c(6:46)]<-dat1$Density*dat1[,c(6:46)]
```

```
dat1[1,]
```

```
## isolate fishing sensitive traits and perform ANOVA
```

```
##~ SIZE=large
```

```
L <- dat1[,c(1:5,10)]
```

```
L <- aggregate(L$S.5, by=list(L$Survey, L$Zone, L$Station.tow), sum)
```

```
names(L) <- c("Survey", "Zone", "Station.tow", "L")
```

```
mod.L<- aov(sqrt(L$L)~L$Zone*L$Survey)
```

```
summary(mod.L)
```

```
TukeyHSD(mod.L)
```

```
##~ SIZE = med-large
```

```
ML <- dat1[,c(1:5,9)]
```

```
ML <- aggregate(ML$S.4, by=list(ML$Survey, ML$Zone, ML$Station.tow), sum)
```

```
names(ML) <- c("Survey", "Zone", "Station.tow", "ML")
```

```
mod.ML <- aov(sqrt(ML$ML)~ML$Zone*ML$Survey)
```

```
summary(mod.ML)
```

```
TukeyHSD(mod.ML)
```

```
##~ LIFESPAN = long (>5 years)
```

```
long <- dat1[,c(1:5,13)]
```

```
long <- aggregate(long$L.3, by=list(long$Survey, long$Zone, long$Station.tow), sum)
```

```
names(long) <- c("Survey", "Zone", "Station.tow", "long")
```

```
mod.long <- aov(sqrt(long$long)~long$Zone*long$Survey)
```

```
summary(mod.long)
```

```
#TukeyHSD(mod.long)
```

```
##~ REPRODUCTIVE METHOD = sexual - mini adults
```

```
MA <- dat1[,c(1:5,17)]
```

```
MA <- aggregate(MA$R.4, by=list(MA$Survey, MA$Zone, MA$Station.tow), sum)
```

```
names(MA) <- c("Survey", "Zone", "Station.tow", "MA")
```

```
mod.MA<- aov(sqrt(MA$MA)~MA$Zone*MA$Survey)
```

```
summary(mod.MA)
```

```
TukeyHSD(mod.MA)
```

```
##~ MOBILITY = none
```

```
none <- dat1[,c(1:5,18)]
```

```
none <- aggregate(none$M.1, by=list(none$Survey, none$Zone, none$Station.tow), sum)
```

```
names(none) <- c("Survey", "Zone", "Station.tow", "none")
```

```
mod.none <- aov(sqrt(none$none)~none$Zone*none$Survey)
```

```
summary(mod.none)
```

```
TukeyHSD(mod.none)
```

```
##~ MOBILITY = low
```

```
low <- dat1[,c(1:5,19)]
```

```
low <- aggregate(low$M.2, by=list(low$Survey, low$Zone, low$Station.tow), sum)
```

```
names(low) <- c("Survey", "Zone", "Station.tow", "low")
```

```
mod.low<- aov(sqrt(low$low)~low$Zone*low$Survey)
```

```
summary(mod.low)
```

```
TukeyHSD(mod.low)
```

```
##~ ATTACHMENT = temporary
```

```
temp <- dat1[,c(1:5,23)]
```

```
temp<- aggregate(temp$A.2, by=list(temp$Survey, temp$Zone, temp$Station.tow), sum)
```

```
names(temp) <- c("Survey", "Zone", "Station.tow", "temp")
```

```
mod.temp<- aov(sqrt(temp$temp)~temp$Zone*temp$Survey)
```

```
summary(mod.temp)
```

```
TukeyHSD(mod.temp)
```

```
##~ ATTACHMENT = permanent
```

```
perm <- dat1[,c(1:5,24)]
```

```
perm<- aggregate(perm$A.3, by=list(perm$Survey, perm$Zone, perm$Station.tow), sum)
```

```
names(perm) <- c("Survey", "Zone", "Station.tow", "perm")
```

```
mod.perm<- aov(sqrt(perm$perm)~perm$Zone*perm$Survey)
```

```
summary(mod.perm)
```

```
TukeyHSD(mod.perm)
```

```
##~ MOVEMENT = sessile
```

```
sessile<- dat1[,c(1:5,25)]
```

```
sessile<- aggregate(sessile$H.1, by=list(sessile$Survey, sessile$Zone, sessile$Station.tow), sum)
```

```
names(sessile) <- c("Survey", "Zone", "Station.tow", "sessile")
```

```
mod.sessile<- aov(sqrt(sessile$sessile)~sessile$Zone*sessile$Survey)
```

```
summary(mod.sessile)
```

```
TukeyHSD(mod.sessile)
```

```
##~ BODY FLEXIBILITY = low (<10 degrees)
```

```
low<- dat1[,c(1:5,31)]
```

```
low<- aggregate(low$F.3, by=list(low$Survey, low$Zone, low$Station.tow), sum)
```

```
names(low) <- c("Survey", "Zone", "Station.tow", "low")
```

```
mod.low<- aov(sqrt(low$low)~low$Zone*low$Survey)
```

```
summary(mod.low)
```

```
TukeyHSD(mod.low)
```

```
##~ BODY FORM = upright
```

```
upright<- dat1[,c(1:5,34)]
```

```
upright<- aggregate(upright$FO.3, by=list(upright$Survey, upright$Zone, upright$Station.tow), sum)
```

```
names(upright) <- c("Survey", "Zone", "Station.tow", "upright")
```

```
mod.upright<- aov(sqrt(upright$upright)~upright$Zone*upright$Survey)
```

```
summary(mod.upright)
```

```
TukeyHSD(mod.upright)
```

```
##~ FEEDING HABIT = filter
```

```
filter<- dat1[,c(1:5,36)]
```

```
filter<- aggregate(filter$FD.2, by=list(filter$Survey, filter$Zone, filter$Station.tow), sum)
```

```
names(filter) <- c("Survey","Zone","Station.tow","filter")
```

```
mod.filter<- aov(sqrt(filter$filter)~filter$Zone*filter$Survey)
```

```
summary(mod.filter)
```

```
TukeyHSD(mod.filter)
```

```
##~ SEXUAL DIFFERENTIATION = gonochoristic
```

```
gono<- dat1[,c(1:5,41)]
```

```
gono<- aggregate(gono$SX.1, by=list(gono$Survey, gono$Zone, gono$Station.tow), sum)
```

```
names(gono) <- c("Survey","Zone","Station.tow","gono")
```

```
mod.gono<- aov(sqrt(gono$gono)~gono$Zone*gono$Survey)
```

```
summary(mod.gono)
```

```
TukeyHSD(mod.gono)
```

```
##~ SOCIABILITY = colonial
```

```
col<- dat1[,c(1:5,46)]
```

```
col<- aggregate(col$SC.3, by=list(col$Survey, col$Zone, col$Station.tow), sum)
```

```
names(col) <- c("Survey","Zone","Station.tow","col")
```

```
mod.col<- aov(sqrt(col$col)~col$Zone*col$Survey)
```

```
summary(mod.col)
```

```
TukeyHSD(mod.col)
```

7.5 Univariate analysis of trait diversity

#~ calculate the diversity of functional traits and their modalities and how this changes with zone and time since closure

two-way ANOVA and Tukey HSD tests

```
## Load the libraries
```

```
library(car)
```

```
library(vegan)
```

```
library(Hmisc)
```

```
library(labdsv)
```

```
## Read the dataset
```

```
setwd("")
```

```
dat <- read.table("combined surveys2.txt", sep="\t", header=T)
```

```
dat[1,]
```

```
## select only the data wanted
```

```
dat1 <- dat[,-c(6)]
```

```
dat1 <- subset(dat1,Survey!="Jun-12")
```

```
dat1[1,]
```

```
## create matrix of trait densities
```



```

dat1[,c(6:41)]<-dat1$Density*dat1[,c(6:41)]

community.mat <- dat1

require(reshape2)

df_melt <- melt(community.mat, id = c("Survey", "Zone", "Station.tow", "Species", "Density"))

community.mat <- dcast(df_melt, Survey + Zone + Station.tow ~ variable, sum, na.rm=T)

rownames(community.mat)
paste(as.character(community.mat$Survey),as.character(community.mat$Station.tow),sep=".")

## calculate shannon diversity

div <- diversity(community.mat[,c(1:3)], index = "shannon", MARGIN = 1, base = exp(1))

div1 <- as.data.frame(cbind(rowname=rownames(div), div))

div1$rownm <- rownames(div1)# add a column which is the same as the rownames

## convert back to long format

dat2<-dat1[,c(1:3,5)]

dat2$rownm <- paste(as.character(dat2$Survey),as.character(dat2$Station.tow),sep=".")

div2 <- merge(dat2, div1, by=c("rownm"), all=T)

## Two-way crossed ANOVA and TukeyHSD test

mod.div<-aov(sqrt(div2$div)~div2$Zone*div2$Survey)

summary(mod.div)

TukeyHSD(mod.div)

```

