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

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

KEY WORDS: Marine protected area · Fishery closure · Scallop dredging · Fishing impact · Epifauna · Natural disturbance · Underwater digital imagery · Side scan sonar

INTRODUCTION

Fishing with bottom towed gears such as beam trawls and scallop dredges impacts populations of by-catch species (Kaiser et al. 1996, Veale et al. 2000, Jenkins et al. 2001), reduces seabed habitat complexity and heterogeneity (Collie et al. 1997, 2000a), causes shifts in community structure and trophic interactions (Carbines & Cole 2009, Hinz et al. 2009, Strain et al. 2012) and alters the physical structure of the sea floor and biogeochemical processes (Schwing-

hamer et al. 1998, Smith et al. 2000, Jennings et al. 2005). The impacts and recovery times post fishing disturbance depend on the magnitude of the fishing disturbance relative to natural disturbance, and the nature of the habitat and species concerned (Collie et al. 2000b, Kaiser et al. 2002, Henry et al. 2006, Kaiser et al. 2006, Lambert et al. 2011). The effects of disturbance are likely to be short-lived for assemblages of biota that are subject to frequent natural perturbations, as animals that inhabit unconsolidated sediments are those with life histories adapted to fre-

quent disturbance by currents and re-suspension of sediment (Jones 1992, Jennings & Kaiser 1998, Collie et al. 2000b).

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

Cardigan Bay, Wales, has been an active scallop fishing ground in the UK for over 30 yr, with most of the scallop dredging occurring beyond 6 nautical miles (n miles) offshore (CCW 2010, Vanstaen & Silva 2010). Until recently, the scallop fishery in Cardigan Bay has been regulated by means of minimum landing size limits, restrictions on gear size, the number of dredges and the imposition of a seasonal closure (Scallop Fishing [Wales] Order 2005). An additional measure involving the permanent closure of the fishery within an area of Cardigan Bay was introduced in March 2010 (Scallop Fishing [Wales] Order 2010). The presence of the year-round spatial closure and the seasonal closure to scallop fishing in Cardigan Bay allowed us to examine the effect of these 2 types of closures on the wider ecosystem effects of scallop dredging.

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

Our study sought to examine the magnitude of impact from scallop dredging on the benthic community in Cardigan Bay and to use this case study to inform the debate about the efficacy of fisheries closed areas for fisheries management and conservation. This was achieved by (1) examining the density of target species (the scallops *Pecten maximus* and *Aequipecten opercularis*) and macro-epifaunal benthic community structure and diversity in the permanently closed area and the adjacent seasonally fished area, (2) examining the temporal changes in the community structure and diversity after the cessation of scallop dredging within the permanently closed area, and (3) examining the relationship between the intensity of scallop dredging and scallop density and community diversity in the seasonally fished area.

MATERIALS AND METHODS

Study area

The study was carried out in the Cardigan Bay Special Area of Conservation (SAC) in Cardigan Bay, Wales (Fig. 1). The SAC (960 km^2) was originally designated in 2004 to protect populations of bottlenose dolphin, grey seal and lamprey. The area is characterized by moderate-energy hydrodynamic conditions (current energy at the seabed: 0.13–1.16 N m^{-2}, wave energy at the seabed: 0.21–1.2 N m^{-2}, UKSeaMap 2010), and is exposed to prevailing south-westerly and westerly gales that can develop a large uninterrupted swell. The seabed in the SAC is characterized by fields of sand ribbons that are principally oriented in a SW–NE direction parallel to the prevailing tidal current (Hinz et al. 2010a,b). The study area is composed entirely of unconsolidated sediment, with sand (<2 mm), gravel (2–4 mm) and pebbles (4–64 mm) being the predominant sediment types (Hinz et al. 2010a,b). The western part of the study area is predominantly gravel, which becomes more sandy towards the east of the area (Hinz et al. 2010a,b). *Pecten maximus* and to a lesser extent *Aequipecten opercularis* are the main target species of the Cardigan Bay scallop fishery, which generally takes place beyond 6 n miles off the coast (Walmsley & Pawson 2007). Potting for lobsters, crabs and

whelks is also common, but this occurs within 6 n miles off the coast (Walmsley & Pawson 2007). Until 2009, the scallop fishery for *P. maximus* in Wales (including in the Cardigan Bay SAC) was mainly managed through minimum landing size, restrictions on the number of dredges and a seasonal closure that ran from 1 June to 31 October for waters beyond 3 n miles offshore (Table 1). Landings of scallops by the UK fleet increased by a factor of 2.6 since 1994, with the bulk of the increase occurring since 2008 (Almond & Thomas 2011). Concerns about the possible effects of increased levels of scallop fishing activ-
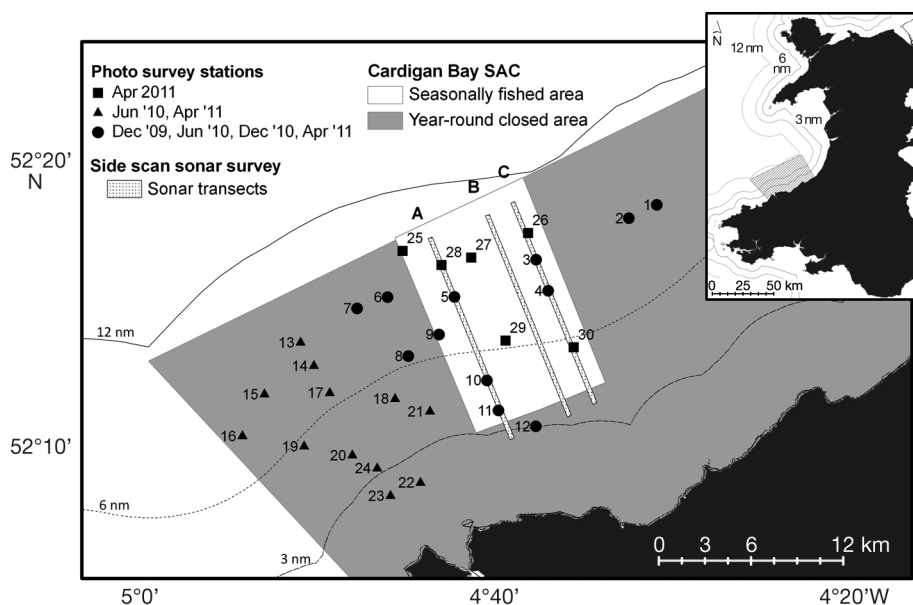

Fig. 1. Cardigan Bay Special Area of Conservation (SAC) along the Welsh coast (inset) and the spatial distribution of the underwater camera stations surveyed during the 4 sampling cruises (1–12, circles) inside the permanently closed area (grey) and the seasonally fished area (white). Stations labelled 13 to 24 (triangles) were surveyed only in June 2010 and April 2011. Stns 25 to 30 (squares) were surveyed inside the seasonally fished area in April 2011. The position of the side scan sonar transects surveyed in December 2009 and June 2010 is also shown (A–C). nm: nautical miles

Table 1. Legislation applicable to Welsh waters and evolution of the permanently closed area and the seasonally fished area in Cardigan Bay Special Area of Conservation (SAC). Sampling cruises are also given in *italics*

Legislation	Timeline	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	
Prohibition of Fishing for Scallops (Wales) Order 2009 No. 2721 (W. 232)	1 Jun 2009–28 Feb 2010	Closed season to SD in all Welsh waters extended to end of Feb 2010	
	10–17 Dec 2009	*Survey 1: photographic & side scan sonar*	
		Permanently closed area	**Seasonally fished 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
	13–19 Jun 2010	*Survey 2: photographic & side scan sonar*	
	1 Nov 2010–30 Apr 2011	Closed to SD	Open to SD
	29 Nov–4 Dec 2010	*Survey 3: photographic*	
	6–9 Apr 2011	*Survey 4: photographic*	
	1 May–31 Oct 2011	Closed to SD	Closed to SD

ity on the Cardigan Bay SAC and its habitat features, namely cobble reefs, resulted in an extended closed season to scallop dredging (from 1 May to 31 October), coupled with a year-round prohibition of scallop dredging within 75% of the SAC (hereafter referred to as the 'permanently closed area') from March 2010 onwards (Table 1, Fig. 1).

Data collection: survey design

Evaluation of the spatial and temporal variation of the macro-epibenthic assemblages between the permanently closed area and the seasonally fished area was carried out over 4 surveys between December 2009 and April 2011 (Table 1). During each of the 4 sampling events, 6 sites were surveyed within the permanently closed area and 6 within the seasonally fished area (Fig. 1). During the June 2010 and April 2011 surveys, an additional 12 sites were surveyed within the permanently closed area (giving a total of 18 sites) to assess community recovery following 13 and 23 mo of no scallop dredging (Fig. 1, Table 1). Additionally, we surveyed a total of 12 sites in the seasonally fished area during the April 2011 survey to examine the relationship between scallop fishing intensity and univariate measures of community response to seasonal fishing (e.g. density, diversity).

Sites were selected based on sediment data quantified from Hamon grab samples and underwater video camera tows carried out during a habitat assessment survey in the Cardigan Bay SAC prior to the present survey (Hinz et al. 2010a,b). Sites that were predominantly composed of gravel (>50% gravel) were selected to minimize confounding factors due to differences in sediment type. At each site, images of the seabed were taken with a high-resolution still camera (Canon 400D) installed in an underwater housing and mounted on a sledge such that the objective lens pointed perpendicularly towards the seabed from a height of 60 cm. The sledge was towed at a speed of approximately 1.0 knot for a period of 10 min, covering an average distance of 300 m, as calculated from the start and end positions of each tow. Tow direction depended on the speed and direction of the tidal current. A 10 megapixel image covering an area of 0.13 m^2 (0.44 × 0.30 m) was taken every 11 s.

Still image analysis

A minimum of 40 images were analysed per camera tow (average number of images analysed: 53 ± 10 SD). Epifaunal organisms were identified to the lowest taxonomic level possible and counted. Despite the high quality of the images, identification and quantification of some sessile epifauna presented a number of significant challenges. First, epifaunal annelids, in particular those belonging to the family Serpulidae, could not be quantified, as it was impossible to distinguish between live and dead specimens because live tubeworms are usually retracted in their tubes. Second, the taxonomy of some species of the phylum Porifera and the classes Hydrozoa, Bryozoa and Ascidiacea could not be resolved below these taxonomic levels, as these organisms necessitated microscopic study to identify distinguishing features. In this case, hydroid, poriferan and bryozoan species were recorded as 'Hydroid turf', 'Porifera indet.' and 'Bryozoan indet.', respectively.

Environmental data

The water depth at each site was calculated as an average of the depth at the start and end of the tow recorded by the echosounder and corrected for tidal state. Estimates of tidal-bed shear stress (N m^{-2}) at the study sites were derived from a 2-dimensional hydrographical model of the Irish Sea (see detailed description on shear stress calculations in Hiddink et al. 2006). Bed shear stress was used as a measure of natural disturbance to quantify tidally generated currents that affect sediment dynamics and hence the structure of the invertebrate community (Hall 1994). The percentage of sand, gravel and cobbles in the sediment was considered as a factor that could affect epifaunal distributions, as it is a surrogate for sediment stability. Substratum type was qualitatively identified from 40 still images selected at random from each tow. Each image was classified as predominantly sand, gravel or cobble when more than 50% of the image's surface area was covered by particles of diameters less than 2 mm, between 2 and 64 mm and between 64 and 256 mm, respectively. The percentage composition of each sediment type was then calculated for each tow.

Side scan sonar survey

While still images give a spatially more restricted impression of sediment types, the side scan sonar delivers spatially larger-scale information on ground topography. We conducted 2 side scan sonar surveys concurrent to the underwater camera surveys: 1 in

December 2009 and the other in June 2010 (Table 1). During each data collection event, we surveyed the same 3 transects in the seasonally fished area (Fig. 1) in order to determine temporal changes in seabed morphology related to the fishing activity or to natural hydrodynamic processes. In December 2009, a sonar range of 100 m (total swath width 200 m and sonar frequency 325 kHz) with the tow-fish altitude above the seabed kept between 5 and 10 m was employed for transect A (Fig. 1). Due to equipment failure halfway through the survey, transects B and C were surveyed using a sonar range of 200 m at a frequency of 100 kHz. In June 2010, all 3 transects were surveyed using a sonar range of 100 m at a frequency of 325 kHz and tow-fish altitude above the seabed between 5 and 10 m. Whenever possible, transects were run perpendicular to the coast as these gave the clearest images with the most distinct shadows.

Fishing intensity

Fishing intensity data for scallop dredging vessels were obtained from the European Community Satellite Vessel Monitoring System (VMS). To investigate the influence of fishing intensity on the benthic assemblage composition inside and outside the permanently closed area, we generated fishing intensity data estimates for the open seasons directly before each sampling event: November 2008 to May 2009 covering the open season prior to the December 2009 survey, March to May 2010 prior to the June 2010 survey, November to December 2010 prior to the December 2010 survey and November 2010 to April 2011 prior to the April 2011 survey. Note that the December 2009 survey was carried out before the establishment of the permanently closed area (refer to Supplement 1 at www.int-res.com/articles/suppl/m480p083_supp.pdf for the spatial distribution and intensity of the scallop fishing activity in the SAC throughout our sampling period). In addition, to examine the long-term effect of fishing on species density and diversity within the seasonally fished area, we generated average fishing intensity estimates over the entire sampling period (i.e. November 2008 to April 2011) for the sites sampled during the last sampling event in April 2011.

To calculate fishing intensities from VMS data, only data records of active scallop dredgers were included in the analysis. Some records did not specify fishing gear type. However, given that the primary fishing activity beyond 3 n miles in and around Cardigan Bay SAC is scallop dredging (CCW 2010,

Vanstaen & Silva 2010), these records were regarded as 'scallop dredgers'. Transmitted vessel speed was used to distinguish fishing from non-fishing records (Lee et al. 2010). Calculations of fishing intensity were restricted to vessel speeds of between 1 and 4 knots. Because our sampling tows covered relatively small areas of the seabed (total tow length = ca. 0.3 km) and because VMS records are transmitted at ~2 h intervals, positional records were interpolated to generate a more accurate estimate of fishing intensity at the spatial scale of our sampling sites. The inverse distance weighted interpolation method was used in ArcGIS 9.3 to interpolate positional records between 2 consecutive records transmitted by the same vessel using the 'heading' information for each VMS record. The modal time interval between interpolated records was 0.22 h.

Fishing intensity was defined as the number of times an area of 0.07 km^2 was swept by scallop dredgers in 1 mo. The area swept by each vessel was calculated as the product of the number of hours fished, average fishing speed (equal to 2.54 knots or 4.7 km h^{-1}) and gear width. Vessels fishing between 3 and 6 n miles were assumed to use 8 dredges (each with a width of 0.85 m) based on regulation, while vessels fishing beyond 6 n miles were assumed to carry 16 and 14 dredges, i.e. the maximum numbers of dredges allowed beyond 6 to 12 n miles before and after 2010, respectively (The Scallop Fishing [Wales] Order 2005, 2010). The actual fishing intensity at each site was then calculated as the sum of the area dredged from all the VMS records falling within the 0.07 km^2 area surrounding each video tow (Table 2).

Since the VMS is only mandatory for vessels over 15 m (EC 2003), the activity of vessels smaller than 15 m, particularly those between 8 and 15 m that have been shown to operate around and beyond 6 n miles offshore in Cardigan Bay (see Vanstaen & Silva 2010), was not represented. Therefore, estimates of fishing frequency may be underestimates of the actual fishing intensity, but are still useful indicators of the relative fishing pressure at the sampled sites.

Data analysis

Analysis of environmental characteristics of sampling sites

Multivariate analysis on normalized environmental data were performed using the analysis of similarity (ANOSIM) routine in PRIMER v.6 to test for differences in habitat characteristics between the 2 man-

Table 2. Summary of fishing intensity at each sampling station, expressed as the number of times an area equivalent to 0.07 km^2 around the study site was dredged per month. Bracketed values under the heading 'Entire sampling period' represent fishing effort as hours fished per month; –: not applicable

| Study site | Fishing frequency (mo^{-1}) | | | | Entire sampling period |
	Survey 1 (Nov 2008–May 2009)	Survey 2 (Mar–May 2010)	Survey 3 (Nov–Dec 2010)	Survey 4 (Nov 2010–Apr 2011)	(Nov 2008–Apr 2011)
1	0.2	0.0	0.0	0.0	–
2	0.6	0.0	0.0	0.0	–
3	0.3	0.1	0.3	0.1	0.1 (0.2)
4	0.8	0.0	2.0	0.3	0.4 (0.5)
5	0.4	0.1	0.7	0.3	0.3 (0.3)
6	0.2	0.0	0.0	0.0	–
7	0.1	0.0	0.0	0.0	–
8	0.3	0.0	0.0	0.0	–
9	0.3	0.0	0.0	0.0	0.1 (0.2)
10	0.2	0.0	0.0	0.0	0.1 (0.2)
11	0.1	0.0	0.0	0.1	0.03 (0.1)
12	0.0	0.0	0.0	0.0	–
25	–	–	–	–	0.1 (0.2)
26	–	–	–	–	0.1 (0.2)
27	–	–	–	–	0.1 (0.2)
28	–	–	–	–	0.1 (0.2)
29	–	–	–	–	0.1 (0.9)
30	–	–	–	–	0.1 (0.1)

agement areas (permanently closed versus seasonally fished) and among the sampling events. The following environmental variables were included: depth, percentage of sand, gravel and cobble, and tidal bed shear stress.

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

Prior to analysis, the abundance and species richness data from 40 images were pooled together for each tow and expressed as ind. m^{-2} and the number of species tow^{-1}, respectively, to facilitate comparisons between sites. The effects of the fishing closure ('Zone', 2 levels: permanently closed area, seasonally fished area) and the time of sampling event ('Time', 4 levels: December 2009, June and December 2010, April 2011) were examined on the following univariate measures: total epifaunal density, scallop density (*Pecten maximus*, *Aequipecten opercularis*), species richness, Shannon-Wiener diversity index and Pielou's evenness (DIVERSE routine in PRIMER-E v6) using a 2-way crossed analysis of variance (ANOVA). Given the nature of the fishing closure in the seasonally fished area, it may be unreasonable to expect an effect of fishing per se (i.e. 'Zone' effect alone), since the effects of fishing during the open season (November to April) may be lost when com-

munity production is at its lowest over the winter season. Rather, it may be expected that an effect of fishing be reflected in a 'Time × Zone' interaction where the abundance in the seasonally fished area is lower than in the permanently closed area during the open season (winter/spring), or else no different than the permanently closed area during the closed season (summer) if recovery processes are rapid enough to allow recovery of the community in the fished area to match that in the permanently closed area. The factor 'Time' can be considered to gather all effects (except fishing and protection) linked to temporal variations such as recruitment, natural mortality, disease, growth, emigration and immigration. Before proceeding with the ANOVAs, the data were examined for normality using the Kolmogorov-Smirnov test and Levene's test for homogeneity of variance. A log$_{10}$ or square root transformation was applied to stabilize variance when necessary.

Multivariate analyses were performed on density data to detect spatial and temporal changes in the epibenthic assemblage composition, using the PRIMER-E v6 statistical package (Clarke & Gorley 2006). The similarity between each pair of samples was calculated using the Bray-Curtis similarity index, after a square root transformation of the data was performed to reduce the influence of highly dominant species. The response of the multivariate epifaunal assemblage to the 2-factor ('Zone' and

'Time') sampling design was examined using permutational multivariate analysis of variance (PERMANOVA). Each factor in the model was tested through permutation tests based on 9999 permutations of residuals under a reduced model to obtain p-values. Canonical analysis of principal coordinates (CAP) was used to produce a constrained ordination to visualize the relationship between multivariate variation in the benthic assemblages and time of sampling event, which was the only factor identified as significant by PERMANOVA.

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

Analysis of temporal changes in the permanently closed area

The recovery of benthic epifauna after 13 mo (June 2010) and 23 mo (April 2011) of the cessation of scallop dredging within the permanently closed area was examined in terms of total density, scallop density (*Pecten maximus* and *Aequipecten opercularis*) and species richness, using 1-way ANOVAs. Whole-community approaches, using total densities to detect impacts of bottom fishing, sometimes miss differential responses between individual community components. Therefore, we also decomposed the total epifaunal density data to the level of taxonomic group to examine for potential shifts in assemblage structure. A log_{10} transformation was performed when necessary to achieve homogeneity of variance. The non-parametric equivalent Kruskal Wallis test was used when assumptions of variance were not met. For the multivariate data, the ANOSIM routine was used to test for changes between the epifaunal assemblages at different durations of closure. Density data were square-root transformed, and a Bray-Curtis similarity index matrix was calculated among samples. Similarity percentages (SIMPER) analysis was conducted to examine the contribution to dissimilarity of individual species between different durations of closure.

Effects of fishing intensity in the seasonally fished area

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

RESULTS

Environmental data: video tows and side scan sonar

The environmental characteristics of the 12 stations sampled inside and outside the permanently closed area did not change significantly among the 4 sampling events (ANOSIM; $R = −0.04$, $p = 0.9$) or between the 2 areas (ANOSIM; $R = 0.06$, $p = 0.05$). Stations within the permanently closed area were predominantly sandy interspersed with cobbles, whereas those within the seasonally fished area were on average composed of equal amounts of sand and gravel (Table 3). Both areas had very sparse cobbles (Table 3). Depth and tidal-bed shear stress did not differ significantly between the permanently closed area and the seasonally fished area (Table 3).

The sediment composition of the 18 stations sampled within the permanently closed area to assess recovery of the benthic community after the complete closure of the scallop fishery changed signifi-

Table 3. Summary of the abiotic habitat characteristics (mean ± SE) at sites sampled in the permanently closed area (Closed) and in the seasonally fished area (Open). A Mann-Whitney test indicated that none of the comparisons was significant

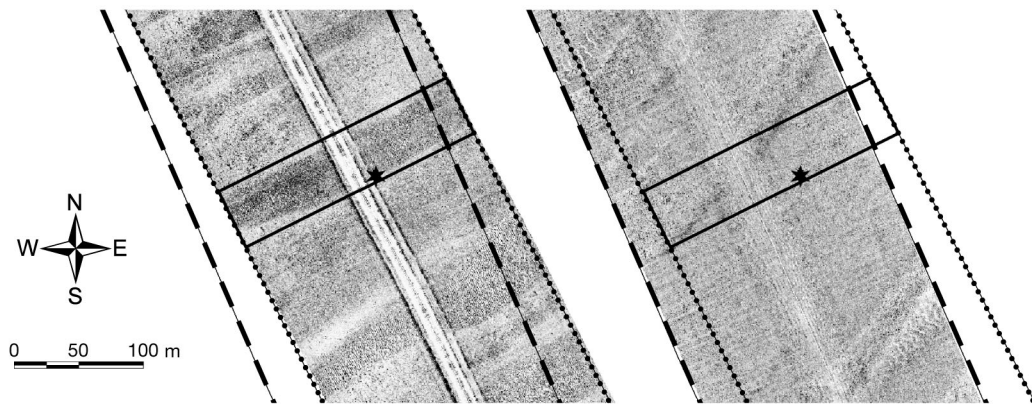| Environmental variable	Closed	Open
Cobble content (%)	3.2 ± 1.3	0.8 ± 0.5
Gravel content (%)	32.3 ± 5.5	50.1 ± 7.9
Sand content (%)	64.5 ± 5.5	49.2 ± 7.9
Bottom shear stress (N m^{-2})	0.4 ± 0.02	0.4 ± 0.01
Depth (m)	30.5 ± 1.5	30.4 ± 0.9

Fig. 2. Two sonar mosaics showing the same area of the seabed from the December 2009 survey (left) and the June 2010 survey (right) (the width of both sonar scans is 200 m). The outer edges of both sonar tracks illustrate the common seabed area covered (dotted: December 2009, dashed: June 2010). The asterisks show the location of a station from the photographic survey aiding correlation between the 2 data sets which are at the same scale and orientation. Features highlighted with a solid line indicate a shift in seabed morphology, whereby the sand ribbons over a coarse substratum (darker shadow) seen in December 2009 were replaced by a landscape dominated by sand ripples in June 2010, and also a change in the orientation of the sand ribbons between surveys
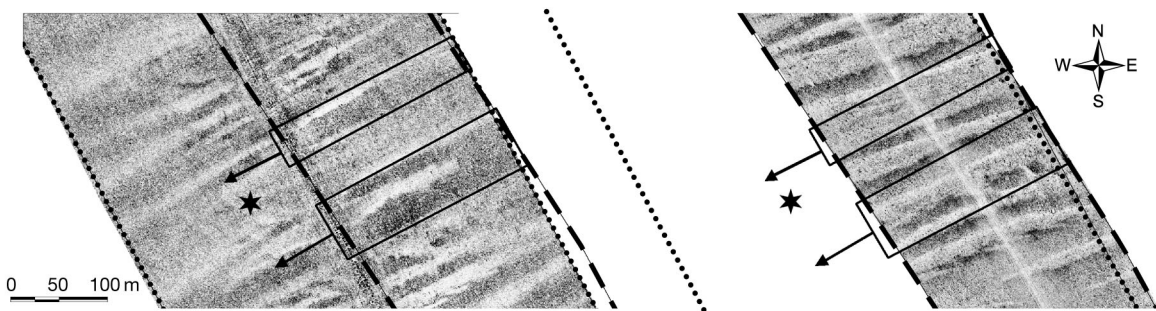

Fig. 3. Two sonar mosaics showing the same area of the seabed from the December 2009 survey (left) and the June 2010 survey (right) (the width of first sonar scan is 400 m and the second scan is 200 m). The outer edges of both sonar tracks illustrate the common seabed area covered (dotted: December 2009, dashed: June 2010). The asterisks show the location of a station from the photographic survey aiding correlation between the 2 data sets which are at the same scale and orientation. Features high lighted with a solid line indicate a change in position of the sand ribbons between surveys

cantly between the 2 sampling events. In June 2010, the dominant sediment type across the study sites was gravel with some cobbles (mean ± SE: % sand = 16.7 ± 4.8; % gravel = 72.1 ± 6.8; % cobbles = 11.2 ± 4.0), whereas in April 2011 stations were on average composed of equal amounts of sand and gravel (% sand = 49.7 ± 8.8; % gravel = 47.8 ± 8.6; % cobbles = 2.5 ± 1.3).

Examination of the side scan sonar records from the repeat surveys in December 2009 and June 2010 indicated temporal variation in seabed configuration. In December 2009, the bedform was characterized by numerous sand ribbons aligned parallel to the main tidal flow, with coarser gravely material in between the ribbons. Within these sand ribbons, mega ripples

occurred that were orientated perpendicular to the main tidal current. The repeat side scan sonar survey in June 2010 indicated a dominance of sand ribbons, but these were less extensive than in December 2009. Transect sections that overlapped significantly between the 2 surveys indicated temporal shifts in seabed morphology such as changes in topographic composition (Fig. 2) and the orientation and position of substratum features (Fig. 3). More examples are given in Supplement 2 at www.int-res.com/articles/suppl/m480p083_supp.pdf. Interestingly, there was little evidence of scallop dredging scour marks in December 2009 compared to June 2010. At the time of the first survey, the seasonally fished area had been closed to scallop dredging for a period of 6 mo,
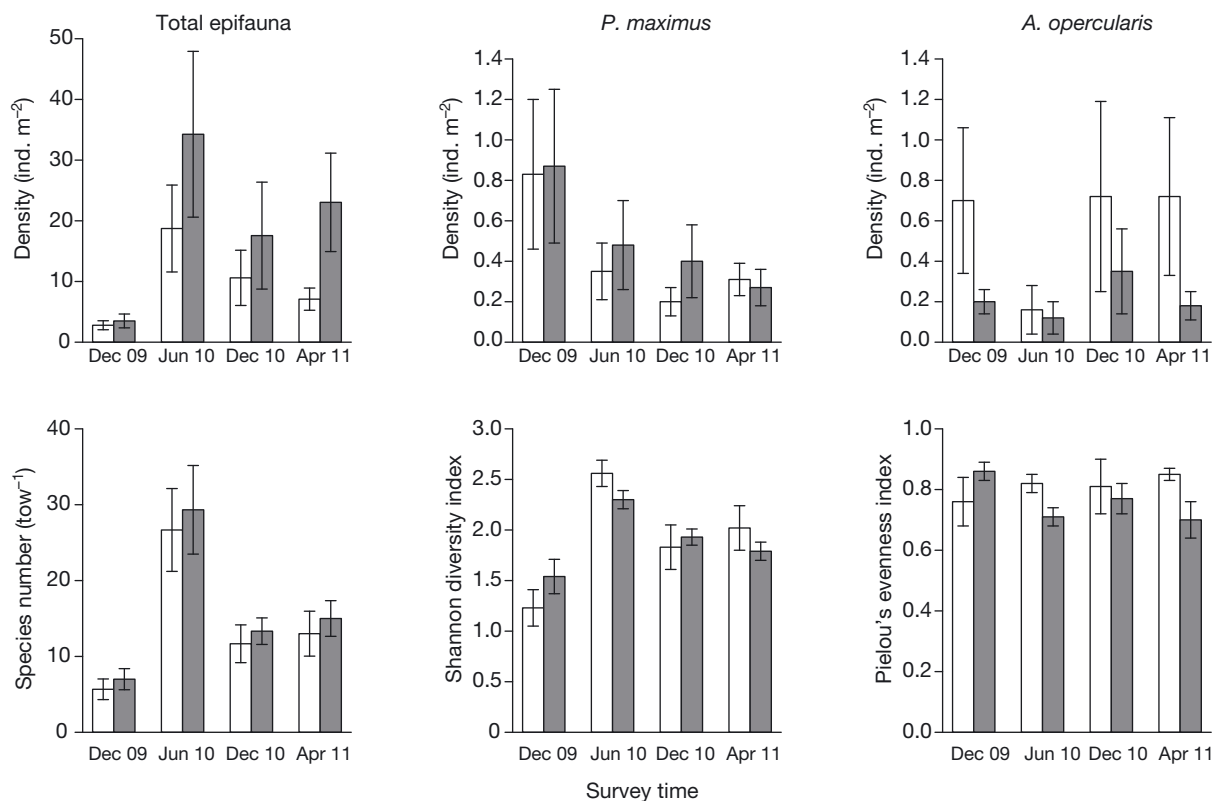
Fig. 4. Mean ± SE total epifaunal density (ind. m^{-2}), *Pecten maximus* density (ind. m^{-2}), *Aequipecten opercularis* density (ind. m^{-2}), species number (tow^{-1}), Shannon-Wiener diversity index (*H'*) and Pielou's evenness index (*J'*) inside the permanently closed area (shaded) and the seasonally fished area (open) during the 4 sampling events (December 2009, June and December 2010, April 2011)

whereas in June 2010, the area had only been closed for 2 wk following a 3 mo open period to scallop dredging. The weathering of dredge tracks may have been due to increased wave action over the winter months which, combined with the prevailing tidal currents, would serve to increase sediment transport at that time.

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

In total, 100 taxa were recorded during the 4 surveys. On average, mean ± SE species richness ranged between 6.3 ± 1.3 and 29.6 ± 5.5 taxa per site (Fig. 4). Only 15 species contributed to more than 80% of the total density (Table 4). Species richness, diversity (*H'*), evenness (*J'*), total epifaunal density and scallop (*Pecten maximus* and *Aequipecten opercularis*) density were similar between the permanently closed area and the seasonally fished area (Fig. 4, 'Zone effect' in Table 5).

Table 4. Macro-epibenthic taxa contributing to more than 80% of the total density at sites sampled within the permanently closed area and seasonally fished area in the Cardigan Bay Special Area of Conservation. Individual taxon contribution to overall density is also shown

Taxon	Taxonomic group	Contribution (%)
Hydroid turf	Hydroid	18
Ophiura albida	Ophiuroid	14.4
Ophiothrix fragilis	Ophiuroid	8.8
Cellaria sp.	Bryozoan	7.9
Epizoanthus couchii	Cnidarian	7.1
Alcyonium digitatum	Soft coral	7
Pecten maximus	Bivalve	3.2
Aequipecten opercularis	Bivalve	2.7
Nemertesia antennina	Hydroid	2.5
Cerianthus lloydii	Cnidarian	2.2
Serpula sp.	Annelid	2.2
Gibbula sp.	Gastropod	1.3
Polychaeta indet.	Annelid	1.3
Bivalvia indet.	Bivalve	1.2
Perophora listeri	Tunicate	1.1

Table 5. Results from a 2-way crossed ANOVA for the effect of management area (Zone) and sampling event (Time) on total mean density (all taxa) and density of scallop species *Pecten maximus* and *Aequipecten opercularis* (ind. m^{-2}), species richness (species tow^{-1}), Shannon-Wiener diversity index (*H′*) and Pielou's evenness (*J′*). Data for total density and species richness were log-transformed, and scallop densities were square-root transformed to meet homogeneity of variance. Significant values are highlighted in **bold**

	All taxa		*P. maximus*		*A. opercularis*	
	F	p	F	p	F	p
Density						
Time effect	4.2	**0.002**	1.7	0.2	0.2	0.4
Zone effect	2.7	0.1	0.4	0.5	2.2	0.1
Time × Zone	0.3	0.9	0.1	0.9	0.2	0.9
Species richness						
Time effect	13.2	**<0.0001**				
Zone effect	0.7	0.4				
Time × Zone	0.1	0.9				
Shannon diversity						
Time effect	10.3	**<0.0001**				
Zone effect	0.3	0.6				
Time × Zone	1.3	0.3				
Pielou's evenness						
Time effect	0.4	0.8				
Zone effect	1.7	0.2				
Time × Zone	2.3	0.1				

Table 6. Permutational multivariate ANOVA (PERMANOVA) on square-root transformed epifaunal density data and Bray-Curtis similarity matrix to examine the effect of management zone (Zone) and survey time (Time) on community composition using a 2-way crossed design. Significant values are highlighted in **bold**

Source	df	SS	MS	Pseudo-*F*	p(perm)
Zone effect	1	4022.8	4022.8	1.6	0.1
Time effect	3	26315	8771.8	**3.5**	**0.0001**
Zone × Time	3	4613.9	1538	0.6	0.9
Residual	40	100920	2522.9		
Total	47	135870			

Total epifaunal density, species richness and diversity were consistently the lowest during the December 2009 survey and the highest in June 2010, and these temporal differences were significant ('Time effect' in Table 5). Furthermore, total epifaunal density and species richness were on average 4 and 2 times lower in December 2009 than in December 2010, respectively (Fig. 4), indicating strong interannual variability of seasons (e.g. frequency and duration of storm surges). Evenness and *A. opercularis* density did not change significantly throughout the
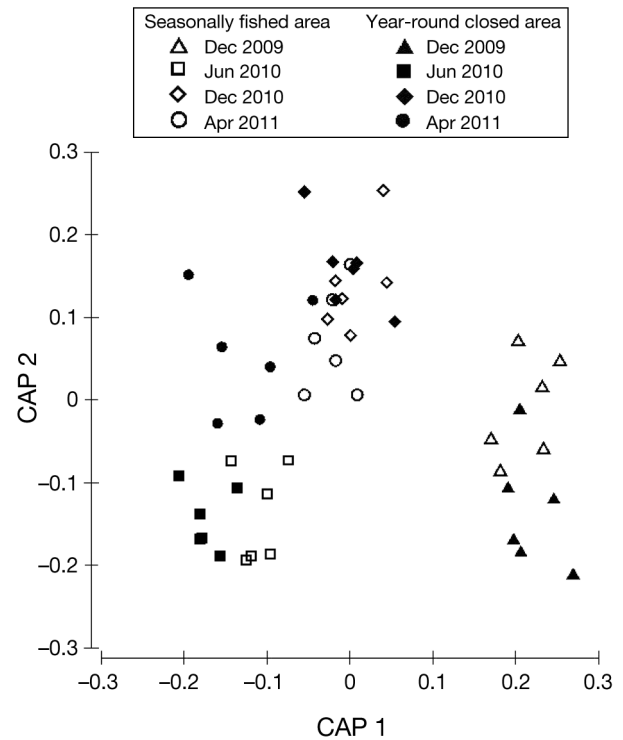

Fig. 5. Two-dimensional ordination plot of the first 2 canonical axes for canonical analysis of principal coordinates (CAP) on square-root transformed epifaunal assemblage density data

sampling period (Table 5) and, although mean density for *P. maximus* appeared to decrease with time (Fig. 4), this temporal trend was not significant (Table 5). The interaction term between 'management area' and 'survey time' (Time × Zone) was not significant for any of the univariate measures examined (Table 5); hence, we did not detect effects due to dredging in the seasonally fished area or due to protection from fishing in the permanently closed area.

Analogous to the results for the univariate measures, the multivariate analysis of the benthic epifaunal assemblage density identified significant differences among the 4 sampling events, but there was no significant zone or interaction effect (Table 6). The ordination plot from the CAP showed clear distinctions between the assemblage sampled in December 2009 and that sampled in June 2010 (CAP1 axis in Fig. 5), and between the assemblage surveyed in summer (June 2010) and those sampled in winter (December 2010) and spring (April 2011; CAP2 axis in Fig. 5). The size of the squared canonical correlations for each of the 2 axes was high, $r^2_1 = 0.95$ and $r^2_2 = 0.82$, indicating a strong association between

the variation in the benthic assemblage and the time of the sampling event. Sessile emergent species such as *Nemertesia* spp., *Alcyonidium diaphanum*, *Epizoanthus couchii* and *Cerianthus llyodii* were more abundant in June 2010 than in December 2009 (Table 7), whereas species that typically senesce in the winter and reproduce during the summer such as *Bugula* spp. and *Clavelina lepadiformis* were more abundant in June 2010 than in December 2010 and April 2011 (Table 8).

Multivariate regression analysis using the DISTLM analysis indicated that total variation was best explained by gravel content, tidal shear stress and survey time (Table 9). However, this model only explained 34% of the total variability in the biological data. 'Survey time' explained the greatest amount of variation in the data at 19.4% and while fishing intensity explained a significant proportion of the variability in assemblage composition, it only accounted for 5% of the total variability (Table 9).

Table 7. Correlation coefficients (corr. coef.) for individual species (|r| ≥ 0.4) with the first canonical axis. A positive correlation indicates higher species density during June 2010 relative to December 2009

Species	CAP 1: Ave. density (ind. m^{-2})				
	corr. coef.	Dec 09	Jun 10	Dec 10	Apr 11
Hydroid turf	0.7	0.1	6.1	2.3	2.0
Nemertesia antennina	0.6	0.01	1.2	0.2	0.1
Alcyonidium diaphanum	0.6	0	0.6	0	0.02
Nemertesia ramosa	0.6	0	0.2	0	0.1
Cerianthus lloydii	0.5	0	0.9	0.3	0.1
Epizoanthus couchii	0.4	0	2.7	0.7	0.8

Table 8. Correlation coefficients (corr. coef.) for individual species (|r| ≥ 0.4) with the second canonical axis. A positive correlation indicates higher species density during June 2010 relative to the other 3 sampling periods

Species	CAP 2: Ave. density (ind. m^{-2})				
	corr. coef.	Dec 09	Jun 10	Dec 10	Apr 11
Anemone indet.	0.6	0.09	0.2	0.02	0.1
Sycon spp.	0.5	0	0.3	0	0
Ebalia spp.	0.4	0.03	0.2	0.01	0.1
Alcyonidium diaphanum	0.4	0	0.6	0	0.02
Clavelina lepadiformis	0.4	0	0.1	0	0
Polymastia spp.	0.4	0	0.1	0	0
Securiflustra/*Bugula* sp.	0.4	0	0.1	0	0
Nemertesia antennina	0.4	0.01	1.2	0.2	0.1

Table 9. Results of the distance-based linear model (DISTLM) for normalized environmental data and Bray-Curtis similarity matrix for square-root transformed epibenthic assemblage density data, using the 'BEST' selection procedure on the basis of the Akaike information criterion (AIC) selection criterion. Significant values are highlighted in **bold**

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

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

Temporal changes in the permanently closed area

On average, total epifaunal density and scallop density did not change significantly with increasing duration of protection from scallop dredging, that is after 13 mo (June 2010) and 23 mo (April 2011) of closure (Table 10). In contrast, species richness was significantly higher in June 2010 than in April 2011 (Table 10). When the analysis was carried out at the level of taxonomic class, we found significant differences among the 2 survey events for 5 out of the 15 taxonomic classes, and densities were lower after 23 mo of closure than after 13 mo (Fig. 6). The multivariate analysis of the benthic assemblage composition found significant differences between the 2 sampling events (ANOSIM on duration of closure; R = 2.6, p = 0.002); however, the species that contributed most to this difference suggest that differences are likely to be due to natural temporal fluctuations in species abundance rather than due to an increase in the density of disturbance-sensitive species (Table 11).

Effects of fishing intensity in the seasonally fished area

The effect of scallop dredging in the seasonally fished area was assessed on species data collected within this area in April 2011. Total epifaunal density, scallop density and species richness were not significantly correlated with fishing intensity (estimated as the number of hours fished per month for the period November 2008 to April 2011): Pearson

Table 10. Epifaunal species density and species richness (mean ± SE) at the permanently closed area, following 13 mo (June 2010) and 23 mo (April 2011) of no scallop dredging

Duration of closure (mo)	Total epifaunal density (ind. m^{-2})	No. of species (tow^{-1})	*Pecten maximus* density (ind. m^{-2})	*Aequipecten opercularis* density (ind. m^{-2})
13	37.2 ± 7.4	26.9 ± 2.5	0.4 ± 0.1	0.5 ± 0.2
23	32.5 ± 4.7	20.3 ± 1.9	0.4 ± 0.1	0.4 ± 0.1
ANOVA	$F = 0.28$, $p = 0.6$	$F = 4.4$, $p = 0.04$	$F = 0.01$, $p = 0.9$	$F = 0.5$, $p = 0.5$
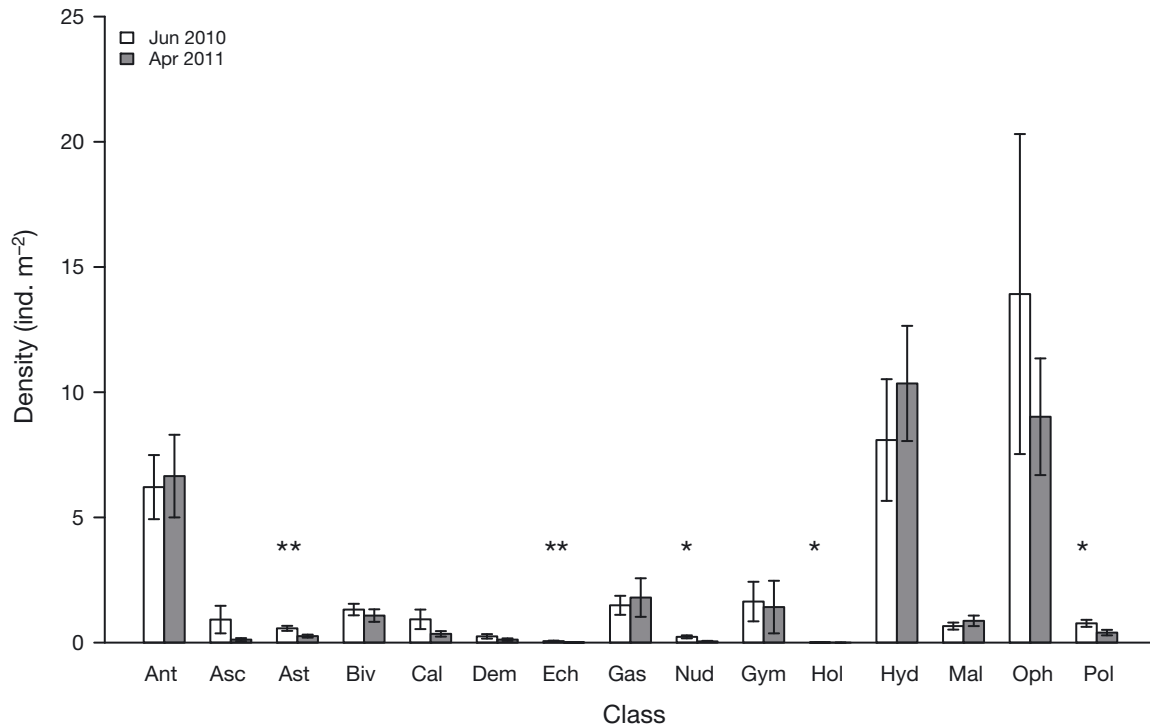
Fig. 6. Mean density (ind. m^{-2}) by taxonomic class for the surveys carried out after 13 mo (June 2010) and 23 mo (April 2011) of closure of scallop dredging in the permanently closed area. Error bars represent SE. Ant: Anthozoa, Asc: Ascidiacea, Ast: Asteroidea, Biv: Bivalvia, Cal: Calcarea, Dem: Demospongiae, Ech: Echinoidea, Gas: Gastropoda (snails), Nud: Nudibranchia, Gym: Gymnolaemata, Hol: Holothuroidea, Hyd: Hydrozoa, Mal: Malacostraca, Oph: Ophiuroidea, Pol: Polychaeta. * and ** indicate significant differences among sampling events at a 0.05 and 0.01 level of significance, respectively

coefficient for log-transformed total density = −0.1, p = 0.9, species richness = −0.1, p = 0.7; Spearman rho for *Pecten maximus* density = 0.4, p = 0.2, *Aequipecten opercularis* = −0.1, p = 0.8.

DISCUSSION

We did not detect differences in the abundance of scallops and the epibenthic community composition between the permanently closed area and the seasonally fished area in the Cardigan Bay SAC ('Zone' effect). Given that the open season for scallop dredg-

ing in the SAC runs from November through to April, we expected an effect of fishing during the open season in the seasonally fished area but not in the permanently closed area. There was no interaction effect between the time of sampling event and the management zone ('Time × Zone'); thus we did not find an effect of fishing at any time throughout our 23 mo sampling period. The lack of any clear 'Zone' or interaction 'Time × Zone' effect could be due to a number of reasons. One reason may be that seasonal fluctuations in species abundance may reduce the potential for fishing effect to be detected during the open season (November to April), which coincides

Table 11. Similarity percentages (SIMPER) analysis giving the mean density (ind. m^{-2}) of those species that contributed to more than 40% of the dissimilarity between the epifaunal assemblages after 13 mo (June 2010) and 23 mo (April 2011) of closure. The % contribution of individual species to the dissimilarity between the 2 sampling events is also shown. % Contrib. = % Contribution

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

with winter and spring. Species that typically senesce in winter (e.g. *Nemertesia antennina*) but reproduce and grow in summer (e.g. *Bugula* spp., *Clavelina lepadiformis*) had the lowest densities during the winter surveys but the highest densities during the summer survey. These seasonal fluctuations are likely to reflect new growth and recruitment processes that generally occur in spring, synchronised with the higher food availability from phytoplankton blooms (Winder & Cloern 2010).

Another possible explanation for the lack of fishing effect between the permanently closed area and the seasonally fished area may be the relatively high level of natural disturbance at the study area that might obscure the effect of fishing on the benthic community. Previous studies have shown that the magnitude of the effect on benthic communities from bottom-towed gears is strongly dependent on habitat type (Collie et al. 2000b, Kaiser et al. 2006); effects in high-energy environments and dynamic habitats, such as shallow sandy sediments are lower in magnitude compared to more stable habitats (Bergman & van Santbrink 2000, Hall-Spencer & Moore 2000). For example, Kaiser et al. (1998) found that beam trawling had no detectable short-term effect on epifaunal communities in mobile sediment compared to more stable sediment habitats in adjacent areas. Gibbs et al. (1980) demonstrated that otter trawling on sandy, estuarine shrimp grounds in New South Wales, Australia, did not cause any detectable changes in macrobenthic fauna, which they attributed to the resilience of coarser sediment fauna and

pre-stressed conditions in the estuary. Stokesbury & Harris (2006) found that the effect of natural disturbance on the epibenthic community prevailed over that of fishing disturbance from the short-term scallop fishery at Georges Bank. The predominance of mobile sediment (sand and fine gravel) aligned parallel to the direction of the main tidal flow, together with the shifting bedforms observed among surveys (side scan sonar surveys) provide evidence of a naturally dynamic environment at our study area. Furthermore, the dominance of taxa such as hydroids, ophiuroids and anthozoans that are morphologically (e.g. high degree of flexibility or low-lying turf) or behaviourally (e.g. high mobility, passive suspension feeders) adapted to dynamic conditions (Labarbera 1984, Okamura 1987, Coma et al. 1998) indicates that the benthic assemblage at Cardigan Bay is composed of species that tolerate the frequent natural perturbations from physical processes such as tidal currents and waves. The extremely low abundance and species richness that we observed at all sampling sites during the first sampling event (December 2009) is unlikely to have resulted from fishing alone, because the entire SAC had been closed to scallop dredging for 6 mo at the time of sampling (see Table 1). Rather, it is likely that the 5 wk of strong winds and heavy sea state that preceded our first survey (M. Sciberras pers. obs.) may explain the relatively impoverished community observed in December 2009. Sessile emergent species such as *Nemertesia* spp., *Alcyonidium diaphanum* and *Cerianthus llyodii*, which are likely to experience high mortality due to displacement from the sediment or from damage due to scouring by pebbles/cobbles, had very low densities during the December 2009 survey relative to the other 3 surveys. Wave-induced mortality is known to impact community structure to a water depth of approximately 50 m (Oliver et al. 1980, Hall 1994, Hiddink et al. 2006, Lambert et al. 2011), and given that all our sampling sites were within 35 m, it is possible that wave scour at the seabed may have resulted in mortality of some species. Nevertheless, the increase in abundance within a few months (i.e. the June 2010 survey) indicates substantial recovery from this natural disturbance by recolonization and re-growth of fauna. The resilience of the community following the storm event, but the lack of difference between the closed and open areas to scallop dredging, suggests that the level of scallop fishing at our survey sites, estimated between 0.07 and 0.52 h of fishing per month, may be insufficient to induce changes large enough to be detected in the presence of strong background natural disturbance. This con-

clusion matches that of Kulbicki et al. (2007); they attributed the lack of a response to the establishment of the Abore reef MPA on fish assemblages to a relatively low fishing pressure and to natural variations that obscured changes due to fishing.

Fishing by bottom-towed gear causes shifts in benthic community composition and structure, from those dominated by slow-moving or sessile erect, filter-feeding species to highly mobile scavengers and predators or small-bodied infaunal species (Kaiser et al. 2000, Jennings et al. 2001, Hermsen et al. 2003, Carbines & Cole 2009, Strain et al. 2012). We expected that the reverse would occur in the permanently closed area after cessation of scallop dredging. There was no effect of 'Duration of closure' on overall epifaunal density, scallop density or species richness; thus, our analysis did not reveal changes in abundance and diversity associated with recovery from fishing disturbance. The observed changes in community composition (see multivariate analysis) were mainly due to temporal patterns of natural variation associated with processes such as recruitment, rather than shifts from robust to fragile species. One possible reason for this lack of recovery with time is that the duration of our study (~2 yr) was not long enough to elicit a visible response in the epibenthos. The recovery of benthic communities from scallop dredging in sand habitats has been shown to occur within 39 d of disturbance, but may take up to 6 mo for some taxa such as annelids and molluscs (Kaiser et al. 2006). Conversely, communities inhabiting relatively stable gravel sediments that tend to support communities with high levels of diversity and biomass may take several years to recover (Kaiser et al. 2006). It must be acknowledged that the studies reviewed by Kaiser et al. (2006) were experimental manipulations; hence, expanding their predictions to the entire fishery comes with some difficulty as the fishery is not spatially or temporally uniform and covers a range of environmental conditions. However, given that the Cardigan Bay SAC is characterized by a naturally highly dynamic environment and a predominance of sand mixed with gravel and pebble, we expected some recovery to have occurred after 23 mo of closure of the fishery if scallop dredging was affecting the benthic community in the first instance. The lack of change in scallop density and community composition after almost 2 yr of no fishing provides further support to the hypothesis that the highly dynamic environment is what primarily drives the community composition and structure in Cardigan Bay. Nevertheless, we recommend that further monitoring be undertaken for a better understanding of the recolonization, recovery and succession process of the epifaunal community in the permanently closed area of the SAC.

Although we did not detect any effects of scallop dredging on the macro-epibenthic community at the Cardigan Bay SAC, it must be recognized that scallop dredging has been a common fishing practice in Cardigan Bay (including the SAC) for over 30 yr. Thus, scallop dredging may have caused previous impacts that are no longer detectable because they have become widespread and long-term. Previous studies have suggested that 5 to 10 yr periods of low to medium intensity mobile fishing can result in long-term declines in epibenthic biogenic reef-forming species and their associated taxa (Bradshaw et al. 2002, Cranfield et al. 2004, Kaiser et al. 2006). In the absence of long-term environmental and biological data in the SAC, dating to before the start of scallop fishing in Cardigan Bay, it is difficult to disentangle the effects of scallop dredging from other environmental disturbances. This is not a unique problem to our study. For instance, in a well-replicated control impact study of the effect of an estuarine prawn-trawl fishery on benthic assemblages at Clarence River, Underwood (2007) found no effect of current trawling practices. The absence of data regarding long-term environmental changes caused by anthropogenic activities (including trawling) precluded the separation of the effects of trawling from other potential confounding long-term disturbances.

CONCLUSIONS

Scallop density and the epibenthic community within the seasonally fished area where scallop dredging is permitted for 6 mo of the year were similar to those in the unfished permanently closed area in Cardigan Bay. Further, the sea floor sediment composition shifted more than the epibenthic community it supported. Hence, our results suggest that the highly dynamic environment may have an effect strong enough to mask or strongly modify the effects of protection from fishing. Gauging the impact of mobile fishing gear requires an understanding of how natural disturbance affects benthic communities (Hall 1994). Unquestionably, dredges disturb the seabed. However, the seabed is also disturbed by natural physical and biological processes, and the biological communities that utilize a particular habitat will adapt to that environment (Krebs 1994). Fishers and managers of fisheries closures set a number of expectations from MPAs, and unexpected results

may provoke conflicts (Agardy et al. 2003). In particular, increases in diversity, density and biomass are expected outputs. Our results have shown that under some circumstances, permanent fishery closures may not necessarily provide detectable increases in target species and their associated communities, at least within a short period of establishment. We argue that the effect of protection from mobile fishing gear on the habitat structure and biological community must be scaled against the magnitude and frequency of seabed disturbance due to natural causes. The imposition of fisheries closed areas without due consideration of the natural environmental conditions and the biology of the species concerned may result in negative impacts on fisheries and limited conservation benefits.

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