ICES Journal of
Marine Science

ICES Journal of Marine Science (2014), 71(4), 834–844. doi:10.1093/icesjms/fst197

Original Article

Impact of scallop dredging on benthic epifauna in a mixed-substrate habitat

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Boulcott, P., Millar, C. P., and Fryer, R. J. 2014. Impact of scallop dredging on benthic epifauna in a mixed-substrate habitat. – ICES Journal of Marine Science, 71: 834–844.

Received 7 June 2013; accepted 23 October 2013; advance access publication 3 January 2014.

Experimental scallop dredging was conducted to assess the vulnerability of emergent epifauna on hard substrates. Three sites were sampled before and after dredging to examine changes in the coverage of faunal turf (hydroid and bryozoan) assemblages and the composition of the wider epifaunal community. Each site had an "impact" box that was dredged, a control box that was in an area that was still open to fishing, and a control box in a special area of conservation (SAC) that had not been fished for two years. Community composition differed significantly after dredging in two of the three sites, with dredged communities becoming less similar to those in the SAC. There was no clear evidence that dredging in the impact boxes reduced the coverage of faunal turfs on hard substrates. However, the coverage of faunal turfs on hard substrates in the SAC was typically greater than in areas that were still being fished commercially, consistent with a dredging effect. The results highlight the role that substrate morphology might play in modifying the severity of dredging effects. This has relevance to marine spatial management, as it suggests that emergent epifauna living on hard substrates that are morphologically suited to dredging, such as pebble and cobble substrates, could be particularly vulnerable to dredging.

Keywords: benthic communities, faunal turfs, Firth of Lorn, fishing impacts, photography, scallop dredging, Special Area of Conservation.

Introduction

There is growing evidence in the scientific literature that towed bottom-fishing gears have a detrimental effect on the viability of many non-target benthic species (Thrush and Dayton, 2002; Kaiser *et al.*, 2006). Such gears can remove, kill or damage non-target species (Bergman and van Santbrink, 2000), reduce the structural complexity of the seabed (Auster *et al.*, 1996; Schwinghamer *et al.*, 1996), and alter the diversity and composition of benthic assemblages (Kaiser and Spencer, 1996; Collie *et al.*, 1997).

The environmental consequences of benthic trawling are complex. The extent of disturbance depends on substrate type (Kaiser *et al.*, 2002), the performance of the gear over the substrate (Caddy, 1973; Currie and Parry, 1999), and the sensitivity of the benthic community under stress (Currie and Parry, 1996; Bergman *et al.*, 1998; Collie *et al.*, 2000a). For example, communities in mobile, sandy substrates tend to be more resilient to towed bottom gear than those in consolidated mud substrates (Kaiser *et al.*, 2006) as they have fewer emergent structures and are composed of species more adapted to disturbance. However, even the viability of communities adapted to disturbance may be compromised by the additional stresses caused by trawling (Kaiser *et al.*, 1998).

Scallop dredging is responsible for some of the most damaging effects to the benthic habitat (Collie *et al.*, 2000b; Kaiser *et al.*, 2006). Small-scale experimental manipulations in sand and gravel habitats have demonstrated that scallop dredging removes and kills many infaunal and epifaunal species (Eleftheriou and Robertson, 1992; Thrush *et al.*, 1995; Currie and Parry, 1996; Kaiser *et al.*, 1998; Hall-Spencer and Moore, 2000), reducing overall habitat complexity (Hill *et al.*, 1999, 2000). Despite growing evidence of short-term fishing impacts on unconsolidated sediment (Collie *et al.*, 2000b), the effect of scallop dredging in hard-bottom areas that support emergent epibiota is poorly understood. This is due in part to the paucity of empirical evidence, but also to the complexity of hard-bottomed areas that are often interspersed with unconsolidated sediments within relatively small scales.

Emergent epifauna colonizing hard substrates are likely to be sensitive to scallop dredging (MacDonald *et al.*, 1996). In a study of the effects of scallop dredging around the Isle of Man (UK), Lambert *et al.* (2011) found that the maximum size and total biomass of emergent epifauna on hard substrates were negatively related to fishing effort. An earlier study, examining scallop dredging on the Georges Bank, also suggested that biota on hard-bottom, gravel/pebble substrates are vulnerable to bottom-trawling activity (Collie *et al.*, 2000a).

However, the effect of dredging on hard substrates varies across taxa (Lambert *et al.*, 2011). In common with other habitats, it is likely that much of this variation is driven by morphological traits, with some species inherently less sensitive to dredging disturbance than others. Nevertheless, the general morphology of hard substrates may also influence dredging effects. Hinz *et al.* (2011) examined the effect of scallop dredging in a highly structured, mixed-substrate habitat in Lyme Bay (Dorset, UK). They compared the abundance of benthic fauna across scallop areas known to differ in fishing pressure and found a significant effect of dredging on three of the nine species analysed. Dredging effects on some potentially sensitive species, such as the pink sea fan, *Eunicella verrucosa*, were not found, indicating that not all species were equally affected by scallop dredging. *E. verrucosa* is closely associated with rocky-reef substrates and the morphological complexity of this substrate may mean that scallop dredges remain out of contact with the seabed for certain periods in these areas. Similar conclusions were drawn from a photographic survey of the effect of scallop dredging on rocky-reefs with complex morphology, which found lower levels of damage than envisaged (Boulcott and Howell, 2011). It has been postulated that emergent epifauna on hard, cobble/pebble substrates may be particularly vulnerable as these substrates provide a seabed which can be dredged effectively using scallop gear (Mason, 1983).

Our study aimed to assess the effect of scallop dredging on benthic epifaunal communities in a mixed-substrate habitat containing several types of hard substrate. We compared benthic communities in three large-scale sites, in existing commercial grounds, before and immediately after dredging. We also compared benthic communities in the dredged sites with those in an adjacent special area of conservation (SAC) where scallop dredging had been suspended for 2 years. To investigate the potential of benthic communities to recover, we resurveyed all sites 2.5 months later.

Material and methods

Study sites

The Firth of Lorn, to the southwest of Oban, Scotland, is a mixed-substrate habitat with areas of bedrock, boulder, cobble, pebble, gravel, shell debris, sand and mud lying close to each other. The area is highly diverse in its bathymetry, hydrography (Dale *et al.*, 2011) and biota and contains the full range of geogenic reef types from bedrock through boulder to stabilized cobble/pebble bed (Howson *et al.*, 2006). In recognition of this diversity, part of the Firth of Lorn was made a Special Area of Conservation (SAC) in March 2005. The seabed in the Firth of Lorn supports an important fishery for the great scallop, *Pecten maximus*, with most fishing activity prosecuted by dredge (Palmer, 2007). Concerns about the vulnerability of emergent epifaunal taxa on hard substrate biotopes to dredging led to the suspension of scallop dredging inside the SAC in spring 2007 pending further investigation. Scallop dredging is still permitted on the hard substrate biotopes outside the SAC.

Benthic surveys

The study consisted of three photographic surveys. The first two, a *before-impact* survey conducted immediately before experimental dredging and an *after-impact* survey conducted 2–3 days after dredging, were undertaken within a 20-day period in May 2009. The short time-span of 2–3 days between the before- and after-impact surveys makes it reasonable to assume that changes in benthic community structure would be negligible in the absence of an impact. In addition, a third, *recovery* survey was conducted in July/August 2009, the timing dictated partly by the availability of the vessel, to examine changes to the benthic community 2.5 months after dredging. This period spans the main summer growth season for many epibenthic species.

Each survey examined three sites on the boundary of the SAC (Figure 1). All sites were mixed-substrate habitats with extensive areas of cobble/pebble and were commercial scallop grounds before the SAC was closed to dredging (Palmer, 2007). Three survey boxes were chosen at each site: a *SAC control* box inside the SAC; an *impact* box outside the SAC; and an *outside control* box outside the SAC. The dimensions of the survey boxes were 2.0 × 0.2 km (site 1), 1.5 × 0.2 km (site 2), and 0.8 × 0.2 km (site 3). All boxes were surveyed during the before-impact and recovery surveys but, due to the limited survey time available, only the impact boxes were surveyed immediately after dredging had taken place. The outside and SAC control boxes acted as two types of control. The outside control box was adjacent to the impact box, but was subject to the possibility of commercial dredging between the before-impact and recovery surveys. The SAC control box was farther from the impact box, but had not been dredged for the previous two years. The effect of dredging within the SAC, whilst of particular interest to policymakers and stakeholders, was not tested directly as experimental dredging in the SAC was not permitted.

Benthic surveys were performed from the RV "Alba na Mara" using a drop camera frame (see Stokesbury, 2002; Stokesbury *et al.*, 2004). The camera frame held a vertically mounted Kongsberg OE14–208 digital still camera (Kongsberg Gruppen ASA, Norway) set to an aperture of *f*/5, with shutter speed selected automatically. Resting on the seabed, the setup provided a fixed focal length of 1.8 m and a photographic area of 1.85 m^2 per image (Figure 2). Light was supplied by 8 SeaLED, MK3 LED lamps (Seatronics Ltd, Aberdeen) fitted with diffusers and mounted around the outside of the frame. Time, depth, and vessel position were recorded for each deployment. Continuous footage from a side-mounted, Micro-SeaCam 2000 video camera (Deepsea Power and Light, California) was also taken. Low-resolution images from this camera provided an alternative viewing angle when needed.

Within each survey box, stations (40 for sites 1 and 2; 30 for site 3) were selected at random using Hawth's Analysis Tools (Beyer, 2004) in ArcGIS (Esri, California). Images of the seabed were taken according to a two-stage sample design, with four quadrats sampled at each station to increase the area covered at each station (Cochran, 1977; Krebs, 1989). Quadrats within each station were placed according to the prevailing drift of the vessel and were all within 15 m of each other. While the same stations were visited at each survey, the quadrat positions varied between surveys. About 4% of quadrat images were unusable—for example, due to camera shake—and were excluded from subsequent analyses. The dominant substrate in each quadrat, in terms of coverage, was recorded.

Dredging

Experimental dredging was performed by a commercial scallop vessel, the "Rambling Rose", whose crew had considerable experience fishing the waters of the Firth of Lorn. The vessel fished eight

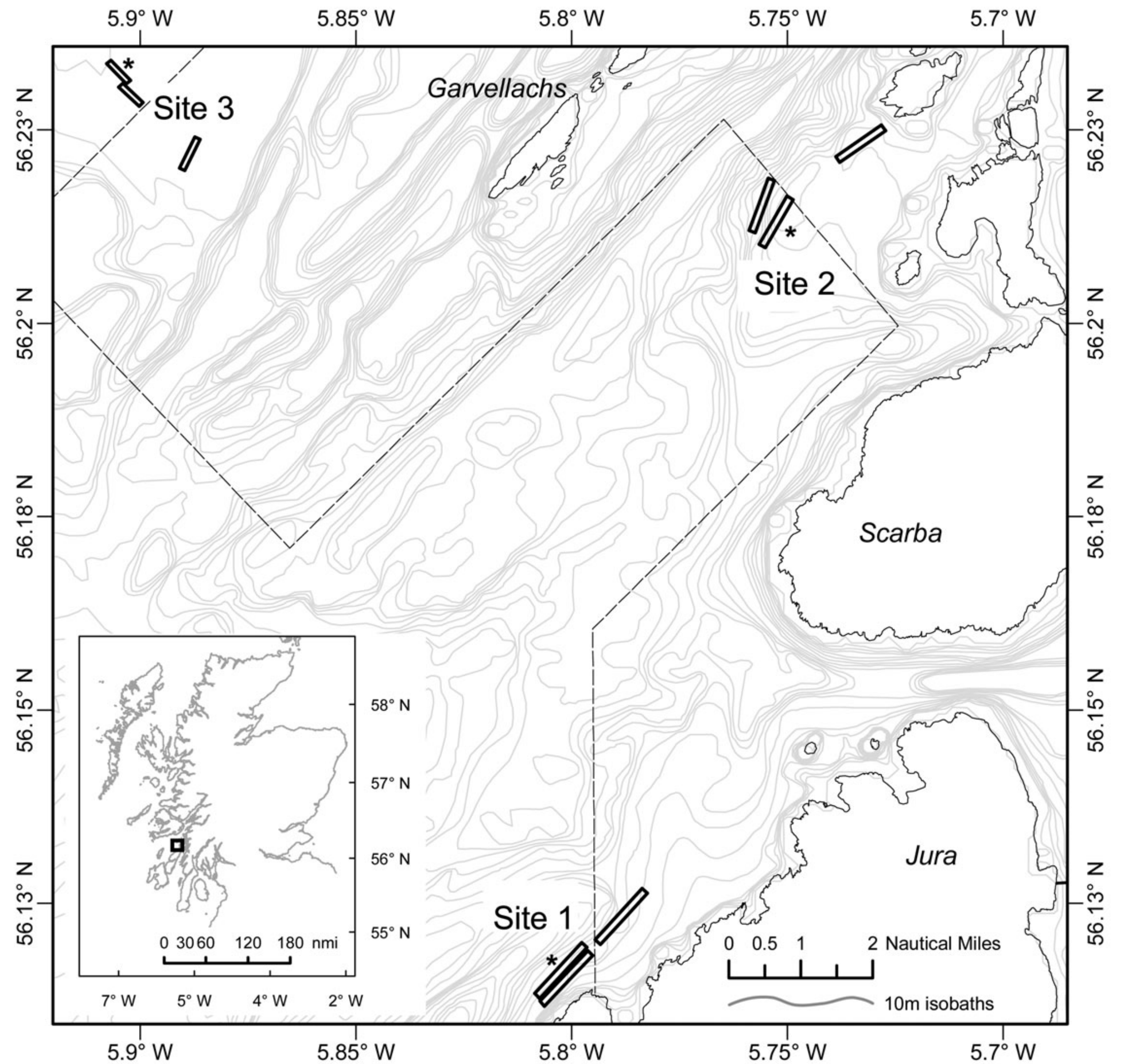

Figure 1. The three sites in the Firth of Lorn surveyed in May and July, 2009. The dotted line shows the SAC. Each site was split into three survey boxes: an impact box that was dredged in May by a commercial scallop dredger (marked by an asterisk); an outside control box; and a control box in the SAC. Light grey contours show bathymetry.

Newhaven scallop dredges per side, as is common practice with much of Scotland's inshore fleet (Keltz and Bailey, 2010). These dredges have a toothed bar which is towed over the substrate, disturbing and lifting partially buried scallops into an attached collecting bag. Dredge lanes were recorded using a Garmin, Map Tour GPS plotter (Garmin Ltd) accurate to 1–5 m. Each impact box was dredged systematically at 2.5 knots in an overlapping pattern for two days, until the whole box had been covered twice by the gear. This dredging intensity was higher than an estimate of commercial dredging activity of 1.2 trawls per year for Lyme Bay (UK) (Hinz *et al.*, 2011).

Evidence for any commercial dredging in the impact and outside control boxes between the before-impact and recovery surveys was assessed using Marine Scotland Vessel Monitoring Data (VMS) for commercial boats >15 m.

Coverage of faunal turfs

Changes in the coverage of hydroids (e.g. *Nemertesia* sp., *Obelia* sp., *Abietinaria sp.*) and bryozoans (e.g. *Flustra* sp., *Bugula* sp., *Alcyonidium* sp.) on hard substrates were used to assess the impact of dredging. Due to the difficulty of identifying hydroids and bryozoans to species level from the photographic images, all erect bryozoan and hydroid species were assessed collectively as "faunal turfs". Faunal turf communities are widely distributed throughout the Firth of Lorn, are closely associated with hard substrates, are vulnerable to towed bottom-fishing gears (Hartnoll, 1998), and their value as an indicator of disturbance has been demonstrated in other photographic, dredge-impact studies (Collie *et al.*, 2000a). Moreover, faunal turfs form emergent structures that provide important settlement substrates for many species, including scallop spat (Lambert *et al.*, 2011). The loss of such structurally complex

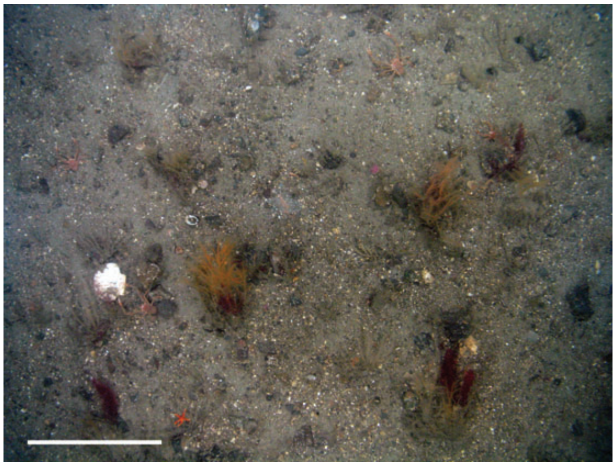

Figure 2. Image of a mixed-substrate quadrat taken within the SAC with faunal turf communities overlying cobbles/pebbles. Scale bar is ~35 cm.

microhabitats is also expected to affect the survival of more mobile species such as juvenile fish (Scharf *et al.*, 2006).

For each survey, three usable quadrat images (where possible) were randomly picked from each station. This achieved approximate balance, with only 2% of stations having only two usable images. For each image, the area of hard substrates (pebble through to bedrock) and the area of hard substrates occupied by faunal turfs were measured using Image J image analysis software (Schneider *et al.*, 2012). To avoid observer bias, all the images were first renamed with randomly generated identifiers and assessed in a randomized order. A repeat assessment of 210 randomly selected images, conducted 14 days later, found no evidence of bias (e.g. Altman and Bland, 1983).

Coverage *c* was defined as the proportion by area of hard substrates occupied by faunal turfs. For each site/box/survey combination, coverage was estimated by a ratio estimator (e.g. Thompson, 2012):

$$\hat{c} = \frac{\sum_{sq} a_{turf,s,q}}{\sum_{sq} a_{hard,s,q}}$$

where $a_{hard,s,q}$ is the area of hard substrates and $a_{turf,s,q}$ the area of hard substrates covered by faunal turfs in quadrat q of station s. A 95% confidence interval for c was obtained using the bootstrap (Efron and Tibshirani, 1994) to avoid making distributional assumptions about the data. Each bootstrap realization involved two levels of resampling: of stations, and of quadrats within stations. A total of 9999 realizations were obtained, and the 250th and 9750th ordered values were used as lower and upper confidence limits respectively.

The coverage estimates were supplemented by a series of one-tailed tests. For each impact box, we tested whether: (i) coverage was lower in the after-impact survey than in the before-impact survey, i.e. was there a reduction in coverage immediately after dredging? (ii) coverage was lower in the recovery survey than in the before-impact survey, i.e. was there a reduction in coverage 2.5 months after dredging?

For each site, we also tested whether coverage in the outside control box was lower than in the SAC control box (in either the before-impact or recovery surveys). This compared boxes that had been protected from dredging for two years with boxes that had not.

One-tailed tests were used because of the *a priori* belief that, if there was an effect of dredging, it would result in lower coverage.

The tests were based on bootstrap confidence intervals. For example, let c_{before} and c_{after} denote the coverage in an impact box in the before- and after-impact surveys respectively, each estimated by ratio estimators as above. Then the *p*-value for a one-tailed test of whether $c_{after} < c_{before}$ was the value α such that an upper $100(1-\alpha)\%$ bootstrap confidence limit for $\log(c_{after}/c_{before})$ was equal to 0. See Efron and Tibshirani (1994) for more details.

All statistical analyses were done in R (R Development Core Team, 2012).

Taxonomic analysis

Taxonomic data were collected to assess community similarity. The abundance of fish and macroinvertebrates down to 40 mm, identified to the lowest taxonomic level possible, were recorded for each quadrat. For analysis, the abundance estimates were fourth root transformed to reduce heteroscedasticity, and the target species *Pecten maximus* and *Aequipecten opercularis* were ignored. Differences between taxonomic communities split according to site/box/survey were calculated using Bray–Curtis ordination (Bray and Curtis, 1957). Derived community similarities were plotted using non-metric multidimensional scaling (nMDS), a technique that has been found to perform well with complex, benthic community data with high levels of variability (Bradshaw *et al.*, 2001). Permutation tests, based on 10 000 permutations, were used to test for pairwise differences in community composition (Edgington, 1980).

Results

The numbers of stations and usable quadrat images, and the range of depths and substrates sampled in each box are given in Table 1. Altogether, 2952 usable quadrat images were produced by the three surveys. The range of depths and substrates sampled is typical of the Firth of Lorn area. All three sites were mixed-substrate habitats (Figure 3). The percentage of quadrats that were predominately hard substrates (pebble through to bedrock) was 26, 22 and 58% at sites 1–3 respectively. The full dataset is given in Boulcott (2013).

Dredging

5861 scallops were caught during the 6 d of experimental dredging in May 2009. The total catch of the seven most abundant species by site is given in Table 2. Physical changes to the seabed were seen in some images in the after-impact survey. Where discernible, the dredge had a homogenizing effect, mixing sediments and flattening natural features. This was most evident at site 3 where 50% of quadrats had gravel megaripples, wave- and current-induced bedforms, before dredging, and only 11% had intact or partially collapsed megaripples afterwards. Parallel teeth marks in sandy substrates were visible in some images.

VMS data indicated that the impact and outside control box at site 1 were probably commercially dredged between the after-impact and recovery surveys. There was no such evidence of commercial dredging at sites 2 and 3.

Coverage of faunal turfs

Faunal turfs were widely distributed, occupying hard substrates in 49% of the assessed quadrats ($n = 2290$). Coverage estimates by

Table 1. A summary of the sites and boxes, with the number of stations and quadrat images available for analysis in each survey.

Site	Box	Depth (m)	Substrate Range	Before-impact Survey Stations (n)	Before-impact Survey Quadrats (n)	After-impact Survey Stations (n)	After-impact Survey Quadrats (n)	Recovery Survey Stations (n)	Recovery Survey Quadrats (n)
1	Outside Control	37–76	mixed (sand/bedrock)	40	159			40	150
	Impact	60–98	mixed (sand/bedrock)	40	158	40	149	40	151
	SAC Control	38–89	mixed (sand/bedrock)	40	157			40	154
2	Outside Control	25–85	mixed (mud/bedrock)	40	158			40	159
	Impact	24–63	mixed (mud/bedrock)	40	157	40	157	40	152
	SAC Control	25–51	mixed (mud/bedrock)	40	154			40	158
3	Outside Control	28–35	mixed (sand/bedrock)	30	117			30	107
	Impact	29–42	mixed (sand/bedrock)	30	119	30	118	30	111
	SAC Control	32–60	mixed (coarse sand/bedrock)	30	112			30	95

Only the impact boxes were surveyed immediately after dredging. The sites and boxes are shown in Figure 1.

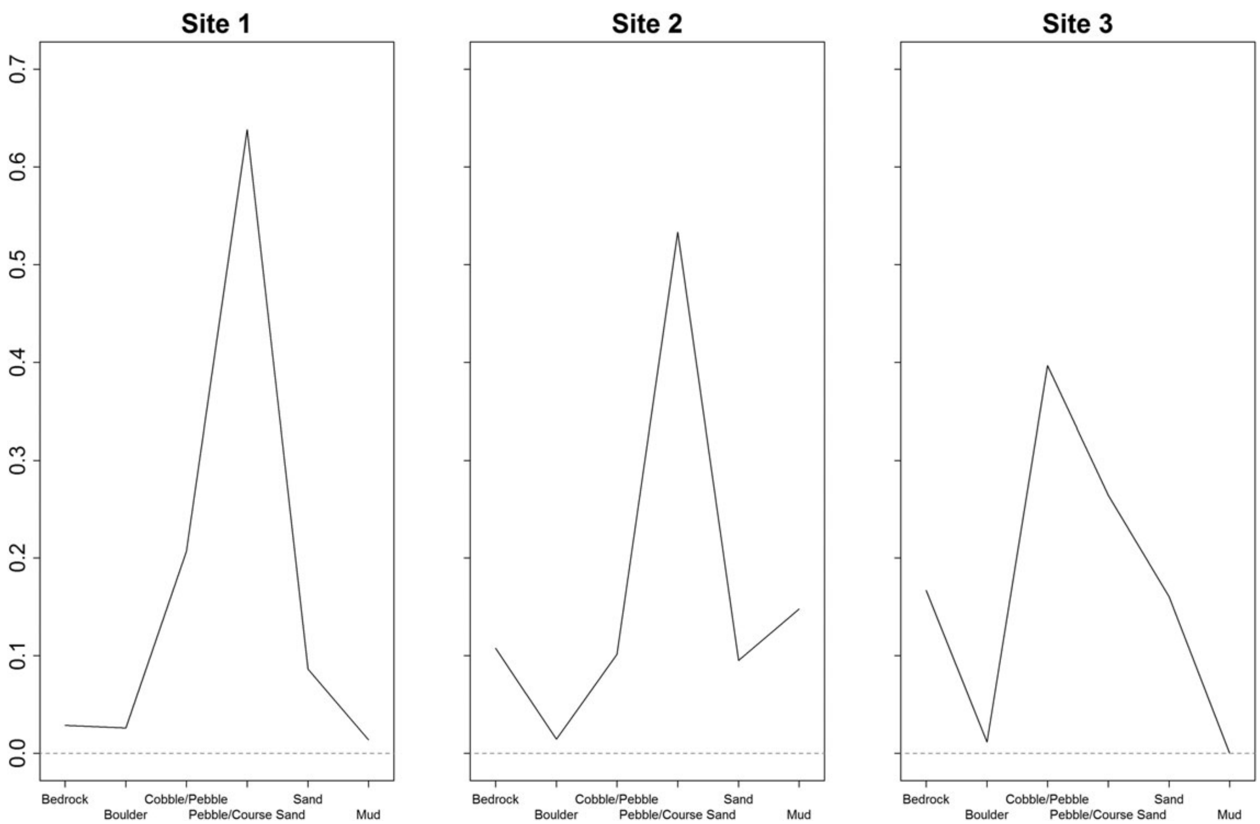

Figure 3. The proportion of each substrate type at each site.

site/box/survey are shown in Figure 4. Point estimates of coverage were lower immediately after dredging in all three impact boxes, although none of these differences was statistically significant ($p = 0.14$, $p = 0.35$, $p = 0.33$ for sites 1–3, respectively). Point estimates of coverage in the impact boxes were also lower in the recovery survey compared with the before-impact survey at sites 1 and 3, but higher at site 2; again, there was no significant reduction in coverage over the 2.5 month period ($p = 0.46$, $p = 0.99$, $p = 0.26$ for sites 1–3, respectively). Coverage in the SAC control boxes was significantly higher than their corresponding outside controls in four of six comparisons (before-impact survey: $p = 0.062$, $p = 0.029$, $p = 0.028$; recovery survey: $p < 0.001$, $p = 0.60$, $p < 0.001$ for sites 1–3, respectively).

Taxonomic data

Abundance data for the 26 categories of fish and epifauna recorded are shown in Table 3, split by site, box and survey. The nMDS plot of transformed community data (Figure 5) shows that community similarity was strongly influenced by site, with boxes from each site clustering together. Across sites, the communities in the SAC boxes were more similar than those in the impact and outside control boxes. Within sites, there were significant differences

Table 2. Total catch by site for the seven most abundant species in the May 2009 dredging trials.

Site	No. Hauls	*Pecten maximus*	*Echinus esculentus*	*Asterias rubens*	*Cancer pagurus*	*Luidia ciliaris*	*Neptunea antiqua*	*Glycymeris glycymeris*
1	25	3444	8	244	134	60	40	0
2	22	1741	0	37	5	13	14	0
3	12	676	121	18	11	13	0	42

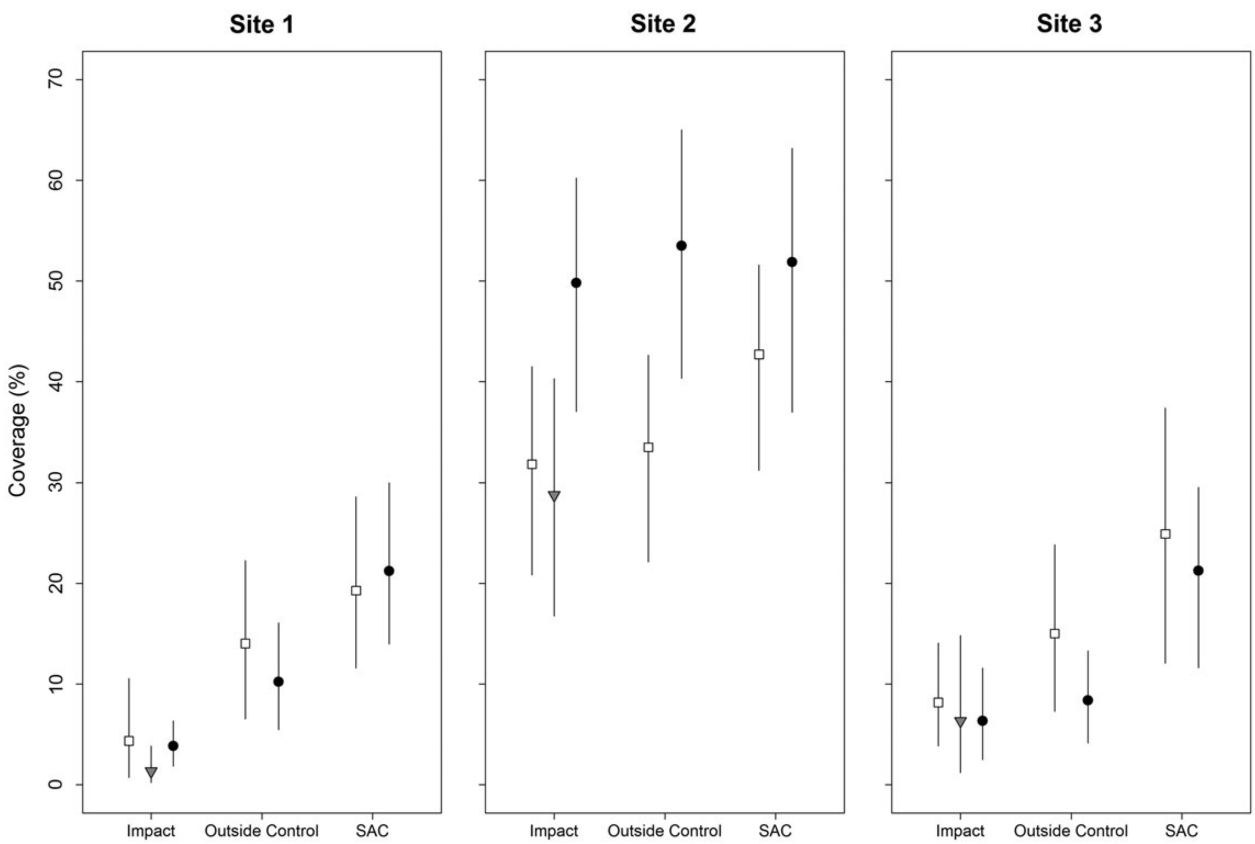

Figure 4. The estimated coverage of hard substrates by faunal turfs for each site and box in the before-impact (white square), after-impact (grey triangle) and recovery (black circle) surveys. The vertical lines show bootstrap 95% confidence intervals.

between the SAC control and outside control communities at all sites in both the before-impact and recovery surveys (Table 4).

The communities in the impact boxes differed significantly between the before- and after-impact surveys at sites 1 and 3, and between the before-impact and recovery surveys at all sites (Table 4). Further, the nMDS plot indicates that the communities in the impact boxes were less similar to their SAC counterparts immediately after dredging at all sites, and remained so 2.5 months after dredging at sites 1 and 3 (Figure 5). Comparing the before-impact and recovery surveys, the community similarities for the impact boxes were lower than those for the outside control boxes at sites 2 and 3, and SAC control boxes at all sites (Table 4).

Discussion

Small-scale dredging impact experiments struggle to reproduce fishing pressures comparable, both temporally and spatially, with commercial activity (Gray *et al.*, 2006). This study investigates dredging pressures at a scale appropriate to scallop fishing in a mixed-substrate environment by dredging an historically active fishing ground for a period and intensity representing moderately high fishing effort. By concentrating on the coverage of emergent epifauna, we have focused on species whose loss would be expected to reduce the available range of ecological niches for associated fauna (Gili and Hughes, 1995; Collie *et al.*, 1997; Bradshaw *et al.*, 2001).

Faunal turf communities

All three impact boxes had lower point estimates of coverage of faunal turf communities immediately after dredging, with estimated reductions of 69, 10 and 22% relative to before-impact coverage at sites 1–3, respectively. However, none of these changes was statistically significant. A *post hoc* power analysis revealed that such reductions would only have been detected with a power of 28, 6 and 14%, respectively, so our design was unlikely to detect the changes (if any) caused by the dredge to faunal turf communities. Although dredging effects on some bryozoan species have been observed elsewhere (Hinz *et al.*, 2011), the ability of field experiments to detect fishing effects is often reduced in habitats that

Table 3. Abundance of taxa in the impact, outside control and SAC control boxes recorded during the before-impact, after-impact and recovery surveys.

Survey	Before-impact									After-impact			Recovery								
Box	Impact			Outside Control			SAC Control			Impact			Impact			Outside Control			SAC Control		
Taxon / Site	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Great Scallop (*Pecten maximus*)	17	42	3	29	39	6	48	53	24	12	26	9	7	18	6	21	56	14	55	47	18
Queen Scallop (*Aequipecten opercularis*)	8	0	0	1	0	5	5	0	3	4	0	0	22	2	1	3	4	2	19	0	6
Squat lobster (*Munida* spp.)	73	49	4	113	188	5	137	258	51	29	45	0	51	69	4	125	182	13	130	203	49
Hermit crab (*Pagurus* spp.)	37	1	1	14	12	0	5	8	4	3	1	4	48	4	1	29	7	0	22	13	5
Edible Crab (*Cancer pagurus*)	1	0	0	0	2	0	1	0	0	0	2	0	1	1	0	1	0	0	1	1	0
Crab (unidentified)	10	1	0	4	4	0	7	2	4	7	0	1	45	4	0	16	3	1	7	9	3
Shrimp (*Caridea*)	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0
Coral worm (*Salmacina dysteri*)	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Burrowing anemone (*Cerianthus lloydii*)	1	8	0	0	175	0	0	2	0	0	3	0	1	0	0	0	59	0	0	3	0
Plumose anemone (*Metridium senile*)	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone (*Sagartia elegans*)	0	0	0	0	1	0	0	0	0	0	2	0	0	4	0	0	0	0	1	0	0
Dahlia anemone (*Urticina felina*)	0	0	0	0	2	0	6	0	0	0	4	0	0	1	0	1	0	0	5	0	0
Tall sea pen (*Funiculina quadrangularis*)	0	10	0	0	2	0	0	0	8	1	5	0	0	4	0	0	10	0	0	0	0
Feather stars (Crinoidea)	10	1	0	6	0	0	56	51	0	2	43	0	7	0	0	9	0	0	20	17	0
Brittle stars (Ophiuroidea)	15	0	3	1	8	53	49	1	66	33	3	0	161	16	0	182	12	2	55	40	13
Edible sea urchin (*Echinus esculentus*)	0	0	2	0	0	9	3	1	2	1	0	3	1	0	0	0	0	6	1	0	0
Starfish (Asteroidea)	4	4	5	10	6	9	14	10	12	4	1	3	6	18	13	17	4	16	12	10	9
Cuckoo skate (*Leucoraja naevus*)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fish (unidentified)	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sea squirt (unidentified)	0	42	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Sponge (*Axinella infundibuliformis*)	0	13	2	0	1	2	9	2	1	0	13	0	0	15	0	0	6	0	5	0	0
Sponge (*Suberites carnosus*)	1	1	0	2	0	0	0	5	5	0	3	0	1	4	0	6	4	2	5	3	0
Sponge (unidentified)	0	18	18	5	19	37	53	3	17	0	6	4	0	6	1	2	19	11	16	1	8
Football sea squirt (*Diazona violacea*)	0	4	0	0	8	0	0	2	0	0	0	0	0	0	1	0	8	0	0	1	0
Dead men's fingers (*A. digitatum*)	3	12	671	54	31	1035	983	3	794	1	0	73	2	5	223	11	289	186	2282	6	268
Caryophyllia spp.	33	690	808	19	453	1583	351	785	227	0	302	843	0	649	857	31	756	531	202	616	279

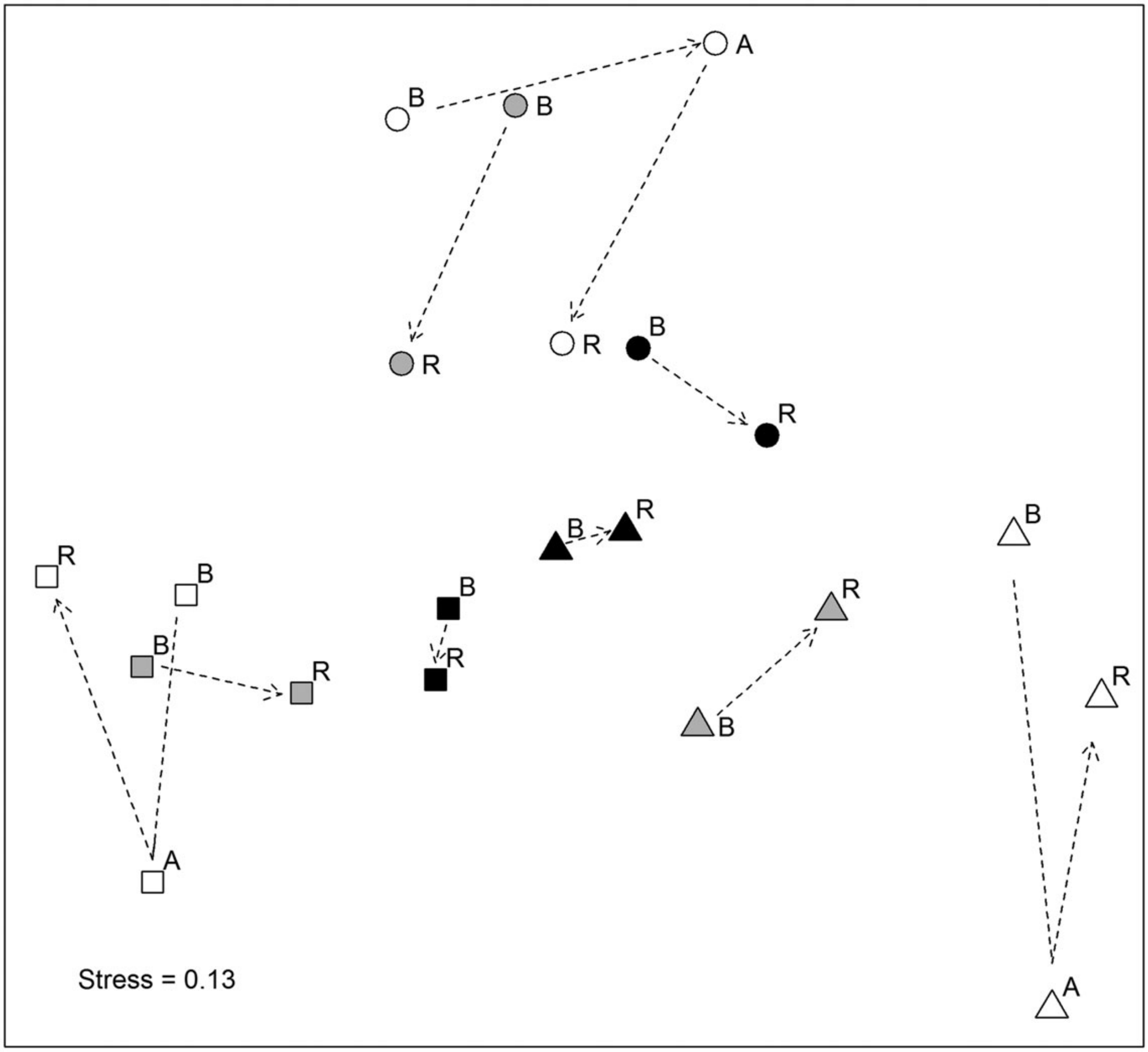

Figure 5. nMDS plot of benthic community data recorded for impact (open symbols), outside control (grey) and SAC control (black) boxes for sites 1 (triangles), 2 (circles) and 3 (squares). Arrows link the surveys completed at each box during the before-impact (B), after-impact (A), and recovery (R) surveys. Plots are based on fourth-root transformed, pooled abundance data with the target species removed.

have already been modified by benthic trawling (Lindeboom, 1995; Hall-Spencer and Moore, 2000). This applies here as the impact (and outer control) boxes had been subject to commercial dredging since the late 1960s (Mason, 1983). Our results could also relate to the fact that coverage might not be as sensitive an indicator of disturbance as biomass (Lambert *et al.*, 2011). Variability in coverage is also likely to be quite high in mixed-substrate habitats such as the Firth of Lorn, since substrate associations can differ considerably among species (Hinz *et al.*, 2011). Such variability will have reduced the power of the study.

Coverage was significantly greater in the SAC control boxes, which had not been dredged for two years at the time of study, than in the outside control boxes in four of six comparisons. Although such differences cannot be formally used to assess the effect of dredging, due to the lack of coverage data collected before the suspension of fishing (see Green, 1993; Underwood, 1994), they are consistent with the hypothesis that dredging reduces the abundance of emergent epifauna such as faunal turfs (Sciberras *et al.*, 2013). Hinz *et al.* (2011) found that the abundance of the bryozoan *Pentapora fascialis* was 73% lower in commercially dredged sites than non-fished sites within the mixed-substrate habitat of Lyme Bay (UK). More generally, a meta-analysis of dredging impacts found 56–96% reductions in the abundance of taxa, depending on substrate type, after a single fishing event (Kaiser *et al.*, 2006). These differences are larger than those observed in the Firth of Lorn, where the median reduction in coverage between the outside and SAC controls was 33%. However, as the recovery of large epifauna can take more than 5 years (Collie *et al.*, 1997; Hermsen *et al.*, 2003) differences in coverage between the outside and SAC control boxes could increase with time.

The coverage estimates at site 2 were all higher than those at sites 1 and 3, regardless of box or survey. The percentage reduction in

Table 4. Bray–Curtis similarity comparing benthic communities from: impact boxes in before- and after-impact surveys; all three boxes in before-impact and recovery surveys; and outside control and SAC control boxes in before-impact surveys and in recovery surveys.

Site	Box type	Survey	Bray–Curtis Similarity	*p*
Impact box before and after dredging				
1	Impact	Before- vs. After-impact	69.2	0.006
2	Impact	Before- vs. After-impact	76.0	0.460
3	Impact	Before- vs. After-impact	66.7	0.0150
Before and recovery surveys by box				
1	Impact	Before-impact vs. Recovery	67.5	$<$0.001
2	Impact	Before-impact vs. Recovery	73.9	0.015
3	Impact	Before-impact vs. Recovery	72.0	0.019
1	Outside Control	Before-impact vs. Recovery	61.0	$<$0.001
2	Outside Control	Before-impact vs. Recovery	82.9	0.230
3	Outside Control	Before-impact vs. Recovery	82.2	0.190
1	SAC Control	Before-impact vs. Recovery	81.2	0.140
2	SAC Control	Before-impact vs. Recovery	75.8	0.007
3	SAC Control	Before-impact vs. Recovery	85.1	0.390
Outside control vs. SAC control boxes				
1	Outside vs. SAC	Before-impact	68.1	0.006
2	Outside vs. SAC	Before-impact	64.1	$<$ 0.001
3	Outside vs. SAC	Before-impact	63.7	$<$ 0.001
1	Outside vs. SAC	Recovery	69.2	0.007
2	Outside vs. SAC	Recovery	72.1	0.013
3	Outside vs. SAC	Recovery	72.6	0.016

P-values give the significance of permutation tests of whether the communities differ.

coverage at site 2 immediately after dredging was also the smallest recorded. The high coverages at site 2 are probably due to its reef morphology (discussed later).

Taxonomic data

There were significant shifts in community composition in the impact boxes between the before- and after-impact surveys at sites 1 and 3 (Table 4), and the communities in all three impact boxes became less similar to their SAC counterparts immediately after dredging (Figure 5). The low similarities before and after dredging were driven by a decrease in the numbers of *Alcyonium digitatum* and sponges, erect epibenthic species that are vulnerable to dredging (Jones, 1992; Collie *et al.*, 1997; Boulcott and Howell, 2011; Hinz *et al.* 2011). Changes in the benthic community caused by mobile fishing gear have been found by other studies on mixed substrates (Auster *et al.*, 1996; Bradshaw *et al.*, 2001). While these studies found that dredging made benthic communities more homogenous, the nMDS plot suggests that the communities in the Firth of Lorn diverged after dredging. This could be partly due to the site differences in our study area, highlighted in the nMDS plot, particularly the strong effect of substratum on the abundance of epifaunal species (Lambert *et al.*, 2011; Hinz *et al.*, 2011). Hydrographical patterns in the Firth of Lorn (Dale *et al.*, 2011) may have also contributed to site differences (see Lambert *et al.*, 2011).

The community similarities between the before-impact and recovery surveys are also generally consistent with the effects of dredging. There were significant differences in community composition in all three impact boxes (Table 4), and the nMDS plot suggests that the communities in the impact boxes at sites 1 and 3 were less similar to their SAC counterparts 2.5 months after dredging (Figure 5). The similarities for the impact boxes at sites 1 and 3 when comparing across surveys were also lower than those for most of the outside and SAC control boxes (Table 4). An exception is the low similarity for the outside control at site 1, which could be because the box was commercially dredged during the study.

Although the study only spanned 2.5 months, the growth of epifaunal species is at its peak during May and June in temperate waters (Hartnoll, 1998) and this period is an opportunity for recovery. An increase in the abundance of individuals of a detectable size, as well as an influx of more mobile species into the survey area, could change community composition (Caddy, 1973; Collie *et al.*, 2000a; Bradshaw *et al.*, 2003). Hence, during the recovery period we might expect benthic communities in both the outside control and impact boxes to become more similar to those in the SAC control boxes. This was indeed the case for the outside control boxes at sites 2 and 3 (where there was no evidence of commercial dredging over the study period) (Figure 5). However, the community composition in the impact boxes at sites 1 and 3 remained affected by dredging after 2.5 months and, along with the potentially impacted outside control box at site 1, these were the only boxes to become less similar to the SAC control boxes during the recovery period (Figure 5). Although the time between surveys in this study was relatively brief, Hinz *et al.* (2011) were unable to detect a recovery in the abundance of epibenthic species 12 months after the exclusion of scallop dredging.

Site differences and the role of reef morphology

Different substrates give different levels of protection from dredging (Hinz *et al.*, 2011). Emerging evidence suggests that bedrock substrates may be more resilient to dredging than other hard substrates due to the morphology of the reef structure (Boulcott and Howell, 2011; Hinz *et al.*, 2011). One explanation for this is that the action of the dredge passing over morphologically complex substrata forces the dredge to lose continuous contact with the substrate, lowering the area of the seafloor under impact. In support, the impact box at site 2 had a higher proportion of bedrock as a component of its hard substrate (Figure 3), and was the only impact box where the community composition did not differ significantly immediately after dredging and became more similar to the SAC control box during the recovery period. That substrate can influence dredging effects might also account for the high faunal turf coverage at site 2 and the small percentage reduction in coverage after dredging: a 10% reduction compared with 69 and 22% at sites 1 and 3 respectively, where there was a greater proportion of cobble/pebble substrates (Figure 4).

As in other studies (Boulcott and Howell, 2011), the action of the dredge moving over bedrock was difficult to discern from quadrat images, supporting the notion that morphologically complex bedrock confers some protection against dredging. Some visual evidence was apparent on cobble/pebble reefs, where rocks and pebbles were displaced or overturned, presumably damaging the emergent structural species colonizing them. Pebbles, cobbles and small boulders were also found in the collecting bag of the dredge, causing further homogenization. The most noticeable change in topography was the flattening of megaripples in the gravel beds to the northwest of the Firth of Lorn. These formations were able to re-establish themselves in the 2.5 months leading up to the recovery survey. However, the impact of the dredge across such substrates is likely to be limited as megaripples can move with the prevailing hydrodynamic conditions (M. Kaiser, pers. comm.) and they had low faunal diversity populated by more disturbance-tolerant species in both the outside and SAC control boxes. Their temporary destruction may be biologically important at certain times of year as they can be spawning grounds for some fish species (Morrison *et al.*, 1991).

Given that cobble/pebble habitats are often suitable scallop grounds (Mason, 1983), provide little impediment to dredges, and were found in this study to support vibrant faunal communities, such areas may be of particular concern.

Conclusion

There is limited empirical evidence with which to assess the harm of scallop dredging on hard substrate habitats due to the difficulties of sampling and the highly structured and interspersed distribution of the substrates. Our study detected changes in the community composition of habitat-forming epifaunal species, which persisted 2.5 months after dredging had taken place. However, we were unable to detect a direct effect of dredging on faunal turf communities. The coverage of faunal turfs in the SAC control boxes was typically greater than in the boxes still fished commercially, and this is consistent with the hypothesis that dredging can result in the loss of such turf communities. In common with Hinz *et al.* (2011), our results also point to the role that substrate morphology might play in modifying the severity of dredging effects. Dense populations of erect, epifaunal species colonizing stable cobble/pebble substrates are of particular concern. Habitats supporting biologically diverse communities that are vulnerable to scallop dredging would benefit from being included in a marine protected area management framework, although the effect of redistributing fishing effort to other areas must also be considered (Greenstreet *et al.*, 2009). Alternatively, vulnerable species from such habitats could be included amongst the secondary effects of bottom-trawling in an ecosystem-based approach to fisheries management (Langton *et al.*, 1990).

Acknowledgements

The authors would like to thank Kevin Stokesbury for early advice in the design of this study and for later revisions to the manuscript. We thank the crew of MRV “Alba na Mara” and Trevor Howell, Marine Scotland Science, for their assistance. We are also indebted to Eoghann MacLachlan and the crew of the FV “Rambling Rose” for their assistance in dredging. Thanks to Bill Turrell and David Donnan for valuable comments and to Rui Catarino for the provision of VMS data. Finally, Martin Burns and Chris Hall, Marine Scotland Science, set up and operated the drop-frame camera system.

Funding

This research was possible with funding from the Scottish Government (Project SU01N0).

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Handling editor: Michel Kaiser