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Implications of a zoned fishery management system for marine benthic communities

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Summary

1. The impacts of trawls and dredges on marine benthic habitats and communities have been studied extensively, but mostly at small scales and over short time periods. To investigate the large-scale chronic impacts of towed fishing gears, zoned commercial fishery management systems allow comparison of habitats and communities between areas of seabed subjected to varying levels of towed-gear use.

2. The Inshore Potting Agreement (IPA) was implemented in 1978 to restrict the use of towed gears in inshore areas that had traditionally been used by static-gear (pot and net) fishers. We used scallop dredges to sample benthic communities at sites within and adjacent to the IPA area that had been subjected to four different commercial fishing regimes since the inception of the system. These were: (i) towed gears only, (ii) annual, seasonal towed-gear use, (iii) temporary towed-gear use but reverting to static-gear use 18–24 months prior to sampling, and (iv) static gears only.

3. There were no significant differences in the total species richness or biomass of benthic communities between sites under regimes (i) and (ii). There was significantly greater total species richness and biomass of benthic communities at sites under regimes (iii) and (iv) than at sites under regimes (i) and (ii). The benthic community biomass under regime (iv) was significantly greater than under all other regimes.

4. The IPA has maintained benthic species that are important for the settlement and survival of others. The cessation of towed-gear fishing for a period of greater than 2 years would be necessary for benthic communities in areas adjacent to the IPA to recover such that they were indistinguishable from areas where towed gears had not been used.

5. *Synthesis and applications.* Members of the fishing industry may object to the creation of permanent closed areas because harvestable stocks can move in space and time. This study indicates that zoned fishery management can allow some sectors of the fishing industry to retain access to fishery resources while protecting benthic species and habitats.

Key-words: community recovery, marine protected area, static gear, trawling effects

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Introduction

Advances in technology have enabled the fishing industry to harvest resources from a progressively greater proportion of the marine environment. There are now few places where marine stocks are not targeted, and overfishing is commonplace (Dayton *et al.* 1995; Vitousek *et al.* 1997; Pauly *et al.* 1998; Pitcher & Pauly 1998; Roberts & Hawkins 1999; Pitcher 2000). To address the resulting problems there is a drive to adopt fishery management systems that incorporate temporal and spatial restrictions on fishing effort (Dugan & Davis 1993; Roberts & Polunin 1993; Roberts 1997; Allison, Lubchenco & Carr 1998; Lauck *et al.* 1998; Babcock *et al.* 1999; Auster & Shackell 2000; Mangel 2000; Rosenberg 2001; Blyth *et al.* 2002; Willis, Millar & Babcock 2003). These restrictions are usually intended to protect significant portions of the stocks of targeted

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species such that spawning events and genetic variability may be at least partially ensured (Malakoff 1997; Roberts 1998).

As well as benefits for targeted species, other important biological benefits may accrue from fishery management systems that restrict the use of certain types of fishing gear. These include the prevention of habitat degradation that inevitably accompanies the use of towed bottom-fishing gear such as trawls or dredges (Dayton *et al.* 1995; Jennings & Kaiser 1998; Auster & Langton 1999; Norse & Watling 1999; Kaiser *et al.* 2002; Schratzberger, Dinmore & Jennings 2002). Benthic communities in areas that are heavily fished with towed gears tend to be less complex and have lower biomass and production than communities in areas that are not fished in this way, or are fished at low levels of effort (Jennings *et al.* 2001; Kaiser *et al.* 2002). In contrast, benthic communities are relatively unaffected by static fishing gears (fish or crustacean pots, long-lines or anchored nets) because of the relatively small area of seabed directly affected (Kinnear *et al.* 1996; Jennings & Kaiser 1998; Eno *et al.* 2001). Hence, the use of static gears might enable some exploitation to occur without negative effects on benthic communities. Few direct comparisons exist of the long-term impacts of static gears and towed gears on benthic communities (Kaiser, Spence & Hart 2000). In addition, few studies have focused on the implications for benthic communities of management strategies that incorporate temporal zonation of fishing effort (Sainsbury *et al.* 1997; Murawski *et al.* 2000).

The Inshore Potting Agreement (IPA) is a zoned fishery management system located off the south coast of Devon, UK (Fig. 1). The IPA has operated since 1978 over an area of approximately 500 km^2 to reduce conflict between different sectors of the fishing industry. The IPA includes areas for the exclusive use of static gears (principally crab pots), and areas for seasonal static-gear use. Towed-gear fishers are able to work in seasonal areas during periods when these are free from static gears (Blyth *et al.* 2002). The success and longevity of the IPA provide a unique opportunity to investigate the characteristics of benthic communities that have been subjected to varying levels of towed and static fishing gear use.

We aimed to use the IPA to investigate the impact of different commercial fishing regimes on benthic communities. Two factors were of particular interest in assessing species richness and biomass of the benthic community: first, the effect of static-gear fishing in comparison to towed-gear fishing; secondly, the effect of annual, seasonal rotation of fishing regime.

Methods

Members of the South Devon and Channel Shellfishermen's Association Ltd were approached in summer 2002 to provide details on the extent to which towed gears had been used in the vicinity of areas where they maintained static-gear territories. Charts of the IPA were provided to 22 static-gear fishers, who were asked to indicate areas where towed gears had never been used, areas where towed gears had been used, but not within the previous year, areas where towed gears were used seasonally on an annual basis, and areas where towed gears were used regularly. Importantly, these sites did not have to correspond exactly with the boundaries of the IPA management system, as towed-gear fishers occasionally infringed the IPA (Blyth *et al.* 2002). Without the input of fishers, these infringements could have unknowingly confounded attempts to attribute different fishing regimes to sites. Towed-gear fishers were not consulted on the use of towed gears in the IPA, as it was thought unlikely that they would co-operate honestly or be willing to incriminate other fishers operating in static-gear areas. In contrast, it was considered that static-gear fishers had no motivation to provide misleading information regarding the illicit use of towed gears inside static-gear areas.

In comparison to other potential sources of data on the use of towed-gears [i.e. fisheries enforcement agency over-flight data or global position system (GPS) monitoring], fishers' information was considered to provide the most detail and accuracy in the area of the IPA. This was because the small spatial variation between sites and the lack of daily agency monitoring precluded the use of fisheries over-flight data. Furthermore, the small boats that prosecute towed-gear fisheries within 6 miles of the UK coastline are not required to carry

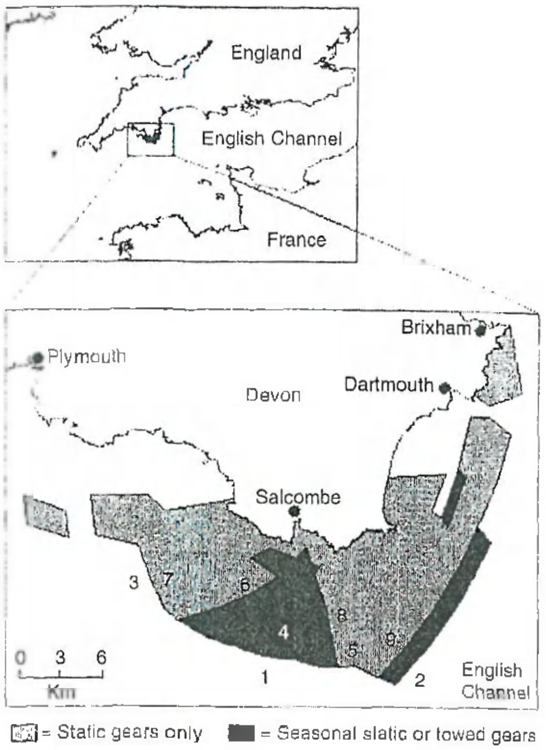

Fig. 1. The location of the Inshore Potting Agreement (IPA). Shaded areas denote the officially recognized fishery management system. Numbers denote locations of sampling sites in areas subjected to different fishing regimes. Sites 1–3, trawl; 4 and 5, seasonal; 6 and 7, ex-trawl; 8 and 9, untrawled.

differential GPS automated position recorders. Importantly, IPA static-gear fishers operate in small territories and typically maintain precise knowledge of all fishing activities in these areas because of conflict issues arising with other fishers (Blyth *et al.* 2002). Finally, charts were cross-referenced between fishers to avoid potential sources of deliberate bias and to corroborate information on towed-gear use at the sites selected for sampling.

Using information provided by fishers, nine sites that had been impacted by fishing gears to varying degrees, and situated as close to each other as possible, were selected and sampled in August 2002 (Fig. 1). Two of these sites were reported as never having been fished with towed gears (called untrawled sites) and two sites were last used by towed-gear fishers 18 months and 2 years prior to sampling (called ex-trawl sites). Two of the other sites selected were trawled seasonally on an annual basis and were last used by towed-gear fishers 3 months and 6 months prior to sampling (called seasonal sites). Three further sites, located just outside the IPA system, were regularly used by the towed-gear fleet (called trawl sites; Table 1).

No data on the precise frequency of fishing gear use at each sampling site were obtained for this study. However, little space exists inside the IPA for additional static gear (Blyth *et al.* 2002) and so it was assumed that crab pots were regularly fished at the untrawled and ex-trawl sites, and the seasonal sites during periods when these were accessible. Due to the perceived catch benefits of operating in the proximity of the IPA, it was reported that the perimeter of the IPA, and hence the trawl sites, were targeted by the towed-gear fleet throughout the year. Seasonal sites were reported to be targeted regularly by the towed-gear fleet when accessible. Both of the ex-trawl sites had been fished regularly over a period of 1–2 months. At the time of sampling, the untrawled, ex-trawl and seasonal sites were occupied by lines of crab and lobster pots.

The substratum at each site was assessed visually, as the mixed coarse substrata encountered within the IPA precluded the use of grab sampling. At each site, a video camera was lowered to the seabed and suspended from the *R.V. Prince Madog* for 30 min. During this period, the vessel was allowed to drift with the tide, so that the camera moved across the seabed. iMovie© V.1.0.2 video software was used to capture a still image on every occasion that the camera came to rest on the seabed during each 30-min deployment. The substratum type in 20 images, selected at random from each site, was allocated a score based on the Φ scale (Buchanan 1984). Scores of between 0 and 5 were allocated for sediments that varied from sand particles of less than 2 mm diameter to gravel of approximately 30 mm diameter (Table 1). Water depth was obtained at the start and end of every tow using the ship's echo-sounder. The mean water depth at each site was calculated as the average of the start and finish depths recorded for all tows at each site (corrected to chart datum). The mean ± SE depth across all sites was 60·5 ± 1·3 m (Table 1).

Following the video surveys, three replicate tows were undertaken at each site using a gang of four Newhaven commercial scallop dredges (each dredge was 850 mm wide). To maximize the collection of smaller organisms, two of the dredges were fitted with 50-mm belly rings and teeth positioned 35 mm apart (called scientific dredges). The other two dredges had 100-mm belly rings and teeth positioned 85 mm apart (called standard dredges). Tows were limited to 10 min bottom time, and were conducted perpendicular to the direction of the main tidal flow to run parallel to any lines of static gear. The distance the dredges travelled over the ground was calculated from differential GPS positions recorded at the time the trawl winch was stopped at the beginning of each tow, and at the moment hauling commenced. Only great scallops *Pecten maximus* Linnaeus were collected from the two standard dredges, while benthos for the community analyses was sampled only from the starboard-most scientific dredge. The catch from the scientific dredge was sorted and identified, and the shells of hermit crabs (Paguridae), as well as other substratum fragments, were removed before all species were separated and weighed wet on a motion-compensated balance (± 1 g). Individuals of each species were not weighed separately due to the difficulty of counting colonial animals.

STATISTICAL METHODS

Biomass data for each species were standardized to the mean ± SE total tow length at all sites of 4408 ± 160 m

Table 1. Environmental characteristics and fishing history for IPA sample sites

Site	Fishing regime	Mean depth (m)	Total tow length (m)	Substrate grade (Φ)	Fisher information
1	Trawl	66·4	4548	0·00	Towed gears used regularly, all year round
2	Trawl	64·4	3951	0·00	Towed gears used regularly, all year round
3	Trawl	56·6	4659	0·00	Towed gears used regularly, all year round
4	Seasonal	63·8	4059	−2·81	Towed gears used annually February–May Towed gears last used 3 months previously
5	Seasonal	66·0	4635	−2·81	Towed gears used annually January–February Towed gears last used 6 months previously
6	Ex-trawl	49·8	3888	−3·81	Towed gears used 18 months previously
7	Ex-trawl	49·2	3963	−1·00	Towed gears used 22 months previously
8	Untrawled	62·3	5340	−2·58	Only static gears used in living memory
9	Untrawled	65·7	4632	−3·32	Only static gears used in living memory

(Table 1). The species richness per tow was not standardized. Data for fish species caught incidentally were excluded from any analyses.

Univariate analyses

Univariate statistical analyses of the biological data were carried out to determine gross differences in species richness and the biomass of the benthic community between sites subjected to different fishing regimes. All univariate statistics were conducted using Minitab V.13.2. Biomass data for each species and the total numbers of species collected at each site were transformed [$x' = \log_{10}(x + 1)$] to stabilize variance. Nested [fishing regime × site(fishing regime)] general linear model (GLM) ANOVA were then undertaken on these data. This model accounts for the enforced lack of orthogonality in the survey design (Underwood 1997). Bonferroni pairwise multiple comparison tests were undertaken when significant differences were found between the fishing regimes. In a further analysis, benthic taxa were then categorized as either 'attached' or 'free' according to their adult life mode. Attached species included bryozoans, hydrozoans and other species that are fixed permanently to the substratum. Free taxa included crabs, starfish, bivalves and other species that are able to move freely (see the Appendix in Supplementary material). For both life modes, nested GLM ANOVA were undertaken on the numbers of species and biomass of species collected at each site. Bonferroni pairwise multiple comparisons were also undertaken when significant differences were found between fishing regimes. Finally, nested GLM ANOVA and Bonferroni pairwise multiple comparisons were undertaken on $\log_{10}(x + 1)$-transformed data for the numbers of scallops greater than 100 mm shell height (the minimum legal landing size in Devon waters) collected at each site using the two standard dredges.

Multivariate analyses

Multivariate statistical analyses of the biological data were carried out to determine differences in the structure of the benthic community between sites subjected to different fishing regimes. All multivariate analyses were performed using the PRIMER© V.5 software package. Data were initially averaged over the three tows conducted at each site. To examine the overall similarity of the benthic communities between sites, a non-metric multidimensional scaling (MDS) ordination plot was created from the community biomass data. This used the Bray–Curtis index of similarity on square root-transformed data (the default PRIMER transformation to down-weight the contribution of common species in relation to rarer ones) and the group average linkage technique. Because of the low number of replicate sites, we then performed an a priori one-way analysis of similarity (ANOSIM), a multivariate analogue of ANOVA, on aggregated data. The untrawled and ex-trawl sites were grouped as 'inside' sites, and the seasonal and trawled sites were grouped as 'outside' sites. A SIMPER analysis was conducted to determine the species that contributed most to the within-fishing regime similarities and between-fishing regime dissimilarities. Finally, a RELATE test was conducted to determine the extent to which patterns observed in the biological community were correlated with abiotic variables resulting from the survey design. This test undertook an element-by-element correlation of a similarity matrix constructed from the square root-transformed community data, with a second similarity matrix constructed from data for the tow length, water depth and substratum type at each site.

Results

UNIVARIATE ANALYSES

Significant differences were determined among different fishing regimes for both the mean total species richness and the mean total biomass of the benthic community (Table 2). Pairwise comparisons showed that a greater

Table 2. Nested GLM ANOVA results for comparisons of (a) number of species and (b) biomass of species, of the total benthic community, attached species and free species observed at sites subjected to different fishing regimes. Bold indicates significant comparisons

Source	d.f.	Adj MS	*F*	*P*
(a) Number of species				
Total				
Fishing regime	3	0·25	25·52	**< 0·001**
Site (fishing regime)	5	0·03	2·96	**0·040**
Error	18	0·01		
Total	26			
Attached				
Fishing regime	3	0·14	9·49	**0·001**
Site (fishing regime)	5	0·06	3·64	**0·019**
Error	18	0·02		
Total	26			
Free				
Fishing regime	3	0·30	35·27	**< 0·001**
Site (fishing regime)	5	0·05	5·84	**0·002**
Error	18	0·01		
Total	26			
(b) Biomass				
Total				
Fishing regime	3	0·72	42·63	**< 0·001**
Site (fishing regime)	5	0·04	2·11	0·111
Error	18	0·02		
Total	26			
Attached				
Fishing regime	3	2·29	17·13	**< 0·001**
Site (fishing regime)	5	0·55	4·09	**0·012**
Error	18	0·13		
Total	26			
Free				
Fishing regime	3	1·49	33·99	**< 0·001**
Site (fishing regime)	5	0·08	1·87	0·150
Error	18	0·04		
Total	26			

Table 3. Bonferroni multiple comparisons of differences in (a) number of species and (b) biomass of species of the total benthic community, attached species and free species observed between sites subjected to different fishing regimes. Bold indicates significant comparisons

	Seasonal	Ex-trawl	Static
(a) Number of species			
Total			
Trawl	0·519	< 0·001	< 0·001
Seasonal		< 0·001	0·003
Ex-trawl			1·000
Attached			
Trawl	0·088	0·017	< 0·001
Seasonal		1·000	0·252
Ex-trawl			0·922
Free			
Trawl	1·000	< 0·001	< 0·001
Seasonal		< 0·001	< 0·001
Ex-trawl			0·165
(b) Biomass			
Total			
Trawl	0·347	< 0·001	< 0·001
Seasonal		0·012	< 0·001
Ex-trawl			0·002
Attached			
Trawl	0·012	0·070	< 0·001
Seasonal		1·000	0·030
Ex-trawl			0·006
Free			
Trawl	0·459	< 0·001	< 0·001
Seasonal		0·004	< 0·001
Ex-trawl			0·099

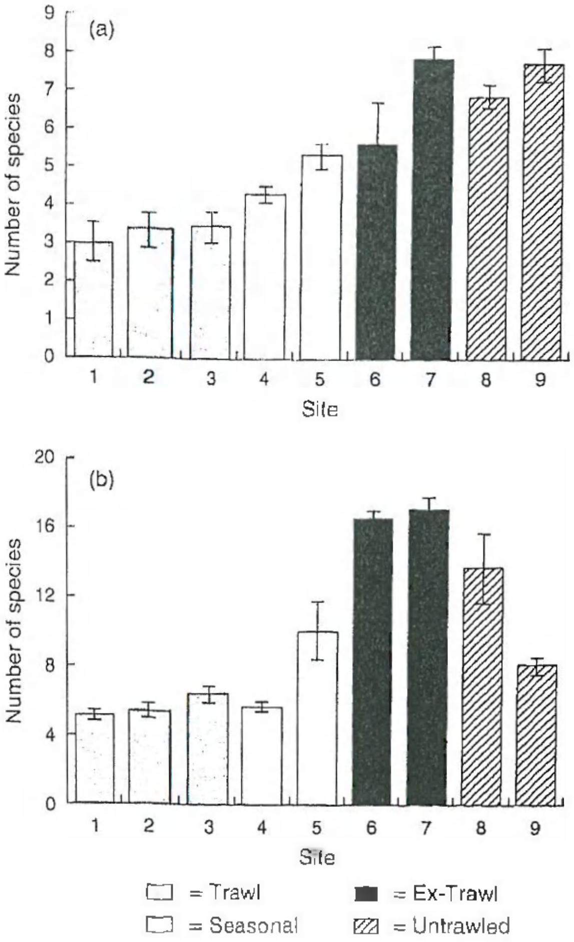

Fig. 2. Mean (± 1 SE) number of (a) attached species and (b) free species observed at sites subjected to different fishing regimes.

total species richness and community biomass were observed at the ex-trawl and untrawled sites than at the trawl and seasonal sites (Table 3). The total community biomass was also significantly greater at the untrawled sites in comparison with the ex-trawl sites. Pairwise comparisons of total species richness and community biomass were not different between other combinations of fishing regimes.

An examination of the life mode components of the benthic community revealed significant differences among fishing regimes for the mean number of species of attached and free animals (Table 2a and Fig. 2a). Pairwise comparisons showed that the mean numbers of attached species at the ex-trawl and untrawled sites were significantly greater than that at the trawl sites (Table 3a). In addition, the mean numbers of free species at the ex-trawl and untrawled sites were significantly greater than at the trawl and seasonal sites (Table 3a). There were also significant differences among fishing regimes in the mean biomass of attached and free species (Table 2b and Fig. 3a,b). Pairwise comparisons showed that the mean biomass of attached species at the untrawled sites was significantly greater than at other fishing regimes (Table 3b). The biomass of attached species at trawl sites was also greater than at the seasonal sites. In addition, the mean biomasses of free species at the ex-trawl and untrawled sites were significantly greater than at the trawl and seasonal sites. Other comparisons among fishing regimes of the mean number or biomass of attached or free species did not differ significantly.

The number of legal-sized scallops caught in the standard dredges differed significantly among areas subjected to different fishing regimes (ANOVA, $F_{1,26} = 9{\cdot}40$, $P = 0{\cdot}001$; Fig. 3c). Pairwise comparisons revealed that fewer scallops were caught at the trawl sites than at either the ex-trawl ($P = 0{\cdot}009$) or untrawled sites ($P \leq 0{\cdot}001$). The comparisons of the numbers of scallops caught at sites subjected to other fishing regimes were not significantly different.

MULTIVARIATE ANALYSES

The relative similarity between the observed composition of the species assemblage of each site was represented by the MDS ordination plot of square root-transformed species data (Fig. 4). The untrawled and ex-trawl sites grouped discretely, while the groupings of the trawl and seasonal sites were less well defined. However, these aggregations of inside and outside sites were significantly different at the 10% level (ANOSIM, $r = 0{\cdot}375$, $P = 0{\cdot}06$). The SIMPER analysis determined that

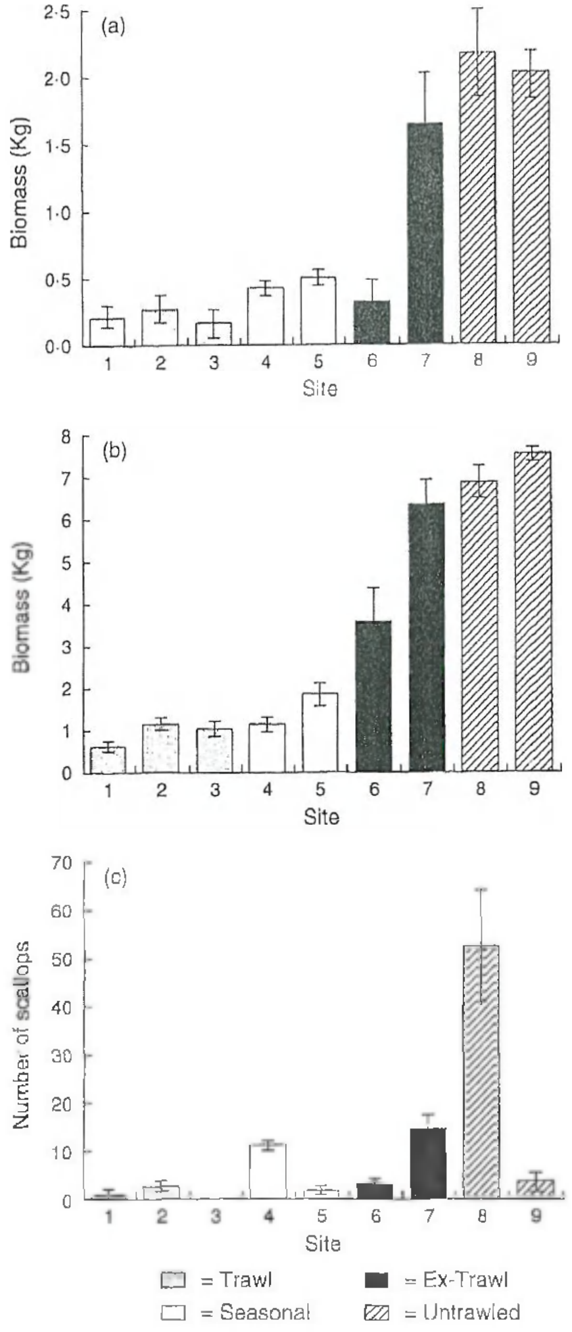

Fig. 3. Mean (± 1 SE) (a) biomass of attached species, (b) biomass of free species and (c) number of legally sized scallops observed at sites subjected to different fishing regimes.

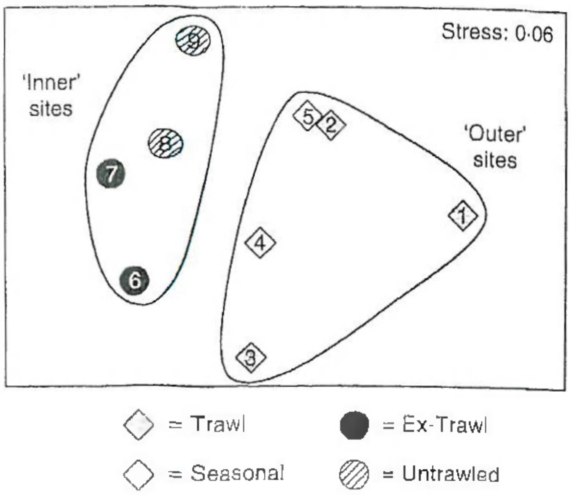

Fig. 4. MDS ordination plot showing square root-transformed community biomass data for IPA sites subjected to different fishing regimes (numbers indicate site). Inner and outer groupings indicate site groupings used in the ANOSIM test.

the overall mean similarities within the trawl, seasonal, ex-trawl and untrawled sites were 10·5%, 16·8%, 24·5% and 40·0%, respectively. The greatest overall mean dissimilarity occurred between the trawl and untrawled sites (89·4%) and the lowest overall mean dissimilarity was between the trawl and seasonal sites (73·9%).

Common taxa that made the greatest contribution to the similarities within sites of all fishing regimes were the attached colonial anthozoan *Alcyonium digitatum* Linnaeus, hydroids and the tube building bristle worm *Chaetopterus variopedatus* Renier (Table 4). The sea urchin *Echinus esculentus* Linnaeus was also found frequently at the ex-trawl and untrawled sites. However, this species contributed greatly to the between-fishing regime dissimilarities because it was not recorded at the trawl or seasonal sites (Table 5). *Alcyonium digitatum* also contributed greatly to the dissimilarities between these combinations of fishing regimes because relatively large quantities of this species were found at the ex-trawl and untrawled sites. The brittle star *Ophiothrix fragilis* Thomson was only found in abundance at the ex-trawl sites, and made the greatest contribution to the dissimilarities between these sites and those of the other fishing regimes.

The RELATE analysis determined that there was no similarity in the patterns observed between the benthic community and the tow length, substratum type and water depth at each site (Rho = −0·116, $P = 0·73$). This result indicated that the abiotic variables tested were not able to predict the variation observed in the biological community.

Discussion

Comparative studies of fishing impacts are prone to the confounding effects of variables such as substratum type that may be autocorrelated with the fishing treatment. In this study, the substrata at the trawl sites were less coarse than those at the sites of other fishing regimes. However, the RELATE analysis indicated that fishing was the only variable that corresponded with the observed differences in the benthic communities between the sites of different fishing regimes. The inference that fishing rather than substratum type brought about the observed differences was further supported by our data, because while the substrata at the seasonal and trawl sites were different, the communities were almost indistinguishable. If it is assumed that the communities at the trawl sites were the most impacted by commercial fishing, then the cessation of towed-gear fishing could enable the communities at all sites around the IPA to recover towards those of the untrawled state.

Table 4. SIMPER results: relative contribution to within-site similarities of the four most similar species observed at each site

	Mean abundance (g)	Mean similarity	Contribution (%)	Cumulative contribution (%)
Trawl				
Hydroids	18·4	2·59	24·6	24·6
Atelecyclus rotundatus	48·3	2·41	22·9	47·5
Nemertesia	15·6	1·07	10·1	57·6
Asterias rubens	10·6	1·01	9·6	67·2
Seasonal				
Alcyonium digitatum	222·8	6·42	38·3	38·3
Chaetopterus variopedatus	53·0	2·86	17·1	55·4
Hydroids	23·4	2·27	13·6	69·0
Aequipecten opercularis	18·9	1·19	7·1	76·1
Ex-trawl				
Marthasterias glacialis	649·1	8·02	32·8	32·8
Echinus esculentus	813·9	7·15	29·2	61·9
Aequipecten opercularis	777·4	2·85	11·6	73·5
Hydroids	123·4	2·53	10·3	83·8
Untrawled				
Alcyonium digitatum	1583·7	25·96	64·9	64·9
Echinus esculentus	589·6	6·40	16·0	80·9
Maia squinado	104·5	1·84	4·6	85·5
Chaetopterus variopedatus	107·4	1·60	4·0	89·5

Table 5. SIMPER results: relative contribution to between-site dissimilarities of the four most dissimilar species observed between each site.

	Mean abundance (g)				
	Regime 1	Regime 2	Mean dissimilarity	Contribution (%)	Cumulative contribution (%)
Trawl vs. seasonal					
Alcyonium digitatum	108·9	222·8	15·59	21·1	21·1
Nemertesia	15·6	186·2	12·48	16·9	38·0
Marthasterias glacialis	158·5	92·5	12·44	16·8	54·8
Pecten maximus	62·9	42·2	5·47	7·4	62·2
Trawl vs. ex-trawl					
Aequipecten opercularis	41·0	777·4	24·70	28·5	28·5
Echinus esculentus	0·0	813·9	18·03	20·8	49·3
Marthasterias glacialis	158·5	649·1	13·10	15·1	64·4
Chaetopterus variopedatus	3·5	203·9	4·17	4·8	69·2
Trawl vs. untrawled					
Ophiothrix fragilis	0·0	1782·4	27·70	31·0	31·0
Alcyonium digitatum	108·9	1583·7	26·14	29·2	60·2
Echinus esculentus	0·0	589·6	10·75	12·0	72·2
Nemertesia	15·6	309·1	5·57	6·2	78·4
Seasonal vs. ex-trawl					
Aequipecten opercularis	18·9	777·4	23·89	27·7	27·7
Echinus esculentus	0·0	813·9	17·43	20·2	47·9
Marthasterias glacialis	92·5	649·1	12·04	14·0	61·9
Alcyonium digitatum	222·8	3·7	5·77	6·7	68·6
Seasonal vs. untrawled					
Ophiothrix fragilis	6·6	1782·4	27·09	33·8	33·8
Alcyonium digitatum	222·8	1583·7	23·49	29·3	63·1
Echinus esculentus	0·0	589·6	10·47	13·0	76·1
Nemertesia	186·2	309·1	4·80	6·0	82·1
Ex-trawl vs. untrawled					
Ophiothrix fragilis	86·2	1782·4	19·76	25·5	25·5
Alcyonium digitatum	3·7	1583·7	19·11	24·6	50·1
Aequipecten opercularis	777·4	10·4	10·12	13·1	63·2
Echinus esculentis	813·9	589·6	6·61	8·5	71·8

The benthic communities in areas that had been open only to static gears in the year preceding sampling were richer and of greater biomass than those in areas that were impacted by towed fishing gears during the same period. However, the benthic communities at the ex-trawl sites remained different to those at the untrawled sites. The lower community biomass but greater species richness at the ex-trawl sites is consistent with the intermediate disturbance theory (Connell 1978). This suggests that regular trawling disturbance will result in a community dominated by a small number of rapidly colonizing and maturing species. In contrast, occasional trawling disturbance may enhance species richness because of opportunities for slower developing species to become established in addition to the fastest colonizers. In the long term absence of vigorous disturbance at the untrawled sites, a community of moderate species richness but greater biomass appears to have become dominant. This finding is not necessarily mirrored by results from other studies. For example, Thrush *et al.* (1998) found that an increase in trawling frequency resulted in a decrease in species richness. The present study was limited in that the dredges used would have been unlikely to sample small species consistently. If additional sampling had been conducted using fine-mesh liners inside the dredges, then it is possible that greater numbers of small species would have changed the observed pattern of benthic community richness between sites.

Arguably the most significant result from this study is that the benthic communities found at the seasonal sites were almost indistinguishable from those found at the trawl sites. Only the biomass of the attached community was greater at the seasonal sites. This indicates that, in the area of the IPA, a 6-month cessation of towed-gear use is insufficient for the benthic community to recover. In contrast, some studies conducted at shallow, coastal sites have reported that the benthic communities in fishing-impacted areas recovered within a short period post-disturbance, and have suggested that natural disturbance events such as storms or tidal scour are likely to have a relatively greater impact than fishing disturbance (Currie & Parry 1996; Kaiser & Spencer 1996; Kaiser *et al.* 1998; Collie *et al.* 2000). However, these were experimental studies, and the reported responses of benthic communities to localized experimental fishing, may not represent the effects of fishing on the large scale and regular basis that occurs with commercial fleets.

In short-term impact experiments (days/months), communities may appear to recover as a result of immigration of fauna from nearby areas, as the recovery trajectories typically described are unlikely to result from the recruitment and growth of settling larvae (Kaiser *et al.* 2002). If towed gears affect a large area, then recovery may be much slower as immigration rates are reduced, and the process of recruitment then becomes increasingly important (Jennings *et al.* 2001). In addition, attached epibenthic species such as *Alcyonium digitatum* and *Chaetopterus variopedatus* are slow growing (Rees 1987; Newell, Seiderer & Hitchcock 1998) and may take many years to attain former biomasses (i.e. the prefishing state). Hence, at the larger scales of operation of commercial fisheries, benthic communities may take years, decades or even thousands of years in deep water areas, to recover (Sainsbury *et al.* 1997; Hall-Spencer & Moore 2000; Hall-Spencer, Allain & Fossa 2002).

The significantly greater biomass of attached species at the untrawled sites in comparison to all other sites is of particular interest because attached epifauna act as settlement sites for many benthic species (Walters & Juanes 1993). The presence of attached epifauna has been shown to increase the survivorship of commercially targeted species including silver hake *Merluccius bilinearis* Mitchill (Auster, Malatesta & Donaldson 1997), cod *Gadus morhua* Linnaeus (Tupper & Boutilier 1995; Lindholm, Auster & Kaufman 1999) and spiny lobster *Panulirus argus* Latreille (Herrnkind, Butler & Hunt 1999). Scallops may be the commercially targeted species most likely to benefit from the IPA, and significant increases in scallop biomass have been reported after the establishment of other closed-area systems (Turner, Tammi & Rice 1996; Brocken & Kenchington 1999; Murawski *et al.* 2000). A number of factors may be implicated in this effect. Primarily, in addition to being captured, scallops may be physically damaged when in direct contact with towed gears, thereby reducing survivorship and fitness (Caddy 1973; Brand, Paul & Hoogesteger 1980). The presence of attached epifauna has also been identified as a critical spat settlement cue for a number of scallop species (Dare & Bannister 1987; Minchin 1992; Stokesbury & Himmelman 1995). Finally, fishery collapses of similar sessile species have been attributed to a reduction in the density of adults, such that mature individuals were too isolated to reproduce successfully (Tegner, Basch & Dayton 1996; Malakoff 1997; Orensanz *et al.* 1998; Roberts & Hawkins 1999; Jennings 2000). Hence, significant cumulative benefits may accrue for the IPA scallop population from greater reproductive output, spat settlement and subsequent juvenile survival. High-density patches of scallops were present at the ex-trawl and untrawled sites within the IPA. However, the implications of these high-density patches for recruitment to the surrounding fishery remain unknown.

Within the IPA system, some areas are rotated seasonally to permit fishers from different sectors equitable access to resources (Blyth *et al.* 2002). Area rotations present a potential problem for the maintenance of benthic communities because towed-gear fishers return regularly to areas that previously produced good catches and are known to be clear of seabed obstructions that could damage the fishing gear (Rijnsdorp *et al.* 1998). Area rotations may therefore relocate fishing effort by forcing fishers to operate away from favoured sites. For example, large-scale fishery closures from 2000 to 2002 in the North Sea, which were designed to protect seasonal spawning aggregations of cod, forced fishers away from traditional grounds. Dinmore *et al.* (2003) argued that the result of this fishery displacement may have had greater long-term impacts on fish stocks and benthic communities, because fishers were forced to operate in areas that had rarely or never been fished before, than if the fleet had simply been allowed to continue operating in traditional locations. However, the greatest impact on the production and biomass of epibenthic communities occurs within the first few passages of towed, demersal gears (Sainsbury *et al.* 1997; Jennings & Kaiser 1998; Jennings 2000). Hence, in open-access systems where fishers are able to target virgin grounds, stable benthic communities may be impacted significantly by even single passes with towed gears.

Preventing towed-gear fleets from operating in closed areas over sufficiently long periods has the potential to allow benthic communities in those areas to recover and be maintained. Findings from this study suggest that the cessation of towed-gear fishing in regions similar to those represented by the IPA must be of a duration longer than 2 years if benefits for the benthic community are to accrue. A 5-year closure on George's Bank, Canada, resulted in significant recovery of the benthic community, including target species such as yellowtail flounder *Limanda ferruginea* Storer and sea scallops *Placopecten magellanicus* Gmelin, such that a rotating closure system was subsequently proposed to increase fishery production (Murawski *et al.* 2000).

CONCLUSIONS

Fishers may object to the creation of permanent marine protected areas because harvestable stocks can move from place to place, and from season to season. In contrast, zoned management systems allow fishers from some sectors of the fishing industry to retain access to marine resources, while having the potential to ensure that sensitive or important habitats, and a significant portion of targeted stocks, remain protected. The argument for adopting zoned systems will be strengthened if it can be shown that these regimes can provide economic benefits to local communities that depend on fishing, while helping to achieve habitat and stock management goals. However, if area rotations are incorporated into management plans, the length of time between switching usage from one area to another must be sufficient for the biomass and diversity of benthic communities to recover. This time period may need to be much longer than is predicted by benthic recovery trajectories constructed from short-term experimental fishing (Collie *et al.* 2000), and will depend on factors that include the depth, tidal regime, susceptibility to weather and substratum and fishery types (Dayton *et al.* 1995; Kaiser *et al.* 2002). In the present study, a cessation of towed-gear fishing for a 2-year period was insufficient for benthic communities to recover to the point that they were indistinguishable from communities found in adjacent areas that had been exclusively subjected to a static-gear fishing regime (i.e. no towed-gear impacts). These results are important for fishery managers given the current drive for using spatial and temporal restrictions on fishing effort as fishery management tools.

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Supplementary material

The following material is available from
http://www.blackwellpublishing.com/products/journals/suppmat/JPE/JPE945/JPE945sm.htm

Appendix. Life mode classification for taxa collected at all sites.

References

Allison, G.W., Lubchenco, J. & Carr, M.H. (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications*, **8**, 79–92.

Auster, P.J. & Langton, R.W. (1999) The effects of fishing on fish habitat. *Fish Habitat: Essential Fish Habitat and Rehabilitation* (ed. L. Benaka), Vol. 22, pp. 150–187. American Fisheries Society, Hartford, CT.

Auster, P.J. & Shackell, N.L. (2000) Marine protected areas for the temperate and boreal northwest Atlantic: the potential for sustainable fisheries and conservation of biodiversity. *Northeastern Naturalist*, **7**, 419–434.

Auster, P.J., Malatesta, R.J. & Donaldson, C.L.S. (1997) Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. *Environmental Biology of Fishes*, **50**, 195–200.

Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W. & Willis, T.J. (1999) Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series*, **189**, 125–134.

Blyth, R.E., Kaiser, M.J., Edwards-Jones, G. & Hart, P.J.B. (2002) Voluntary management in an inshore fishery has conservation benefits. *Environmental Conservation*, **29**, 493–508.

Brand, A.R., Paul, J.D. & Hoogesteger, J.N. (1980) Spat settlement of the scallops *Chlamys opercularis* (L.) and *Pecten maximus* (L.) on artificial collectors. *Journal of the Marine Biological Association of the United Kingdom*, **60**, 379–390.

Brocken, F. & Kenchington, E. (1999) *A Comparison of Scallop (Placopecten magellanicus) Population and Community*

Characteristics between Fished and Unfished Areas in Lunenburg County, NS, Canada. Report No. 2258. Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Canada.

Buchanan, J.B. (1984) Sediment analysis. *Methods for the Study of Marine Benthos* (eds N.A. Holme & A.D. McIntyre), pp. 41–65. Blackwell Scientific Publications, Oxford, UK.

Caddy, J.F. (1973) Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. *Journal of the Fisheries Research Board of Canada*, 30, 173–180.

Collie, J.S., Hall, S.J., Kaiser, M.J. & Poiner, I.R. (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology*, 69, 785–799.

Connell, J.H. (1978) Diversity in tropical rainforests and coral reefs. *Science*, **199**, 1302–1310.

Currie, D.R. & Parry, G.D. (1996) Effects of scallop dredging on a soft sediment community: a large-scale experimental study. *Marine Ecology Progress Series*, **134**, 131–150.

Dare, P.J. & Bannister, R.C.A. (1987) Settlement of scallop *Pecten maximus* spat on natural substrates off south-west England: the hydroid connection (abstract only). *The Sixth International Pectinid Workshop* (eds A.R. Beaumont & J. Mason). CM 1987/K: 3. ICES, Copenhagen, Denmark.

Dayton, P.K., Thrush, S.F., Agardy, M.T. & Hofman, R.J. (1995) Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 5, 205–232.

Dinmore, T.A., Dupilsea, D.E., Rackham, B.D., Maxwell, D.L. & Jennings, S. (2003) Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. *ICES Journal of Marine Science*, **60**, 371–380.

Dugan, J.E. & Davis, G.E. (1993) Applications of marine refugia to coastal fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2029–2042.

Eno, N.C., MacDonald, D.S., Kinnear, J.A.M., Amos, S.C., Chapman, C.J., Clark, R.A., Bunker, F.S.P.D. & Munro, C. (2001) Effects of crustacean traps on benthic fauna. *ICES Journal of Marine Science*, **58**, 11–20.

Hall-Spencer, J.M. & Moore, P.G. (2000) Scallop dredging has profound, long-tem impacts on maerl habitats. *ICES Journal of Marine Science*, **57**, 1407–1415.

Hall-Spencer, J.M., Allain, V.-A. & Fossa, J.H. (2002) Trawling damage to Northeast Atlantic ancient coral reefs. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **269**, 507–511.

Herrnkind, W.F., Butler, M.J. IV & Hunt, J.H. (1999) A case for shelter replacement in a disturbed spiny lobster nursery in Florida: why basic research had to come first. *Fish Habitat: Essential Fish Habitat and Rehabilitation* (ed. L. Benaka), Vol. 22, pp. 421–437. American Fisheries Society, Hartford, CT.

Jennings, S. (2000) Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries*, 10, 209–231.

Jennings, S. & Kaiser, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology* (eds J.H.S. Blaxter, A.J. Southward & P.A. Tyler), Vol. 34, pp. 203–354. Academic Press, London, UK.

Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Warr, K.J. (2001) Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series*, 213, 127–142.

Kaiser, M.J. & Spencer, B.E. (1996) The effects of beam trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology*, 65, 348–358.

Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S. & Poiner, I.R. (2002) Modification of marine habitats by trawling activities: prognosis and solutions. *Fish and Fisheries*, 3, 114–136.

Kaiser, M.J., Edwards, D.B., Armstrong, P.J., Radford, K., Lough, N.E.L., Flatt, R.P. & Jones, H.D. (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES Journal of Marine Science*, **55**, 353–361.

Kaiser, M.J., Spence, F.E. & Hart, P.J.B. (2000) Fishing-gear restrictions and conservation of benthic habitat complexity. *Conservation Biology*, 14, 1515–1525.

Kinnear, J.A.M., Barkel, P.J., Mojsiewicz, W.R., Chapman, C.J., Holbrow, A.J., Barnes, C. & Greathead, C.F.F. (1996) *Effects of Nephrops Creels on the Environment.* Report No. 2/96. Scottish Office, Agriculture, Environment and Fisheries Department, Aberdeen, UK.

Lauck, T., Clark, C.W., Mangel, M. & Munro, G.R. (1998) Implementing the precautionary principle in fisheries management through marine reserves. *Ecological Applications*, 8, 72–78.

Lindholm, J.B., Auster, P.J. & Kaufman, L.S. (1999) Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, **180**, 247–255.

Malakoff, D. (1997) Extinction on the high seas. *Science*, **277**, 486–488.

Mangel, M. (2000) Irreducible uncertainties, sustainable fisheries and marine reserves. *Evolutionary Ecology Research*, 2, 547–557.

Minchin, D. (1992) Biological observations on young scallops, *Pecten maximus*. *Journal of the Marine Biological Association of the United Kingdom*, 72, 807–819.

Murawski, S.A., Brown, R., Lai, H.-L., Rago, P.J. & Hendrickson, L. (2000) Large-scale closed areas as a fishery-management tool in temperate marine systems: the Georges Bank experience. *Bulletin of Marine Science*, **66**, 775–798.

Newell, R.C., Seiderer, L.J. & Hitchcock, D.R. (1998) The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. *Oceanography and Marine Biology: An Annual Review*, **36**, 127–178.

Norse, E.A. & Watling, L. (1999) Impacts of mobile fishing gear: the biodiversity perspective. *Fish Habitat: Essential Fish Habitat and Rehabilitation* (ed. L. Benaka), Vol. 22, pp. 31–40. American Fisheries Society, Hartford, CT.

Orensanz, J.M., Armstrong, J., Armstrong, D. & Hilborn, R. (1998) Crustacean resources are vulnerable to serial depletion: the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. *Reviews in Fish Biology and Fisheries*, **8**, 117–176.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, J.F. (1998) Fishing down marine food webs. *Science*, **279**, 860–863.

Pitcher, T.J. (2000) Ecosystem goals can reinvigorate fisheries management, help dispute resolution and encourage public support. *Fish and Fisheries*, 1, 99–103.

Pitcher, T.J. & Pauly, D. (1998) Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. *Reinventing Fisheries Management* (eds T. J. Pitcher, P. J. B. Hart, & D. Pauly), pp. 311–329. Kluwer Academic Publishers, London, UK.

Rees, H.L. (1987) *A Survey of the Benthic Fauna Inhabiting Gravel Deposits off Hastings, Southern England.* Report No. CM 1987/L: 19. ICES, Copenhagen, Denmark.

Rijnsdorp, A.D., Buijs, A.M., Storbeck, F. & Visser, E. (1998) Micro-scale distribution of beam trawl effort in the south-eastern North Sea in relation to the trawling frequency on the sea bed and the impact on benthic organisms. *ICES Journal of Marine Science*, **55**, 403–419.

Roberts, C.M. (1997) Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution*, **12**, 35–38.

Roberts, C.M. (1998) Sources, sinks, and the design of marine reserve networks., 23, 16–19.

Roberts, C.M. & Hawkins, J.P. (1999) Extinction risk in the sea. *Trends in Ecology and Evolution*, **14**, 241–246.

Roberts, C.M. & Polunin, N.V.C. (1993) Marine reserves: simple solutions to managing complex fisheries? *AMBIO*, **22**, 363–368.

Rosenberg, A.A. (2001) Marine reserves and population recovery or how do closed areas affect exploited population dynamics. *Reviews in Fish Biology and Fisheries*, **10**, 519–520.

Sainsbury, K.J., Campbell, R.A., Lindholm, R. & Whitelaw, A.W. (1997) Experimental management of an Australian multi-species fishery: examining the possibility of trawl-induced habitat modification. *Global Trends: Fisheries Management* (eds E.K. Pikitch, D.D. Huppert & M.P. Sissenwine), Vol. 20, pp. 107–112. American Fisheries Society, Bethesda, MD.

Schratzberger, M., Dinmore, T.A. & Jennings, S. (2002) Impacts of trawling on the diversity, biomass and structure of meiofauna assemblages. *Marine Biology*, **140**, 83–93.

Stokesbury, K.D.E. & Himmelman, J.H. (1995) Biological and physical variables associated with aggregations of the giant scallop *Placopecten magellanicus*. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 743–753.

Tegner, M.J., Basch, L.V. & Dayton, P.K. (1996) Near extinction of an exploited marine invertebrate. *Trends in Ecology and Evolution*, **11**, 278–280.

Thrush, S.F., Thrush, S.F., Hewitt, J.E., Cummings, V.J., Dayton, P.K., Cryer, M., Turner, S.J., Funnell, G.A., Budd, R.G., Milburn, C.J. & Wilkinson, M.R. (1998) Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecological Applications*, **8**, 866–879.

Tupper, M. & Boutilier, R.G. (1995) Effects of habitat on settlement, growth, and post-settlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1834–1841.

Turner, W.H., Tammi, K.A. & Rice, M.A. (1996) 'Bags to drags', the story of the bay scallop restoration project. *Journal of Shellfish Research*, **16**, 276.

Underwood, A.J. (1997) *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge, UK.

Vitousek, P.M., Mooney, H.A., Lubchenko, J. & Melillo, J.M. (1997) Human domination of the Earth's ecosystems. *Science*, **277**, 494–499.

Walters, C.J. & Juanes, F. (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2058–2070.

Willis, T.J., Millar, R.B. & Babcock, R.C. (2003) Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagurus auratus* (Sparidae) in northern New Zealand marine reserves. *Journal of Applied Ecology*, **40**, 214–227.

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