

Accepted Manuscript

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PII: S1385-1101(13)00230-X
DOI: doi: [10.1016/j.seares.2013.11.005](https://doi.org/10.1016/j.seares.2013.11.005)
Reference: SEARES 1164

To appear in: *Journal of Sea Research*

Received date: 11 September 2012
Revised date: 30 August 2013
Accepted date: 13 November 2013



Please cite this article as: Handley, Sean J., Willis, Trevor J., Cole, Russell G., Bradley, Anna, Cairney, Daniel J., Brown, Stephen, Carter, Megan, The importance of benchmarking habitat structure and composition for understanding the extent of fishing impacts in soft sediment ecosystems, *Journal of Sea Research* (2013), doi: [10.1016/j.seares.2013.11.005](https://doi.org/10.1016/j.seares.2013.11.005)

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The importance of benchmarking habitat structure and composition for understanding the extent of fishing impacts in soft sediment ecosystems

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ABSTRACT

Trawling and dredge fisheries remove vulnerable fauna, homogenise sediments and assemblages, and break down biogenic habitats, but the full extent of these effects can be difficult to quantify in the absence of adequate control sites. Our study utilised rare control sites containing biogenic habitat, the Separation Point exclusion zone, formally protected for 28 years, as the basis for assessing the degree of change experienced by adjacent areas subject to benthic fishing. Sidescan sonar surveys verified that intensive trawling and dredging occurred in areas adjacent to, but not

inside, the exclusion area. We compared sediment composition, biogenic cover, macrofaunal assemblages, biomass, and productivity of the benthos, inside and outside the exclusion zone. Disturbed sites were dominated by fine mud, with little or no shell-gravel, reduced number of species, and loss of large bodied animals, with concomitant reductions in biomass and productivity. At protected sites, large, rarer molluscs were more abundant and contributed the most to size-based estimates of productivity and biomass. Functional changes in fished assemblages were consistent with previously reported relative increases in scavengers, predators and deposit feeders at the expense of filter feeders and a grazer. We propose that the colonisation of biogenic species in protected sites was contingent on the presence of shell-gravel atop these soft sediments. The process of sediment homogenisation by bottom fishing and elimination of shell-gravels from surficial sediments appeared to have occurred over decades – a ‘shifting baseline’. Therefore, benchmarking historical sediment structure at control site like the Separation Point exclusion zone is necessary to determine the full extent of physical habitat change wrought by contact gears on sheltered soft sediment habitats to better underpin appropriate conservation, restoration or fisheries management goals.

Keywords: assemblage structure, benthos, dredging, New Zealand, Separation Point, trawling impact

1. Introduction

Trawling and dredging cause physical disturbance to the sea floor, homogenise habitats and their benthic assemblages, and reduce biodiversity (Jennings & Kaiser 1998, Kaiser et al. 2006, Thrush & Dayton 2002, Tillin et al. 2006, Rice 2006). Much of the published literature regarding bottom fishing comprises assessments of the effects on the abundances of organisms, either individually or at the assemblage level (Gray et al. 2006, Jennings & Kaiser 1998, Kaiser et al. 2006, Thrush & Dayton 2002). Investigations have also focussed on the effects of trawl disturbance on other ecological parameters like the importance of size structure of invertebrates and their relative contribution to biomass and productivity (Blanchard et al. 2004, Cartes et al 2009, Hermsen et al. 2003, Hidding et al 2006, Jennings et al. 2003). As benthic disturbance by fishing gear selects for smaller invertebrates (Duplisea et al. 2002, Tserpes et al. 2006) a shift to the dominance of smaller-sized species could increase productivity per unit biomass at the expense of standing biomass which will decrease (Cartes et al. 2009, Queirós et al. 2006). While bottom fishing gear breaks down and removes diverse biogenic habitats (Tserpes et al. 2006, Watling & Norse 1998) causing reductions in sediment habitat heterogeneity, species diversity and ecological function (Hewitt et al. 2008), few studies have investigated the effects of fishing on the heterogeneous mollusc shell gravel component of coastal soft sediments. Bivalve shells act as ecosystem engineers in the succession of biogenic habitats as shells provide substratum for the recruitment of plants and animals that bind the shell fragments together (Powell & Klinck 2007). Shells from dead bivalves can also provide important ecosystem services including; stabilising sediments (Hewitt et al.

2005), provide refugia from predation, buffer physical or physiological stress, and control transport of solutes and particles in the benthic environment (Gutiérrez et al. 2003, Powell & Klinck 2007). Biogenic structure, in turn, may provide recruitment habitat and shelter for small fish (Kaiser et al. 2003, Thrush et al. 2002) or invertebrates (Kamenos et al. 2004). Of importance to fisheries managers, habitats that are less damaged are suggested to contribute more recruits to fisheries (Auster et al. 1996, Carlines et al. 2004), and to contain greater diversity than disturbed habitats (Auster & Langton 1999, Thrush et al. 1998).

Without adequate benchmarking, it is difficult to predict how much fishing (in terms of the intensity or frequency of activity), and over what time scales, such changes are brought about. Because of the ubiquitous nature of bottom fishing (Cryer et al. 2002) and the potential for shifting baselines (Pauly 1995), it is unlikely that public and institutional knowledge can be used to benchmark the pre-impact potential of affected assemblages and habitats. Without attempts to benchmark lost assemblage structure, in the absence of adequate control sites, we cannot determine the past environmental conditions, the rate, direction and magnitude and cause of change in relation to natural variability (Saunders and Taff 2009, Smol 2008). In the context of fishing effect studies, the magnitude and scale of effects can be estimated using appropriate control sites if available, by using gradient approaches (e.g. Thrush et al. 1998, Tillin et al. 2006), or by using marine reserves and marine protected areas (MPA's) to measure recovery rates and successional processes following cessation of bottom fishing (e.g. Asch & Collie 2008). When adequate control sites are not available it is difficult to examine the true range of effect size. This potential disjuncture between the pre- and post-impact compositions of fished habitats has

important implications for conservation, ecosystem approaches to fisheries management and restoration goals for depleted fishery species.

Various forms of exclusion zones or temporal closures have been used to evaluate the nature and magnitude of effects of fishing on benthic and demersal composition and production (e.g. Asch and Collie 2008, Duineveld et al 2007, Dimech et al 2008, McConnaughey et al 2000, Murawski et al 2000). No studies have examined the effects of fishing on benthic invertebrate productivity in the southern hemisphere in shallow, productive, euphotic waters. Due to the late colonisation of New Zealand (Wilmshurst et al. 2008), there is a relatively short history of human disturbance. With the foresight of early fisheries managers, some areas of soft sediment habitats have been preserved to protect unique biogenic habitats that would otherwise have been modified or removed by bottom fishing gears (Bradstock and Gordon 1983, Mace 1981). Such sites offer a unique opportunity to benchmark the effects of fishing on the benthos. Here we utilise the Separation Point exclusion zone, an area that has not been trawled, seined or dredged for at least 28 years to estimate the degree to which trawling may alter the benthic habitat and associated biota. This area contains a relict biogenic bryozoan assemblage atop shell gravel substratum providing rare control sites from which to demonstrate the importance of benchmarking habitat composition in the study of fishing effects. We compare protected areas with neighbouring sites that have been intensively trawled and historically dredged, by measuring sediment characteristics, and invertebrate abundance, size, biomass, productivity, and functional composition.

2. MATERIALS AND METHODS

2.1 Study location and fishing history

Separation Point lies between Golden and Tasman Bays, in the north of the South Island of New Zealand (Fig. 1). The seabeds of the two bays slope gradually to ca.50 m depth. The Golden and Tasman Bay seabeds are intensively fished, by trawling and seining for finfishes including flatfish species (*Rhombosolea plebius*, *R. leporina*, *R. tapirina*), barracouta (*Thyrstites atun*), snapper (*Pagrus auratus*), tarakihi (*Nemadactylus macropterus*) and red cod (*Pseudophycis bachus*) and by dredging for scallops (*Pecten novaezelandiae*) and oysters (*Ostrea chilensis*). Recreational fishers are also permitted to dredge for scallops and oysters.

In December 1980 commercial trawling, seining and shellfish dredging were excluded from a 146-km² sector from the coastline out to ca.50 m depth offshore of Separation Point (hereafter the “exclusion zone”, Fig. 1) to protect an area of bryozoans, mainly *Celleporaria agglutinans* and *Hippomenella vellicata*, which was perceived to be important recruitment habitat for fishes (Bradstock & Gordon 1983, Mace 1981). Due to the robust nature of the Separation Point bryozoan ‘corals’, fishers avoided these grounds until pair trawling began between 1972-74 allowing nets to be “flown” above the seabed to avoid nets filling with bryozoa that caused damage to catch and longer catch sorting times (Grange et al. 2003). Thus, although the area cannot be considered “completely pristine”, the robustness of the bryozoan beds provided innate protection from fishers who adapted their fishing methods to avoid bottom contact. Declines in numbers of juvenile snapper and tarakihi (Saxton

1980) subsequently led to protection of the bryozoan beds. A post-protection survey using sidescan sonar and remotely operated vehicle in 2003 reported bryozoans covered ca. 38% of the protected area (Grange et al. 2003). Recreational fishing is permitted in the exclusion zone, so densities of angling species, potential benthic feeders, are likely to be similar inside and outside the exclusion zone, especially given the small size of the exclusion area in relation to demersal fish movement. Recreational dredging for scallops is likely to be unproductive due to the biogenic nature of the sediments.

Bottom trawling was recorded as occurring both west and south of the exclusion zone in the two years preceding our sampling since records began in 2007. Over twice as many trawls occurred south of the exclusion zone in 2007, but trawling was relatively consistent either side of the zone during 2008 (Handley, unpub. data). The majority of trawls targeted demersal flat fish species including sand flounder (Tuck et al. 2011). Commercial scallop dredging occurred west and south of the exclusion zone since at least 1989, with little dredging south of the exclusion zone since 2002-03 and moderate dredging pressure west of the exclusion zone in 2007 in Golden Bay (Williams and Michael 2011).

Field sampling was carried out in May 2008. Data for a number of additional explanatory variables were collected or modelled as below.

2.2 Infaunal and sediment sampling

We sampled benthic organisms from sediments by using a Van Veen grab (bite area 0.069 m²). We collected groups of samples either side of the borders of the protection zone between 20-30 m depth, with 12 samples from the fished area on the western

side of the zone, and 12 samples nearby but within the protection zone (Fig. 1). An identical distribution of sampling effort (another 24 samples) was allocated at the southern side. Fished and control samples were thus separated by 0.95 to 3.8 km, whereas the two sampling zones (west and south) were separated by 5.4 to 8.3 km. Grab stations were assigned randomly by use of the random point tool in ArcMap 9.1.3 (ESRI Inc. 1999-2009). For grain size analysis, a 5 x 5 cm tube corer was used to vertically subsample sediments from each grab. An additional 5 ml scoop of surficial sediment was removed from each grab sample for analysis of chlorophyll *a*. These subsamples were frozen for later analysis, whereas the remaining grabs were preserved in 70% ethanol. Preserved fauna were sieved over a log-series of mesh sieves down to 0.5 mm, and analysed for abundance. Biomass, and productivity of infauna were estimated using the size based conversion factors and methodology of Edgar (1990) and Taylor (1998). Size classes are presented as equivalent organism weights (ash-free dry mass: AFDM) on the \log_2 scale (Queirós et al. 2006). Data were not normalised. Sediments were wet sieved through 2 and 1 mm sieves and the filtrate collected on a 63 μm sieve. The 1 and 2 mm fractions were then re-dried to constant weight and re-weighed to derive percent mud, sand and shell gravel. Chlorophyll α content of sediment scoops was analysed using fluorescence spectrophotometry (Cary Eclipse) by freezing (0°C), sonicating in acetone to extract pigments at 4°C for 4 hr (Untrasonics, Inc, Cell Disruptor, W-225, 20HZ), and centrifuging at 3000 rpm for 15 minutes (expressed both as a raw value and as a percentage).

2.3 Sidescan sonar

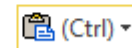
Furrows or scars from dredges, trawl doors, ropes, bobbins and chains as they are dragged across the seafloor (Kaiser et al. 2006) were assessed by sidescan sonar (Humborstad et al. 2004, Malik & Mayer 2007). As sidescan sonar views the seafloor horizontally, any structure rising above the seafloor casts a shadow. The presence of shadows and their relative density can be used to estimate relative habitat height and complexity (e.g. Ehrhold et al. 2006). We obtained four 60-m wide, >500 m long, sidescan swaths within each of the inside/outside areas, using a high-frequency (675 kHz) Tritech towfish connected to a Garmin 72 GPS receiver (Fig. 1). Vessel speed was maintained between 1 and 2 knots. The recorded files were subsequently viewed using Seagnet Pro V1.1.6 software (Tritech International Ltd., UK.). The variables derived were (i) count of trawl / dredge marks, (ii) estimated percentage cover of biogenic habitat, (iii) an index of trawl / dredge mark age (0 = none, 1 = old, 2 = new, based on intensity of acoustic shadow within each transect), (iv) an index of biogenic reflectance (0 = none, 1 = low, 2 = high), and (v) an index of habitat height/complexity. The habitat height/complexity was judged by the degree of shadow cast in the images per geographic-second displayed by the Seagnet software (0 = smooth, 1 = medium, 2 = coarse). Objects extending above the seabed were assumed to be biogenic in nature as bryozoan colonies are reported widespread inside the exclusion zone, and rocky substratum is rare inside the zone (Bradstock & Gordon 1983, Grange et al. 2003). Subsequent video transects have confirmed this assumption (Handley unpub. data). We used biogenic reflectance and habitat complexity as

indexed from sidescan as predictor variables, under the assumption that biogenic structure will influence infaunal assemblages.

2.4 Functional groups

Scores were assigned to functional feeding categories for all organisms collected, following the method of Hewitt et al. (2008). As our organisms were classified by size using log-series sieves, the relative importance of size per feeding category was accounted for by using the following equation for each species within each grab sample:

$$\text{Functional group importance} = \sum (n_{ij}) \cdot F_i$$



$$\text{Functional group importance} = \sum (n_{ij}) \cdot F_i$$

Where n = abundance of the i th species in sieve size j , and F = functional feeding category (Hewitt et al. 2008) for species i .

2.5 Current and wave models

As the exclusion zone lies off a headland, we used modelled current and wave data along with depth to test the null hypothesis that the assemblages were not affected by proximity to a headland. Current speed in Tasman and Golden Bays was modelled using the ROMS model, which is a widely used ocean/coastal model (Haidvogel et al. 2008, Warner et al. 2008). The model was set up on a rectangular 130×128 grid with spacing of 1 km. The outputs used as covariates in our analyses

were the mean and maximum near-bottom modelled current layers. Wave modelling was carried out using NIWA's operational forecasting system called NZWAVE_12 which incorporates wind inputs from the weather forecasting model NZLAM_12 where the "12" in both instances indicates a horizontal grid spacing of 12 km, and both these models are nested in coarser-scale global models. Output wave and wind statistics were available for the 24 months from March 2009 through February 2011. A simulation of wave conditions in the greater Cook Strait during January 2008 was then nested inside the NZWAVE_12 domain using a grid of approximately 1 km. The same 12 km resolution wind fields were used as for the operational forecasting, but the finer resolution allowed nearshore wave processes to be better estimated. Maximum and mean wave heights were used as covariates in our analyses.

2.6 Statistical analysis

Abundance data were converted to a Bray-Curtis similarity matrix (Bray & Curtis 1957) without transformation, as abundance did not vary by more than one order of magnitude among taxa. Differences between fished and unfished habitat were examined using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001). Relationships between the benthic assemblage composition and predictor variables were examined using forward selection of the multivariate multiple regression using the DistLM routine (distance-based linear model; Legendre & Anderson 1999, McArdle & Anderson 2001) and distance-based redundancy analysis (dbRDA; Legendre & Anderson 1999). Tests for multi-collinearity were carried out between all predictor variables (Biogenic Reflectance; Estimated percent cover; Habitat complexity; % Gravel; % Mud; Mean No. Trawl Marks; Mean

Currents; Maximum Currents; Mean Waves; Maximum Waves; Depth; Chl-a (ug/g); % Pheo) by Draftsman plots and correlation analyses, with none of the predictor variable's $|r|$ values exceeding the recommended 0.95 correlation threshold (Anderson et al. 2008, Clarke & Gorley 2006). To visualise relationships between the dbRDA sample ordination and species densities, environmental variables, and functional feeding modes, Spearman's correlations of the variables with individual dbRDA axes were plotted as vector biplots, whereby the length of the biplot vectors represent the correlation score. Species and variables with a $\rho > 0.4$ and a frequency of occurrence in $\geq 15\%$ of the samples were considered to have a meaningful correlation with the ordination axes. We chose 15% as a cutoff point to avoid emphasising spurious correlations that might have been generated by rare species. Multivariate statistical analyses were performed using the PERMANOVA+ for PRIMER package (Anderson et al. 2008). Differences between the exclusion zone and fished habitats for "functional group importance" scores were estimated using maximum likelihood in a generalised linear model (Proc GENMOD in SAS 9.3) that included location effects. These effect sizes were expressed as percentages with 95% Wald confidence limits. Significant interaction terms indicated that effect differed between locations, and therefore additional estimates were made by location. We used Proc Means (SAS 9.3) to calculate 95% confidence intervals for the effect size (the difference between "exclusion zone" minus "fished") for counts, biomasses, and productivity estimates, for combinations of site (west and south) by organism size class.

3. RESULTS

3.1 Sidescan

A total of 144 'benthic trawling scars' (Fig. 2a) was recorded on the south side of the exclusion zone, compared with 13 on the west. No evidence of trawling occurred within the exclusion zone, where biogenic bryozoan habitat was present (Fig. 2b). The estimated percentage cover of biogenic material showed four-fold increase between inside and outside the exclusion zone, and biogenic habitat was more prevalent to the west inside the exclusion zone (Fig. 3a).

3.2 Sediments

Sediment samples from within the exclusion zone comprised appreciably less mud (Fig. 2d), and more sand and shell gravel, than samples from the fished areas (Figs. 2c, 3b). In the fished areas, the mean percentage of mud was $96.3\% \pm 0.7$, whereas in the no-trawl zone the mean percentage of mud was 14.2% less – $82.1\% \pm 3.1$. Shell-gravel was 8.3% more abundant in the exclusion zone, with an average of $10.3\% \pm 2.4$ of samples from the exclusion zone, compared with less than $2\% \pm 0.6$ in the trawled area. Shells present in the gravel fraction were dominated by *Dosinia*, *Chlamys*, *Protula*, *Maoricolpus* and *Limaria* species.

3.3 Assemblage characteristics and explanatory variables

There were significant differences between benthic assemblages collected on the west and south of the exclusion zone ($F_{1,44} = 2.48$, $P = 0.001$) and inside and outside the exclusion zone ($F_{1,44} = 4.62$, $P = 0.0002$), with no significant interaction between them ($F_{1,44} = 1.39$, $P = 0.1$). Permutational multivariate regression of variables fitted individually (independently of each other) indicated that 12 of the 14 environmental and sidescan variables made statistically significant contributions to explaining variability in the benthic assemblages inside and outside the exclusion zone. Only seven of these explained $> 5\%$ of the modelled variation (Table 1a). Biogenic reflectance, estimated percent biogenic cover and habitat complexity (measured from sidescan) each explained ca. 10% of the variability, followed by the percent shell-gravel and percent mud (8.87 and 8.12% respectively). However, since many of the variables are correlated with each other, we built a sequential model with forward selection that accounted for collinearity among the variables. This reduced the number of significant explanatory variables to four, which collectively accounted for just over 23% of the variability (Table 1b). dbRDA ordination separated all but one of the fished from the protected samples on the first dbRDA axis, accounting for 50.6 % of the fitted variation (Fig. 4a). After the removal of collinear environmental variables, Biogenic Reflectance and % Gravel were strongly negatively correlated with the first dbRDA axis (i.e. characterised closed area samples), whereas Mean Waves and Depth were weakly correlated with the second dbRDA axis (Fig. 4b), and the overlap of one datum between fished and exclusion zone assemblages occurred in a shallow area less likely to be fished.

Correlations of individual species with the dbRDA axes showed that exclusion zone samples contained higher abundances of polychaete worms (including eunicids, opheliids *Armandia maculata* and syllids), the bivalve *Limaria orientalis* and the grazer *Leptochiton* sp. (Fig. 4c). Samples in fished locations were dominated by nephtyiid polychaetes (in samples with high mud content), whereas the bivalves *Nucula hartvigiana* and *Ennucula strangei* and the brittlestar *Amphiura* sp. increased in frequency with increasing depth (compare Fig 4c with Fig 4b, Table 2).

The higher abundance of suspension feeders and the grazer were correlated with exclusion zone samples, whereas greater numbers of deposit feeders, scavengers and predators were correlated with fished samples (Fig. 4d). Grazers were 502% and suspension feeders 241% significantly more abundant in the exclusion zone than in fished areas (Table 3). Deposit feeders were 42.5% more abundant in fished samples, but these differences were not significant. A significant end \times treatment effect was detected for scavengers and predators, with them being 73.1 and 57.9% more abundant in fished habitats at the south end respectively, but their effect sizes were smaller to the west. Increased productivity and biomass were positively correlated with exclusion zone samples (Fig. 4e). Although small organisms were numerically most abundant in the exclusion zone, their contributions to biomass and productivity estimates were minor and insignificant compared to contributions from large rare organisms also found in the exclusion zone (Fig 5a, b). The numerically dominant species within the exclusion zone were ostracods, amphipods, and the bivalve *Thracia vegrandi*, whereas the larger rare organisms included the following: bivalves; *Limaria orientalis*, *Dosina zelandica*, *Talochlamys zelandiae*, *Modiolus areolatus*, *Venericardia purpurata*; gastropods; *Austrofusus glans*, *Xymene plebeius*, *Alcithoe arabica*, the crab *Notomithrax* sp. and aphroditid scale worms. In contrast, the mid-

range size class (8 mm, \log_2 -4.7 g) were 38.7% more abundant in fished samples to the south than exclusion samples (Fig 5c), and represented by the brittlestar *Amphiura* sp. and polychaetes of the families Maldanidae, Trichobranchidae, Sigalionidae and Nephtyidae.

4. DISCUSSION

This study demonstrated large differences in habitats and fauna between trawled and untrawled areas at small spatial scales that we attribute to bottom fishing rather than a location or headland effect. This is because environmental variables (waves, depth and currents) were only minor contributors to modelled variability, whereas differences between fished and protected assemblages – spatially separated by only hundreds of m to ca. 1 km – were much greater than location effects of 5-6 km. Furthermore, analyses of sediment composition showing fished areas had a higher silt-mud component, and less shell-gravel, irrespective of location. Sidescan sonar surveys showed significantly greater habitat complexity, percent cover of epibiota (mainly large bryozoans, Grange et al. 2003) and biogenic reflectance inside the exclusion zone. This contrasted with low estimates of biogenic cover and reflectance in the fished habitat, and high numbers of scars in the sediment that we attribute to disturbance from bottom fishing gear, an assumption corroborated by trawl effort data (Handley unpub. data). Laudably, no trawling or dredging marks were evident in the sediments within the exclusion zone demonstrating the fishing industry's respect for the closure as a means of protecting potential juvenile fish habitat (Bradstock & Gordon 1983).

Sediment homogenisation occurs where fishing gear breaks down biogenic habitat (Hewitt et al. 2005, Thrush et al. 2006, Watling & Norse 1998), physically erodes shell, and fishers remove and displace large coarse substratum that is retained in dredges and nets. The mollusc shell component of sediments can provide important ecosystem roles including providing the primary settlement surface for encrusting organisms such as bryozoans that create biogenic reefs (Hewitt et al. 2005, Manley et al. 2010, Thrush et al. 2006). Comparisons of benthic fauna between fished and unfished areas at Separation Point showed reduced size structure, biomass and productivity of organisms in disturbed habitats. In contrast to the soft mud dominated sediments in the fished habitat, the protected sediments were an unsorted heterogeneous matrix of mollusc shell, sand and mud. If it takes decades for the shell component supporting biogenic habitats like those at Separation Point to be broken down and eroded, being displaced or buried by resuspended fines by bottom fishing, it would be difficult to empirically demonstrate such change. We assert that the soft sediments dominant in our fished sites are the result of a ploughing-effect described by Trimmer et al. (2005), whereby bottom fishing gear repeatedly resuspends sediments resulting in larger shell-gravels removed, eroded, and/or settling first, then sand grains followed by fine mud settling last (Durrieu de Madron et al. 2005) thus dominating the surface substratum.

Disturbance from bottom fishing can affect the size range of macrofauna by the removal of large, long-lived and rare organisms (Ball et al. 2000, Blanchard et al. 2004, Queirós et al. 2006), and as responses to trawling depend on organismal traits, disturbed habitats contain smaller opportunistic species less susceptible to bottom fishing (Blanchard et al. 2004, Gray & Elliot 2009). This reinforces the importance of examining organism size in the study of disturbance effects. We found higher

numbers of large and small organisms and more individuals inside the exclusion zone. The larger, rare individuals contributed the most to the biomass and productivity estimates within the exclusion zone. In contrast, the numerically dominant smaller species made comparatively little contribution to biomass and productivity. This supports findings that benthic productivity may decrease as fishing intensity increases, with the loss of productivity attributed to the removal of high-biomass species composed mostly of emergent or suprabenthic species (Asch & Collie 2008, Cartes et al. 2009, Kaiser et al. 2002). As rare species are underrepresented by point sampling techniques (e.g. Kaiser 2003, McGill 2003) our estimates of biomass and productivity derived from larger species are likely to be conservative. Although the more abundant invertebrates <2 mm (mostly ostracods and amphipods) inside the exclusion zone accounted for low biomass and productivity, these species could be important as food for small fishes, contributing to fishery production at the next trophic level (Aarnio et al. 1996, Gee 1989).

Results of functional trait analyses in this study corroborate evidence that disturbance from bottom fishing reduces functional biodiversity (Thrush & Dayton 2002) and narrows assemblages to species with traits tolerant of disturbance (Watling & Norse 1998). Functional changes to benthic assemblages as indicators of trawling disturbance have been used to demonstrate changes to soft sediment benthic communities not considered especially vulnerable to trawling activity (de Juan et al. 2007). Organisms from fished habitats at Separation Point were dominated by scavengers, predators and deposit feeders, functional categories sensitive to fishing disturbance (de Juan et al. 2007). In contrast, suspension feeders then grazers characterised the exclusion zone fauna. Mobile scavengers attracted to carrion in the wake of fishing may be less vulnerable to trawling along with motile burrowing

deposit feeders and predators which avoid bottom fishing gear by burrowing into the sediments (Demestre et al. 2000, de Juan et al. 2007, Kaiser & Spencer 1994, Ramsay et al. 1998). Large emergent sessile filter feeders are susceptible to gear contact and increases in suspended sediments following trawling making them vulnerable to fishing disturbance (Allen & Clarke 2007, Caddy 1973, de Juan et al. 2009). Grazers are also susceptible to fine sediments which can inhibit feeding efficiency (De Troch et al. 2006) but also likely require hard surfaces provided by shell-gravels, have limited mobility, as well as being directly vulnerable to trawl disturbance. Sensitivity scores derived from biological trait analysis, have been used to evaluate the vulnerability of different habitats to trawling disturbance in the Greater North Sea (Bolam et al. 2013). This approach has shown that poorly-sorted substrates containing gravels and muds similar to those described herein from Separation Point are more productive, but also more sensitive to disturbance from fishing. In contrast, productivity and sensitivity to disturbance was lower in well-sorted sandy substrates Bolam et al (2013).

Of importance to fisheries managers, the self-structuring nature of soft sediment communities (Reise 2002) can complicate the study of fishing effects on soft sediments, because shell gravels, as elements of the habitat can be both a response (to bottom fishing - extraction) and a driver of faunal composition (settlement substrata) in and of itself. Molluscs have been termed ecosystem engineers, as not only do their shells become substrata for attachment of epibionts, but also provide refuges from predation, physical or physiological stress, and control transport of solutes and particles in the benthic environment (Gutiérrez et al. 2003, Hewitt et al. 2005). As habitat heterogeneity is a driver of functional composition and diversity (Hewitt et al. 2005, 2008), the coarse shell component of the sediments within the exclusion zone is

likely to drive settlement of biogenic species. As shell debris can last for hundreds to thousands of years (Smith 1993), and biogenic habitats are sensitive to fishing disturbance, the coarse heterogeneous shell-gravel at Separation Point likely represents a relict 'climax' sediment type arising from long-term successional processes of colonisation and senescence of infauna and epifauna. For the future management and restoration of biogenic habitats like the bryozoan assemblage at Separation Point (Bradstock & Gordon 1983, Grange et al. 2003) the contingent settlement, growth and death of large bivalves at the sediment water interface in the absence of high disturbance will be required – a process akin to an evolving biogenic reef over a foundation of soft sediment. Not only do molluscan shells provide habitat when they are alive (Cummings et al. 1998, Dame et al. 1997, Thrush & Dayton 2002) but they are also vital to successional processes allowing biogenic habitats to become established and persist (Hewitt et al. 2005, Powell & Klinck 2007).

The opportunity to utilise an area, unimpacted by bottom fishing gears for 28 years, with which to compare fished substrata is rare. Most studies are forced to estimate the effects of fishing-induced disturbance by comparing areas with varying fishing histories (Cryer et al. 2002, Jennings & Kaiser 1998, Kaiser et al. 2006, Thrush & Dayton 2002, Thrush et al. 1998). While there is little doubt that bottom fishing does cause major changes to the benthos, the necessary use of impacted "control" sites means that the effects are nonetheless likely to have been underestimated (Dayton et al. 1998, Gray et al. 2007). This is because relatively little fishing effort is needed to remove slow-growing epifauna (Ash & Collie 2008, Clark & Rowden 2009, Kaiser & Spencer 1994) and alter the composition of surface sediments with consequent effects on infauna. Mensurative studies that compare frequently fished areas with infrequently fished areas may detect differences between

them, but cannot detect the differences brought about by the transformative changes to the substratum that occur at the beginning of an area's fishing history. In an undisturbed state, many "soft" sediment environments possess habitats that are functionally "hard" substrata. For example, in this study samples from unfished areas contained a small chiton grazer that lives on mollusc shell. In heavily fished soft sediments, hard substrata could become functionally extinct if it becomes ploughed under. Sampling along gradients of fishing to define fishing effects is thus not a particularly powerful means of doing so, because in defining gradients it is difficult to differentiate between the intensity of fishing in space and the frequency of disturbance in time. However, gradient approaches have the advantage of potentially identifying thresholds of change or providing useful continuous data for modelling (e.g. Tillin et al 2006), but without knowing the extent of the change, management may be misguided. The largest changes in habitats (and hence in biological assemblages) may be brought about with relatively little fishing effort (Ash & Collie 2008, Dinmore et al. 2003), and subsequent recovery in time then occurs in an alternative state of simplified habitat structure. A study of recovery rates in an exclusion zone in the Georges Bank found sessile colonial species including sponges were particularly vulnerable to bottom fishing and recovery rates of colonial epifauna were greater than two years on gravel habitat, with even infrequent trawling prolonging changes in epifaunal composition (Ash & Collie 2008). The presence of diverse unsorted calcareous habitat in the Separation Point exclusion zone suggests the time scale of habitat recovery in the absence of bottom fishing disturbance is likely to be much greater than that for biological recovery to a stable equilibrium within a particular habitat type. The first cut may not only be the deepest (Dinmore et al. 2003, Jennings

& Kaiser 1998), but take the longest to recover from (Bolam et al. 2013, Hiddink et al. 2006).

As bottom fishing can homogenise soft sediments and associated faunal assemblages that in many respects are 'self-structuring' (Reise 2002), benchmarking pre-impact sediment composition appears very important. Notably, maximum productivity of the benthos has been correlated with sediments containing diverse granulometry classes sampled from sheltered low energy sites like those in this study and in the Greater North Sea (Bolam et al. 2013). Because undisturbed sediments that contain large molluscs appear to self-structure their granulometry, we assert that benchmarking the pre-fished sediment granulometry and composition is required to determine the full extent of bottom fishing impacts. If diverse granulometry was present before bottom fishing took place, fisheries managers could forgo lost productivity inherent in biogenic habitats if sediment homogenisation has taken place, especially in ecosystem approaches to fisheries management that attempt to model potential productivity of fished habitats. The importance of benchmarking has been extolled for other highly impacted ecosystems including estuaries and lakes where palaeoecological methods have been used to reconstruct historic benthic and pelagic assemblages from which to set management goals and assess effectiveness of management actions (e.g. Saunders & Taffs 2009, Smol 2008). Such benchmarking has been incorporated at a policy level, in North America and Europe in relation to fresh water quality monitoring and estuarine eutrophication (Kemp et al. 2005, Saunders & Taffs 2009, USEPA 2006). Benchmarking pre-impact state of sediment characteristics should thus be attempted in areas where homogenisation of diverse granulometry sediments is likely to have occurred, to manage these ecosystems to their inherent full potential. Such benchmarking could be achieved using

palaeoecological techniques (e.g. Saunders & Taffs 2009), the use of unfished control sites – although these areas are unfortunately rare (Caveen et al. 2012) – or alternatively, long-term research is required utilising MPA's, to investigate the importance of heterogeneity of granulometry in the succession and re-colonisation of biogenic habitats.

Acknowledgements. We thank the New Zealand Foundation for Research Science and Technology, NIWA Capability Funds CREL084 and CRAL094 for financial support. Thanks to Richard Taylor for assistance with biomass and productivity estimates, Drew Lohrer for contributions to species information and comments on the MS, Judi Hewitt for contributions to feeding modes, Barry and Lyn Bird for boating, Chris Cunningham for fluorometry analysis, Jenny McLean and Ken Grange for administration, Don Morrissey for his review, Mark Hadfield for providing hydrodynamic data, and Richard Gorman for providing modelled wave data. Helpful comments from anonymous referees helped to focus the manuscript.

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Table 1. Results of multivariate regression of benthic assemblages inside and outside the Separation Point fishing exclusion zone on environmental variables for (a) each variable individually (ignoring other variables), and (b) forward selection of variables where each variable added to the model is followed by a possible backward elimination of a variable until no improvement in the achievement criteria can be made by adding or removing a term.

Variable	F	P	Variability explained (%)	Cumulative variability (%)
<i>(a) Variables fitted individually</i>				
Biogenic Reflectance	5.3752	0.0002	10.46	
Estimated Percent Cover	4.8847	0.0002	9.60	
Habitat Complexity	4.8581	0.0002	9.55	
% Gravel	4.4785	0.0002	8.87	
% Mud	4.0667	0.0002	8.12	
Mean No. Trawl Marks	3.0171	0.0002	6.15	
Mean Currents	2.7204	0.0012	5.58	
Mean Waves	1.7314	0.0272	3.63	
Depth	1.7288	0.0324	3.62	
Maximum Currents	1.7264	0.0328	3.62	
Maximum Waves	1.6205	0.0494	3.40	
Chla (ug/g)	1.6199	0.0500	3.40	
Pheo (ug/g)	0.70099	0.8434	1.50	
<i>(b) Variables fitted sequentially</i>				
Biogenic Reflectance	5.3752	0.0002	10.46	10.46
% Gravel	2.8028	0.0002	5.25	15.71
Mean Waves	2.1386	0.0028	3.82	19.53
Depth	1.9974	0.0072	3.66	23.19

Table 2. Spearman's correlations (ρ dbRDA1), functional group scores (mean and standard error: se) for species selected with correlations greater than 0.4 from the Spearman's bi-plot (Fig. 4c).

Exclusion zone	ρ dbRDA1	Suspension	Deposit	Predator	Scavenger	Grazer
<i>Limaria orientalis</i>	-0.67	1	0	0	0	0
Eunicidae	-0.60	0	0	0.5	0.5	0
<i>Scintillona zelandica</i>	-0.56	1	0	0	0	0
<i>Armandia maculata</i>	-0.55	0	1	0	0	0
Syllidae	-0.54	0	0	0.5	0.5	0
<i>Leptochiton sp.</i>	-0.47	0	0	0	0	1
	Mean	0.33	0.17	0.17	0.17	0.17
	S.E.	(0.19)	(0.15)	(0.10)	(0.10)	(0.15)
Fished						
Nephtyiidae	0.63	0	0	0.5	0.5	0
<i>Ennucula strangei</i>	0.49	0	1	0	0	0
<i>Nucula hartvigiana</i>	0.49	0	1	0	0	0
<i>Amphiura sp.</i>	0.37	0	0	0.5	0.5	0
	Mean	0	0.50	0.25	0.25	0
	(se)	(0)	(0.25)	(0.13)	(0.13)	(0)

Table 3. Comparisons of “functional group importance” scores inside and outside the Separation Point fishing exclusion zone. Means, percent effect size and Wald’s 95% confidence limits for the effect size are presented along with Chi-square and P values. Note: when significant interaction terms were detected between location and treatment, south and west were tested independently.

Functional Group	Exclusion zone mean	Fished mean	Effect size (%)	Wald Low CL (%)	Wald Upper CL (%)	Chi-square	P
Grazers	2.37	0.39	502	138.1	866.1	6.8	0.0091
Suspension	70.77	20.75	241.0	111.4	370.8	11.73	0.0006
Deposit	24.6	35.06	42.5	2.1	84.2	3.36	0.0669
Scavengers	31.27	42.77	36.8	10.0	63.5	8.06	0.0045
South	32.50	56.24	73.1	35.2	110.9	11.22	0.0008
West	30.04	29.29	2.5	-28.0	33.0	0.03	0.8704
Predators	35.84	45.42	26.7	14.8	52.0	4.12	0.0423
South	38.29	60.48	57.9	21.6	94.3	8.19	0.0042
West	33.39	30.35	10.0	-20.0	40.0	0.42	0.5156

Figure captions

Fig. 1 Inset: location of Separation Point ($40^{\circ} 47' S$, $172^{\circ} 59' E$), between Golden and Tasman Bays, in the north of New Zealand's South Island. Main Figure: grey shading indicates Separation Point power-fishing exclusion zone. Locations of grab samples are indicated by circled dots, sidescan paths as lines, and depth contours in metres as dashed lines.

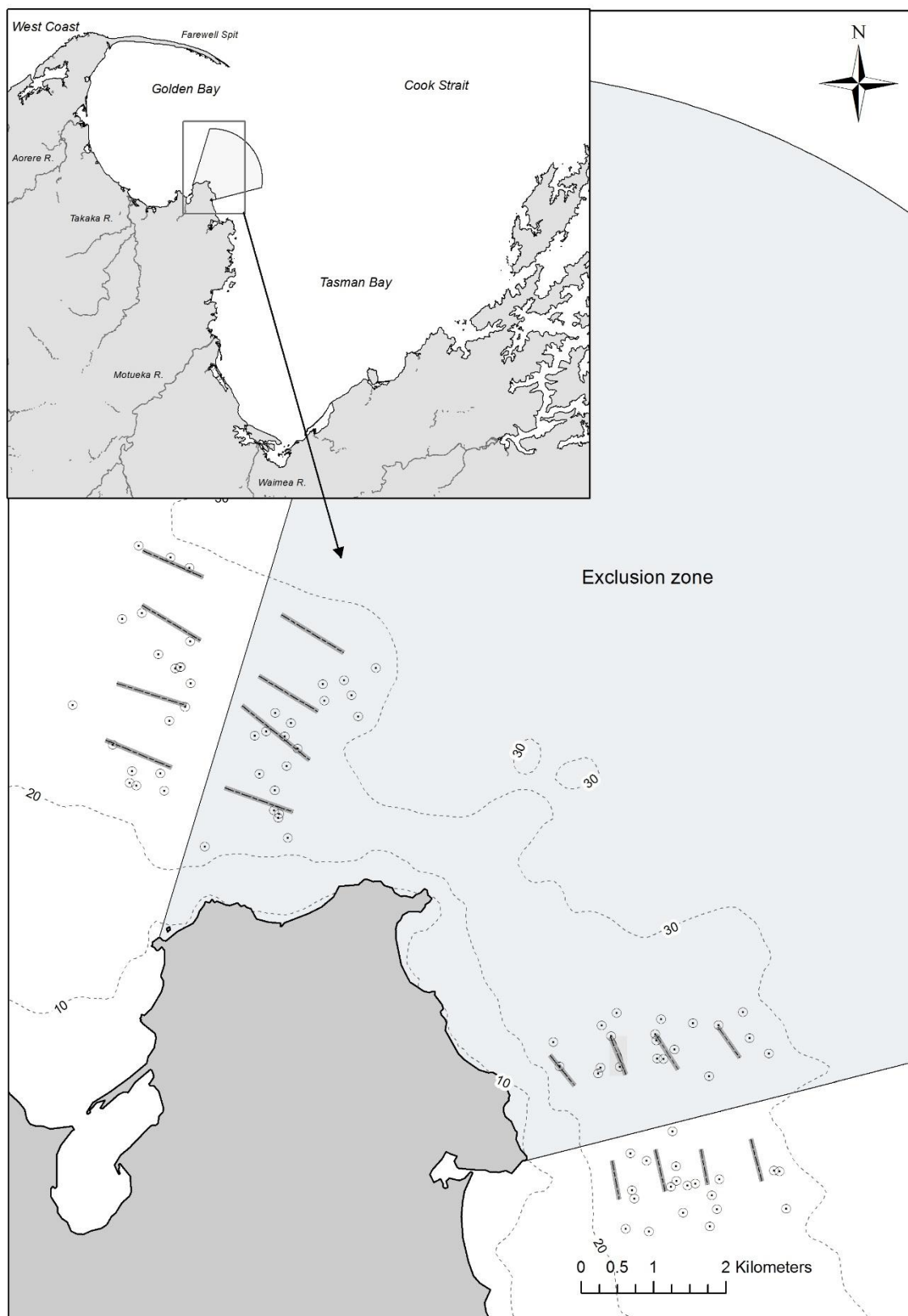
Fig. 2 Examples of sidescan sonar swathes and mud sediment characteristics from (a & c) outside exclusion zone showing tracks from contact fishing gear and mud sediment, and (b & d) inside the exclusion zone showing heterogeneous biogenic bryozoan habitat and shelly sediment.

Fig. 3 (a) Estimated percentage cover of biogenic material. Error bars are 95% confidence intervals. (b) Percentage of sand and shell/gravel in sediment grab samples collected at Separation Point. Mud content not shown, but totals = 100%. See Fig. 1 for sampling locations.

Fig. 4 dbRDA (distance based redundancy analysis) discriminating fished and protected samples (inside and outside). The vector plots show Spearman correlations r of (b) habitat and sediment variables, (c) species, (d) feeding modes, and (e) estimates of biomass and productivity with the two dbRDA axes, where $|r| > 0.5$ and frequency of occurrence > 0.15 .

Fig. 5 Size-class specific mean “effect sizes” (“exclusion zone” minus “fished”) calculated from (a) estimates of productivity plotted by size class (\log_2 g AFDM) of organisms (b) counts, and (c) estimates of biomass. Note: bars with 95% confidence limits that do not intercept zero, are significantly different between inside and outside the exclusion zone in the direction indicated.

ACCEPTED MANUSCRIPT

**Fig. 1.**

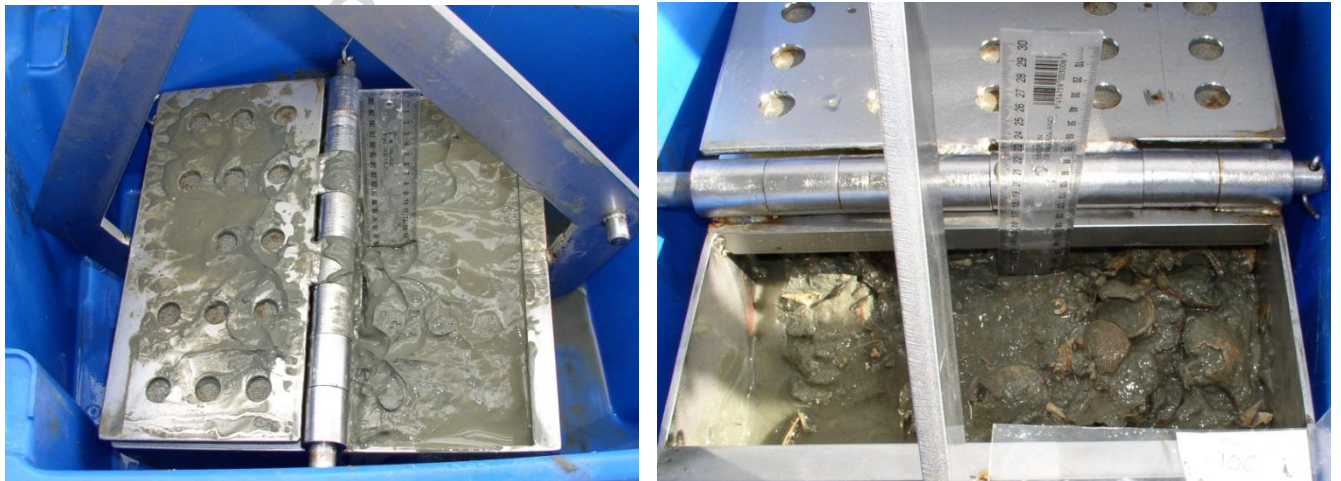
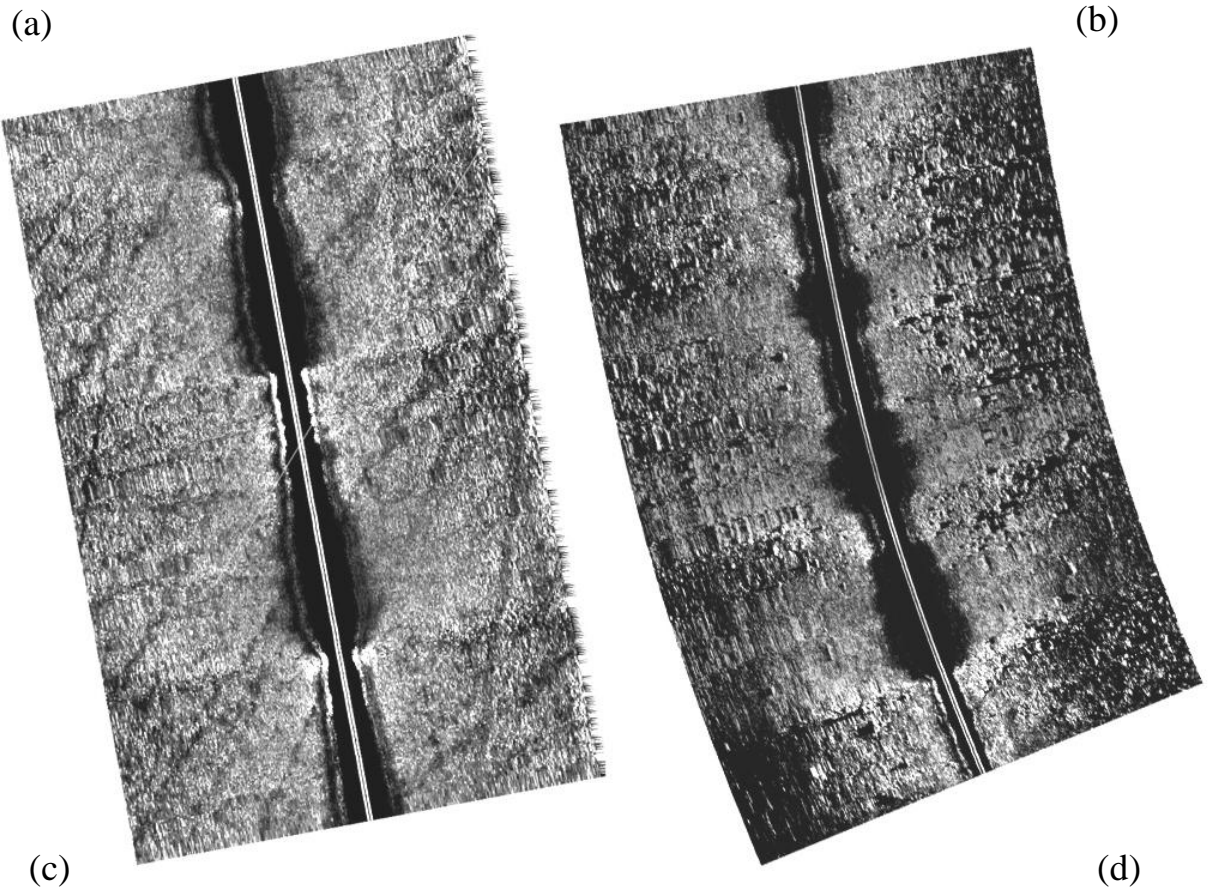
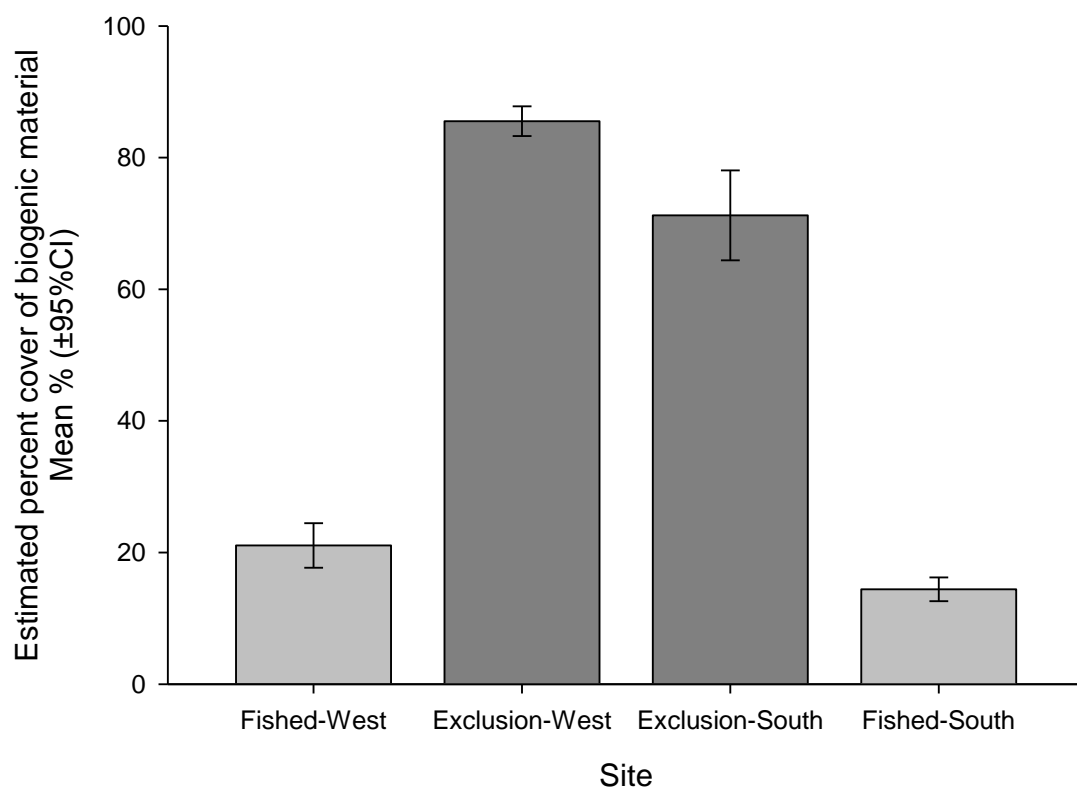
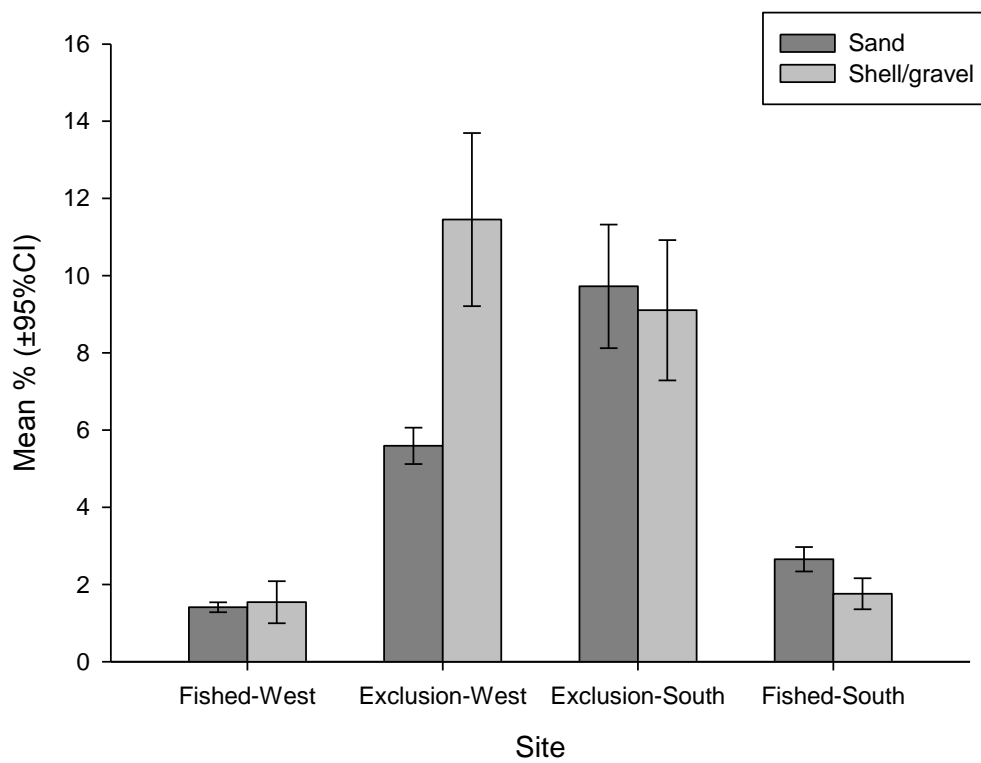


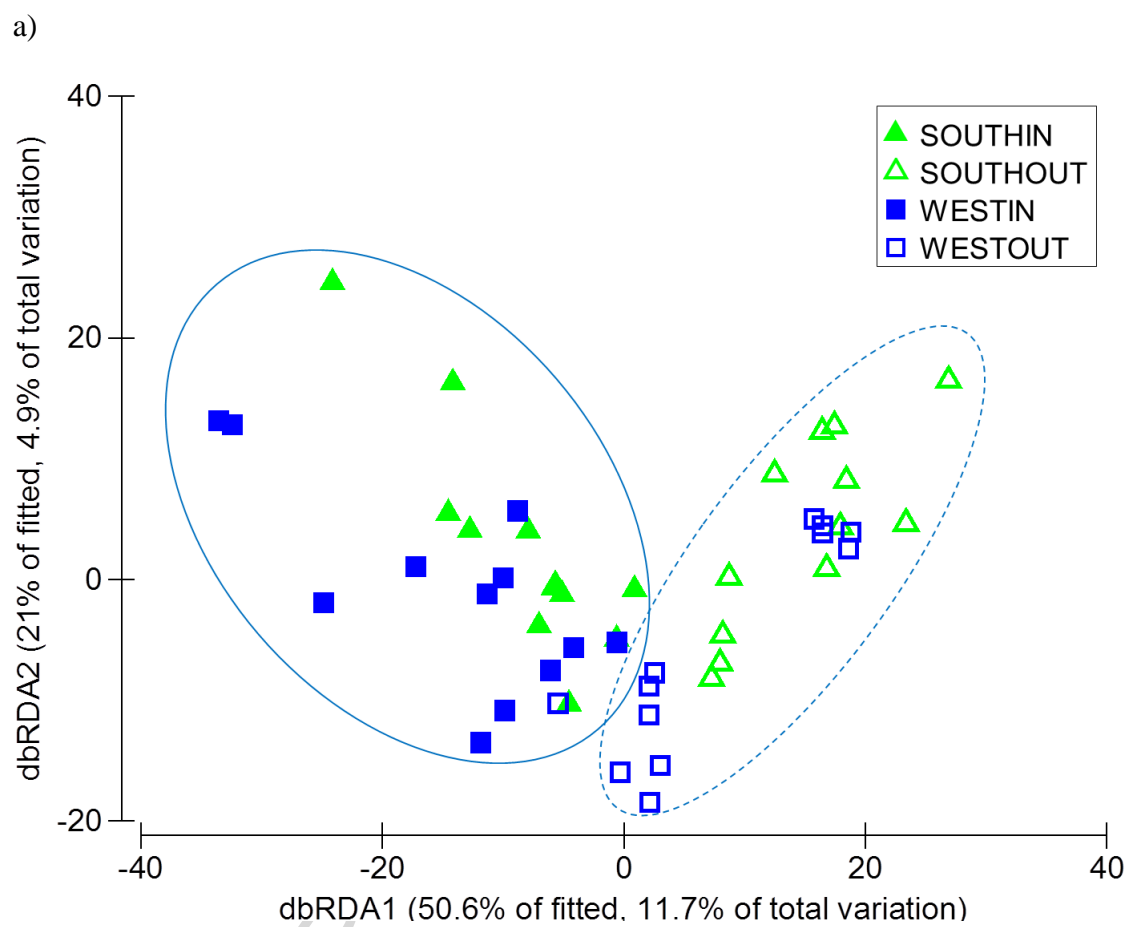
Fig. 2.

(a)



(b)

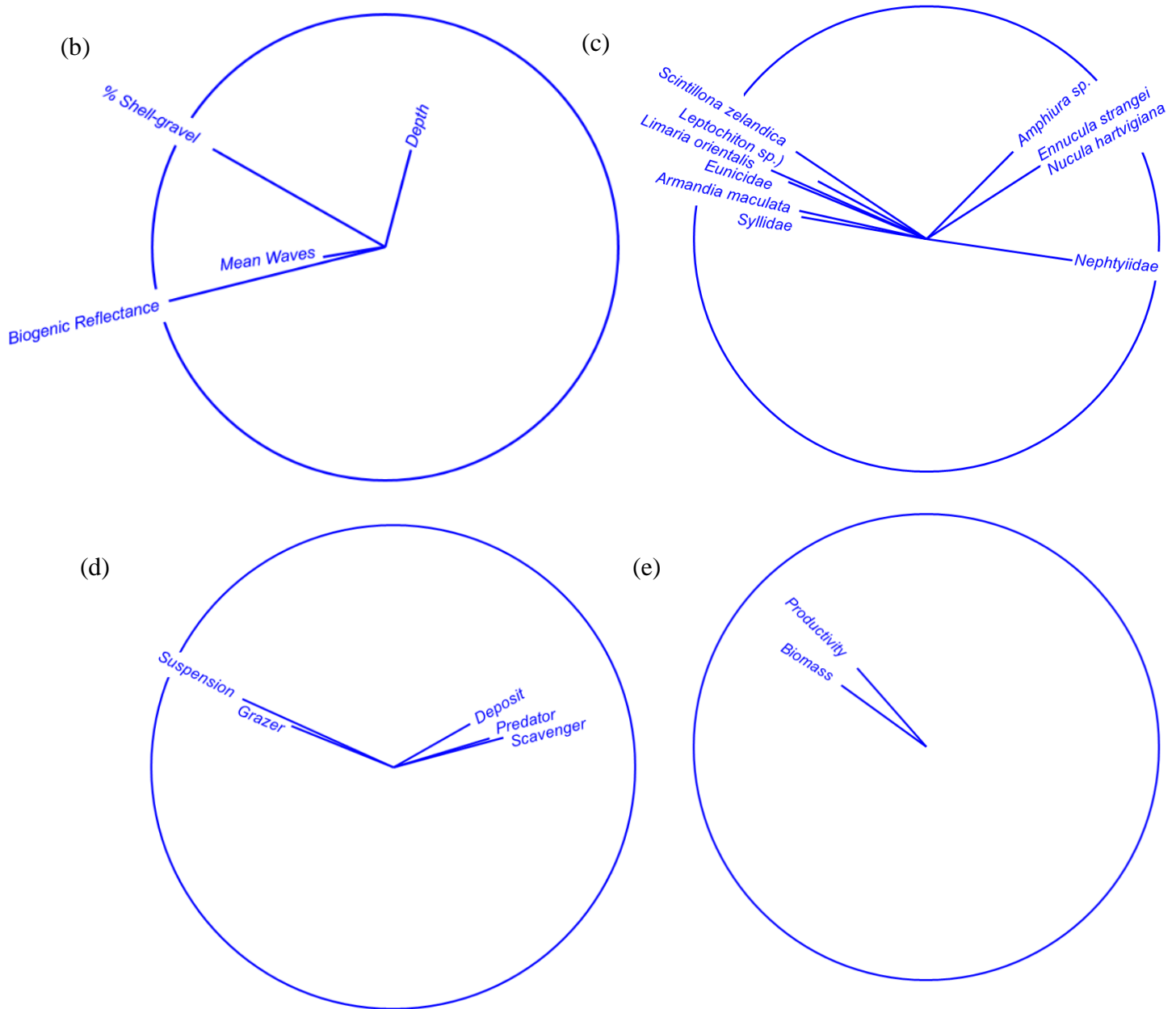
**Fig. 3.**



Continued over...

Fig. 4.

Fig 4. Cont...



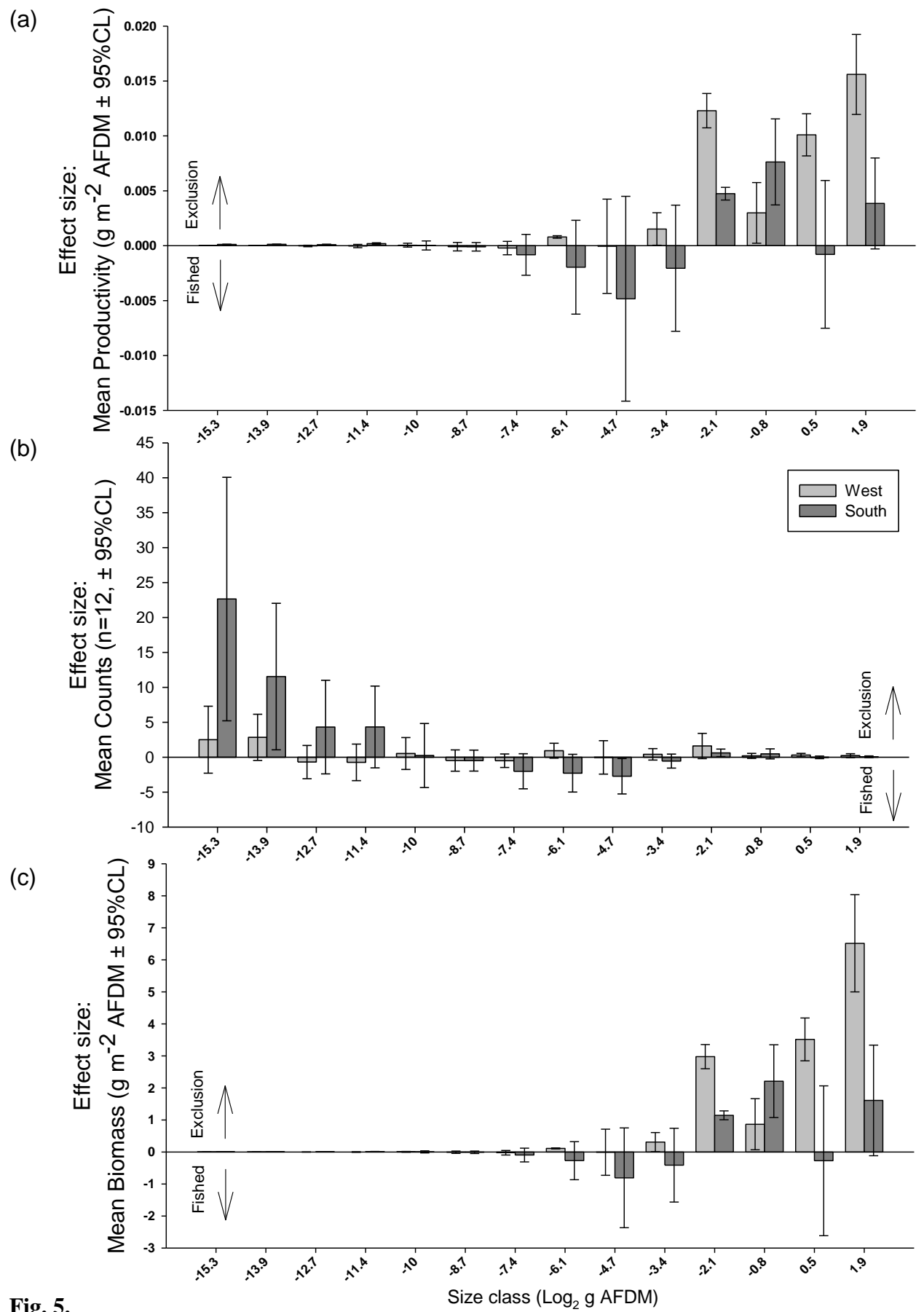


Fig. 5.

Highlights

- We compared sediment and macrofauna inside and outside a 28 year old fishing exclusion zone.
- Fished habitats contained little shell-gravel, more mud, and lower macrofaunal productivity and biomass.
- Fished assemblages had increased numbers of scavengers, predators and deposit feeders.
- To understand the full extent of bottom fishing impacts, we recommend benchmarking the pre-impact sediment granulometry of soft sediment ecosystems where homogenisation by fishing is likely to have occurred.