The effects of bottom trawling and primary production on the biological traits composition of benthic assemblages

Howarth, Leigh M.; Waggitt, James J.; Bolam, S.G.; Eggleton, J; Hiddink, Jan; Somerfield, P.J.

Marine Ecology Progress Series

DOI:
10.3354/meps12690

Published: 23/08/2018

Peer reviewed version

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Howarth, L. M., Waggitt, J. J., Bolam, S. G., Eggleton, J., Hiddink, J., & Somerfield, P. J. (2018). The effects of bottom trawling and primary production on the biological traits composition of benthic assemblages. *Marine Ecology Progress Series*, *602*, 31-48. https://doi.org/10.3354/meps12690

The effects of bottom trawling and primary production on the biological traits composition of benthic assemblages

Howarth, L.M.,[1*] Waggitt, J.J.,[1] Bolam, S.G.,[2] Eggleton, J.,[2] Somerfield, P.J.,[3] & Hiddink, J.G.[1]

[1]Bangor University, School of Ocean Sciences, Menai Bridge, UK, LL59 5AB
[2] Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, Suffolk, UK, NR33 0HT
[3] Plymouth Marine Laboratory, Prospect Place, Plymouth, UK, PL1 3DH
* Corresponding author. Tel: +1 (902) 494-3557. Email: leigh.howarth@dal.ca

Running page head: Trawling and production on benthic functioning

Key words: Interactive effects; ecosystem function; ecosystem services; fishing impacts; fuzzy coding; macroecology; multiple stressors

Abstract

Although many studies have investigated the effects of disturbance and environmental drivers on marine ecosystems, comparatively few have studied their interactions. Using fuzzy coded biological traits, we compared the functional composition, diversity and evenness of benthic communities in the English Channel, and Celtic and Irish Seas, across interacting gradients of bottom trawling and primary production. Fuzzy correspondence analysis indicated greater similarity in traits composition at sites of high trawling pressure than those of low trawling. In contrast, the analysis revealed no relationship between traits composition and primary production. Trawling and primary production had no effect on the traits “longevity”, “sediment position” and “feeding mode”. However, trawling had negative effects on all modalities within the trait “living habit”, which were strongest for attached and epifaunal organisms, but weakest for burrow- and tube-dwelling species. Trawling also negatively affected most modalities within the trait “maximum weight”, which were strongest for organisms weighing between < 0.1 g and 1 kg. Conversely, trawling positively affected organisms weighing > 10 kg. For the trait “bioturbation”, upward conveyors were positively related with primary production, whilst other modalities exhibited no clear pattern. Because trawling affected some traits more than others, community biomass was less evenly distributed across traits in highly trawled areas, which resulted in lower levels of functional diversity and evenness. Overall, the effects of bottom trawling were greater in areas of high primary production.

Introduction

Marine ecosystems are subject to a range of anthropogenic stressors, many of which are increasing in intensity and occurrence (Lotze et al. 2006, Poloczanska et al. 2013). The use of bottom trawls has greatly increased over the last century (Watson et al. 2013, Howarth et al. 2014). In contacting the seafloor, bottom trawling can damage benthic habitats (Kaiser et al. 2000), reduce the abundance of target and non-target species (Hiddink et al. 2017), and truncate age and size distributions (Beamish et al. 2006, Jørgensen et al. 2007). In parallel, ocean acidification, eutrophication, and climate change are altering global levels of primary production (Frederiksen et al. 2006, Tait & Schiel 2013), which could significantly alter food web dynamics, fisheries production and ocean biogeochemistry (Gregg et al. 2003, Brander 2007, Blanchard et al. 2012). In areas where primary production increases, benthic communities should receive a greater input of energy, increasing their growth, reproduction and resilience to bottom trawling (Blanchard et al. 2009, Hiddink et al. 2017). Investigating the interactive effects of bottom trawling and primary production could therefore help to inform management and improve understanding of how multiple drivers affect marine ecosystems.

Most studies quantify the ecological effects of disturbance by measuring changes in species abundances (Mouillot et al. 2013, Stuart-Smith et al. 2013). However, species-based approaches convey little direct information on how disturbances affect ecosystem processes, such as nutrient cycling and habitat provisioning (Bremner & Frid 2005), which play a greater role in maintaining ecosystem integrity than the abundance of a particular species (Loreau et al. 2001). Hence, biological traits are increasingly being used to describe the physical, behavioural and life-history characteristics of species to evaluate their potential vulnerability to disturbance (‘response traits’) and contribution towards ecosystem function (‘effect traits’– see Bolam *et al.* 2016). For example, bioturbation can be considered an ‘effect trait’ as the burrowing of benthic infauna can transport nutrients and oxygen from the sediment surface to deeper layers (Olsgard et al. 2008, Sciberras et al. 2016). In contrast, bottom trawls are more likely to damage sessile organisms than pelagic organisms (Kaiser et al. 2000, Tillin et al. 2006), meaning living habit can be considered a ‘response trait’. Given that some disturbances affect life histories and functions more than others, biological traits can help disentangle the ecological effects of multiple stressors (Bremner et al. 2006)

Numerous studies show bottom trawling can change benthic traits composition. By reducing the abundance of large predators, trawling can increase the abundance of small and fast-growing species, which can recover quickly from disturbance and benefit from reduced predation (Bremner & Frid 2005, Tillin et al. 2006). Additionally, trawling can increase the availability of organic matter and dead / injured animals, boosting the local abundance of mobile scavengers (Tillin et al. 2006, Kaiser & Hiddink 2007, Craven et al. 2013). Trawling can also plough and re-suspend sediments which can reduce the feeding efficiency of suspension feeders (Collie et al. 2000, Bradshaw et al. 2003). Compared to bottom trawling, little is known about the effects of primary production on traits composition. Nonetheless, areas of high primary production often support greater abundances of small-bodied organisms that can quickly incorporate pulses of energy into growth and reproduction (Macpherson et al. 2002, Jennings & Blanchard 2004, Gómez-Canchong et al. 2013). High levels of primary production should also result in greater quantities of phytoplankton and other organic matter sinking to the seafloor, which would benefit suspension and deposit feeders (Blanchard et al. 2009).

Given that trawling and primary production likely have contrasting consequences, their interaction may produce different effects to them acting alone (Crain et al. 2008). These interactions could be synergistic or additive, where the effects of one driver equal or exceed the sum of each in isolation (see Gunderson *et al.* 2016). For example, the positive relationship between primary production and small body size might be intensified by trawling, because fishing removes the largest individuals (Beamish et al. 2006, Jørgensen et al. 2007, Fu et al. 2018). Alternatively, interactions may be antagonistic, where the cumulative effect of several drivers is less than them acting alone. For instance, the increased detritus and organic matter caused by high primary production levels may increase population growth rates of suspension and deposit feeders, reducing recovery times and their sensitivity to trawling effects.

Persistent and intense disturbances can reduce species abundances to levels that eliminate their influence on ecosystem function (Howarth et al. 2014). Given that multiple species can perform the same functional role (Fonseca & Ganade 2001), high species diversity presumably increases ecosystem resilience because of the low probability of losing all species capable of performing a specific function (Loreau et al. 2001, Cardinale et al. 2002). Biological traits can therefore measure the distribution (functional evenness) and range (functional diversity) of functional roles present within an ecosystem (Díaz & Cabido 2001, Mooney et al. 2009). Given the greater effects of bottom trawling on some groups, trawling is expected to reduce the functional diversity and evenness of marine communities, and reduce their resilience to further disturbance (Schleuter et al. 2010, Howarth et al. 2014).

In order to evaluate how primary production and fishing influence the functioning of benthic ecosystems, we compare the functional composition, diversity and evenness of benthic communities in the English Channel, and Celtic and Irish Sea, across interacting gradients of bottom trawling and primary production. First, we hypothesize that bottom trawling will reduce the functional diversity and evenness of benthic communities by reducing the abundance of long-lived predatory fish and attached and suspension feeding invertebrates. Second, we hypothesize that both trawling and primary production increase abundances of scavengers and small, short-lived species. Last, we hypothesize reduced effects of trawling on suspension feeders in areas of high primary production, but intensified effects of trawling on body size.

Methods

Outline

Benthic organisms were sampled over gradients of trawling intensity and primary production at sampling stations with otherwise homogeneous environmental conditions. Their biological trait composition, functional diversity and functional evenness were then related to trawling intensity and primary production.

Study area

This work was carried out in the Irish Sea, Celtic Sea, and western English Channel. These areas are characterised by moderate levels of wave energy, depths of 20 – 100 m, and similar circalittoral sediments of muddy sand and gravel (Cooper et al. 2010). However, they also differ slightly in that sea surface temperatures are often lower, and primary production levels higher, within the Irish Sea. Between March and May, the Celtic Sea undergoes a distinct algal bloom that originates south of Ireland and temporarily increases chlorophyll a concentrations in the Celtic Sea, southern Irish Sea and western English Channel (Fasham et al. 1983, Garcia-Soto & Pingree 2009). This algal bloom can increase chlorophyll a levels to such an extent that it can homogenise any spatial differences that typically exist during the rest of the year. European beam and otter trawlers operate throughout these regions and target a wide range of species such as hake (*Merluccius merluccius*), plaice (*Pleuronectes platessa*), sole (*Solea solea*), monkfish (*Lophius piscatorius*) and whiting (*Merlangius merlangus*). However, the Irish Sea is characterised by a greater presence of otter trawlers targeting Nephrops prawns (*Nephrops norvegicus*), the Celtic Sea is characterised by a greater presence of beam trawlers targeting flat fish, and the western English Channel is the focus of a large king scallop (*Pecten maximus*) dredge fishery (Guénette & Gascuel 2012, Campbell et al. 2014, Howarth & Stewart 2014).

Data sources

Water column depths (m) were extracted from GEBCO (www.gebco.net) at a resolution of half-minute intervals. Information on seabed substrate type and bed shear stress was obtained from the UkSeaMap 2016 (http://jncc.defra.gov.uk/ukseamap). Annual levels of primary production (mg C m^{-2} yr^{-1}) between 2009 and 2013 (estimated by the MODIS satellite sensor) were provided by NEODAAS (www.neodaas.ac.uk) at a resolution of 1.1 x 1.1 km and averaged across all years. These data used Morel & Berthon's (1989) algorithm to convert depth, surface chlorophyll, and photosynthetically active radiation (PAR) into estimates of net primary production. However, like most satellite chlorophyll algorithms, it can over-estimate primary production in waters of high sediment loads or coloured dissolved organic matter. Fishing effort (hours spent bottom trawling and dredging) between

2011 and 2013 was provided by the MMO (www.gov.uk/government/organisations/marine-management-organisation) at a resolution of 3.5 x 3.5 km, which was averaged by year. Trawling intensity (swept area ratio yr^{-1}) averaged between the years 2010 and 2012 was supplied by Eigaard *et al.* (2016) at a resolution of 1.8 x 1.8 km. Their data take into account differences in trawl size and trawl type, which can strongly influence the level of disturbance trawling gears have on the benthos (Hiddink et al. 2007). Swept area ratio can be interpreted as the mean number of times fishing gear impacts an area in a year. A swept area ratio of one indicates that the swept area equals the cell area (Gerritsen et al. 2013). Because swept area ratio is more informative than the number of hours spent fishing, the MMO measures of fishing effort were converted to swept area ratio as described by Gerritsen *et al.*, (2013). For this, we assumed that the average fishing vessel towed gears 24 m in width at a speed of two knots. Our study solely used fishing effort provided by (Eigaard et al. 2017) except for two stations (O and P) where we used MMO data instead. Beam trawlers in North Devon intensively target this area (Campbell et al. 2014) which was not highlighted in the Eigaard dataset, likely because of a lack of French and Spanish VMS data for their trawl fleets operating in the Celtic Sea.

Experimental design

Trawling intensity and primary productivity were both divided into four categorical levels (Table 1) and 1.8 x 1.1 km sampling stations were chosen to cover all combinations within the Irish Sea, Celtic Sea and English Channel. To ensure comparability and to avoid confounding effects, stations were restricted to “sand” and “muddy sand” substrates, between 40-100 m in depth, and of “moderate” bed shear stress as defined by the UkSeaMap. Final sampling stations were selected based on their proximity to one another, and their distance from restricted (military and fishing) zones and offshore structures; greater distances were preferred in all cases. Stations were also selected based on their similarity in depth and sediment composition. Some treatment combinations were rarer than others, meaning there were instances where we had to sample stations coarser in substrate or located at greater depth. Hence, there is some spatial clustering of sampling stations, and differences in environmental characteristics may provide some scope for confounding effects which we test for in our analyses.

Sample collection

A total of 20 stations were sampled both in September 2015 and April 2016 (Figure 1 and Table S1) and data were pooled across both sampling events. Most benthic recovery processes are seasonal and rely on distinct pulses in recruitment, which require time for larvae to settle and grow (Rodríguez et al. 1993, Mann 2009). Hence, by sampling during and after the spring algal bloom, we aimed to account for these seasonal differences.

At each station, seabed water samples were taken to quantify the chlorophyll a (Chl-a) content at time of sampling, and to allow comparisons with the satellite-generated measures of primary production. At each sampling station, a one-litre Niskin bottle fitted with a digital reversing thermometer was deployed to one metre above the seafloor and triggered with a brass messenger three times. Upon retrieval, the mean of 15 temperature measurements were recorded along with their standard deviation (SD). For each station, we filtered between 900 and 1800 ml of seawater over 47 mm GF/F filter papers in triplicate and stored these filters at -20˚C in the dark until further processing.

Five 0.1 m^2 Day grabs were taken within each sampling station. These samples were later used to quantify sediment size, Chl-a, and infauna. To quantify sediment Chl-a, we subcored using a cut-off syringe 14.5 mm in diameter to a depth of 8 mm which was preserved at -20˚C in the dark. To sample meiofauna, we took two subcores 25 mm in diameter to a depth of 40 mm which were preserved in a 4% buffered formalin seawater solution. To sample infauna, we washed whatever sediment remained of the Day grab samples over a 1-mm sieve before preserving the remaining material in 4% formalin.

Epifaunal organisms were sampled using two 2 m beam trawls (fitted with a 10 mm mesh and 2 mm cod-end liner) which were towed for five minutes along the seafloor at a speed of 1.5 knots. Benthic megafauna and demersal fish were sampled using two 4 m beam trawls (fitted with a chain matrix and an 82 mm diamond cod-end) which were towed for 30 minutes at a speed of 3 knots. All organisms caught by the trawls were identified to species level where possible, counted, and weighed using a motion compensating balance. Subsampling was used for species comprising of more than 50 individuals. Small animals < 1 g were weighed in groups and their mean individual weight calculated.

Particle size analysis (PSA)

Sediment samples collected by the Day grab were analysed for particle size using both dry sieving and a laser particle analyser. Both datasets were then combined as described in Mason (2011).

Chl-a analysis

Water samples were analysed for Chl-a content using the methods and equations described in Lorenzen (1966) and JGOFS (1994). The same method was applied to the sediment cores, however, these were centrifuged for 20 minutes at 2400 rpm before analysis in order to separate sediments from the supernatant.

Invertebrate sorting and identification

Approximately 10 ml of 0.1% Rose Bengal was added to the formalin-preserved grab samples, gently mixed, and left to stain for at least one hour before sorting. Samples were then washed over a 1-mm sieve to remove all traces of formalin and moved to a white tray. All organisms were separated from the sediment and preserved in 70% industrial methylated spirit (IMS). These organisms were sorted into broad taxonomic groups using a dissection microscope and methyl blue dye. All individuals were then identified to at least family level, counted, blotted dry, and weighed to the nearest 1 mg. Body parts were reassembled to make whole organisms but were discarded if less than 20% of the individual remained. Individuals were not counted if they did not possess a head. Mollusc shells were smashed and discarded if empty. Tube-dwelling animals were separated from their tubes before weighing, and hermit crabs were removed from their shells or epibionts and weighed separately.

Data analysis

Comparisons of environmental characteristics

Multivariate tests were used to test if differences in measured environmental characteristics existed between sampling sites, and whether they could confound the effects trawling and primary production. These environmental data were mean particle size, percentage gravel, percentage mud, percentage sand, and water depth. A resemblance matrix using a Euclidean Distance measure was created and visualised using non-Metric Dimensional Scaling (nMDS) with clusters generated from a Similarity Profile (Simprof) routine. This analysis indicated two sampling stations (D and P) were dissimilar to the others (S1). As station D had a very low outlying mean particle size (69 µm ± 2 SE) and station P had a very high outlying mean particle size (937 µm ± 203 SE), these two stations were excluded from further analysis.

Verification of experimental treatments

Trawling intensity, sediment and water Chl-a content were compared between the categorical levels of fishing effort and primary productivity. Trawling intensity increased exponentially across levels of fishing effort (S2a). The Chl-a content of the sediment samples displayed no relationship with levels of primary production (S2b). In contrast, water Chl-a correlated tightly with levels of primary production in September but not in April (S2c).

Gear calibrations

Because we used multiple types of sampling gears to capture several components of the benthic ecosystem, each gear partly overlapped in the size of organisms they captured, but differed in sampling area and catch efficiency. For each sampling gear, small animals were undersampled because they passed through the sieves or nets of the gear, and large animals were rarely found because their abundance was too low relative to the area sampled. This meant that the abundance and biomass values obtained by the different sampling gears could not be combined until they were corrected to represent the same sampling area and sampling efficiency, and were restricted to the size ranges that were sampled effectively. Hence, we scaled the data from the different sampling gears based on the assumption that the abundance of size ranges that were sampled by two sampling gears should be the same after correction. We carried out the following correctional procedure on the whole dataset for all stations combined to get the most robust correction factors.

Normalised biomass size spectra were created as described in Sprules & Barth (2015). The size spectrum of each individual sampling gear showed an optimum relationship with different minimum and maximum size ranges of organisms sampled (S3a). The size range of organisms sampled effectively by each gear was identified as the range where the size spectrum exhibited a monotonic decline (S3b). Abundance values from the Day grab samples were used as the base for the corrections because the area sampled by the grab was known to be exactly 0.1 m^2. The abundance of organisms sampled by the 2-m beam trawl were then corrected by performing a linear regression on the normalised biomass per size class captured by the Day grab and 2-m beam trawl for the size ranges in which they overlapped (S4a). This procedure was then repeated for the combination of the 2-m and the 4-m beam trawl (S4b). To correct those size classes that were sampled by multiple gears, the total biomass within each size class was then divided by the number of gears contributing to each size class.

Constructing a fuzzy coded database

Many traits-based studies assign species to discrete functional roles, such as ‘predator’ or ‘detritivore’ (e.g. Friedlander & DeMartini 2002; Micheli & Halpern 2005; Williams *et al.* 2015). However, this approach is overly simplistic because most aquatic species exhibit multiple traits (e.g. part-predator, part-detritivore) and express ontogenetic shifts in their ecology as they develop (e.g. from planktivorous larvae, to piscivorous adults). Hence, we used a method known as ‘fuzzy coding’ to help overcome these issues. Fuzzy coding divides traits (e.g. maximum weight) into categories, or ‘modalities,’ that cover the full range of possible values for that trait (e.g. < 10 g; 10 – 100 g; > 100 g). We then assigned scores to each trait indicating the affinity of species to those modalities; where low scores represented no affinity, and high scores represented total and exclusive affinity (Chevenet *et* *al.* 1994; Tillin *et al.* 2006). These scores were then converted to proportions totalling to one, and multiplied by species biomass or abundance, effectively spreading out their abundance across multiple traits.

We modified an existing fuzzy coded traits database of species, genus's and families compiled by Bolam *et al.* (2017) to include maximum biomass and demersal fish (Table 2). These additional information came from FishBase (www.fishbase.org), the BIOTIC database (www.marlin.ac.uk/biotic) and Jennings *et al.* (2001). For taxa identified at a resolution higher than species (e.g. genus and family), the database assigned scores based on their most closely-related taxa using the Best Professional Judgement (BPJ) approach (Bolam et al. 2014). This strategy resulted in a reasonably accurate completion of modalities wherever the entries across closely related taxa were fairly consistent, but we were less confident where traits were variable across closely related taxa, making it necessary to spread the fuzzy-scores across a wider number of modalities.

Overall, our functional traits database included information on six biological traits spanning across 32 modalities (Table 2). There is currently no accepted methodology for selecting the most appropriate traits for a given study. However, the traits used in our study were intended to cover a combination of response and effect traits with the potential to reflect an organism's life history (e.g. life span), ecology (e.g. living habit), vulnerability (e.g. sediment position), and contribution towards ecosystem processes (e.g. bioturbation). We also aimed to ensure our selected traits did not overlap in the information they conveyed. For instance, both maximum weight (g) and maximum length (cm) can describe an organism's size. However, maximum weight is more informative about how much energy an organism has invested into its own growth (Brose et al. 2005, Gómez-Canchong et al. 2012), and can more accurately reflect the size of an organism that does not exhibit bilateral symmetry. Hence, we chose maximum weight over maximum length as a biological trait.

Relating functional indices to trawling and primary production

Functional diversity and evenness were estimated from the Shannon-Wiener Diversity Index and Pielou's Evenness using the biomass of each modality as described in Schleuter *et al.* (2010). To test whether functional diversity and evenness were significantly related to primary production and trawling intensity, two linear models were constructed as follows:

$$\text{Functional diversity} \sim \log_{10}(\text{trawling intensity}) * \log_{10}(\text{primary production})$$

$$\text{Functional evenness} \sim \log_{10}(\text{trawling intensity}) * \log_{10}(\text{primary production})$$

For visualisation purposes, fitted values were plotted against continuous levels of trawling and compared between categorical levels of primary production, and vice a versa. These visualisations therefore differed from the models, as the models fitted these as continuous variables. This was done using the *predict* function in R (Team 2017) across trawling gradients and the mean of each level of primary production, and vice a versa. Linear models are used throughout our analyses because previous studies show the log biomass of communities decrease linearly with the log of trawling pressure (Hiddink et al. 2006). This pattern occurs because a fixed fraction of benthic biomass is typically removed with every pass of a trawl.

Relating functional composition to trawling and primary production

To visualise the influence of trawling pressure and primary production on overall functional composition, a fuzzy correspondence analysis (FCA) was performed using the R package "ade4" (Dray et al. 2017). FCA is a type of correspondence analysis that can describe relationships among objects of interest (i.e. sampling stations) based on the abundances of fuzzy coded variables (i.e. modalities). To aid interpretation, the total biomass of each modality was summed across both survey periods. The scores generated by the first two FCA axes were then plotted for each station and modality. This meant each bubble represented an individual sampling station, the size of which was based on its trawling intensity or primary production. Stations that are plotted closer together in the ordination have similar patterns of biomass distributions across modalities. Hence, distances between the stations reflect differences in the proportional biomass of modalities. For example, if the trawling ordinations clearly separated the larger bubbles from the small, then trawling intensity could be interpreted as having a strong influence on trait composition. In addition, modalities labelled closely to the larger bubbles would be more associated with areas of high trawling pressure than areas of low trawling pressure.

Relating modality biomass to trawling and primary production

To determine whether modality biomasses were significantly related with trawling pressure and primary production, linear models were created as:

$$\mathrm{Log}_{10}(\mathrm{biomass}) \sim \mathrm{modality} * \log_{10}(\mathrm{trawling\ intensity}) * \log_{10}(\mathrm{primary\ production})$$

and repeated for each trait, creating a total of six models. We based this approach assuming that a significant interaction between modality and trawling and / or primary production would indicate unequal response in the modalities within a trait to these pressures. Significant interactions were then plotted using the visualisation methods described earlier.

Results

Dataset description

This study identified 332 different taxa, 52 (or 16%) of which were identified to species level, 221 were to genus (63%) and 59 (21%) were to family. The modalities with the fewest taxa (< 20) were organisms weighing > 10 kg, organisms buried > 10 cm deep within the sediment, and upward and downward bioturbators (Table 2). In contrast, surface-depositors, free-living organisms and animals living on the sediment surface contained the most taxa (> 200). The modalities with the lowest biomass (< 100 g m^{-2}) were organisms with a life span of < 1 year, organisms weighing > 10 kg, crevice-dwelling organisms, and pelagic species. In contrast, the most abundant modalities (> 3000 g m^{-2}) were free-living animals, organisms with a life span between 3 – 10 years, and animals buried down to 5 cm in the sediment.

Effect of trawling and primary production on functional indices

Functional diversity and functional evenness related positively to primary production and negatively to trawling (Table 3); the highest levels of functional evenness and diversity therefore coincided with low trawling and high primary production (Figure 2). The interaction between trawling and primary production was significantly negative, with the strongest trawling effect at high primary production. At low primary production, trawling did not affect functional evenness and diversity.

Effect of trawling and primary production on traits composition

FCA ordinations showed greater similarity in traits composition at stations subjected to high levels of trawling pressure than stations subjected to lower levels of trawling (Figure 3A). Intensively trawled stations were characterised by a greater biomass of organisms that weighed over 1 kg (g1001 and g10000), lived for over 10 years (l10), resided deep within the sediment (sp10) or were pelagic (spPelagic), did not contribute to bioturbation (bNone), and were predatory (fPred) and / or crevice-dwelling (lhCrev). In contrast, stations subjected to low levels of trawling were characterised by animals that attached to the seabed (lhAtt) or other animals (lhEpi), lived high up (sp0.5 and sp6.10) or on top of the sediment (spSurf), were diffusive (bDiff) bioturbators, weighed between 11 g – 1 kg (g11 and g101), lived < 1 year to 3 years (l1 and l1.3), and were suspension (fSusp) and / or surface-feeders (fSurf). Unlike these comparisons in trawling pressure, the FCA ordinations did not clearly separate stations of low and high primary production (Figure 3B).

Effect of trawling and primary production on modality biomass

Linear models relating modality biomass with primary production and trawling pressure for each biological trait showed significant interactions between modality and trawling and / or primary production, thus indicating different reactions by modalities to these two stressors (Table 4). Trawling and primary production did not interact significantly with modality biomass for the traits “longevity”, “sediment position” and “feeding mode”. For “living habit”, we observed significant interactions between modality and primary production, and between modality and trawling pressure. Trawling had negative effects on all modalities within this trait, and these effects were more pronounced under high levels of primary production (Figure 4). This negative relationship was strongest for attached and epifaunal organisms, and weakest for burrow- and tube-dwelling species. For “maximum weight”, the three-way interaction between modality, trawling, and primary production was significant. This meant trawling had negative effects on most modalities within this trait, with the negative effect of trawling strengthening under high levels of primary production (Figure 5). These negative relationships were strongest in organisms weighing between < 0.1 g and 1000 g. In contrast, organisms weighing > 10 kg exhibited a broadly positive relationship with trawling, which strengthened with increasing primary production. Primary production had positive effects on the biomass of most modalities when plotting primary production as a continuous variable (Figures S5 and S6), and that the positive effect of primary production weakened under high levels of trawling. For “bioturbation”, only the interaction between modality and primary production was significant. Of the modalities within this trait, upward conveyors related positively to primary production (Figure 6), whilst the other modalities exhibited no clear pattern.

Discussion

Our study is the first to measure the joint effects of trawling and primary production on the functional diversity and traits composition of benthic communities. Overall, bottom trawling had negative effects on the functional diversity, evenness, and biomass of 12 of the 32 modalities investigated, whilst primary production had positive effects. We also observed strong interactive effects between the two, in that the degree to which one influenced the benthic community depended on the strength of the other. This meant greater effects of bottom trawling on benthic communities in areas of high primary production.

Community biomass was less evenly distributed across modalities in highly trawled areas, resulting in lower levels of functional diversity and functional evenness. Whilst some studies suggest fishing can reduce functional diversity and evenness (Worm et al. 2006, Martins et al. 2012), ours is the first to directly relate reductions to incremental increases in trawling pressure. We also found stronger effects of trawling on functional diversity and evenness in areas of high primary production. The cause of this pattern remains unclear, especially considering recent evidence which suggests that high primary production should buffer benthic communities from trawling impacts (Hiddink et al. 2017). Then again, highly productive freshwater systems often coincide with high community biomass but low species diversity (McQueen et al. 1989, Rudstam et al. 1993), and should therefore be less resilient (Macpherson et al. 2002, Jennings & Blanchard 2004, Gómez-Canchong et al. 2013). Given the effects of climate change, acidification, and eutrophication on global levels of primary production, such a relationship could make marine ecosystems and the fisheries they support less resilient to the impacts of fishing, particularly in areas where primary production increases (Blanchard et al. 2012, Tait & Schiel 2013).

Intensely trawled areas were characterised by lower biomasses of attached and epiphytic organisms such as sea squirts (Tunicata), sponges (Porifera), bryozoans (e.g. *Flustra foliacea*, Crisiidae and *Cellaria* spp), and soft (e.g. *Alcyonium digitatum*) and hard corals (e.g. *Caryophyllia smithii*). Many studies document strong impacts on these organisms by mobile gears through physical disruption of sediments (Kaiser et al. 2000, 2006, Bradshaw et al. 2003, Howarth, Pickup, et al. 2015) and associated negative effects on suspension feeders (Collie et al. 2000, Bradshaw et al. 2003). However, these organisms are functionally important to temperate marine ecosystems because they add three dimensional structure to the seabed (Howarth, Roberts, et al. 2015). In doing so, they can provide nursery habitats to a wide range of fish and invertebrates, supporting local levels of biodiversity and the recruitment of commercially important species (Beck et al. 2001, Kamenos et al. 2004, Gibb et al. 2007, Howarth, Roberts, et al. 2015). Consequently, negative effects of bottom trawling could potentially reduce their nursery habitat function (Kaiser et al. 2000, Bradshaw et al. 2001, Howarth et al. 2011).

High levels of fishing pressure are expected to reduce the abundance of large predators, and favour smaller competitor and prey species with shorter life histories (Bremner & Frid 2005, Tillin et al. 2006). Alternatively, all body sizes could be affected given that bottom trawling is non-selective, causing mortality in a wide range of non-target and target species ranging from nematodes to large sharks (Fennessy 1994, Hiddink et al. 2006, Hinz et al. 2008, 2009). However, we found negative effects of bottom trawling on a variety of body sizes (< 0.1 g to 10 kg) but no relationship with feeding mode. Hence, our results indicate that bottom trawling removes biomass from most of the benthic community, and not just large predators. Our results therefore suggest that fishing mortality is more important for small-bodied organisms than the release from predation pressure caused by the removal of targeted fish species.

Surprisingly, trawling had a broadly positive effect on the biomass of large organisms weighing > 10 kg such as rays (e.g. *Amblyraja radiata* and *Dipturus batis*), sharks (e.g. *Mustelus Asterias*), gadoids (e.g. *Gadus morhua* and *Molva molva*) turbot (*Scophthalmus maximus*) and monkfish (*Lophius piscatorius*). This unexpected result may reflect the low number of species (i.e. 11) represented in this modality. Hence, any differences in the spatial distribution of these species across our sampling stations would have had disproportionally strong effects on our results. Alternatively, this finding may reflect the confounding effects of using fishing effort as an indicator of fishing disturbance. Logic suggests fishing pressure should concentrate in areas with larger, more commercially viable species. If true, this would reduce our ability to detect a negative relationship between fishing effort and the abundance of large predatory fish.

The abundance of mobile scavengers can increase by up to 200 times in trawled areas as a result of increased availability of carrion and other organic matter (Tillin et al. 2006, Kaiser & Hiddink 2007). However, we detected no relationship between bottom trawling and the biomass of scavenging organisms such as hermit crabs (e.g. *Pagurus* spp). Then again, given the dispersion of odour plumes, resettlement of sediment and predation of damaged / injured organisms, high scavenger densities on fishing grounds are likely to be relatively short-lived events (Howarth, Pickup, et al. 2015). Hence, our approach, which was designed to detect long-term and large-scale changes, is unlikely to detect such an event. However, our results support two other studies that suggest the benefits of an increased food supply to scavengers cannot compensate for the direct mortality caused by bottom trawling (Bolam 2014, Bolam et al. 2017). These two studies also observed recovery of bioturbating species in 3 – 5 months following bottom fishing. In our study, this modality was composed primarily of burrowing polychaetes (e.g. Pectinariidae, Maldanidae and Eunicidae) which recover quickly from disturbance (reviewed in Jennings, Kaiser, et al. 2001). This capacity may explain why we observed no relationship between bottom trawling and the biomass of bioturbating organisms.

High levels of primary production should provide more energy to benthic deposit and suspension feeders (Blanchard et al. 2009). However, we detected no relationship between primary production and the biomass of deposit and suspension feeding organisms, such as bivalves (e.g. Cardiidae and *Abra* spp), polychaetes (e.g. *Lagis koreni*), and anemones (Actiniaria). This may reflect the depth of our sampling stations. Detritus is a poor energy resource, subject to degradation through microbial action and consumption as it sinks through the water column towards the seabed (Gerlach et al. 1985). Given that our sampling sites were located at depths between 40 and 90 m, the detritus reaching the seabed may have been too low in energy to offer measurable benefit to deposit and suspension feeders. We also expected a positive relationship between primary production and small body size, and for this relationship to intensify under high trawling pressure. Whilst we found evidence of primary production increasing the biomass of small-bodied organisms, in reality, this relationship weakened with increasing trawling pressure. Hence, this pattern suggests the fishing mortality inflicted on small organisms outweighs any benefits they receive from enhanced growth rates under high primary production (Posey et al. 2002).

In summary, our evidence suggests that bottom trawling and primary production can cause functional changes to benthic communities. Bottom trawling had negative effects on functional diversity, functional evenness, and the maximum weight and living habit of the benthic community, and no effects on their feeding mode, longevity, bioturbation, and sediment position. We also found greater effects of trawling on benthic ecosystem functioning in areas of high primary production. Noting changing levels of primary production globally, this interaction may reduce resiliency of ecosystems and fish stocks to future fishing impacts. We therefore suggest further study of the interactions between fishing disturbance and environmental perturbations, which could have strong implications for conservation and fisheries management.

Data accessibility

Data used in this paper are archived in the British Oceanographic Data Centre (www.bodc.ac.uk) under doi:10.5285/674d4224-7cc5-4080-e053-6c86abc0626e.

Acknowledgements

This work was supported by the Natural Environment Research Council and Department for Environment, Food and Rural Affairs [grant number NE/L003279/1, Marine Ecosystems Research Programme]. We thank Camille Maurin, Marine Cendrier, Susan Allender, Ian Pritchard, Wendy Robertson, Tanya Riley, Maria Giulia Moretti-Bushin, Jack Buckingham, Hannah Hernon, Charlotte Mathews, Claude Eric-Marquet, Craig Robertson, Marija Sciberras, Kathryn Hughes, Sowmiya Shivaji, Tom Perkins, Michael Spence, James Pilkington, Julia Rulent, Anna Canning, Gillian Peacock, Pascal Dubois, Anna Krystali, Nichola Lacey, Federico Ghiazza, Lucy Hawkesworth, Sarah Holmes, Sarah Dashfield, Christine Pascoe and Natalie Welden for their assistance with sampling and laboratory work.

References

Aller RC (1982) The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: McCall PL, Tesz MJS (eds) Animal-Sediment Relations. Plenum Publishing Company, New York, p 53–102

Beamish RJ, McFarlane GA, Benson A (2006) Longevity overfishing. Prog Oceanogr 68:289–302

Beck MW, Heck KL, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2001) The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. Bioscience 51:633–641

Bergmann M, Wieczorek SK, Moore PG, Atkinson RJA (2002) Discard composition of the *Nephrops* fishery in the Clyde Sea area, Scotland. Fish Res 57:169–183

Blanchard JL, Jennings S, Holmes R, Harle J, Merino G, Allen JI, Holt J, Dulvy NK, Barange M (2012) Potential consequences of climate change for primary production and fish production in large marine ecosystems. Philos Trans R Soc B Biol Sci 367:2979–2989

Blanchard JL, Jennings S, Law R, Castle MD, McCloghrie P, Rochet MJ, Benoît E (2009) How does abundance scale with body size in coupled size-structured food webs? J Anim Ecol 78:270–280

Bolam SG (2014) Predicting the effect of trawling based on biological traits of organisms and functional correlates of these traits to predict which functions may be disproportionally affected. BENTHIS Deliverable 4.3.

Bolam SG, Coggan RC, Eggleton J, Diesing M, Stephens D (2014) Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. J Sea Res 85:162–177

Bolam SG, Garcia C, Eggleton J, Kenny AJ, Buhl-Mortensen L, Gonzalez-Mirelis G, Kooten T van, Dinesen G, Hansen J, Hiddink JG, Sciberras M, Smith C, Papadopoulou N, Gumus A, Hoey G Van, Eigaard OR, Bastardie F, Rijnsdorp AD (2017) Differences in biological traits composition of benthic assemblages between unimpacted habitats. Mar Environ Res 126:1–13

Bolam SG, McIlwaine PSO, Garcia C (2016) Application of biological traits to further our understanding of the impacts of dredged material disposal on benthic assemblages. Mar Pollut Bull 105:180–192

Borrvall C, Ebenman B, Tomas Jonsson TJ (2000) Biodiversity lessens the risk of cascading extinction in model food webs. Ecol Lett 3:131–136

Bradshaw C, Collins P, Brand AR (2003) To what extent does upright sessile epifauna affect benthic biodiversity and community composition? Mar Biol 143:783–791

Bradshaw C, Veale LO, Hill AS, Brand AR (2001) The effect of scallop dredging on Irish Sea benthos: experiments using a closed area. Hydrobiologia 465:129–138

Brander KM (2007) Global fish production and climate change. Proc Natl Acad Sci USA 104:19709–19714

Bremner J, Frid C. (2005) Biological traits of the North Sea benthos: does fishing affect ecosystem function? Am Fish Soc Symp 41:477–489

Bremner J, Rogers SI, Frid CLJ (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecol Indic 6:609–622

Brose U, Cushing L, Berlow EL, Jonsson T, Banasek-Richter C, Bersier L-F, Blanchard J, Brey T, Carpenter SR, Blandenier M-F, Cohen J, Dawah H, Dell T, Edwards F, Harper-Smith S, Jacob U, Knapp R, Ledger M, Memmott J, Mintenbeck K, Pinnegar J, Rall B, Rayner T, Ruess L, Ulrich W, Warren PH, Williams RJ, Woodward G, Yodzis P, Martinez N (2005) Body sizes of consumers and their resources. Ecology 86:2545

Campbell MS, Stehfest KM, Votier SC, Hall-Spencer JM (2014) Mapping fisheries for marine spatial planning: Gear-specific vessel monitoring system (VMS), marine conservation and offshore renewable energy. Mar Policy 45:293–300

Cardinale BJ, Palmer MA, Collins SL (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. Nature 415:426–429

Chevenet Fran, Doleadec S, Chessell D (1994) A fuzzy coding approach for the analysis of long-term ecological data. Freshw Biol 31:295–309

Collie JS, Hall SJ, Kaiser MJ, Poiner IR (2000) A quantitative analysis of fishing impacts on shelf-sea benthos. J Anim Ecol 69:785–798

Cooper R, Long D, Doce D, Green S, Morando A (2010) Creating and assessing a sediment data layer for UKSeaMap 2010. British Geological Survey Commercial Report, CR/09/168.

Crain CM, Kroeker K, Halpern BS (2008) Interactive and cumulative effects of multiple human stressors in marine systems. Ecol Lett 11:1304–1315

Craven HR, Brand AR, Stewart BD (2013) Patterns and impacts of fish bycatch in a scallop dredge fishery. Aquat Conserv Mar Freshw Ecosyst 23:152–170

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655

Dray S, Bu-four A-B, Thiolouse J (2017) Package ‘ade4’. Analysis of ecological Data: exploratory and Euclidean methods in environmental sciences. Cran R Project.

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock H, Geitner K, Gerritsen H, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Mirelis GG, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith C, Vanelslander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: distribution, intensity and seabed integrity. ICES J Mar Sci 74:847–865

Fasham MJR, Holligan PM, Pugh PR (1983) The Spatial and Temporal Development of the Spring Phytoplankton Bloom in the Celtic Sea , April 1979. Prog Oceanogr 12:87–145

Fennessy ST (1994) Incidental capture of elasmobranchs by commercial prawn trawlers on the Tugela Bank, Natal, South Africa. South African J Mar Sci 14:287–296

Fonseca CR, Ganade G (2001) Species functional redundancy, random extinctions and the stability of ecosystems. J Ecol 89:118–125

Frederiksen M, Edwards M, Richardson AJ, Halliday NC, Wanless S (2006) From plankton to top predators: Bottom-up control of a marine food web across four trophic levels. J Anim Ecol 75:1259–1268

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–264

Fu C, Travers-Trolet M, Velez L, Grüss A, Bundy A, Shannon LJ, Fulton EA, Akoglu E, Houle JE, Coll M, Verley P, Heymans JJ, John E, Shin Y-J (2018) Risky business: The combined effects of fishing and changes in primary productivity on fish communities. Ecol Modell 368:265–276

Garcia-Soto C, Pingree RD (2009) Spring and summer blooms of phytoplankton (SeaWiFS/MODIS) along a ferry line in the Bay of Biscay and western English Channel. Cont Shelf Res 29:1111–1122

Gerlach SA, Hahn AE, Schrage M (1985) Size spectra of benthic biomass and metabolism. Mar Ecol Prog Ser 26:161–173

Gerritsen HD, Minto C, Lordan C (2013) How much of the seabed is impacted by mobile fishing gear? Absolute estimates from Vessel Monitoring System (VMS) point data. ICES J Mar Sci 70:523–531

Gibb FM, Gibb IM, Wright PJ (2007) Isolation of Atlantic cod (Gadus morhua) nursery areas. Mar Biol 151:1185–1194

Gómez-Canchong P, Blanco JM, Quiñones RA (2013) On the use of biomass size spectra linear adjustments to design ecosystem indicators. Sci Mar 77:257–268

Gómez-Canchong P, Quiñones RA, Brose U (2012) Robustness of size–structure across ecological networks in pelagic systems. Theor Ecol 6:45–56

Gregg WW, Conkright ME, Ginoux P, O’Reilly JE, Casey NW (2003) Ocean primary production and climate: global decadal changes. Geophys Res Lett 30

Guénette S, Gascuel D (2012) Shifting baselines in European fisheries: The case of the Celtic Sea and Bay of Biscay. Ocean Coast Manag 70:10–21

Gunderson AR, Armstrong EJ, Stillman JH (2016) Multiple Stressors in a Changing World: The Need for an Improved Perspective on Physiological Responses to the Dynamic Marine Environment.

Ann Rev Mar Sci 8

Hiddink JG, Jennings S, Kaiser MJ (2007) Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. J Appl Ecol 44:405–413

Hiddink JG, Jennings S, Kaiser MJ, Queiros AM, Duplisea DE, Piet GJ (2006) Cumulative impacts of seabed trawl disturbance on benthic biomass, production and species richness in different habitats. Can J Fish Aquac Sci 63:721–736

Hiddink JG, Jennings S, Sciberras M, Szostek C., Hughes KM, Ellis N, Rijnsdorp AD, McConnaughey RA, Mazor T, Hilborn R, Collie JS, Pitcher R, Amoroso RO, Parma AM, Suuronen P, Kaiser MJ (2017) Global analysis of depletion and recovery of seabed biota following bottom trawling disturbance. Proc Natl Acad Sci In press

Hinz H, Hiddink JG, Forde J, Kaiser MJ (2008) Large-scale responses of nematode communities to chronic otter-trawl disturbance. Can J Fish Aquat Sci 732:723–732

Hinz H, Prieto V, Kaiser MJ (2009) Trawl distrubance on benthic communities: chronic effects and experimental predications. Ecol Appl 19:761–773

Howarth LM, Pickup SE, Evans LE, Cross TJ, Hawkins JP, Roberts CM, Stewart BD (2015) Sessile and mobile components of a benthic ecosystem display mixed trends within a temperate marine reserve. Mar Environ Res 107:8–23

Howarth LM, Roberts CM, Hawkins JP, Steadman DJ, Beukers-Stewart BD (2015) Effects of ecosystem protection on scallop populations within a community-led temperate marine reserve. Mar Biol 162:823–840

Howarth LM, Roberts CM, Thurstan RH, Stewart BD (2014) The unintended consequences of simplifying the sea: Making the case for complexity. Fish Fish 15:690–711

Howarth LM, Stewart BD (2014) The dredge fishery for scallops in the United Kingdom (UK): effects on marine ecosystems and proposals for future management. Marine Ecosystem Management Report no. 5, University of York. York

Howarth LM, Wood HL, Turner AP, Beukers-Stewart BD (2011) Complex habitat boosts scallop recruitment in a fully protected marine reserve. Mar Biol 158:1767–1780

Jennings S, Blanchard JL (2004) Fish abundance with no fishing: Predictions based on macroecological theory. J Anim Ecol 73:632–642

Jennings S, Kaiser MJ, Reynolds JD (2001) Marine fisheries ecology. Blackwell, Oxford.

Jennings S, Pinnegar JK, Polunin NVC, Boon TW (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. J Anim Ecol 70:934–944

Jennings S, Pinnegar JK, Polunin NVC, Warr KJ (2002) Linking size-based and trophic analyses of benthic community structure. Mar Ecol Prog Ser 226:77–85

JGOFS (1994) Joint Global Ocean Flux Study (JGOFS) Protocols. Woods Hole Oceanographic Institution, Massachusetts.

Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B, Gårdmark AG, Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino M, Rijnsdorp AD (2007) Ecology: Managing Evolving Fish Stocks. Science (80-) 318:1247–1248

Kaiser MJ, Clarke KR, Hinz H, Austen MC V, Somerfield PJ, Karakassis I (2006) Global analysis of response and recovery of benthic biota to fishing. Mar Ecol Prog Ser 311:1–14

Kaiser M., Hiddink JG (2007) Food subsidies from fisheries to continental shelf benthic scavengers.

Mar Ecol Prog Ser 350:267–276

Kaiser MJ, Spence FE, Hart PJB (2000) Fishing-Gear Restrictions and Conservation of Benthic Habitat Complexity. Conserv Biol 14:1512–1525

Kamenos N, G. Moore P, Hall-Spencer J (2004) Nursery-area function of maerl grounds for juvenile queen scallops Aequipecten opercularis and other invertebrates. Mar Ecol Prog Ser 274:183–189

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science (80-) 294:804 LP-808

Lorenzen CJ (1966) A method for the continuous measurement of the in vivo chlorophyll concentration. Deep Sea Res 13:223–227

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. Science (80-) 312:1806 LP-1809

Macpherson E, Gordoa A, García-Rubies A (2002) Biomass Size Spectra in Littoral Fishes in Protected and Unprotected Areas in the NW Mediterranean. Estuar Coast Shelf Sci 55:777–788

Mann KH (2009) Ecology of Coastal Waters. John Wiley & Sons, New York

Martins GM, Arenas F, Neto AI, Jenkins SR (2012) Effects of Fishing and Regional Species Pool on the Functional Diversity of Fish Communities. PLoS One 7:e44297

Mason C (2011) NMBAQC's Best Practice Guidance. Particle Size Analysis (PSA) for Supporting Biological Analysis. National Marine Biological AQC Coordinating Committee.

McGrady-Steed J, Harris PM, Morin PJ (1997) Biodiversity regulates ecosystem predictability. Nature 390:162

McQueen DJ, Johannes MRS, Post JR, Stewart TJ, Lean DRS (1989) Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol Monogr 59:289–309

Mermillod-Blondin F (2011) The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. J North Am Benthol Soc 30:770–778

Micheli F, Halpern BS (2005) Low functional redundancy in coastal marine assemblages. Ecol Lett 8:391–400

Mooney H, Larigauderie A, Cesario M, Elmquist T, Hoegh-Guldberg O, Lavorel S, Mace GM, Palmer M, Scholes R, Yahara T (2009) Biodiversity, climate change, and ecosystem services. Curr Opin Environ Sustain 1:46–54

Morel A, Berthon J-F (1989) Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications. Limnol Oceanogr 34:1545–1562

Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR (2013) A functional approach reveals community responses to disturbances. Trends Ecol Evol 28:167–177

Musick JA (1999) Ecology and conservation of long-lived marine animals. Am Fish Soc Symp 23:1–10

Olsgard F, Schaanning MT, Widdicombe S, Kendall MA, Austen MC (2008) Effects of bottom trawling on ecosystem functioning. J Exp Mar Bio Ecol 366:123–133

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr Mar Biol Annu Rev 16:229–311

Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, Moore PJ, Brander K, Bruno JF, Buckley LB, Burrows MT, Duarte CM, Halpern BS, Holding J, Kappel C V, O/'Connor MI, Pandolfi JM, Parmesan C, Schwing F, Thompson SA, Richardson AJ (2013) Global imprint of climate change on marine life. Nat Clim Chang 3:919–925

Rodríguez S, Ojeda F, Inestrosa N (1993) Settlement of benthic marine invertebrates. Mar Ecol Prog Ser 97:193–207

Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. Netherlands J Sea Res 34:303–317

Rudstam LG, Lathrop RC, Carpenter SR (1993) The Rise and Fall of a Dominant Planktivore: Direct and Indirect Effects on Zooplankton. Ecology 74:303–319

Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. Ecol Monogr 80:469–484

Sciberras M, Parker R, Powell C, Robertson C, Kroger S, Bolam S, Geert Hiddink J (2016) Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. Limnol Oceanogr 61:2076–2089

Sprules WG, Barth LE (2015) Surfing the biomass size spectrum: some remarks on history, theory, and application. Can J Fish Aquat Sci 73:477–495

Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE, Baker SC, Thomson RJ, Stuart-Smith JF, Hill NA, Kininmonth SJ, Airoldi L, Becerro MA, Campbell SJ, Dawson TP, Navarrete SA, Soler GA, Strain EMA, Willis TJ, Edgar GJ (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501:539–42

Tait LW, Schiel DR (2013) Impacts of Temperature on Primary Productivity and Respiration in Naturally Structured Macroalgal Assemblages. PLoS One 8:e74413

Team RC (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Tillin HM, Hiddink JG, Jennings S, Kaiser MJ (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Mar Ecol Prog Ser 318:31–45

Watson RA, Cheung WWL, Anticamara JA, Sumaila U, Zeller D, Pauly D (2013) Global marine yield halved as fishing intensity redoubles. Fish Fish 14:493–503

Williams ID, Baum JK, Heenan A, Hanson KM, Nadon MO, Brainard RE (2015) Human, oceanographic and habitat drivers of central and western pacific coral reef fish assemblages. PLoS One 10:1–19

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. Science (80-) 314:787–790

Figures

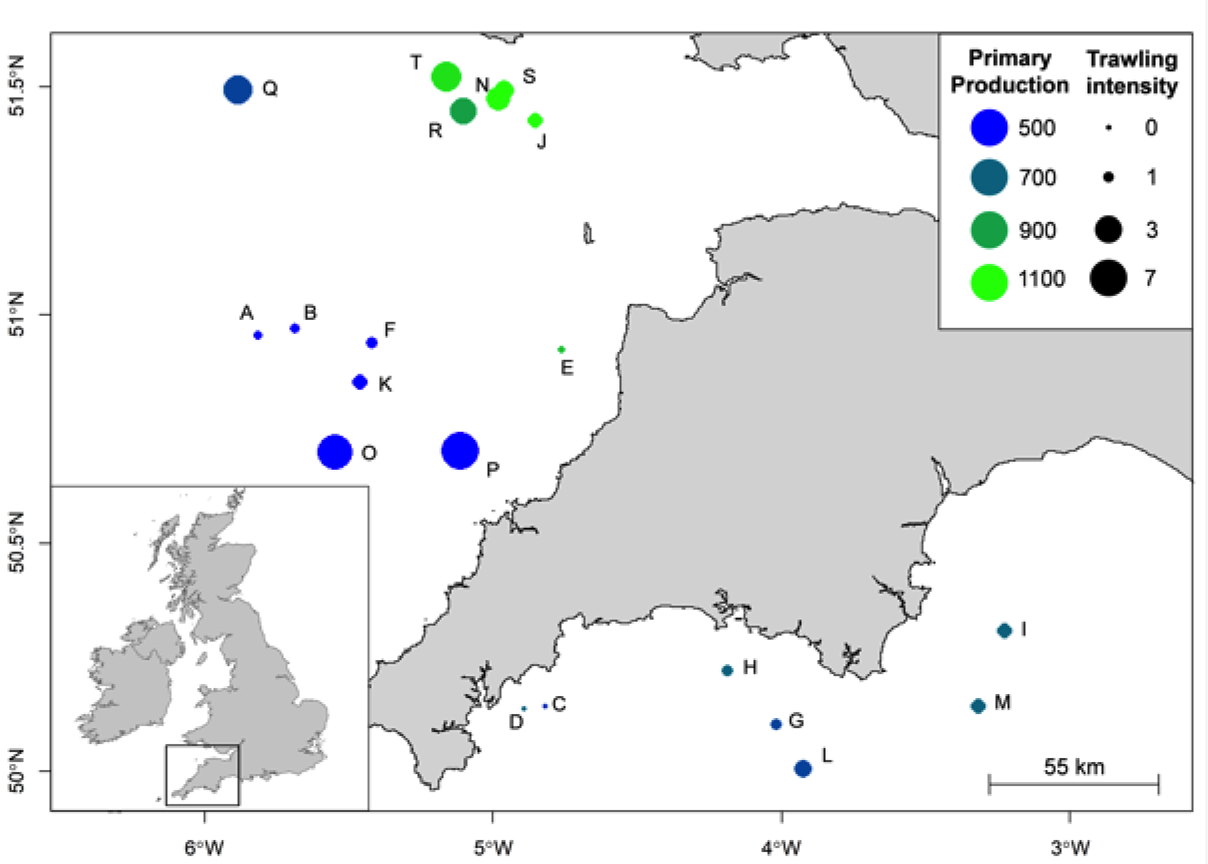


Figure 1. Sampling stations. Each point represents a 1 x 0.6 nautical mile box, the shade and size of which signifies the level of primary production (mg C m^{-2} yr^{-1}) and trawling intensity (yr^{-1}).

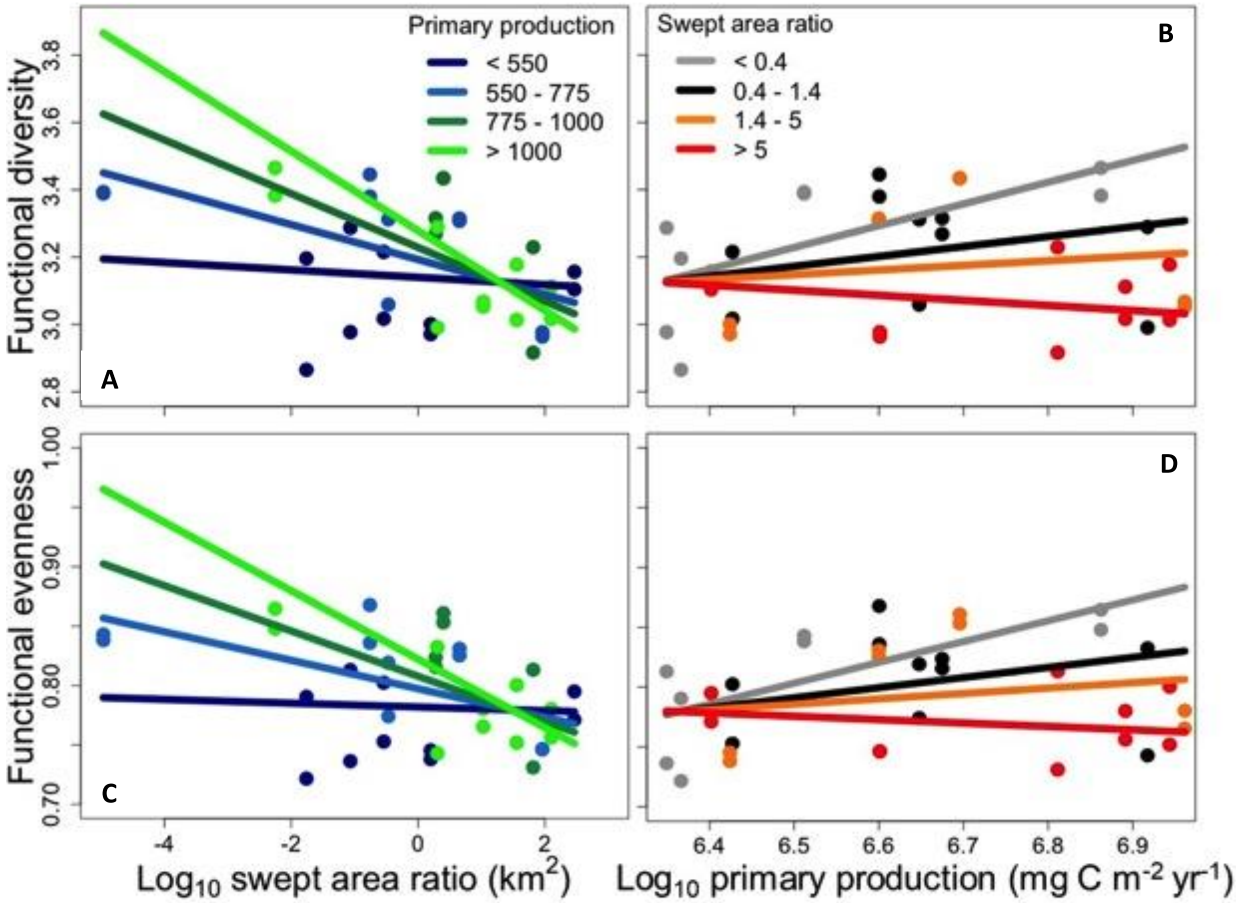


Figure 2: Functional diversity (A) and functional evenness (B) plotted against trawling intensity and categorical levels of primary production. Functional diversity (C) and functional evenness (D) plotted against primary production and categorical levels of trawling intensity. Trend lines fitted by linear models.

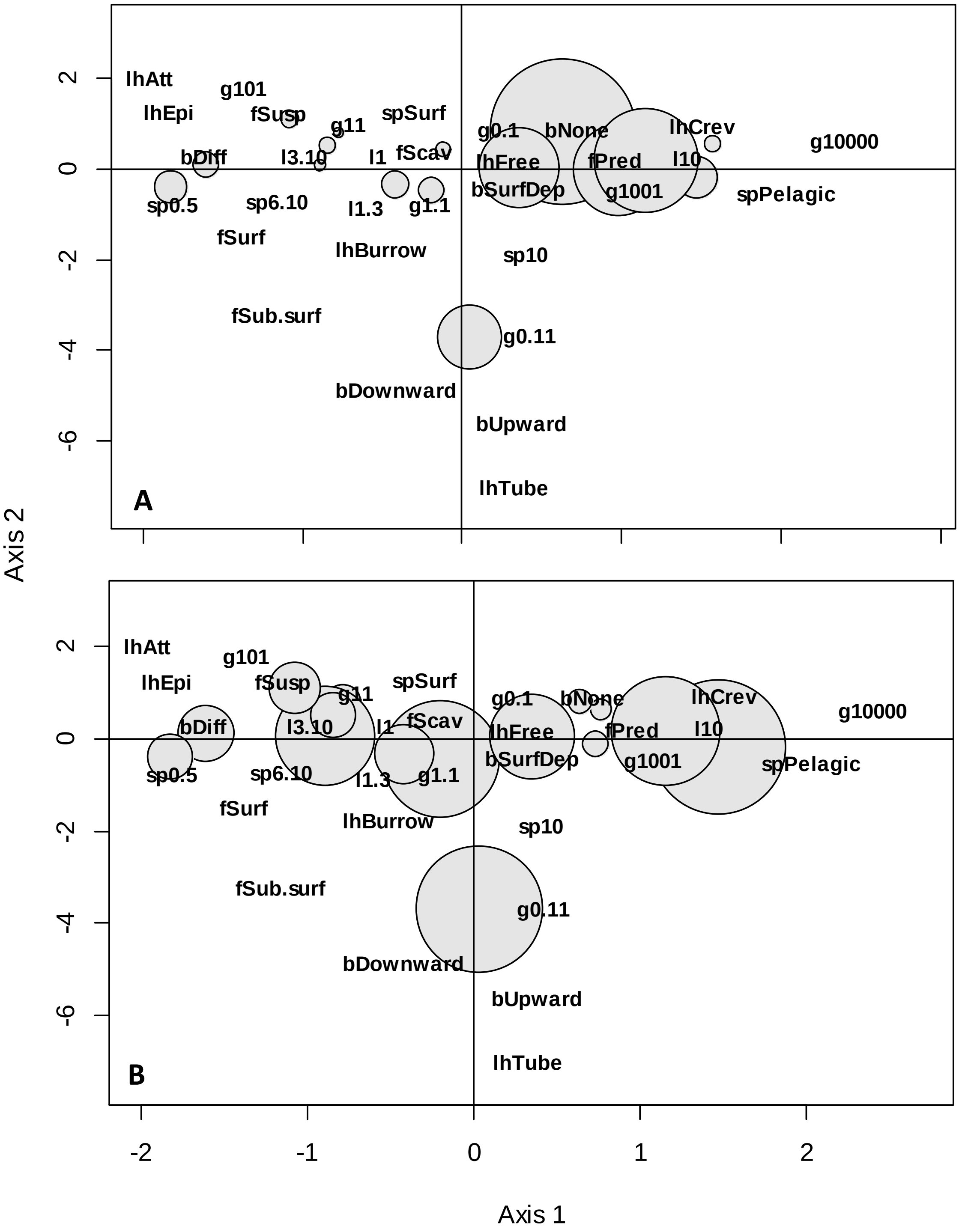


Figure 3. Plots of ordination scores from fuzzy correspondence analysis of modality biomass. Each bubble indicates a sampling station. Plots are identical except for the area of circles: (A) trawling intensity (yr–1); (B) primary production (mg C m-2 yr-1). The abbreviations give the names of the modalities. Stations that appear further apart have greater differences in overall trait composition. The location of the modalities indicates the types of stations with which they are associated.

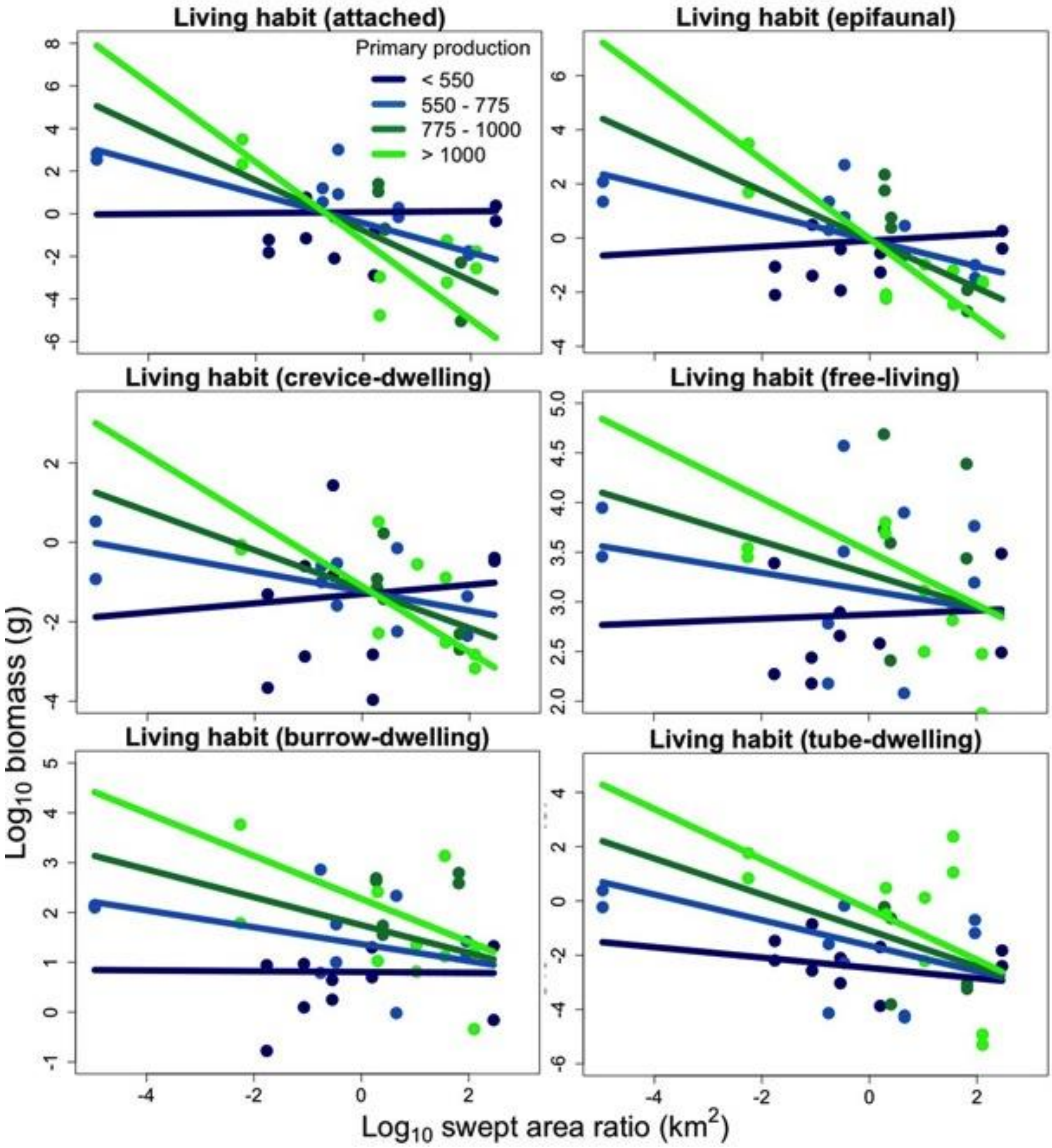


Figure 4. Biomass of modalities within the trait "living habit", plotted against trawling intensity (swept area ratio) and categorical levels of primary production. Trend lines fitted by linear models.

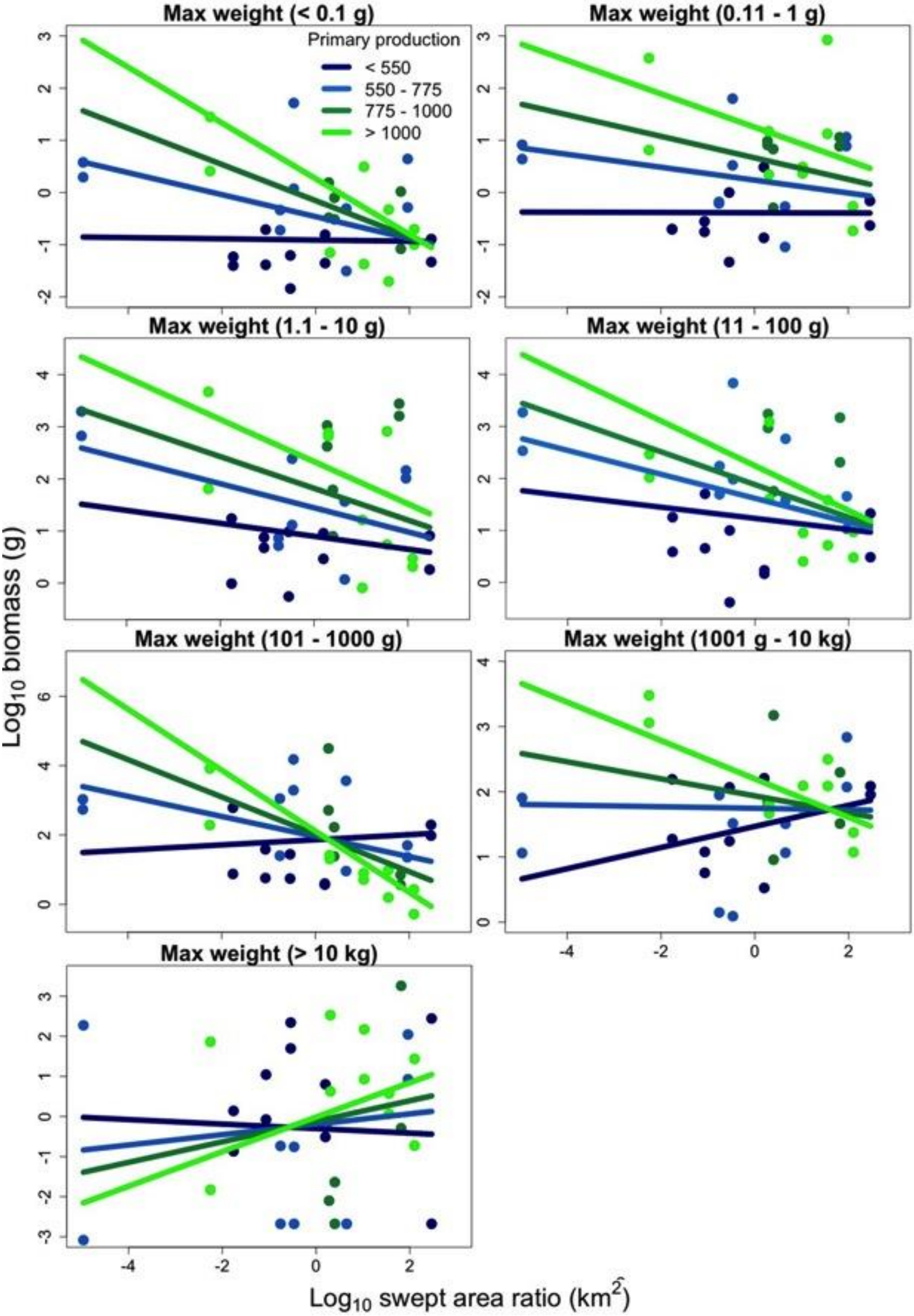


Figure 5. Biomass of modalities within the trait “maximum weight”, plotted against trawling intensity (swept area ratio) and categorical levels of primary production. Trend lines fitted by linear models.

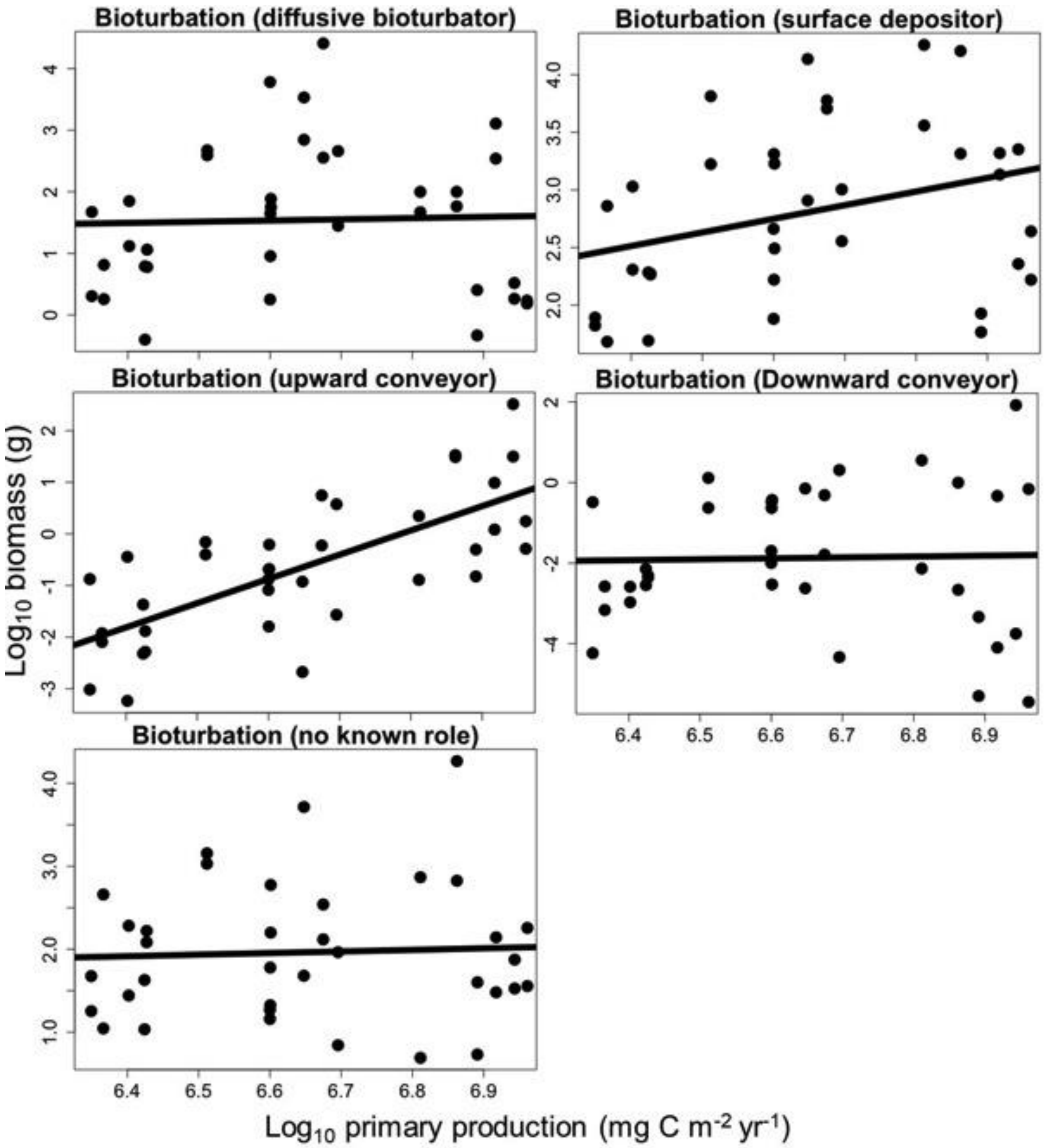


Figure 6. Biomass of modalities within the trait "bioturbation", plotted against primary production. Trend lines fitted by linear models.

Table 1. The range of values that defined the four experimental treatments of trawling intensity and primary production sampled in this study.

Treatment	Swept area ratio (km^2)	Primary production (mg C m^{-2} yr^{-1})
1 - Low	≤ 0.4	≤ 550
2 - Medium low	$\geq 0.4 \leq 1.4$	$> 550 \leq 775$
3 - Medium high	$\geq 1.4 \leq 5$	$> 775 \leq 1000$
4 - High	> 5	> 1000

Table 2. Description of biological traits used in this study, and the total biomass (pre-gear calibration) and number of taxa that fell within each modality.

Trait	Code	Description	No. of taxa	Biomass (g m^{-2})	Relevance
Maximum weight	g0.1	< 0.1 g	108	298.1	Reflects trophic position, metabolic rate, energy requirements, generation time, commercial value, and catchability (Jennings et al. 2002, Brose et al. 2005, Sprules & Barth 2015).
	g0.11	0.11 - 1 g	71	801.8	
	g1.1	1.1 - 10 g	105	2305.8	
	g11	11 - 100 g	84	936.5	
	g101	101 - 1000 g	46	1421.8	
	g1001	1001 - 10000 g	33	256.5	
	g10000	> 10000 g	11	33	
Longevity	l1	< 1 yrs	45	15.3	Reflects age at maturity, somatic growth, and disturbance frequency / severity (Pearson & Rosenberg 1978, Musick 1999).
	l1-3	1 - 3 yrs	125	1152.2	
	l3-10	3 - 10 yrs	171	3557.9	
	l10	> 10 yrs	83	1328.1	
Living habit	lhTube	Tube-dwelling	31	329	Indicates potential to evade, or to be exposed to disturbance and predation pressure (Kaiser et al. 2000).
	lhBurrow	Burrow-dwelling	89	2015.8	
	lhFree	Free-living	222	3266.5	
	lhCrev	Crevice-dwelling	48	62.1	
	lhEpi	Epiphytic	34	140.6	
	lhAtt	Attached	29	239.5	
Location within sediment	spPelagic	Pelagic	63	79.9	Implications for sediment-water biogeochemistry and oxygen availability, and susceptibility to disturbance (Aller 1982, Collie et al. 2000).
	spSurf	Atop of sediment	233	1366.5	
	sp0-5	0 - 5 cm deep	124	3731.3	
	sp6-10	6 - 10 cm deep	53	729.2	
	sp10	> 10 cm deep	26	146.5	
Feeding mode	fSusp	Suspension feeder	127	1847.6	Implications for energy flow and susceptibility to disturbance (Rosenberg 1995, Bergmann et al. 2002, Craven et al. 2013).
	fSurf	Surface deposit feeder	107	1434	
	fSub-surf	Sub-surface deposit feeder	49	1559.7	
	fScav	Scavenger	60	355.8	
	fPred	Predator	163	854.9	
Bioturbation	bDiff	Diffusive bioturbator	112	2304.8	Implications for sediment-water biogeochemistry and oxygen availability (Mermillod-Blondin 2011).
	bSurfDep	Surface depositor	249	2897.3	
	bUpward	Upward conveyor	12	303.5	
	bDownward	Downward conveyor	17	186.4	
	bNone	None	88	361.4	

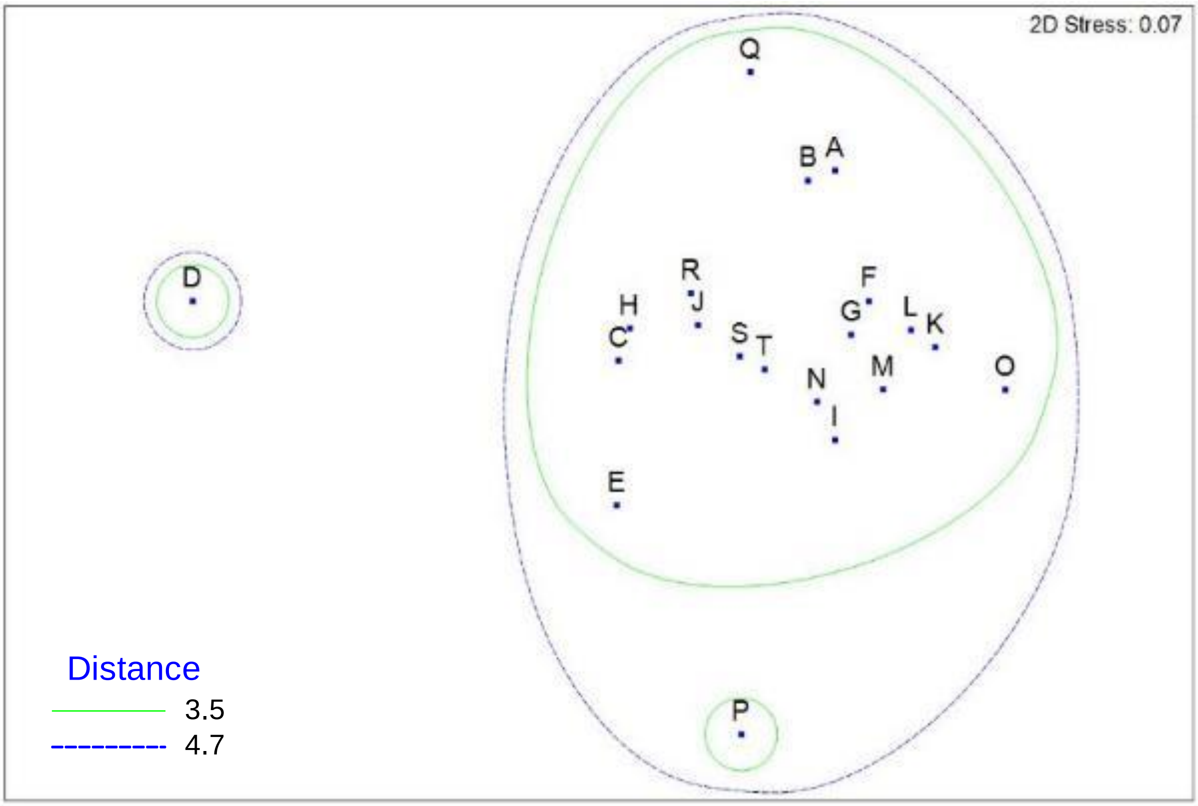
Table 3. Linear model outputs modelling functional diversity and functional evenness to trawling intensity and primary production.

Model	Predictor	Value	SE	*t*	*P*	R^2
Functional diversity	Intercept	1.23	0.99	1.25	0.233	0.37
	log(trawling)	1.6	0.61	2.61	0.020	
	log(primary production)	0.3	0.15	2.1	0.044	
	log(trawling):log(primary production)	-0.25	0.09	-2.7	0.018	
Functional evenness	Intercept	0.26	0.24	1.07	0.305	0.38
	log(trawling)	0.4	0.15	2.68	0.018	
	log(primary production)	0.08	0.04	2.25	0.041	
	log(trawling): log(primary production)	-0.06	0.02	-2.77	0.015	

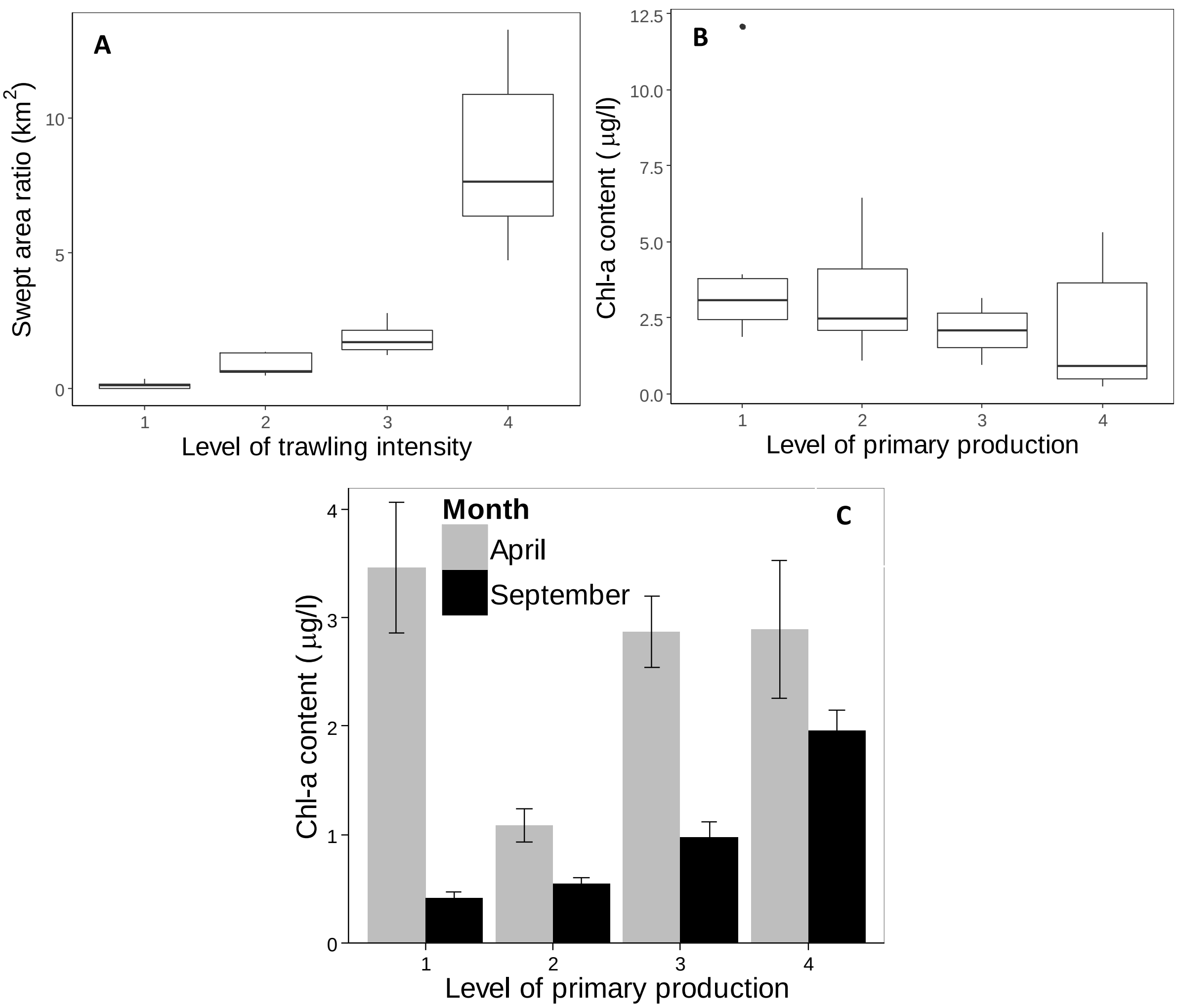
Table 4. Linear model outputs modelling trait biomass to modality, trawling intensity, and primary production.

Trait	Predictor	df	MSE	*F*	*P*	R^2
Living habit	Modality	5	126.2	59.9	<0.001	0.69
	log(trawling)	1	75.6	35.9	<0.001	
	log(production)	1	1.5	0.7	0.401	
	Modality : log(trawling)	5	9.1	4.3	<0.001	
	Modality : log(production)	5	8.6	4.1	0.002	
	log(trawling) : log(production)	1	67.6	32.1	<0.001	
	Modality : log(trawling) : log(production)	5	4.6	2.2	0.057	
Maximum weight	Modality	6	52.3	17.4	<0.001	0.39
	log(trawling)	1	7.9	2.7	0.104	
	log(production)	1	33.2	11.1	0.001	
	Modality : log(trawling)	6	1.4	0.5	0.822	
	Modality : log(production)	6	1.7	0.6	0.734	
	log(trawling) : log(production)	1	2.7	0.9	0.339	
	Modality : log(trawling) : log(production)	6	8.1	2.7	0.015	
Longevity	Modality	3	351.7	274.9	<0.001	0.87
	log(trawling)	1	13.6	10.6	0.001	
	log(production)	1	7	5.5	0.02	
	Modality : log(trawling)	3	0.8	0.6	0.605	
	Modality : log(production)	3	0.6	0.5	0.711	
	log(trawling) : log(production)	1	16.2	12.7	<0.001	
	Modality : log(trawling) : log(production)	3	0.4	0.3	0.799	
Bioturbation	Modality	4	136.1	110.6	<0.001	0.39
	log(trawling)	1	7.8	6.5	0.011	
	log(production)	1	22.1	18	<0.001	
	Modality : log(trawling)	4	1.2	1	0.432	
	Modality : log(production)	4	4.7	3.8	0.005	
	log(trawling) : log(production)	1	10.5	8.6	0.004	
	Modality : log(trawling) : log(production)	4	0.4	0.3	0.863	
Sediment position	Modality	4	101.4	89	<0.001	0.71
	log(trawling)	1	5	4.4	0.037	
	log(production)	1	9.5	8.3	0.004	
	Modality : log(trawling)	4	2.3	2	0.091	
	Modality : log(production)	4	1.1	1.1	0.376	
	log(trawling) : log(production)	1	9.2	9.2	0.002	
	Modality : log(trawling) : log(production)	4	1.2	1.2	0.319	
Feeding mode	Modality	4	28.7	28.7	<0.001	0.51
	log(trawling)	1	6.3	6.3	0.013	
	log(production)	1	16.2	16.2	<0.001	
	Modality : log(trawling)	4	1.21	1.2	0.305	
	Modality : log(production)	4	0.45	0.4	0.769	
	log(trawling) : log(production)	1	19.2	19.2	<0.001	
	Modality : log(trawling) : log(production)	4	1.2	1.2	0.315	

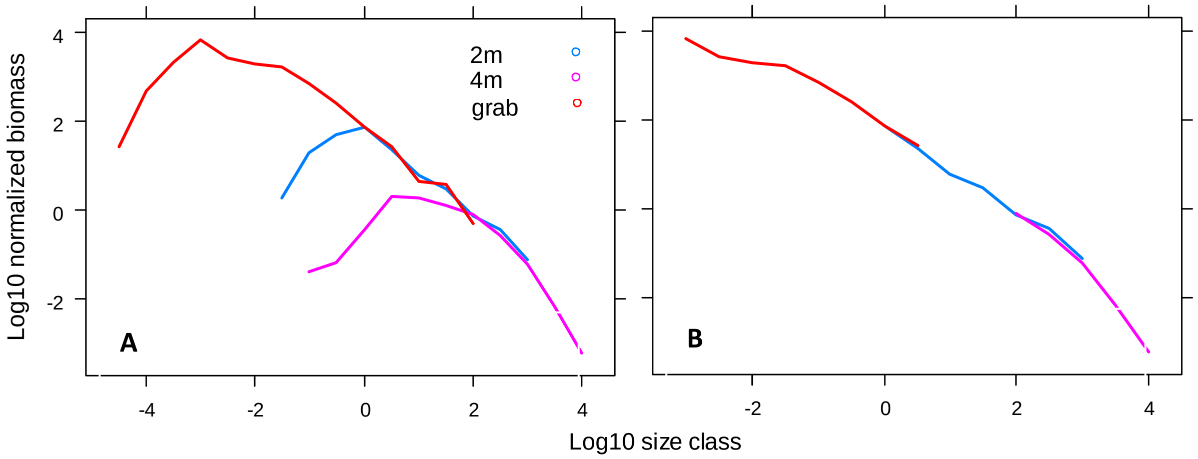
Electronic supplementary material



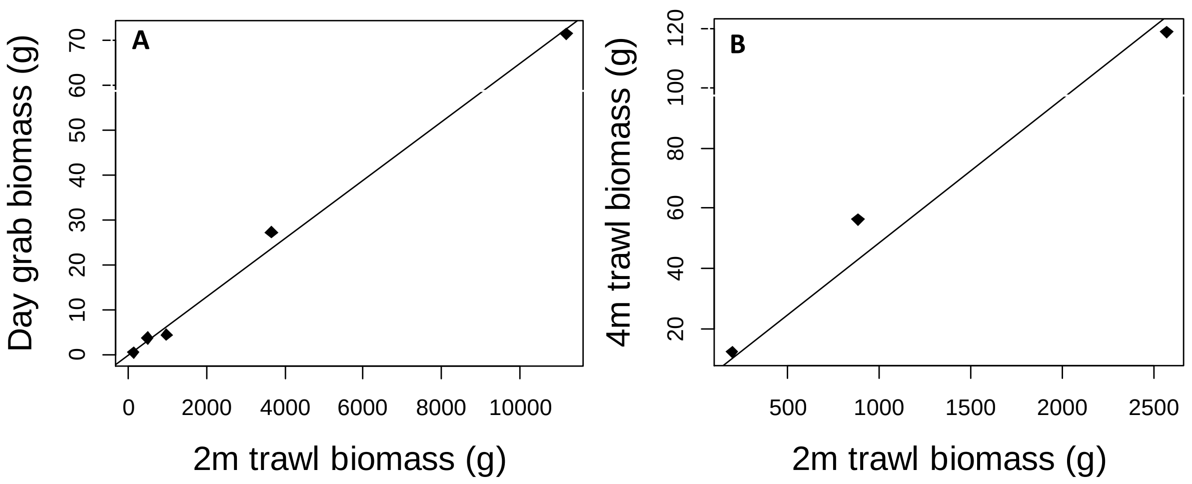
S1. nMDS plots of the different stations and their environmental characteristics before removing outliers.



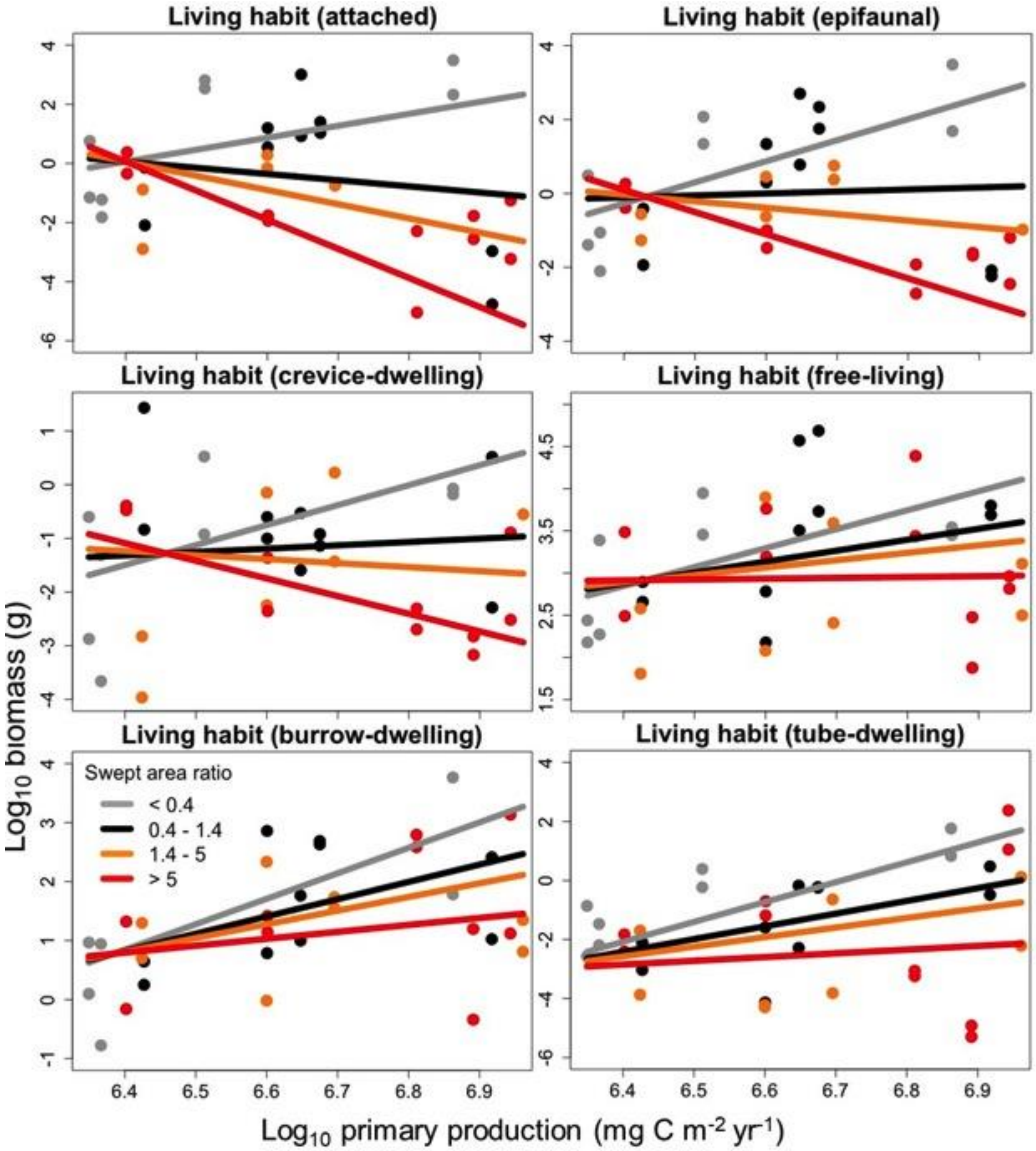
S2. The mean swept area ratio of the sampling stations plotted against their *a priori* experimental level of trawling intensity (A). The mean total Chl-a content of the sediment samples collected in April plotted against their *a priori* experimental level of primary production (B). The mean total Chl-a content of the water samples collected in September and April plotted against their *a priori* experimental level of primary production (C). Error bars represent ±1 SE.



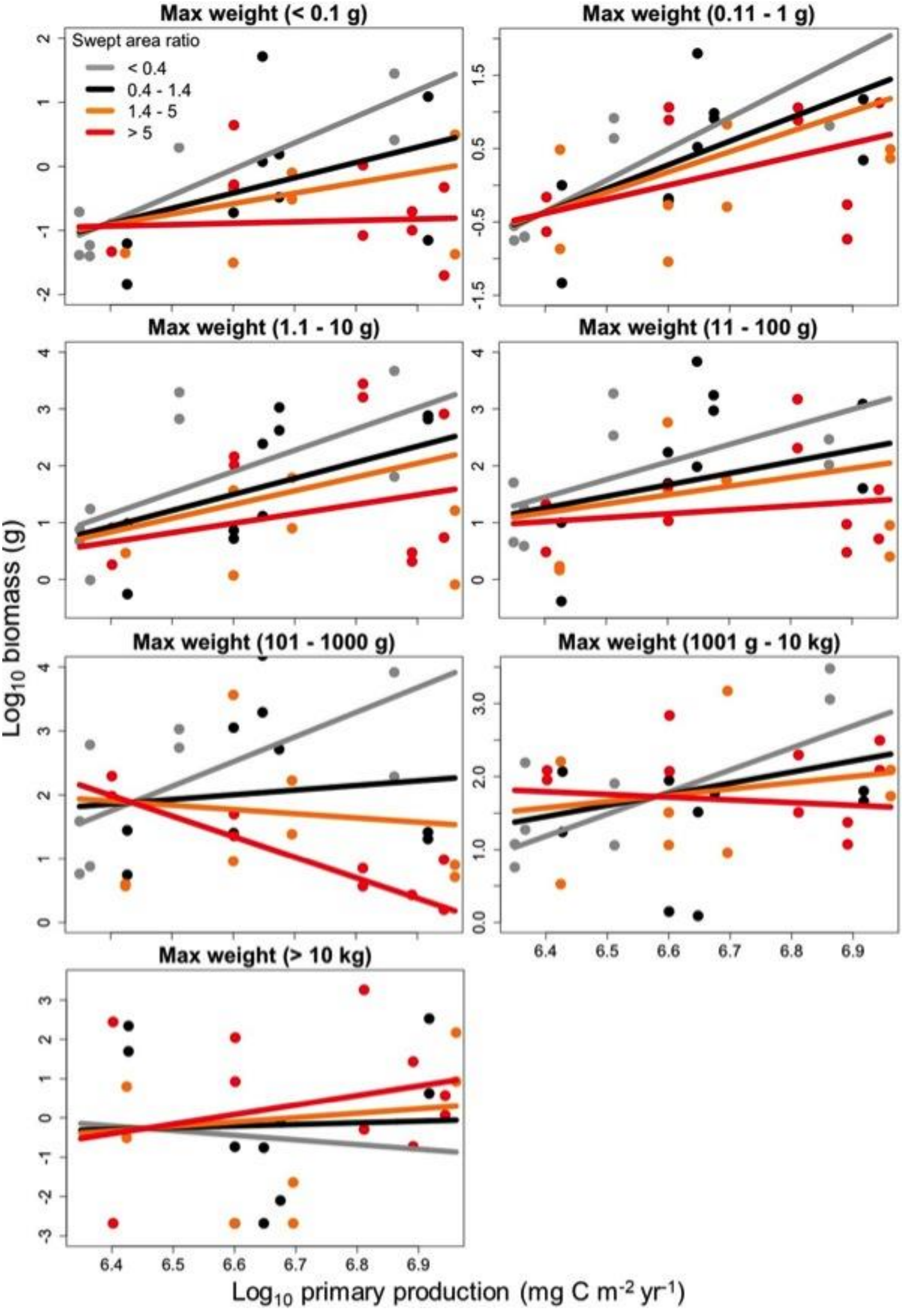
S3. The sampling gears captured organisms of markedly different size ranges (A). The amount of biomass each gear contributed was corrected to represent the same sampling area and were restricted to the size ranges that were sampled effectively. The extreme size classes inefficiently captured by each gear were then removed, resulting in a clear negative slope (B).



S4. Linear regressions models used to generate the catch coefficients. These were used to determine how much biomass the various gears contributed towards the final dataset. x and y axes represent normalised biomass.



S5. Biomass of modalities within the trait "living habit", plotted against primary production and categorical levels of trawling intensity. Trend lines fitted by linear models.



S6. Biomass of modalities within the trait "maximum weight", plotted against primary production and categorical levels of trawling intensity. Trend lines fitted by linear models.

Table S1. The latitude, longitude, mean annual primary productivity, mean annual trawling pressure, depth and mean particle size of the 1 x 0.6 nautical mile stations sampled in this study.

Station	Longitude	Latitude	Primary production (mg C m^{-2} yr^{-1})	Swept area ratio (yr^{-1})	Depth (m)
A	50.95762	-5.81468	581	0.17	86.5
B	50.96952	-5.68377	572	0.34	83.4
C	50.14108	-4.81793	672	0.01	62.0
D	50.13779	-4.89094	777	0.01	47.7
E	50.92419	-4.76168	955	0.11	41.6
F	50.94027	-5.42183	618	0.58	76.3
G	50.10285	-4.01841	735	0.47	64.0
H	50.2217	-4.19	770	0.63	41.3
I	50.3062	-3.22847	792	1.32	53.5
J	51.42451	-4.85315	1009	1.36	55.3
K	50.8516	-5.46147	616	1.22	77.0
L	50.00633	-3.9267	735	1.92	70.0
M	50.14212	-3.31622	808	1.49	62.0
N	51.49193	-4.96128	1054	2.80	51.4
O	50.69918	-5.5469	603	11.76	75.3
P	50.7029	-5.11145	613	13.23	59.4
Q	51.49384	-5.8869	735	7.10	96.0
R	51.44706	-5.10275	907	6.14	57.0
S	51.47474	-4.98225	1036	4.74	50.8
T	51.52256	-5.15893	983	8.18	43.7