Deliverable 4.3

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.

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SUMMARY

Fisheries research was traditionally driven by the requirement to manage single stocks of exploited species. In the last 2 decades, however, research efforts have increasingly been focused on the wider environmental global effects of fishing on non-target fauna and marine habitats. This focus is consistent with policy frameworks such as the Marine Strategy Framework Directive in the EU and the increasing need for fisheries management plans to adopt an Ecosystem Approach to Fisheries; both of which require an increased appreciation of the functional impacts of human activities on marine ecosystems. While studies that focus on changes in taxonomic composition of benthic communities as a result of bottom fishing have led to a fundamentally important understanding of the impacts of fishing, assessments based on trait composition have been shown to afford greater insights into ecosystem function than assessments based on the taxonomic structure of benthic communities. In this study, we examine whether; (i) the initial effect of bottom fishing on the abundance of benthic invertebrates vary among species with different biological traits, (ii) the magnitude of response to fishing varies among different habitat types and fishing gears, and (iii) the temporal trajectory for recovery from bottom fishing activity varies among species with different biological traits. Systematic review methodology was used to conduct a comprehensive search of peer-reviewed scientific literature and grey literature and to compile a database of studies that documented and compared the biological effects of experimentally fished areas with bottom mobile fishing gear (the impacted area) to non-fished areas (the control area). There were 59 different experimental manipulations or observations of the effects of fishing disturbance on benthic fauna and communities, extracted from 30 separate publications, which were included in the meta-analysis to examine the magnitude of the response of benthic invertebrates to bottom fishing gear and recovery trajectories following the disturbance. A suite of eleven traits that have been defined by WP3 were selected to describe the life history and morphological and behavioural characteristics of the species that may determine the potential sensitivity of benthic taxa to trawling and their contribution to ecosystem functioning. Bottom fishing resulted in significant negative impacts on total benthic community abundance; reductions were significantly higher following dredging (33% loss) compared to otter trawling and beam trawling (5% loss), and they were most severe for benthic communities in biogenic habitats and coarse and mixed sediment relative to sandy and muddy sediments. The effects of otter trawling on total benthic community abundance were short-lived and recovery was relatively quicker than for dredged areas, which were predicted to take about 3.5 years to recover. The damage from bottom fishing on communities in biogenic habitats may be irreversible as recovery did not appear to take place at any point after the disturbance. Recovery of total benthic community abundance in coarse and mixed sediment habitats was predicted to take up to a year after the fishing impact to occur, whereas only 5 months in sandy sediment. As for total community abundance, bottom fishing resulted in significant reductions in abundance in the fished area relative to the non-fished area for a number of modalities, and these differences were more pronounced following dredging than after otter trawling. Motility and burrowing behaviour proved to be important traits in determining

vulnerability to dredging, as organisms that burrow deeper than the penetration depth of the gear may avoid fishing disturbance. Predatory species showed very little reduction in abundance in the fished area relative to the non-fished area (6% loss), whereas scavengers (35% loss), deposit feeders (37% loss) and suspension feeders (22% loss) proved vulnerable to dredging, as significantly lower densities of these organisms were recorded in the fished area. Dredging was also found to result in significant reductions of short-lived species (41% loss) and of sexually reproducing species that produce pelagic eggs (31% loss) and planktotrophic larvae (26% loss), which may have profound long-term implications for population recovery or for the recolonization of other impacted areas further afield that depend on an external source of larvae for their survivability. Recovery times following dredging were significantly shorter for short-lived species (<1 – 3 years), free-living and tube-dwelling species and for scavenging or opportunistic species, than for medium-lived species (3 – 10 years), burrow-dwelling species and suspension feeders. In trawled areas, recovery times were significantly shorter for free-living species, species covered by an exoskeleton or a hard tunic and species that produce pelagic or benthic eggs than for epiphytic/zoic species, species that grow attached to the substratum and have an erect or stalked body form and species that reproduce asexually. Fishing resulted in substantial loss in the bioturbation potential of the benthic community immediately following fishing (25% reduction in the fished area), however, species capable of bioturbation were estimated to recover within 3 – 5 months following bottom fishing, indicating that fishing may reduce the bioturbation potential of a community in the short term but not in the long term. The present study provides insight into the magnitude of fishing effect and the recovery trajectories following fishing for species characterized by different biological traits, which may influence directly or indirectly ecosystem functioning. This is a step towards furthering our understanding of the potential influences of bottom fishing on ecosystem processes and functions governed by benthic species.

TABLE OF CONTENTS

1 INTRODUCTION

Policy frameworks such as the Marine Strategy Framework Directive in the EU, and the paradigm of ecosystem-based management inherently require an increased appreciation of the functional impacts of human activities on marine ecosystems (Hall and Mainprize 2004; Pikitch et al. 2004). Therefore, there is an increasing need to understand not only the impacts of anthropogenic activities on the structural composition of benthic invertebrate communities, but how such communities function and how this functionality is altered by anthropogenic pressures (Bremner 2008; Bremner et al. 2006; Reynoldson and Metcalfe-Smith 1992; Thrush and Dayton 2002). Over recent years, many studies have specifically aimed to understand the impacts of the various bottom trawling gear on benthic communities and most have focused on changes in community structural composition (e.g. Bergman et al. 2002; Dayton et al. 1995; Hall 1999; Jennings and Kaiser 1998; Jennings et al. 2001; Kaiser et al. 2000; Queiros et al. 2006). A meta-analysis of multiple studies on the effects of bottom fishing disturbance on benthic organisms highlighted that the largest negative impacts are generally observed for anthozoans, malacostracans, polychaetes, holothurians and ophiuroids whereas ostracods, echinoids, asteroids and bivalves appear to be less sensitive to fishing disturbance (Collie et al. 2000). Furthermore, these studies have shown that the effects of bottom trawling on the structure of benthic communities depend on factors such as the gear, intensity and the nature of the seabed habitats (Kaiser et al. 2006; Smith et al. 2000; Sciberras et al. 2013). For example, it has become apparent that there is a great variability in the susceptibility of different benthic habitats to a given fishing pressure (de Juan et al. 2007; Hiddink et al. 2007; Kaiser et al. 2006). More stable, sheltered or complex habitats (e.g. biogenic habitats and muddy sediments) that experience fewer natural disturbances are usually more profoundly affected by fishing activity, and can result in long-term community changes (Jennings and Kaiser 1998). Conversely, soft-sediment habitats which experience a relatively high level of natural physical disturbance are generally found to be less impacted by fishing (Prantoni et al. 2013; Sciberras et al. 2013).

Species composition changes do not necessarily equate to the same changes in trait composition. Several studies have shown that the functional trait composition of biological communities is a key component that most often explains ecosystem functioning better than attributes based on community structure or species composition (Bolam and Eggleton 2014; Hooper et al. 2004; Mouillot et al. 2008). Assessments based on trait composition may thus afford greater insights into ecosystem function than assessments based on the taxonomic structure of benthic communities (Bolam 2012; Bolam et al. 2014a; Bremner 2008; Paganelli et al. 2012; Van Der Linden et al. 2012; van Son et al. 2013). Benthic organisms perform a number of ecosystem-level processes that include dynamic processes such as sediment bioturbation, active re-suspension and decomposition, which in turn influence ecosystem functions such as secondary production (Bolam and Eggleton 2014), the transfer of oxygen and nutrients through the ecosystem (Bertics et al. 2010; Queirós et al. 2011), the recycling of waste material and the sequestration of harmful substances (Gilbert et al.

1994). Whilst two species may be taxonomically unrelated, it is possible to perform the same function given they have the same suite of traits. For example, deep burrows formed by the spatangoid urchin, *Echinocardium cordatum*, and the polychaete worm, *Nereis* sp. play a similar role in the redistribution and ventilation of sediment (Covich et al. 2004).

Whilst it is widely agreed that the loss or reduction in abundance and diversity of benthic fauna due to bottom-fishing may have far-reaching implications for the integrity of marine ecosystems, our understanding of the benthic structural variability of shelf seas (Barrio Froján et al. 2012; Heip and Craeymeersch 1995) is not matched by a comparable appreciation of its functional variability (Bolam et al. 2010). This is partly a reflection of the methodological and logistical difficulties encountered when assessing functional properties of seabed systems. Alternative approaches that utilize biological traits information have been increasingly used to link changes in community composition to changes in ecosystem functioning (Bremner 2008). A biological trait is simply a description of a particular characteristic of an individual (often defined for the species), for example body size, feeding mode and reproductive mode. Although caution must be encouraged as an understanding of the trait composition of a community provides only a qualitative assessment regarding ecological function, there has been an increasing number of experimental studies that link trait-function relationships. For example, in soft bottom habitats certain feeding and movement behaviours (primarily deposit-feeding and burrowing activities) can redistribute sediments, thus increasing the depth of oxygen and detritus penetration and consequently enhancing organic matter decomposition (Bertics et al. 2010; Kristensen 2001; Pearson 2001). Other traits, such as tube-building, have been shown to affect the transport of toxins into and through sediments (Aller 1983). Norkko et al. (2013) demonstrated that body size trait was important for oxygen and nutrient flux across the sediment–water interface. Bolam et al. (2014b) revealed that the highest total secondary production estimates are exhibited by assemblages dominated by suspension-feeders and/or surface-deposit-feeders, planktotrophic larval developers, those sessile taxa possessing an exoskeleton and those found on the sediment surface.

In this study, we examine how bottom trawling affects the functional composition of benthic invertebrate communities. Therefore, several biological traits that were considered important in determining the response of the benthos to fishing activities (functional response traits), and in determining the potential for changes in ecosystem function (functional effect traits) were selected. For example, the motilities of the organisms and their positions in or on the sediments influence their vulnerability to bottom fishing. Sedentary surface organisms are strongly affected by bottom-towed gear (Bergman and Hup 1992, Thrush et al. 1995, Auster et al. 1996, Wassenberg et al. 2002). External protecting structures and the morphological characteristics of organisms can also affect exposure and vulnerability to bottom fishing. Species protected with a hard shell, or vermiform organisms are considered less vulnerable to trawling impact (Bremner et al. 2003, Blanchard et al. 2004). Assemblages dominated by individuals that recruit via planktotrophic larvae are likely to respond more rapidly following large-scale physical disturbance than one reliant on benthic or lecithotrophic larvae (Thrush and Whitlatch 2001). Assemblages typified by r-strategists that are typically characterized by short life cycles and high fecundity have been shown to recover faster following fishing than assemblages characterized by k-strategists (Hixon and Tissot 2007; McConnaughey et al. 2000). Body size and feeding mode may also influence vulnerability to trawling. Numerous studies have detected significant increases of motile scavengers following trawling (Kaiser and Spencer 1994, Collie et al. 1997, Ramsay et al. 1998, Demestre et al. 2000, Rumohr and Kujawski 2000). Deposit feeders can also be favoured as trawling increases the availability of organic matter on the sediments (Frid et al. 2000), whereas filter feeders are generally negatively affected by the increase of suspended sediment following trawling (Hermsen et al. 2003; Carbines and Cole 2009; Strain et al. 2012). Large organisms are generally more strongly impacted than small organisms as these are more likely to come in direct contact with the fishing gear (Kaiser et al. 2000). Body size and feeding mode may also influence ecosystem functioning; large deposit feeders have been shown to play an important role in oxygen and nutrient distribution across the sediment-water interface (Norkko et al. 2013). It is well documented that infaunal invertebrates exhibit significant influence over benthic sedimentary geochemical environments in soft sediments through bioturbation (Rhoads 1974; Volkenborn et al 2010), which has been shown to influence oxygen, pH and redox gradients (Pischedda et al. 2008), sediment granulometry (Montserrat et al. 2009), pollutant release (Gilbert et al. 1994), macrofauna diversity (Volkenborn et al. 2007), bacterial activity and composition (Mermillod-Blondin and Rosenberg 2006; Gilbertson et al., 2012) and metal (Teal et al. 2008; 2009), carbon (Kristensen 2001), nutrient and nitrogen cycling (Bertics et al. 2010; Queirós et al. 2011).

In a previous synthesis of the global trends in the response of benthic biota and habitats to fishing disturbance, a collection of fishing-impact studies was investigated to ascertain patterns in the responses of biota to fishing disturbance, and how these might vary with habitat, depth, disturbance type and among different taxonomic groups (Collie et al. 2000; Kaiser et al. 2006). In this study, we meta-synthesize studies that have conducted experimental fishing-impact studies to examine how the response to disturbance varies for species groups with different biological traits. This approach will provide useful insights on potential influences of bottom fishing on certain ecosystem functions (e.g. nutrient cycling) through ecosystem processes (e.g. bioturbation) carried out by different functional species groups. Additionally, it will also shed light on the wider environmental global effects on marine ecosystems which is the focus of an Ecosystem Approach to Fisheries (EAF) (Sinclair and Valdimarsson 2003; Hall and Mainprize 2004). This study addresses the following specific questions and objectives:

1) Does the initial effect of bottom fishing on the abundance of benthic invertebrates vary among species with different biological traits? That is to determine whether all species groups are impacted equally by fishing or whether some species groups are more severely impacted by bottom fishing than others immediately following the disturbance.
2) The interactions between fishing gear type and habitat type are most pressing in terms of fisheries policy and management given the need for managers to understand which fishing gear have the most deleterious effects on benthic assemblages. Therefore, this study

determines whether the magnitude of response to fishing varies among different habitat types and fishing gears.

3) Bottom fishing necessarily removes surficial sediments, thus resulting in changes in sediment characteristics and biological communities in these areas. It follows then that the most relevant management-related issue becomes the rate at which fished areas and their associated communities recover. Among different species, the rate of recovery is most certainly influenced by species' life history and ecological traits. Therefore, we also examined whether the temporal trajectory for recovery from bottom fishing activity varies among species with different biological traits.

2 METHODS

We used systematic review methodology (Pullin and Stewart 2006; Higgins and Green 2008) and meta-analysis (Arnqvist and Wooster 1995; Gurevitch and Hedges 1999) to examine the magnitude of the response of benthic invertebrates to bottom fishing gear. A comprehensive search of peer-reviewed scientific literature and grey literature (up until February 2014) was conducted to compile a database of studies that documented and compared the biological effects of experimentally fished areas with bottom mobile fishing gear (the impacted area) to non-fished areas (the control area) (Hughes et al. 2014). Non-fished areas were generally areas of similar environmental characteristics to the fished areas that have not been fished for years, for example because of the presence of marine protected areas or area closures to mobile bottom fishing gear, or areas that were only very lightly fished.

2.1 Data sources and study inclusion criteria

The search was conducted in multiple electronic databases (e.g. Aquatic Sciences and Fisheries Abstracts, ISI Web of Science, Science Direct, Natural Environment Research Council UK, NOAA Library and information network catalog) and the internet (including organizational websites) using a range of Boolean search terms that included the terms 'bottom fishing', 'mobile fishing', 'trawling', 'dredging', 'benthos', 'invertebrate', 'experimental', 'fishing disturbance' and 'protected area' to capture the diverse range of experimental studies on fishing impacts that have been carried out. A full list of the search terms used and databases and websites searched is given in Hughes et al. 2014. The bibliographies of articles included in this review and other relevant review articles were also searched.

Studies were retained if they explicitly compared an area that was experimentally fished to a non-fished area or protected area where no bottom fishing was allowed or an area that was only very lightly fished (established through local knowledge of study authors or estimated using fishing effort from VMS data). This analysis does not include comparative studies that studied areas of the seabed subjected to different levels of fishing activity, as these have an unknown level of fishing frequency and intensity and it was not possible to estimate the time taken for recovery (e.g. Sciberras et al. 2013; Smith et al. 2013; Stokesbury & Harris, 2006; Svane et al. 2009; Tillin et al. 2006). Furthermore, studies would need to have examined and presented biological data (e.g. density, biomass, CPUE, diversity) for benthic marine invertebrates, either reported as univariate summary data, i.e. the total numbers of individuals and species richness or reported data for individual species or genera. As we wanted to carry out a meta-analysis weighted by the inverse of the study variance, studies were included if mean, sample size values (e.g. number of transects or trawl hauls) and an appropriate error measure (standard deviation, standard error, variance, 95% confidence interval) were reported. These values were extracted as presented from tables or within text. When values were presented in figures, these were extracted using the data extraction software TechDig v.2. Whenever means, sample sizes or error measures were not available in the paper, the corresponding authors were contacted to provide the data.

2.2 Dataset and covariates

There were 59 different experimental manipulations or observations of the effects of fishing disturbance on benthic fauna and communities, extracted from 30 separate publications, which were included in the meta-analysis (Table 1). Some articles were subdivided into different studies as they incorporated distinctly different experimental manipulations conducted; (i) under different environmental conditions, for example comparable manipulations of a fishing disturbance but in two distinctly different habitats or in different locations separated by tens or hundreds of kilometres, (ii) using different fishing gear to create the disturbance, (iii) employing different fishing intensity during the experiment (e.g. fished 4 times vs. fished 20 times). A further nine publications were identified as relevant but could not be included in the analysis because the data (e.g. mean, standard deviation) required for meta-analysis could not be extracted from the paper, for example when data was presented in multidimensional scaling plots or not all the data was available in the article, for example tables with mean data but no standard deviation (Table 1). Authors were contacted but did not send us the missing data.

Experimental studies were classified with respect to a range of variables that might affect the degree of trawling impact, including fishing gear type, intensity of disturbance regime, water depth (m), the minimum dimension of the reported scale of disturbance (e.g. the width of a trawl), the season when the experiment was conducted, habitat type (mud, muddy sand, sand, gravel), the background disturbance level of the experimental areas and biological trait grouping (e.g. feeding mode, degree of mobility). The definition of the habitat types is not precise, as many authors did not give particle-size ranges but provided only qualitative description regarding sediment; however, we take mud, muddy sand and sand to fall within those definitions used by the Folk classification, while gravel is defined as coarse sediments that include a high proportion of gravel and/or broken shell debris (Holme and MacIntyre 1984). For the sake of consistency with other BENTHIS work packages, habitats were grouped into different EUNIS level 3 habitats (EEA, 2007) and fishing gear were classified into different categories using the fishing metiers defined in Eigaard et al. (in prep).

Habitats described as sand & gravel and pebbles & cobbles were classified as 'Sublittoral coarse / mixed sediment (A5.1 / A5.4)'; sand, fine sand with shell debris and muddy sand were classified as 'Sublittoral sand' (A5.2), fine silt, clay, silt & shell and sand & silt were classified as 'Sublittoral mud' (A5.3) and *Modiolus* beds, mussel beds, mearl beds and seagrass beds were classified as 'Sublittoral biogenic reef' (A5.6). According to the description of fishing gear and targeted species provided in the articles the following BENTHIS fishing metiers were included in the analysis, for beam trawls – TBB_DMF and TBB_MOL, for dredges – DRB_MOL, and for otter trawls – OT_CRU, OT_MIX_DMF_PEL, OT_MIX_ARA, OT_MIX (see Table 1 for definitions). A further otter trawl category was added to the list provided by WP2; OT_MOL to describe otter trawls used to collect bivalves such as *Aequipecten opercularis* (e.g. Hinz et al. 2011).

Table 1. Studies identified by the literature search as relevant to the review questions; (I) studies included in the meta-analysis (n = 59), (II) studies not included in the meta-analysis (n = 9). Given in table information are the study area name (Site) and geographical location, the type of EUNIS level 3 habitat in which the study was carried out (EUNIS code: A5.1 / A5.4 – Sublittoral coarse sediment / Sublittoral mixed sediment, A5.2 – Sublittoral sand, A5.3 – Sublittoral mud, A5.6 – Sublittoral biogenic reef), the type of fishing gear used to create the disturbance (Fishing gear: TBB – Beam trawl, DRB – Dredge, OT – Otter trawl) and the equivalent WP2 fishing metier category, the number of times the area was swept by the fishing gear during the experimental fishing (Idis), depth in metres and the response variables for which data was extracted from the articles. *WP2 fishing metiers given in Eigaard et al. (in prep): TBB_MOL – beam trawling for molluscs; TBB_DMF – beam trawling for demersal fish; DRB_MOL – dredging for molluscs; OT_CRU – otter trawling for crustaceans; OT_MIX_DMF_PEL – otter trawling for bentho-pelagic fish; OT_MIX_ARA – otter trawling for shrimps; OT_MIX – otter trawling (no information as to which species are targeted by the fishery is given). †OT_MOL – otter trawling for molluscs such as *Aequipecten opercularis* – was added as it did not fit any of the categories defined by Eigaard et al. (in prep).

I. Studies identified as relevant to review question and included in meta-analysis

Study ID	Study reference	Site	Geographical location	EUNIS code	Fishing gear	*WP2 fishing metier	Idis	Depth (m)	Response variable
1	Bergman, M.J.N & Hup, M. 1992. ICES J Mar Sci, 49: 5-11	ICES quadrant 36F5	Northern Europe	A5.2	TBB	TBB_DMF	2	30	Individual species abundances
2	Bishop et al. 2005. fishery Bulletin, 103(4): 712-719	North Carolina	East North America	A5.6	DRB	DRB_MOL	1	1.5	Individual species abundances
3	Constantino, R., Gaspar, M.B., Tata-Regala, J. et al. 2009. Mar Env Res, 67: 89-99	Vale do Lobo, Algarve, Portugal	Southern Europe	A5.2	DRB	DRB_MOL	1	6	Total abundance, Diversity
4	Constantino, R., Gaspar, M.B., Tata-Regala, J. et al. 2009. Mar Env Res, 67: 89-99	Vale do Lobo, Algarve, Portugal	Southern Europe	A5.1 / A5.4	DRB	DRB_MOL	1	18	Total abundance, Diversity

5	Cook et al. 2013. PLOS One, 8(8)	Point of Ayre, Isle of Man	Northern Europe	A5.6	OT	OT_MIX	1	33	Individual species abundances, Total abundance, Diversity
6	Cook et al. 2013. PLOS One, 8(8)	North of the Lleyn Peninsula, Caernarfon Bay, Wales	Northern Europe	A5.6	DRB	DRB_MOL	1	30	Individual species abundances, Total abundance, Diversity
7	Currie & Parry 1999. Can J Fish Aquat Sci, 56: 539-550	St. Leonards - Port Philip Bay	Australia / New Zealand	A5.2	DRB	DRB_MOL	2	13	Individual species abundances
8	Currie, D.R. & Parry, G.D. 1996. Mar Ecol Prog Ser, 134: 131-150	St. Leonards, Sector 43	Australia / New Zealand	A5.2	DRB	DRB_MOL	2	NA	Individual species abundances
9	Currie, D.R. & Parry, G.D. 1999. Can J Fish Aquat Sci, 56: 539-550	Dromana, Port Philip Bay	Australia / New Zealand	A5.2	DRB	DRB_MOL	2	15	Individual species abundances
10	Currie, D.R. & Parry, G.D. 1999. Can J Fish Aquat Sci, 56: 539-550	Portarlington, Port Philip Bay	Australia / New Zealand	A5.3	DRB	DRB_MOL	4	14	Individual species abundances
11	DeBiasi, A.M. 2004. ICES J Mar Sci, 61: 1260-1266	Tyrrhenian Sea	Southern Europe	A5.3	OT	OT_MIX	14	33	Individual species abundances
12	Dolmer, P., Kristensen, T., Christiansen, M.L., et al 2001. Hydrobiologia 465: 115–127	Limfjorden	Northern Europe	A5.6	DRB	DRB_MOL	12	7.4	Diversity
13	Dolmer, P., Kristensen, T., Christiansen, M.L., et al 2001. Hydrobiologia 465: 115–127	Limfjorden	Northern Europe	A5.6	DRB	DRB_MOL	12	7.4	Diversity
14	Drabsch et al. 2001. ICES J Mar Sci: 58(6), 1261-1271.	Gulf St. Vincent, location1	Australia / New Zealand	A5.2	OT	OT_CRU	2	20	Individual species abundances, Total abundance, Diversity

15	Drabsch, S.L., Tanner, J.E., Connell, S.D. 2001. ICES J Mar Sci: 58(6), 1261-1271.	Gulf St. Vincent	Australia / New Zealand	A5.3	OT	OT_CRU	2	20	Individual species abundances, Total abundance, Diversity
16	Drabsch, S.L., Tanner, J.E., Connell, S.D. 2001. ICES J Mar Sci: 58(6), 1261-1271.	Gulf St. Vincent	Australia / New Zealand	A5.2	OT	OT_CRU	2	20	Individual species abundances, Total abundance, Diversity
17	Gilkinson, K.D., Gordon, D.C., MacIsaac, K.G. et al. 2005. ICES J Mar Sci, 62:925-947	Banquereau, Scotian Shelf	East North America	A5.2	DRB	DRB_MOL	1	NA	Total abundance, Diversity
18	Hall, S.J., Basford, D.J., Robertson, M.R. 1990. Neth J Sea Res, 27: 119-125	Loch Gairloch	Northern Europe	A5.2	DRB	DRB_MOL	1	7	Individual species abundances, Total abundance, Diversity
19	Haywood, M., Hill, B., Donovan, A. et al. 2005.Quantifying the effects of trawling on seabed fauna in the Northern Prawn Fishery. Final Report on FRDC Project 2002/102. CSIRO, Cleveland. 488 pp.	East Mornington	Australia / New Zealand	A5.2	OT	OT_CRU	4	NA	Individual species abundances
20	Haywood, M., Hill, B., Donovan, A. et al. 2005.Quantifying the effects of trawling on seabed fauna in the Northern Prawn Fishery. Final Report on FRDC Project 2002/102. CSIRO, Cleveland. 488 pp.	East Mornington	Australia / New Zealand	A5.2	OT	OT_CRU	20	NA	Individual species abundances

21	Haywood, M., Hill, B., Donovan, A. et al. 2005.Quantifying the effects of trawling on seabed fauna in the Northern Prawn Fishery. Final Report on FRDC Project 2002/102. CSIRO, Cleveland. 488 pp.	West Mornington	Australia / New Zealand	A5.1 / A5.4	OT	OT_CRU	4	NA	Individual species abundances
22	Haywood, M., Hill, B., Donovan, A. et al. 2005.Quantifying the effects of trawling on seabed fauna in the Northern Prawn Fishery. Final Report on FRDC Project 2002/102. CSIRO, Cleveland. 488 pp.	West Mornington	Australia / New Zealand	A5.1 / A5.4	OT	OT_CRU	20	NA	Individual species abundances
23	Henry, L.A., Kenchington, E.L.R., Kenchington, T.J. et al. 2006, Mar Ecol Prog Ser, 306: 63-78	Western Bank, Scotian Shelf	East North America	A5.1 / A5.4	OT	OT_MIX_DMF_PEL	12	70	Total abundance, Diversity
24	Henry, L.A., Kenchington, E.L.R., Kenchington, T.J. et al. 2006, Mar Ecol Prog Ser, 306: 63-78	Western Bank, Scotian Shelf	East North America	A5.1 / A5.4	OT	OT_MIX_DMF_PEL	12	70	Total abundance, Diversity
25	Henry, L.A., Kenchington, E.L.R., Kenchington, T.J. et al. 2006, Mar Ecol Prog Ser, 306: 63-78	Western Bank, Scotian Shelf	East North America	A5.1 / A5.4	OT	OT_MIX_DMF_PEL	12	70	Total abundance, Diversity
26	Hinz, H., Murray, L.G., Malcolm, F.R. et al. 2012. Mar Env Res, 73: 85-95	NE Isle of Man	Northern Europe	A5.2	DRB	DRB_MOL	1	21.5	Individual species abundances

27	Hinz, H., Murray, L.G., Malcolm, F.R. et al. 2012. Mar Env Res, 73: 85-95	NE Isle of Man	Northern Europe	A5.2	OT	†OT_MOL	1	21.5	Individual species abundances, Total abundance
28	Hinz, H., Murray, L.G., Malcolm, F.R. et al. 2012. Mar Env Res, 73: 85-95	NE Isle of Man	Northern Europe	A5.2	DRB	DRB_MOL	1	21.5	Individual species abundances, Total abundance
29	Kaiser, M.J., Edwards, D.B., Armstrong, D.B. et al. 1998 ICES J Mar Sci, 55:353-361	Liverpool Bay, UK	Northern Europe	A5.2	TBB	TBB_DMF	15	30	Individual species abundances, Total abundance, Diversity
30	Kaiser, M.J., Edwards, D.B., Armstrong, D.B. et al. 1998 ICES J Mar Sci, 55:353-361	Liverpool Bay, UK	Northern Europe	A5.2	TBB	TBB_DMF	15	30	Individual species abundances, Total abundance, Diversity
31	Kaiser, M.J., Hill, A.S., Ramsay, K. et al. 1996. Aquat. Conserv: Mar Freshw Ecocsyst, 6: 269-285	SW Isle of Man	Northern Europe	A5.1 / A5.4	TBB	TBB_MOL	10	NA	Individual species abundances
32	Kaiser, M.J., Hill, A.S., Ramsay, K. et al. 1996. Aquat. Conserv: Mar Freshw Ecocsyst, 6: 269-285	SW Isle of Man	Northern Europe	A5.1 / A5.4	DRB	DRB_MOL	10	NA	Individual species abundances
33	Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G. et al. 2006. J Sea Res, 56: 249-270	Western Bank, Scotian Shelf	East North America	A5.1 / A5.4	OT	OT_MIX_DMF_PEL	13	70	Individual species abundances
34	Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G. et al. 2006. J Sea Res, 56: 249-270	Western Bank, Scotian Shelf	East North America	A5.1 / A5.4	OT	OT_MIX_DMF_PEL	13	70	Individual species abundances
35	Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G. et al. 2006. J Sea Res, 56: 249-270	Western Bank, Scotian Shelf	East North America	A5.1 / A5.4	OT	OT_MIX_DMF_PEL	13	70	Total abundance, Diversity

36	Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G. et al. 2006. J Sea Res, 56: 249-270	Venice Lagoon, Italy	Southern Europe	A5.3	DRB	DRB_MOL	0.5	1.75	Individual species abundances, Diversity
37	Kenchington, E.L.R., Gilkinson, K.D., MacIsaac, K.G. et al. 2006. J Sea Res, 56: 249-270	Western Bank, Scotian Shelf	East North America	A5.1 / A5.4	OT	OT_MIX_DMF_PEL	13	70	Individual species abundances
38	Kenchington, E.L.R., Prena, J., Gilkinson, K.D. et al 2001. Can J Fish Aquat Sci, 58: 1043-1057	Grand Banks, Newfoundland	East North America	A5.2	OT	OT_MIX_DMF_PEL	12	133	Individual species abundances, Total abundance, Diversity
39	Kenchington, E.L.R., Prena, J., Gilkinson, K.D. et al 2001. Can J Fish Aquat Sci, 58: 1043-1057	Grand Banks, Newfoundland	East North America	A5.2	OT	OT_MIX_DMF_PEL	12	133	Individual species abundances, Total abundance, Diversity
40	Kenchington, E.L.R., Prena, J., Gilkinson, K.D. et al 2001. Can J Fish Aquat Sci, 58: 1043-1057	Grand Banks, Newfoundland	East North America	A5.2	OT	OT_MIX_DMF_PEL	12	133	Individual species abundances, Total abundance, Diversity
41	Pitcher et al. 2009. Fisheries Research, 99: 168-183	northern Great Barrier Reef, Australia	Australia / New Zealand	A5.1 / A5.4	OT	OT_CRU	1	32.5	Individual species abundances
42	Pranovi, F. & Giovanardi, O. 1994. Sci Mar, 58(4): 345-353	Venice Lagoon, Italy	Southern Europe	A5.3	DRB	DRB_MOL	0.5	1.75	Individual species abundances, Diversity
43	Pranovi, F., Raicevich, S., Franceschini, G. et al. 2000. ICES J Mar Sci, 57: 517-524	Adriatic Sea	Southern Europe	A5.2	DRB	DRB_MOL	0.5	24	Individual species abundances, Total abundance, Diversity
44	Prantoni, A.L., Da Cunha Lana, P., Sandrini-Neto, L., et al. 2013. J Mar Biol Ass UK, 93: 495-502	Brazillian coast	East South America	A5.2	OT	OT_MIX_ARA	2	10	Individual species abundances, Total abundance, Diversity

45	Ramsay, K., Kaiser, M.j., Hughes, R.N. 1998. JEMBE, 224: 73-89	Anglesey, UK	Northern Europe	A5.1 / A5.4	TBB	TBB_DMF	10	40	Individual species abundances
46	Ramsay, K., Kaiser, M.j., Hughes, R.N. 1998. JEMBE, 224: 73-89	Red Wharf Bay, UK	Northern Europe	A5.2	TBB	TBB_DMF	10	12	Individual species abundances
47	Ramsay, K., Kaiser, M.j., Hughes, R.N. 1998. JEMBE, 224: 73-89	Red Wharf Bay, UK	Northern Europe	A5.2	DRB	DRB_MOL	4	12	Individual species abundances
48	Ramsay, K., Kaiser, M.j., Hughes, R.N. 1998. JEMBE, 224: 73-89	Red Wharf Bay, UK	Northern Europe	A5.2	TBB	TBB_DMF	4	12	Individual species abundances
49	Ramsay, K., Kaiser, M.j., Hughes, R.N. 1998. JEMBE, 224: 73-89	Walney Island, UK	Northern Europe	A5.3	TBB	TBB_DMF	10	36	Individual species abundances
50	Robinson, S.M.C., Bernier, S., MacIntyre, A. 2001. Hydrobiologia, 465: 103-114	Ministers Island, Bay of Fundy	East North America	A5.1 / A5.4	DRB	DRB_MOL	2	8	Individual species abundances
51	Robinson, S.M.C., Bernier, S., MacIntyre, A. 2001. Hydrobiologia, 465: 103-114	Grand Manan Island, Bay of Fundy	East North America	A5.1 / A5.4	DRB	DRB_MOL	2	8	Individual species abundances
52	Sanchez, P., Demestre, M., Ramon, M. et al 2000. ICES J Mar Sci, 57: 1352-1358	NW Mediteranean	Southern Europe	A5.3	OT	OT_MIX	1	30	Individual species abundances, Total abundance, Diversity
53	Sanchez, P., Demestre, M., Ramon, M. et al 2000. ICES J Mar Sci, 57: 1352-1358	NW Mediteranean	Southern Europe	A5.3	OT	OT_MIX	2	40	Individual species abundances, Total abundance, Diversity
54	Sparks-McConkey, P.J. & Watling, L. 2001. Hydrobiologia, 456: 73-85	Penobscot Bay, Maine	East North America	A5.3	OT	OT_MIX_ARA	4	60	Individual species abundances, Total abundance, Diversity

55	Tanner, J.E. 2003. Can J Fish Aquat Sci, 60: 517-526	Gulf St. Vincent	Australia / New Zealand	A5.6	OT	OT_MIX_ARA	2	20	Individual species abundances
56	Thrush, S.F., Hewitt, J.E., Cummings, V.J. et al. 1995. Mar Ecol Prog Ser, 129: 141-150	Hahei, Mercury Bay, New Zealand	Australia / New Zealand	A5.2	DRB	DRB_MOL	1	24	Individual species abundances, Total abundance, Diversity
57	Thrush, S.F., Hewitt, J.E., Cummings, V.J. et al. 1995. Mar Ecol Prog Ser, 129: 141-150	Opito Bay, Mercury Bay, New Zealand	Australia / New Zealand	A5.1 / A5.4	DRB	DRB_MOL	1	24	Individual species abundances, Total abundance, Diversity
58	Tuck, I.D., Hall, S.J., Robertson, M.R., et al. 1998. Mar Ecol Prog Ser, 162: 227-242	Loch Gareloch, Scotland	Northern Europe	A5.3	OT	OT_MIX	5	32	Individual species abundances, Total abundance, Diversity
59	vanDolah, R.F., Wendt, P.H., Nicholson, N. 1987. Fish Res, 5: 39-54	St. Catherines Island, Georgia	East North America	A5.1 / A5.4	OT	OT_MIX	1	20	Individual species abundances

II. Studies identified as relevant to review questions but could not be included in meta-analysis

Study ID	Site name	Geographical location	Study reference
#60	SW Isle of Man, UK	Northern Europe	Bradshaw et al. 2001. Hydrobiologia, 465: 129 - 138
#61	Gulf of Alaska	East North America	Freese, L. 2001. Mar Fish Rev, 63(3): 7 - 13
#62	Gulf of Alaska	East North America	Freese, L., Auster. P.J., Heifetz, J. et al. 1999. Mar Ecol Prog Ser, 182: 119 - 126
#63	Gullmarsfjorden, Sweden	Northern Europe	Hansson, M., Lindegarth, M., Valentinsson, D. et al. 2000. Mar Ecol Prog Ser, 198: 191-201

#64	North of Monte Bello Islands, NW Australia	Australia / New Zealand	Moran, M.J. & Stephenson, P.C. 2000. ICES J. Mar. Sci. 57: 510-516
#65	Ancona Maritime District, Adriatic Sea	Northern Europe	Morello, E.B., Froglia, C., Atkinson, R.J.A. et al. 2005. Can. J. Fish. Aquat. Sci. 62: 2076-2087
#66	Parangipettai, India	Asia	Muthuvelu, S., Murugesan, P., Muniasamy, M. et al. 2013. Ocean Science Journal, 48: 183-195
#67	Cuddalore, India	Asia	Muthuvelu, S., Murugesan, P., Muniasamy, M. et al. 2013. Ocean Science Journal, 48: 183-195
#68	Cochin-Munambam area, Kerala	Asia	Thomas, J.V., Sreedevi, C. Kurup, B.M. 2006. Indian J Mar Sci, 35: 249-256

2.3 Biological traits

Some studies included the effects of fishing disturbance on univariate summary data, i.e. the total numbers of individuals and species richness, whereas others reported the effects at different phylogenetic levels. Given that the main objective of this work is to quantify the magnitude of effect of trawling based on biological traits of benthic invertebrates, studies that reported data for organisms at the species, genus or family level were retained in the analysis. Biological traits were then assigned to each individual taxon retained in the database. Whenever data was reported for taxonomic levels higher than family (i.e. order, class, phylum) the data was not included as it is not possible to assign biological traits accurately at these taxonomic levels. Furthermore, pelagic species, mainly fish species, and meiofauna species, mainly nematodes, were not included in the analysis.

A suite of eleven traits that have been defined by WP3 were selected to describe the life history and morphological and behavioural characteristics of the species that may determine the potential sensitivity of benthic taxa to trawling and their contribution to ecosystem functioning (Table 2). Each of these traits was subdivided into multiple ‘modalities’ chosen to encompass the range of possible attributes of all the taxa; for example, modalities for mobility were ‘swimming’, ‘burrowing’, ‘crawling’ and ‘sessile’. A total of 53 modalities among the eleven selected traits were selected (Table 2).

Information regarding the 11 biological traits was needed for 408 taxa (family, genus or species) for which data was presented in the studies. Traits information was collected from a variety of sources; biological traits database generated for BENTHIS WP3 (data for 176 taxa), published journal papers, books and websites of various scientific institutions (see Appendix I). While it was possible to access reliable information for many taxa regarding certain traits (e.g. larval development and morphology), published information describing other traits (e.g. longevity) was not available for large proportions of the taxa. In such cases, we adopted the category entries for congeneric species or the most closely-related taxa, i.e., within family but whenever this was not possible a score of zero was assigned to all categories for that particular trait. It was not possible to obtain biological traits data for 46 taxa, the majority of which were from Australian waters. Each taxon was coded using a “fuzzy coding” approach (Chevenet et al. 1994) on the basis of the extent to which it displayed the modalities of each trait. Traits were coded for a scoring range of 0–3, where 0 conveys no affinity, 1 or 2 express partial affinity and 3 indicates total and exclusive affinity (Bolam et al. 2014b).

When all taxa had been coded for the ‘taxon × trait’ matrix, the codes were converted to proportions for each taxon and trait category, so that the total added up to 1 within each trait. The ‘taxon × trait’ matrix was then used to derive a ‘study × trait’ matrix using the faunal data extracted from the articles in two ways. Firstly, the 'taxon × trait' matrix was combined with taxon abundance data (numbers per unit area) to produce an 'abundance × trait' matrix. To generate this, the abundance of each taxon was multiplied by its fuzzy-coded trait proportion. These values were then summed across all taxa for each study and each trait modality to generate a 'study × trait' matrix for each of the eleven traits.

Table 2. Description of traits and modalities used in the biological trait meta-analysis (adapted from Bolam et al. 2014b, c).

Trait	Modality	Trait Definition	Functional significance and/or vulnerability to fishing
Body size (mm)	<10 11 – 20 21 – 100 101 – 200 201 – 500 > 500	Maximum recorded size of adult (as individuals or colonies)	Indicates potential for the adult stage to be exposed to physical disturbance (larger individuals stand a higher chance of by-catch or damage from gear). Implications for the movement of organic matter within the benthic system as large organisms hold organic matter (low turnover) within the system relative to small-bodied species (high turnover) (Pearson and Rosenberg, 1978).
Morphology	Soft	External tissue is soft and not covered by any form of protective casing	External characteristics of the taxon. Indicates potential for the adult stage to be exposed to physical disturbance. Stalked, erect individuals and individuals not covered by a think shell (e.g. soft and cushion forms) stand a higher chance of damage from gear.
	Tunic	Body is covered by a protective outer tissue made up of, for example, cellulose (e.g. tunicates)	
	Exoskeleton	Body is covered or encased in either a thin chitinous layer or calcium carbonate shell	
	Cushion	Body is soft and forms a cushion-like layer over the substratum and/or flora/fauna	
	Stalked	Typically attached and erect	
	Erect	Typically attached, erect, bushy and branching	
	Encrusting	Grows over the substratum	

Trait	Modality	Trait Definition	Functional significance and/or vulnerability to fishing
Longevity (yrs)	<1 1 – < 3 3 - 10 > 10	Maximum reported life span of the adult stage	Indicates the relative investment of energy in somatic rather than reproductive growth and the relative age of sexual maturity, i.e. a proxy for relative r- and k- strategy (Pearson and Rosenberg, 1978).
Larval development location	Pelagic planktotrophic	Larvae feed and grow in the water column, generally pelagic for several weeks	Indicates the potential for dispersal of the larval stage prior to settlement. Affects ability to recover from disturbance with planktonic recruitment affording potentially faster recolonization than lecithotrophic and direct development (Thrush and Whitlatch 2001).
	Pelagic lecitotrophic	Larvae feed on yolk reserves, pelagic for short periods	
	Benthic direct	Larval stage missing (eggs develop into juvenile forms) or larvae are limited to the bed	
Egg development location	Asexual / budding	Species can reproduce asexually, either by fragmentation, budding, epitoky, etc.	Indicates dispersal via the egg stage and the potential susceptibility of eggs to damage from fishing. Benthic eggs are generally more concentrated over smaller areas. Asexual reproduction allows the potential to increase numbers rapidly, particularly following disturbance.
	Sexual - Pelagic eggs	Eggs are released into the water column	
	Sexual - Benthic eggs	Eggs are released onto/into the bed, either free or maintained on bed by mucous or other means	
	Sexual - brood eggs	Eggs are maintained by adult for protection, either within parental tube or within body cavity	

Trait	Modality	Trait Definition	Functional significance and/or vulnerability to fishing
Living habit	Tube-dwelling	Tube may be lined with sand, mucus or calcium carbonate	Indicates potential for the adult stage to evade, or to be exposed to physical disturbance.
	Burrow-dwelling	Lives within a permanent or temporary burrow	
	Free-living	Not limited to any restrictive structure at any time. Able to move freely within and/or on the sediments	
	Crevice-dwelling / under stones	Adults are typically cryptic, predominantly found inhabiting spaces made available by coarse/rock substrate and/or tubes made by biogenic species or algal holdfasts	
	Epi/endo zoic/phytic	Live on or in other organisms	
	Attached	Attached to larger substrata or rock	
Sediment position	Surface	Found on or just above the seabed	Typical living position in sediment profile. Organisms occupying shallower positions in the sediment are more likely to contact bottom gear than those living deeper. Sediment position also has implications for the effect of the organism to affect sediment-water nutrient and/or oxygen exchange.
	Infauna (0 – 5 cm)	Species whose bodies are found almost exclusively below sediment surface between 0 and 5 cm sediment depth	
	Infauna (6 – 10 cm)	Species whose bodies are partly or exclusively found below sediment surface at a depth generally between 5 and 10 cm	
	Infauna (>10 cm)	Species whose bodies are partly or exclusively found below sediment surface at a depth greater than 10 cm	

Trait	Modality	Trait Definition	Functional significance and/or vulnerability to fishing
Feeding mode	Suspension	The removal of particulate food taken from the water column, generally via filter-feeding	Feeding mode has important implications for the potential for transfer of carbon between the sediment and water and within the sediment matrix. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg, 1995). Furthermore, whilst scavengers may benefit from higher food availability as a result of carrion, suspension feeders may suffer damage to their filtering devices due to high concentration of suspended sediment following the fishing disturbance event.
	Surface deposit	Active removal of detrital material from the sediment surface. This class includes species which scrape and/or graze algal matter from surfaces	
	Subsurface deposit	Removal of detrital material from within the sediment matrix	
	Scavenger / opportunist	Species which feed upon dead animals	
	Predator	Species which actively predate upon animals (including the predation on smaller zooplankton)	
	Parasite	Species which have a parasitic mode of life on other invertebrate species	
Mobility	Sessile	Species in which the adults have no, or very limited, mobility either because they are attached or are limited to a (semi-) permanent tube or burrow	Adults of faster moving species are more likely to evade capture by trawl gear than slow-moving or sessile individuals. Mobility also affects the ability for adult recolonization of disturbed areas.
	Burrower	Infaunal species in which adults are capable of active movement within the sediment	
	Crawl/creep/climb	Capable of some, generally limited, movement along the sediment surface or rocky substrata	
	Swim	Species in which the adults actively swim in the water column (many usually return to the bed when not feeding)	

Trait	Modality	Trait Definition	Functional significance and/or vulnerability to fishing
Bioturbation	Diffusive mixing	Vertical and/or horizontal movement of sediment and/or particulates	Describes the ability of the organism to rework the sediments. Can either be upward, downward, onto the sediment or mixing of the sedimentary matrix. Bioturbation mode has important implications for sediment-water exchange and sediment biogeochemical properties.
	Surface deposition	Deposition of particles at the sediment surface resulting from e.g. defecation or egestion (pseudofaeces) by, for example, filter and surface deposit feeding organisms	
	Upward conveyor	Translocation of sediment and/or particulates from depth within the sediment to the surface during subsurface deposit feeding or burrow excavation	
	Downward conveyor	The subduction of particles from the surface to some depth by feeding or defecation	
	None	Do not perform any of the above and/or not considered as contributing to any bioturbatory capacity	
Protection	No protection	Body is not covered by a thick skin, exoskeleton or shell and organism does not have the ability to regenerate	Describes the capacity to withstand physical disturbance and thus the potential for the adult population to remain viable following acute fishing.
	Fragile	Body is covered by a fragile shell	
	Tough skin or exoskeleton	Body is covered by a thick skin or by exoskeleton	
	Robust	Body is covered by a hard shell or organism has ability to regenerate	

2.4 Meta-analysis

Meta-analysis is defined as the quantitative summary of data from multiple studies (Arnqvist and Wooster 1995; Gurevitch and Hedges 1999). The result of each independent study is expressed as an index of effect; these effect estimates are then combined across studies to produce a summary of the findings. For the meta-analysis of trawling/dredging impacts on fished areas, a “study” was defined as being composed of (i) an experimentally fished area (Impt) and a non-fished area (Ctrl) or, (ii) an area that was sampled before (Ctrl) and after (Impt) experimental fishing, or (iii) a fished and non-fished area that were sampled before and after experimental fishing (BACI, refer to schematic in Figure 1). Within each control and impacted area, one or more “stations” were studied at which one or more individual “samples” (cores, sediment grabs, trawl, etc.) were collected (Figure 1). In the majority of studies, replicate “stations” (or replicate “samples” when only one station was sampled) were used to calculate the mean, standard deviation and sample size for the impact or control areas used in the meta-analysis.

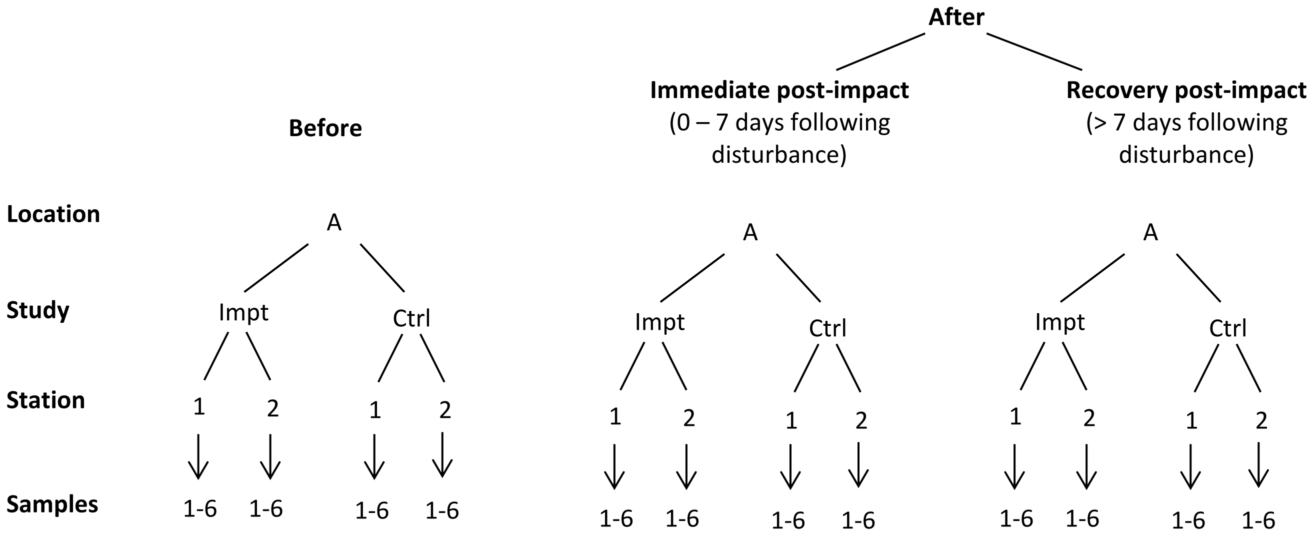


Figure 1. Schematic representation of the experimental study designs for studies included in the meta-analysis. Impt - Impacted area, Ctrl – Control area.

52% of the experimental fishing studies involved sampling the impact and control areas at multiple time periods following the experimental fishing event, whereas 48% of the studies sampled only once following the impact. Data extracted from studies was treated as “immediate post-impact”, if the data was collected within 7 days of the fishing disturbance event and “recovery post-impact”, if the data was collected more than 7 days following the impact (range = 13 – 730 days) (Figure 1). With no exception, sampling occurred only once prior to the impact.

Two meta-analyses were therefore carried out, one using the "immediate post-impact" data and another using "immediate" and "recovery post-impact" data. Using these two datasets, the following questions were addressed in the analyses:

1) How large is the reduction in abundance of benthic invertebrates within the first 7 days following a fishing event for (a) the benthic community and (b) benthos with different biological traits? For the latter (b), categorical meta-analysis was used to assess whether benthos with different modalities (e.g. swimmer vs. crawler vs. burrower vs. sessile) responded differently to bottom fishing. The effect on benthic community was assessed using total abundance values as reported in papers for the impact and control areas.

2) Fishing gear type, habitat type (which is strongly correlated with depth) and the intensity of the fishing disturbance regime were considered the most important predictors of the magnitude of fishing impact on benthic communities. Therefore, we asked:
    a. Does the magnitude of response to fishing vary among different habitat types and fishing gears?
    b. What is the relationship between the intensity of fishing and the response of the biological community? The intensity of fishing is hereby defined as the number of times or the number of fishing gear passes over the entire experimental box.

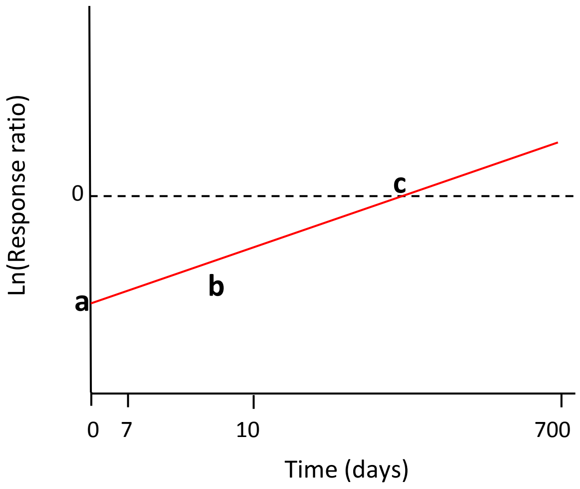
   A categorical meta-analysis and meta-regression were used to explicitly examine whether the effect of bottom fishing on biological traits, expressed as the effect size (response variable), depends on these explanatory variables. Although it was planned to examine the magnitude of fishing effect among the fishing metiers defined by BENTHIS WP2, this was not possible as the number of studies within each fishing metier was too low to support this analysis (generally in the range of 1 to 4 studies). Therefore, fishing metier categories were combined as beam trawl (TBB), otter trawl (OT) and dredges (DRB). Differences in effect sizes among categories were tested using Q_M statistic, which partitions the total variance (of all categories about the grand mean effect size) into variance within categories and variance between categories (of category means about the grand mean).

3) What is the temporal trajectory for recovery of the biological community from bottom fishing activity and does the rate of recovery vary among biological traits?

   A meta-regression model consisting of two main effect terms *Modality* and *Time* and a two-way interaction term between modality and time (*Modality x Time*) was examined to determine whether the time for recovery and the rate of recovery differed among modalities of a biological trait. Time was $\log_{10}$-transformed to make the distribution of values on the time-axis more symmetric (i.e. to reduce positive skewness in the data that results from a few very large values along the time-axis). Selection of the final (most parsimonious) model was undertaken using the Akaike's Information Criterion (AIC) estimated with a maximum likelihood (ML) fit to compare a sequence of models in which non-significant interaction and main effects were incrementally removed (Zuur et al. 2009).

The model with the lowest value of AIC was identified as the most parsimonious model. After completing model selection, the final model was refitted with the restricted maximum-likelihood (REML) method for reporting significant relationships. All statistical tests were performed at $\alpha = 0.05$ level. Whenever the interaction term (*Modality x Time*) or the factor *Modality* was significant, pairwise tests were carried out to determine those modalities for which the rates of recovery or the time for recovery differed significantly.

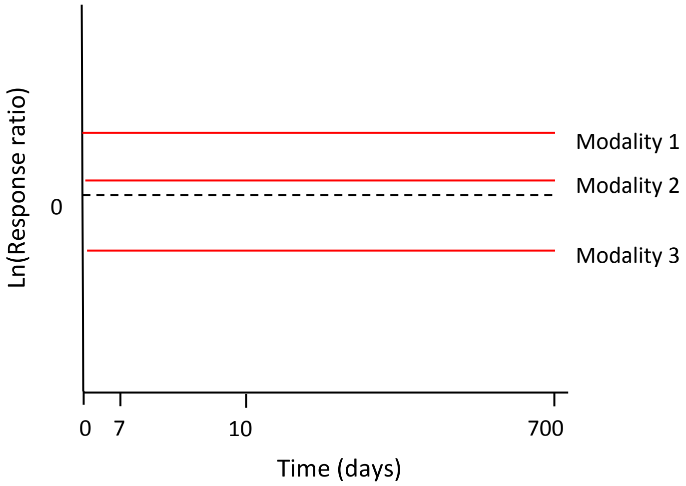
To facilitate interpretation of model outputs later in the results, we present an explanation of a number of possible different scenarios of model outputs. Figure 2 defines a number of terms that will be used throughout the rest of the document; initial effect of fishing, time to recovery, rate of recovery. Figure 3 presents interpretation of the different possible model output scenarios.



a = initial effect of fishing immediately following a fishing disturbance event (intercept)
b = rate of recovery (slope)
c = time to recovery, assuming that recovery occurs when abundance in fished area is the same as that in the control area, Ln(Response ratio) = 0.

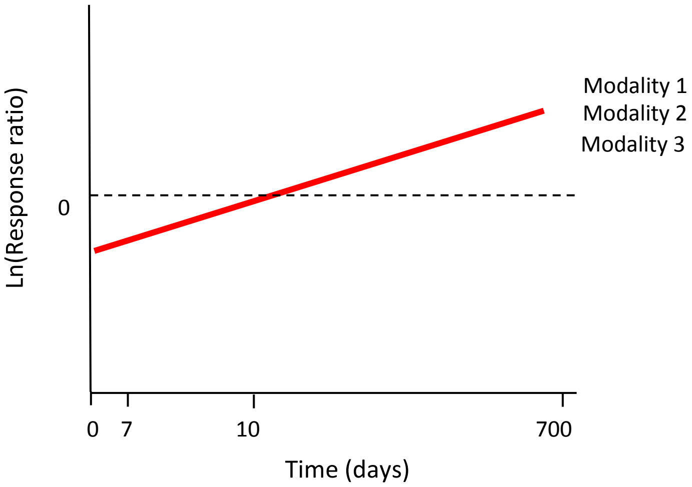
Figure 2. A diagrammatic representation of the response to fishing (ln-transformed response ratio) with time since the last fishing disturbance event (in days).

Scenario 1: Interaction term and the covariate *time* are not significant but factor *modality* is significant. Parsimonious model = intercept + *Modality*



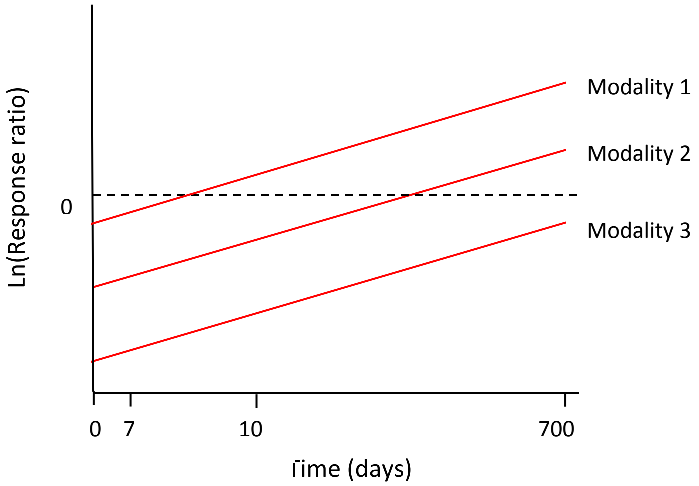
The interaction term *(Modality x Time)* is not significant indicating that the rate of recovery does not differ significantly among modalities. *In this scenario* ***b*** *= 0. Time* is also not significant suggesting that there is no significant recovery in species abundance in the fished area through time (**c** = NA). However, the initial impact of fishing differs significantly among modalities as suggested by a significant *Modality* term in the model and different values for **a** among the modalities.

Scenario 2: Covariate *time* is significant but the interaction term and the factor *modality* are not significant. Parsimonious model = intercept + *Time*



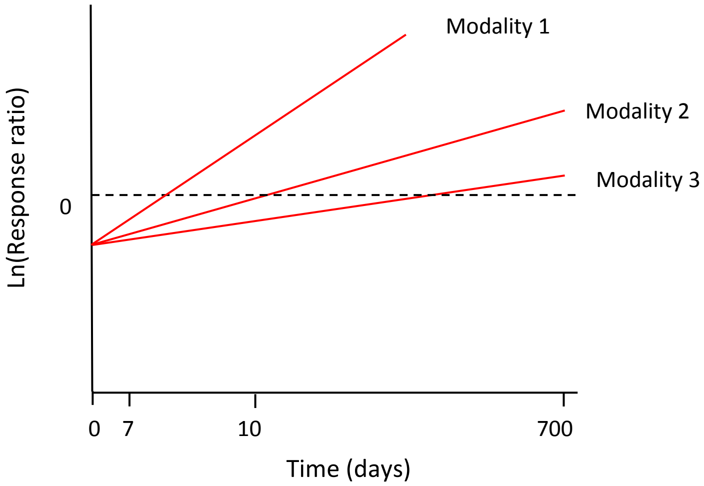
The rate of recovery **(b)**, the initial impact of fishing **(a)** and the time to recovery **(c)** does not differ significantly among the modalities; however there is an overall increase in abundance in fished area following fishing disturbance over time.

Scenario 3: The additive model between the covariate *time* and factor *modality* is significant. Parsimonious model = intercept + *(Time + Modality)*



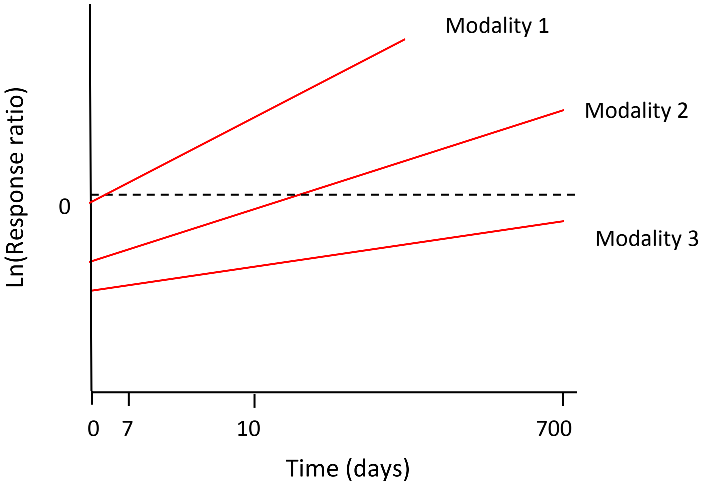
Although the rate of recovery **(b)** does not differ significantly among modalities, the time to recovery **(c)** changes significantly among different modalities. One reason for this is that the initial effect of fishing **(a)** is much larger (or smaller) for some modalities than for others, which in turn may influence the time necessary for a population to recover.

Scenario 4A: The interactive model between the covariate *time* and factor *modality* is significant, but intercept is the same among modalities. Parsimonious model = intercept + *(Time x Modality)*



Fishing results in similar reductions in abundance in the fished area to begin with (i.e. the initial effect of fishing **(a)** is the same among modalities), but the rate of recovery is faster for some modalities than for others **(b)** and consequently the time to recovery **(c)** also differs among modalities.

Scenario 4B: The interactive model between the covariate *time* and factor *modality* is significant, and intercept differs among modalities. Parsimonious model = intercept + *(Time x Modality)*



The initial impact of fishing **(a)** varies significantly among modalities. Furthermore, a significant interaction term suggests that the rate of recovery **(b)** and time to recovery **(c)** differs significantly among modalities, whereby some modalities recover faster than others.

Figure 3. Interpretation of scenarios of possible model outputs from a meta-regression model that examines the main effect terms *Modality* and *Time*, and the interaction term *Modality x Time*.

2.4.1 Effect size

The natural logarithm transformed response ratio, LnRR (Hedges et al. 1999) was used as the effect size, which is better suited than other metrics for a study of changes brought about by an impact because it is designed to quantify the proportionate change that results from the intervention (Goldberg et al. 1999; Hedges et al. 1999). LnRR was used instead of response ratio (RR) because it linearizes the metric so that changes in the denominator and numerator are treated equally and yields better sampling distributions (Hedges et al. 1999). The response ratio is defined as the ratio of the mean abundance estimate measured inside (impact) and outside (control) the fished area for a control-impact design study or before (control) and after (impact) for a before-after study (Hedges et al. 1999):

$$LnRR = Ln\left(\frac{\overline{X}_{Impact}}{\overline{X}_{Control}}\right) \qquad \text{Eq. 2.1}$$

The response ratio for a BACI design was calculated as shown in Eq. 2.2 to correct for differences in observed abundances due to temporal variation rather than due to the fishing impact per se:

$$LnRR = Ln\left(1 + \frac{Impact_{Diff} - Control_{Diff}}{Impact_{Before}}\right) \qquad \text{Eq. 2.2}$$

where

$$Impact_{Diff} = Impact_{After} - Impact_{Before} \qquad \text{Eq. 2.3}$$

$$Control_{Diff} = Control_{After} - Control_{Before} \qquad \text{Eq. 2.4}$$

For the meta-regression analysis of the change in effect size with time following the fishing disturbance, it was considered inappropriate to calculate effect sizes using before and after data that have been collected months or in some cases years apart. Natural temporal variation and seasonal variation (if before and after data were collected during different seasons) may mask the effect of fishing. Therefore, for this analysis only after control-impact (ACI) and BACI studies were included and the effect size was generated using data collected inside (impact) and outside (control) the fished area.

In a meta-analysis, effect sizes are commonly weighted to ensure a greater contribution of the most robust studies. Robustness is usually based on (inversed) sample variance (Rosenberg et al. 2000), which takes into account both the sample size and the variability among replicates “stations” or “samples” within a study. Therefore, this weighting procedure reduces the influence of studies with high variance or small sample size relative to those studies with lower variance or greater sample size. The variance associated with the response ratio (V_{LnRR}) (Hedges et al. 1999) was estimated as:

$$V_{LnRR} = \frac{SD^2_{Impact}}{n_{Impact}\left(\overline{X}_{Impact}\right)^2} + \frac{SD^2_{Control}}{n_{Control}\left(\overline{X}_{Control}\right)^2} \qquad \text{Eq. 2.5}$$

where $\overline{X}_{Impact}$ and $\overline{X}_{Control}$ are the mean abundance, SD_{Impact} and $SD_{Control}$ are the standard deviation associated with the mean and n is the sample size for estimation of the mean (i.e. the number of hauls or transects sampled) in the impacted and control area or after and before trawling, respectively.

A weighted summary effect size ($\overline{LnRR}$) across the different experimental studies was calculated by conducting a random effects meta-analysis, which acknowledges that differences in observed effects may be due to differences among studies such as different designs and characteristics of studies rather than due to sampling error alone. The restricted maximum-likelihood (REML) estimator method was used to calculate the summary effect size (Gurevitch and Hedges 1999; Hedges et al. 1999; Rosenberg et al. 2000):

$$\overline{LnRR} = \frac{\sum_{i=1}^{k} W_i \, LnRR_i}{\sum_{i=1}^{k} W_i} \qquad \text{Eq. 2.6}$$

where $LnRR_i$ and W_i are the effect size and weight (inverse variance) associated with each experimental study included in the analysis, respectively, and k is the number of studies.

Negative values of the summary effect size ($\overline{LnRR}$) indicate lower abundance in fished areas relative to non-fished areas, or after relative to before the fishing disturbance. Positive values indicate the opposite. The summary effect size ($\overline{LnRR}$) is considered to be significantly different from zero (i.e. there is a significant either positive or negative effect of fishing) when the 95% confidence interval (CI) does not overlap zero.

All meta-analyses were performed using the package Metafor in R (version 3.0.2).

3 RESULTS

3.1 Qualitative description of data

The majority of studies included in the analysis were conducted in Northern Europe (n = 19), Eastern North America (n = 16) and Australia (n = 15), fewer studies were conducted in Southern Europe (n = 8) and Eastern South America (n = 1) (Figure 4). The small number of studies examining the effect of different fishing metier as defined in WP2 on the benthos did not support an analysis using these categories, rather the metiers were aggregated into three fishing gear types; beam trawl (TBB), otter trawl (OT) and dredges (DRB) (Table 3). The main fishing gears studied were dredges and otter trawls perhaps reflecting a higher degree of concern regarding the effects of these methods of fishing (Table 3). Otter trawl gear mainly targeted *Nephrops* or groundfish, primarily cod and plaice, whereas dredges primarily targeted scallops, *Pecten* spp. Soft-sediment communities were those most commonly studied and most studies were carried out on sand habitats (Table 3). The number of studies assessing the fishing impact in some sediment type and fishing gear combinations was either very low (e.g. Dredge on Coarse / mixed sediment) or lacking altogether (e.g. Beam trawl in muddy sediment) (Table 3). The latter may reflect the inability of particular fishing gear to be used effectively on some sediment types (e.g. a beam trawl would sink into a mud substratum). There were relatively more studies that examined the effect of fishing on the benthos immediately following the fishing disturbance (Table 4). The majority of the studies (68%) were carried out between April and September (spring / summer); fewer (32%) were carried out between October and March (autumn / winter). Experimental fishing was generally carried out in areas where there was no bottom fishing recorded or in areas where bottom fishing had not taken place for at least 4 months (range: 4 months – 20 years) prior to the experiment. Thrush et al. (1995) however, carried out their study in a regularly exploited commercial fishing ground (Opito Bay). The intensity of experimental fishing applied among the included studies ranged from low to high fishing intensity (Figure 5).

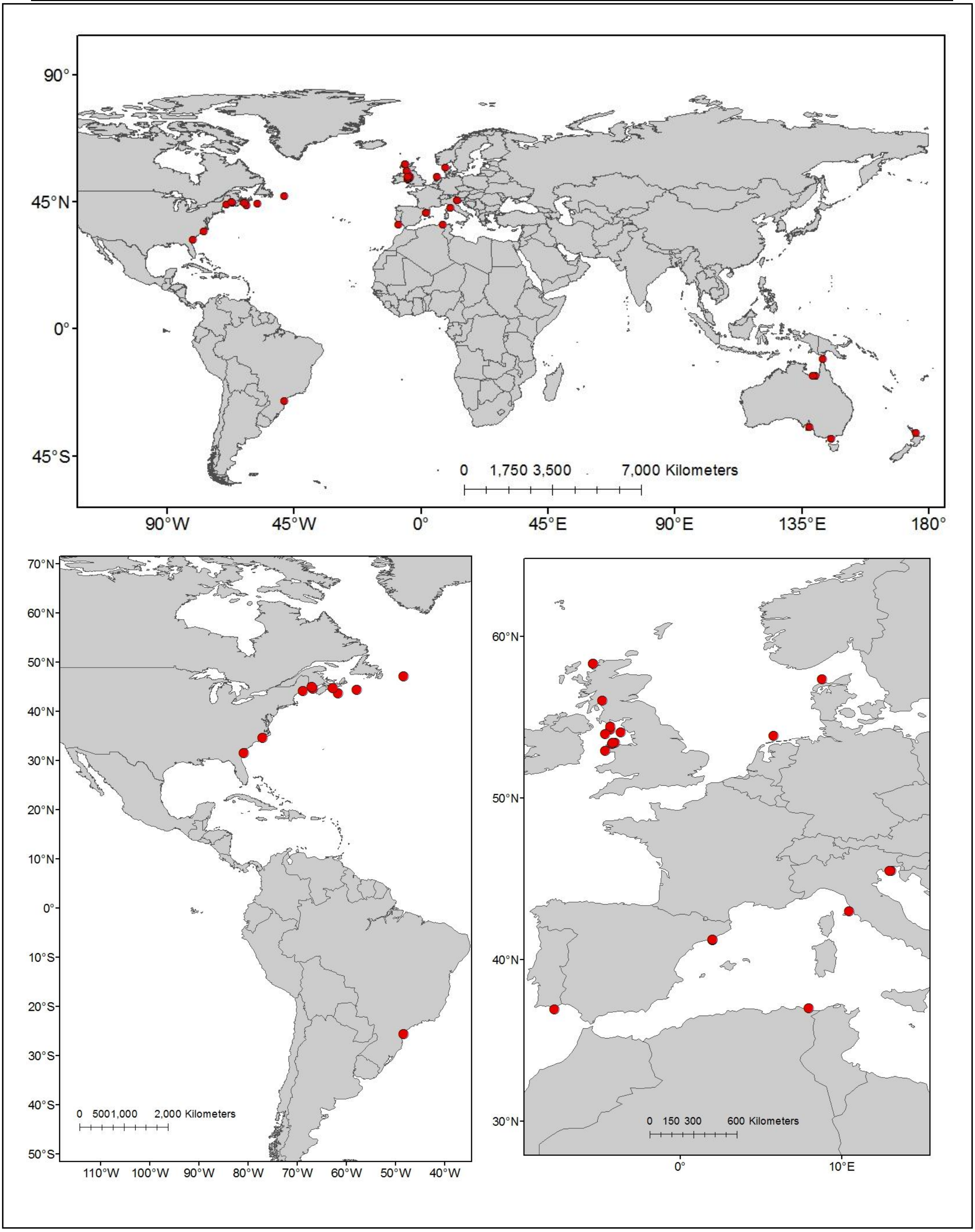


Figure 4. The distribution of studies (red dots) included in the meta-analysis. The insets in the bottom half of the figure illustrate more clearly the distribution of American studies (left) and European studies (right).

Table 3. Number of studies included in the meta-analysis that examined the effect of different fishing gear on the benthos in different habitat types.

			EUNIS L3 habitat type			
			Coarse (A5.1), Mixed (A5.4) sediment	Sand (A5.2)	Mud (A5.3)	Biogenic (A5.6)
Fishing gear (BENTHIS WP2 fishing metiers)	Dredging (DRB)	DRB_MOL	5	11	4	3
	Otter Trawling (OT)	OT_CRU	3	4	1	-
		OT_MIX	1	-	4	1
		OT_MIX_ARA	-	1	1	1
		OT_MIX_DMF_PEL	7	3	-	-
		OT_MOL	-	1	-	-
	Beam trawling (TBB)	TBB_MOL	1	-	-	-
		TBB_DMF	1	5	1	-

Table 4. Distribution of studies among different response variables and among fixed time periods following the fishing disturbance event.

		Time after fishing disturbance (days)		
		0 – 7 days	8 – 60 days	> 60 days
Response variable	Diversity	27	8	13
	Total abundance	25	4	14
	Individual species abundance	44	9	19

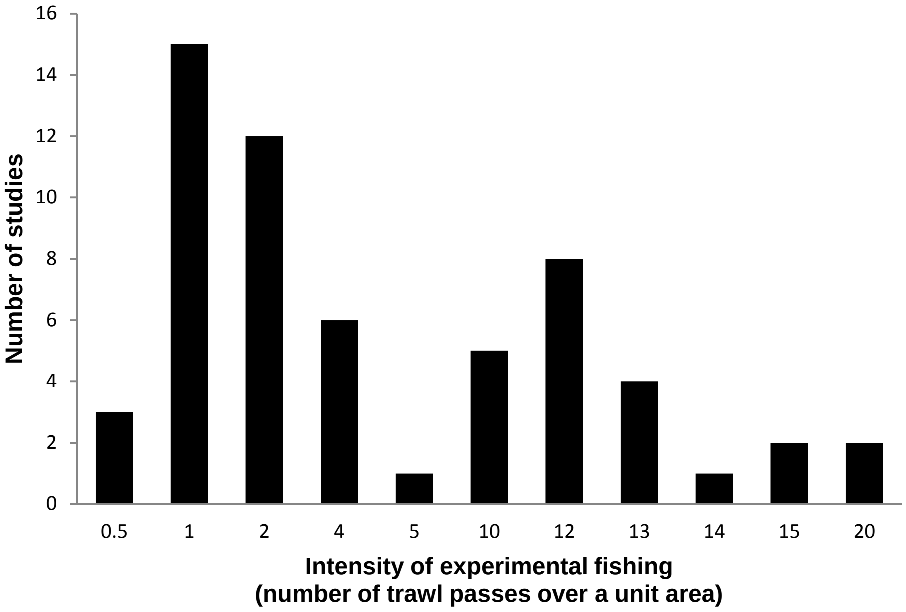


Figure 5. The intensity of fishing, defined as the number of times or the number of fishing gear passes over the entire experimental box, applied to the fished area in the studies included in the meta-analysis.

3.2 Meta-analysis of the effect of bottom fishing on total community abundance within the first 7 days following the fishing disturbance event

A subset of 25 studies reported the responses for two whole community descriptors: total number of species and total 'abundance', which included studies that provided density or biomass data. There was no significant response to fishing for total number of species ($\overline{LnRR}$ = -0.02, confidence interval (CI) = -0.09 to 0.04, number of studies (k) = 27) (Figure 6), and the effect did not differ significantly with sediment type or fishing gear type (Table 5). In contrast, there was a significant negative response to fishing for the total abundance. On average, benthic community abundance was 17% lower in fished areas relative to control areas, and ranged between a 4% and 27% reduction after experimental fishing with bottom towed gear ($\overline{LnRR}$ = -0.17, CI = -0.31 to -0.04, k = 25). The reduction in community abundance was most severe in coarse & mixed sediment (Figure 7, $\overline{LnRR}$ = -0.38, CI = -0.69 to -0.08, k = 25, 32% reduction) and following the application of dredges (Figure 8, $\overline{LnRR}$ = -0.34, CI = -0.62 to -0.07, k = 27, 29% reduction). A further analysis was carried out to examine the heterogeneity among responses in sand and following otter trawling, using the interaction terms between sediment type and fishing gear type (Table 6). Interactions between some gear and sediment types could not be examined because of an inadequate sample size for a meta-analysis (e.g. Dredge on Coarse / mixed sediment) or because of the lack of studies altogether (e.g. Beam trawl in muddy sediment) (Table 6). In sand communities, dredging resulted in a significantly higher reduction in total abundance than otter trawling ($Q_M = 4.92$, $p = 0.03$; Table 6). On average, total abundance of the benthos in sand undergoes a 33% reduction following dredging and a 5% reduction following otter trawling. However, otter trawling resulted in a 41% reduction in abundance of coarse / mixed sediment communities (Table 6). Otter trawling in mud led to a slight (14%) but non-significant reduction in total abundance (Table 6).

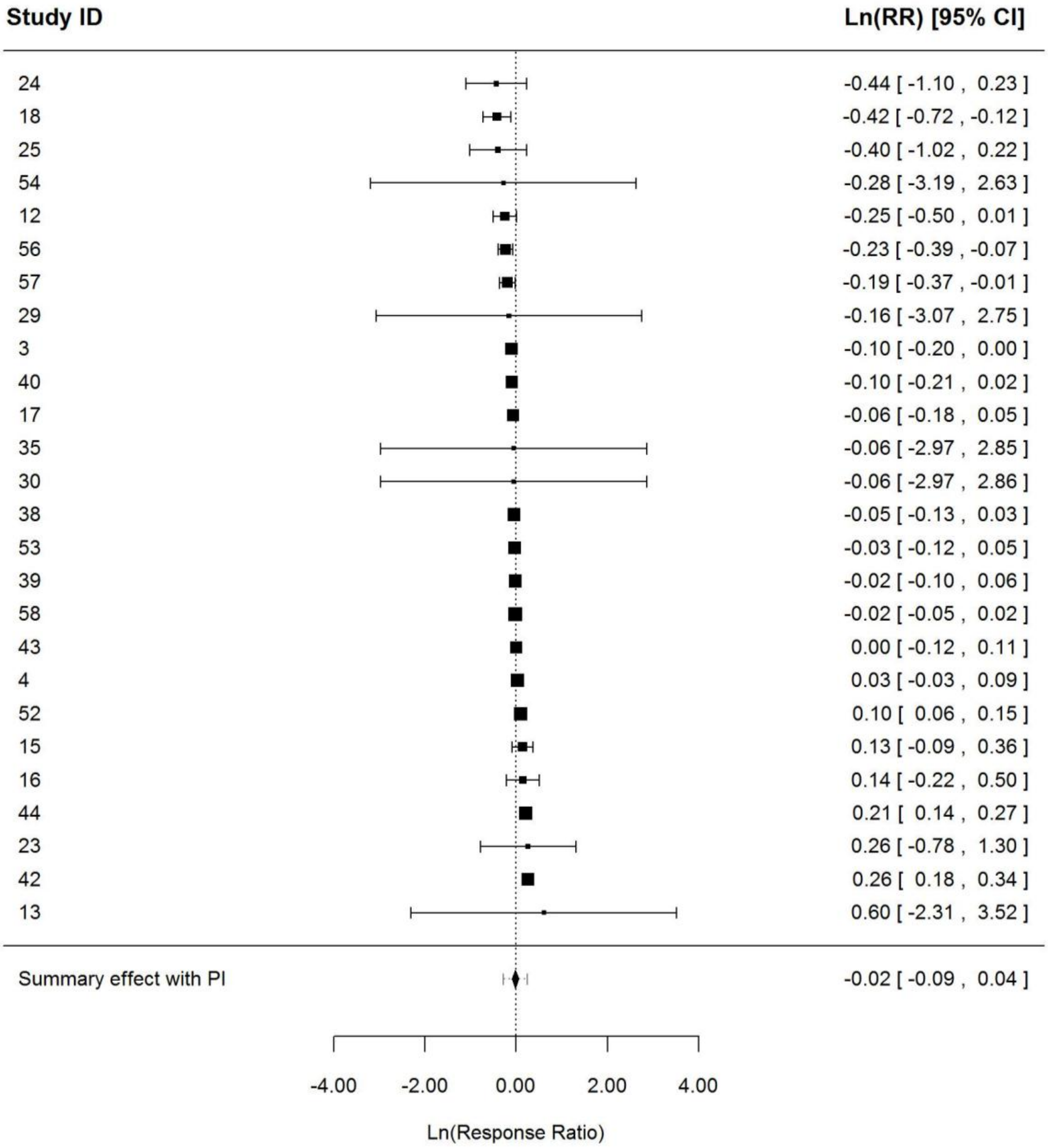


Figure 6. Forest plot of the effect of bottom fishing on benthic community diversity. Effect sizes are based on species number data in the fished and control area. Each row represents a study: paired Fished – Control comparison or Before-After comparison. The vertical dotted line at LnRR = 0 represents equal abundance in fished and control area; LnRR > 0 indicates higher abundance in fished area, LnRR < 0 indicates lower abundance in the fished area. The squares are the effect size for each study, the error bars are the 95% confidence interval for each study, whose values are given on the right hand side of the figure. The size of each square is proportional to the weight of the study. Summary effect: the diamond represents the weighted mean calculated from the

random effects meta-analysis of all studies included in the analysis. The width of the diamond is proportional to the estimation in the error of the mean (95% CI) and the horizontal dotted line is the prediction interval were 95% of true effects are predicted to occur.

Table 5. Mean response ratio ($\overline{LnRR}$) based on species number data in the fished and control area for benthos in different sediment type categories and exposed to different types of fishing gear.

EUNIS sediment type	**Mean response ratio, 95% confidence interval, number of studies (k)**	
Coarse & mixed sediment (A5.1, A5.4)	$\overline{LnRR}$ = -0.11, CI = -0.29 to 0.09, k = 6	Q_M (df = 3) = 2.62, p = 0.45 (Test of significance among the different habitats, H_0: coarse sediment = sand = mud = biogenic = 0)
Sand (A5.2)	$\overline{LnRR}$ = -0.02, CI = -0.11 to 0.08, k = 13	
Mud (A5.3)	$\overline{LnRR}$ = 0.04, CI = -0.11 to 0.18, k = 5	
Biogenic (A5.6)	$\overline{LnRR}$ = -0.24, CI = -0.6 to 0.13, k = 2	

Fishing gear	**Mean response ratio, 95% confidence interval, number of studies (k)**	
Beam trawl (TBB)	$\overline{LnRR}$ = -0.12, CI = -2.21 to 1.95, k = 2	Q_M (df = 2) = 1.53, p = 0.47 (Test of significance among the different habitats, H_0: TBB = DRB = OT = 0)
Dredge (DRB)	$\overline{LnRR}$ = -0.07, CI = -0.17 to 0.03, k = 10	
Otter trawl (OT)	$\overline{LnRR}$ = 0.02, CI = -0.07 to 0.1, k = 14	

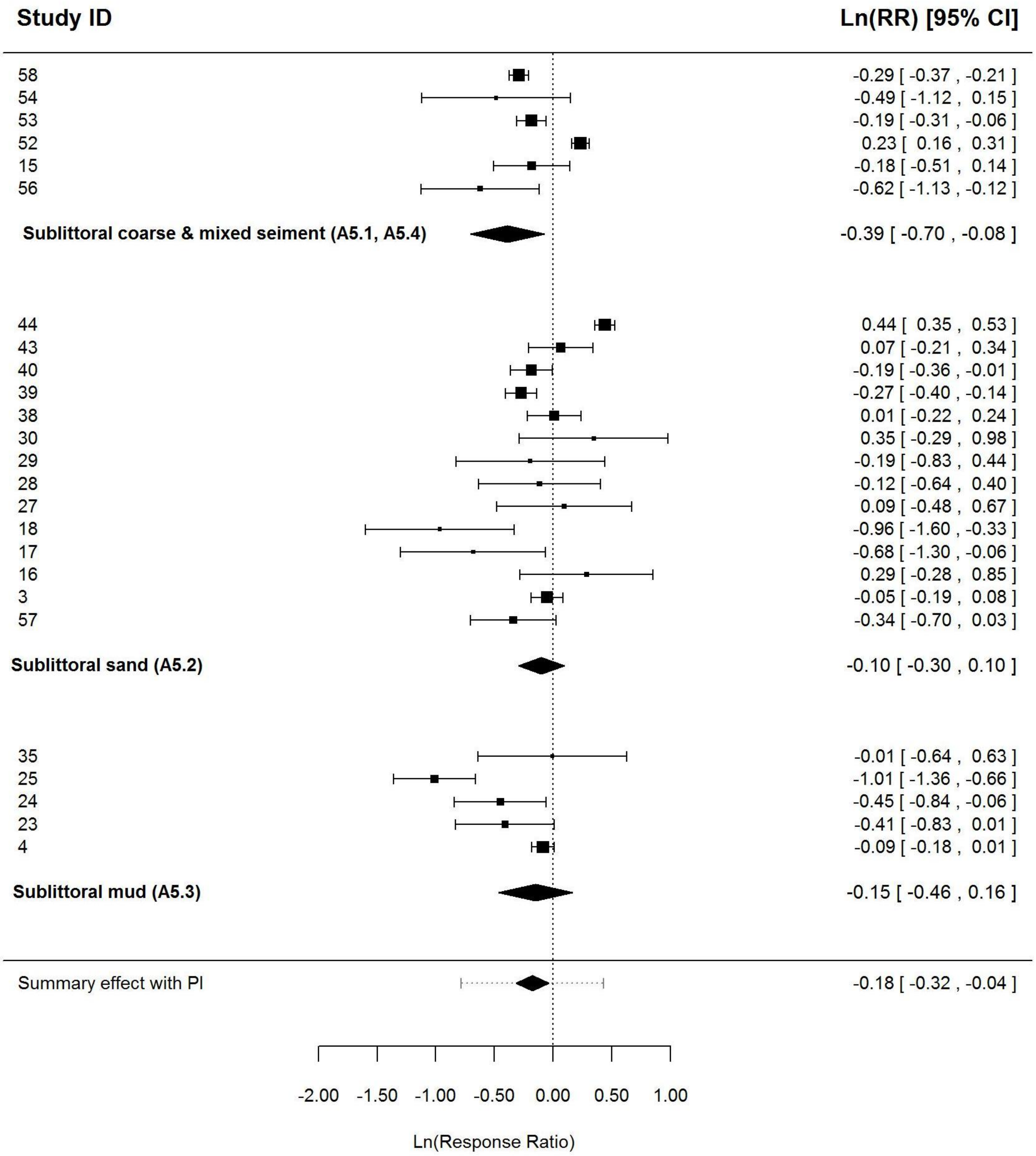


Figure 7. Forest plot of benthic community effect sizes based on total abundance data in the fished and control area for each of the habitat type examined (coarse & mixed sediment, sand, mud).

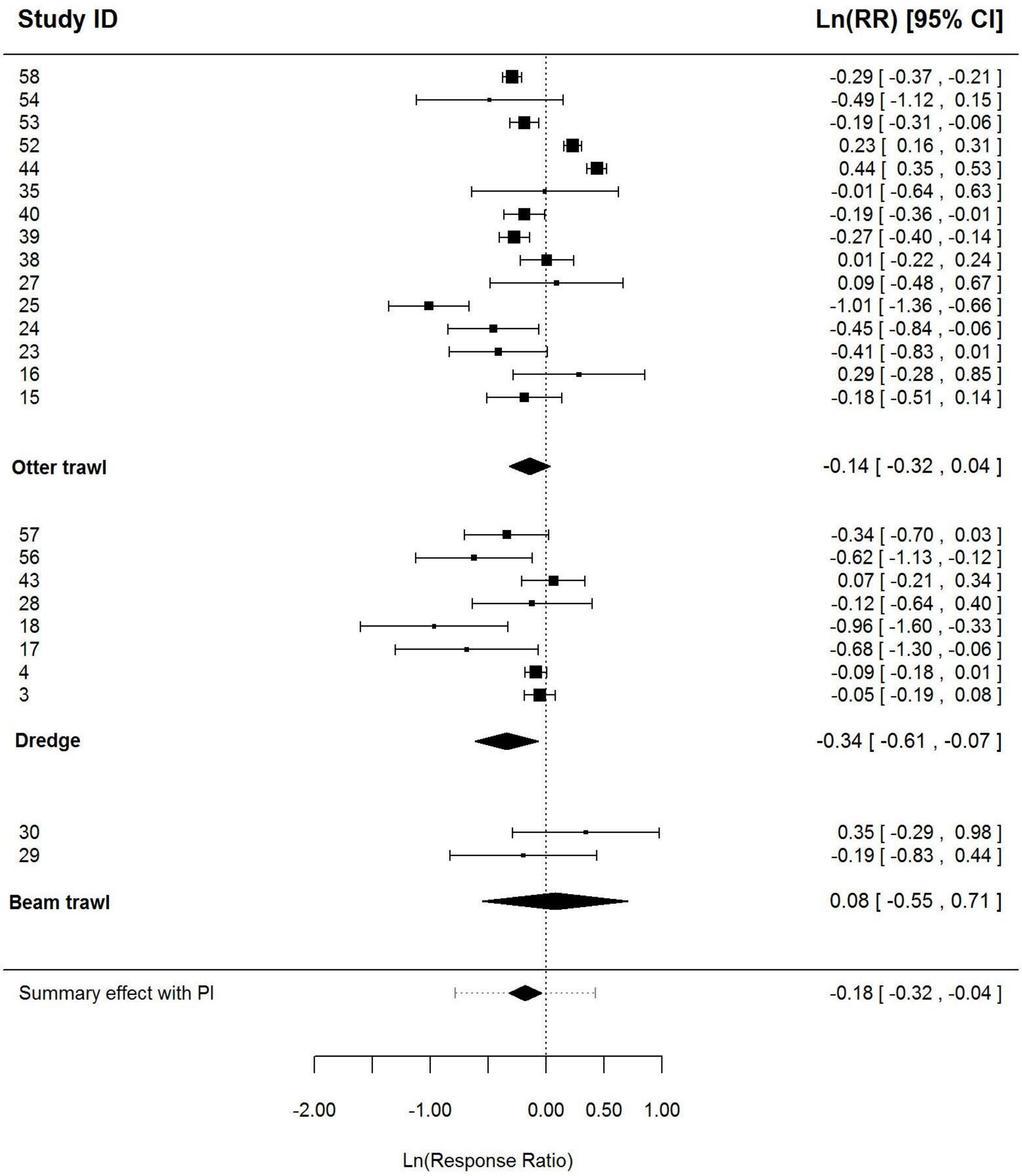


Figure 8. Forest plot of benthic community effect sizes based on abundance data in the fished and control area for each of the fishing gear types examined (otter trawl, dredge, beam trawl).

Table 6. Summary of the weighted summary effect sizes and confidence intervals for each of the habitat type x fishing gear combination comparing total benthic community abundance in the fished area relative to the control area. Bold indicates significant differences. k = number of studies.

	Fishing gear			
EUNIS L3 habitat type	*Otter trawl*	*Beam trawl*	*Dredge*	
Coarse & mixed sediment (A5.1, A5.4)	**$\overline{LnRR}$ = -0.53, CI = -0.92 to -0.12, k = 4**	No data	k = 2	-
Sand (A5.2)	$\overline{LnRR}$ = -0.05, CI = -0.19 to 0.28, k = 7	k = 2	**$\overline{LnRR}$ = -0.40, CI = -0.72 to -0.08, k = 5**	Q_M = 4.92, p = 0.03 (Test of significance of different fishing gear in sand community, H_0: coarse sediment = sand = mud = biogenic = 0)
Mud (A5.3)	$\overline{LnRR}$ = -0.15, CI = -0.46 to 0.17, k = 15	No data	No data	-
	Q_M = 5.35, p = 0.07 (Test of significance of the effect of otter trawling among the different habitats, H_0: coarse sediment = sand = mud = biogenic = 0)	-	-	

3.3 Meta-analysis of the effect of bottom fishing on species' biological traits within the first 7 days following the fishing disturbance event

In this section the overall response of species with different biological traits to bottom fishing was examined. Two hypotheses were tested in this analysis. First, that fishing results in significantly higher or lower abundance of species of a particular modality in the fished area relative to the non-fished area. Significant differences occur when the 95% confidence interval (CI) around the mean effect size ($\overline{LnRR}$) does not overlap zero. Second, that the effect of fishing differs significantly among modalities of a biological trait. For example, in examining the effect of fishing on the biological trait 'Mobility', the analysis determines whether the effect of fishing is significantly different between species with different degrees of mobility (Mobility: sessile vs. burrower vs. crawler vs. swimmer). A significant difference among modalities is given by a significant p-value for the Q_M statistic.

3.3.1 Effect of fishing on species' traits

The effect of fishing was not significantly different between any of the modalities examined for the eleven biological traits included in this study (refer to Q_M statistic in Table 7). However, fishing did result in significantly lower species' abundance in the fished area relative to the control area for several modalities (refer to 95% CI in Table 7). Small (< 10 mm) to medium (101 – 200 mm) sized species showed significant negative responses to fishing with bottom towed gear; an overall 40% reduction in abundance was observed following the fishing event (Figure 9, Table 7). Perhaps not surprising given that the extent of gear penetration within the sediment is most significant in the first 5 – 8 cm, epifauna and infauna inhabiting sediment down to 5 cm exhibited the strongest impact of bottom fishing; a 22% reduction in abundance on average (Figure 9, Table 7). Interestingly, the abundance of the shortest lived species group (life span < 1 year) (Figure 9) and species with medium mobility (burrowers and crawlers) (Figure 9) was significantly reduced in fished areas immediately after experimental fishing relative to the control areas (Table 7). Although the abundance of sessile and long-lived species was reduced by bottom fishing these reductions were not significant (Table 7). The impact of fishing was significantly more severe on organisms which reproduce asexually (e.g. by budding) or produce pelagic eggs and for those with a planktotrophic larval development (Figures 9, 10). Slightly equivocal responses were obtained among modalities within the traits 'Feeding group' and 'Protection'. Bottom fishing resulted in a significant 35% reduction in abundance of scavenging / opportunistic species, and although the abundance of deposit feeders and suspension feeders was on average 22% lower in fished areas than in control areas, this reduction in abundance was not significant (Table 7). Significant negative effects of fishing was observed for species with no protection from tough exoskeleton or shell or with no regeneration ability, but also for species classified as robust that are characterized by the presence of shells or high regeneration ability (Figure 10, Table 7). Nevertheless, the highest loss in abundance occurred for species with no protection; a 45% reduction relative to a 30% reduction for robust species (Table 7). Among the 'Living habit' modalities examined, significant reductions in abundance to fishing were observed for epiphytic / epizoic organisms, burrow-dwelling organisms and free-living organisms (Table 7, Figure 10). Organisms that work the sediment through sediment deposition underwent a significant 28% reduction in their abundance following fishing (Table 7, Figure 10). None of the species with different morphological characteristics were found to differ significantly between fished and non-fished areas (Figure 9).

Table 7. The percentage change in modality abundance between fished and non-fished areas following the fishing disturbance event. Significant differences in abundance between fished and non-fished areas for different modalities occur are shown in red. The Q_M statistic tests for significant differences in response to fishing among different trait modalities.

Biological trait category	**% change between fished and non-fished area (range)**	**Biological trait category**	**% change between fished and non-fished area (range)**
Body size (mm)		***Protection***	
< 10 mm	- 38 % (-12 to -57 %)	None	- 46 % (-2 to -70 %)
11- 20 mm	- 22 % (+3 to -42 %)	Fragile	- 14 % (+17 to -37 %)
21 – 100 mm	- 22 % (+0.2 to -40 %)	Exoskeleton	- 23 % (+7 to -45 %)
101 – 200 mm	- 31 % (-6 to -50 %)	Robust	- 31 % (-5 to -51 %)
201 – 500 mm	- 18 % (+10 to -39 %)		Q_M = 1.97, p = 0.78
> 500 mm	- 25 % (+10 to -49 %)		
	Q_M = 1.77, p = 0.90		
Sediment position		***Mobility***	
Surface	- 22 % (-4 to -36 %)	Sessile	- 22 % (+2 to -41 %)
0 – 5 cm	- 20 % (-1 to -36 %)	Burrower	- 26 % (-3 to -43 %)
6 – 10 cm	- 20 % (+2 to -38 %)	Crawler	- 28 % (-10 to -43 %)
> 10 cm	- 10 % (+27 to -36 %)	Swimmer	- 26 % (+1 to -46 %)
	Q_M = 0.47, p = 0.92		Q_M = 4.42, p = 0.96
Living habit		***Egg development***	
Attached	- 16 % (+25 to -44 %)	Asexual	- 33 % (-2 to -54 %)
Burrow-dwelling	- 23 % (-1 to -41 %)	Pelagic eggs	- 27 % (-6 to -44 %)
Tube-dwelling	- 7 % (+31 to -36 %)	Benthic eggs	+ 2 % (+45 to -28 %)

Crevice / under stone	- 16 % (-27 to -45 %)	Brooder	- 18 % (+7 to -38 %)
Epi/Endo phytic/zoic	- 53 % (-33 to -67 %)		Q_M = 3.22, p = 0.36
Free-living	- 21 % (-1 to -37 %)		
	Q_M = 8.92, p = 0.25		
Larval development		***Longevity***	
Direct	- 26 % (+4 to -45 %)	< 1 year	- 39 % (-9 to -58 %)
Lecitotrophic	- 10 % (+30 to -38 %)	1 – 3 yrs	- 20 % (+5 to -40 %)
Planktotrophic	- 25 % (-3 to -42 %)	3 – 10 yrs	- 17 % (+5 to -35 %)
	Q_M = 0.72, p = 0.69	> 10 yrs	- 15 % (+16 to -39 %)
			Q_M = 1.97, p = 0.58
Feeding mode		***Bioturbation***	
Suspension	- 17 % (+6 to -36 %)	Diffusive mixer	- 7 % (+21 to -29 %)
Surface deposit	- 15 % (+9 to -34 %)	Surface deposition	- 28 % (-8 to -43 %)
Subsurface deposit	- 21 % (+7 to -42 %)	Downwards conveyer	- 13 % (+23 to -38 %)
Scavenging / Opportunistic	- 35 % (-15 to -51 %)	Upwards conveyer	+ 2 % (+64 to -37 %)
Predator	- 19 % (+5 to -37 %)	None	- 25 % (+19 to -52 %)
Parasite	- 37 % (+73 to -77 %)		Q_M = 2.88, p = 0.58
	Q_M = 3.55, p = 0.89		

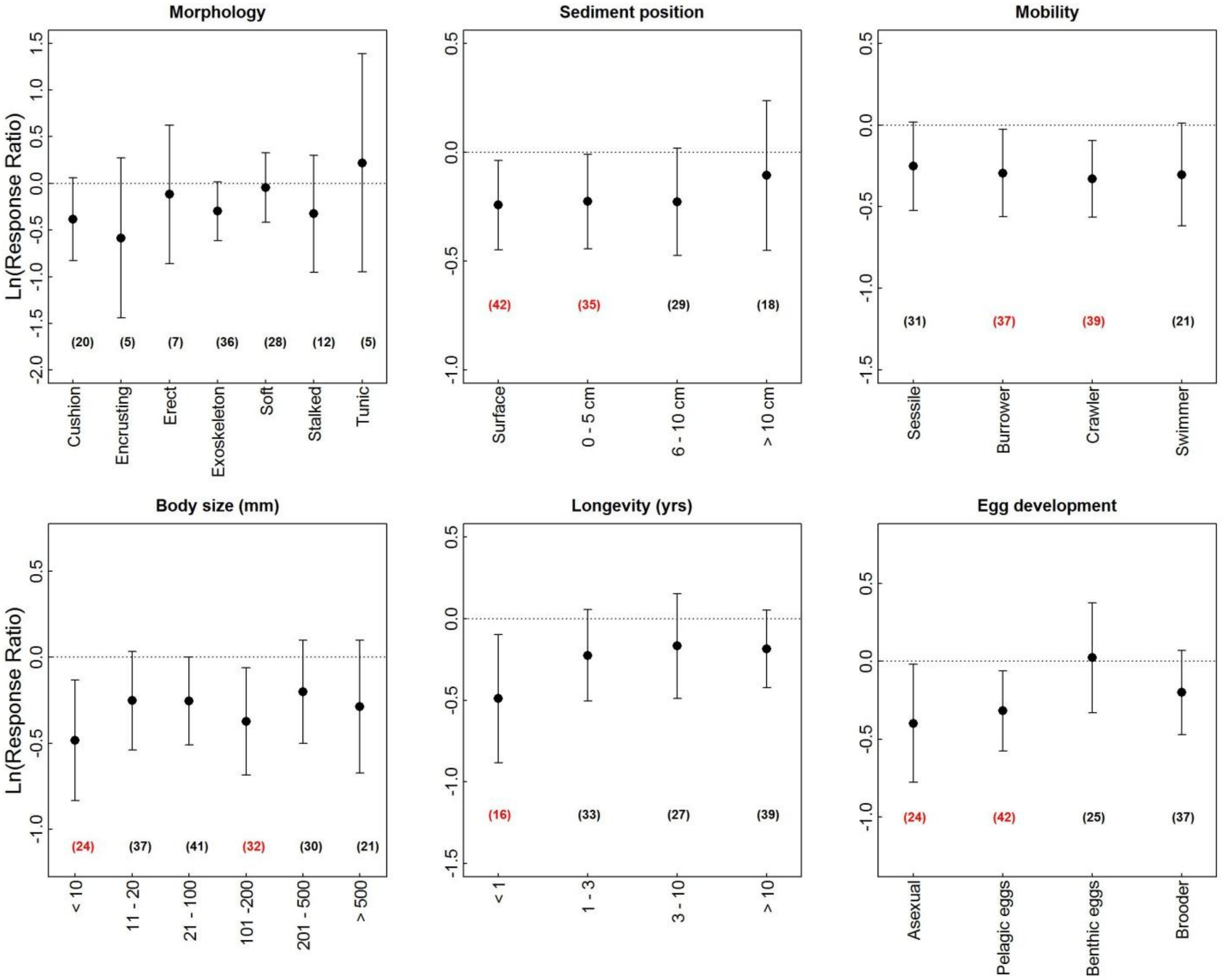


Figure 9. The response ($\overline{LnRR}$) of species groups with different biological (morphology, body size, longevity, egg development, sediment position, mobility) characteristics to disturbance by bottom fishing. Error bars represent the 95% confidence interval. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area; LnRR > 0 indicates higher abundance in the fished area, LnRR < 0 indicates lower abundance in the fished area. Significant differences in abundance between fished and non-fished areas are shown in red.

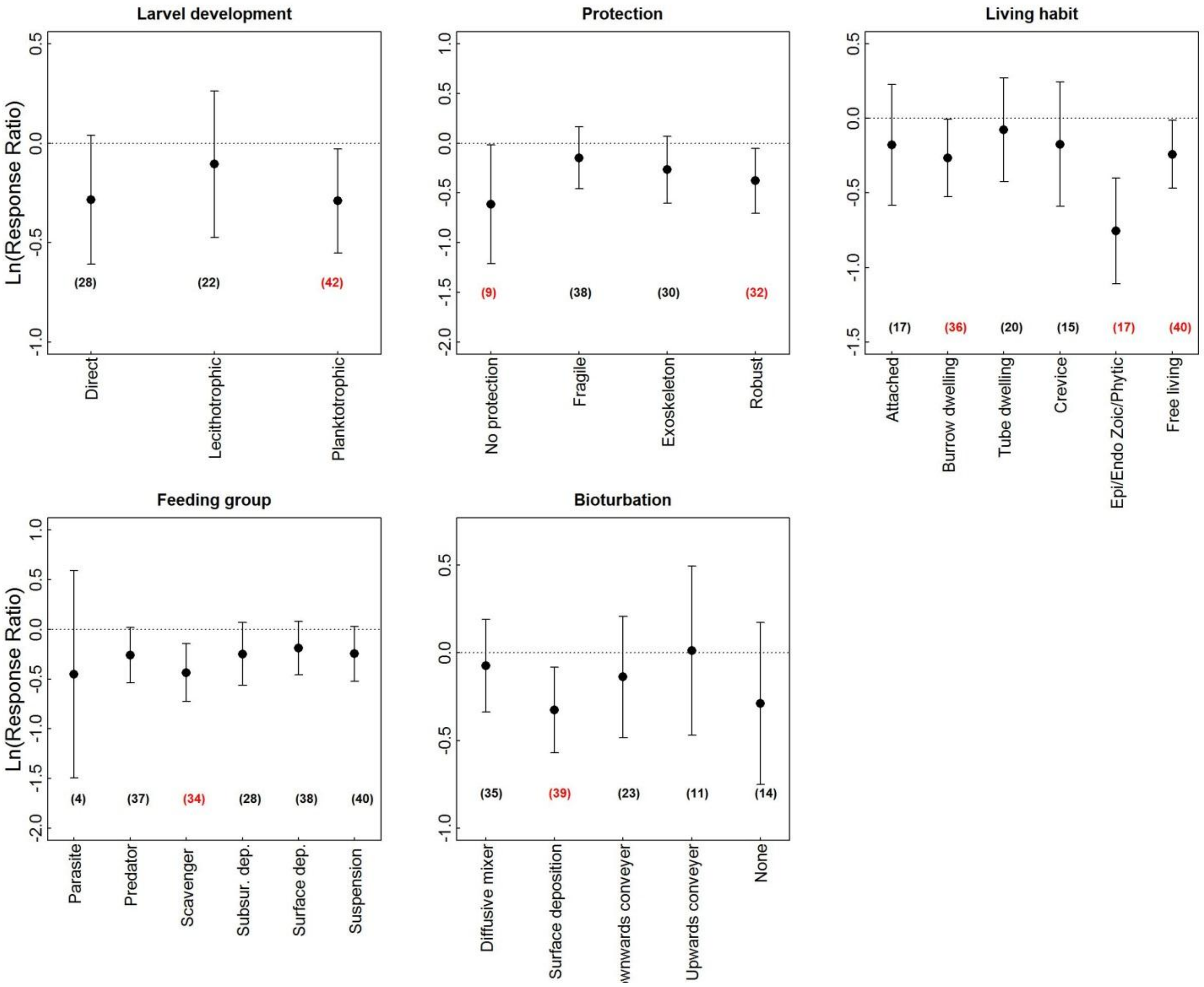


Figure 10. The response ($\overline{LnRR}$) of species groups with different biological (larval development) and ecological (feeding group, living habit, bioturbation, protection) characteristics to disturbance by bottom fishing. Error bars represent the 95% confidence interval. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. The vertical dotted line at ($\overline{LnRR}$) = 0 represents equal abundance in fished and control area; $\overline{LnRR}$ > 0 indicates higher abundance in the fished area, $\overline{LnRR}$ < 0 indicates lower abundance in the fished area. Significant differences in abundance between fished and non-fished areas are shown in red (as an example, null hypothesis tested: fishing has no effect on the abundance of scavenging species).

3.3.2 Effect of fishing gear on species' traits (Interaction: *Fishing gear x Modality*)

To assess whether the response of species' traits is influenced by the type of fishing gear used to create the fishing disturbance, the interaction between fishing gear type and modality (*Fishing gear x Modality*) was examined. No significant interactions were observed for any of the biological traits examined. This is not to say that there is no impact of fishing, but rather that the initial reductions in abundance in the fished area as a result of beam trawling or otter trawling or dredging are similar among different modalities of a biological trait (Table 8).

Fishing did however result in significant differences between the fished and non-fished area for a number of modalities, and these differences were more pronounced for dredging than for otter trawling and beam trawling (refer to significant differences marked in red in Figures 11 – 14). Although, beam trawling resulted in an overall reduction in abundance in the fished area relative to the control area for all the trait groups, these reductions were not significant. In contrast, significant reductions in species' abundance were observed in the fished area following dredging for a number of modality groups. Dredging impact was most severe on infauna organisms occurring within the first 10 cm of the sediment ('Sediment position' in Figure 11). From among the feeding modalities assessed, dredging resulted in a significant negative effect on scavengers and deposit feeders; a 35% loss in abundance of scavengers, a 37% loss of subsurface deposit feeders and a 27% loss in abundance of surface deposit feeders occurred following dredging ('Feeding group' in Figure 12). Otter trawling and dredging resulted in different effects on species characterized by different living habits; whereas the impact of dredging was most severe for burrow-dwelling organisms, otter trawling impacted epi/endo phytic/zoic species the most ('Living habit' in Figure 12). Dredging had a negative impact on bioturbating organisms; downwards conveyors underwent a loss of 37% (range: -2 to – 59%) post-fishing ('Bioturbation' in Figure 12). Sessile and burrow-dwelling organisms showed a significant reduction in abundance following dredging; a 30% (range: -2 to – 49%) loss in abundance for sessile species and a 45% (range: -21 to – 62%) loss for burrowers ('Mobility' in Figure 13). Interestingly, both dredging and otter trawling produced a significant negative short-term effect for highly mobile species; a 33% loss in abundance for swimming species following dredging and a 27% loss following otter trawling ('Mobility' in Figure 13). The abundance of asexually reproducing organisms was significantly reduced by otter trawling; whereas dredging had a stronger impact on sexually reproducing organisms that produce pelagic eggs ('Egg development' in Figure 14). Dredging also resulted in significant loss in abundance of small-bodied species (maximum body size is less than 10 mm) ('Body size' in Figure 11) and short-lived species (maximum life span is less than 1 year) ('Longevity' in Figure 13). Although the overall effect of fishing was negative for species characterized by different morphological characteristics and protection capacity to fishing with bottom towed gear, none of the differences in abundance between fished and non-fished areas were significant ('Protection' in Figure 11, 'Morphology' in Figure 12).

Table 8. Summary of a 2-way interaction meta-analysis between fishing gear type and modality to examine if the effect of fishing on trait modalities depends on fishing gear type used to cause fishing disturbance.

	Biological trait	**Test of significance to examine 'Fishing gear x Modality' interaction**
Biological traits	*Body size (mm)*	Q_M (df = 24) = 14.80, p = 0.93
	Longevity	Q_M (df = 11) = 6.56, p = 0.83
	Egg development	Q_M (df = 11) = 7.57, p = 0.75
	Larval development	Q_M (df = 7) = 1.78, p = 0.97
	Feeding group	Q_M (df = 20) = 9.02, p = 0.98
	Morphology	Q_M (df = 16) = 5.55, p = 0.99
Ecological traits	Mobility	Q_M (df = 19) = 13.66, p = 0.8
	Sediment position	Q_M (df = 11) = 6.24, p = 0.86
	Living habit	Q_M (df = 21) = 15.44, p = 0.8
	Bioturbation	Q_M (df = 13) = 10.3, p = 0.67
	Protection	Q_M (df = 14) = 9.3, p = 0.81

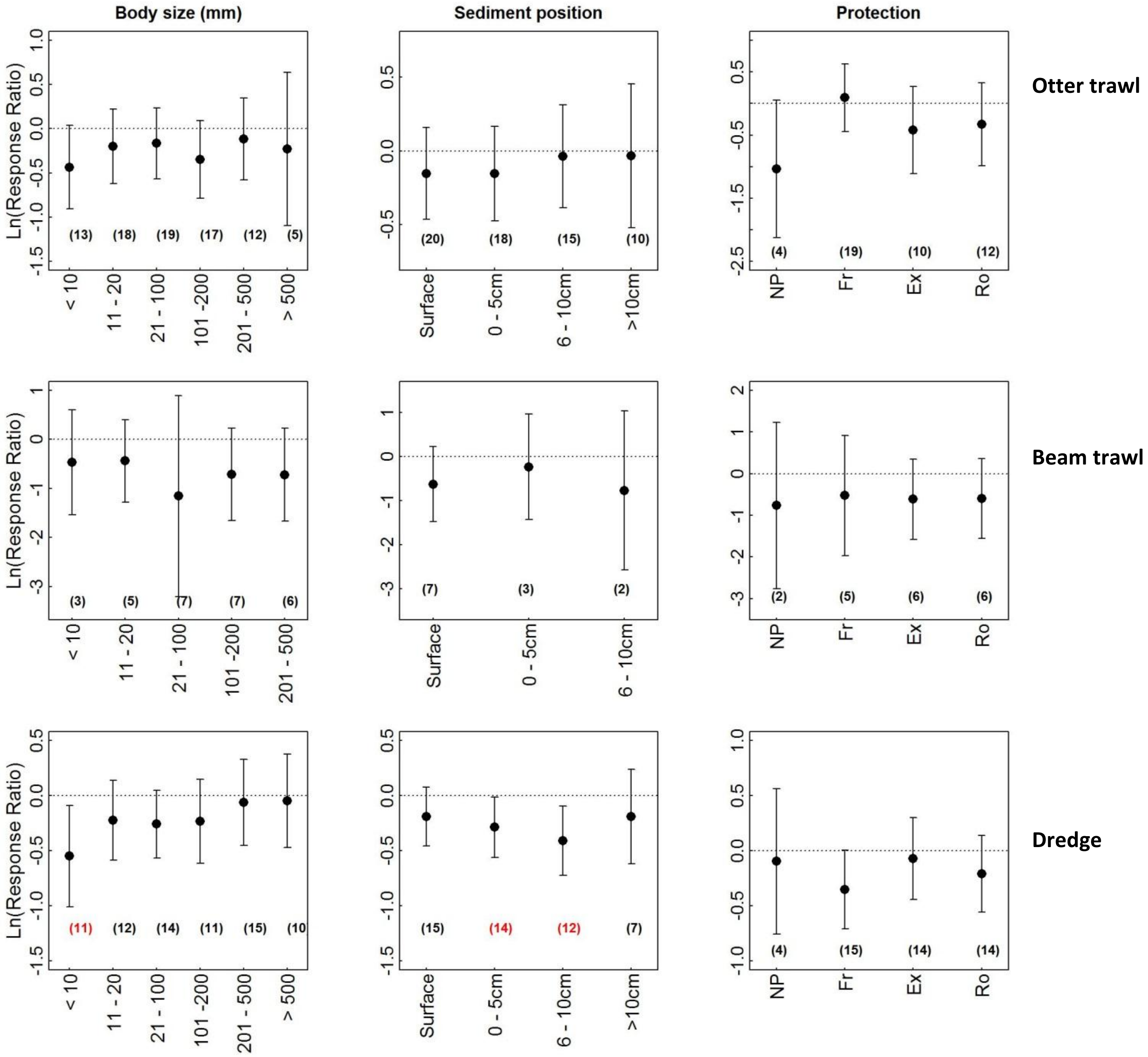


Figure 11. Initial response (up to 7 days after impact) with 95% CI, of species with different body size, sediment position and protection capacity to otter-trawling, beam trawling and dredging. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait ‘Protection’: NP = no protection or no regeneration ability, Fr = fragile, Ex = exoskeleton, Ro = robust (hard shell or high regeneration ability).

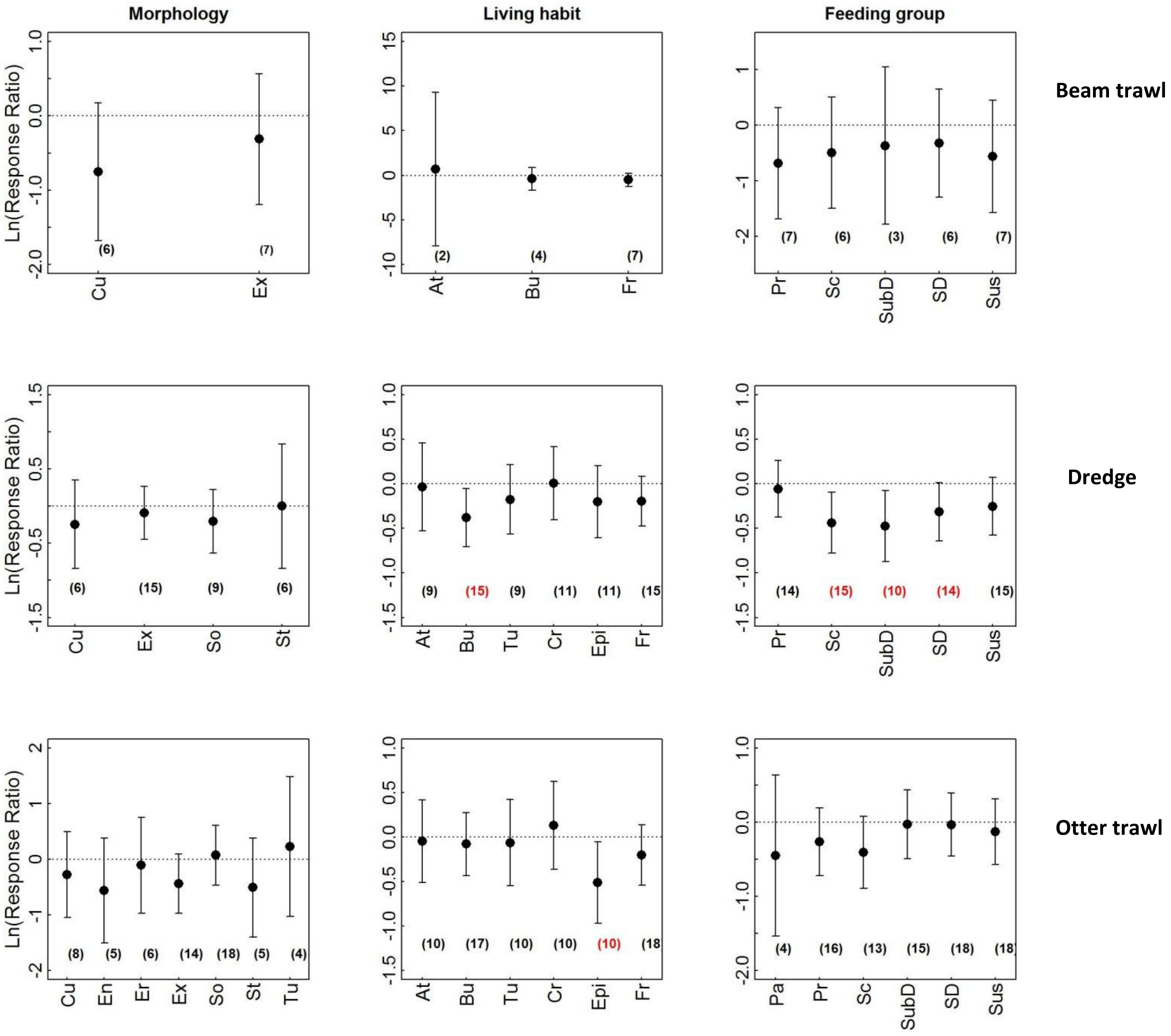


Figure 12. Initial response (up to 7 days after impact) with 95% CI, of species with different morphology, living habit and feeding mode to otter-trawling, beam trawling and dredging. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait 'Morphology': Cu = Cushion, En = encrusting, Er = erect, Ex = exoskeleton, So = soft, St = stalked, Tu = tunic. For the trait 'Living habit': At = attached, Bu = Burrow-dwelling, Tu = tube-dwelling, Cr = crevice or under stone, Epi = epi/endo phytic/zoic, Fr = free-living. For the trait 'Feeding group': Pa = parasite, Pr = predator, Sc = scavenging or opportunistic species, SubD = subsurface deposit feeder, SD = surface deposit feeder, Sus = suspension feeder.

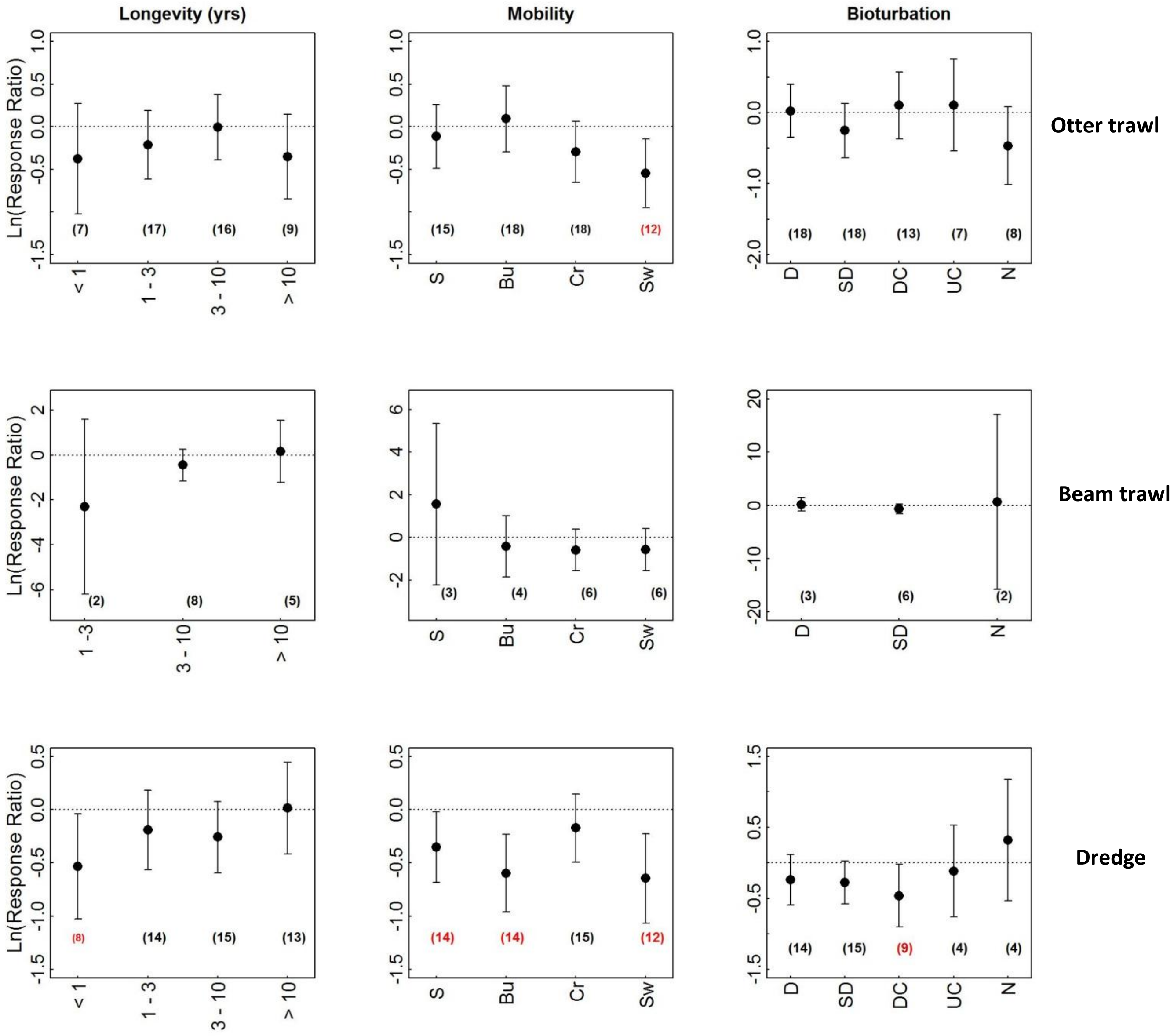


Figure 13. Initial response (up to 7 days after impact) with 95% CI, of species with different lifespan, mobility and bioturbation ability, to otter-trawling, beam trawling and dredging. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait ‘Mobility’: S = sessile, Bu = burrower, Cr = crawler or creeper, Sw = swimmer. For the trait ‘Bioturbation’: D = diffusive mixer, SD = surface deposition, DC = downwards conveyor, UC = upwards conveyor, N = no bioturbation.

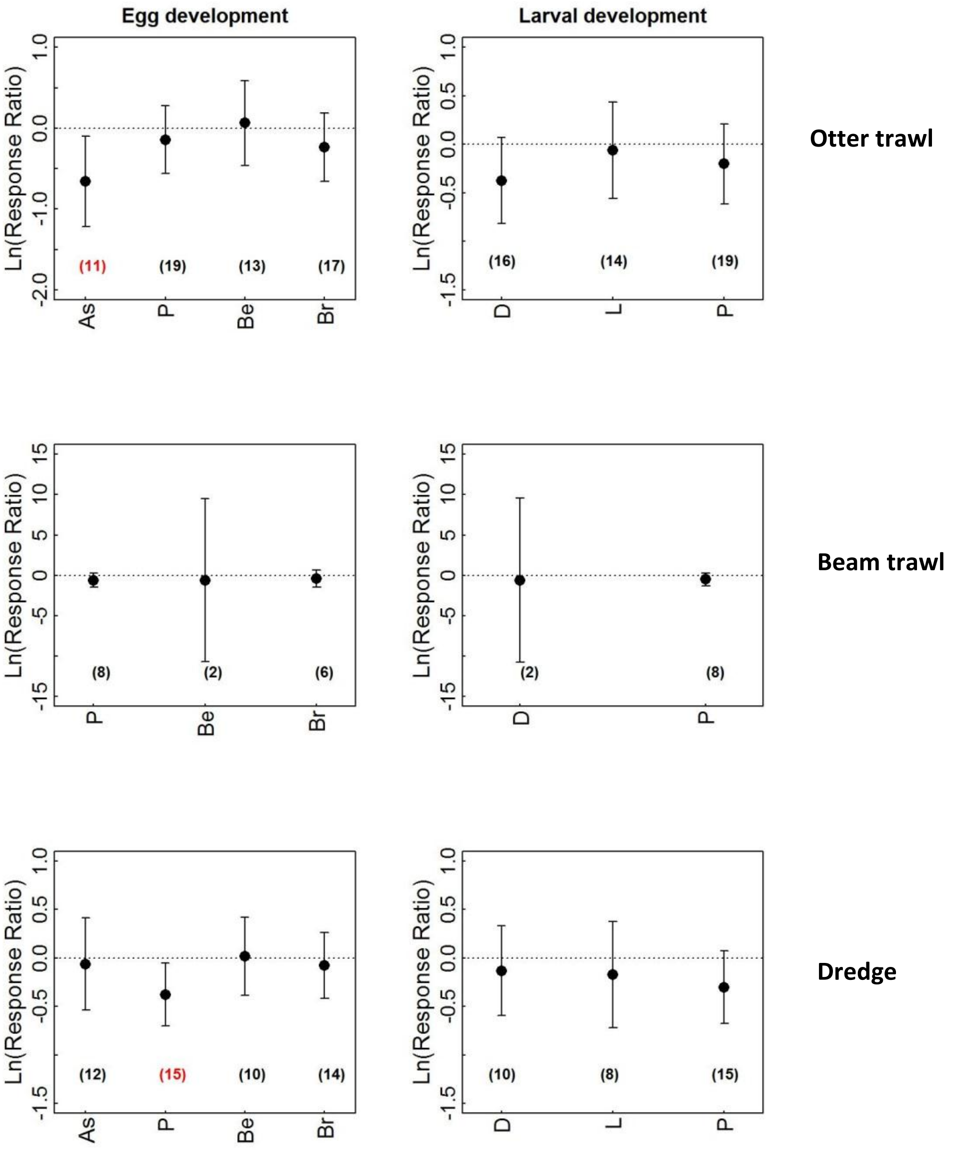


Figure 14. Initial response (up to 7 days after impact) with 95% CI, of species with different egg and larval development to otter-trawling, beam trawling and dredging. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait ‘Egg development’: As = asexual or budding, P = sexual and produced pelagic eggs, Be = sexual and produces benthic eggs, Br = sexual and species broods the eggs. For the trait ‘Larval development’: D = direct development, L = lecitotrophic larvae, P = planktotrophic larvae.

3.3.3 Effect of fishing on species' traits in different sediment types (Interaction: Sediment type *x Modality*)

As per section 3.3.2, to assess whether the response to fishing for different modalities of a species' trait is influenced by sediment type, the interaction between sediment type and modality (*Sediment type x Modality*) was examined. No significant interactions were observed for any of the biological traits examined, although the interaction between modality and sediment type was only marginally non-significant for the biological trait 'Living habit' (Table 9).

Fishing did however result in significant differences between the fished and non-fished area for a number of modalities particularly in sand and in coarse and mixed sediment (Figures 15 to 18). In sand, the abundance of small (< 10 mm) to medium (101 – 200 mm) sized species was significantly reduced in the fished area immediately following bottom fishing ('Body size' in Figure 15). On average, their abundance was 68% lower in the fished area compared to the non-fished area. The abundance of large species (> 500 mm) was found to be the lowest in mud, however this mean effect size should be viewed with caution given that there were only 2 studies that assessed the impact of fishing in mud for this modality ('Body size' in Figure 15). In sand, species with no protection capacity from bottom-towed gear ('Protection' in Figure 15) and those characterized by direct larval development were significantly less abundant compared to the control area ($\overline{LnRR}$ = -0.67, 95% CI = -1.21 to -0.12) ('Larval development' in Figure 18). Short-lived species (< 1 year) and infauna species occupying the first 10 cm of coarse and mixed sediments undergo a significant 32% reduction in abundance following fishing ('Sediment position' in Figure 15, 'Longevity' in Figure 17).

Some interesting contrasting observations were found between sandy and coarse & mixed sediment communities. Whereas scavengers and opportunists underwent the highest reduction in abundance in sand following fishing ($\overline{LnRR}$ = -0.54, 95%CI = -1.01 to -0.07), subsurface deposit feeders were impacted the most in coarse and mixed sediment ($\overline{LnRR}$ = -0.56, 95% CI = -1.01 to -0.13) ('Feeding group in Figure 16). Whereas the abundance of epi- phytic/zoic species was reduced the most in sand (77% reduction on average), burrow-dwelling species were significantly impacted in coarse and mixed sediments (34% reduction on average) ('Living habit' in Figure 16). Accordingly, sessile species were lowest in sand ($\overline{LnRR}$ = -0.39, 95% CI = -0.77 to -0.01), and crawlers were lowest in coarse and mixed sediments ($\overline{LnRR}$ = -0.49, 95% CI = -0.93 to -0.05) ('Mobility' in Figure 17). Interestingly, highly mobile species that should be able to swim away from an approaching bottom towed gear were found to undergo significant reductions in abundance on both sand and coarse and mixed sediments ('Mobility' in Figure 17). In sand, the abundance of highly mobile species in the fished area was reduced by 53% relative to the non-fished area, whereas the abundance in coarse and mixed sediment was reduced by 30% on average.

Although the overall effect of fishing was negative for species characterized by different morphological characteristics and bioturbation ability, none of the differences in abundance between fished and non-fished areas were significant ('Protection' in Figure 15, 'Morphology' in Figure 16, 'Bioturbation' in Figure 17).

Table 9. Summary of a 2-way interaction meta-analysis between sediment type and modality to examine if the effect of fishing on trait modalities depends on the sediment type in which the community occurs.

	Biological trait	**Test of significance to examine 'Sediment type x Modality' interaction**
Biological traits	Body size (mm)	Q_M (df = 26) = 23.14, p = 0.62
	Longevity	Q_M (df = 11) = 5.55, p = 0.91
	Egg development	Q_M (df = 11) = 6.68, p = 0.83
	Larval development	Q_M (df = 8) = 9.13, p = 0.33
	Feeding group	Q_M (df = 24) = 14.55, p = 0.93
	Morphology	Q_M (df = 18) = 14.48, p = 0.7
Ecological traits	Mobility	Q_M (df = 21) = 18.29, p = 0.63
	Sediment position	Q_M (df = 11) = 8.86, p = 0.63
	Living habit	Q_M (df = 24) = 36.76, p = 0.05
	Bioturbation	Q_M (df = 13) = 9.6, p = 0.73
	Protection	Q_M (df = 16) = 14.94, p = 0.53

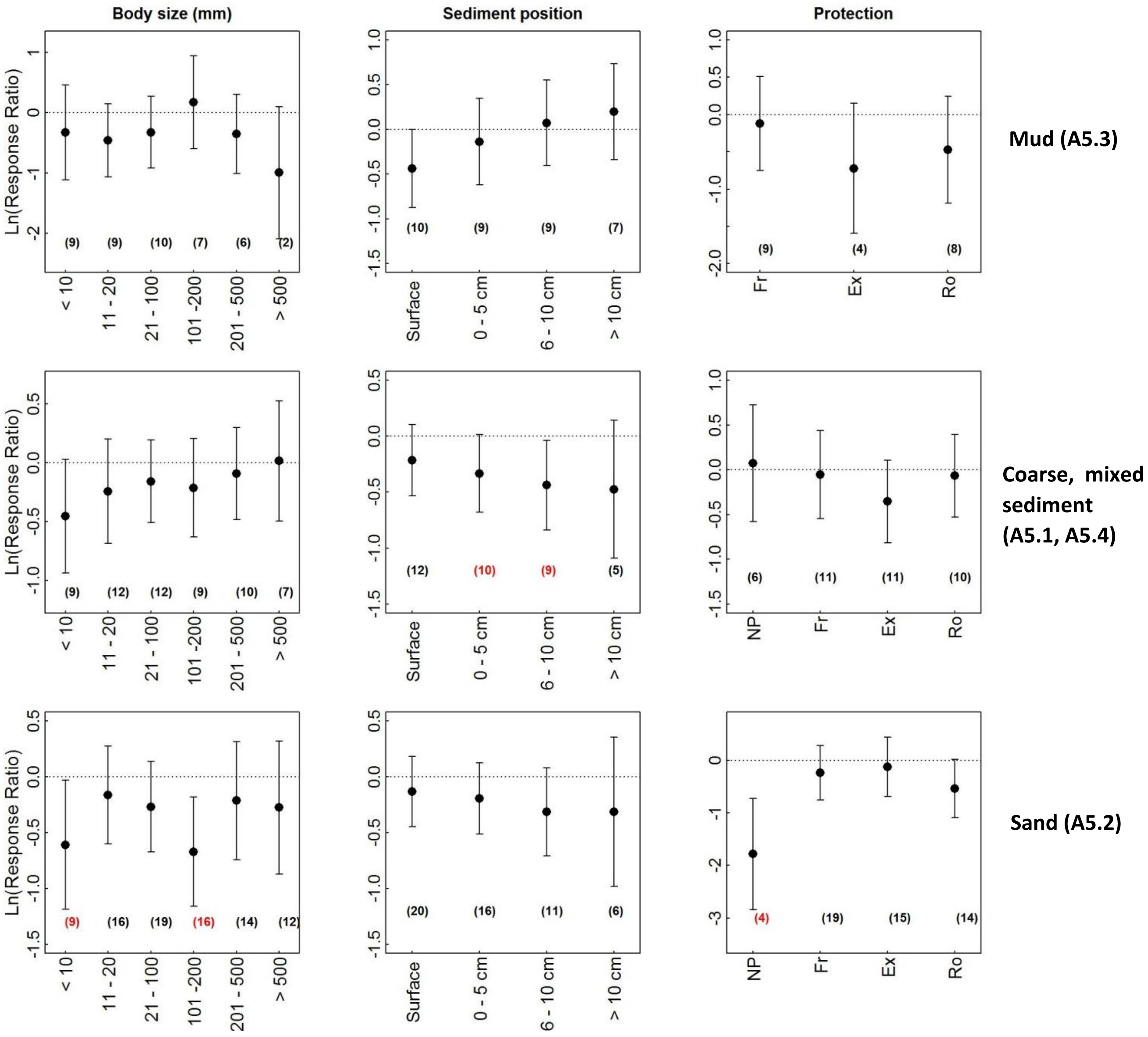


Figure 15. Initial response (up to 7 days after impact) with 95% CI, of species with different body size, sediment position and protection capacity in coarse sediment, sand and mud. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait ‘Protection’: NP = no protection or no regeneration ability, Fr = fragile, Ex = exoskeleton, Ro = robust (hard shell or high regeneration ability).

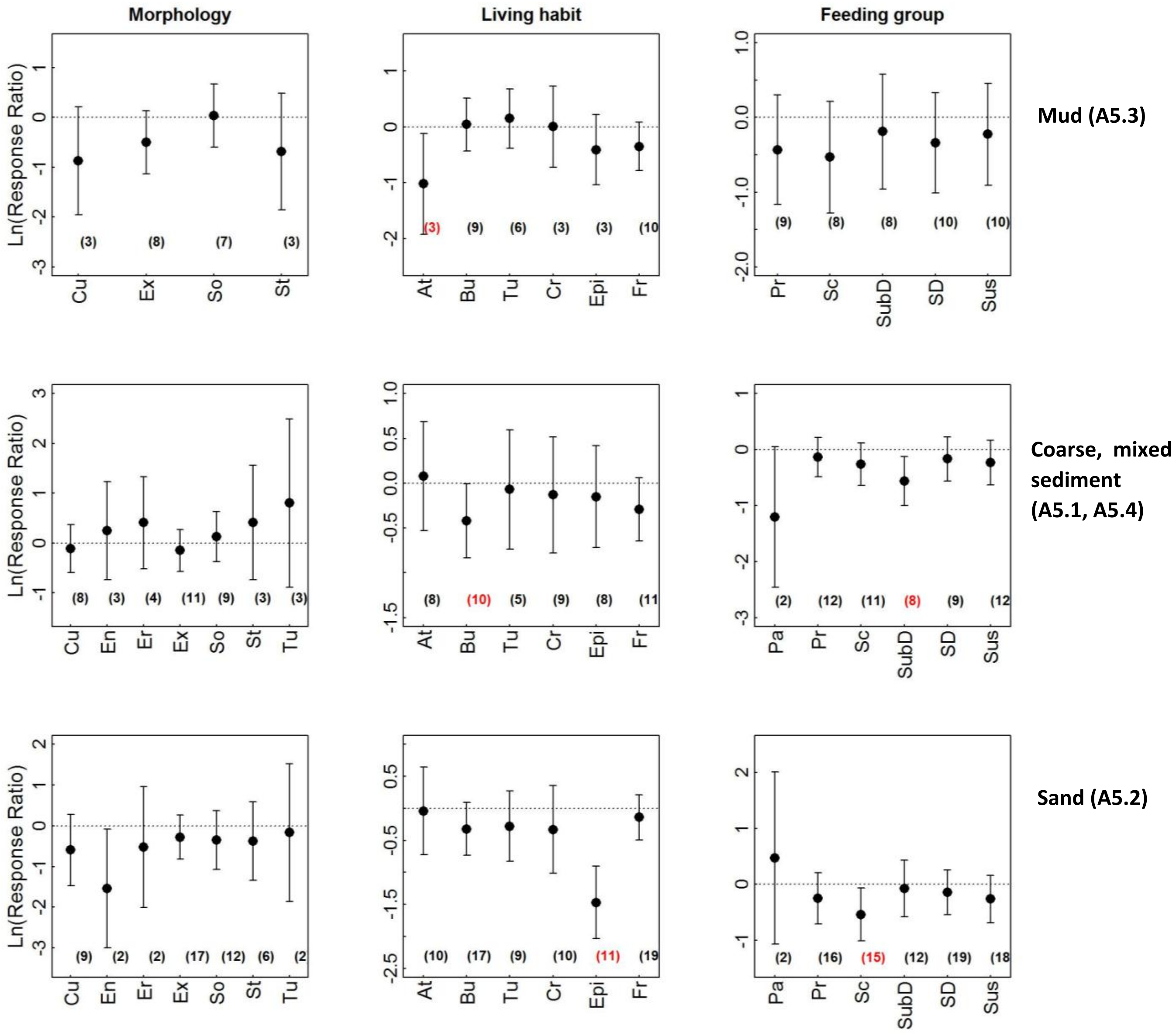


Figure 16. Initial response (up to 7 days after impact) with 95% CI, of species with different morphology, living habit and feeding mode in coarse sediment, sand and mud. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait 'Morphology': Cu = Cushion, En = encrusting, Er = erect, Ex = exoskeleton, So = soft, St = stalked, Tu = tunic. For the trait 'Living habit': At = attached, Bu = Burrow-dwelling, Tu = tube-dwelling, Cr = crevice or under stone, Epi = epi/endo phytic/zoic, Fr = free-living. For the trait 'Feeding group': Pa = parasite, Pr = predator, Sc = scavenging or opportunistic species, SubD = subsurface deposit feeder, SD = surface deposit feeder, Sus = suspension feeder.

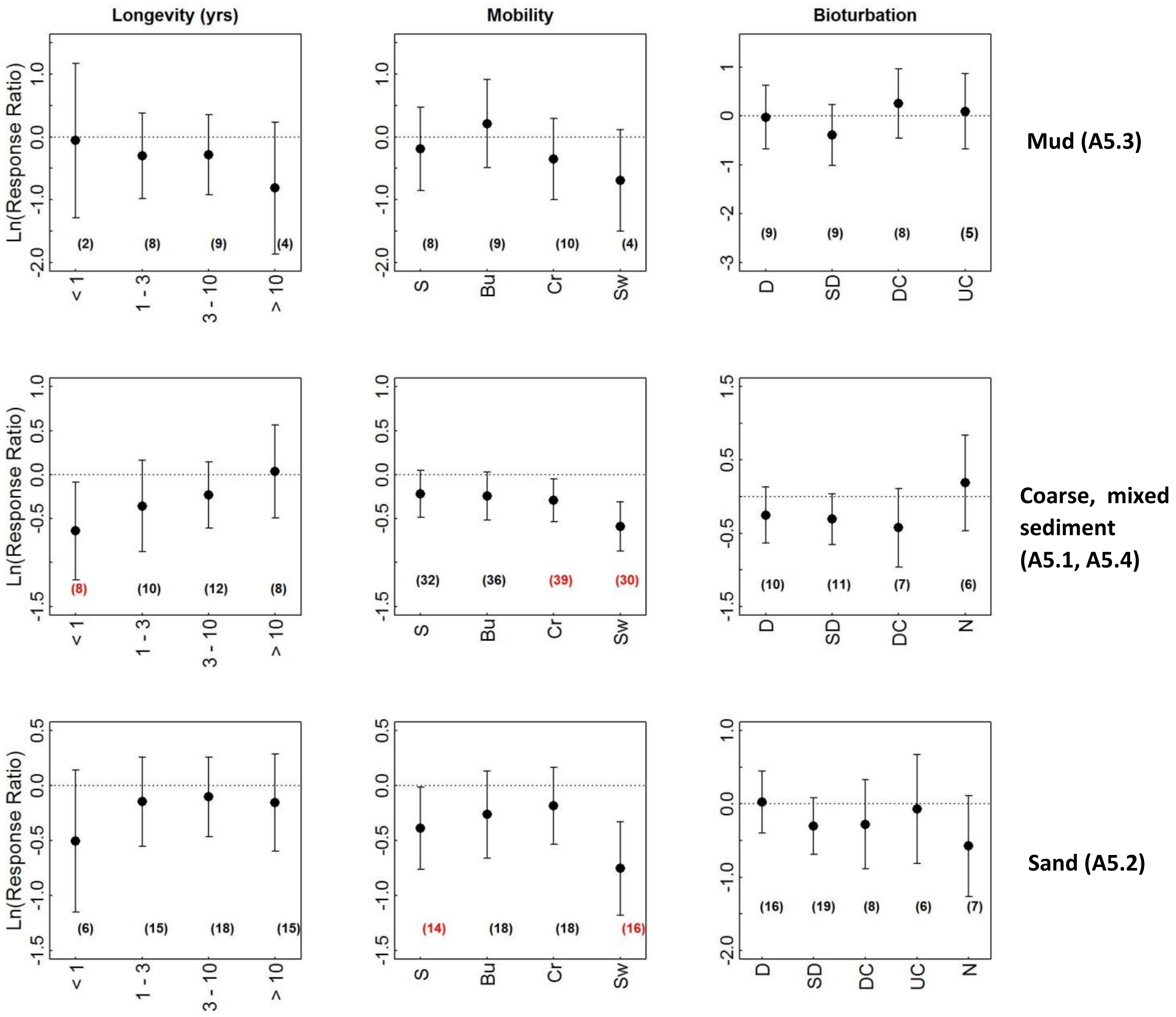
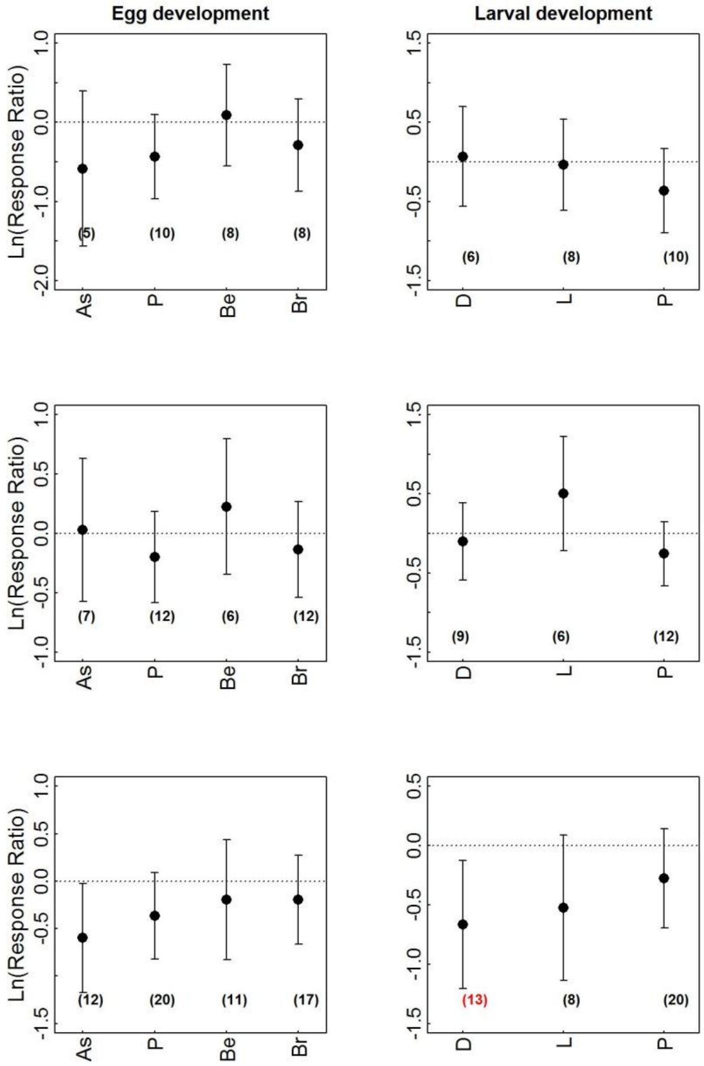


Figure 17. Initial response (up to 7 days after impact) with 95% CI, of species with different longevity, mobility and bioturbation ability in coarse sediment, sand and mud. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait 'Mobility': S = sessile, Bu = burrower, Cr = crawler or creeper, Sw = swimmer. For the trait 'Bioturbation': D = diffusive mixer, SD = surface deposition, DC = downwards conveyor, UC = upwards conveyor, N = no bioturbation.



Mud (A5.3)

Coarse, mixed sediment (A5.1, A5.4)

Sand (A5.2)

Figure 18. Initial response (up to 7 days after impact) with 95% CI, of different egg and larval development stages in coarse sediment, sand and mud. Sample size (i.e. the number of studies) for each response ratio is shown in parentheses. Significant differences between fished and non-fished areas are shown in red. For the trait ‘Egg development’: As = asexual or budding, P = sexual and produced pelagic eggs, Be = sexual and produces benthic eggs, Br = sexual and species broods the eggs. For the trait ‘Larval development’: D = direct development, L = lecitotrophic larvae, P = planktotrophic larvae.

3.4 Meta-analysis of the effect of bottom fishing on total community abundance with time (0 – 730 days following the fishing disturbance event)

There was no significant influence of time since bottom fishing on total community abundance, Q_M (df = 1) = 1.68, p = 0.2, indicating that recovery following the initial reduction in abundance immediately after fishing was not detected (Figure 19). However, when the effect of bottom fishing was partitioned by the fishing gear type used to create the disturbance, different recovery patterns were observed when the area was fished using an otter trawl or a dredge. There were only four studies measuring the response of fishing using a beam trawl; two studies immediately after the disturbance event (i.e. time = 0 days) and two after 180 days. This number of data-points was considered insufficient to examine the relationship of effect size with time; therefore the rate of recovery of benthic community was only examined separately for otter trawl and dredge studies. Both otter trawls and dredges resulted in an overall negative effect on total benthic community abundance immediately after fishing; however the impact for dredging was significantly higher than that of otter trawling (Table 10). Total abundance was reduced by 27% following dredging, and by 3% following otter trawling. Consequently, abundance recovery was faster following otter trawling than following dredging; trawled areas were predicted to recover within less than a week, whereas dredged areas would take about 3.5 years to recover (Figure 20).

The initial effect of fishing and the time to recovery from fishing was also found to differ significantly among benthic communities in different sediment types (Table 11). On average, biogenic habitats underwent a 62% loss in total species abundance on impact with bottom-towed fishing gear, whereas benthic communities in coarse & mixed sediments and sand experienced a 23% loss in abundance (Table 11). Total species abundance in sandy sediments was predicted to occur within 5 months following fishing, whereas abundance in coarse and mixed sediments was estimated to take a year to recover (Figure 21). Biogenic habitats did not show any sign of recovery. Benthic communities in muddy sediments did not show any significant losses in abundance following bottom fishing (Figure 21).

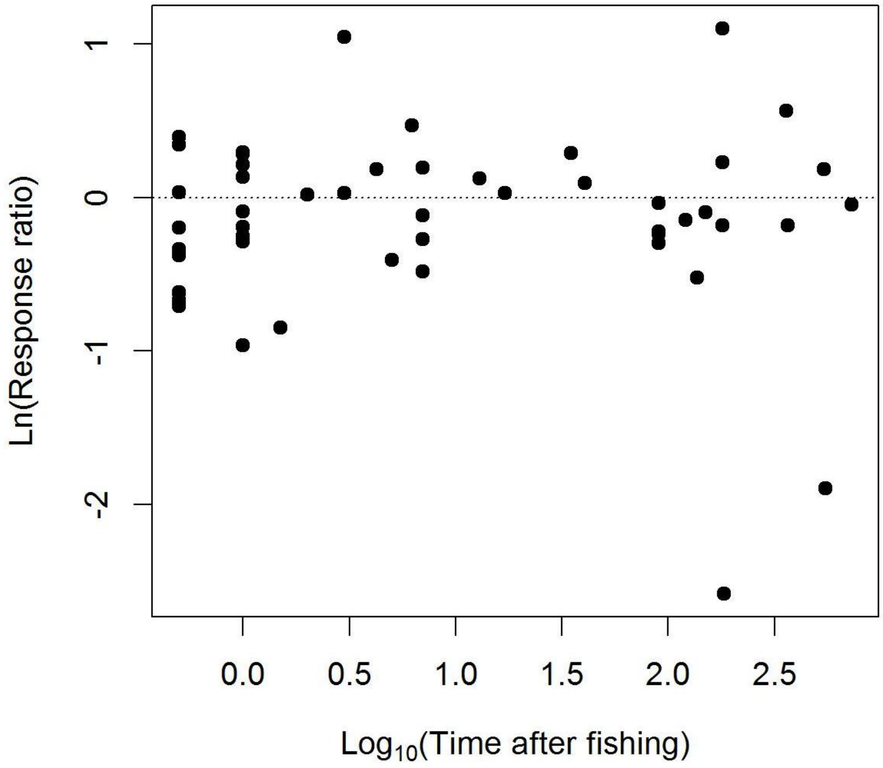


Figure 19. The effect of bottom fishing on total benthic community abundance through time following a fishing disturbance event. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

Table 10. Assessment of the influence of fishing gear type on the rate of recovery of the benthos: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Gear x Log_{10}(Time) and main (Gear, Log_{10}(Time) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of total benthic community abundance to bottom fishing.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Gear x Log_{10}(Time)	68.19	-29.10
Additive model: Gear + Log_{10}(Time)	**66.29**	**-29.15**
Main term: Gear	67.80	-30.90
Main term: Log_{10}(Time)	70.22	-32.11
Null model: no moderators	69.95	-32.98

(II) Output of parsimonious model: Additive model: Gear + Log_{10}(Time)

Q_M(df = 2) = 7.9850, p-val = 0.02
R^2 (amount of heterogeneity accounted for by additive model): 22.21%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.31 (-0.50 to -0.13)
Gear(Otter trawl) = 0.28 (-0.06 to 0.51)
Log_{10}(Time) = 0.1 (-0.01 to 0.21)

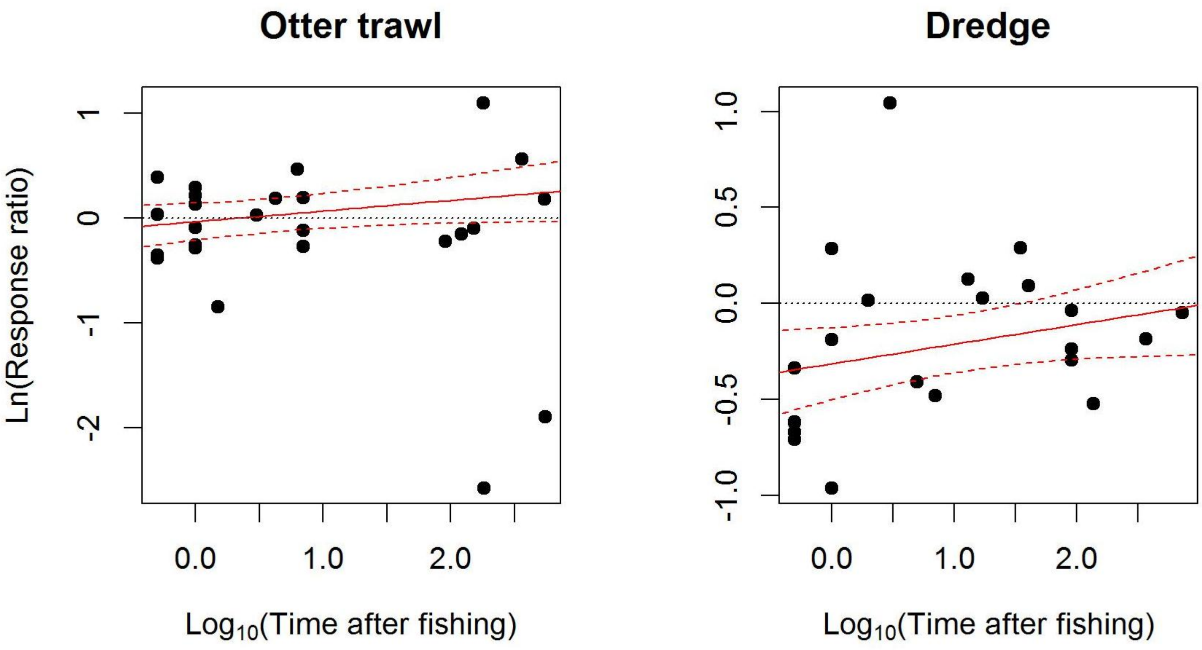


Figure 20. The change in response of total benthic community abundance, estimated as the ln-transformed ratio of abundance in the fished area relative to the control area (Ln(Response ratio), through time following an otter trawling and dredging event. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area. The fitted model and 95% confidence intervals are plotted in red (Fitted model for otter trawling: $y = -0.03 + 0.1\log_{10}$time; fitted model for dredging: $y = -0.31 + 0.1\log_{10}$time).

Table 11. Assessment of the influence of sediment type on the rate of recovery of the benthos: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Sediment type x Log_{10}(Time) and main (Sediment type, Log_{10}(Time) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of total benthic community abundance to bottom fishing, (III) Pairwise tests of significance among levels of different sediment types.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Sediment type x Log_{10}(Time)	73.93	-27.96
Additive model: Sediment type + Log_{10}(Time)	**70.96**	**-29.48**
Main term: Sediment type	74.30	-27.5
Main term: Log_{10}(Time)	82.11	-38.05
Null model: no moderators	83.84	-39.02

(II) Output of parsimonious model: Additive model: Sediment type + Log_{10}(Time)

Q_M(df = 3) = 15.54, p-val = 0.001
R^2 (amount of heterogeneity accounted for by additive model): 32.88%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.31 (-0.51 to -0.12)
Sediment type(Sublittoral sand, A5.2) = 0.05 (-0.21 to 0.30)
Sediment type(Sublittoral mud, A5.3) = 0.41 (0.14 to 0.67)
Sediment type (Sublitoral biogenic habitat, A5.6) = -0.67 (-1.27 to -0.05)
Log_{10}(Time) = 0.12 (0.01 to 0.23)

(III) Pairwise tests among the levels of the categorical moderator, Sediment type

	A5.1, A5.4	A5.2	A5.3
A5.1, A5.4	-	-	-
A5.2	Q_M = 13.72, p = 0.001	-	-
A5.3	Q_M = 11.39, p = 0.003	Q_M = 10.96, p = 0.004	-
A5.6	Q_M = 17.44, p = 0.002	Q_M = 13.75, p = 0.003	Q_M = 13.22, p = 0.001

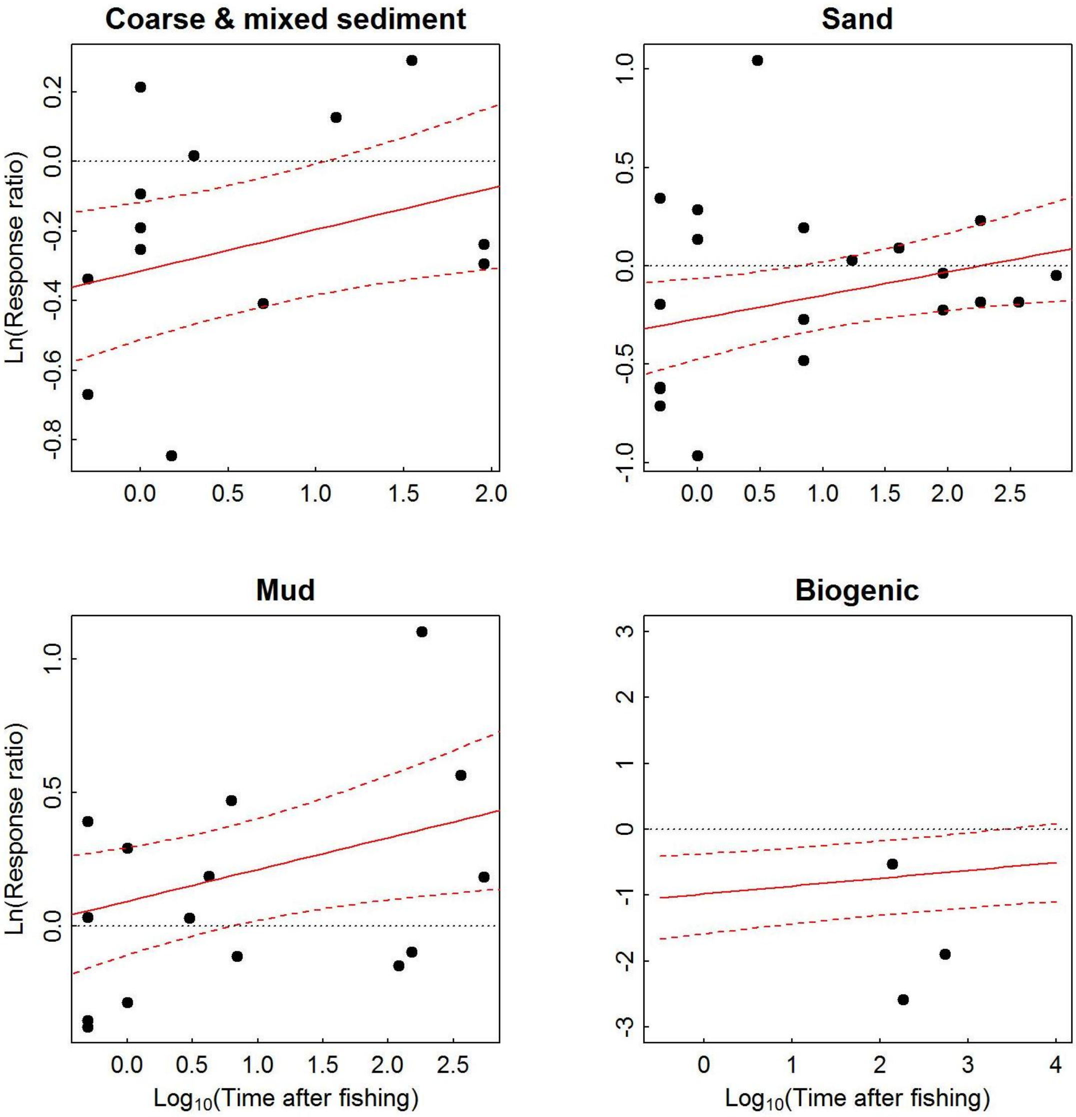


Figure 21. The change in response of total benthic community abundance with time following a fishing event, for benthos occurring in coarse and mixed sediment, sand, mud and in biogenic substrata. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area. The fitted model and 95% confidence intervals are plotted in red (Fitted model for coarse & mixed sediment: $y = -0.31 + 0.12\log_{10}$time; fitted model for sandy sediment: $y = -0.26 + 0.12\log_{10}$time; fitted model for muddy sediment: $y = 0.1 + 0.12\log_{10}$time; fitted model for biogenic habitats: $y = -0.98 + 0.12\log_{10}$time).

3.5 Meta-analysis of the effect of otter trawling on species' biological traits with time (0 – 730 days following the fishing disturbance event)

To examine the patterns of recovery from otter trawling for species with different modalities of a biological trait, the response (ln-transformed response ratio) to trawling was examined over time (log-transformed) using a mixed-effects model consisting of two main effect terms *Modality* and *log_{10}Time* and a two-way interaction term between modality and time (*Modality x log_{10}Time*). The results of model selection using the Akaike's Information Criterion (AIC) are presented in section (I) of Tables 12, 13, 14, 15, 16, 17, 19, 21, 23, 25, 26 for each of the eleven biological traits examined. The relationship between the response to trawling and time for each modality is depicted in Figures 22 - 32 in Appendix II. The model was fitted to the data of a particular biological trait whenever a significant relationship between the effect size and time was identified.

There was no relationship between the response to trawling and *Modality* or *log_{10}Time* (i.e. model with no moderators was the parsimonious model) for a number of biological traits; Sediment position (Table 12), Longevity (Table 13), Mobility (Table 14), Larval development (Table 15) and Protection (Table 16). However, the main effect terms *Modality* and/or *log_{10}Time* explained a significant amount of heterogeneity in the response to trawling for the remaining biological traits. Whereas, the main term *Modality* indicates significant differences in the initial effect of trawling among modalities but no significant changes in response through time (Scenario 1, section 3.4), the additive model *Modality + log_{10}Time* suggests significant differences in the time to recovery between modalities potentially reflecting the differences in the initial impact of trawling among modalities (Scenario 3, section 3.4). There was no significant interaction term for any of the traits, indicating that the rate of recovery did not differ significantly among modalities (Scenario 4, section 3.4). However, changes in response to trawling among modalities through time (i.e. *Modality + log_{10}Time)* were found for species with different morphological and living habit characteristics, and for species with different egg development and bioturbation mechanisms. For ease of interpretation, the results for each of these traits are presented separately below.

Morphology: The initial reduction in abundance following trawling was most severe for encrusting, erect and stalked species compared to cushion-shaped species such as asteroids (Table 17 sections II, III). On average, encrusting, erect and stalked species underwent a 35% loss in abundance following trawling, whereas cushion-shaped species suffered a 14% loss in abundance. A low rate of recovery was observed for all species groups, and the predicted recovery times indicated that cushion-shaped species took about 3 years to recover, whereas encrusting, erect and stalked species did not show signs of recovery (Table 18). As indicated by the positive initial effect, species covered by an exoskeleton or a hard tunic or soft-bodied species such as anemones did not show any significant losses in abundance following trawling (Table 17 sections II, III).

Living habit: The predicted recovery times based on numerical abundance of benthic species with different living habits, suggest faster recovery times for free-living species (24 days) than for species growing attached to the substratum (316 days) and epiphytic or epizoic organisms, which showed no signs of recovery following trawling (Table 20). The initial effect of trawling was disproportionately higher for epiphytic or epizoic organisms (Table 19), potentially resulting in the failure for recovery for this species group. The initial positive effect following trawling for burrowers, tube- and crevice-dwelling species suggests that these species' groups were not significantly impacted by trawling (Table 19, section II).

Egg development: Asexually reproducing species were negatively impacted by trawling (ca. 24% reduction in abundance) and this impact was significantly higher than for sexually reproducing species (Table 21). Sexually reproducing species that produce pelagic or benthic eggs recovered within 6 and 18 days, respectively, following trawling, whereas asexually reproducing species did not appear to recover within two years following the trawling disturbance (Table 22). Sexually reproducing organisms that brood their eggs did not show any significant losses in abundance following trawling (Table 21 sections II, III).

Bioturbation: Non-bioturbating organisms were severely impacted by trawling compared to bioturbating organisms, and these did not show signs of recovery (Table 23, 24). Abundance recovery was faster for diffusive mixers and surface deposition bioturbators (< 2 days), but slower for upward conveyors (147 days) (Table 23, 24). The initial positive effect following trawling for downward conveyors suggests that this species' group was not significantly impacted by trawling (Table 23, 24).

The main effect term *Modality* was the only significant moderator to explain differences in the response to fishing for species belonging to different size classes (Body size) and feeding strategies (Feeding group). This suggests that there is no apparent change in species abundance in the fished area relative to the control area with time for any of the species' size classes (Table 25) and feeding groups (Table 26) examined. The initial effect of trawling was significantly more severe for medium-sized species (101 – 200 mm) than for smaller-sized species (11 – 20 mm) (Table 25 sections II, III). Similarly, the initial effect of trawling was significantly higher for predators and scavengers than for deposit feeders and suspension feeders. On average, the abundance of predators and scavengers was reduced by 5% immediately after a trawling disturbance event (Table 26 sections II, III).

Table 12. Assessment of the influence of otter trawling on the recovery of epibenthic and infaunal species (Biological trait: *Sediment position*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model examining the differences in the initial effect of otter trawling on epifauna and infauna species (no pairwise tests were carried out as initial effect of fishing did not differ significantly among species occupying different position in the sediment).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Sediment position) x Log_{10}(Time)	295.23	-138.62
Additive model: Trait(Sediment position) + Log_{10}(Time)	291.98	-139.99
Main term: Trait(Sediment position)	**291.19**	**-140.59**
Main term: Log_{10}(Time)	292.17	-143.08
Null model: no moderators	291.8	-143.89

(II) Output of parsimonious model: Main term: Trait(Sediment position)

Q_M(df = 3) = 6.64, p-val = 0.08
R^2 (amount of heterogeneity accounted for by additive model): 8.19%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.23 (-0.49 to 0.03)
Sediment position (Surface) = 0.34 (0.04 to 0.64)
Sediment position (0 – 5 cm) = 0.39 (0.09 to 0.69)
Sediment position (6 – 10 cm) = 0.29 (-0.03 to 0.61)

Table 13. Assessment of the influence of otter trawling on the recovery of species with different lifespans (Biological trait: *Longevity*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model examining the differences in the effect of otter trawling on species with different lifespans (no pairwise tests were carried out as initial effect of fishing and time to recovery following fishing did not differ significantly among species with different lifespans).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Longevity) x Log_{10}(Time)	232.99	-107.50
Additive model: Trait(Longevity) + Log_{10}(Time)	**230.65**	**-109.32**
Main term: Trait(Longevity)	230.95	-110.48
Main term: Log_{10}(Time)	225.89	-109.95
Null model: no moderators	226.16	-111.08

(II) Output of parsimonious model: Main term: Trait(Longevity) + Log_{10}(Time)

Q_M(df = 4) = 3.38, p-val = 0.49
R^2 (amount of heterogeneity accounted for by additive model): 0.01%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.02 (-0.34 to 0.3)
Longevity (1 – 3 yrs) = 0.09 (-0.26 to 0.44)
Longevity (3 – 10 yrs) = -0.0001 (-0.35 to 0.35)
Longevity (> 10 yrs) = -0.03 (-0.39 to 0.34)
og_{10}(Time) = 0.05 (-0.02 to 0.13)

Table 14. Assessment of the influence of otter trawling on the recovery of species with different mobility characteristics (Biological trait: *Mobility*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model (modality and time were not found to explain differences in the effect of otter trawling on species with different mobility characteristics, therefore no model was fitted to the data).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Mobility) x Log_{10}(Time)	282.15	-132.08
Additive model: Trait(Mobility) + Log_{10}(Time)	280.12	-134.06
Main term: Trait(Mobility)	279.36	-134.68
Main term: Log_{10}(Time)	278.31	-136.15
Null model: no moderators	**277.51**	**-136.76**

Table 15. Assessment of the influence of otter trawling on the recovery of species with different larval development mechanisms (Biological trait: *Larval development*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model (modality and time were not found to explain differences in the effect of fishing on species with different larval development mechanisms, therefore no model was fitted to the data).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Larval development) x Log_{10}(Time)	253.53	-119.77
Additive model: Trait(Larval development) + Log_{10}(Time)	250.69	-120.35
Main term: Trait(Larval development)	249.37	-120.68
Main term: Log_{10}(Time)	247.03	-120.51
Null model: no moderators	**245.74**	**-120.87**

Table 16. Assessment of the influence of otter trawling on the recovery of species with different protection capacities to the mechanical impact of bottom-towed gear (Biological trait: *Protection*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model examining the relationship of benthic abundance with time (no pairwise tests were carried out as recovery following fishing did not differ significantly among species with different protection capacities).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Protection) x Log_{10}(Time)	214.78	-98.39
Additive model: Trait(Protection) + Log_{10}(Time)	210.35	-99.17
Main term: Trait(Protection)	211.59	-100.79
Main term: Log_{10}(Time)	**205.70**	**-99.85**
Null model: no moderators	206.26	-101.13

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 2.53, p-val = 0.11
R^2 (amount of heterogeneity accounted for by additive model): 2.4%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.03 (-0.17 to 0.11)
Log_{10}(Time) = 0.06 (-0.01 to 0.13)

Table 17. Assessment of the influence of otter trawling on the recovery of species with different morphological characteristics (Biological trait: *Morphology*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different morphological characteristics to bottom fishing, (III) Pairwise tests of significance to compare the magnitude of the initial effect of otter trawling among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Morphology) x Log_{10}(Time)	377.38	-173.69
Additive model: Trait(Morphology + Log_{10}(Time)	**369.98**	**-175.99**
Main term: Trait(Morphology)	369.94	-176.97
Main term: Log_{10}(Time)	381.28	-187.64
Null model: no moderators	379.93	-187.97

(II) Output of parsimonious model: Main term: Trait(Morphology + Log_{10}(Time)

Q_M(df = 7) = 24.14, p-val = 0.001
R^2 (amount of heterogeneity accounted for by additive model): 16.95%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.15 (-0.4 to 0.09)
Morphology (Encrusting) = -0.16 (-0.52 to 0.2)
Morphology (Erect) = -0.26 (-0.6 to 0.06)
Morphology (Exoskeleton) = 0.22 (-0.04 to 0.49)
Morphology (Soft) = 0.24 (-0.05 to 0.53)
Morphology (Stalked) = -0.24 (-0.57 to 0.1)
Morphology (Tunic) = 0.37 (-0.05 to 0.8)
Log_{10}(Time) = 0.05 (-0.02 to 0.12)

(III) Pairwise tests among the levels of the categorical moderator, Morphology

	Cushion	Encrusting	Erect	Exoskeleton	Soft	Stalked

Encrusting	Q_M = 2.57, p = 0.28	-	-	-	-	-
Erect	**Q_M= 6.86, p = 0.03**	Q_M = 2.66, p = 0.26	-	-	-	-
Exoskeleton	Q_M = 3.53, p = 0.17	Q_M = 5.58, p = 0.06	**Q_M = 10.0, p = 0.01**	-	-	-
Soft	Q_M = 2.09, p = 0.35	Q_M = 4.26, p = 0.12	**Q_M = 8.01, p = 0.02**	Q_M = 2.69, p = 0.26	-	-
Stalked	**Q_M = 5.84, p = 0.05**	Q_M = 2.23, p = 0.33	Q_M = 3.39, p = 0.18	**Q_M = 9.0, p = 0.01**	**Q_M = 7.15, p = 0.03**	-
Tunic	Q_M = 3.32, p = 0.19	Q_M = 5.26, p = 0.07	**Q_M = 8.4, p = 0.02**	Q_M = 4.05, p = 0.13	Q_M = 3.77, p = 0.15	**Q_M = 7.67, p = 0.02**

Table 18. The recovery time (in days) of benthic species with different morphological characteristics following otter trawling. The species in the fished area were assumed to have recovered from trawling when the abundance in the fished area was the same as that in the absence of trawling (i.e. LnRR = 0).

Trait modality	Model	Days to recovery
Cushion	LnRR = -0.15 + 0.05 $\log_{10}$time	1000
Encrusting	LnRR = -0.31 + 0.05 $\log_{10}$time	No recovery
Erect	LnRR = -0.41 + 0.05 $\log_{10}$time	No recovery
Exoskeleton	LnRR = 0.07 + 0.05 $\log_{10}$time	Not impacted by trawling
Soft	LnRR = 0.09 + 0.05 $\log_{10}$time	Not impacted by trawling
Stalked	LnRR = -0.39 + 0.05 $\log_{10}$time	No recovery
Tunic	LnRR = 0.22 + 0.05 $\log_{10}$time	Not impacted by trawling

Table 19. Assessment of the influence of otter trawling on the recovery of species with different living habit characteristics (Biological trait: *Living habit*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different living habit characteristics to otter trawling, (III) Pairwise tests of significance to compare the magnitude of the initial effect of fishing among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Living habit) x Log_{10}(Time)	396.96	-185.48
Additive model: Trait(Living habit) + Log_{10}(Time)	**390.01**	**-187.01**
Main term: Trait(Living habit)	393.48	-189.74
Main term: Log_{10}(Time)	394.38	-194.19
Null model: no moderators	395.56	-195.8

(II) Output of parsimonious model: Main term: Trait(Living habit) + Log_{10}(Time)

Q_M(df = 6) = 18.03, p-val = 0.01
R^2 (amount of heterogeneity accounted for by additive model): 14.67%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.2 (-0.46 to 0.05)
Living habit (Burrow-dwelling) = 0.27 (-0.01 to 0.56)
Living habit (Crevice / under stone) = 0.36 (-0.01 to 0.74)
Living habit (Epi/endo phytic/zoic) = -0.15 (-0.46 to 0.16)
Living habit (Free-living) = 0.09 (-0.17 to 0.36)
Living habit (Tube-dwelling) = 0.36 (-0.02 to 0.75)
Log_{10}(Time) = 0.08 (0.01 to 0.15)

(III) Pairwise tests among the levels of the categorical moderator, Living habit

	Attached	Burrow-dwelling	Crevice / under stone	Epi/endo phytic/zoic	Free-living

Burrow-dwelling	$Q_M = 3.65$, $p = 0.16$	-	-	-	-
Crevice / under stone	$Q_M = 4.06$, $p = 0.13$	$Q_M = 4.92$, $p = 0.09$	-	-	-
Epi/endo phytic/zoic	**$Q_M = 9.50$, $p = 0.01$**	**$Q_M = 9.01$, $p = 0.01$**	**$Q_M = 7.32$, $p = 0.03$**	-	-
Free-living	$Q_M = 3.21$, $p = 0.20$	$Q_M = 3.92$, $p = 0.14$	$Q_M = 3.7$, $p = 0.16$	$Q_M = 3.18$, $p = 0.20$	-
Tube-dwelling	$Q_M = 3.92$, $p = 0.14$	$Q_M = 4.83$, $p = 0.09$	$Q_M = 5.28$, $p = 0.07$	**$Q_M = 6.98$, $p = 0.03$**	$Q_M = 3.51$, $p = 0.17$

Table 20. The recovery time (in days) of benthic species with different living habit characteristics following otter trawling. The species in the fished area were assumed to have recovered from trawling when the abundance in the fished area was the same as that in the absence of trawling (i.e. LnRR = 0).

Trait modality	Model	Days to recovery
Attached	$LnRR = -0.2 + 0.08 \log_{10}time$	316
Burrow-dwelling	$LnRR = 0.07 + 0.08 \log_{10}time$	Not impacted by trawling
Crevice / under stone	$LnRR = 0.16 + 0.08 \log_{10}time$	Not impacted by trawling
Epi/endo phyte/zoic	$LnRR = -0.35 + 0.08 \log_{10}time$	No recovery
Free-living	$LnRR = -0.11 + 0.08 \log_{10}time$	24
Tube-dwelling	$LnRR = 0.16 + 0.08 \log_{10}time$	Not impacted by trawling

Table 21. Assessment of the influence of otter trawling on the recovery of species with different egg development mechanisms (Biological trait: *Egg development*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x $\mathrm{Log_{10}}$(Time) and main (Modality, $\mathrm{Log_{10}}$(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different egg development mechanisms, (III) Pairwise tests of significance to compare the magnitude of the initial effect of otter trawling among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Egg development) x $\mathrm{Log_{10}}$(Time)	281.03	-131.52
Additive model: Trait(Egg development) + $\mathrm{Log_{10}}$(Time)	**275.79**	**-131.9**
Main term: Trait(Egg development)	275.73	-132.87
Main term: $\mathrm{Log_{10}}$(Time)	278.36	-136.18
Null model: no moderators	278.01	-137.01

(II) Output of parsimonious model: Main term: Trait(Egg development) + $\mathrm{Log_{10}}$(Time)

Q_M(df = 4) = 10.15, p-val = 0.04
R^2 (amount of heterogeneity accounted for by additive model): 7.56%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.28 (-0.48 to -0.08)
Egg development (Benthic eggs) = 0.25 (0.003 to 0.49)
Egg development (Brooder) = 0.33 (0.10 to 0.55)
Egg development (Pelagic eggs) = 0.23 (-0.001 to 0.45)
$\mathrm{Log_{10}}$(Time) = 0.04 (-0.02 to 0.10)

(III) Pairwise tests among the levels of the categorical moderator, Egg development

	Asexual / Budding	Sexual – pelagic eggs	Sexual – benthic eggs
Sexual – pelagic eggs	Q_M = 5.83, p = 0.05	-	-
Sexual – benthic eggs	Q_M = 6.02, p = 0.05	Q_M = 4.95, p = 0.08	-

Sexual - brooder	**Q_M = 8.08, p = 0.02**	**Q_M = 8.04, p = 0.02**	**Q_M = 8.24, p = 0.02**

Table 22. The recovery time (in days) of benthic species with different egg development mechanisms following otter trawling. The species in the fished area were assumed to have recovered from trawling when the abundance in the fished area was the same as that in the absence of trawling (i.e. LnRR = 0).

Trait modality	Model	Days to recovery
Asexual / Budding	LnRR = -0.28 + 0.04 log$_{10}$time	No recovery
Sexual (pelagic eggs)	LnRR = -0.05 + 0.04 log$_{10}$time	5.6
Sexual (benthic eggs)	LnRR = -0.03 + 0.04 log$_{10}$time	17.8
Sexual (brooder)	LnRR = 0.05 + 0.04 log$_{10}$time	Not impacted by trwaling

Table 23. Assessment of the influence of otter trawling on the recovery of species with different bioturbation mechanisms (Biological trait: *Bioturbation*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log$_{10}$(Time) and main (Modality, Log$_{10}$(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different bioturbation mechanisms, (III) Pairwise tests of significance to compare the magnitude of the initial effect of otter trawling among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)		
	AIC	logLik
Interactive model: Trait(Bioturbation) x Log$_{10}$(Time)	270.67	-124.34
Additive model: Trait(Bioturbation) + Log$_{10}$(Time)	**264.02**	**-125.01**
Main term: Trait(Bioturbation)	265.19	-126.59
Main term: Log$_{10}$(Time)	268.68	-131.34
Null model: no moderators	269.02	-132.51
(II) Output of parsimonious model: Main term: Trait(Bioturbation) + Log$_{10}$(Time)		

Q_M(df = 5) = 15.2, p-val = 0.01
R^2 (amount of heterogeneity accounted for by additive model): 13.1%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.01 (-0.21 to 0.18)
Bioturbation (Surface deposition) = -0.001 (-0.23 to 0.23)
Bioturbation (Downwards conveyor) = 0.26 (-0.02 to 0.54)
Bioturbation (Upwards conveyor) = -0.12 (-0.44 to 0.21)
Bioturbation (No bioturbation) = -0.28 (-0.54 to -0.02)
Log_{10}(Time) = 0.06 (-0.01 to 0.13)

(III) Pairwise tests among the levels of the categorical moderator, Bioturbation

	Diffusive mixer	Surface deposition	Downwards conveyor	Upwards conveyor
Surface deposition	Q_M = 0.03, p = 0.98	-	-	-
Downwards conveyor	Q_M = 4.16, p = 0.13	Q_M = 4.04, p = 0.13	-	-
Upwards conveyor	Q_M = 0.75, p = 0.69	Q_M = 0.53, p = 0.76	Q_M = 4.96, p = 0.08	**-**
No bioturbation	**Q_M = 6.37, p = 0.04**	Q_M = 5.49, p = 0.06	**Q_M = 12.15, p = 0.002**	Q_M = 4.36, p = 0.11

Table 24. The recovery time (in days) of benthic species with different bioturbation mechanisms following otter trawling. The species in the fished area were assumed to have recovered from trawling when the abundance in the fished area was the same as that in the absence of trawling (i.e. LnRR = 0).

Trait modality	Model	Days to recovery
Diffusive mixing	LnRR = -0.01 + 0.06 log_{10}time	1.47
Surface deposition	LnRR = -0.012 + 0.06 log_{10}time	1.59
Downwards conveyor	LnRR = 0.25 + 0.06 log_{10}time	Not impacted by trawling
Upwards conveyor	LnRR = -0.13 + 0.06 log_{10}time	146.7
No bioturbation	LnRR = -0.29 + 0.06 log_{10}time	No recovery

Table 25. Assessment of the influence of otter trawling on the recovery of small, medium and large species (Biological trait: *Body size*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different body size, (III) Pairwise tests of significance to compare the magnitude of the initial effect of otter trawling among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Body size) x Log_{10}(Time)	388.39	-181.2
Additive model: Trait(Body size) + Log_{10}(Time)	380.22	-182.11
Main term: Trait(Body size)	**379.34**	**-182.67**
Main term: Log_{10}(Time)	382.29	-188.14
Null model: no moderators	381.32	-188.66

(II) Output of parsimonious model: Main term: Trait(Body size)

Q_M(df = 5) = 12.0, p-val = 0.03
R^2 (amount of heterogeneity accounted for by additive model): 32.88%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.001 (-0.19 to 0.19)
Body size (11 – 20 mm) = 0.15 (-0.09 to 0.39)
Body size (21 – 100 mm) = 0.12 (-0.12 to 0.36)
Body size (101 – 200 mm) = -0.14 (-0.39 to 0.11)
Body size (201 – 500 mm) = -0.09 (-0.35 to 0.18)
Body size (> 500 mm) = -0.23 (-0.59 to 0.13)

(III) Pairwise tests among the levels of the categorical moderator, Body size (mm)

	< 10	11 – 20	21 – 100	101 – 200	201 – 500
11 – 20 mm	Q_M = 3.31, p = 0.2	-	-	-	-
21 – 100 mm	Q_M = 2.64, p = 0.27	Q_M = 1.53, p = 0.47	-	-	-

101 – 200 mm	Q_M = 3.02, p = 0.22	**Q_M = 6.33,** **p = 0.04**	Q_M = 5.66, p = 0.05	-	-
201 – 500 mm	Q_M = 0.86, p = 0.65	Q_M = 3.75, p = 0.15	Q_M = 3.17, p = 0.2	Q_M = 1.26, p = 0.53	-
> 500 mm	Q_M = 2.18, p = 0.34	Q_M = 4.93, p = 0.08	Q_M = 4.38, p = 0.11	Q_M = 2.03, p = 0.36	Q_M = 1.60, p = 0.45

Table 26. Assessment of the influence of otter trawling on the recovery of species with different feeding strategies (Biological trait: *Feeding group*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different feeding strategies, (III) Pairwise tests of significance to compare the magnitude of the initial effect of otter trawling among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Feeding group) x Log_{10}(Time)	358.47	-168.23
Additive model: Trait(Feeding group) + Log_{10}(Time)	351.17	-168.58
Main term: Trait(Feeding group)	**350.35**	**-174.18**
Main term: Log_{10}(Time)	354.35	-174.18
Null model: no moderators	353.08	-174.54

(II) Output of parsimonious model: Main term: Trait(Feeding group)

Q_M(df = 4) = 10.7, p-val = 0.03
R^2 (amount of heterogeneity accounted for by additive model): 5.85%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.04 (-0.21 to 0.12)
Feeding group (Scavenger / Opportunist) = -0.02 (-0.26 to 0.21)
Feeding group (Subsurface deposit feeder) = 0.16 (-0.08 to 0.41)
Feeding group (Surface deposit feeder) = 0.25 (0.01 to 0.48)
Feeding group (Suspension feeder) = 0.27 (0.04 to 0.52)

(III) Pairwise tests among the levels of the categorical moderator, Feeding group

	Predator	Scavenger / Opportunist	Subsurface deposit feeder	Surface deposit feeder
Scavenger / Opportunist	Q_M = 0.86, p = 0.65	-	-	-
Subsurface deposit feeder	Q_M = 1.91, p = 0.39	Q_M = 2.51, p = 0.28	-	-
Surface deposit feeder	**Q_M = 5.97, p = 0.05**	**Q_M = 6.19, p = 0.05**	Q_M = 4.41, p = 0.11	-
Suspension feeder	**Q_M = 7.73, p = 0.02**	**Q_M = 7.70, p = 0.02**	Q_M = 5.44, p = 0.07	**Q_M = 6.54, p = 0.04**

3.6 Meta-analysis of the effect of dredging on species' biological traits with time (0 – 730 days following the fishing disturbance event)

The results of model selection using the Akaike's Information Criterion (AIC) are presented in section (I) of Tables 27, 28, 29, 30, 31, 33, 35, 37, 38, 39, 40 for each of the eleven biological traits examined. The relationship between the response to trawling and time for each modality is depicted in Figures 33 – 43 in Appendix III. The model was fitted to the data of a particular biological trait whenever a significant relationship between the effect size and time was identified.

There was no significant initial effect of dredging on species' abundance (*Modality)* or a significant relationship between the response to dredging and time (*$log_{10}Time$)* observed for the following biological traits; Morphology (Table 27), Larval development (Table 28), Egg development (Table 29) and Protection (Table 30). A significant interaction term between Modality and time (i.e. *Modality x $log_{10}Time$)* was found for species with different living habit characteristics, feeding mechanisms and for species with different lifespans, indicating that the rate of recovery differed significantly among species groups of these biological traits (Scenario 4, section 3.4). The results for each of these traits are presented separately below for ease of interpretation.

Living habit: As for otter trawling, the initial reduction in abundance following dredging was disproportionately higher for epiphytic and/or epizoic organisms (Table 31 section II), and although the rate of recovery for this species group was significantly faster than that of the other species groups (Table 31 sections II, III), full recovery of epiphytic or epizoic organisms was predicted to take about 4 months to occur (Table 32). The fitted model predicted short recovery times for tube-dwelling species and free-living species (ca. 10 days) compared to burrow-dwelling species which required 8 to 9 months to recover (Table 32). The initial positive effect and relative decline in abundance following dredging for crevice-dwelling species and species that grow attached to the substratum suggests that these species' groups were not significantly impacted by dredging (Table 31, 32).

Feeding group: Dredging did not have a negative impact on predators and scavengers. The initial 8% increase in predator abundance in the fished area relative to the control area suggests that predators may benefit slightly from dredging. Scavengers undergo minimal loss in abundance immediately after dredging (2% reduction), and recovery is very fast for this species group (2 days, Table 33). Conversely, dredging resulted in significant reduction in abundance of deposit feeders and suspension feeders immediately after the fishing disturbance event. Although the initial loss in abundance was higher for deposit feeders (40%) than for suspension feeders (17%), the former recovered within 2 months following dredging whereas suspension feeders showed no signs of recovery (Table 34). The rate of recovery was significantly higher for subsurface deposit feeders than for surface deposit feeders; surface deposit feeders took twice as long to recover following dredging (Table 34).

Longevity: Although the initial effect of dredging was most severe for species with relatively short lifespans, less than 3 years (35 - 44% loss in abundance), the rate of recovery was fastest for this group (Table 35, 36). The predicted time of recovery for species with a maximum lifespan of 1 year was 34 days, whereas for those with a maximum lifespan of 3 years recovery would take about 39 days. Species that live up to 10 years have slower rates of recovery and may take up to 100 days following the dredging impact to recover (Table 36). Interestingly, the initial positive effect and relative decline in abundance following dredging for longer-lived species (more than 10 years) suggests that these species' groups were not significantly impacted by dredging (Table 35, 36).

Mobility, Body size, Sediment position, Bioturbation: The initial effect of dredging on species' abundance was negative irrespective of the size and mobility of the organism, or of whether the species lives on or within the sediment or whether it is a bioturbating species or not. Overall, all four traits indicated a positive recovery of species' abundance over time following a fishing disturbance event (only time was found to be a significant moderator for these traits, Tables 37 – 40). Recovery times based on the fitted models for *Mobility, Body size and Sediment position* ranged from 39 days to 49 days (Fitted model for Mobility: $y = -0.27 + 0.17\log_{10}\text{time}$, Body size: $y = -0.22 + 0.13\log_{10}\text{time}$, Sediment position: $y = -0.29 + 0.18\log_{10}\text{time}$). The initial loss in abundance of species with different bioturbation mechanisms amounted to a 25% reduction in the fished area, indicating a substantial loss in the bioturbation potential of the benthic community immediately following dredging. Recovery based on abundance of species capable of bioturbation was predicted to occur within 85 days following a dredging disturbance event (Fitted model for Bioturbation: $y = -0.27 + 0.14\log_{10}\text{time}$).

Table 27. Assessment of the influence of dredging on the recovery of species with different morphological characteristics (Biological trait: *Morphology*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model examining the differences in the initial effect of dredging species with different morphological characteristics (no pairwise tests were carried out as initial effect of fishing did not differ significantly among species with different morphological characteristics).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Morphology) x Log_{10}(Time)	117.59	-51.79
Additive model: Trait(Morphology + Log_{10}(Time)	115.42	-52.71
Main term: Trait(Morphology)	115.53	-53.76
Main term: Log_{10}(Time)	**111.86**	**-52.93**
Null model: no moderators	111.98	-53.99

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 2.08, p-val = 0.15
R^2 (amount of heterogeneity accounted for by additive model): 0.21%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.19 (-0.39 to 0.01)
Log_{10}(Time) = 0.1 (-0.04 to 0.24)

Table 28. Assessment of the influence of fishing on the recovery of species with different larval development mechanisms (Biological trait: *Larval development*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model (modality and time were not found to explain differences in the effect of fishing on species with different larval development mechanisms, therefore no model was fitted to the data).

(I) Model selection using Akaike's Information Criterion (AIC)	AIC	logLik
Interactive model: Trait(Larval development) x Log_{10}(Time)	140.07	-63.04
Additive model: Trait(Larval development) + Log_{10}(Time)	137.25	-63.62
Main term: Trait(Larval development)	137.25	-64.62
Main term: Log_{10}(Time)	137.15	-65.58
Null model: no moderators	**137.05**	**-66.53**

Table 29. Assessment of the influence of dredging on the recovery of species with different egg development mechanisms (Biological trait: *Egg development*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model examining the differences in the initial effect of dredging species with different egg development mechanisms (no pairwise tests were carried out as initial effect of fishing did not differ significantly among species with different egg development mechanisms).

(I) Model selection using Akaike's Information Criterion (AIC)	AIC	logLik
Interactive model: Trait(Egg development) x Log_{10}(Time)	184.44	-83.22
Additive model: Trait(Egg development) + Log_{10}(Time)	185.88	-86.94
Main term: Trait(Egg development)	185.83	-87.91
Main term: Log_{10}(Time)	**182.57**	**-88.28**
Null model: no moderators	182.67	-89.33

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 2.12, p-val = 0.15
R^2 (amount of heterogeneity accounted for by additive model): 0.1%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.19 (-0.38 to -0.02)
Log_{10}(Time) = 0.09 (-0.03 to 0.21)

Table 30. Assessment of the influence of dredging on the recovery of species with different protection capacities to bottom fishing (Biological trait: *Protection*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main effect (Modality, Log_{10}(Time)) terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model examining the differences in the initial effect of dredging species with different protection capacities to bottom fishing (no pairwise tests were carried out as initial effect of fishing did not differ significantly among modalities).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Protection) x Log_{10}(Time)	148.94	-67.47
Additive model: Trait(Protection) + Log_{10}(Time)	149.12	-69.56
Main term: Trait(Protection)	149.29	-70.64
Main term: Log_{10}(Time)	**145.87**	**-69.94**
Null model: no moderators	146.06	-71.03

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 2.16, p-val = 0.14
R^2 (amount of heterogeneity accounted for by additive model): 0.1%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.19 (-0.36 to -0.02)
Log_{10}(Time) = 0.09 (-0.03 to 0.21)

Table 31. Assessment of the influence of dredging on the recovery of species with different living habit characteristics (Biological trait: *Living habit*): (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different living habit characteristics to dredging, (III) Pairwise tests of significance to compare the rate of recovery following dredging among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Living habit) x Log$_{10}$(Time)	**211.76**	**-92.88**
Additive model: Trait(Living habit) + Log$_{10}$(Time)	213.6	-98.80
Main term: Trait(Living habit)	218.77	-102.39
Main term: Log$_{10}$(Time)	213.2	-101.58
Null model: no moderators	213.83	-104.91

(II) Output of parsimonious model: Main term: Trait(Living habit) * Log$_{10}$(Time)

Q$_M$(df = 11) = 25.75, p-val = 0.01
R^2 (amount of heterogeneity accounted for by additive model): 35.05%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = 0.20 (-0.5 to 0.9)
Log$_{10}$(Time) = -0.2 (-0.66 to 0.25)
Living habit (Burrow-dwelling) = -0.54 (-1.31 to 0.24)
Living habit (Crevice / under stone) = 0.23 (-0.71 to 1.16)
Living habit (Epi/endo phytic/zoic) = -1.18 (-2.04 to 0.33)
Living habit (Free-living) = -0.39 (-1.15 to 0.36)
Living habit (Tube-dwelling) = -0.39 (-1.18 to 0.41)
Living habit (Burrow-dwelling):Log$_{10}$(Time) = 0.34 (-0.17 to 0.85)
Living habit (Crevice / under stone):Log$_{10}$(Time) = 0.04 (-0.52 to 0.6)
Living habit (Epi/endo phytic/zoic):Log$_{10}$(Time) = 0.68 (0.14 to 1.21)
Living habit (Free-living):Log$_{10}$(Time) = 0.38 (-0.12 to 0.87)
Living habit (Tube-dwelling):Log$_{10}$(Time) = 0.39 (-0.13 to 0.92)

(III) Pairwise tests among recovery rates of different Living habit modalities

	Attached): Log$_{10}$(Time)	Burrower: Log$_{10}$(Time)	Crevice: Log$_{10}$(Time)	Epiphytic/zoic: Log$_{10}$(Time)	Free-living :Log$_{10}$(Time)
Burrower:Log$_{10}$ (Time)	Q$_M$ = 1.87, p = 0.39	-	-	-	-
Crevice:Log$_{10}$ (Time)	Q$_M$ = 0.38, p = 0.83	Q$_M$ = 3.04, p = 0.22	-	-	-

Epiphytic/zoic): Log_{10}(Time)	**Q_M = 7.92, p = 0.02**	**Q_M = 6.88, p = 0.03**	**Q_M = 10.84, p = 0.004**	-	-
Free-Living :Log_{10}(Time)	Q_M = 2.65, p = 0.27	Q_M = 2.22, p = 0.33	Q_M = 4.37, p = 0.11	**Q_M = 6.64, p = 0.04**	-
Tube-dwelling):Log_{10} (Time)	Q_M = 2.46, p = 0.29	Q_M = 2.23, p = 0.33	Q_M = 3.79, p = 0.15	**Q_M = 6.38, p = 0.04**	Q_M = 2.42, p = 0.3

Table 32. The recovery time (in days) of benthic species with different living habit characteristics following dredging. The species in the fished area were assumed to have recovered from trawling when the abundance in the fished area was the same as that in the absence of trawling (i.e. LnRR = 0).

Trait modality	Model	Days to recovery
Attached	LnRR = 0.2 – 0.2 log_{10}time	10
Burrow-dwelling	LnRR = -0.34 + 0.14 log_{10}time	268
Crevice-dwelling	LnRR = 0.43 – 0.16 log_{10}time	Not impacted by dredging
Epi/endo phyte/zoic	LnRR = -0.98 + 0.48 log_{10}time	110
Free-living	LnRR = -0.19 + 0.18 log_{10}time	11
Tube-dwelling	LnRR = -0.19 + 0.19 log_{10}time	10

Table 33. Assessment of the influence of dredging on the recovery of species with different feeding strategies (Biological trait: *Feeding group)*: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different feeding strategies to dredging, (III) Pairwise tests of significance to compare the rate of recovery following dredging among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)		
	AIC	logLik

Interactive model: Trait(Feeding group) x Log$_{10}$(Time)	**168.86**	**-73.43**
Additive model: Trait(Feeding group) + Log$_{10}$(Time)	174.99	-80.49
Main term: Trait(Feeding group)	180.97	-84.49
Main term: Log$_{10}$(Time)	171.65	-82.82
Null model: no moderators	177.6	-86.8

(II) Output of parsimonious model: Interactive model: Trait(Feeding group) x Log$_{10}$(Time)

Q_M(df = 9) = 28.95, p-val = 0.001
R^2 (amount of heterogeneity accounted for by additive model): 52.56%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = 0.08 (-0.14 to 0.3)
Log$_{10}$(Time) = -0.02 (-0.17 to 0.12)
Feeding group (Scavenger / Opportunist) = -0.28 (-0.64 to 0.07)
Feeding group (Subsurface deposit feeder) = -0.66 (-1.07 to -0.26)
Feeding group (Surface deposit feeder) = -0.57 (-0.9 to -0.25)
Feeding group (Suspension feeder) = -0.27 (-0.57 to 0.04)
Feeding group (Scavenger / Opportunist):Log$_{10}$(Time) = 0.09 (-0.15 to 0.33)
Feeding group (Subsurface deposit feeder):Log$_{10}$(Time) = 0.4 (0.15 to 0.66)
Feeding group (Surface deposit feeder):Log$_{10}$(Time) = 0.29 (0.07 to 0.52)
Feeding group (Suspension feeder):Log$_{10}$(Time) = 0.07 (-0.14 to 0.28)

(III) Pairwise tests among recovery rates of different Feeding group modalities

	Scavenger: Log$_{10}$ (Time)	Subsurface deposit:Log$_{10}$ (Time)	Surface deposit :Log$_{10}$ (Time)	Suspension:Log$_{10}$ (Time)
Sub-surface deposit:Log$_{10}$ (Time)	Q_M = 9.59, p = **0.008**	-	-	-
Surface deposit: Log$_{10}$ (Time)	Q_M = 6.43, p = **0.04**	Q_M = 11.73, p = **0.003**	-	-
Suspension:Log$_{10}$ (Time)	Q_M = 0.68, p = 0.71	Q_M = 9.86, p = **0.01**	Q_M = 6.66, p = **0.04**	-
Predator:Log$_{10}$ (Time)	Q_M = 0.76, p = 0.68	Q_M = 9.81, p = **0.01**	Q_M = 6.6, p = **0.04**	Q_M = 0.64, p **= 0.73**

Table 34. The recovery time (in days) of benthic species with different feeding strategies following dredging. The species in the fished area were assumed to have recovered from trawling when the abundance in the fished area was the same as that in the absence of trawling (i.e. LnRR = 0).

Trait modality	**Model**	**Days to recovery**
Predator	LnRR = 0.08 – 0.02 log$_{10}$time	Not impacted by dredging
Scavenger / opportunist	LnRR = -0.02 + 0.07 log$_{10}$time	2
Subsurface deposit feeder	LnRR = -0.58 + 0.38 log$_{10}$time	34
Surface deposit feeder	LnRR = -0.49 + 0.27 log$_{10}$time	65
Suspension feeder	LnRR = -0.19 +0.05 log$_{10}$time	No recovery

Table 35. Assessment of the influence of dredging on the recovery of species with different lifespans (Biological trait: *Longevity)*: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log$_{10}$(Time) and main (Modality, Log$_{10}$(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model with moderators that have been found to account for a significant amount of heterogeneity in the response of species with different lifespans to dredging, (III) Pairwise tests of significance to compare the rate of recovery following dredging among different modalities. Significant differences are shown in bold.

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Longevity) x Log$_{10}$(Time)	**135.82**	**-58.91**
Additive model: Trait(Longevity) + Log$_{10}$(Time)	146.83	-67.41
Main term: Trait(Longevity)	148.68	-69.34
Main term: Log$_{10}$(Time)	141.61	-67.81
Null model: no moderators	143.38	-69.69

(II) Output of parsimonious model: Interactive model: Trait(Longevity) * Log$_{10}$(Time)

Q_M(df = 7) = 23.15, p-val = 0.002

R^2 (amount of heterogeneity accounted for by additive model): 45.26%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.58 (-1.03 to -0.12)
Log_{10}(Time) = 0.38 (0.08 to 0.68)
Longevity (1 – 3 yrs) = 0.15 (-0.38 to 0.68)
Longevity (3 – 10 yrs) = 0.36 (-0.17 to 0.88)
Longevity (> 10 yrs) = 0.9 (0.33 to 1.48)
Longevity (1 – 3 yrs):Log_{10}(Time) = -0.11 (-0.47 to 0.25)
Longevity (3 – 10 yrs):Log_{10}(Time) = -0.27 (-0.61 to 0.08)
Longevity (> 10 yrs):Log_{10}(Time) = -0.73 (-1.12 to -0.34)

(III) Pairwise tests among recovery rates of different Longevity modalities

	< 1 yrs: Log_{10}(Time)	1 - 3 yrs: Log_{10}(Time)	3 – 10 yrs: Log_{10}(Time)
1 - 3 yrs: Log_{10}(Time)	Q_M = 7.87, p = **0.02**	-	-
3 - 10 yrs: Log_{10}(Time)	Q_M = 13.56, p = **0.001**	Q_M = 2.79, p = 0.25	-
> 10 yr: Log_{10}(Time)	Q_M = 6.26, p = **0.04**	Q_M = 17.98, p = **0.0001**	Q_M = 14.51, p = **0.001**

Table 36. The recovery time (in days) of benthic species with different lifespans following dredging. The species in the fished area were assumed to have recovered from trawling when the abundance in the fished area was the same as that in the absence of trawling (i.e. LnRR = 0).

Trait modality	Model	Days to recovery
< 1 yr	LnRR = -0.58 + 0.38 log_{10}time	34
1 – 3 yrs	LnRR = -0.43 + 0.27 log_{10}time	39
3 – 10 yrs	LnRR = -0.22 + 0.11 log_{10}time	100
> 10 yrs	LnRR = 0.32 – 0.35 log_{10}time	Not impacted by dredging

Table 37. Assessment of the influence of dredging on the recovery of species with different mobilities (Biological trait: *Mobility)*: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model

with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model which examines the relationship of effect size with time (no pairwise tests were carried out as the initial effect of dredging or the rate of recovery following dredging did not differ significantly among modalities).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Mobility) x Log_{10}(Time)	148.67	-65.34
Additive model: Trait(Mobility) + Log_{10}(Time)	144.89	-66.44
Main term: Trait(Mobility)	152.86	-71.43
Main term: Log_{10}(Time)	**141.06**	**-67.53**
Null model: no moderators	147.91	-71.96

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 8.99, p-val = 0.002
R^2 (amount of heterogeneity accounted for by additive model): 15.01%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.27 (-0.44 to -0.1)
Log_{10}(Time) = 0.17 (0.06 to 0.28)

Table 38. Assessment of the influence of dredging on the recovery of small, medium and large species (Biological trait: *Body size)*: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model which examines the relationship of effect size with time (no pairwise tests were carried out as the initial effect of dredging or the rate of recovery following dredging did not differ significantly among modalities).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Body size) x Log_{10}(Time)	234.25	-104.12

Additive model: Trait(Body size) + Log_{10}(Time)	232.12	-108.06
Main term: Trait(Body size)	235.72	-110.86
Main term: Log_{10}(Time)	**224.33**	**-109.16**
Null model: no moderators	228.42	-112.21

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 6.08, p-val = 0.01
R^2 (amount of heterogeneity accounted for by Log_{10}(Time)): 4.59%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.22 (-0.37 to -0.08)
Log_{10}(Time) = 0.13 (0.03 to 0.23)

Table 39. Assessment of the influence of dredging on the recovery of epifauna and infauna species (Biological trait: *Sediment position)*: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model which examines the relationship of effect size with time (no pairwise tests were carried out as the initial effect of dredging or the rate of recovery following dredging did not differ significantly among modalities).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Sediment position) x Log_{10}(Time)	114.36	-48.18
Additive model: Trait(Sediment position) + Log_{10}(Time)	114.06	-51.03
Main term: Trait(Sediment position)	123.86	-56.93
Main term: Log_{10}(Time)	**111.99**	**-52.99**
Null model: no moderators	120.85	-58.43

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 11.36, p-val = 0.0007
R^2 (amount of heterogeneity accounted for by additive model): 23.11%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.29 (-0.45 to -0.13)
Log_{10}(Time) = 0.18 (0.08 to 0.29)

Table 40. Assessment of the influence of dredging on the recovery of species with different bioturbation mechanisms (Biological trait: *Bioturbation)*: (I) Model selection using Akaike's Information Criterion (AIC) to compare a sequence of models in which non-significant interaction (Modality x Log_{10}(Time) and main (Modality, Log_{10}(Time)) effects terms are incrementally removed from the model. The model with the lowest value of AIC was identified as the most parsimonious model, (II) Output of parsimonious model which examines the relationship of effect size with time (no pairwise tests were carried out as the initial effect of dredging or the rate of recovery following dredging did not differ significantly among modalities).

(I) Model selection using Akaike's Information Criterion (AIC)

	AIC	logLik
Interactive model: Trait(Bioturbation) x Log_{10}(Time)	157.34	-67.67
Additive model: Trait(Bioturbation) + Log_{10}(Time)	150.73	-68.37
Main term: Trait(Bioturbation)	153.97	-70.98
Main term: Log_{10}(Time)	**144.22**	**-69.11**
Null model: no moderators	148.09	-72.04

(II) Output of parsimonious model: Main term: Log_{10}(Time)

Q_M(df = 1) = 5.86, p-val = 0.02
R^2 (amount of heterogeneity accounted for by additive model): 8.17%

Model moderators: coefficient (lower and upper 95% confidence limits)
Intercept = -0.27 (-0.45 to -0.09)
Log_{10}(Time) = 0.14 (0.03 to 0.26)

4 DISCUSSION

4.1 Severity of impact and recovery of total community abundance

Bottom fishing resulted in significant negative impacts on total benthic community abundance. Reductions were significantly higher following dredging compared to otter trawling and beam trawling, and they were most severe for benthic communities in biogenic habitats and coarse and mixed sediment relative to sandy and muddy sediments. These observations are in general agreement with those obtained by previous syntheses of global trends in the response of benthic biota and habitats to bottom fishing disturbance (Collie et al. 2000; Kaiser et al. 2006).

Otter trawling had a significant initial effect on the benthos, however, these effects were short-lived and recovery was relatively quicker than for dredged areas, which were predicted to take about 3.5 years to recover. Biogenic habitats undergo the biggest loss in abundance on impact with bottom-towed gear, and the damage in these habitats may be irreversible as recovery did not appear to take place at any point after the disturbance. Coarse and mixed sediment habitats, which are relatively stable and tend to support communities with high levels of diversity and biomass, were negatively affected by bottom fishing both in the short- and long-term; a 41% loss in abundance was estimated to occur immediately following the disturbance and community recovery was predicted to take up to a year after the fishing impact to occur. Blyth et al. (2004) had also shown that the benthic community of a mixed coarse substratum area impacted by towed gear was approaching the composition of an adjacent non-impacted area 2 years post-fishing. Collie et al. (2005) showed significant increases in abundance and biomass 2-5 years after the closure of a gravel sediment area of the Georges Bank, but increases in numbers and biomass of certain species were still observed up to 5 years after the closure. The reduction in abundance of benthos in sandy and muddy sediments was lower than that for biogenic or coarse and mixed sediment (14% and 5% reductions, respectively). This may be partly due to the highly energetic nature of shallow, subtidal, soft-sediment habitats in which physical processes will have a significant habitat-structuring influence (e.g. wave action and bed scour). Benthic communities in sandy habitats were predicted to occur within 5 months of the disturbance, which fits in with estimates obtained from large-scale studies. Dernie et al. (2003) studied the effects of two intensities of physical disturbance on both the habitat and fauna of a sheltered sand flat, and found that benthic community recovery from the lower intensity disturbance occurred within 2 months of the disturbance, whereas recovery after higher intensity disturbance occurred 5 – 7 months post-disturbance.

4.2 Severity of fishing impact among modalities within trait categories

Fishing resulted in significant reductions in abundance in the fished area relative to the non-fished area for a number of modalities, and these differences were more pronounced following dredging than after otter trawling. This suggests that dredging causes more severe impacts and potentially more profound effects on ecosystem functioning than otter trawling. Motility and burrowing behaviour proved to be important traits in determining vulnerability to dredging, as organisms that burrow deeper than the penetration depth of the gear may avoid fishing disturbance (Philippart 1998, Ramsay et al. 1998, Frid et al. 2005). Conversely, sessile organisms and infauna species that occur within the first 10 cm of the sediment were most vulnerable to dredging. Predatory species showed very little reduction in abundance in the fished area relative to the non-fished area, whereas scavengers, deposit feeders and suspension feeders proved vulnerable to dredging, as significantly lower densities of these organisms were recorded in the fished area. The decrease in abundance of suspension feeders agrees with predictions that these species can be negatively affected by fishing due to increased suspended sediment concentrations that may damage their filtering devices (Caddy 1973). Previous studies have reported deposit feeders and scavengers to benefit from the increase of organic matter available in the sediment column (Frid et al. 2000) and from the increase of carrion supply (Kaiser and Spencer 1994, Ramsay et al. 1998, Demestre et al. 2000) in the fished area following fishing. However, our results indicate that the magnitude of loss in abundance on direct contact with the dredge outweighs the benefits that may potentially result from increased food supply for scavengers and deposit feeders following fishing. Bremner et al. (2005) found that the abundance of scavengers and predators decreased with an increase in fishing intensity. It may be then that whereas scavengers and deposit feeders may benefit from fishing at low fishing intensity, this may not hold true in areas of high fishing intensity. There is, however, no evidence for this, as we found no significant relationship between effect size and intensity of experimental fishing for both scavenging and deposit feeding species groups.

Dredging was also found to result in significant reductions of short-lived species and of sexually reproducing species that produce pelagic eggs and planktotrophic larvae. This may have profound long-term implications for population recovery or for the recolonization of other impacted areas further afield that depend on an external source of larvae for their survivability. Previous studies have shown these species groups to be less impacted by fishing compared to longer-lived species and species that lay or attach their eggs to the seabed (Phillippart 1998; Tillin et al. 2006). It is therefore interesting that we observe the strongest impact following fishing for these modalities. A principal component analysis among biological traits (Appendix IV) revealed high positive correlation among species that produce pelagic eggs and burrowing species that occupy the first 5 cm of the sediment, and between short-lived (<1 – 3 years) species and small-bodied species and species with no form of protection (such as an exoskeleton or hard shell or high regeneration ability) from fishing; modalities which have also been found to be negatively impacted by dredging. Although each traits was assessed in isolation in our analysis, it is important to keep in mind that species are characterized by a whole suite of biological traits and whereas some characteristics may make them highly vulnerable to fishing in the first instance (e.g. the absence of a shell or occurrence on or slightly below the sediment surface), others increase the rate of recoverability of the same species (e.g. short lifespans and planktotrophic larvae). A case in point is shown by the time taken for short-lived species to recover. Our results showed that although short-lived species undergo the highest reduction in abundance immediately after fishing (perhaps because of no external protection from fishing), these organisms recovered within a month. Although assessing each trait in isolation may have some short-comings, an assessment that investigates differences in the composition of each trait separately has a number of advantages over assessments in which all traits are considered simultaneously. Firstly, the results are less dependent upon the choice and/or selection of which traits are included within the study. Secondly, an appraisal of the actual trait categories displaying a significant change between the various studies, when combined, may be used to infer aspects of functional change.

Although bottom fishing resulted in a reduction in the abundance of all modalities with different biological traits, on average, we did not find significant differences in the response to fishing among the different modalities for any of the traits examined. This indicates that the initial reductions in abundance in the fished area as a result of bottom fishing are similar among different modalities of a biological trait. The lack of significant differences in the response to fishing among different modalities is likely a result of highly variable effects of fishing among studies. This is reflected by a high variance around the values for mean ln-response ratio (i.e. wide 95% confidence intervals). This variability potentially arises from a host of factors including differences in measurements used to monitor impact, methodology used to collect data, geographic locations of studies, timing of fishing (season), size of impacted areas, local physical environmental conditions and local and regional management policies. Although no formal analysis of the influence of season on the response to fishing was carried out, the majority (80%) of studies that sampled the benthos immediately after or within a week of the fishing disturbance were carried out during summer, therefore although the influence of season cannot be ruled out, the high variability of response around the mean cannot be solely attributed to lower or higher recruitment and re-colonization rates associated with different seasons. Differences in the level of background fishing among the experimentally fished areas may also contribute to variation in the response of benthos to fishing, however this is unlikely the case for this synthesis as the majority (95%) of studies were undertaken in areas that have been closed to fishing, or in areas that are known from vessel monitoring system (VMS) data to experience only limited or no fishing effort or are known to have remained unexploited for reasons such as seabed obstructions.

4.3 Recovery patterns for species characterized by different biological traits

Recovery times following dredging were significantly shorter for short-lived species (<1 – 3 years), free-living and tube-dwelling species and for scavenging or opportunistic species, than for medium-lived species (3 – 10 years), burrow-dwelling species and suspension feeders. In trawled areas, recovery times were significantly shorter for free-living species, species covered by an exoskeleton or a hard tunic and species that produce pelagic or benthic eggs than for epiphytic/zoic species, species that grow attached to the substratum and have an erect or stalked body form and species that reproduce asexually. Differences in the recoverability of different species groups following fishing may result in changes in community composition and ecosystem functioning over the long term. These results are in agreement with experimental and observational studies that have observed changes in benthic community composition and structure; from those dominated by slow-moving or sessile erect, filter-feeding species to highly mobile scavengers and predators or small-bodied infaunal species (Kaiser et al. 2000; Jennings et al. 2001; Hermsen et al. 2003; Carbines and Cole 2009; Strain et al. 2012). Unlike in dredged areas, burrow-dwelling species did not appear to be impacted by trawling, presumably because the net and bridle does not penetrate as deep as a scallop or hydraulic dredge within the sediment and therefore burrow formations remain intact.

The present study demonstrates the potential of some species groups to start recovering during the first year post-fishing disturbance but others to take more than two years. Previous recovery estimates from meta-analyses and large-scale long-term studies range from <3 years to 5–10 years (Cranfield et al. 2001; Blyth et al. 2004; Collie et al. 2005; Kaiser et al. 2006). Collie et al. (2005) showed significant increases in abundance and biomass 2-5 years after the closure of a gravel sediment area of the Georges Bank, but increases in numbers and biomass of certain species were still observed up to 5 years after the closure. Although these studies are not directly comparable to results obtained from this synthesis as we have looked at biological trait groups rather than taxonomic groups, our results may appear optimistic in some cases. One possible reason for this is that small-scale experimental studies may have immigration rates that are not realistic for real fishing grounds, and therefore may result in an overestimation of recovery times. In contrast, real fishing grounds consist of a mosaic of communities fished with different frequencies and at different intensities, and consequently a source of immigrants cannot be relied on. On a cautionary note, therefore, recovery times that are estimated from small-scale experimental trawling studies should be viewed with caution.

The relationship between effect size and time was not comparable across all traits, which may indicate that some of the biological traits considered in this synthesis are more or less important at affecting recovery. For example, the absence of a relationship with time for traits such as ‘Sediment position’, ‘Mobility’ and ‘Protection’ may reflect the fact that recovery is not ultimately governed by these traits (e.g. whether a species is covered by a shell or not). Rather these traits influence more the vulnerability of an organism to mortality and/or removal following trawling. It is surprising, however, that those traits that are expected to influence the recoverability of species following disturbance (e.g. larval and egg development location, longevity) did not always show a significant relationship with time. For example, one would expect species that have a planktotrophic larval stage to recover faster, as planktonic recruitment affords potentially faster recolonization for these species than for species with lecithotrophic larvae (pelagic for shorter periods of time) or direct developers (lack a larval stage altogether). There was no relationship with time for ‘Larval development’ for studies examining effects of otter trawling or dredging. A significant relationship with time for Longevity was found for studies examining the effects of dredging but not for otter trawling, whereas a relationship with time for Egg development was found for studies examining the effects of trawling but not for dredging. The reasons for these inconsistent recovery patterns are unclear, but it may reflect the year-to-year variations in environmental attributes, such as variations in primary productivity, and possible differences in patchiness in fished versus non-fished areas. Furthermore, factors such as tidal velocity, the proximity of areas with high abundances of benthic invertebrates and wave stress, which have been found to be important drivers of recovery time (Lambert et al. 2014), may be different among study sites and may thus also account for variability in effect between studies.

4.4 Implications for ecosystem functioning

Bottom fishing may affect ecosystem functioning indirectly through selective effects on animals with specific life histories and ecological traits. The present study has shown that species belonging to different modalities exhibit differences in the vulnerability to and recoverability from fishing (as discussed in sections 4.2 and 4.3). Changes that alter the functional diversity within an ecosystem alter resource use and would be expected to have an effect on the productivity of the ecosystem (Tilman 2001). If functional diversity is reduced by depletion or deletion of a functional group, then certain resources would be under exploited or unexploited relative to undisturbed communities, or redirected to other compartments such as the microbial loop (Diaz and Cabido 2001, Baird et al. 2004). This would be expected to lead to a reduction in the productivity of the ecosystem. Whilst some ecosystem functions can be undertaken by a variety of different organisms, it is generally believed that a greater diversity of species increases the stability and resilience of an ecosystem's capacity to perform its various functions (Cardinale et al. 2000, 2002).

Deposit and suspension feeders were particularly vulnerable to trawling. These have been shown to affect benthic biodiversity by capturing and utilizing large quantities of particles from the sediment and water column and may directly and indirectly regulate primary and secondary production (Gili and Coma 1998). Suspension-feeding bivalves can remove 60 to 90% of suspended matter, depending on particle size, from the horizontal particle flux (Loo and Rosenberg 1989). By ejecting unsuitable particles, such as mucous wrapped pseudofaeces, deposit and suspension feeders also increase the rate of particle deposition to the seafloor and stimulate microbial production (Newell 2004). Reduction of biomass within these groups may alter the pattern of resource use in the community and change energy flow through the benthic ecosystem.

It is well documented that infaunal invertebrates exhibit significant influence over ecosystem functions such as secondary production (Bolam and Eggleton 2014), the transfer of oxygen and nutrients through the ecosystem (Bertics et al. 2010; Queirós et al. 2011), the recycling of waste material and the sequestration of harmful substances (Gilbert et al. 1994) through bioturbation. The initial loss in abundance of species with different bioturbation mechanisms amounted to a 25% reduction in the fished area, indicating a substantial loss in the bioturbation potential of the benthic community immediately following fishing. However, species capable of bioturbation were estimated to recover within 3 – 5 months following bottom fishing, indicating that fishing may reduce the bioturbation potential of a community in the short term but not in the long term.

4.5 Limitations of study

Most often studies included in this review reported differences in mean abundance between control and fished area rather than biomass. Fishing-impact studies rarely reported community responses to fishing disturbance in terms of biomass (compared to abundance), which may be a more important ecological indicator of community structure and recovery. In a smaller number of cases, authors reported data for mean biomass, particularly when dealing with biogenic fauna, which in many cases are taxa that form colonies in which it is not easy to differentiate individuals. A number of studies have shown that body size and/or biomass of the benthic community provides a more accurate reflection of benthic function than that based on abundance (Bremner et al. 2006; Cesar and Frid 2009; Lohrer et al. 2004). Furthermore, while a measure of abundance may adequately describe comparisons of small-bodied fauna such as annelids, it may not adequately describe recovery for larger biota such as sponges and soft corals. An overall positive response may represent an increase in the abundance of smaller-bodied fauna, but a possible overall decrease in biomass in response to trawling (Jennings et al. 2001, Duplisea et al. 2002). For these, a consideration of body-size is paramount, as biota of large body-size are more vulnerable and have lower intrinsic rates of increase and hence a lower capacity to sustain elevated mortality. Indicators such as the slope of the body-size spectrum of the benthic assemblage may provide a better effect size against which to measure the state of the entire assemblage in response to disturbance treatments (Duplisea and Kerr 1995, Duplisea et al. 2002, Jennings et al. 2002).

It is a challenge to balance the uncertainty surrounding the results of meta-analysis against their potential impact when considering management implications. Throughout the study selection process, as specified by the systematic review methodology, we have applied stringent study inclusion and quality assessment criteria in the hope of providing the best quality evidence for evaluating the effect of bottom fishing on benthic communities. As part of the study quality control, we have undertaken a weighted meta-analytical approach to factor in for sample size and within-study variance in the overall effect of fishing and have thus excluded studies that did not provide sample sizes and variance measures. While acknowledging that these strict criteria might have led to a reduction in the pool of available studies, we believe that there is little benefit in including biased or confounded studies.

Pooling of individual species responses for study level analyses may introduce methodological bias. For example, studies that have measured large numbers of species may exhibit stronger negative responses due to the higher probability of including species that are impacted negatively by fishing. However, the alternative of using each individual species response as if they were statistically independent of each other goes against the concept of a meta-analysis, which demands that no study contributes more than one point to each analysis, the presumption being that since different studies take place at different places, times and under different environmental conditions there will be greater variance between studies than between response values within a study, and the ‘proper’ level of residual variation to test against is that between studies.

Small sample sizes and lack of power are clearly problematic in some instances, for example studies in muddy sediments and following beam trawling were particularly lacking. The limited number of studies made it hard to draw firm conclusions about the impact of beam trawling and on organisms in muddy sediments.

4.6 Conclusion

The Ecosystem Approach to Fisheries requires managers to consider the environmental impacts of fishing in management plans. Our synthesis provides insight into the magnitude of fishing effect and the recovery trajectories following fishing for species characterized by different biological traits, which may influence directly or indirectly ecosystem functioning. This is a step towards furthering our understanding of the potential influences of bottom fishing on ecosystem processes and functions governed by benthic species. Furthermore, this work provides useful insights for changes in the resilience of seabed habitats as a result of the loss of species with specific traits following bottom fishing. Information on seabed recovery times and resilience can be used to define spatial management plans that minimize seabed impacts. Management plans that reduce the relative impacts of fishing, if effective, may also help to move fisheries towards ‘best practice’ in terms of minimizing impacts on the seabed and to move fisheries a step closer towards ecosystem-based management.

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Databases

Traits access database provided by Tom Webb (email: t.j.webb@sheffield.ac.uk)

Appendix II: The relationship between the response to otter trawling and time since last trawling event is given in Figures 22 - 32 for each biological trait. The model was fitted to the data of a particular biological trait whenever a significant relationship between the effect size and time was identified (section 3.5).

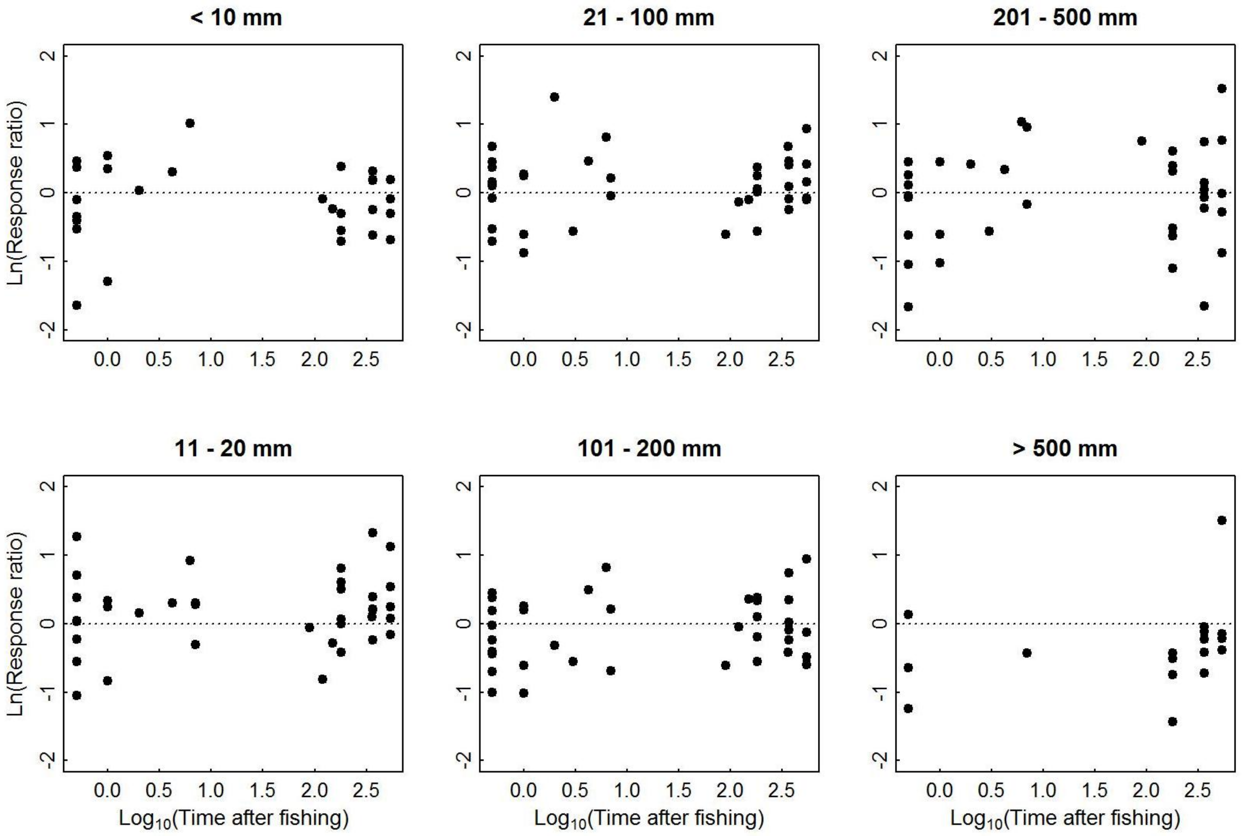

Figure 22. The recovery in the response of different modalities of the trait 'Body size' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

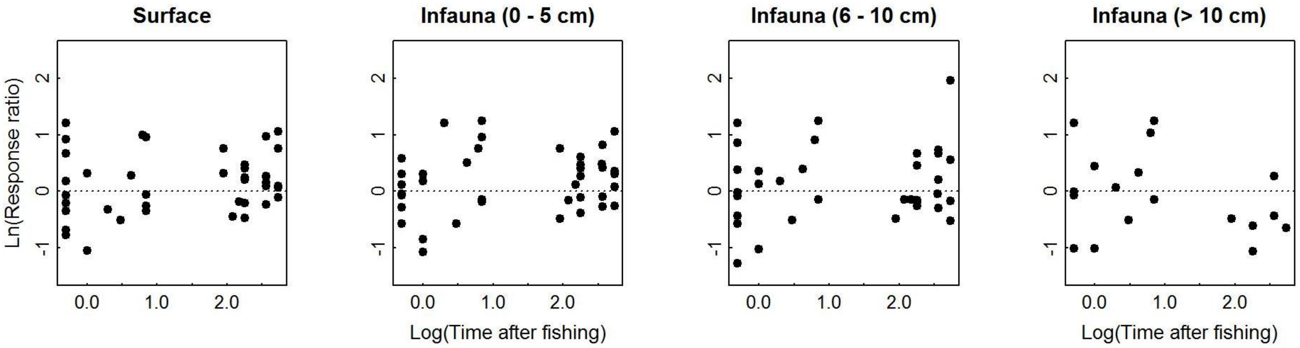

Figure 23. The recovery in the response of different modalities of the trait 'Sediment position' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

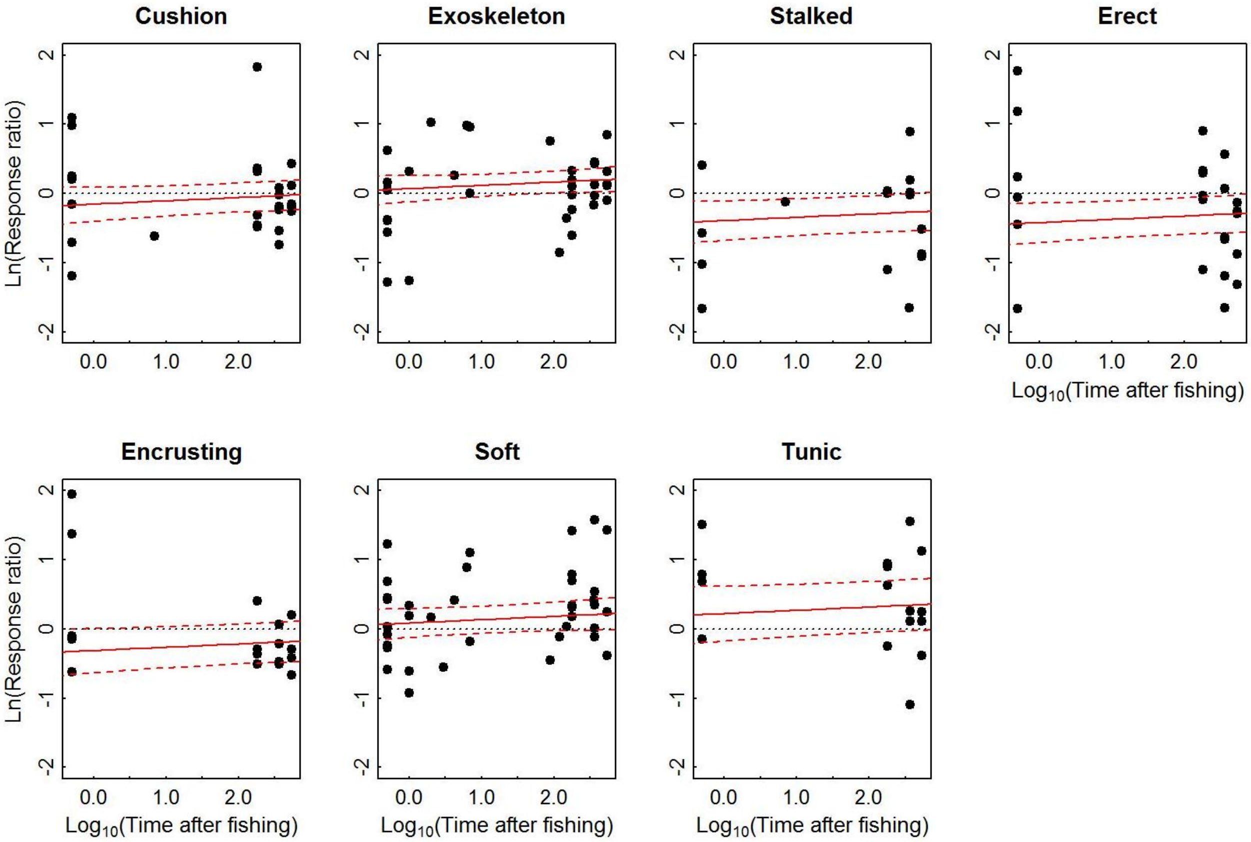

Figure 24. The recovery in the response of different modalities of the trait ‘Morphology’ following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

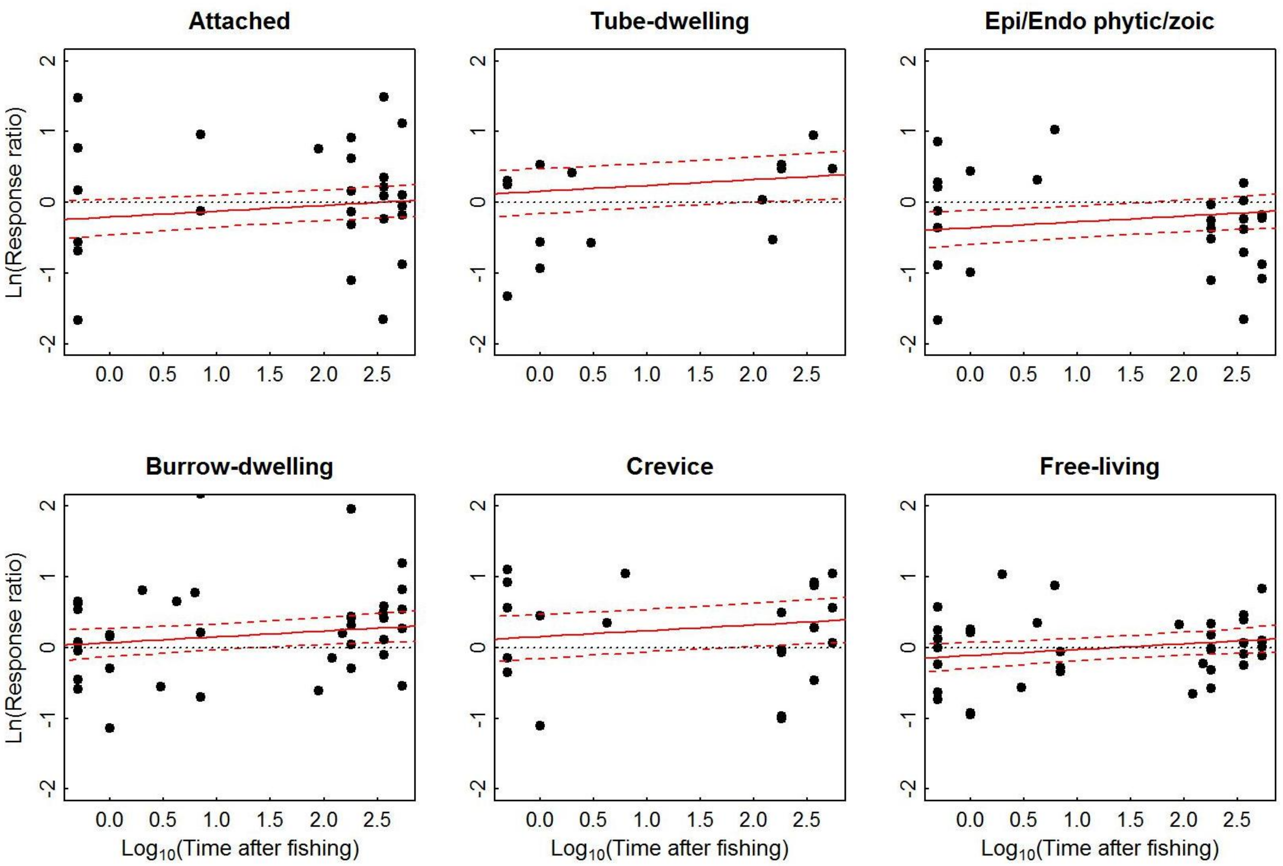

Figure 25. The recovery in the response of different modalities of the trait 'Living habit' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

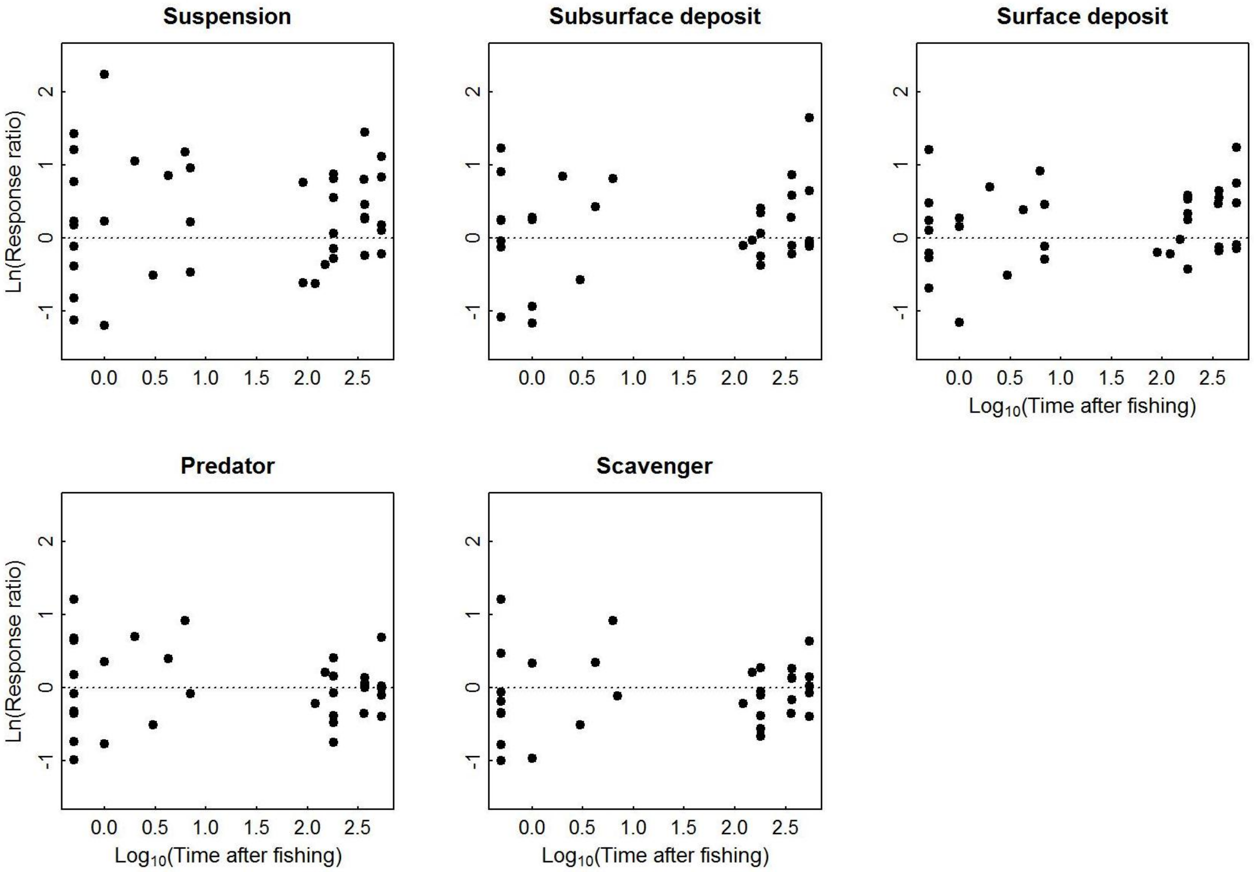

Figure 26. The recovery in the response of different modalities of the trait 'Feeding group' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

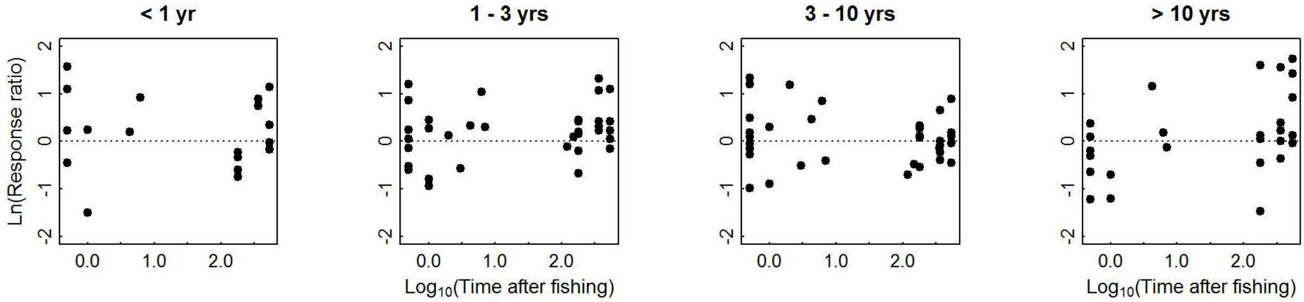

Figure 27. The recovery in the response of different modalities of the trait 'Longevity' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

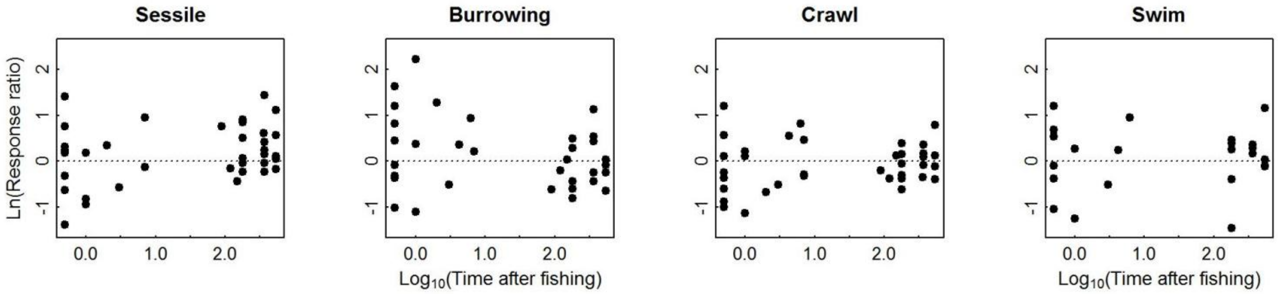

Figure 28. The recovery in the response of different modalities of the trait 'Mobility' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

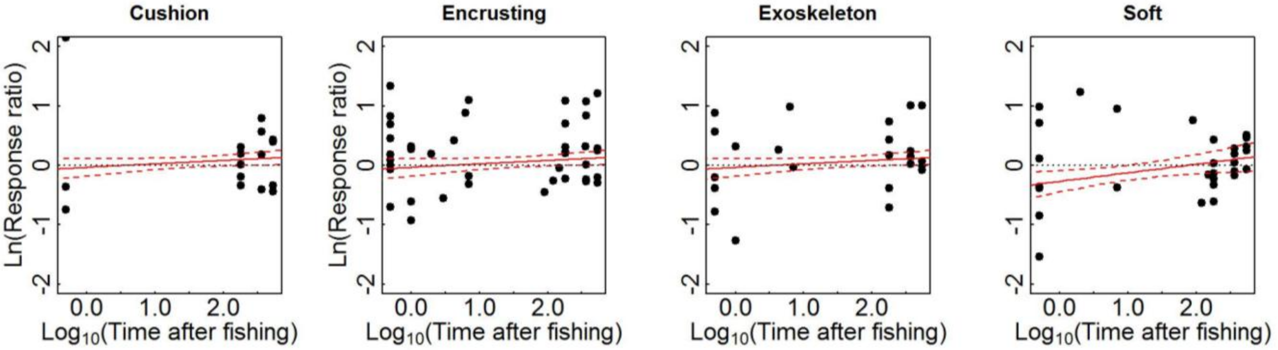

Figure 29. The recovery in the response of different modalities of the trait 'Protection' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

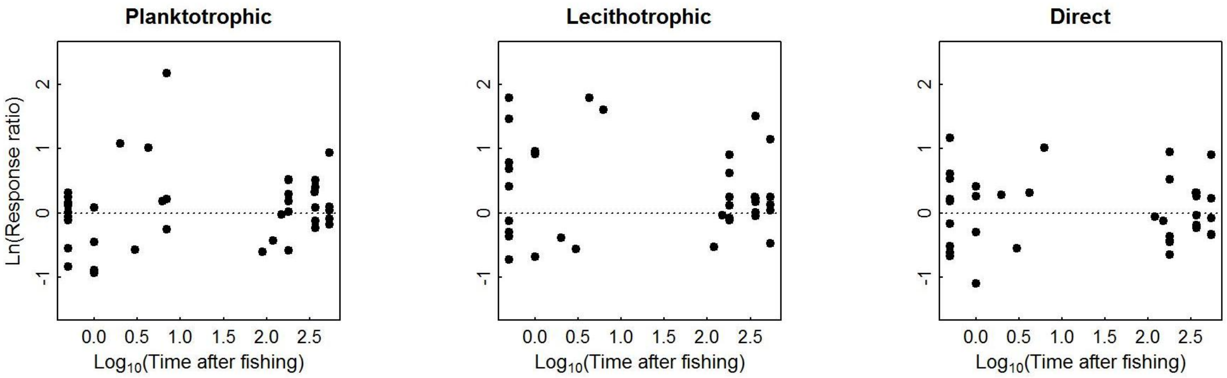

Figure 30. The recovery in the response of different modalities of the trait 'Larval development' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

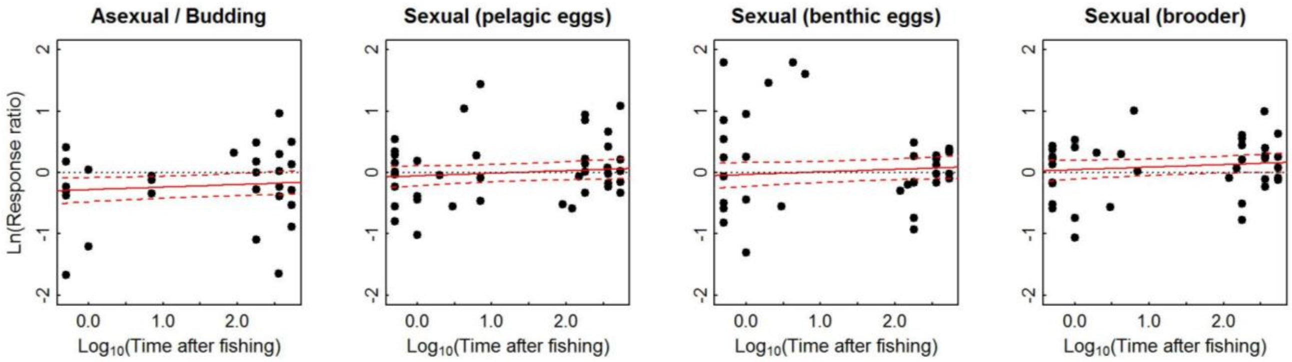

Figure 31. The recovery in the response of different modalities of the trait 'Egg development' following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

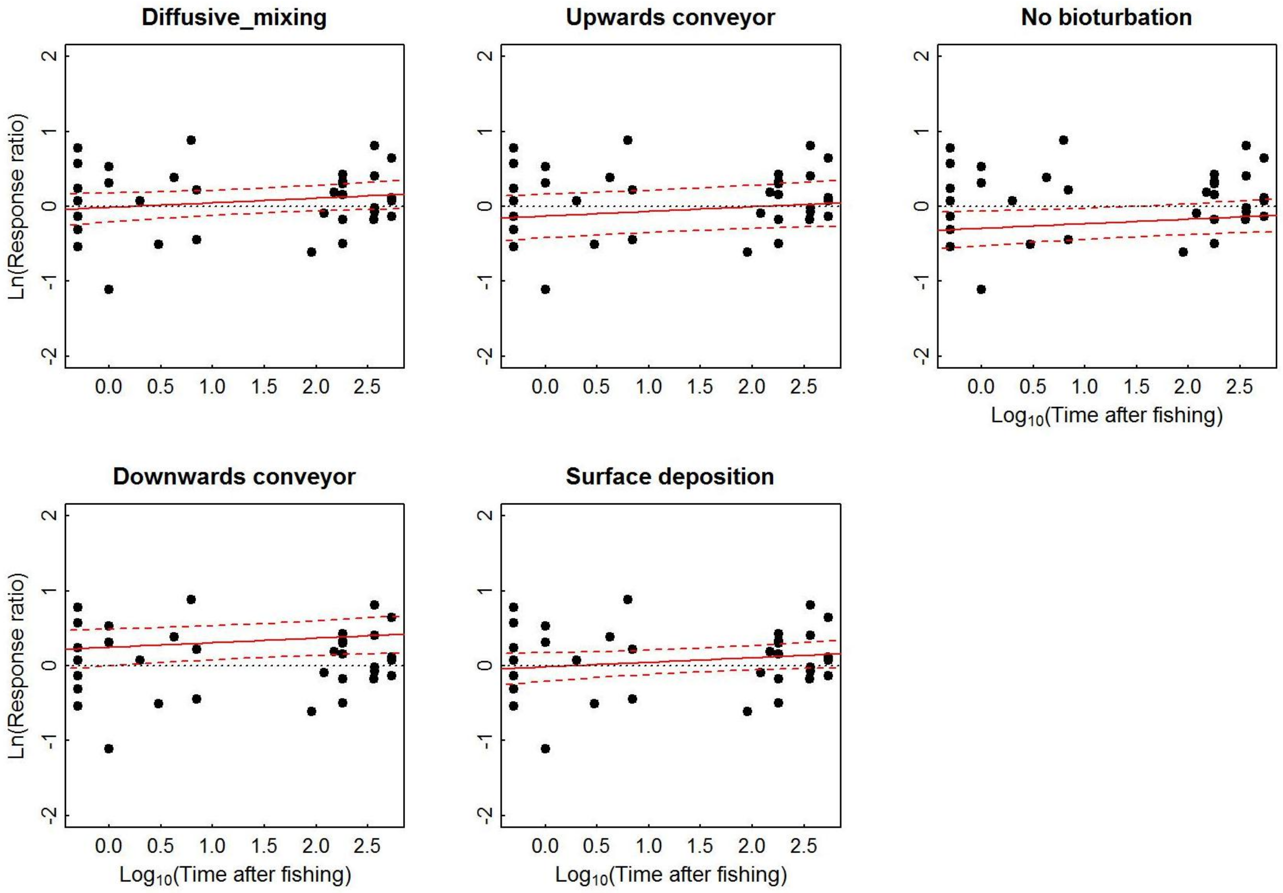

Figure 32. The recovery in the response of different modalities of the trait ‘Bioturbation’ following otter trawling. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

Appendix III: The relationship between the response to dredging and time since last trawling event is given in Figures 33 - 43 for each biological trait. The model was fitted to the data of a particular biological trait whenever a significant relationship between the effect size and time was identified (section 3.6).

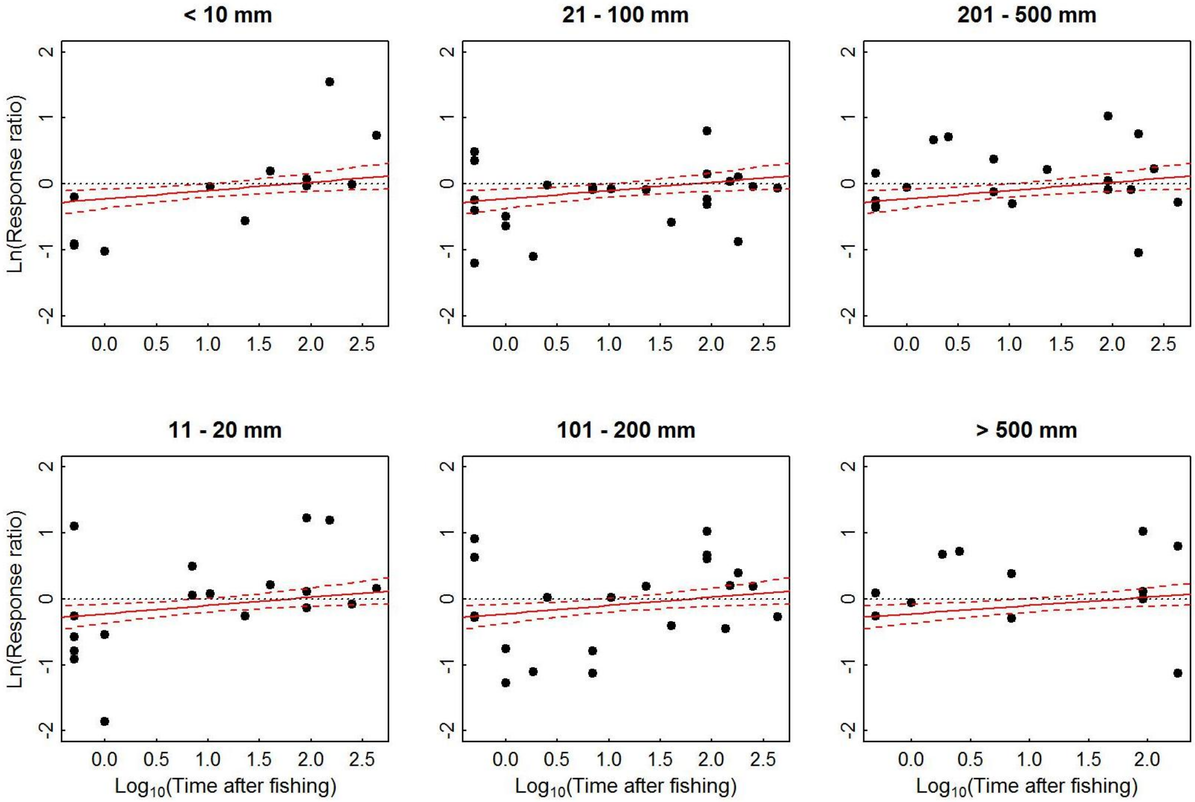

Figure 33. The recovery in the response of different modalities of the trait 'Body size' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

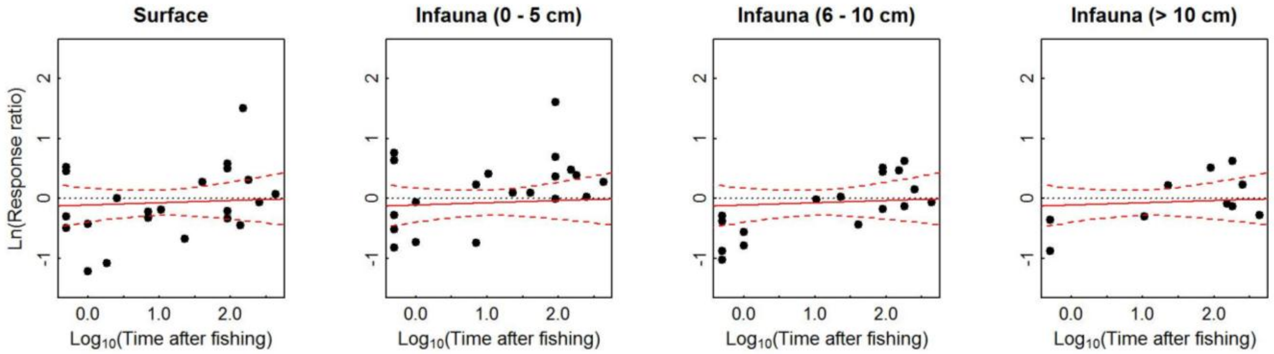

Figure 34. The recovery in the response of different modalities of the trait 'Sediment position' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

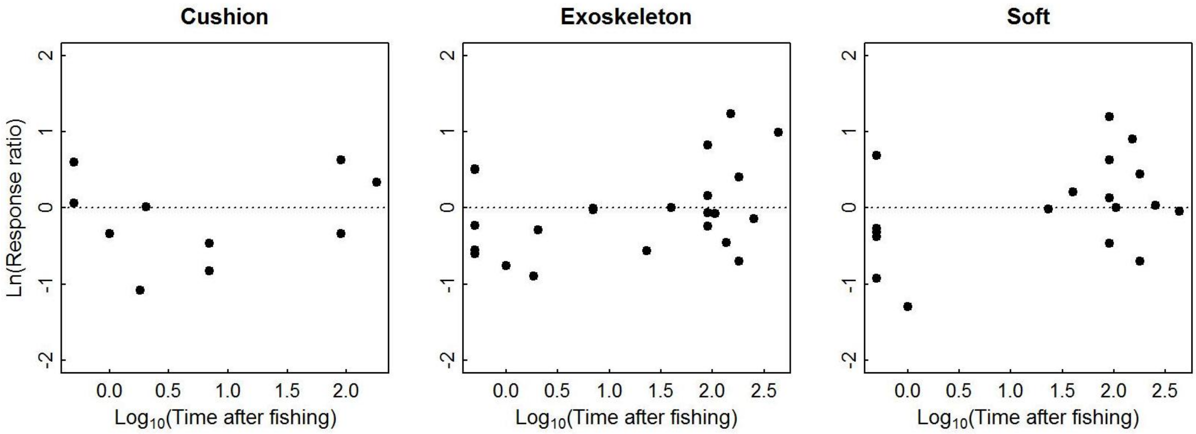

Figure 35. The recovery in the response of different modalities of the trait 'Morphology' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area. There was no data available for the following modalities; erect, stalked and tunic.

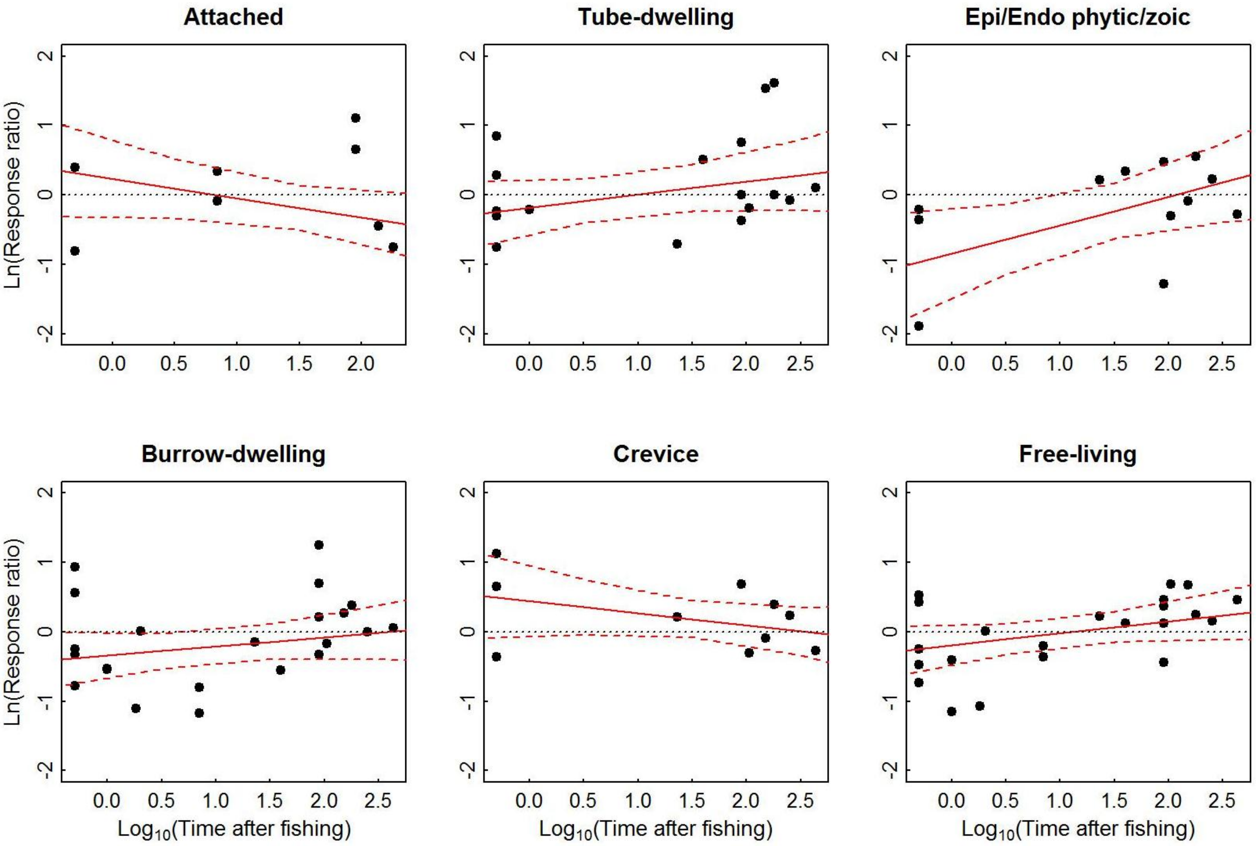

Figure 36. The recovery in the response of different modalities of the trait 'Living habit' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area. The fitted model and 95% confidence intervals are plotted in red.

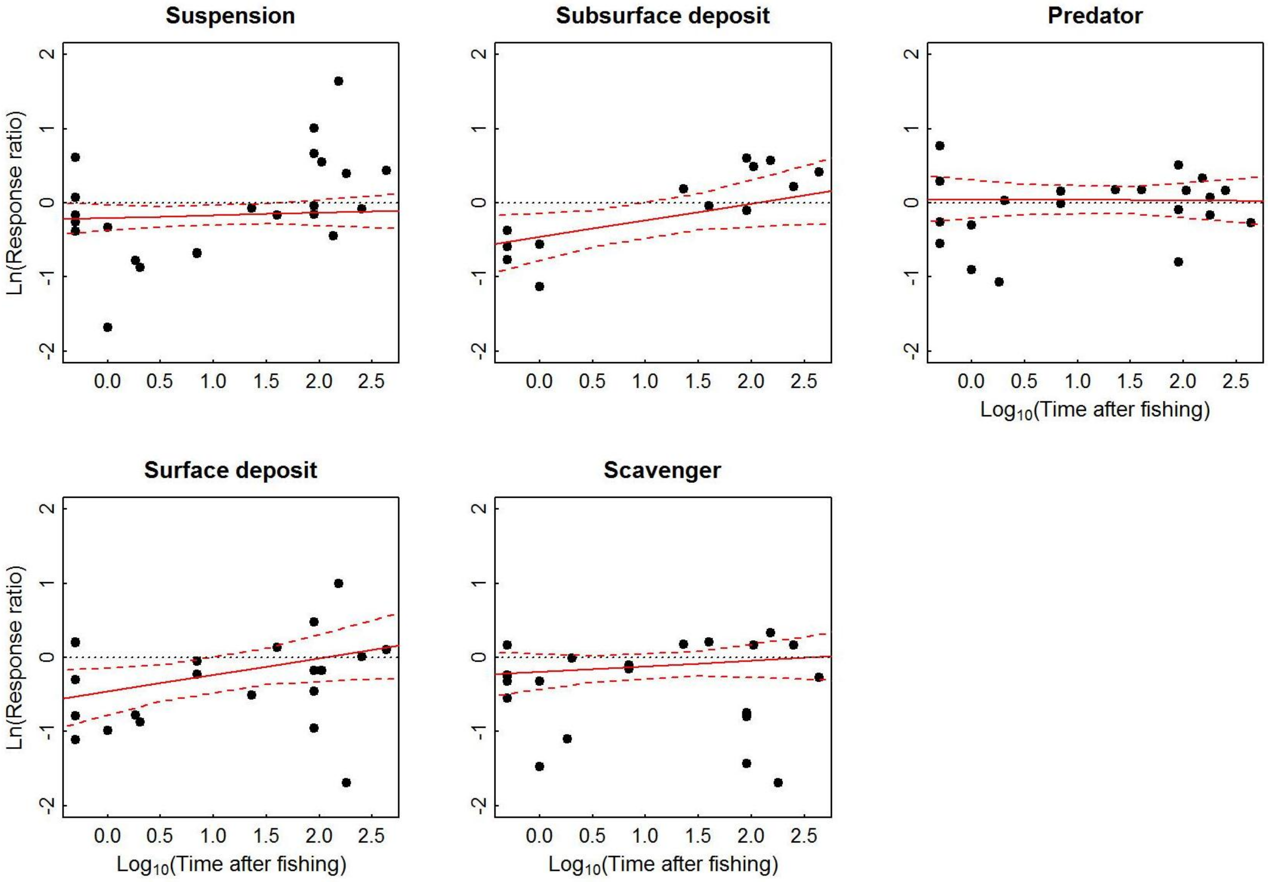

Figure 37. The recovery in the response of different modalities of the trait ‘Feeding group’ following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area. The fitted model and 95% confidence intervals are plotted in red.

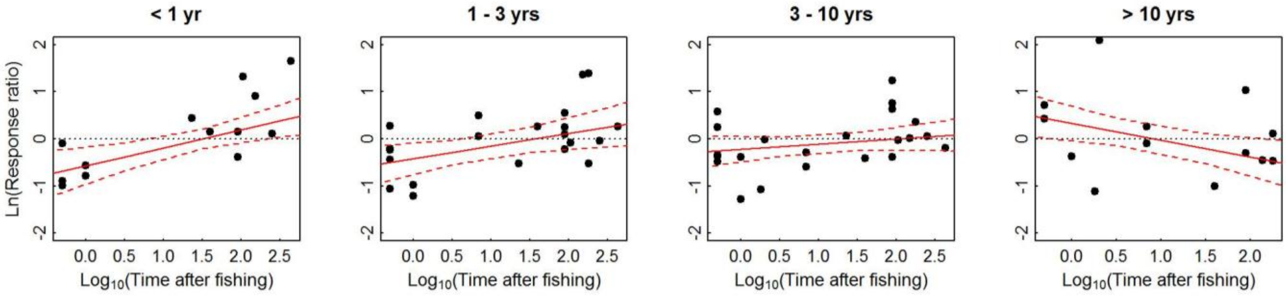

Figure 38. The recovery in the response of different modalities of the trait ‘Longevity’ following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area. The fitted model and 95% confidence intervals are plotted in red.

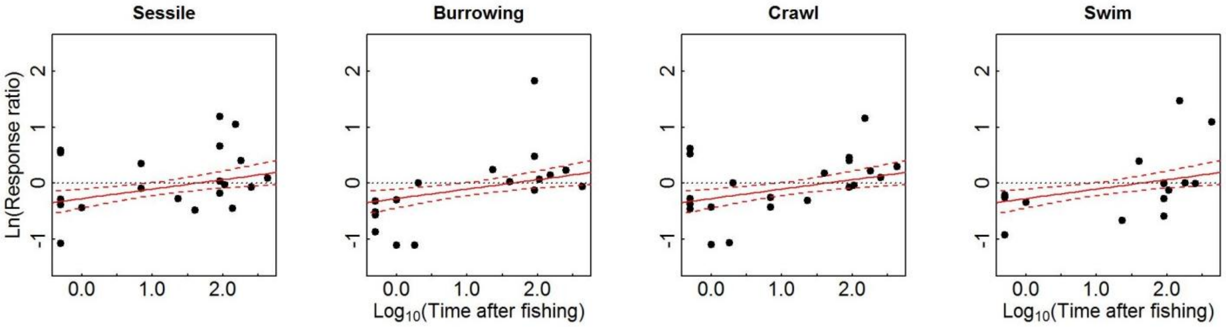

Figure 39. The recovery in the response of different modalities of the trait 'Mobility' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

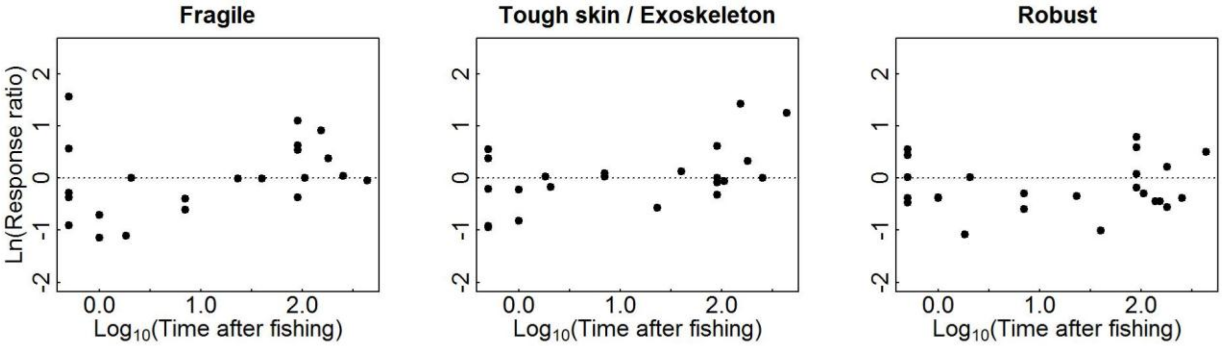

Figure 40. The recovery in the response of different modalities of the trait 'Protection' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area. There was no data available for 'no protection' modality.

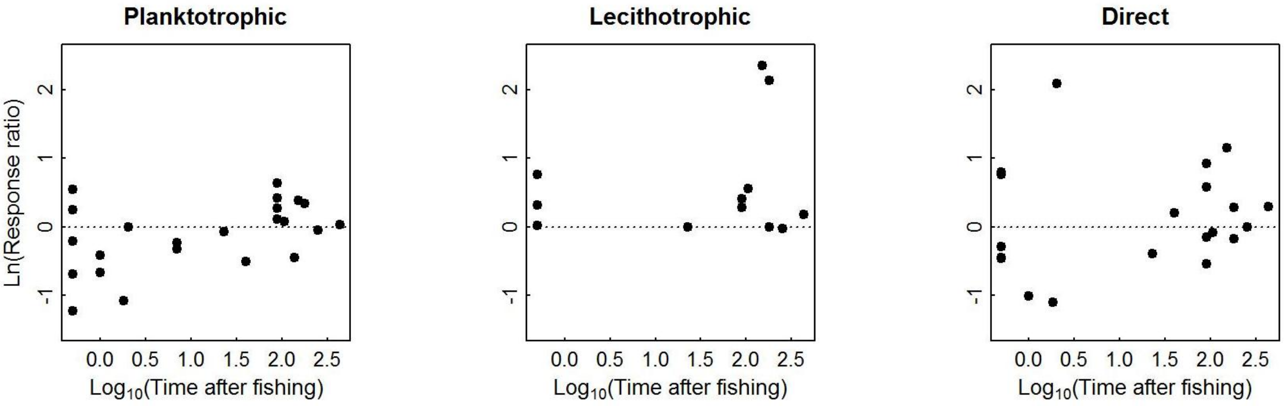

Figure 41. The recovery in the response of different modalities of the trait 'Larval development' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

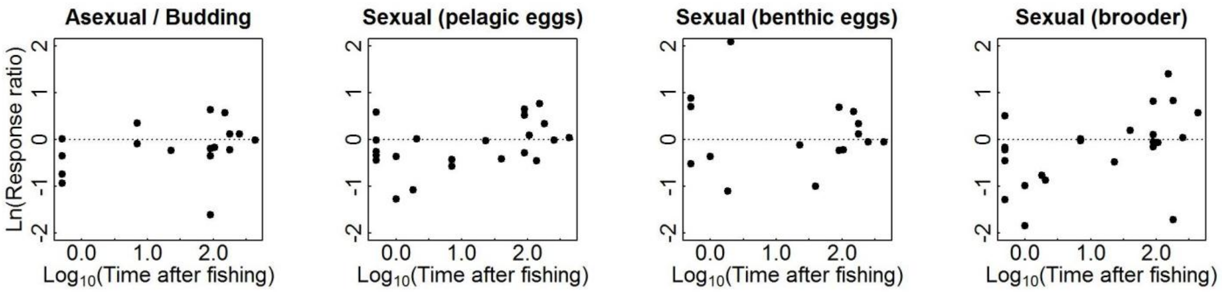

Figure 42. The recovery in the response of different modalities of the trait 'Egg development' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

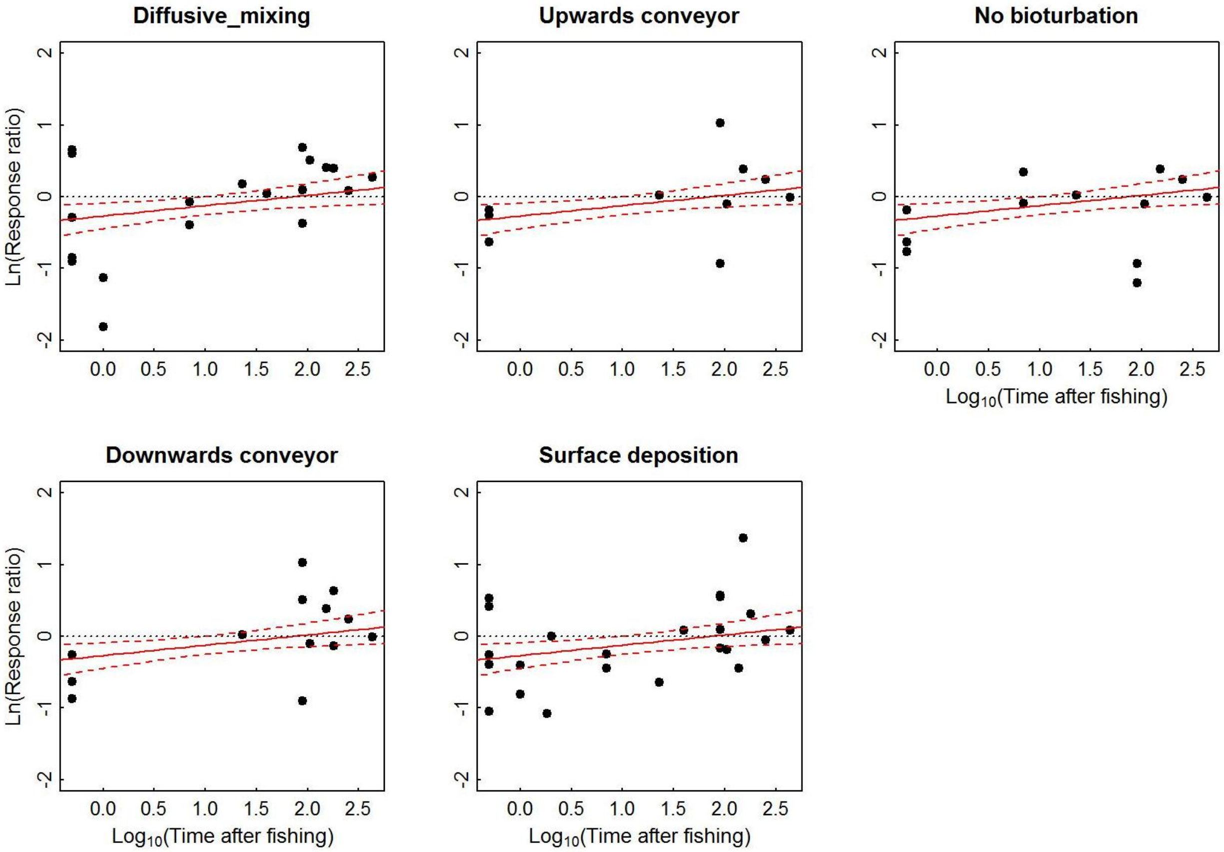

Figure 43. The recovery in the response of different modalities of the trait 'Bioturbation' following dredging. The vertical dotted line at (LnRR) = 0 represents equal abundance in fished and control area.

Appendix IV: Principal component analysis to examine correlations between species' biological traits and modalities