

A quantitative analysis of fishing impacts on shelf-sea benthos

JEREMY S. COLLIE*, STEPHEN J. HALL†, MICHEL J. KAISER‡ and IAN R. POINER§

*Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA; †The Flinders University of South Australia, GPO Box 2100, Adelaide 5001, Australia; ‡School of Ocean Sciences, University of Wales-Bangor, Menai Bridge, Gwynedd, LL59 5EY, UK; and §CSIRO Division of Marine Research, PO Box 120, Cleveland, Queensland 4163, Australia

Summary

1. The effects of towed bottom-fishing gear on benthic communities is the subject of heated debate, but the generality of trawl effects with respect to gear and habitat types is poorly understood. To address this deficiency we undertook a meta-analysis of 39 published fishing impact studies.

2. Our analysis shows that inter-tidal dredging and scallop dredging have the greatest initial effects on benthic biota, while trawling has less effect. Fauna in stable gravel, mud and biogenic habitats are more adversely affected than those in less consolidated coarse sediments.

3. Recovery rate appears most rapid in these less physically stable habitats, which are generally inhabited by more opportunistic species. However, defined areas that are fished in excess of three times per year (as occurs in parts of the North Sea and Georges Bank) are likely to be maintained in a permanently altered state.

4. We conclude that intuition about how fishing ought to affect benthic communities is generally supported, but that there are substantial gaps in the available data, which urgently need to be filled. In particular, data on impacts and recovery of epifaunal structure-forming benthic communities are badly needed.

Key-words: benthic organisms, fishing impact, habitat disturbance, meta-analysis, predictive models.

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Introduction

Fishing gears used to catch demersal fish and shellfish often disturb both the seabed and the organisms living within or on it. The potential impact of this disturbance has become a subject of heated debate (Malakoff 1998). Experimental manipulations of fishing disturbance at the relevant scales are time-consuming and expensive to undertake. Few workers have deliberately incorporated factors such as depth, habitat type, scale of disturbance or disturbance regime into their design. Thus, the results of any single study are highly specific with respect to fishing gear, disturbance regime, habitat and environment. Viewing each study in isolation makes it difficult to draw general conclusions. In recent years, there have been at least 12 publications in the

primary literature that review experimental studies to some extent (e.g. Jennings & Kaiser 1998; Watling & Norse 1998; Auster & Langton 1999; Hall 1999), but none has attempted a quantitative analysis of the responses from which general predictions might be drawn. Current debates about the selection and utility of marine protected areas would benefit greatly from predictions on the sensitivity and possible recovery rate of different habitats derived from models based on quantitative data.

As a step toward quantitative synthesis, we have extracted summary data from a population of fishing impact studies and undertaken a meta-analysis of this combined data set to ask the following questions:

1. Are there consistent patterns in the responses of benthic organisms to fishing disturbance?
2. How does the magnitude of this response vary with habitat, depth, disturbance type and among taxa?

3. How does the recovery rate of organisms vary with these same factors?

Meta-analysis, the summary of multiple, independent studies to detect general relationships is growing in popularity with ecologists (see, for example, Gurevitch & Chester 1986; Gurevitch *et al.* 1992; Arnqvist & Wooster 1995; Osenberg & St Mary 1998). Using this approach, the results from each study are regarded as independent replicates, permitting ecological questions to be examined on a much larger scale than would otherwise be possible. The purpose of this study was to examine whether sufficient data were available on fishing impacts on benthos to answer the questions above and, if not, to identify those areas where more work was especially needed.

Materials and methods

DATA EXTRACTION

We found 57 different manipulations or observations of the effects of fishing disturbance on benthic fauna and communities, extracted from 39 separate publications (Table 1). We believe we have assembled the majority of studies relevant for a large-scale synthesis, but there will undoubtedly be some that we have missed. Some studies were considered more than once as they incorporated distinctly different experimental manipulations conducted at different depths or locations. Experimental studies were classified with respect to a range of variables that might affect the degree of trawling impact (Table 2). Gear type was subdivided into different fishing activities according to differences in their mode of action. Regime describes the number of discrete periods of disturbance. We also distinguished the acute disturbance of experimental fishing impact studies from comparisons of fished (chronically disturbed) and unfished areas. Size of experimental plot was included as the minimum dimension of any disturbed area because this is the smallest distance over which adults or larvae need to migrate to recolonize an area. Habitat was classified as mud, muddy sand, sand, gravel and biogenic. Each habitat category may contain a range of sediment sizes. The biogenic category includes seagrass meadows or reef-forming organisms such as mussel beds, sponge or coral reefs. The remaining variables were geographical region, water depth of the study and taxonomic grouping (phylum, class, genus).

From 33 of these studies, estimates of the effects of fishing disturbance on the numbers of individuals and species richness were extracted, together with effects at the genus level where available and at higher taxonomic levels otherwise. Responses for specific taxa were then treated as independent observations to examine the effects of our potential explanatory

variables on population responses, irrespective of taxon.

The magnitude of the response of each variable to the fishing treatment was calculated from the following equation, using the mean values for fished and unfished plots in any given study:

$$\% \text{ Difference} = \left(\frac{A_f - A_c}{A_c} \right) \times 100$$

where A_f = abundance in fished plots and A_c = abundance in control plots.

In cases where the study involved a before fishing–after fishing comparison for the same plot(s), rather than a treatment–control design, these data were used to calculate percentage difference. For 17 studies, data on the longer-term recovery of benthos was also extracted and analysed.

The potential and pitfalls of meta-analysis are described in detail by Arnqvist & Wooster (1995), and the need to formulate biologically appropriate metrics of effect size discussed at length by Osenberg & St Mary (1998) and Osenberg *et al.* (1999). With respect to effect size, the measure described above comes from a family that are commonly used in meta-analysis. In the context of examining competition experiments, for example, abundance in fished plots in the equation above would be replaced by the abundance in the presence of competitors and the metric used to measure ‘relative competitive intensity’ (RCI, e.g. Paine 1992; Goldberg *et al.* 1999).

One common feature of most meta-analyses is that measures of effect size are weighted by the within study variance, thereby giving more weight to the results of those studies about which one is more confident. Unfortunately, sample variance was often not reported in the studies that we examined, making it impossible for us to apply such weighting. In effect, therefore, we have treated the experimental design and the precision of estimates for all studies as equivalent. Although this is clearly not the case, and meta-analysis conducted in the absence of within study variance estimates is not ideal, as Gurevitch & Hedges (1999) note, ‘where there is no alternative, they [meta-analyses] may provide useful information where otherwise none is available’.

STATISTICAL ANALYSIS

For study of the initial impacts of fishing we examined the effect of each variable on the response of benthic organisms to fishing disturbance within a generalized linear modelling framework (McCullagh & Nelder 1989). Minimal, adequate models were obtained by a sequential process of model fitting. Explanatory variables were systematically added or subtracted from the model, and were included in the final model if they led to a statistically significant

Table 1. Summary table showing the 56 fishing impact studies used in the analysis, sorted by fishing gear, habitat and region. Some publications appear more than once because they incorporated distinctly different experimental manipulations. Missing values indicate that the information was not provided in the original publication. The Use column indicates whether the data was used for the formal statistical analysis (values in brackets denote use in the recovery analysis). Recovery, denotes the period in days over which recovery was followed. An asterisk in the regime column denotes a study on a fishing ground, where the level of disturbance was unknown. For a description of the other variables see Table 2

Reference	Use	Gear	Habitat	Region	Scale (m)	Depth (m)	Regime	Recovery period (days)
Kaiser & Spencer (1996)	x	Beam trawling	Gravel	Northern Europe	40	40	1	
Kaiser <i>et al.</i> (1998)	x	Beam trawling	Gravel	Northern Europe	40	40	1	180
Kaiser & Spencer (1996)		Beam trawling	Gravel	Northern Europe	40	40	1	
Lindeboon & de Groot (1998)	x	Beam trawling	Muddy sand	Northern Europe	60	43	1	
Lindeboon & de Groot (1998)	x	Beam trawling	Sand	Northern Europe	60	20	1	
Bergman & Hup (1992)		Beam trawling	Sand	Northern Europe	200	30	1	
Kaiser & Spencer (1996)	x	Beam trawling	Sand	Northern Europe	40	27	1	
Kaiser <i>et al.</i> (1998)		Beam trawling	Sand	Northern Europe	40	27	1	180
Ismial (1985)		Hydraulic dredging	Muddy sand	East North America	150	3	1	300
Peterson <i>et al.</i> (1987)		Inter-tidal dredging	Biogenic	East North America	35	1	2	730
Brown & Wilson (1997)	x	Inter-tidal dredging	Mud	East North America	1	0	4	
Kaiser <i>et al.</i> (1996)		Inter-tidal dredging	Mud	Northern Europe	2	0	1	210
Kaiser <i>et al.</i> (1998)	x (x)	Inter-tidal dredging	Muddy sand	Northern Europe	1.5	0	1	365
Wynberg & Branch (1994)		Inter-tidal dredging	Muddy sand	South Africa	3	0	1	606
Peterson <i>et al.</i> (1987)		Inter-tidal dredging	Sand	East North America	35	1	2	730
Hall & Harding (1997)	x (x)	Inter-tidal dredging	Sand	Northern Europe	45	0	1	56
Cryer <i>et al.</i> (1987)		Inter-tidal dredging	Sand	Northern Europe	5	0	1	180
McLusky <i>et al.</i> (1983)	x (x)	Inter-tidal dredging	Sand	Northern Europe	1	0	1	140
Heiligenberg (1987)	x (x)	Inter-tidal dredging	Sand	Northern Europe	7	0	1	140
Heiligenberg (1987)	x (x)	Inter-tidal dredging	Sand	Northern Europe	1	0	1	180
Heiligenberg (1987)	x (x)	Inter-tidal dredging	Sand	Northern Europe	1	0	1	140
Hall <i>et al.</i> (1990)		Inter-tidal dredging	Sand	Northern Europe	50	7	1	40
Brown & Wilson (1997)	x	Inter-tidal raking	Mud	East North America	1	0	2	
Cotter <i>et al.</i> (1997)	x (x)	Inter-tidal raking	Sand	Northern Europe	20	0	1	400
Hall & Harding (1997)	x (x)	Inter-tidal raking	Sand	Northern Europe	45	0	1	56
Kaiser <i>et al.</i> (1998)	x	Otter trawling	Biogenic	East Australia	40	25	1	
Kaiser <i>et al.</i> (1998)	x	Otter trawling	Biogenic	East Australia	40	50	1	
Van Dolah <i>et al.</i> (1987)	x (x)	Otter trawling	Biogenic	East North America		20	1	365
Bradstock & Gordon (1983)		Otter trawling	Biogenic	New Zealand		10	*	
Magorrian <i>et al.</i> (1995)		Otter trawling	Biogenic	Northern Europe			*	
Sainsbury (1987)		Otter trawling	Biogenic	North-western Australia		50	*	
Guillen <i>et al.</i> (1994)		Otter trawling	Biogenic	Southern Europe			*	1095
Kaiser <i>et al.</i> (1996)		Otter trawling	Gravel	East North America		94	*	
Freese <i>et al.</i> (1999)		Otter trawling	Gravel	West North America	5	206	1	
Lindeboon & de Groot (1998)	x	Otter trawling	Mud	Northern Europe	40	35	1	
Tuck <i>et al.</i> (1998)	x (x)	Otter trawling	Mud	Northern Europe	200	30	16	540
Lindeboon & de Groot (1998)	x	Otter trawling	Mud	Northern Europe	40	75	1	
Sanchez <i>et al.</i> (in press)		Otter trawling	Mud	Southern Europe	100	20	1	180
Brylinsky <i>et al.</i> (1994)	x	Otter trawling	Sand	East North America			1	
Van Dolah <i>et al.</i> (1991)	x (x)	Otter trawling	Sand	East North America	500	8	*	180
Auster <i>et al.</i> (1996)		Otter trawling	Sand	East North America		30	*	3650
Van Dolah <i>et al.</i> (1991)	x (x)	Otter trawling	Sand	East North America	200	20	*	180
Pitcher <i>et al.</i> (1996)		Otter trawling	Sand	Eastern Australia	1200	25	1	1440
Pitcher <i>et al.</i> (1996)		Otter trawling	Sand	Eastern Australia	20	25	13	1440
Gibbs <i>et al.</i> (1980)		Otter trawling	Sand	Eastern Australia		10	1	
Engel & Kvitek (1998)		Otter trawling	Sand	West North America	3700	180	*	
Fonseca <i>et al.</i> (1984)		Scallop dredging	Biogenic	East North America			1	
Hall-Spencer (1995)		Scallop dredging	Biogenic	Northern Europe				
Collie <i>et al.</i> (1997)	x	Scallop dredging	Gravel	East North America	5000	42	*	1275
Collie <i>et al.</i> (1997)	x	Scallop dredging	Gravel	East North America	5000	83	*	1275
Bradshaw <i>et al.</i> (1999)	x (x)	Scallop dredging	Gravel	Northern Europe				
Watling <i>et al.</i> (unpublished)	x (x)	Scallop dredging	Muddy sand	East North America	50	15	1	180
Currie & Parry (1996)	x (x)	Scallop dredging	Muddy sand	South Australia	600	12	2	420
Thrush <i>et al.</i> (1995)	x (x)	Scallop dredging	Sand	New Zealand	20	24	1	90
Thrush <i>et al.</i> (1995)	x (x)	Scallop dredging	Sand	New Zealand	20	24	1	90
Eleftheriou & Robertson (1992)	x	Scallop dredging	Sand	Northern Europe			1	
Langton & Robinson (1990)	x	Scallop dredging		East North America			*	

Table 2. Description of each of the potential explanatory variables extracted from the published studies for the meta-analysis of fishing effects studies

Parameter	Description
Gear type	Subdivided into different fishing activities according to differences in their mode of action. For example, beam and otter trawls and scallop dredges all disrupt sediment to some degree, but the depth and percentage of seabed affected varies between gears (Kaiser <i>et al.</i> 1996). Hydraulic dredging is treated as a distinct category because it physically removes sediment from the seabed. Tractor and cockle dredging were grouped together as 'inter-tidal raking' because both rake sediment. In contrast, bait digging, clam kicking, bait dredging and clam suction harvesting are grouped as 'inter-tidal dredging' because each of these activities directly removes sediment, creating pits or trenches.
Regime	Describes the number of discrete periods of disturbance. Thus, in the case of an experimental plot that was trawled completely 10 times in one day this was counted as one disturbance event. In contrast, a study that disturbed the same plot on two dates separated by weeks or months was classed as a multiple disturbance regime.
Minimum scale	Experimental studies were usually conducted within defined plots. In many cases, the plots had rectangular dimensions. We considered that the minimum dimension of any disturbed area would be the most important to consider in terms of recolonization rate since this is the smallest distance over which adults or larvae need to migrate.
Region	The broad geographical region in which each study was located.
Depth	Most studies were undertaken at a constant depth. When minimum and maximum depths were specified, we extracted minimum depth only. Only two studies had a depth range that exceeded 5 m.
Habitat	Subdivided into mud, muddy sand, sand, gravel and biogenic habitats. Each habitat category is a general description of a range of habitats. For example, sand habitat incorporates a range of grain sizes from 125 to 250 μ m. Gravel habitat describes those studies in which gravel was a major component, normally these are actually mixed sediments with gravel, shell debris, coarse sand and silt. Biogenic habitat describes those studies that have examined the responses of seagrass meadows or reef-forming organisms, such as mussel beds, sponge or coral reefs. Some of the sedimentary habitats are interspersed with biogenic reefs, but these were not usually the main object of study.

reduction in deviance. In all models the response variable was transformed to $\log(x + 101) - \log(101)$, where x is the percentage difference described above. This transformation made the distribution of residuals approximately normal and centred the data such that zero corresponds to no effect. For individual taxa responses were recorded at the genus level where possible. To test for non-linear responses to the continuous variables depth and experimental scale, generalized additive models (GAM's) were used. This approach extends the linear modelling framework by allowing the relationship between a response and explanatory variable to be defined by a low dimensional smoothing function, rather than a single linear parameter. If inclusion of a smoothed function failed to account for a significant proportion of the deviance we concluded that the response to that variable was linear. For further details on GAM's see Hastie & Tibshirani (1990) and Hastie (1993). Analysis of variance (ANOVA) for unbalanced designs was used for models containing only categorical variables.

In addition to the statistical modelling approaches described above, we also employed tree-based regression modelling, in which a data set is progressively split into increasingly homogenous subsets until it is unfeasible to continue. This approach is becoming increasingly popular as a means for devising prediction rules and for summarizing large multivariate data sets in ways that are sometimes more

informative than linear models. We adopted the technique because it seems especially appropriate for an initial attempt to develop a predictive framework for fishing impacts. Compared with linear models, tree-based models are also more adept at capturing non-additive behaviour and allow more general interactions between predictor variables. Clark & Pregibon (1993) give a good description of the approach.

To examine patterns of recovery following fishing disturbance, responses were considered only for those taxa that responded negatively to fishing impact. Because the data for a particular taxon in a given study follow the same population over time, these data can be considered as repeated measures in which the error structure in each recovery time-series is likely to be serially correlated. To account for this feature of the data, we fitted linear mixed effects models, which included time as a random variable and treated the within population errors as having an auto-regressive (order 1) structure. First, single-factor models (plus time) were constructed with and without a time \times factor interaction term. These models were then compared with each other and with a model in which only time was included. Likelihood ratio tests were used to determine whether the inclusion of a particular factor in the model led to a significant improvement in fit. When inclusion of a time \times factor interaction led to a significant reduction in model deviance, we included

this in a full model. The effect of removing each individual term from the full model was then examined to determine those factors that explained (in a statistical sense) the recovery process.

Results

Most (89%) of the studies were undertaken at depths less than 60 m; of these 13 (23%) were intertidal (Table 1, Fig. 1a). This bias to intertidal and shallow water studies almost certainly reflects the logistic difficulties and high cost of conducting experiments in deeper water, although it is encouraging to note two recent studies off the west coast of North America that were conducted at depths of about 200 m. All the intertidal studies were conducted at small spatial scales (< 50 m), and most of the subtidal studies had spatial scales less than 200

m (Fig. 1b). The largest scale studies were those that compared commercially-fished grounds with closed areas or areas of different fishing intensity. Most of the experiments consisted of a single disturbance event. Seven studies manipulated the disturbance regime, but only four of these contained data suitable for our analyses (Fig. 1c). Hence, we used the regime variable to distinguish experimental studies (acute disturbance) from the 12 studies comparing fished and unfished areas (chronic disturbance). Otter trawling was the gear type most frequently studied, which reflects the wide use of otter trawls around the world (Fig. 1d). Geographically, the studies are heavily dominated by Northern Europe and East North America, which perhaps reflects the fact that bottom fishing gear was first developed in these regions. The North Atlantic has a longer exploitation history than other regions and concerns about

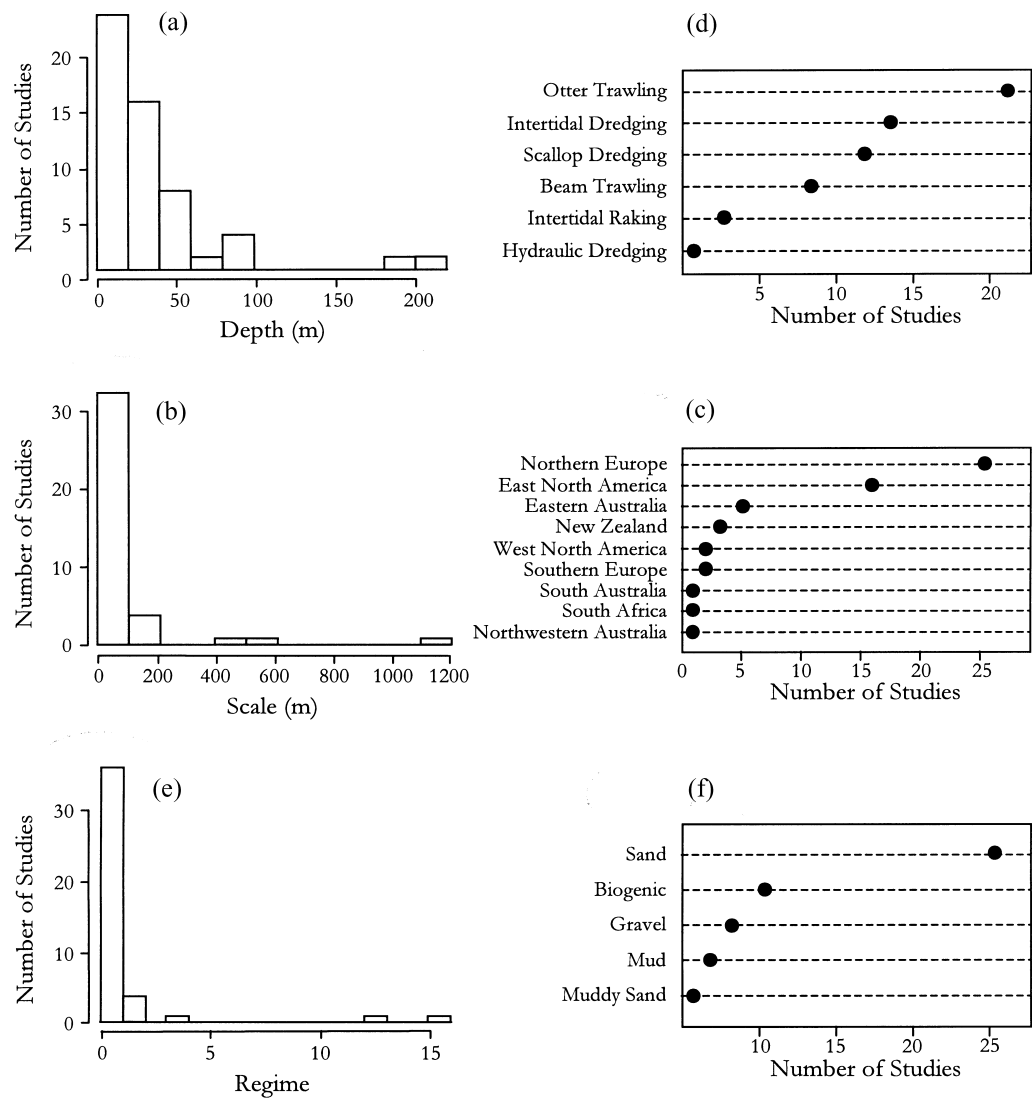


Fig. 1. Summary of the distribution of published fishing impact studies with respect to a range of potential explanatory variables. Fifty-seven studies were identified in 39 publications.

Table 3. Initial impacts on total number of individuals and total number of species for all levels of three factors, gear, habitat and geographical region. Values are mean percent changes for each level of each factor

Factor (level)	Total number of individuals	Total number of species
Gear		
Inter-tidal dredging	-56	-39
Scallop dredging	-51	-30
Otter trawling	-51	1
Beam trawling	3	-23
Habitat		
Biogenic	-59	N/A
Mud	-57	-36
Gravel	-58	-34
Sand	-21	-15
Region		
East North America	-55	-18
Australia & New Zealand	-47	-14
Northern Europe	-33	-40

the impacts of bottom fishing were raised correspondingly earlier (Fig. 1e). Sand was by far the most commonly studied habitat, reflecting the predominance of sand on continental shelves around the world (Fig. 1f). The effects of fishing in biogenic and structured habitats were of particular interest, as we anticipated that these would be the most vulnerable to fishing disturbance. However, only four of the 10 studies listed for this habitat contained data suitable for incorporation in our analyses.

EFFECTS ON TOTAL NUMBER OF INDIVIDUALS AND TOTAL NUMBER OF SPECIES

Of the 33 studies that provided data suitable for analysis of the immediate effects of fishing, 24 of the studies reported summary data on the total number of individuals and, of these, 18 also contained the total number of species. The mean of the standar-

dized response for the number of individuals was -0.61, which corresponds to a 46% decrease in the total number of individuals within disturbed plots. Although none of the explanatory variables explained a statistically significant proportion of the deviance, the mean values for the levels of each factor are worthy of comment (Table 3). For example, dredging had a more negative impact than trawling, which is not surprising as dredges tend to penetrate deeper into the sediments than trawls. Interestingly, however, beam trawling studies in sand habitats in Northern Europe had remarkably less impact than the other gear types and other habitats. As expected, the largest negative impact occurred in biogenic habitats, in this case off the East Coast of Australia (Sainsbury *et al.* 1997). These biogenic habitats are largely composed of relatively slow growing species, and are typified by sponges and corals.

The mean response for number of species was -0.31, which corresponds to a 27% reduction. Again, no statistically significant effects were detected, but larger impacts were observed in mud and gravel habitats than in sand. Inter-tidal dredging had the most negative impact on species richness and otter trawling had the least impact.

In summary, despite some suggestive patterns in the responses of number of individuals and species to fishing disturbance, none of the tests showed statistically significant effects. We suspect this lack of significance is largely due to the low statistical power, but it may also be that negative responses of some taxa are counteracted by positive responses of others.

EFFECTS ON POPULATIONS

Examining the initial responses of individual taxa to fishing, the grand mean response was -0.79 or a percentage reduction of 55%. The final ANOVA contained five factors (Table 4). Gear type was highly significant, with inter-tidal dredging having the most negative impact, followed by scallop dredging and inter-tidal raking; otter trawling and beam trawling had less negative effects (Fig. 2a). The geo-

Table 4. Summary of ANOVA of initial response data. Each row indicates the increase in the residual sum of squares (RSS) that would result from dropping that term from the linear model

Factor	D.f.	RSS	F-value	Probability
Regime	1	792	3.73	NS ($P = 0.054$)
Class	12	839	2.81	***
Habitat	4	801	2.33	NS ($P = 0.055$)
Region	4	852	10.53	***
Gear type	4	898	17.84	***
Residual	500	786		

NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

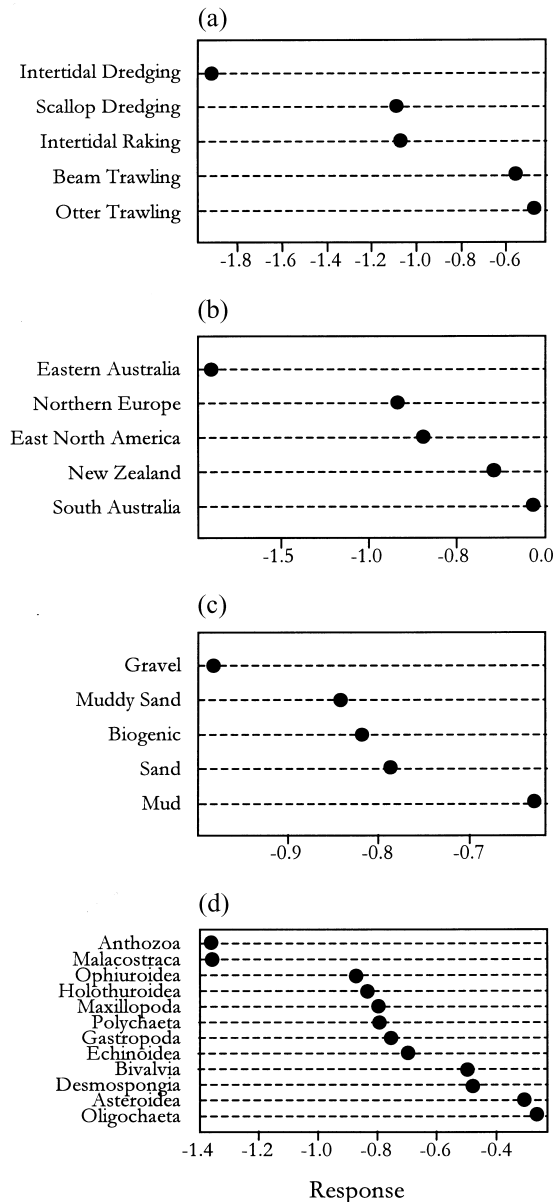


Fig. 2. Predicted means from the ANOVA of initial responses (Table 4). The coefficients have been standardized to make the treatment effects orthogonal. Data are on a transformed scale (see text) where values correspond to percentage declines from controls as follows: $-0.1 = 10\%$; $-0.22 = 20\%$; $-0.35 = 30\%$; $-0.5 = 40\%$; $-0.68 = 50\%$; $-1.35 = 75\%$; $-4.61 = 100\%$

graphical region of study was also highly significant. The largest negative impacts were observed in Eastern Australia followed by Northern Europe and the least impact was observed in South Australia (Fig. 2b). Habitat and regime were almost significant at the 5% level. The most negative impacts occurred in muddy sand and gravel habitats. Surprisingly, the least impact was observed in mud habitats, not sand—a result that was not consistent with that obtained above for total number of individuals or species richness (Fig. 2c). Taxa in the one study of

chronic disturbance included in this meta-analysis (Collie *et al.* 1997) had more negative responses (mean = -0.98 , 62%) than the acute fishing experiments (mean = -0.77 , 54%).

The variable 'Class' also had a significant effect on the response to disturbance. The largest negative impacts were observed for Anthozoa and Malacostraca; their means of -1.36 correspond to a 75% reduction in density (Fig. 2d). The other arthropod class, maxillopoda (copepods and ostracods), was less negatively affected. Among the echinoderms, the holothurians and ophiuroids were more negatively impacted than the echinoids and asteroids. Bivalves appeared to be less sensitive to fishing disturbance than gastropod molluscs. Polychaetes were more negatively affected than oligochaetes, which appeared to be the least sensitive class. Interestingly, none of the predicted means was positive. Taxa differed in their response to disturbance, but on average, none increased in abundance.

A seven-node regression tree shows the most important contrasts in the response data (Fig. 3). The first split, accounting for the largest reduction in model deviance, separated inter-tidal dredging, inter-tidal raking, and scallop dredging on the left from beam trawling and otter trawling on the right. The trawling studies were then split by taxonomic class: anthozoans, echinoids, gastropods, holothurians, malacostracans and ophiuroids had more negative responses than the other classes. The dredging studies split by region and then by habitat. The muddy sand studies had more negative responses than the other sediment types, while in the other habitats, anthozoa, malacostraca, ophiuroidea and polychaeta were the more sensitive classes, and had more negative responses to chronic than to acute disturbance. The regression tree can be followed from its root to the branches to make predictions about how a particular taxon would be affected initially by disturbance from a particular fishing gear in a particular habitat.

We extracted the records for genera with six or more records to investigate the extent to which individual taxa exhibited similar responses to disturbance in different studies. Most of these common genera are from the North Atlantic. A three-way ANOVA was fit to these data to factor out the significant effects of habitat and gear type (Table 5). As with the full data set, dredging had a larger impact than trawling; unlike the previous analysis, intertidal raking had the least effect (Fig. 4a). The mean response in muddy sand was much more negative than in the other habitats (Fig. 4b). The most negative responses were for the polychaete species *Arenicola*, *Scoloplos*, *Heteromastus* and *Glycera* (Fig. 4c). *Arenicola*, which is harvested as bait for sport fishing, was completely removed in five of the six studies in which it occurred. The bivalves *Macoma* and *Cerastoderma* were also more negatively impacted

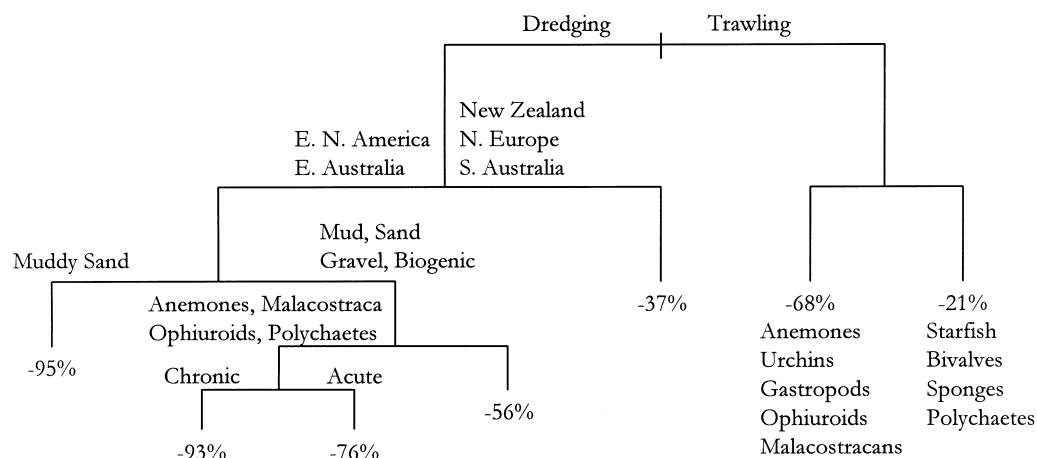


Fig. 3. Regression tree of the initial response data. A binary partitioning algorithm recursively splits the data in each node until the node is homogeneous or contains too few observations. The vertical height of each branch indicates the importance of that split. The number under each node is the mean response for that combination of variables.

than the other genera, perhaps because they are specifically targeted by some fishing gears. The genera least impacted by disturbance were bivalves: *Nucula*, *Ensis*, *Chamelea*, *Abra* and *Corbula*. The mean response for *Nucula* was slightly positive. Many of these bivalves are small in size or have particularly

well armoured shells that protect them from physical damage. Recent studies show that smaller bodied organisms are displaced by pressure waves that form in front of fishing gear as they move through the water (Gilkinson *et al.* 1998).

Table 5. Summary of ANOVA of the initial responses of individual genera. Each row indicates the increase in the residual sum of squares (RSS) that would result from dropping that term from the linear model. NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Factor	D.f.	RSS	F-value	Probability
Genus	17	145	2.70	***
Habitat	3	113	3.07	*
Gear type	4	120	4.47	**
Residual	119	104		

PATTERNS OF RECOVERY

For single-factor recovery models (plus time) significant interaction terms were obtained for gear type, habitat type, scale, and the phylum or class to which a taxon belonged (Table 6). Since all these factors also accounted for a significant proportion of the deviance when removed from a full model, these results suggest that they are significantly correlated with recovery rate. For the initial impact data, depth and scale were either insignificant or had inconsistent effects among models, yet they both had significant main effects in the recovery analysis.

Table 6. Summary of single factor models of recovery data for negative initial responses. Values are likelihood ratios for main effects and interactions. Statistically significant main effects indicate that models of the form response = $f(\text{time} + \text{factor})$, gave significant improvements in fit over a model with time only. Statistically significant interactions were determined by comparing response = $f(\text{time} + \text{factor})$ models with those in which a time:factor interaction was included. A significant main effect suggests that the magnitude of response was statistically different for different levels of the factor. Significant interactions suggest that the rate of recovery differed between levels

Factor	Main effect	Interaction
Gear type (fixed)	$L_{7,10} = 5.34$ NS	$L_{10,13} = 18.04$ ***
Habitat (fixed)	$L_{7,10} = 1.82$ NS	$L_{10,13} = 21.03$ ***
Scale (random)	$L_{7,8} = 13.38$ ***	$L_{8,9} = 26.11$ ***
Depth (random)	$L_{7,8} = 4.01$ *	$L_{8,9} = 3.69$ NS ($P = 0.055$)
Phylum (fixed)	$L_{7,9} = 6.13$ *	$L_{9,11} = 25.41$ ***
Class (fixed)	$L_{7,12} = 9.22$ NS	$L_{12,17} = 47.48$ ***

NS, $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

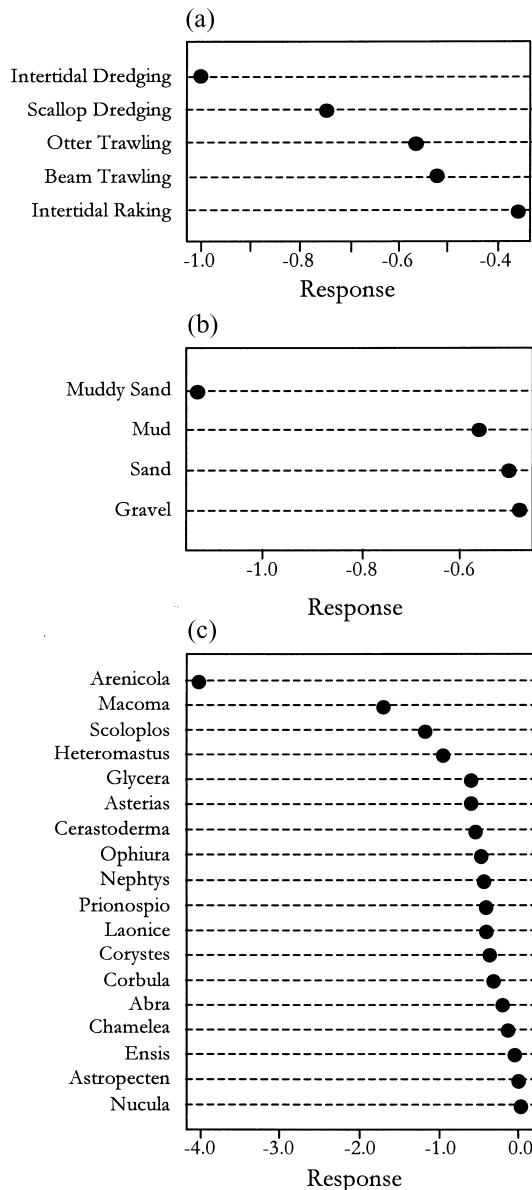


Fig. 4. Predicted means from the ANOVA of initial responses for gear type, habitat and individual genera (Table 5). The coefficients have been standardized to make the treatment effects orthogonal. Data are on a transformed scale (see text) where values correspond to percentage declines from controls as follows: $-0.1 = 10\%$; $-0.22 = 20\%$; $-0.35 = 30\%$; $-0.5 = 40\%$; $-0.68 = 50\%$; $-1.35 = 75\%$; $-4.61 = 100\%$.

The interaction term was also significant for scale, while for depth it was almost so ($P = 0.055$). These results seem intuitively reasonable since, while both these factors could be expected to affect the recovery process, there is no particular reason to suppose that they would influence initial mortality rates.

The recovery data are notably sparse and scattered (Fig. 5), but some features are worthy of comment. First, recovery (as indicated by the trend line) was rarely less than 100 days, regardless of the basis for classification. Indeed, when considered by taxo-

mic classes, for which the density and distribution of records over time was rather more complete, recovery was closer to 500 days. With respect to gear type, the plots suggest that the source of the statistically significant interaction term is the greater initial impact for inter-tidal dredging. Interestingly, although initial impact is greater, these plots also suggest that the time taken to reach control values does not differ markedly from other gear types. Inter-tidal dredging gives the greatest initial responses because it is the most efficient gear of those considered, completely removing the substratum and its attendant fauna. In addition, accurate sampling is more easily achieved on inter-tidal compared with subtidal areas. For habitat, it would appear that the relatively lower initial impacts in mud and biogenic habitats is the source of the significant interaction term. Nevertheless, recovery appears to occur most rapidly in sand as opposed to the other habitat types. Another interesting feature of these data is the location of records with maximal impact (i.e. 100% removal relative to controls). Of the 12 observations in this category, nine were for bivalves, affected by inter-tidal dredges in sandy habitats (*Macoma balthica* and *Cerastoderma edule*). Although it was more common to observe 100% removal of fauna in the inter-tidal dredging studies, there may be much greater ecological significance attached to the removal of 50% of resident biogenic fauna (see below).

Discussion

Despite the obvious limitations of our analyses, consistent patterns have emerged that would otherwise be unsupported by single studies. On average, the immediate impact of fishing disturbance was to remove about half the individuals. However, the magnitude of the response varied significantly with gear type, habitat and among taxa.

With respect to gear type our results are broadly consistent with expectations—inter-tidal dredging has more marked initial effects than scallop dredging, which in turn is greater than otter trawling. Although, at first sight, the apparent lack of effect from beam trawling is somewhat surprising, we suspect that the relative paucity of data for this gear is almost certainly part of the explanation. It should also be borne in mind, however, that beam-trawling studies were generally conducted in relatively dynamic sandy areas, where initial effects may be less apparent.

Our expectations for a habitat effect were that initial responses and rates of recovery from trawling impacts would be related to, and could be predicted from, the physical stability of the sea bed. It makes intuitive sense that animals living in unconsolidated sediments are adapted to periodic sediment resuspension and smothering. Indeed, such intuition has

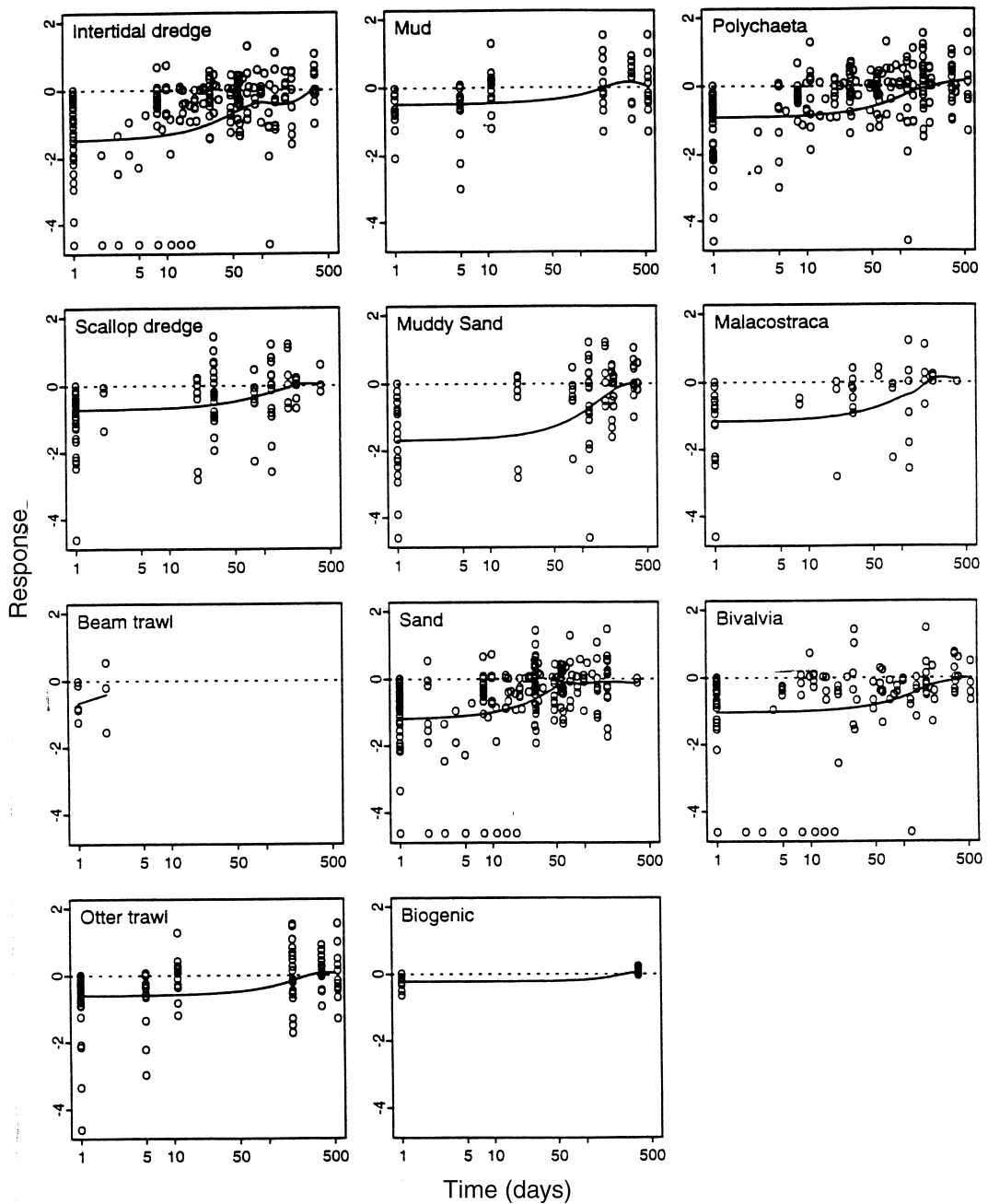


Fig. 5. Scatter plots of recovery data for categorical variables for which there was a significant interaction term. Trend lines are fitted by loess smooth, with identical smoothing parameters for each panel. Data are on a transformed scale (see text) where values correspond to percentage declines from controls as follows: $-0.1 = 10\%$; $-0.22 = 20\%$; $-0.35 = 30\%$; $-0.5 = 40\%$; $-0.68 = 50\%$; $-1.35 = 75\%$; $-4.61 = 100\%$.

been the cornerstone of our own thinking about impacts and recovery dynamics for benthos (e.g. Hall 1994; Jennings & Kaiser 1998). However, our initial impact results with respect to habitat were somewhat inconsistent among analyses. It does appear that responses in sand habitats were usually less negative than in the other habitats, but a clear ranking for expected impacts did not emerge. The inconsistencies may reflect interactions between the factors arising from the unbalanced nature of the

data, with many combinations of gear and habitat unrepresented. For example, the relatively low impact on mud habitats may be explained by the fact that most studies were done with otter trawls. If data were also available for the effect of dredgers a more negative response for this habitat may have been observed. Whether these inconsistencies can be explained in this way can only await further study.

Perhaps the most consistently interpretable result was with respect to faunal vulnerability, with a

ranking of initial impacts that seems broadly congruent with expectations based on morphology and behaviour.

Our regression tree analysis provides the first quantitative basis for predicting the relative impacts of fishing under different situations. Following the tree from its root to the branches we can make predictions, for example, about how a particular taxon would be affected initially by disturbance from a particular fishing gear in a particular habitat. Thus, we would predict from Fig. 3 that trawling would reduce anthozoans by 68%, whereas Asteroids would only be reduced by 21%. Similarly, for dredging chronic exposure (repeated dredging) is predicted to lead to 93% reductions for anthozoa, malacostraca, ophiuroidea and polychaeta, whereas acute fishing (a single dredge event) is predicted to lead to a 76% reduction. At this stage, it would clearly be unwise to use this analysis as anything other than illustrative, but we argue that the approach might ultimately provide a useful quantitative framework for predicting fishing impacts, particularly because it is readily amenable to updating in the light of new data.

RECOVERY FROM TRAWLING IMPACTS

Our recovery data, while very preliminary, permit us to speculate about the level of physical disturbance that is sustainable in a particular habitat. For example, if, as our results suggest, sandy sediment communities are able to recover within 100 days, this implies that they could perhaps withstand 2–3 incidents of physical disturbance per year without changing markedly in character. This is the average predicted rate of disturbance for the whole of the southern North Sea, for example. However, when fishing effort data is collected at fine spatial (9 km²) resolution (Rijnsdorp *et al.* 1998), it becomes clear that effort is patchily distributed and that some relatively small areas of the seabed are visited by > 400 trawlers per year. This level of fishing equates to a total disturbance of approximately eight times per year (Rijnsdorp *et al.* 1998). If our recovery rate estimates for sandy habitats are realistic, this is a rate that will result in a resident community that is not representative of the fauna that originally occurred in that habitat.

While the above example is illustrative, there are some important caveats. First, the small spatial scale of most of the trawl impact studies make it likely that much of the recolonization was through immigration into disturbed patches, rather than reproduction within patches. We found recovery to be slower if the spatial scale of impact was larger, as it would be on heavily fished grounds. Secondly, it should be noted, that while we might accurately predict the recovery rate for small-bodied taxa such as polychaetes, which dominate the data set, sandy

sediment communities often contain one or two long-lived and therefore vulnerable species. Note, for example, the occurrence of the large bivalve *Mya truncata* in the inter-tidal zone of the Wadden Sea. While the majority of the benthos in this environment recovered within 6 months of lugworm dredging, the biomass of *M. truncata* remained depleted for at least 2 years (Beukema 1995). Given the effects observed in many studies, we anticipate a shift from communities dominated by relatively high biomass species towards dominance by high abundances of small-sized organisms.

It is clear that intensively fished areas are likely to be maintained in a permanently altered state, inhabited by fauna adapted to frequent physical disturbance. This is, of course, much more likely for the most stable types of habitats containing structural biogenic components. It is for these habitats that the paucity of data is most apparent and where recovery rates will be longest. While it would appear that none of the habitats included in our study for which recovery data are available fall into this category, some data are emerging. Recent work by Hall-Spencer & Moore (1999) on Maerl beds, for example, showed that 4 years after the initial disturbance had occurred, certain fauna, such as the nest building bivalve *Limaria hians*, had still not recolonized trawl tracks. Similarly, work by Sainsbury *et al.* (1997) suggests that recovery rates may exceed 15 years for sponge and coral habitats off the western coast of Australia. As a matter of urgency we need to identify other habitats that show long recovery times—the most likely candidates are of course those that, like Maerl beds, contain a high proportion of structural fauna.

Despite our efforts to predict the outcome of fishing activities for existing benthic communities, we are often unable to deduce the original composition of the fauna because data gathered prior to the era of intensive bottom fishing are sparse. This is an important caveat because recent analyses of the few existing historical datasets suggest that larger bodied organisms (both fish and benthos) were more prevalent prior to intensive bottom trawling (Greenstreet & Hall 1996; Frid & Clark 1999; Veale *et al.* in press). Moreover, in general, epifaunal organisms are less prevalent in areas subjected to intensive bottom fishing (Collie *et al.* 1997; Sainsbury *et al.* 1997; Thrush *et al.* 1998; Veale *et al.* in press). An important consequence of this effect is the reduction in habitat complexity (architecture) that accompanies the removal of sessile epifauna, which appears to have important consequences for fish communities (see, for example, Sainsbury *et al.* 1997). Our current understanding of the functional role of many of the larger-bodied long-lived species (e.g. as habitat features, bioturbators, etc.) is limited and should be addressed to predict the outcome of permitting

chronic fishing disturbance in areas where these animals occur.

While short-term, site-specific fishing impact studies have yielded useful quantitative data, there is clearly a need for continued synthesis. More studies are needed, particularly of recovery dynamics from comparative studies that examine the large-scale effects of fishing disturbance at intensities imposed by commercial fleets (e.g. Collie *et al.* 1997). There is also a paucity of quantitative studies undertaken in deeper water (> 100 m), or in stable and structurally complex habitats for which the recovery trajectory will be measured in years.

With respect to the design of future studies, we feel that experimentalists wishing to address the fishing impacts issue will be best served by abandoning short-term, small-scale pulse experiments (*sensu* Bender *et al.* 1984). Instead, the scientific community should be arguing for support to undertake much larger scale press and relaxation experiments. One half of the experiment has already been done—since fishing activity has been providing the press for many years, what we now require are carefully designed closed area contrasts. There are two principal advantages to this approach. First, the results obtained are clearly interpretable in terms of real world intensities of fishing disturbance. Secondly, the spatial scale of the protected areas can probably be relatively small (and hence replicated to fulfil the requirements for sound experimental design) without compromising unduly the interpretation of recovery dynamics: estimates of recovery in small protected areas in a sea of disturbance are likely to be conservative, while recovery in small deliberately disturbed patches are not. Thirdly, the experiments would be conducted in the very habitats (i.e. real fishing grounds) about which the question of recovery is actually being posed.

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References

- Arnqvist, F.R. & Wooster, D. (1995) Meta-analysis – synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution*, **10**, 236–240.
- Auster, P.J. & Langton, R.W. (1999) The effects of fishing on fish habitat. *Fish Habitat: Essential Fish Habitat and Rehabilitation* (ed. L. Benaka), pp. 150–187. American Fisheries Society, Bethesda, Maryland.
- Auster, P.J., Malatesta, R.J., Langton, R.W., Watling, L., Valentine, P.C., Donaldson, C.L.S., Langton, E.W., Shepard, A.N. & Babb, I.G. (1996) The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest Atlantic): implications for conservation of fish populations. *Reviews in Fisheries Science*, **4**, 185–202.
- Bender, E.A., Case, T.J. & Gilpin, M.E. (1984) Perturbation experiments in community ecology: theory and practice. *Ecology*, **65**, 1–13.
- Bergman, M.J. & Hup, M. (1992) Direct effects of beam trawling on macrofauna in a sandy sediment in the southern North Sea. *ICES Marine Science Symposium*, **49**, 5–11.
- Beukema, J.J. (1995) Long term effects of mechanical harvesting of lugworms *Arenicola marina* on the zoobenthic community of a tidal flat in the Wadden Sea. *Netherlands Journal of Sea Research*, **33**, 219–227.
- Bradshaw, C., Veale, L.O., Hill, A.S. & Brand, A.R. (1999) The effects of scallop dredging on gravely seabed communities. *The Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-Economic Issues* (eds M.J. Kaiser & S.J. de Groot). Blackwell Science, Oxford, UK.
- Bradstock, M. & Gordon, D.P. (1983) Coral-like bryozoan growths in Tasman Bay, and their protection to conserve local fish stocks. *New Zealand Journal of Marine and Freshwater Research*, **17**, 159–163.
- Brown, B. & Wilson, W.H. (1997) The role of commercial digging of mudflats as an agent for change of infaunal intertidal populations. *Journal of Experimental Marine Biology and Ecology*, **218**, 49–61.
- Brylinsky, M., Gibson, J. & Gordon, D. (1994) Impacts of flounder trawls on the intertidal habitat and community of the Minas Basin, Bay of Fundy. *Canadian Journal of Fisheries and Aquatic Science*, **51**, 650–661.
- Clark, L.A. & Pregibon, D. (1993). Tree-Based Models. *Statistical Models in S*. (eds J.M. Chambers & T.J. Hastie), pp. 377–419. Chapman & Hall, London.
- Collie, J.S., Escanero, G.A. & Valentine, P.C. (1997) Effects of bottom fishing on the benthic megafauna of Georges Bank. *Marine Ecology Progress Series*, **155**, 159–172.
- Cotter, A., Walker, P., Coates, P., Cook, W. & Dare, P. (1997) Trial of a tractor dredger for cockles in Burry Inlet, South Wales. *ICES Journal of Marine Science*, **54**, 72–83.
- Cryer, M., Whittle, G.N. & Williams, R. (1987) The impact of bait collection by anglers on marine intertidal invertebrates. *Biological Conservation*, **42**, 83–93.
- Currie, D.R. & Parry, G.D. (1996) Effects of scallop dredging on a soft sediment community – a large scale experimental study. *Marine Ecology Progress Series*, **134**, 131–150.
- Eleftheriou, A. & Robertson, M.R. (1992) The effects of experimental scallop dredging on the fauna and physical environment of a shallow sandy community. *Netherlands Journal of Sea Research*, **30**, 289–299.
- Engel, J. & Kvitek, R. (1998) Effects of otter trawling on a benthic community in Monterey Bay National Marine Sanctuary. *Conservation Biology*, **12**, 1204–1214.

- Fonseca, M.S., Thayer, G.W. & Chester, A.J. (1984) Impact of scallop harvesting on eelgrass (*Zostera marina*) meadows: implications for management. *North American Journal of Fisheries Management*, **4**, 286–293.
- Freese, L., Auster, P.J., Heifetz, J. & Wing, B. (1999) Effects of trawling on seafloor habitat and associated invertebrate taxa in the Gulf of Alaska. *Marine Ecology Progress Series*, **182**, 119–126.
- Frid, C.L.J. & Clark, R.A. (1999) Long-term changes in North Sea benthos: discerning the role of fisheries. *The Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-Economic Issues* (eds M.J. Kaiser & S.J. de Groot), pp. 198–216. Blackwell Science, Oxford, UK.
- Gibbs, P.J., Collins, A.J. & Collett, L.C. (1980) Effect of otter prawn trawling on the macrobenthos of a sandy substratum in a New South Wales estuary. *Australian Journal of Marine and Freshwater Research*, **31**, 509–516.
- Gilkinson, K., Paulin, M., Hurley, S. & Schwinghamer, P. (1998) Impacts of trawl door scouring on infaunal bivalves: results of a physical trawl door model/dense sand interaction. *Journal of Experimental Marine Biology and Ecology*, **224**, 291–312.
- Goldberg, D.E., Rajaniemi, T.K., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118–1131.
- Greenstreet, S.P.R. & Hall, S.J. (1996) Fishing and groundfish assemblage structure in the northwestern North Sea: an analysis of long-term and spatial trends. *Journal of Animal Ecology*, **65**, 577–598.
- Guillen, J., Ramos, A., Martinez, L. & Sanchez Lizaso, J. (1994) Antitrawling reefs and the protection of *Posidonia oceanica* (L.) delile meadows in the western Mediterranean Sea: demands and aims. *Bulletin of Marine Science*, **55**, 645–650.
- Gurevitch, J. & Chester, S.T.J. (1986) Analysis of repeated experiments. *Ecology*, **67**, 46–57.
- Gurevitch, J. & Hedges, L.V. (1999) Statistical issues in ecological meta-analysis. *Ecology*, **80**, 1142–1149.
- Gurevitch, J., Morrow, L.L., Wallace, A. & Walsh, J.S. (1992) Analysis of repeated experiments. *Ecology*, **67**, 46–57.
- Hall, S.J. (1994) Physical disturbance and marine benthic communities: life in unconsolidated sediments. *Oceanography and Marine Biology. An Annual Review*, **32**, 179–239.
- Hall, S.J. (1999) *The Effects of Fishing on Marine Ecosystems and Communities*. Blackwell Science, Oxford.
- Hall, S.J., Basford, D.J. & Robertson, M.R. (1990) The impact of hydraulic dredging for razor clams *Ensis* sp. on an infaunal community. *Netherlands Journal of Sea Research*, **27**, 119–125.
- Hall, S.J. & Harding, M.J.C. (1997) Physical disturbance and marine benthic communities: the effects of mechanical harvesting of cockles on non-target benthic infauna. *Journal of Applied Ecology*, **34**, 497–517.
- Hall-Spencer, J. (1995) *Evaluation of the Direct Impact of Fishing Gears on the Substratum and on the Benthos*. European Commission, Brussels.
- Hall-Spencer, J.M. & Moore, P.G. (1999) Impacts of scallop dredging on maerl grounds. *The Effects of Fishing on Non-Target Species and Habitats: Biological, Conservation and Socio-Economic Issues* (eds M.J. Kaiser & S.J. de Groot), pp. 105–118. Blackwell Science, Oxford, UK.
- Hastie, T.J. (1993) Generalized additive models. *Statistical Models in S* (eds J.M. Chambers & T.J. Hastie), pp. 249–308. Chapman & Hall, London.
- Hastie, T. & Tibshirani, R. (1990) *Generalized Additive Models*. Chapman & Hall, London.
- Heiligenberg, T. (1987) Effects of mechanical and manual harvesting of lugworms *Arenicola marina* L. on the benthic fauna of tidal flats in the Dutch Wadden sea. *Biological Conservation*, **39**, 165–177.
- Ismail, N.S. (1985) The effects of hydraulic dredging to control oyster drills on benthic macrofauna of oyster grounds in Delaware Bay, New Jersey. *Internationale Revue der Gesamten Hydrobiologie*, **70**, 379–395.
- Jennings, S. & Kaiser, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 201–352.
- Kaiser, M.J., Edwards, D., Armstrong, P., Radford, K., Lough, N., Flatt, R. & Jones, H. (1998) Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES Journal of Marine Science*, **55**, 353–361.
- Kaiser, M.J., Edwards, D.B. & Spencer, B.E. (1996) A study of the effects of commercial clam cultivation and harvesting on benthic infauna. *Aquatic Living Resources*, **9**, 57–63.
- Kaiser, M.J. & Spencer, B.E. (1996) Behavioural responses of scavengers to beam trawl disturbance. *Aquatic Predators and Their Prey* (eds S. P. R. Greenstreet & M. L. Tasker), pp. 116–123. Fishing News Books, Oxford.
- Langton, R.W. & Robinson, W.E. (1990) Faunal associations on scallop grounds in the western Gulf of Maine. *Journal of Experimental Marine Biology and Ecology*, **144**, 157–171.
- Lindeboon, H.J. & de Groot, S.J. (1998) *The Effects of Different Types of Fisheries on the North Sea and Irish Sea Benthic Ecosystems*. The Netherlands Institute for Sea Research, Den Burg, Texel.
- Magorrian, B.H., Service, M. & Clarke, W. (1995) An acoustic bottom classification survey of Strangford Lough, Northern Ireland. *Journal of the Marine Biological Association (UK)*, **75**, 987–992.
- Malakoff, D. (1998) Papers posit grave impact of trawling. *Science*, **282**, 2168.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, New York.
- McLusky, D.S., Anderson, F.E. & Wolfe-Murphy, S. (1983) Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging. *Marine Ecology Progress Series*, **11**, 173–179.
- Osenberg, C.W., Sarnelle, O., Cooper, S.D. & Holt, R.D. (1999) Resolving ecological questions through meta-analysis: goals, metrics and models. *Ecology*, **80**, 1105–1117.
- Osenberg, C.W. & St. Mary, C.M. (1998) Meta-analysis: synthesis or statistical subjugation? *Integrative Biology: Issues, News and Views*, **1**, 43–48.
- Paine, R.T. (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature (London)*, **355**, 73–75.
- Peterson, C.H., Summerson, H.C. & Fegley, S.R. (1987) Ecological consequences of mechanical harvesting of clams. *Fishery Bulletin*, **85**, 281–298.
- Pitcher, C.R., Burrige, C.Y., Wassenberg, T.J. & Poiner, I.R. (1996) The effects of prawn trawl fisheries on GBR seabed habitats. The Great Barrier Reef, science, use and management: National Conference. *Proceedings, Great Barrier Reef Marine Park Authority*, pp. 107–123.
- Rijnsdorp, A.D., Buijs, A.M., Storbeck, F. & Visser, E. (1998) Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the

- impact on benthic organisms. *ICES Journal of Marine Science*, **55**, 403–419.
- Sainsbury, K.J. (1987) Assessment and management of the demersal fishery on the continental shelf of northwestern Australia. *Tropical Snappers and Groupers: Biology and Fisheries Management* (eds J. J. Polovina & S. Ralston), pp. 465–503. Westview Press, Boulder, CO.
- Sainsbury, K.J., Campbell, R.A., Lindholm, R. & Whitlaw, A.W. (1997) Experimental management of an Australian multispecies fishery: examining the possibility of trawl-induced habitat modification. *Global Trends: Fisheries Management* (eds K. Pikitch, D. D. Huppert & M. P. Sissenwine), pp. 107–112. American Fisheries Society, Bethesda, Maryland.
- Sanchez, P., Demestre, M., Ramon, M. & Kaiser, M.J. (in press) The impact of otter trawling on mud communities in the NW Mediterranean. *ICES Journal of Marine Science*.
- Thrush, S.F., Hewitt, J.E., Cummings, V.J. & Dayton, P.K. (1995) The impact of habitat disturbance by scallop dredging on marine benthic communities: what can be predicted from the results of experiments? *Marine Ecology Progress Series*, **129**, 141–150.
- Thrush, S.F., Hewitt, J.E., Cummings, V.J., Dayton, P.K., Cryer, M., Turner, S.J., Funnell, G.A., Budd, R.G., Milburn, C.J. & Wilkinson, M.R. (1998) Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecological Applications*, **8**, 866–879.
- Tuck, I.D., Hall, S.J., Robertson, M.R., Armstrong, E. & Basford, D.J. (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea-loch. *Marine Ecology Progress Series*, **162**, 227–242.
- Van Dolah, R.F., Wendt, P.H. & Levisen, M.V. (1991) A study of the effects of shrimp trawling on benthic communities in two South Carolina sounds. *Fisheries Research*, **12**, 139–156.
- Van Dolah, R.F., Wendt, P.H. & Nicholson, N. (1987) Effects of a research trawl on a hard-bottom assemblage of sponges and corals. *Fisheries Research*, **5**, 39–54.
- Veale, L.O., Hill, A.S., Hawkins, S.J. & Brand, A.R. (in press) Effects of long-term physical disturbance by commercial scallop fishing on subtidal epifaunal assemblages and habitats *Marine Biology*.
- Watling, L. & Norse, E.A. (1998) Disturbance of the seabed by mobile fishing gear: a comparison to forest clear-cutting. *Conservation Biology*, **12**, 1180–1197.
- Wynberg, R.P. & Branch, G.M. (1994) Disturbance associated with bait-collection for sandprawns (*Callinassa kraussi*) and mudprawns (*Upogebia africana*): long-term effects on the biota on intertidal sandflats. *Journal of Marine Research*, **52**, 523–558.

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