

Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing

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Summary

1. The Ecosystem Approach to Fisheries requires that managers take account of the environmental impacts of fishing. Towed bottom-fishing gears disturb seabed habitats and cause mortality of benthic invertebrates. Measurements of recovery rates of marine habitats after fishing disturbance can provide insight into spatial variations in resilience and may be used to assess the sustainability of these fishing impacts and inform the development of appropriate management strategies.
2. To measure recovery on real fishing grounds at fishery- and management-relevant scales, we estimated the post-disturbance recovery rates of epifaunal marine benthic communities on coarse and hard substrata across > 4000 km² of seabed where the patchy distribution of bottom fishing in space and time creates a mosaic of habitat patches at different stages of recovery.
3. The history of fishing events at each location was described using satellite vessel monitoring system (VMS) data. Recovery rates were extrapolated from the relationship between time since the last fishing event and abundance of epifaunal benthic invertebrates with life-history traits that are expected to make them sensitive to fishing.
4. Recovery of abundance of all species and functional groups (medium to medium-large size, medium to long life span, suspension feeding, high body flexibility and low mobility species) was estimated to take < 1 to > 10 years, depending on the group, with faster recovery in areas with faster tidal currents.
5. The recovery of large species was faster when conspecifics were abundant within a radius of 6 km, suggesting an important role for maintaining local sources of recruits to repopulate impacted areas.
6. *Synthesis and applications.* We used a new method to estimate the recovery rate of benthic communities and to describe spatial differences in sensitivity to fishing. Bottom fishing in areas that recover quickly will minimize overall impacts, while leaving unfished patches of seabed will enhance recovery rates in fished areas. We conclude that management plans which limit bottom trawls and dredge fisheries to more resilient areas and maintain unfished patches within these areas will minimize the collective impacts of a given amount of fishing effort on seabed habitats.

Key-words: Ecosystem-based fisheries management, fishing impact, otter trawling, recovery, scallop dredging, vessel monitoring system, VMS

Introduction

Towed bottom-fishing gears modify the biomass, diversity, productivity and composition of benthic communities (Collie, Escanero & Valentine 1997; Jennings *et al.* 2001;

Hiddink *et al.* 2006b). These changes, in turn, affect a variety of ecosystem processes, such as nutrient cycling, sediment stabilization, enhancement of structural habitat complexity and provision of habitat and food for fish (Rhoads & Germano 1982; Bolam, Fernandes & Huxham 2002; Solan *et al.* 2004).

The resilience of a habitat, community or process to fishing impacts can be measured as the inverse of the recovery time following a defined impact (Hiddink, Jennings &

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Kaiser 2007). Resilience is higher and higher fishing rates can be sustained if the habitat, community or process recovers quickly from fishing. Quantification of spatial variation in recovery times can be used to support the identification and selection of fishing grounds that are least affected by the impacts of fishing, and similarly would enable the identification of sensitive habitats where fishing should be reduced or avoided.

The allocation of fishing rights based on a 'habitat-impact quota' has been suggested as a potential approach to encourage targeting of more resilient habitats by fisheries that use towed bottom-fishing gears (e.g. Holland & Schnier 2006). Implementation of this approach would require the mapping and identification of more resilient habitats. Recovery time of benthic communities depends on their exposure to natural disturbance as well as the intensity of fishing disturbance (Kaiser 1998). Communities found in unconsolidated mobile sediments are expected to be better adapted to natural disturbance than those found in consolidated sediment and in hard-bottom areas (Collie *et al.* 2000; Kaiser *et al.* 2006). Consequently, a given fishing impact will account for a larger proportion of the total disturbance when natural disturbance is low (Dernie *et al.* 2003).

Recovery rates of species and communities have often been assessed at small temporal and spatial scales using 'Before-After Control-Impact' experimental designs (Underwood 1994). Some of these studies suggest recovery times of less than a year (e.g. Robinson, Bernier & MacIntyre 2001; reviews Kaiser *et al.* 1998 and Pitcher *et al.* 2009), but it is debatable whether such fast recovery rates apply at larger scales. While immigration may account for much of the 'recovery' reported in experimental studies (Collie *et al.* 2000; Jennings *et al.* 2001), entire fishing grounds will have different recovery dynamics because reproduction and growth may be the main source of observed recovery if immigration from surrounding areas is limited. Meta-analyses and large-scale long-term studies suggest recovery times from <3 years (Cranfield *et al.* 2001; Blyth *et al.* 2004) to 5–10 years (Collie *et al.* 2000, 2005; Kaiser *et al.* 2006) for sessile epifauna on hard-bottom habitats.

Existing empirical studies of recovery have focused on a single location or a small number of replicate locations. In reality, fishing pressure is patchily distributed in space and time (e.g. Rijnsdorp *et al.* 1998) such that there will be a mosaic of habitat patches at different stages of recovery on any fishing ground, depending on the history of fishing in these patches. With the advent of satellite vessel monitoring systems (VMS) that describe the fine-scale distribution of fishing activity in space and time (e.g. Lambert *et al.* 2012), there is the potential to use the patchiness of fishing activity to examine recovery trajectories. This provides a novel and powerful means by which to measure recovery on actual fishing grounds at fishery- and management-relevant scales.

The Isle of Man territorial sea (c. 4000 km²) provides an ideal opportunity to assess recovery of benthic

communities on hard substrata following bottom-fishing disturbance, because, in recent years, most of the scallop dredging and bottom trawling vessels fishing in the territorial sea have been monitored with VMS. Here, we take advantage of the comprehensive VMS monitoring to link the status of epifaunal communities at multiple locations to the known history of fishing at those locations. We estimated the post-disturbance recovery rates of epifaunal marine benthic communities on coarse and hard substrata to measure recovery on actual fishing grounds at fishery- and management-relevant scales. The approach enabled us to describe patterns and rates of recovery in space and time and the proportions of locations where communities were at different stages of recovery.

Materials and methods

The study was conducted in the territorial waters of the Isle of Man, United Kingdom, that have been fished for over 60 years. The study was conducted in three stages. First, we quantified the abundance and species richness of benthic epifaunal communities around the island (see Biological data collection). Secondly, we estimated the date when each sampled station was last fished (see Estimating fishing intensity). Thirdly, we linked the date of this 'last fishing event' to some benthic communities metrics to infer recovery trajectories (see Recovery of epifaunal communities).

BIOLOGICAL DATA COLLECTION

Seabed habitats were surveyed in August 2008. Photographs of the seabed were taken at 120 stations located on a regular grid with 5-km spacing within the 12 nautical miles limit of the territorial sea. A sledge, on which a high-resolution Canon 400D digital camera was fitted, was towed on the seabed for 15 min at each station over a distance (on average) of 370 m (range 110–810 m). Every 9 s, a 10 megapixel photograph was taken (c. 100 pictures per station); each photograph recorded an area of 0.14 m².

The pictures were used to identify and quantify the benthic epifauna presents at each station at the highest possible taxonomic resolution (Lambert *et al.* 2011). Stations with a soft substratum (mud and sand) were removed from the analyses as the major component of the benthic communities in those habitats comprised infaunal species that could not be photographed. For all other stations, the identity and abundance of epifauna were recorded from a variable number of pictures. To obtain similar sample sizes at each station, we selected stations where a minimum of 15 photographs had been taken and analysed. A total of 67 stations met this criterion and were selected. For stations with >15 photographs, subsamples of 15 photographs were randomly selected 100 times and the resulting estimates of abundance and species richness (the total number of species per unit area) averaged out to provide a comparable estimate of abundance and species richness that would account for the variability among photographs. Functional composition, measured in terms of the abundance of organisms with particular life-history traits, was described from the taxonomic composition and the abundance of species at each station.

The matrix of functional composition was computed as follows. First, a matrix of species by subtraits was created.

To assign values to matrix entries, subtraits were clustered into traits. For example, the subtraits 'suspension feeder', 'deposit feeder', 'scavenger', 'predator' and 'grazer' were all linked to the trait 'feeding behaviour'. The matrix entries for all clusters of subtraits that comprised a trait were always constrained to add up to 1 (or 100%), for example, the subtraits 'suspension feeder' and 'deposit feeder' could have entries of 0.5 and 0.5 if a species showed both feeding behaviours. The resulting matrix of species by subtraits was multiplied by species abundance (individuals m^{-2}), at any defined station, to produce a matrix of species abundance by subtrait for each station. The species abundance entries for each subtrait in the matrix of species abundance were summed to give total abundance by subtrait at any given station.

The recovery of each functional group, or subtrait, could then be analysed separately. The traits were chosen to include information on morphology, life history and ecology of the benthic species. We chose to study categories of traits which were expected to be sensitive to fishing disturbance based on the literature, that is, medium, medium-large and large size animals (11–20, 21–50 and >50 cm), medium and long life span animals (2–5 and >5 years), animals with no or low mobility, permanently attached species, species with soft bodies with high flexibility (able to bend >45°) and suspension feeders (e.g. <http://www.marlin.ac.uk/>; Bremner, Rogers & Frid 2003; Bremner 2005; Tillin *et al.* 2006). Before studying the recovery of the organisms with those particular functional traits, we also checked whether they were sensitive to fishing in our study area. We did this by comparing the abundance of each functional group, as well as total abundance of species and species richness, between low and high fishing intensity areas with analysis of variance. Fishing intensity was categorized based on its median value (see Estimating fishing intensity). Species richness,

abundance of large size species, of immobile species and of species with permanent attachment did not differ significantly between areas of low and high fishing intensity and were excluded from the analysis of recovery (Fig. 1).

ESTIMATING FISHING INTENSITY AND THE TIME OF THE 'LAST' FISHING EVENT

Vessel monitoring system (VMS) position, time, speed and anonymous vessel identification data for king scallop dredgers and queen scallop otter trawlers for 2007–2008 were provided by the Isle of Man Department of Environment, Food & Agriculture (DEFA). The data included all Isle of Man vessels regardless of their size and UK vessels ≥ 15 m. The positions of all vessels ≤ 15 m fishing in the 3 nm zone were also reported. Prior to analysis, the VMS data set was screened to remove duplicate position records, records close to port (<1 km), erroneous records allocated to land and records not associated with fishing (Lambert *et al.* 2012). Interpolation methods were used to recreate the course of the vessels and to map fishing activity. Scallop dredging tracks were interpolated by straight lines and otter trawling tracks using cubic Hermite splines (Hintzen, Piet & Brunel 2010) because previous studies have shown that these methods were the most appropriate to model the fishing tracks of those two fisheries (Lambert *et al.* 2012). Fishing intensity was estimated from the interpolated positions that fell into a 9-km² circle centred on each station and was expressed as the number of times the area was fished in a year (see Lambert *et al.* 2012 for details).

The interpolated tracks were also used to estimate the timing of the 'last fishing event' at each station. Vessels tend to fish a

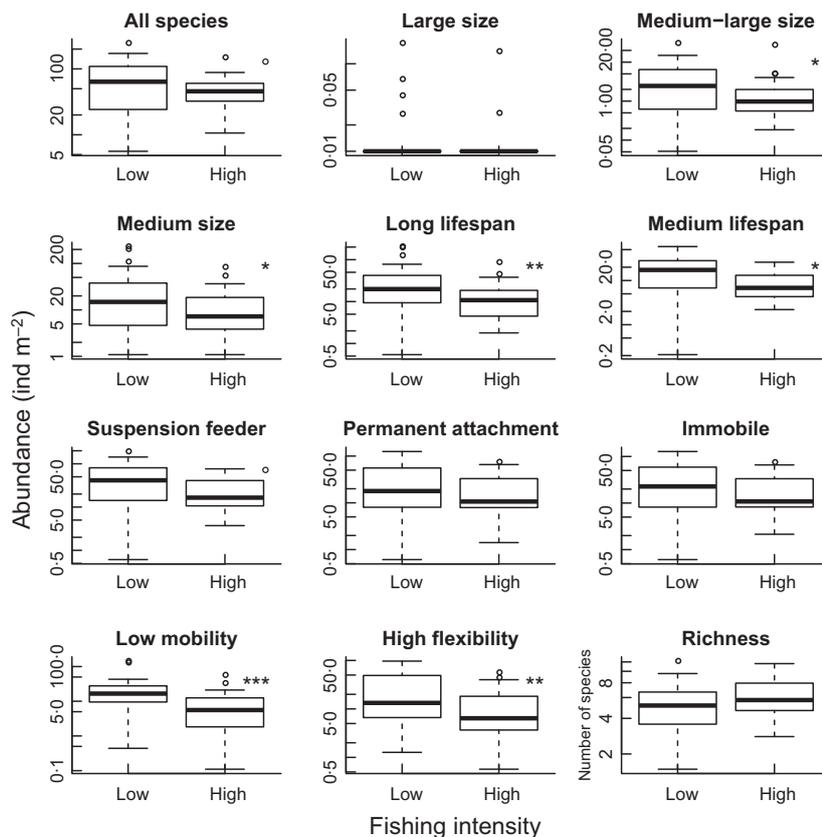


Fig. 1. Impact of fishing on the abundance of different functional groups and species richness. Fishing categories 'low' and 'high' are defined as lower and higher than the median fishing intensity (in year⁻¹). Symbols to the top right of each panel indicate when abundance in the 'low' fishing intensity category was significantly greater than the 'high' category: ° 0.05 < $P \leq 0.1$, * 0.01 < $P \leq 0.05$, ** 0.001 < $P \leq 0.01$, *** $P \leq 0.001$.

patch for several days or weeks before moving on to the next one. Vessels in this fishery do not normally return to the fished patch for several weeks or months to allow more scallops to reach the minimum landing size (e.g. Veale *et al.* 2000). For these reasons, the date of the last tow over a patch provides a good approximation of the last time when the whole patch was fished. Interpolated VMS data do not provide estimates of the fishing tracks that are sufficiently accurate to determine whether a given seabed photograph or sample falls precisely on the track, so the last date of fishing was estimated from the density of fishing tracks within a defined distance of the sampling station. The choice of distance, expressed here as the radius of a circle centred on each station and enclosing a defined area around each station, might affect the estimated date of the 'last fishing event'. For that reason, the date of the 'last fishing event' at each station was assessed at three spatial scales, 0.25, 0.5 and 1 km², and the results were compared. At all scales, a 'fishing event' was defined as any group of tows separated by ≤ 14 days. A single tow was also treated as a fishing event if it

was separated from any other tow by >14 days. Cumulative fishing effort for the period spanning fishing events was calculated as the cumulative effort prior to the sampling date in August 2008. Fishing effort was calculated from interpolated fishing positions following the methods and assumptions detailed in Lambert *et al.* (2012). The fishing event accounting for the highest proportion of cumulative effort between July 2007 and August 2008 was defined as the largest fishing event, and the last date in this period was assumed to be the date of the 'last fishing event'. The approach is illustrated in Fig. 2. This approach was adopted to take account of the fishing strategies used in this fishery and to exclude any subsequent and isolated tows that would have small impacts in relation to the fishing event and a low probability of impacting the sampled station. Another option for estimating that date of the 'last fishing event' would have been to determine an absolute cumulative effort threshold, ideally 1, equivalent to the whole area having been fished once. However, because the range of fishing intensities was low (Lambert *et al.* 2011), we used an approach

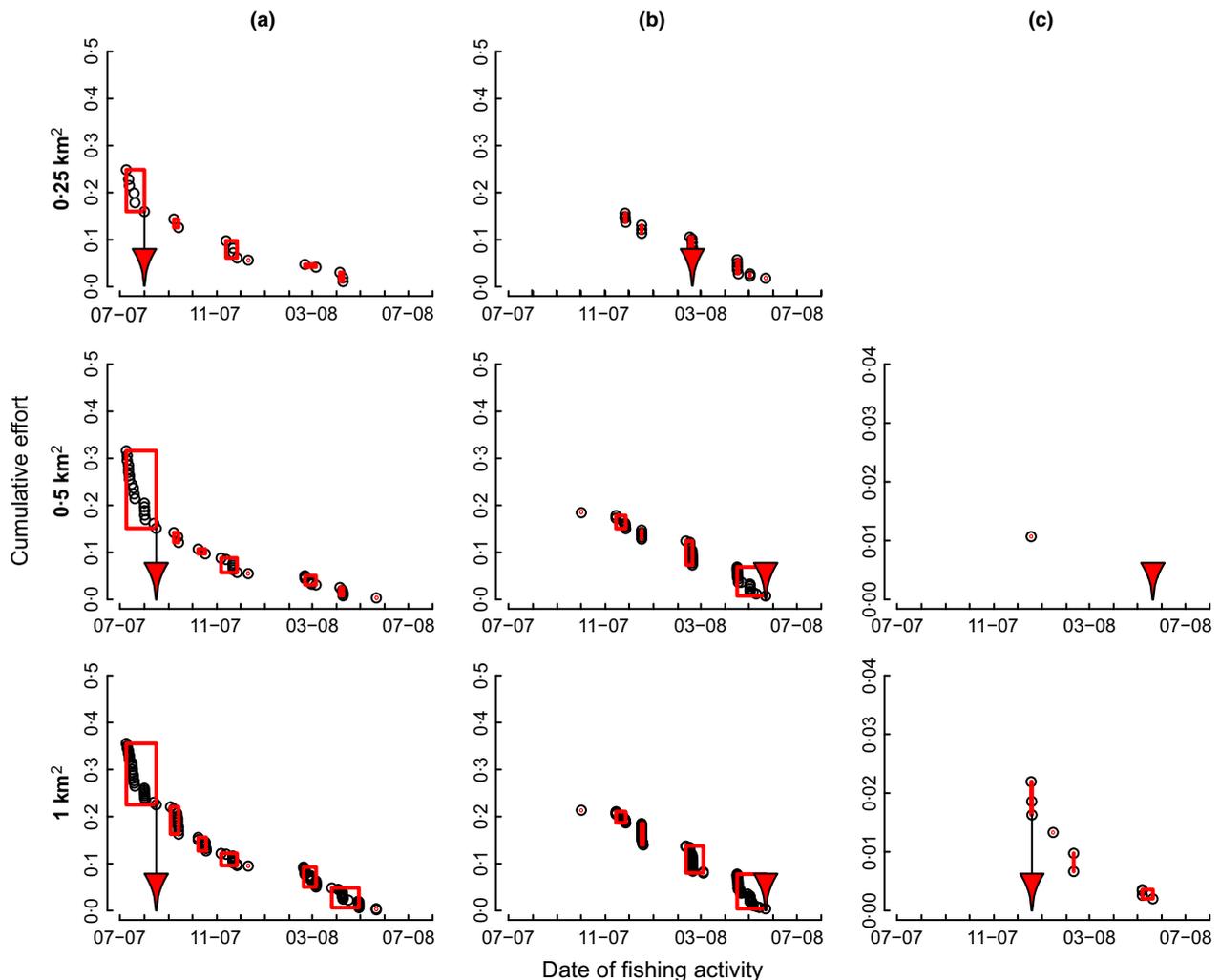


Fig. 2. Examples of history of fishing activity at three stations (a–c). At each station, fishing activity was estimated over three spatial scales, 0.25, 0.5 and 1 km² (top to bottom). Cumulative fishing effort is the cumulative proportion of the area fished prior to the sampling date in August 2008 (mm-yy). The red rectangles identify fishing events, and the red arrow is the date defined as the 'last fishing event' (see Materials and methods). The top-right figure is missing because no fishing activity was found around this station at the small scale of 0.25 km².

that maximized the probability that the 'last fishing event' had impacted the sampled station.

RECOVERY OF EPIFAUNAL COMMUNITIES

The recovery of abundance of all species and of abundance by functional groups was described in relation to the estimated dates of the last fishing events. In the absence of empirical data on the form of recovery dynamics, the logistic equation was assumed to describe the recovery in abundance (Pitcher *et al.* 2000):

$$dN/dt = rN(1 - N/K) \quad \text{eqn 1}$$

where r is the intrinsic rate of increase, K the carrying capacity and N the abundance. This equation describes an initial exponential increase in a population which slows as the carrying capacity of the environment is reached. We made the simplifying assumption that all species in a defined community recovered collectively. In reality, the body size and species composition of a recovering community would change owing to the different intrinsic rates of increase in the component species, but the resolution of the photographs and sample sizes for individual species are not sufficient to investigate these processes.

Equation 1 was integrated between $N_{(t=0)}$ and N to express N as a function of time since 'last fishing event' t :

$$N = N_{t=0}/[N_{t=0}/K + e^{-rt}(1 - N_{t=0}/K)] \quad \text{eqn 2}$$

Equation 2 was fitted on \log_e -transformed values of N and K (i.e. $\log_e(100x + 1)$). The approaches used to estimate the 3 parameters, r , $N_{t=0}$ and K , are described below.

Estimating K

K had to be estimated prior to fitting the model as the strong correlation between r and K , and the limited number of data points, would lead to potentially unrealistic fits. Two approaches were used and compared. *Fixed K* : In this first approach, we made the simplifying assumption that we did not have enough information to estimate a site-specific carrying capacity and assumed that variation in site-specific carrying capacity would be insignificant. K was thus estimated as the 95th upper quantile of the value of abundance across all stations (fished and unfished). *Variable K* : In this second approach, we investigated the effect of varying K among stations. Carrying capacity was estimated by fitting a linear quantile regression on the 95th quantile of the distribution of abundance as a function of environmental variables (Lambert *et al.* 2011). Two variables were tested separately, tidal velocity and wave stress. These environmental variables were chosen because they are known to drive sessile epifauna abundance around the Isle of Man and affect feeding rates of suspension feeders as well as mortality, settlement and larval supply (Lambert *et al.* 2011). The analysis included all stations because the range of variation in the selected environmental variables was low at the unfished stations. In the variable K approach, to fit the model described by eqn 2, relative abundance, denoted n , was expressed in terms of N and K at station i , following Ellis *et al.* (2008):

$$n_i = N_i/K_i * 100 \quad \text{eqn 3}$$

Relative abundance, n , can then be substituted for absolute abundance, N , in eqn 2:

$$n = n_{t=0}/[n_{t=0}/100 + e^{-rt}(1 - n_{t=0}/100)] \quad \text{eqn 4}$$

Equation 4 was fitted on square root-transformed values of n and K (100 here).

Estimating r

The intrinsic rate of increase, r , being positive or close to null, was estimated as an exponential, and r was replaced in the above equations by $r = \exp(x)$. It was further expected to vary as a function of the environment. We therefore tested three alternate models where $\log_e(r)$ was assumed to be linearly related to an environmental variable X : tidal velocity (Nm^{-2}), wave stress (ms^{-2}) or surrounding abundance (\log_e -transformed individuals m^{-2}).

$$r = \exp(a + bX) \quad \text{eqn 5}$$

We defined 'surrounding abundance' as the mean abundance of the communities located within a 6 km radius of the station. A distance of 6 km was chosen because, in effect, this selected the closest stations given the sampling grid was spaced at 5 km.

Estimating $N_{t=0}$

First, we made the simplifying assumption that $N_{t=0}$ did not vary among stations. Then, we tested the hypothesis that $N_{t=0}$ varied among stations and included a random effect on $N_{t=0}$ in a mixed-effects model. However, $N_{t=0}$ could not be considered site-specific as the logistic curve did not follow site-specific recovery trajectories. Two models were therefore tested, one with $N_{t=0}$ being substratum-specific (with five mixed substratum categories: sand, maerl, gravel, cobble and rock) and one with $N_{t=0}$ being dependent on past fishing impact (with fishing intensity classified into five categories based on quantiles of the distribution of intensity, between 0.01 and 3.95 year^{-1}).

All models were fitted using the *gnls* and *nlme* functions of the *nlme* package in R, with a maximum-likelihood approach (see model selection in Table S1, Supporting information). To identify the most parsimonious model, we used the Akaike Information Criterion (AIC) corrected for small sample sizes (Venables & Ripley 2002; Burnham & Anderson 2004). Models were considered further if their AIC was lower than the AIC of the null model by at least 2. If several models had similar AIC values (within ± 2), then a visual assessment of the residuals was used to select the best model. This was done by plotting the residuals against the variables selected in the different models and selecting the model that showed the least or no pattern. This approach did not allow for comparison of the models with fixed K and variable K based on absolute and relative abundance. This is because AIC is only comparable when the models include the same response variable. Therefore, we reported the preferred models for fixed K and variable K separately. Model selection by AIC, residuals of the selected model and diagnostics are presented in the Supporting information (Tables S1–S2, Figs S5–S10).

The models were all tested at the three different spatial scales that were used to estimate the last fishing event. The selected models were used to estimate the recovery time of the communities by extrapolation. Recovery was assumed to have occurred at the time (t_R) when 90% of the carrying capacity, K , was reached. t_R was estimated by rearranging eqns 2 and 4 to estimate t and by substituting $0.9K$ for N . If one of the environmental covariates

was found to significantly influence the intrinsic rate of increase, r and t_R were defined as ranges using the lowest and highest values of the covariate.

Results

At scales of 0.25, 0.5 and 1 km², fishing activity was respectively detected at 43, 50 and 52 of the 67 stations selected for the analyses. The spatial scale at which the last fishing event was calculated further affected the estimated date of last fishing event (Fig. 2). The standard deviation around this date was ± 19 days among scales, with a minimum of 0 days (i.e. same date of last fishing event) and a maximum of 109 days at one station.

Variation in the estimated dates of the last fishing events among scales led to variation in estimated recovery time. For the recovery trajectory of absolute abundance of all species (Fig. 3), for example, extrapolation of the recovery curve for absolute abundance indicates that recovery may take 0.3–0.5 years in areas where tidal velocity is high and 5.6–11.2 years in areas where tidal velocity is low, depending on the scale at which the last fishing event is estimated. The recovery trajectory of relative abundance leads to estimates of recovery time from 2.3 to 2.7 years depending on scale. The effects of the environment on recovery time, t_R , were broadly consistent among scales, notwithstanding variation in estimated times since last fishing event among scales.

Modelled recovery trajectories of absolute abundance with covariates always provided better fits to data (lower

AIC) than the null models (Table 1). The modelled intrinsic rate of increase in abundance of all species groups increased with tidal velocity (Table 1, Fig. 4). For most groups, the nonlinear mixed-effect model fitted better than the simple nonlinear model, with the initial abundance $N_{t=0}$ being dependent on past fishing intensity or substratum type (Table 1, Table S1 and residual analysis Figs S5, S7 & S9, Supporting information).

Results were broadly consistent among scales (Table 1, Figs 4, S1 & S3, Supporting information). Based on the fitted models, t_R was estimated to be between <0.1 and >12 years. In high tidal velocities, all species groups were predicted to recover in less than a year, with low mobility species recovering slightly faster than other groups (recovery in 0–0.1 year). In low tidal velocities, t_R varied between 3.8 years for suspension feeders to >12 years for long life span, medium life span and low mobility species.

Relative abundance could only be estimated for four groups: all species, medium-large size, medium life span and high flexibility species. The abundance of all the other groups was not significantly limited by tidal velocity or wave stress, and therefore, no site-specific variable K could be estimated. Only tidal velocity was shown to affect carrying capacity (Figs 5, S2 & S4, Supporting information). As a result, tidal velocity was not a significant covariate of recovery rates for relative abundance (Table 1). The ranges in estimates of recovery time fell within the range estimated by models of absolute abundance recovery with t_R being predicted between 0.9 and ≤ 4 years. Only medium life span species did not show any relationship with time since last fishing event. The t_R of relative abundance of all species did not vary with the environment. Wave stress appeared to have a positive impact on recovery rates of relative abundance of medium-large size and high body flexibility species. Medium-large size species also recovered faster where there were higher abundances in surrounding areas at the 0.25 km² scale.

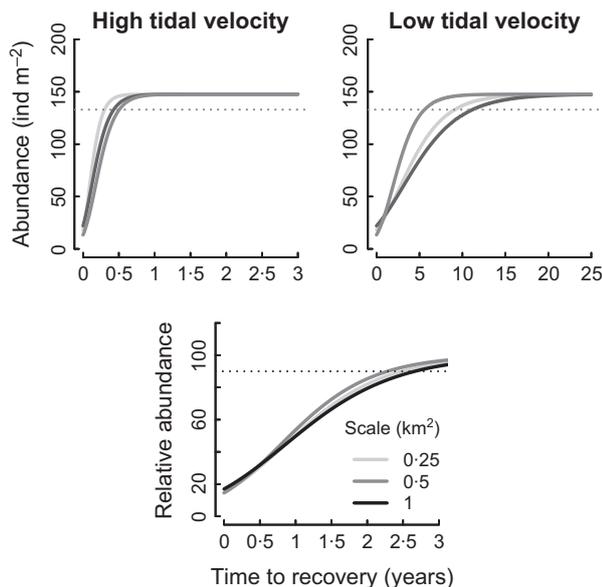


Fig. 3. Extrapolated recovery trajectory of absolute (top panels) and relative (bottom panel) abundance of all species as a function of the spatial scale at which the last fishing event was estimated. Note the x-axes differ between the two hydrodynamic regimes. The dotted lines represent 90% of the estimated carrying capacity K . Predicted abundance and K were back-transformed from \log_e estimates. Note: The predictions at 0.25 and 1 km² overlap in the bottom panel.

Discussion

We have shown that the fishing grounds consisted of a mosaic of communities at different stages of recovery since the last fishing event. Our approach could be used to assess recovery at large spatial scales and with high levels of replication on many fishing grounds by taking advantage of the dynamic patchiness created by fisher behaviour (e.g. Rijnsdorp *et al.* 1998; Fulton *et al.* 2010; Tidd *et al.* 2012). Such work complements experimental studies of fishing impacts and recovery (Kaiser *et al.* 2006). Our approach provides information on the drivers of recovery as well as providing spatially resolved estimates of recovery time on fishing grounds wherever substratum type and environmental variables are known (e.g. Fig. 6, see also Fig. S11 and S12, Supporting information for all other species groups and scales). Linked with information on current fishing pressure, such maps would

Table 1. Recovery time (t_R) estimates and model parameters for each community descriptor that was affected by fishing activities

Response	Group	Scale (km ²)*	Model†	Covariate‡	Random covariate†	$N_t = 0$ (individuals m ⁻²)§	K^{\ddagger}	r ($\times 10^{-3}$) (day ⁻¹)¶	ΔAIC^{\S}	t_R (years)‡
Abundance (fixed K models)	All species	0.25	Mixed	Tidal velocity	Substratum	18.29 ± 2.24	147.63	0.97–29.37	14.15	0.3–9.1
		0.5	Nls	Tidal velocity		13.38	147.63	1.67–18.46	17.75	0.5–5.6
		1	Mixed	Tidal velocity	Substratum	22.02 ± 3.47	147.63	0.76–19.90	15.86	0.4–11.2
	Medium-large size spp.	0.25	Mixed	Tidal velocity	Fishing intensity	0.32 ± 0.02	12.90	1.5–45.43	18.38	0.3–7.8
		0.5	Mixed	Tidal velocity	Substratum	0.57 ± 0.3	12.90	1.76–16.65	21.66	0.6–6.2
		1	Mixed	Tidal velocity	Substratum	0.44 ± 0.03	12.90	1.69–17.88	14.24	0.6–6.6
	Medium size spp.	0.25	Nls	Tidal velocity		3.15	83.32	1.35–22.06	9.50	0.5–7.9
		0.5	Nls	Tidal velocity		2.55	83.32	2.24–13.97	14.94	0.8–4.9
		1	Mixed	Tidal velocity	Substratum	4.44 ± 1.25	83.32	1.23–14.46	12.84	0.7–8.2
	Long life span spp.	0.25	Mixed	Tidal velocity	Substratum	7.22 ± 2.13	79.51	0.66–35.35	8.59	0.3–>12
		0.5	Mixed	Tidal velocity	Substratum	7.14 ± 1.91	79.51	0.97–12.49	9.71	0.8–9.7
		1	Mixed	Tidal velocity	Substratum	7.84 ± 2.53	79.51	0.80–13.90	10.67	0.7–11.6
	Medium life span spp.	0.25	Mixed	Tidal velocity	Substratum	5 ± 0.47	41.64	0.57–59.84	18.08	0.2–>12
		0.5	Mixed	Tidal velocity	Substratum	4.76 ± 0.66	41.64	0.85–42.19	24.35	0.2–10.7
		1	Mixed	Tidal velocity	Substratum	5.19 ± 0.56	41.64	0.62–50.55	22.73	0.2–>12
Suspension feeding spp.	0.25	Mixed	Tidal velocity	Fishing intensity	6.69 ± 0.75	100.80	1.82–23.01	12.20	0.4–5.4	
	0.5	Nls	Tidal velocity		5.92	100.80	2.65–14.54	17.37	0.7–3.8	
	1	Nls	Tidal velocity		8.05	100.80	1.88–15.40	12.80	0.6–5.1	
High body flexibility spp.	0.25	Mixed	Tidal velocity	Fishing intensity	3.63 ± 0.43	61.92	0.91–21.71	13.61	0.5–11	
	0.5	Nls	Tidal velocity		2.48	61.92	2.00–18.13	22.65	0.6–5.3	
	1	Mixed	Tidal velocity	Fishing intensity	4.27 ± 0.58	61.92	0.94–17.17	18.61	0.6–10.5	
Low mobility spp.	0.25	Nls	Tidal velocity		3.18	42.35	0.36–167.4	10.16	0.1–>12	
	0.5	Mixed	Tidal velocity		4.63 ± 0.93	42.35	0.07–639.97	9.77	0–>12	
	1	Mixed	Tidal velocity	Substratum	4.61 ± 1.04	42.35	0.07–596.73	10.72	0–>12	
Relative abundance (variable K models)	All species	0.25	Nls	None	Substratum	14.79	100.00		5.21	2.5
		0.5	Nls	None		14.57	100.00		7.04	2.3
		1	Nls	None		16.98	100.00		5.33	2.7
	Medium-large size spp.	0.25	Nls	Abundance		7.55	100.00	2.67–4.00	3.13	2.7–4
		0.5	Nls	Wave		7.88	100.00	3.19–13.49	12.82	0.8–3.3
		1	Nls	Wave		6.18	100.00	3.77–15.52	17.73	0.7–2.9
Medium life span spp. High body flexibility spp.	ALL	Null model is better								
	0.25	Nls	None		10.39	100.00	2.76	12.82	3.6	
	0.5	Nls	Wave		7.99	100.00	3.59–12.68	17.73	1–2.9	
1	Nls	Wave		8.35	100.00	3.31–14.37	12.82	0.9–3.1		

*Scale† refers to the scale at which the last fishing event was calculated.

†Only the significant models and environmental variables are listed (see Tables S1 and S2 in Supporting information).

‡All covariates had a positive effect. The range in r and t_R is estimated from minimum and maximum values of the fixed covariate.

§ ΔAIC corresponds to the difference between AIC of the given model and the null model.

¶ $N_t = 0$ is the estimate of the fixed part of the model, \pm standard error. The standard error is estimated from the best linear unbiased predictors (BLUPs – random part of the model). Note that $N_t = 0$ and K are log_e-transformed in eqn 2 and square root-transformed in eqn 4 (see Materials and methods).

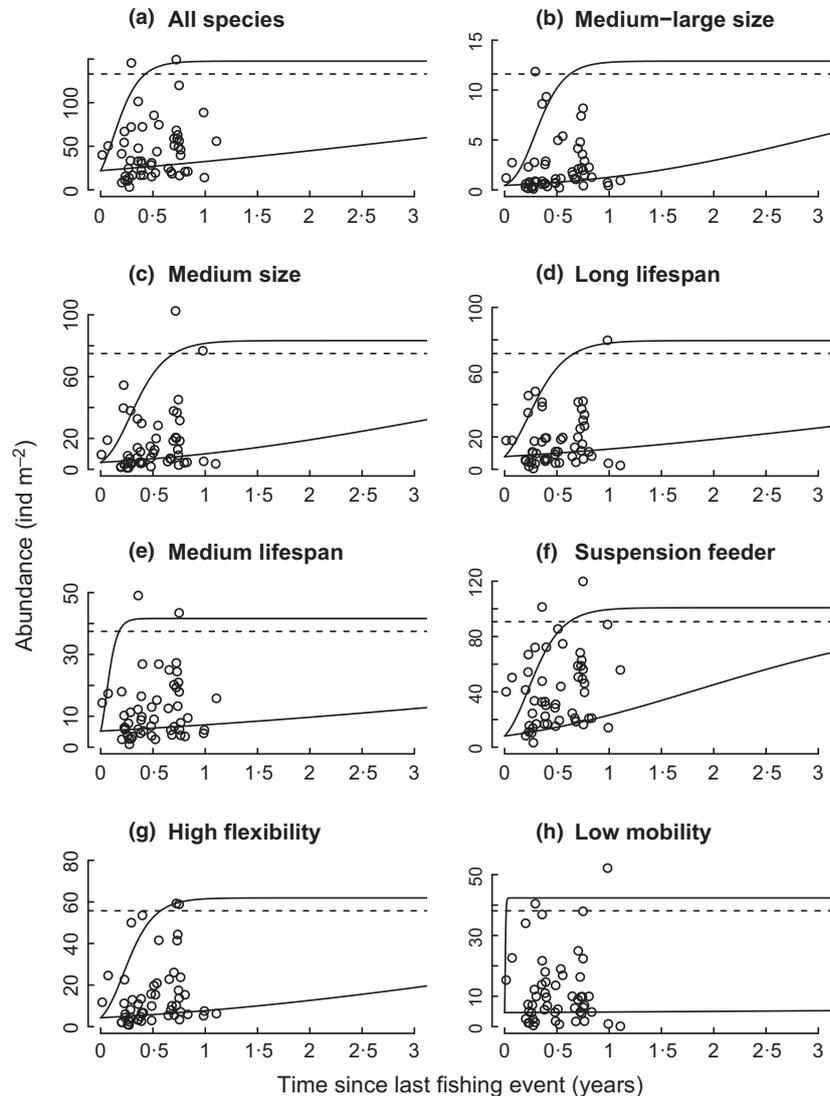


Fig. 4. Recovery of absolute abundance for (a) all species, (b) medium-large size spp., (c) medium size spp., (d) long life span spp., (e) medium life span spp., (f) suspension feeding spp., (g) high flexibility and (h) low mobility spp. as a function of time since the last fishing event, when a spatial scale of 1 km² was used to detect the last fishing event. The dotted lines represent 90% of carrying capacity K . The continuous lines are the modelled recovery trajectories for the minimum and maximum value of the associated covariate (see Table 1 and Fig. 3). Corresponding results for spatial scales of 0.25 and 0.5 km² are provided in the Supporting information.

provide valuable information to assess the state of benthic habitats and the consequences of management actions on the cumulative impacts of fishing vessels or fleets (Hiddink *et al.* 2006a).

Our approach for calculating the time since the last fishing event was tailored to the Isle of Man scallop fishery. There fishing disturbance is applied in acute pulses, where a ground is intensively fished for a few days before the fleet moves on, potentially returning to the same ground once more before the end of the season (Veale *et al.* 2000). This fleet behaviour led us to estimate the timing of the last fishing event after identifying and accounting for the episodes of intensive fishing activity. In other fisheries and other countries, the method for estimating prior fishing activity should be tailored to the characteristics of those fisheries. For fishing grounds world-wide where VMS or other GPS positioning records are less frequent, a probabilistic framework for estimating the timing of previous fishing activity may be more appropriate (e.g. building on the approaches of Gerritsen, Minto & Lordan 2013).

The magnitude of recovery has to be assessed in relation to a reference point (Thrush & Dayton 2010). Most studies use pre-impact values or values from neighbouring areas as reference points (Newell *et al.* 2004; Kaiser *et al.* 2006). Here, the recovered state was estimated from the overall community characteristics of the mixed to hard substratum grounds around the Isle of Man. We used a fixed or a variable estimate of carrying capacity that did not account for long-term fishing impacts which may have modified the system as a whole (Veale *et al.* 2000). Recovery rates seemed to be fairly consistent under all environmental conditions when we studied the relative abundance of species groups that showed a limiting effect of tidal velocity, that is, for which a carrying capacity could be estimated at each site. For these groups, recovery time was estimated between *c.* 8 months and 4 years based on relative abundance, while it was estimated to be >12 years in areas with low tidal velocity when studying absolute abundance with a fixed estimate of carrying capacity. This meant that it was more complex to interpret the results for areas of low tidal velocities as they could either take

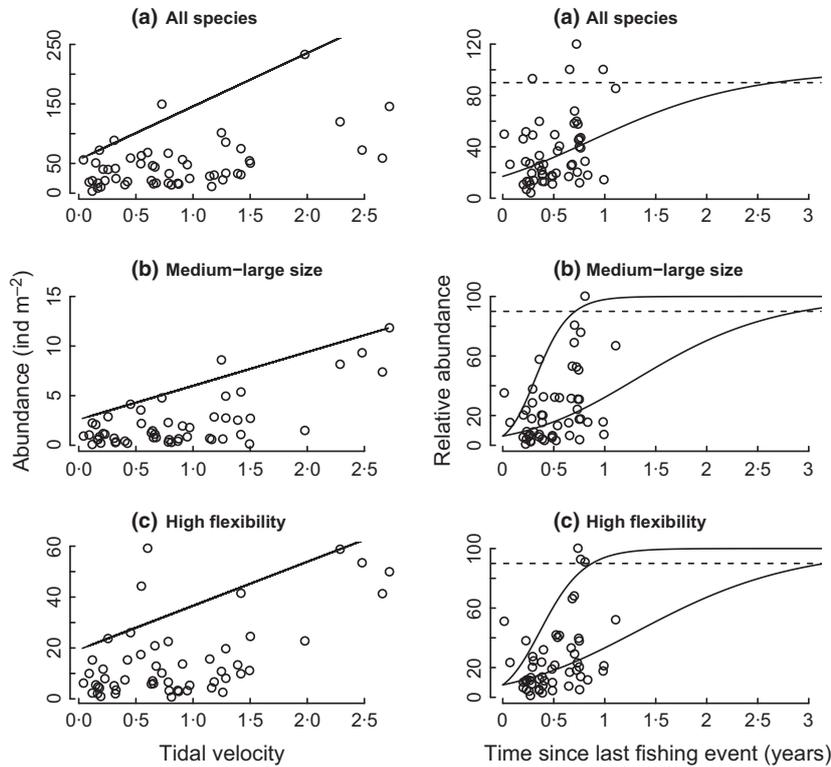


Fig. 5. Recovery of relative abundance of (a) all species, (b) medium-large spp. and (c) high body flexibility spp. as a function of time since the last fishing event, when a spatial scale of 1 km² was used to detect the last fishing event. The panels on the left show the relationship between abundance and tidal velocity from which relative abundances have been calculated. The fitted line is the 95th quantile (treated as carrying capacity). The panels on the right are the recovery curves for relative abundances. See Fig. 4 legend for further details.

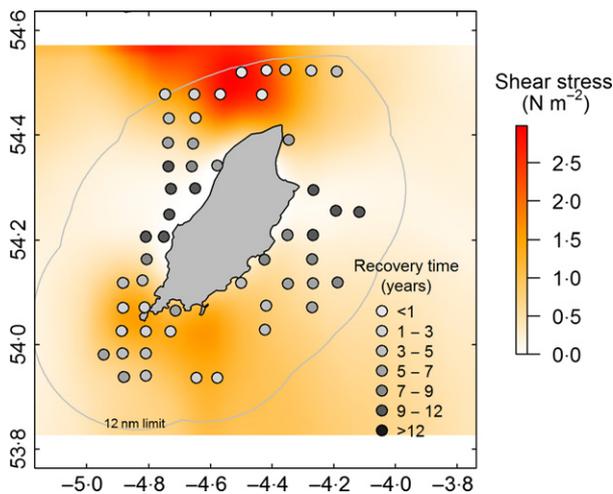


Fig. 6. Estimated recovery time (t_R) of absolute abundance of all species after fishing impact at stations sampled in the territorial waters of the Isle Man, UK, when a spatial scale of 1 km² was used to detect the last fishing event. The colour gradient represents tidal velocity, measured as peak bottom stress in Nm^{-2} at the time of mean tides. The corresponding model of recovery in relative abundance predicts that recovery should occur everywhere within 2.7 years.

much longer to recover or be areas of low carrying capacity. Further, carrying capacity is potentially dynamic as it will be influenced by stochastic processes and environmental parameters. Given the large and consistent variation in estimated recovery times as a function of the

environment, we consider our approaches for estimating carrying capacity suitable for comparing relative rates of recovery among stations, but the absolute rates of recovery will be influenced by the stability and magnitude of benthic carrying capacity and the extent to which it can be treated as a fixed 'reference point'. Nonetheless, our approaches do allow comparison of the relative resilience and sensitivity of different habitats in different environments and provide essential evidence for managers tasked with reducing the benthic impacts of towed bottom-fishing gears while maintaining a viable fishing industry.

Despite the potential uncertainties in absolute estimates of recovery time, our estimates of recovery time for numbers of individuals correspond with previous estimates from meta-analyses and large-scale long-term studies, which range from <3 years to 5–10 years (Cranfield *et al.* 2001; Blyth *et al.* 2004; Collie *et al.* 2005; Kaiser *et al.* 2006). The present study, alongside a few other published studies, demonstrates the potential of heavily fished grounds to start recovering during the first year post-fishing disturbance. 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. Recovery from aggregate extraction in similar

habitats was also reported to take from 2–4 years to >7 years (Desprez 2000; Cooper *et al.* 2007).

We estimated recovery from changes at many sites and revealed that the most important drivers of recovery time were tidal velocity and the proximity of areas with high abundances of benthic invertebrates and potentially wave stress. Tidal velocity will affect food availability, feeding, and recolonization rates of the adult, juvenile and larval stages in soft sediment communities (Wildish & Kristmanson 1997). The relationship between the rate of recovery and the proximity of areas with high abundances of benthic invertebrates is important as it implies that reserves or unfished areas can replenish fished areas of the seabed with larvae and juveniles across relatively short distances (e.g. Allison 2004). Wave stress also had a positive impact on recovery rates in the models of relative abundance, but high energy habitats generally have less biomass around the Isle of Man (Lambert *et al.* 2011). Therefore, these habitats may appear to recover more quickly because the maximum biomass potential is lower.

The Ecosystem Approach to Fisheries (FAO 2003) requires managers to consider the environmental impacts of fishing in management plans. Our method for estimating recovery rates provides insight into spatial variation in resilience and may be used to assess how fishing impacts change with the distribution and intensity of trawling of individual fishing vessels and fleets. In Europe, advisory processes supporting the implementation of the Marine Strategy Framework Directive (MSFD; EC 2008a) seek to define targets for 'Good Environmental Status' (GES) for ecosystem components and attributes such as the seabed (EC 2010). Beyond establishing targets consistent with sustainable impacts, parts of the MSFD imply that targets for GES should be consistent with lower levels of pressure and impact than those needed to achieve sustainable use. Information on the resilience of seabed habitats will help to inform debate about those targets, but it will be the role of society to define them. In contrast to the MSFD, the European Common Fisheries Policy (CFP; EC 2002; in revision at the time of writing) has not sought to define explicit targets for fishing impacts on the environment, but makes general commitments to minimize impacts. Consequently, CFP indicators of the effects of fishing are intended to show trends in the environmental performance of fishery management (EC 2008b). One practical interpretation of a commitment to 'minimize' is that managers should seek to reduce the impacts of fishing per unit catch weight or value as well as fulfilling any objectives to manage catch rates or fishing effort. Information on seabed recovery times 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 strengthen a case for fisheries certification or move a fishery towards 'best practice' in terms of minimizing impacts on the seabed.

A variety of European and national legislations have stimulated the designation of various types of marine

protected area (MPA). The associated management measures may displace fishing activity, the consequences of which can be assessed with data on the distribution of recovery rates of different benthic habitats (e.g. Dinmore *et al.* 2003; Hiddink *et al.* 2006c). Our results suggest that speed of habitat recovery can be increased if patches of nearby habitat are left unfished and that even small changes in fleet distribution could have significant impact on the sensitivity of the habitats they impact. In general terms, we conclude that management plans that limit bottom trawls and dredge fisheries to more resilient areas and maintain permanently unfished patches within these areas will minimize the impacts of a given amount of towed bottom-fishing effort on seabed habitats. Our approach is an addition to methods that have thus far been used to assess recovery of seabed habitats because it provides a broader (fishery-scale) assessment of recovery rates than single experimental studies or studies of area closures that have supported previous assessments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Tables S1 & S2. Model selection for recovery of absolute and relative abundance of all species and functional groups at all spatial scales.

Figs S1–S4. Recovery of absolute and relative abundance of all species and functional groups when scales of 0.25 and 0.5 km² were used to detect the last fishing event.

Figs S5–S10. Residual analysis for the selected absolute and relative abundance recovery models when scales of 0.25, 0.5 and 1 km² were used to detect the last fishing event.

Figs S11 & S12. Maps of estimated recovery time (t_R) of absolute and relative abundance of all species and other groups at all scales.