



# Recovery linked to life history of sessile epifauna following exclusion of towed mobile fishing gear

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## Abstract

1. The use of reserves as conservation tools is widespread. However, evaluating the effectiveness of reserve implementation for long-lived species has been problematic as it requires sampling programmes over long timescales that are appropriate to species' longevity and recovery rates. In the sea, towed bottom fishing gears alter the biodiversity and ecosystem services provided by benthic communities and habitats. Marine reserves have been used to manage these impacts but our understanding of the drivers of their effectiveness for the conservation of temperate reefs is incomplete.
2. We examined the effectiveness of marine reserves for recovery of temperate reef fauna in relation to their life history. We used an underwater video to sample six species with different life histories across 60 sites that varied in the duration of protection from towed mobile fishing gear at 0, 1, 8 and 10 years.
3. Species with a high dispersal potential and less habitat specific requirements such as soft corals and king scallops recovered to close to their carrying capacity in <3 years. In contrast, the longer-lived Ross coral and pink seafans increased in abundance but had not fully recovered; with their projected recovery time being 17–20 years.
4. Ongoing recovery was evident for long-lived species as their mean body size increased significantly across all treatments, whereas shorter-lived species such as queen scallops did not change in size and were assumed to have fully recovered.
5. *Synthesis and applications.* This study shows that the recovery rates of biota depend on life-history factors, such as larval longevity and dispersal potential. Recovery for species that had low dispersal potential and specific habitat requirements was slow and could take >20 years. This suggests activities such as bottom trawling or dredging should be avoided where such species occur if their conservation is an objective. In contrast, species with high dispersal potential and less habitat specific requirements had shorter recovery timescales of c. 2–3 years and would be more amenable to managed trawl frequencies in areas where activities such as fishing occur.

## KEYWORDS

biogenic reefs, *Eunicella verrucosa*, marine protected areas, pink seafans, Ross coral, scallop dredging, towed mobile fishing gears

## 1 | INTRODUCTION

Marine protected areas (MPAs) or reserves are one of the many management tools that can contribute to the ecosystem-based approach to fisheries management (Jennings & Kaiser, 1998; Roberts, Hawkins, & Gell, 2005), which seeks to promote the sustainable use of marine resources whilst maintaining biodiversity and protecting habitats (Worm et al., 2006). MPAs can provide partial or total protection from fishing activities and can have positive outcomes within the boundaries of MPAs (Auster & Shackell, 2000; Blyth-skyrme, Kaiser, Hiddink, Edwards-Jones, & Hart, 2006; Sciberras et al., 2013).

Marine protected areas are of particular value as conservation tools when they are used to limit (or remove) activities that directly threaten particular seabed habitats or sessile species associated with those habitats (Hinz, Tarrant, Ridgeway, Kaiser, & Hiddink, 2011; Sheehan, Cousens, et al., 2013; Sheehan, Stevens, Gall, Cousens, & Attrill, 2013). The implementation and design of effective MPAs requires a multi-disciplinary approach, together with an understanding of the ecological and life-history traits of the protected species, physical environment and natural disturbance regime (Claudet et al., 2010; Sciberras et al., 2013; Stewart et al., 2009). Many marine species are highly mobile and migratory (Willis, Millar, Babcock, & Tolimieri, 2003), ranging over vast areas that exceed the boundaries of an MPA, potentially reducing their effectiveness.

### 1.1 | Effects of scallop dredging on seabed biota

In Europe, scallop fisheries have increased considerably over that last 10 years and were ranked as the third most valuable fishery in the UK in 2014 (MMO, 2014). Although they are economically valuable, scallop dredge fisheries have well-known adverse effects on benthic communities, leading to reductions in diversity and production (Kaiser, Collie, Hall, Jennings, & Poiner, 2002; Lambert, Jennings, Kaiser, Davies, & Hiddink, 2014). Nevertheless, the effects of scallop dredging vary considerably according to the environmental context in which scallop dredging occurs, such that some benthic communities exhibit higher resilience to disturbance than others (Hiddink et al., 2006, 2017). Of particular concern are the effects of dredges (and other towed mobile fishing gears) on stable biogenic habitats, such as reefs, or on longer-lived fauna. The species that create biogenic habitats, such as corals, often form complex ecological associations and tend to be long-lived, slow growing and fragile, sensitive to disturbance and vulnerable to damage (Coma, Pola, Ribes, & Zabala, 2004; Garcia, Ragnarsson, & Eiríksson, 2006; Hinz et al., 2011). Despite their ecological importance, our understanding of the recovery potential of biogenic habitats following disturbance by towed bottom fishing gears has been restricted by the limited opportunities to study recovery dynamics in such environments, and more importantly the long timescales over which such studies need to be carried out to allow detecting recovery (Boulcott, Millar, & Fryer, 2014; Cook et al., 2013; Hall-Spencer & Moore, 2000; Hinz et al., 2011; Williams et al., 2010). Estimates either suggest that no recovery occurs within the timescale of the study (e.g. Hall-Spencer & Moore, 2000 [4 years] and Cook et al., 2013 [5 years]) or suggest

that some biogenic habitats (particularly sponges and soft corals) could require up to, or more than, 20–30 years before signs of recolonisation and recovery may occur (Williams et al., 2010).

Evaluating the effectiveness of reserve implementation for long-lived species has been problematic as it requires sampling regimes over the long timescales that are appropriate to their longevity and recovery rates. Here, we examine the link between the life history of species and reserve effectiveness. This study reports the changes that have occurred over 10 years in a MPA (Lyme Bay special area of conservation [SAC] [UK]) by comparing the abundance and size of benthic fauna at varying periods after closure to towed mobile fishing gear. It is important to note that the SAC has remained open to fishing with static fishing gear that have little physical impact on the seabed (Coleman, Hoskin, Von Carlshausen, & Davis, 2013). We anticipated that species that have fast growth rates and high dispersal potential would have achieved their maximum abundance and size in the 10 years since closure (king and queen scallops, dead men's fingers), whereas slower growing species or those with limited dispersal capability may not have recovered fully to their unimpacted status (Ross coral, pink seafans, white sea squirts).

## 2 | MATERIALS AND METHODS

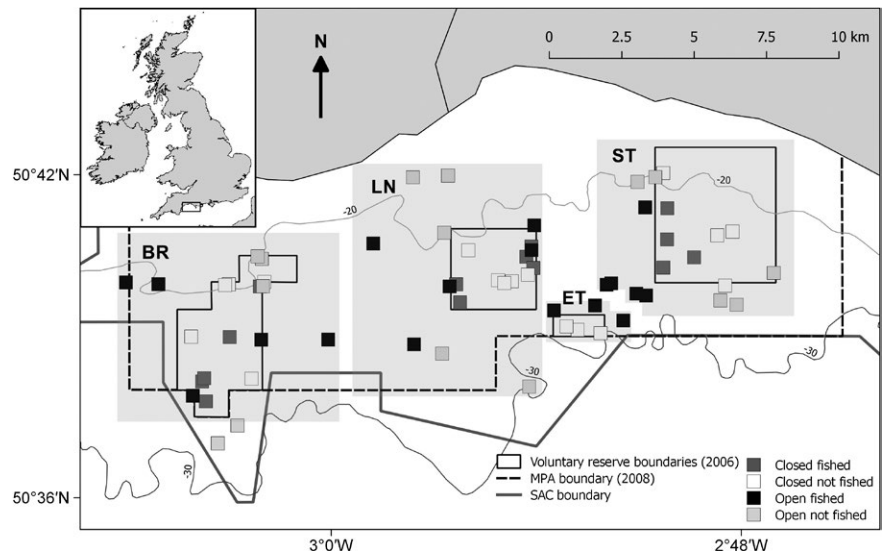
### 2.1 | Study context

In 2007, to investigate the effects of protection and fishing activity on epifaunal community composition, a survey conducted by Hinz et al. (2011) assessed differences in the size and abundance of nine species under different levels of protection and previous fishing activity. The same nine species were studied herein (Hinz et al., 2011) with a view to recording changes in the size and abundance of these species with time (Figure 1). The species included; the nationally protected pink sea fan *Eunicella verrucosa* (Pallas, 1766), branched sponge *Axinella dissimilis* (Bowerbank), dead men's fingers *Alcyonium digitatum* (L.), Ross corals *Pentapora foliacea* (Ellis & Solander, 1786) and white sea squirts *Phallusia mammillata* (Cuvier, 1815). Four commercially important species were also quantified; king scallop *Pecten maximus*, queen scallop *Aequipecten opercularis*, brown crab *Cancer pagurus* (L.) and spider crab *Maja squinado* (Herbst).

### 2.2 | Experimental design

The experimental design was implemented across the four voluntary reserves that were established in 2006. The first factor examined was fishing-history and the protection status in 2006 (hereafter termed *fishing history*) with four different levels: *closed not-fished* (CNF), within the voluntary reserve boundaries and not previously scallop-dredged; *closed fished* (CF), within the voluntary reserve boundaries but scallop-dredged previously; *open not-fished* (ONF), outside of the voluntary reserve boundaries but not previously scallop-dredged; and *open fished* (OF), outside of the voluntary reserve boundaries and previously scallop-dredged. The second factor was *year* with two different levels: 2007 and 2016. In the original study we undertook two

**FIGURE 1** Positions of the sample sites (squares) used to investigate temporal changes in epifaunal community composition in Lyme Bay following closure to towed demersal fishing gears over a 10 year period. The same survey design and sample sites used in the baseline survey were adopted (Hinz et al., 2011). The four voluntary reserves implemented in 2006 are outlined in thicker lines and the light blue shaded areas outline the sample sites for the corresponding reserve (BHG, Beer Home Ground; LN, Lanes Grounds; ET, East Tennents; STL, Saw Tooth Ledges). The current Marine protected area (MPA) boundary, implemented in 2008, is outlined in black. Grey shaded squares represent the sampling sites and colour denotes the four fishing history treatments. East Tennents was not analysed in this study due to inadequate sample replication. The inset boxes show the UK and wider Lyme Bay with the red rectangle and box indicating the study area, respectively



separate surveys in 2007, these have been combined and values averaged. Data for the East Tennents reserve was eventually eliminated from the analysis due to the poor quality of the video footage obtained and the lack of sufficient replication.

For the 2007 surveys, previous fishing effort was determined, using high-resolution track plots continuously recorded from fishermen's chart plotter data conducted between 2000 and 2006 (Hinz et al., 2011). This information was voluntarily provided by fishermen from five scallop dredge boats in the area, accounting for approximately 12% of the local fleet, and was considered representative of effort distribution by the South West Inshore Fishermen's Association. Fishing effort was calculated in ArcGIS 9.2 (ESRI) as the number of times a 500 × 500 m area was dredged between 2000 and 2006 (Hinz et al., 2011). Local fisheries by-laws meant that all vessels fishing within 6 nautical miles of the shore were under 12 m in length and were restricted to fishing with a total of 12 dredges (V. Gravestock, Southern Inshore Fisheries and Conservation Association, pers. comm.). The data significantly correlated with fisheries patrol aircraft sightings of the whole fleet during the same time-period and so was considered the most accurate data source for describing the general fishing effort and spatial coverage within Lyme Bay prior to implementation of the MPA (Hinz et al., 2011). Five replicate sample sites were selected at random for each of the remaining treatment combinations in each reserve (Figure 1; Hinz et al., 2011). Sixty-six of the sites sampled in 2007 were resampled in 2016, of which 60 were considered valid for the temporal comparisons with the baseline survey.

### 2.3 | Video sampling

In 2007, epifaunal communities were sampled using a towed high definition digital camera system on a towed sled with parallel laser

points for scale reference measuring only those animals that occurred at a consistent point in the field of view of the digital image (see Hinz et al., 2011). In 2016, epifaunal communities were sampled, using video footage taken from a towed flying array (Sheehan, Stevens, & Attrill, 2010). A silver *Hero 4 GoPro* camera, was used to record high definition video footage of the benthos, and three *XTAR D26 LED* dive torches (1,000 lumen), were attached to the array and were all positioned at a 45° angle to the seabed (Stevens, Sheehan, Gall, Fowell, & Attrill, 2014), congruent with the angle used in the baseline survey (Hinz et al., 2011). Two green lasers mounted in parallel projected parallel dots 17.5 cm apart to provide a constant reference for size measurements (Stevens et al., 2014). The *GoPro* video cameras were set to a standard resolution of 720p, 30 frames per second to reduce blurring and a narrow field of view to reduce image distortion.

At each sample site, the array was towed for approximately 10 min at a speed of c. 0.5 knots (0.25 m/s). GPS positions were recorded, using a handheld *Garmin eTrex 10* plotter, at the point when the array reached the seafloor and at the point when it was lifted clear from the seabed and were used to calculate the distance travelled by the array for each tow, using the GPS positions (see [www.datadryad.org](http://www.datadryad.org)). Video tows were positioned as close as possible to the corresponding location sampled in the baseline survey (Figure 1). From the digital images, the following data were extracted: abundance and body or colony-size of the epifaunal species listed in the introduction, a visual classification of the surficial seabed sediment habitat (see S1 for methods).

Given that we used different vessels and camera systems for the 2007 and 2016 surveys there is the potential to introduce survey artefacts which may have influenced the results. We consider that the survey vessel effect is irrelevant in this instance as the video material provides a direct measure of sample quality. In addition, the effect of a changing field of view was an issue in both surveys (due to wave action), however this effect could be accounted for by the

use of parallel laser pointers which provided a constant reference point in both surveys. If a scaling error was present, this would be presented as a consistent affect across all species, however the results indicate that size of individuals or colonies was either consistent or increased, but not in a uniform fashion across the two surveys. For these reasons, we consider that the data generated across the surveys is comparable.

## 2.4 | Statistical analysis

A full two-way factorial design with interaction terms was used to analyse the data. The two factor levels were fishing history and year (2007 vs. 2016; see Table 1). The data collected during the 2007 March and August surveys were pooled (and averaged) to increase the statistical power to detect temporal changes that occurred between 2007 and 2016. Samples obtained at East Tennents were removed from the statistical analyses due to a lack of replication for this site. All univariate analyses were performed, using R v.3.3.0.

The effect of previous fishing history and time on epifaunal species abundance and size was analysed in R GLMs with a Gaussian distribution (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Model assumptions were checked visually in R and transformations were applied to the data when appropriate. If the data did not conform to a Gaussian distribution, then log transformations were applied ( $\log(n + 1)$ ). We raised the level at which we accepted a significant effect had occurred to  $\alpha = 0.1$  to reduce the risk of Type II errors. We did this because the species studied are protected by legislation and hence it was important to be precautionary in the interpretation of our data. A Tukey LSD post hoc test was used to determine pair-wise difference when treatment effects were detected, again with  $\alpha = 0.1$  (see Thrusch, Hewitt, Cummings, & Dayton, 1995 for a justification of taking this precautionary approach).

Given the timeline of the implementation of the various area closures, we were able to explore the potential recovery rate of the individual species, using the following method. We treated the areas that had never been fished (the ONF and CNF sites) as an indicator of the carrying capacity  $K$  of the system for each species. We calculated the mean abundance for each species for each of these treatments (calculated from the mean of each of the replicate locations for each treatment) in both 2007 and 2016. This provided us with four measures of  $K$ . We then calculated the mean value of  $K$  and used this as a reference point that would indicate full recovery. For the areas that were exposed previously to fishing, our sampling regime provided estimates of abundance at year 0, 1, 8 and 10 years post-fishing (for explanation see Table 1). By calculating the mean of the mean abundance at each replicate site per treatment, we have only one data point per time period, however, given that we have some replication with time we consider that precision of the estimate at each time point is of greater value for the calculation of recovery. Given the low level of replication using this approach, we treat this analysis with caution. Logistic curves of the change in abundance vs. time were fitted and the time to 80% and 95% recovery of mean  $K$  was estimated (hereafter  $t_{80}$  and  $t_{95}$ ) using the nonlinear regression ( $\text{Abundance} \sim B_t \times K /$

**TABLE 1** Illustration of the number of years of protection (i.e. recovery timescale) for each of the different fishing treatments. Open not-fished (ONF) and closed not-fished (CNF) are both considered to represent the baseline condition and were used to calculate  $k$  for each species ( $n = 4$ ). The voluntary closure was implemented in August 2006 which means that the closed fished (CF) treatment was sampled 1 and 10 years post-closure. The open fished (OF) treatment was only protected at the point that Lyme Bay special area of conservation (SAC) was designated in 2008, and hence this site was sampled 8 years post-closure

	OF	CF	ONF	CNF
2007	0	1	>10	>10
2016	8	10	>10	>10

$(B_t + (K - B_t) \times \exp(-r \times t))$ , where  $B_t$  is the abundance at time  $t =$  years of protection and  $K$  was estimated as specified above). This analysis was not attempted for *C. pagurus* or *M. squinado* as these are mobile species and continued to be fished by static gear fisheries.

Size measurements could not be obtained from all of the individual organisms or colonies (note pink seafans, dead men's fingers and Ross corals form colonies) observed in the video footage. To calculate the mean size of a particular species at a given site, only sites with three or more size measurements contributed to the calculation of mean size. Four species: dead men's fingers, pink sea fans, queen and king scallops, met these quality assurance criteria. While there were an insufficient number of replicates for a temporal analysis of possible change in mean size of Ross coral and white sea squirts, there were a sufficient number of replicates to make comparisons between the four fishing history treatments, using only the 2016 data. The effect of previous fishing history and time on the size of each of these species was analysed as outlined above. We undertook a more in-depth examination of size-frequency distributions of pink sea fans for 2007 and 2016 across the four fishing treatments. Pearson's chi-squared tests were used to test for differences in the frequency distributions ( $\alpha = 0.1$ ).

## 3 | RESULTS

### 3.1 | Variation in substratum type

Univariate analysis showed that the percentage cover of gravel recorded in the surveys in 2016 was marginally higher than in 2007 (increase from c. 5% to 10%) (Mann-Whitney  $U$ -test,  $W = 1,148$ ,  $p < .002$ ; Figure 2). The percentage cover of all other substratum types did not vary between years. Thus, the habitats surveyed in 2007 and 2016 were highly consistent between surveys and did not introduce habitat confounding effects when considering any changes in species abundance, size and habitat association.

### 3.2 | Species abundance

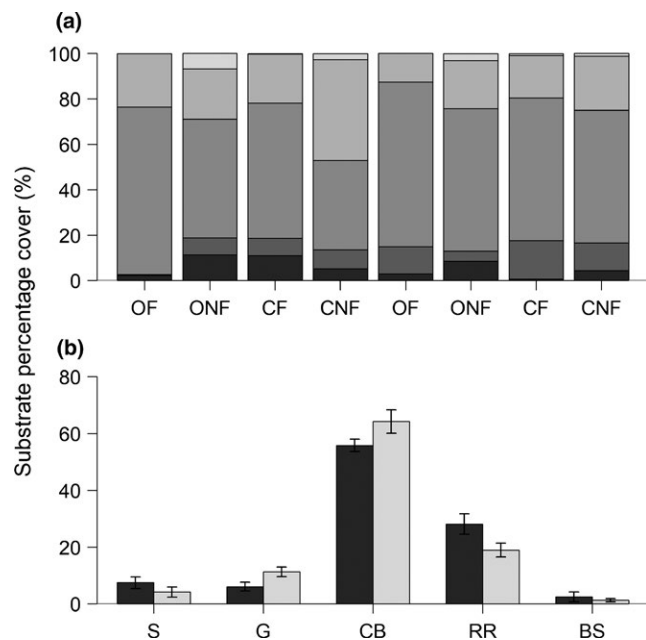
When we pooled the data from the two surveys undertaken in 2007 for the nine species of interest, a total of 7,675 individuals were observed from 11,838  $m^2$  of the seabed (65 indiv per 100  $m^2$ ). In

contrast, 12,757 individuals were observed from 11,969 m<sup>2</sup> of the seabed in 2016 (107 indiv per 100 m<sup>2</sup>), which is a 65% increase in abundance.

Analyses of the change in the abundance of each of the nine species with time and among fishing-history treatments were not consistent among the species. Pink sea fans, Ross coral and branched sponges had identical responses such that there was no change in their abundance across the fishing-history treatments with time, whereas there was a significant effect of fishing-history with the highest abundance of individuals in the CNF sites (Figure 3, Table 2). In contrast, the two other sessile species, dead men's fingers and white sea squirts, had significant effects for both time and fishing-history treatments, with a significant interaction term for dead men's fingers. In both cases, there was a consistent increase in abundance across all fishing history treatments. For the commercially important species, there was no significant effect of time or fishing-history treatment for king and queen scallops and brown crab but there was a significant decrease in the abundance of spider crab that varied with time and with fishing history (Figure 3, Table 2).

### 3.3 | Species recovery trajectories

Species recovery plots indicated that recovery to 80% of carrying capacity (t80) would take between 2.5 and 6 years for king scallops and dead men's fingers, respectively (although neither of these fitted



**FIGURE 2** (a) Mean substrate percentage cover across the four previous fishing treatment (OF, open fished; ONF, open not-fished; CF, closed fished; CNF, closed not-fished) and the two years (2007 and 2016). (b) Mean percentage cover ( $\pm$ SE) of the five substratum categories sampled across video transects during the 2007 (dark grey) and 2016 (light grey) surveys. S = sand; G = gravel; CB = cobbles and boulders; RR = rocky reef; BS = brittlestar beds. Only the percentage cover of gravel sediment differed significantly between 2007 and 2016 (Mann-Whitney  $W = 1,148$ ,  $p = .002$ )

relationships was significant), whereas recovery to t80 was projected to occur from 17 to 20 years for Ross coral, white sea squirts and pink sea fans, respectively (Figure 4). The maximum time to recovery for t95 was 51 years for yellow branched sponges. No recovery times were calculated for queen scallops as the abundance of this species was well above  $K$  in the previously fished stations at the start of the study and remained above  $K$  throughout.

### 3.4 | Changes in size

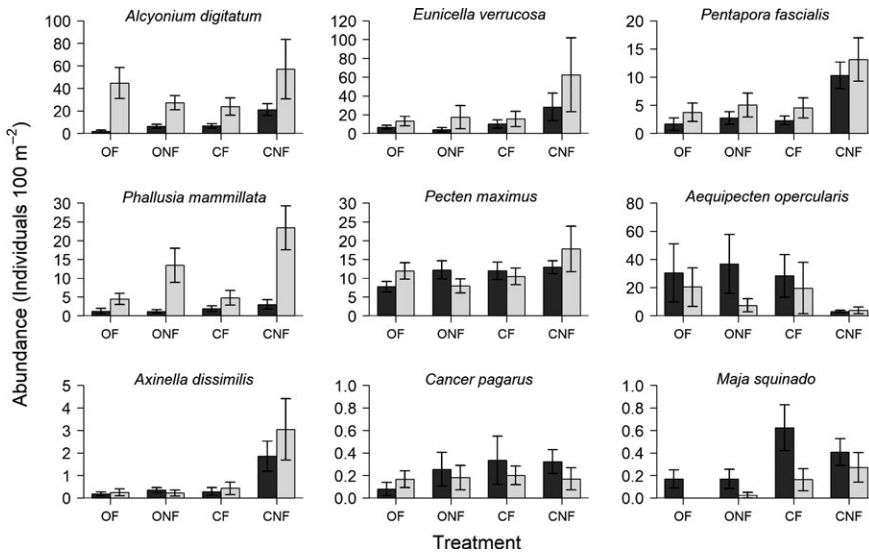
The mean size of dead men's fingers increased from 2007 to 2016 in the OF, ONF and CF sites (4.3, 1.7 and 2.9 times greater in size, respectively, Figure 5, Table 2), however, no significant difference was seen between years at CNF sites (Figure 5). Similarly, in 2016, pink sea fans were significantly larger than in 2007 at CNF and OF sites (2.4 and 3.1 times bigger, respectively) overall there was no difference in mean size between fishing history treatments (Figure 5, Table 2 and S2). Analysis of the mean size of Ross corals and white sea squirts in 2016 showed no significant effect of fishing history on Ross coral size, however, white sea squirts were larger in the ONF sites compared to the CNF sites (Figure 5, Tables 2 and 3). King scallops increased in size across all fishing-history treatments from 2007 to 2016 in contrast to the size of the shorter-lived queen scallops which did not change in mean size with time (S2). The size frequency distributions of pink sea fans were significantly different between years at ONF, OF and CF sites ( $\chi^2 = 40$ ,  $df = 18$ ,  $p = .04$ ;  $\chi^2 = 40$ ,  $df = 28$ ,  $p = .07$ ;  $\chi^2 = 50$ ,  $df = 35$ ,  $p = .05$ ), but not at CNF sites ( $\chi^2 = 60$ ,  $df = 54$ ,  $p = .27$ ). At ONF and CF sites, a significant increase in the number of pink sea fan individuals in larger size classes was observed between 2007 and 2016 (S3).

## 4 | DISCUSSION

This study enabled us to investigate the temporal changes in the abundance and body-size distribution of temperate reef fauna with contrasting life-history strategies following the exclusion of towed bottom-fishing gears. Most importantly we have gained some insight into the recovery rate of long-lived species such as pink sea fans and Ross corals which have recovery times (to t80: 80% of carrying capacity) of between 17 and 20 years. Shorter-lived species such as scallops and dead men's fingers had much shorter recovery times of 2.5–6 year. Although neither predictive relationship was significant in the formal analysis for the latter two species, these recovery times are similar to other studies (Lambert et al., 2014; Sciberras et al., 2013). We set out to be precautionary and avoid Type II errors by setting  $\alpha = 0.1$  as our level of significance (Thrush et al., 1995), but in the majority of cases the effects of fishing had probabilities  $\ll 0.05$ .

### 4.1 | Effects of the closure on species abundance

The effects reported herein share similarities with those reported elsewhere (Boulcott et al., 2014; Cook et al., 2013; Hall-Spencer & Moore, 2000). Hinz et al. (2011) reported negative effects of fishing



**FIGURE 3** Mean abundance ( $\pm 1SE$ ) of the nine epibenthic species sampled to investigate temporal changes following the implementation of the Marine protected area (MPA) in Lyme Bay in 2008, at previously open fished (OF), open not-fished (ONF), closed fished (CF) and closed not-fished (CNF) sites, for the years 2007 (dark grey) and 2016 (light grey)

on the abundance of dead men's fingers, and Ross corals, and on and the presence of branching sponges in Lyme Bay in 2007, but no effect of fishing was observed for pink seafans. This finding was contrary to expectation, and it was concluded that the impacts from gangs of scallop dredges was less severe within rocky habitats, perhaps due to the uneven topography of the seabed which may provide areas of protection or refuge from gears different gear (Boulcott & Howell, 2011; Hinz et al., 2011). This contrasts with the findings of this present study in which there was a positive effect of the MPA (Lyme Bay SAC) on the abundance and size of pink seafans that had been protected from towed mobile fishing gear for a much longer period of time.

In this study, we found that despite increases in the average abundance of Ross coral across each fishing treatment since the Lyme Bay SAC was implemented, no significant effect of time on abundance was found. This differs to the findings of the short-term studies, that were conducted 3 years following the establishment of the MPA (Sheehan, Cousens, et al., 2013; Sheehan, Stevens, et al., 2013), which observed significant increases in abundance over time. Hinz et al. (2011) also observed an increase in Ross coral abundance over a period of 5 months following implementation of the four initial reserves in 2006, however this increase was perceived to reflect seasonal differences rather than a recovery response. Typically Ross coral are considered sensitive species (Milazzo, Chemello, Badalamenti, Camarda, & Riggio, 2002) with a growth rate estimated at 2–3 cm per year. Ross coral have a lecithotrophic larval phase, lasting less than 1 day (Cocito, Sgorbini, & Bianchi, 1998), a life-history characteristic that limits dispersal and would favour habitat specialists (Hinz et al., 2011; Lombardi, Cocito, Occhipinti-Ambrogi, & Porter, 2008). Thus, it is perhaps not surprising that in this study, our projected recovery time to  $t_{80}$  was 16.6 years given the low rate of dispersal of larvae to areas around the adult population.

Eight years following the implementation of the MPA, white sea squirts were considerably more abundant than in 2007. White sea squirts appear to begin recovery within the first 3 years after the MPA was implemented (Hinz et al., 2011; Sheehan, Cousens, et al.,

2013; Sheehan, Stevens, et al., 2013). White sea squirts, similar to pink seafans and Ross coral, produce free swimming larvae that settle rapidly onto the seabed after a few days (Berrill, 1930). This short larval duration means that recruitment will be entirely reliant on local populations of adults (e.g. Lambert et al., 2014) and would explain why our predicted time to reach  $t_{80}$  was nearly 20 years (Figure 4).

In contrast to the species above, dead men's fingers have a higher recovery potential compared to other longer-lived sessile emergent species, due to their high fecundity and spawning strategies (Budd, 2008). Once fertilised, the lecithotrophic planulae can remain in the water column more than 10 days and can disperse more than 10 km (Budd, 2008; Hartnoll, 1975;). Sheehan, Cousens, et al. (2013) found an increase in the abundance of dead men's fingers within the MPA but not outside the MPA, 3 years after closures were implemented. In this study, dead men's fingers increased across all fishing treatments and remained most abundant in the CNF area. Our predicted time to  $t_{95}$  was 2.5 years which is similar to the recovery timescales reported by Lambert et al. (2014) for the Isle of Man (c. 5 years).

## 4.2 | Changes in size of individuals

Dead men's fingers increased in size across all treatments except in the CNF sites, which suggested that individuals within this area represent the upper-limit of body-size for this species in this locality. No differences in Ross coral size were found between the four fishing history treatments, suggesting that maximum size had been reached (Table 3). Pink seafans increased in size across all fishing-history treatments. The apparent increase in body size within the closed not fished (CNF) treatment may be attributed to a reduction in the frequency of interactions with static fishing gear (Eno et al., 2001). Anecdotal evidence from the local management agency (Inshore Fisheries and Conservation Association) suggests that whilst static gear effort within the MPA has not increased since the closures were implemented in 2008, static gear effort appears to have spread out over a wider

**TABLE 2** General linear model outputs on ln transformed data for the abundance of individuals 100 m<sup>2</sup> and on square root transformed body-size (surface area mm<sup>2</sup>) of individuals of each species, with fishing history (see Table 1) and year (2007 and 2016) as factors. Multiple pair-wise test are given in Table 3

Abundance	df	SS	MS	F	p	Body size	df	SS	MS	F	p
<i>Alcyonium digitatum</i>						<i>Alcyonium digitatum</i>					
Fishing history	3	18	6.01	5.11	<.001	Fishing history	3	2,576.4	858.8	3.2	.03
Year	1	54.1	54.1	46	<.001	Year	1	5,490.5	5,490.5	20.6	<.001
Fishing history × year	3	13.6	4.54	3.87	0.01	Fishing history × year	3	651.3	217.1	0.8	.49
Error	110	129	1.17			Error	67	17,899	267.2		
Total	117	216				Total	74	25,984			
<i>Eunicella verucosa</i>						<i>Eunicella verucosa</i>					
Fishing history	3	32.5	10.8	4.7	<.001	Fishing history	3	4,274.1	1,424.7	0.97	.42
Year	1	1.62	1.62	0.71	.4	Year	1	22,384	22,384	15.2	.0001
Fishing history × year	3	1.11	0.36	0.16	.92	Fishing history × year	3	575	191.7	0.1	.94
Error	110	254	2.3			Error	42	61,872	1,473.1		
Total	117	289				Total	49	90,779			
<i>Pecten maximus</i>						<i>Pecten maximus</i>					
Fishing history	3	2.36	0.79	1.31	.27	Fishing history	3	672.1	224	0.9	.44
Year	1	0.57	0.57	0.95	.33	Year	1	10,421	10,421	42.2	<.001
Fishing history × year	3	3.31	1.1	1.83	.15	Fishing history × year	3	400.5	133.5	0.5	.66
Error	110	66.2	0.6			Error	94	23,224	247.1		
Total	117	72.4				Total	101	34,969			
<i>Aequipecten opercularis</i>						<i>Aequipecten opercularis</i>					
Fishing history	3	2.26	0.75	0.31	.82	Fishing history	3	606.4	202.1	1.78	.17
Year	1	5.59	5.59	2.32	.13	Year	1	38.5	38.5	0.3	.56
Fishing history × year	3	2.48	0.82	0.34	.79	Fishing history × year	3	232.1	77.4	0.7	.57
Error	110	265	2.41			Error	27	3,062.9	113.4		
Total	117	276				Total	34	3,947.8			
<i>Pentapora fascialis</i>						<i>Pentapora fascialis</i>					
Fishing history	3	27.7	9.25	8.52	<.001	Fishing history	3	1,851	617	0.9	.42
Year	1	2.36	2.36	2.18	.14	Error	24	15,095	629		
Fishing history × year	3	1.18	0.39	0.36	.49	Total	27	16,946			
Error	110	120	1.08								
Total	117	151									
<i>Phallusia mammillata</i>						<i>Phallusia mammillata</i>					
Fishing history	3	19.7	6.58	6.46	<.001	Fishing history	3	473	157	0.9	.45
Year	1	30.6	30.6	30.1	<.001	Error	30	5,212	174		
Fishing history × year	3	5.01	1.67	1.64	.18	Total	33	5,686			
Error	110	112	1.02								
Total	117	166									
<i>Axinella dissimilis</i>						<i>Axinella dissimilis</i>					
Fishing history	3	8.49	2.83	10	<.001						
Year	1	0.01	0.01	0.04	.84						

(Continues)

**TABLE 2** (Continued)

Abundance	df	SS	MS	F	p	Body size	df	SS	MS	F	p
Fishing history × year	3	0.16	0.05	0.19	.9						
Error	110	31.1	0.28								
Total	117	39.8									
<i>Cancer pagurus</i>											
Fishing history	3	0.13	0.04	0.57	.63						
Year	1	0.02	0.02	0.35	.55						
Fishing history × year	3	0.12	0.04	0.54	.66						
Error	110	8.52	0.07								
Total	117	8.81									
<i>Maja squinado</i>											
Fishing history	3	0.94	0.31	4.49	.01						
Year	1	0.71	0.71	10.1	<.001						
Fishing history × year	3	0.14	0.05	0.71	.55						
Error	110	7.71	0.07								
Total	117	9.54									

area such that fishing intensity is lower (S. Pengelly, pers. comm., 14 September 2016). Such a response would occur as the risk of negative interaction between the towed gear sector and static gear sector was removed (Blyth, Kaiser, Hart, & Edwards-Jones, 2002). Thus, a reduction in the intensity of fishing activities *per se* may have led to an increase in the body size distribution of individuals of some species such as pink sea fans.

**4.3 | Change in abundance and size of target species**

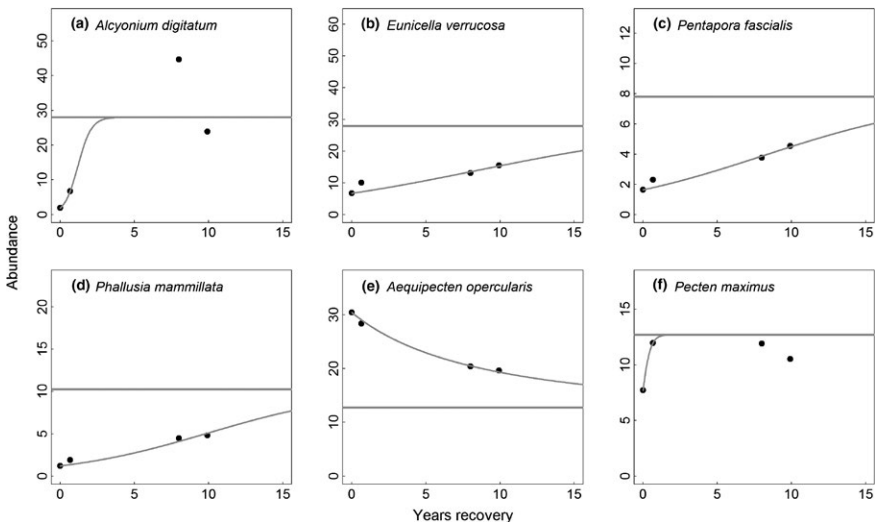
In contrast to expectations based on other studies (Beukers-Stewart, Vause, Mosley, Rossetti, & Brand, 2005; Sciberras et al., 2013), there was only a modest increase in the abundance of king scallops with time. However, our predicted recovery trajectory suggested that the scallop population may already be at carrying capacity in Lyme Bay.

Sheehan, Cousens, et al. (2013) and Sheehan, Stevens, et al. (2013) reported much higher abundances of king scallops in the areas of seabed they studied within Lyme Bay, which could suggest that the areas (type) of seabed surveyed in this study may have been less suitable for king scallops, or these differences may relate to temporal and spatial variation in recruitment.

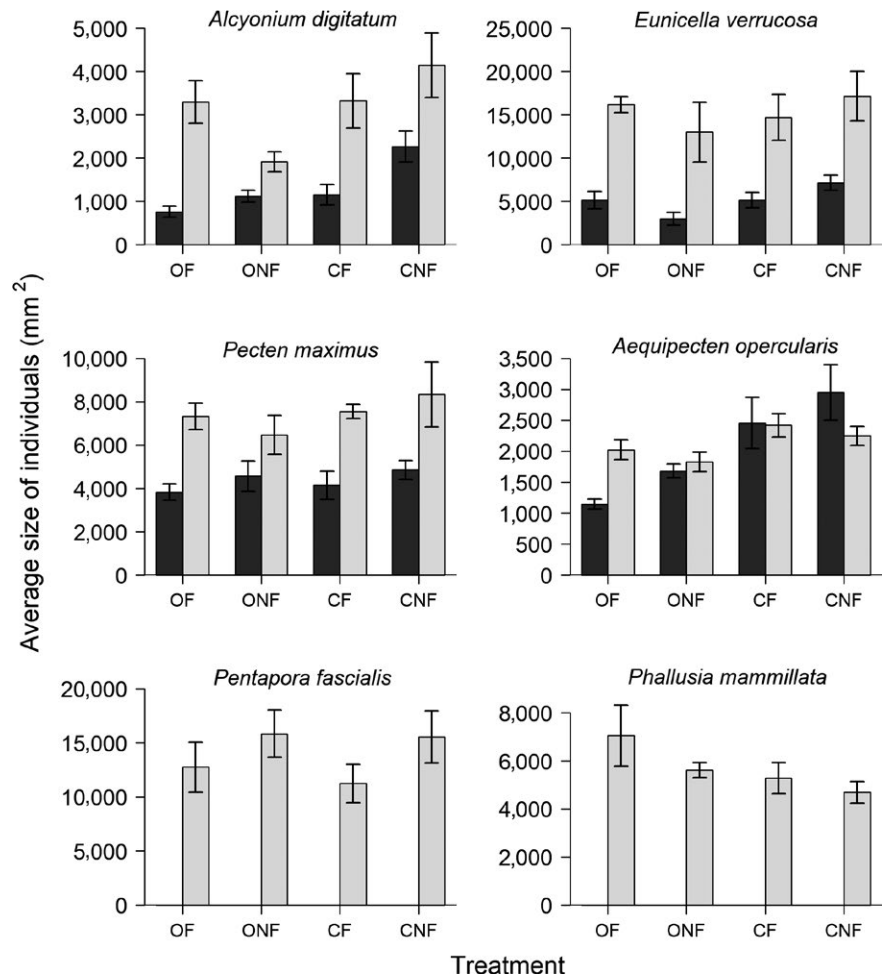
**5 | CONCLUSIONS**

**5.1 | Implications for management**

The implementation of reserves as conservation tools define spatial areas within which human activities can be managed. However, reserves are still subject to diffuse anthropogenic disturbances such as pollution and environmental changes such as warming sea



**FIGURE 4** Recovery plots for six sessile species sampled in Lyme Bay, showing the mean carrying capacity *K* (black horizontal line) and the fitted relationship for change with time in abundance showing the time to 80% (*t*80) and 95% (*t*95) recovery relative to *K*



**FIGURE 5** Mean individual size ( $\text{mm}^2$ ) ( $\pm 1\text{SE}$ ) of six epibenthic species for which we had adequate levels of replication to investigate temporal changes in body-size following the implementation of a Marine protected area (MPA) in Lyme Bay in 2008, at previously open fished (OF), open not-fished (ONF), closed fished (CF) and closed not-fished (CNF) sites, for the years 2007 (dark grey) and 2016 (light grey). Due to insufficient levels of replication, it was not possible to make a temporal comparison for *Pentapora fascialis* and *Phallusia mammillata* hence only the data for 2016 are shown

**TABLE 3** Coefficient ( $r$ ) for the logistic recovery curves, probability ( $p$ ) and the mean carrying capacity ( $K$ ) for each of the species for which recovery curves were fitted, plus the time (year) to recover to 80% ( $t_{80}$ ) and 95% ( $t_{95}$ ) of  $K$  (see Figure 4)

	$r$	$p$	$t_{80}$	$t_{95}$	$K$ mean
<i>Alcyonium digitatum</i>	2.21	.51	1.8	2.5	28.03
<i>Axinella dissimilis</i>	.09	.03	34.6	51.1	1.37
<i>Eunicella verrucosa</i>	.14	.005	18.7	30.2	27.91
<i>Pentapora fascialis</i>	.16	.001	16.6	26.1	7.81
<i>Phallusia mamillata</i>	.2	.001	16.9	24.7	10.25
<i>Aequipecten opercularis</i>	.05	.001	NaN	NaN	12.7
<i>Pecten maximus</i>	3.54	.31	0.3	0.7	12.71

temperatures. We cannot rule out the latter as potentially contributing to some of the effects we observed, such as some of the increases in organism size which could be related to temperature. Nevertheless, following the implementation of protection from fishing in Lyme Bay, this study has provided evidence that over the last 10 years the change in status for most species was positive and had either reached or is moving towards carrying capacity. Increases in size for the longer-lived species indicated recovery towards an improved size-structure in

these populations. The study highlights that differences in species life-history traits may be useful predictors of recovery rate. We found that all of the species with poor dispersal capability had slow predicted recovery rates, whereas species that had high larval dispersal (e.g. dead men's fingers and scallops) had relatively rapid recovery rates.

Any future consideration of towed mobile fishing activities within the boundaries of the current MPA should avoid entirely the rock reef and other areas of substantial hard substrata that have a strong affinity with species with poor dispersal capabilities (Hinze et al., 2011). Alleviation of the intensity of static gear fishing pressure may have contributed to some of the positive outcomes detected in this study (i.e. increasing body-size in pink sea fans) and would warrant further investigation. When the conservation of long-lived species is the objective of spatial management measures, our findings suggest that activities that lead to a reduction in species abundance such as trawling and dredging are incompatible within such areas. It may also be important to define the upper threshold of the intensity of other activities that may cause mortality of long-lived species (e.g. pot fishing), such that management measures (e.g. effort control) can be implemented that maintains the long-lived species in a favourable status. In contrast, some species such as dead men's fingers are more resilient to the effects of towed fishing gear given their shorter recovery timescale and low intensities of trawling may be sustainable for this species.

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## AUTHORS' CONTRIBUTIONS

M.J.K., S.H., J.R.B. collected and analysed the data, J.G.H. analysed the recovery plots, M.J.K., J.G.H. and H.H. conceived the original study. All authors wrote the paper and gave approval for publication of the final version.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.p8p8q> (Kaiser, Hormbrey, Booth, Hinz, & Hiddink, 2018).

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