

Variable population responses by large decapod crustaceans to the establishment of a temperate marine no-take zone

M.G. Hoskin, R.A. Coleman, E. von Carlshausen, and C.M. Davis

Abstract: In 2003, an area adjacent to Lundy Island was designated as the United Kingdom's first no-take zone (NTZ) for nature conservation. The only significant fishery at Lundy was for lobster (*Homarus gammarus* L.) and various crabs. The Lundy NTZ provided an opportunity to test hypotheses about the recovery of crustacean populations from fishing. Using an experimental potting program, we simultaneously compared changes in the crustacean populations within the NTZ with those in proximal control (Near Control) locations and two distant control (Far Control) locations. Comparisons were replicated over 4 years, and the results analysed using asymmetrical analysis of variance. There was evidence of a rapid, large increase in the abundance and sizes of legal-sized lobsters within the NTZ, and evidence of spillover of sublegal lobsters from the NTZ to adjacent areas. The NTZ also appeared to cause a small, but significant increase in the size of brown crab (*Cancer pagurus* L.) and a decrease in the abundance of velvet crabs (*Necora puber* L.) (the latter potentially owing to predation and (or) competition from lobsters). Unlike many previous studies, these results are unambiguous, owing to a robust asymmetrical experimental design. We suggest that regulatory and conservation agencies use this approach, which we have demonstrated to be relatively straightforward, whenever the NTZ requiring evaluation cannot be replicated.

Résumé : En 2003, une région adjacente à l'île de Lundy a été désignée la première zone de pêche interdite (NTZ, no-take zone) pour la conservation de la nature au Royaume-Uni. La seule pêche commerciale d'importance à Lundy était celle de homards (*Homarus gammarus*) et de divers crabes. La NTZ de Lundy fournit l'occasion de tester des hypothèses concernant le rétablissement des populations de crustacés après la pêche. En utilisant un programme expérimental de captures au moyen de casiers, nous avons comparé les changements dans les populations de crustacés dans la NTZ et en même temps dans des sites témoins avoisinants et deux sites témoins éloignés; nous avons répété l'expérience pendant quatre ans et avons analysé les changements au moyen d'une analyse de variance asymétrique. Il y avait des indications d'un accroissement rapide et important dans l'abondance et la taille des homards de taille légale dans la NTZ et d'un débordement vers les régions adjacentes de homards de taille inférieure à la taille légale. La NTZ semble aussi avoir produit un accroissement petit mais significatif de la taille des crabes dormeurs (*Cancer pagurus*) et un déclin de l'abondance des étrilles communes (*Necora puber*) — ce déclin sans doute dû à la prédation et(ou) à la compétition par les homards. Contrairement aux études antérieures, nos résultats sont sans ambiguïté à cause d'un plan expérimental asymétrique robuste. Nous suggérons aux agences de réglementation et de conservation d'utiliser cette même méthodologie que nous avons démontrée être relativement simple lorsque les NTZ à évaluer ne peuvent être étudiées par répétition.

[Traduit par la Rédaction]

Introduction

The two greatest threats facing biodiversity are anthropogenically associated habitat degradation and species loss. Whilst the ultimate mechanisms for these, i.e., human population increase, urbanization, and climate change, are receiving increasing attention, far more effort has been focused on proximate causes. In the case of the marine environment, the most studied anthropogenic disturbance is that of fishing

(e.g., Myers and Worm 2003; Dankel et al. 2008 and others cited therein). A frequently used tool in the protection, recovery, and restoration of marine systems are marine protected areas (MPAs), which may vary in the strength of protection (Allison et al. 1998). The strongest level of protection is the "no-take zone" (NTZ), or as they are now more often termed "sanctuary zones." Often, these NTZs are applied with minimal evaluation of their ecological impacts. The key aspect here is that when evaluating the eco-

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logical effects of conservation measures (or any anthropogenic intervention in the environment), proper monitoring design is crucial to be able to accurately and precisely detect potential impacts (Underwood 1994, 1995). Here we report on one of the first evaluations of a marine protected area using a fully replicated asymmetric monitoring scheme.

Reviews of the now-extensive body of empirical evidence associated with NTZs all conclude that highly-protected marine areas can trigger lasting, often rapid, increases in the abundance, diversity, and productivity of marine organisms (Roberts and Polunin 1993; Halpern and Warner 2002; Lubchenco et al. 2003). The potential for NTZs to promote local enhancement of natural populations is of interest for both biodiversity conservation and fisheries management. Of further and perhaps even-greater interest to fisheries managers is the theory that increased production within NTZs can “spill over” into surrounding areas via adult migration and larval dispersal, causing increased catches in these areas (Dugan and Davis 1993; Roberts and Polunin 1993; Guénette et al. 1998). Direct evidence of spillover benefits to fisheries is much more limited, however, than evidence of enhanced production within NTZs (Russ and Alcalá 1996; Roberts et al. 2001; Goñi et al. 2006). If such effects were a commonplace effect of NTZs, this would be a compelling argument for their widespread use as a tool for fisheries management.

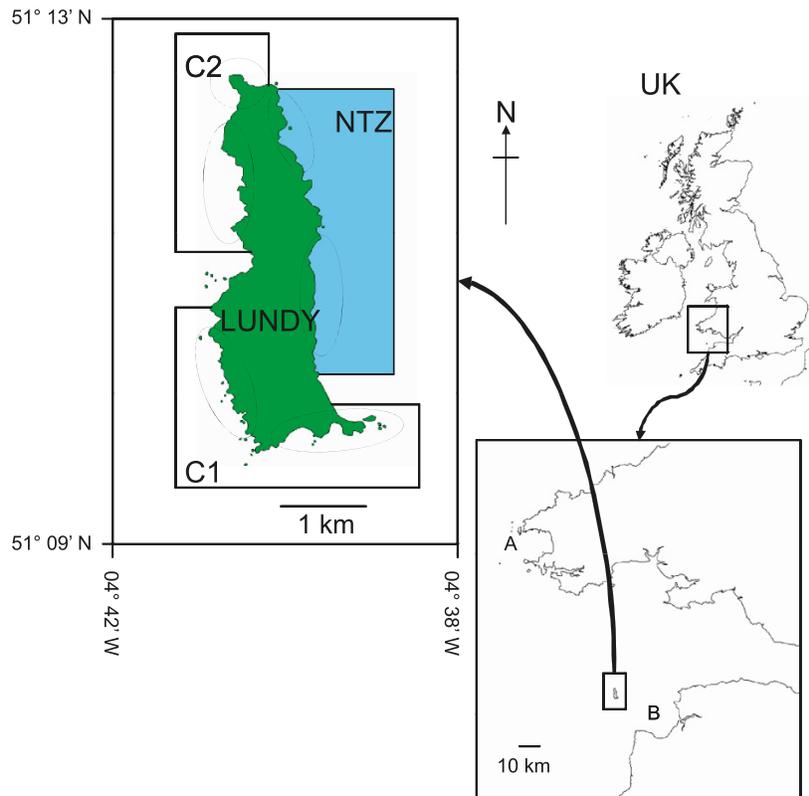
The first requirement for effective monitoring of any managerial action with respect to the environment is an a priori decision as to what outcome would constitute (and demonstrate) success. Once a “success goal” has been set, it must be translated into a precise, testable hypothesis to inform the design of sampling and statistical analyses that will reliably test that hypothesis (Underwood 1994, 1995). Without a testable a priori hypothesis, monitoring yields results that are difficult and sometimes impossible to interpret reliably. Hypotheses are implicit in managerial decision-making (Underwood 1998), but this fact may be overlooked if managers believe that the decision to act (or not to act) is the end-point of management. Implicit in the decision to implement a NTZ is the general hypothesis that previously-exploited populations inside the NTZ will experience positive changes (e.g., increased abundance, size, fecundity, etc.) that are significantly greater than those experienced by similar populations in areas that continue to be fished. Testing this hypothesis requires that time-series data from the NTZ are compared with contemporaneous data from similar places that are not NTZs. Tests for effectiveness of marine reserves are often done badly. Some studies (e.g., Narvarte et al. 2006) compare a single established MPA with only one other site. Other studies (e.g., Francini-Filho and Moura 2008, and others reviewed by Halpern et al. 2004), have improved on this approach by also having used a before–after comparison, i.e., the classic “before–after control–impact”, or, BACI design. Unfortunately, such studies are always confounded, as they rely on an unreplicated interaction. If Site I is the MPA and Site II is a control location, each sampled before, I_{bef} and II_{bef} , and after, I_{aft} and II_{aft} , then the hypothesis under test is that II_{bef} should not differ from II_{aft} , but I_{aft} should differ from I_{bef} . Since there is no reason to expect that the natural temporal variations in Sites I and II will be similar, however, acceptance of this hypothesis

cannot be reliably interpreted as an effect of the MPA. A much better design (i) compares the single MPA with multiple control sites, to account for variation among places, and (ii) compares those sites multiple times before and after the study to account for temporal variation. The analytical mechanisms to disentangle impact effects from spatial and temporal variation when using such asymmetric designs have been determined (Underwood 1994). It is also possible to apply such analyses to assess potential ecological impacts after a disturbance (or other anthropogenic intervention) has occurred (Glasby 1997). Thus, even without “before” data, it is relatively easy to develop and apply “gold standard” asymmetric analytical tests for evaluating the effectiveness of a MPA. Unfortunately, only one study has done this (Claudet et al. 2008); however, this was a meta-analysis from many, less rigorous evaluations. In our study, we were unable to obtain “before” data (owing to fisheries regulators implementing faster than funding agencies); so, we present the first asymmetric, post-impact field-evaluation of the effect of a NTZ in the context of natural variation in response variables close to the NTZ (1–5 km) and further away from it (20–100 km), and at smaller spatial scales nested within these locations.

Lundy Island is off the southwest coast of England ($51^{\circ} 10'N$, $4^{\circ}40'W$, Fig. 1). The closest mainland coast lies ~ 18 km to the south. Lundy is about 5 km long and about 1.25 km wide and its long axis lies approximately north–south. In 1986, Lundy’s intertidal zone and surrounding marine area were designated as the UK’s first Marine Nature Reserve (MNR). In 2000, this area also became a Special Area of Conservation (SAC) under the European Union’s Habitats Directive. Despite Lundy’s statutory conservation designations, there was concern that whilst the island’s important marine habitats and species were still subject to commercial and recreational fishing, there was no reliable knowledge of potential ecological impacts from these activities. The main commercial fishery around Lundy is potting (fishing with baited traps) for lobster and crabs. Fisheries using trawls, dredges, or nets were banned on designation of the MNR. Recreational angling and shellfish harvesting by scuba divers are still permitted at Lundy, but are relatively limited (Keith Hiscock, Marine Biological Association of the United Kingdom, Plymouth, UK, personal communication May 2004). Concern for the potential impacts of continuing fishing led to designation of part of the Lundy MNR/SAC as the UK’s first statutory NTZ in February 2003. The NTZ extends ~ 3.6 km along the east coast of Lundy and ~ 1 km out to sea, encompassing an area of ~ 4 km² (Fig. 1). Rocky and sedimentary habitats are present within the NTZ, with the latter occupying the greater portion.

This study focuses on the decapod crustaceans targeted by the commercial potting fishery at Lundy. The hypotheses in this study came from the general model that the NTZ would remove or reduce fishing mortality and fishing-related disturbances, causing marine populations that were previously affected by fishing within the NTZ to prosper relative to those in similar places where fishing was ongoing. The specific hypotheses tested were as follows: (1) The mean abundances of commercially fished crustaceans will increase in the NTZ relative to mean abundances in areas that continue to be fished; (2) The mean abundances of commercially

Fig. 1. Location of Lundy in the United Kingdom. Inset shows the boundary of the Lundy no-take zone (NTZ). C1 and C2, Near Controls; A, South Wales Far Control; B, North Devon Far Control. Sites of sampling for the potting study to assess effects of the Lundy NTZ on lobster and crabs are indicated by ellipses.



fished crustaceans will increase within the NTZ and adjacent areas relative to mean abundances in more-distant areas that continue to be fished (note that acceptance of this hypothesis will indicate that spillover may have occurred, but it will not support it conclusively); (3) The mean sizes of commercially fished crustaceans will increase in the NTZ relative to mean sizes in areas that continue to be fished.

Materials and methods

Sampled species and design

Potential effects of the Lundy NTZ were assessed for four species of commercially-fished crustaceans. These were (i) lobster (*Homarus gammarus* L.); (ii) velvet crab (*Necora puber* L.); (iii) brown crab (*Cancer pagurus* L.); and (iv) spider crab (*Maja squinado* (Herbst)).

The potential effects of the Lundy NTZ on abundances and body-sizes were tested at small (1–5 km) and large (20–100 km) spatial scales over 4 years (2004–2007). At the smaller scale, there was a comparison between the Lundy NTZ and two adjacent control locations (Near Controls); at the larger scale, there was a comparison between the Lundy NTZ and two Far Control locations, one in South Wales and one in North Devon (Fig. 1). All control locations were approximately the same size as the Lundy NTZ (areas ~3–4 km in length, parallel to shore, and ~100 m wide), similar in bathymetry, benthic habitat, etc., and all are important areas for commercial lobster and crab potting. Each sampling location was divided into two replicate sites, each ~1–1.5 km in length approximately parallel to the shore.

By comparing abundance data from the Lundy NTZ with data from Near Control and Far Control locations, it was possible to assess potential spillover effects arising from any increases in abundance within the NTZ. If spillover of lobster or crabs occurred, it was expected that this should cause abundances within Near Control locations to increase (becoming more like that within the NTZ) whilst abundances in Far Control locations remain more-or-less unchanged. It was assumed that Far Control locations were far enough away from Lundy to not be significantly affected by any spillover from the NTZ (based on the small proportions of regional crustacean populations protected within the Lundy NTZ, and the expectation that the rate of spillover, be it via larvae, juveniles, or adults, into receiving areas would decline steeply with increasing distance from Lundy; Kinlan and Gaines 2003).

Sampling lobster and crabs

Lobsters and crabs were sampled using standard commercial shellfish pots baited with salted whole mackerel (*Scomber scombrus* L.). The catch-rate of a pot depends on animals encountering and entering it, and is thus strongly related to the local abundances of the target species. The pots used for this study were “parlour pots” (71 cm in length with 25 cm entrances), which catch lobsters and crabs. “Ink well” pots were judged less suitable, as lobsters can readily escape (Lovewell et al. 1988).

Pots were deployed in “strings” of 10, with approximately 15 m between each pot. At both ends of each string

there was a heavy metal weight (~ 20 kg) serving as an anchor and a rope attached to a surface marker-buoy. Adjacent pots on a string were sufficiently close to each other that they could not safely be considered as independent replicates as the presence of individuals in one pot may influence the probability of another entering an adjacent pot and additionally, the bait odour plumes from closely spaced traps on a string will overlap and “compete” for hungry animals (Miller 1983). Hence, strings of pots rather than individual pots were replicates, with $n = 4$ in each of the two sites per location. Within each site, strings were set parallel to the shoreline with 50–100 m between the ends of adjacent strings. The same sites in each location were sampled in each year.

In each location, in each year, there were five consecutive replicate days of sampling, with pots therefore having a ~ 24 h “soak” prior to each sampling event. Sampling was done within June/July each year. On a few (5%) occasions, bad weather meant that some strings were soaked for 48 h rather than 24 h. While it might be assumed that a longer soak-time would increase the catch proportionately, evidence for lobsters suggests that when soak-time is 5 d or less, small variations in soak-time have no consistent and significant effect on the catch rate (Bennet and Lovewell 1977). Thus, there was little cause for concern about systematic bias.

Within each year, sampling was not done simultaneously at all locations, except for those at Lundy (i.e., the NTZ and the two Near Control locations), because of logistical constraints and the number of pots available to the study (240 in total). In each year, sampling was done first in North Devon, then in South Wales, and finally at Lundy. Our inability to sample all locations simultaneously in each year meant that some spatial differences were potentially confounded with an unknown amount of temporal (weekly) variation. It was considered unlikely, however, that sampling the different locations in the same order each year would cause any problems of bias, since there was no reason to expect any consistent tidal or weather trend during the sampling “window” in each year.

Measurement of variables and other methodological details

The measure of abundance of lobster and crabs was the number of individuals per string of 10 pots. As each string was hauled, lobsters and crabs were removed from the pots and placed in separate fish boxes according to species. Once each string had been hauled and cleared of its catch, pots were re-baited (if needed) and the string was immediately re-deployed in approximately the same position. Measuring of lobsters and crabs and their immediate return to the sea proceeded whilst the string of pots was being re-deployed.

For lobsters, the measure of size was carapace length (CL); the distance from the rear of the eye-socket to the posterior edge of the carapace. Measurements of carapace length were obtained using a Vernier calliper. For crabs, the measure of size was carapace width (CW), measured at the widest point using either the Vernier calliper, or a measuring board if the shell was wider than the maximum gape of the calliper (~ 15 cm).

Analysis of the abundances of lobster and crabs (hypotheses 1 and 2)

Univariate hypotheses about potential effects of the Lundy NTZ on mean abundances of lobster and crabs were tested using analysis of variance (ANOVA). With the exception of lobster, hypotheses about changes in abundance were tested using data that comprised all sampled individuals, regardless of size. For lobster, data on the abundance of individuals larger than the minimum landing size (MLS) ($CL \geq 90$ mm) were analysed separately from abundance data for individuals smaller than the MLS. This was because preliminary analyses of abundance data for lobster had revealed different responses to the NTZ in these two size-classes (referred to subsequently as “legal sized” and “sublegal,” respectively).

For lobster and crabs, small-scale comparisons between the NTZ and Near Control locations were done separately from comparisons with Far Control locations. The required ANOVA in each case was an asymmetric model, in which the single NTZ location was compared with the two Near Control locations (or two Far Control locations, as appropriate) (see Underwood 1992, 1994; Glasby 1997 for the theory and application of asymmetrical ANOVA in environmental monitoring). It was necessary to use two separate ANOVAs because a single model encompassing comparisons of NTZ versus Near Control (NTZ vs. Nr) and NTZ versus Far Control (NTZ vs. Far) would have had such complex asymmetry that the likelihood of obtaining valid F ratios for the important ANOVA tests would have been excessively small (A.J. Underwood, University of Sydney, Centre for Research on Ecological Impacts of Coastal Cities (EICC), New South Wales, Australia, personal communication). Asymmetric ANOVA computations for the different variables were constructed from sums of squares calculated by the ANOVA software WinGMAV5 (EICC, The University of Sydney, Australia). Computationally, the two asymmetric ANOVAs for the different spatial scales were identical. In each case, the asymmetric ANOVA for analysing data on the abundances of lobster and crabs was a mixed model comprising four experimental factors. The first factor was “Location” (Lo), for which there were three levels, the NTZ (a fixed component) and two Control locations (Near or Far, as appropriate; random components). The second factor was “Year” (Ye), which was a fixed factor with four levels (the years 2004, 2005, 2006, and 2007). The third factor was the random factor “Site” (Si), nested in “Location” with two levels. Factor four was the random factor “Time” (Ti), nested in “Year” with five levels (the five replicate days of sampling in each year). The testable factors in the two asymmetric ANOVA models based on this experimental design are listed and interpreted in the online supplementary data,² Tables S1a and S1b.

For the purpose of testing Hypothesis 1 for each species, the main ANOVA factors of interest were $Ye \times Lo$: NTZ vs. Nr, for the small-scale comparison, and $Ye \times Lo$: NTZ vs. Far, for the large-scale comparison. Hypothesis 2, the potential spillover hypothesis, was tested via the two ANOVAs described above and an additional ANOVA that was only required for this hypothesis. Three distinct ANOVAs were needed to assess potential spillover because there were three parts to this hypothesis. The first part was that there

would be significant increase in mean abundance within NTZ and Near Control locations: this was tested via the factor Year, in the previously-described ANOVA for these locations. The second part of the spillover hypothesis was that there should be no significant increase in Far Control locations relative to the NTZ: this was tested via the factor $Ye \times Lo$: NTZ vs. Far, in the ANOVA for these locations. The third part of the spillover hypothesis was that the increase in abundance in Near Control locations should be significant relative to Far Control locations: this was tested via a third ANOVA comparing these locations (see supplementary data,² Table S1c). This third ANOVA was only done where significant changes consistent with the first and second parts of the test for potential spillover had already been confirmed. Unlike the first two ANOVAs, this third ANOVA was a symmetrical analysis, because Near Control and two Far Control locations were equally replicated.

Initial analyses of lobster and velvet crab data using the planned ANOVA models revealed significant haphazard variation (i.e., “noise”) from time-to-time within some years, which necessitated a slight modification of the models. With the planned models, this temporal noise meant that valid ANOVA tests for $Ye \times Lo$: NTZ vs. NR and $Ye \times Lo$: NTZ vs. Far (the critical factors of interest) were not available. This was remedied by averaging the abundance data for each string of 10 pots across the five replicate times of sampling per year prior to analysis (this was only possible because each string of pots sampled the same area each time). Unfortunately, averaging across times within years reduced the power of tests (by reducing n by 20%), however, by also reducing temporal “noise” in the data, it made important tests possible that could not have been done otherwise. Apart from the absence of “Times(Year)”-factors and use of a 5 d average variable, the ANOVA models applied to lobster and velvet crab were identical to the planned analyses and tests for the other factors can be interpreted in exactly the same way.

Prior to ANOVA, abundances of lobster and crabs were transformed to either $\ln(X+1)$ if the species was generally abundant, or $\ln(X+0.1)$ if it was present only infrequently. With either transformation, the hypothesis tested was one of relative, rather than absolute difference among treatments (Underwood 1997). This was considered appropriate because changes in relative abundance are more informative than changes in absolute abundance when assessing the performance of a NTZ. A logarithmic transformation also has the general effect of reducing heterogeneity of variances, which reduces the rate of Type-I error in ANOVA tests (i.e., false rejection of a true null hypothesis). In an experiment such as this, however, with a relatively large number of treatments and balanced sampling, mild heterogeneity of variances should not be problematic (Underwood 1997). Nevertheless, heterogeneity of variance was tested for each ANOVA using Cochran’s Test (Underwood 1997) and the results reported for information in the relevant tables. ANOVA in general is robust against non-normality of data; this is especially true for large, balanced designs (Underwood 1997) and so normality tests were not done. For all ANOVA models, α was 0.05. Where appropriate, post-hoc pooling of nonsignificant

factors ($P > 0.25$; Winer et al. 1991) was used to create new denominators allowing more powerful tests for key ANOVA factors. In some instances, critical interpretation required the use of Student–Newman–Keuls (SNK) multiple comparison tests to investigate the patterns of change or difference responsible for significant ANOVA tests. For the purpose of describing and plotting results, the abundance of each species was expressed as the untransformed mean abundance per string of pots ± 1 standard error (SE).

Hypotheses about potential effects of the NTZ on the mean sizes of lobster and crabs were tested using untransformed data. The ANOVA model for testing size data was identical to that for testing abundance data, except that the factors Site and Time were dispensed with. This was because there were frequent combinations of Site and Time for which a mean size could not be calculated because abundance was ≤ 1 (interpretations of factors in the asymmetric ANOVA for size data are provided in the supplementary data,² Table S1d). Because the four species of crustacean differed in their patterns of abundance, the sample sizes for analysing their body sizes (and hence the power of these analyses) also varied amongst species. These variations in abundance also made it necessary to randomly subsample the available size data to balance sample sizes prior to analyses. All other aspects of the statistical interpretation and presentation of size data were as per analyses of abundances.

For brevity, this paper focuses only on results that directly relate to a priori hypotheses about potential effects of the NTZ. Significant differences due to other factors are reported in the accompanying tables and figures, but not described or discussed thereafter.

Results

The abundance of lobster and crabs (hypotheses 1 and 2)

Of the four species of commercially-fished crustaceans that were monitored for this study, only lobster and velvet crab showed significant changes in abundance that were potentially attributable to the NTZ.

Abundance of lobster

There was a substantial increase in the abundance of legal-sized lobsters within the NTZ relative to abundances in both Near and Far Control locations. For legal-sized lobsters, evidence for a positive effect of the NTZ came from significant results for the factors $Ye \times Lo$: NTZ vs. Nr (Table 1) and $Ye \times Lo$: NTZ vs. Far (Table 2). By 2007, mean abundance within the NTZ had increased by 127%, while abundances in Near Control and Far Control locations had not changed significantly (Fig. 2a). This increase, on top of the initial difference, meant that by 2007, legal-sized lobsters were 5× more-abundant within the NTZ compared with the other locations (Fig. 2a).

There were increases in the average abundance of sublegal lobsters within the NTZ and Near Control locations, but relatively constant mean abundances in Far Control locations (Fig. 2b). For sublegal lobsters, there was no significant effect of $Ye \times Lo$: NTZ vs. Nr (Table 3), but the

²Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>).

Table 1. Asymmetric analysis of variance (ANOVA) of $\ln(x+1)$ -transformed abundances of legal-sized lobsters (carapace length, $CL \geq 90$ mm) per string of 10 pots for NTZ versus near control locations ($n = 4$).

Source of variation	df	SS	MS	Planned tests		
				Denominator	F	P
<i>Location</i>	2	20.47	20.476			
Lo: NTZ vs. Nr	1	20.38	20.375	Lo: Nr	200.73	$P < 0.05$
Lo: Nr	1	0.10	0.102	Site (Lo: Nr)	1.30	ns
<i>Site (Location)</i>	3	0.35	0.117			
Site (NTZ)	1	0.19	0.195	Res: NTZ	1.35	ns
Site (Nr)	2	0.16	0.078	Res: Nr	1.41	ns
<i>Year</i>	3	2.17	0.724	Ye × Lo: Nr	6.79	ns
<i>Year × location</i>	6	2.35	0.391			
Ye × Lo: NTZ vs. Nr ^a	3	2.03	0.676	Ye × Lo: Nr	6.33	ns
Ye × Lo: Nr ^b	3	0.32	0.107	Ye × Si (Lo: Nr)	0.97	ns
<i>Year × site (Location)^b</i>	9	0.68	0.076	Residual	0.89	ns
Ye × Si (Lo: NTZ)	3	0.02	0.007	Res: NTZ	0.05	ns
Ye × Si (Lo: Nr)	6	0.66	0.110	Res: Nr	1.98	ns
<i>Residual^a</i>	72	6.13	0.085			
Res: NTZ	24	3.47	0.145			
Res: Nr	48	2.66	0.055			
Total	95	32.15				

Note: NTZ, no-take zone; Nr, near; Ye, year; Lo, location; Si, site; ns, not significant. Location was a random factor with three levels (NTZ, Near Control 1, and Near Control 2), the contrast between NTZ and Near Controls used fixed terms. Site was a random factor to estimate spatial variance and Year represented the 4 years of the study (fixed). Heteroscedasticity was checked by Cochran's test (Underwood 1997). Cochran's Test $C = 0.2055$ ($P < 0.05$). Largest variance = 0.420, this occurred in the NTZ, Site 1 in 2005.

^aPost hoc tests: $F = 7.96$; $P < 0.001$.

^bFactors that were pooled to create the denominator for testing Ye × Lo: Ntz vs. Nr.

Table 2. Asymmetric analysis of variance (ANOVA) of $\ln(x+1)$ -transformed abundances of legal-sized lobsters (carapace length, $CL \geq 90$ mm) per string of 10 pots for the no-take zone (NTZ) versus Far Control locations ($n = 4$).

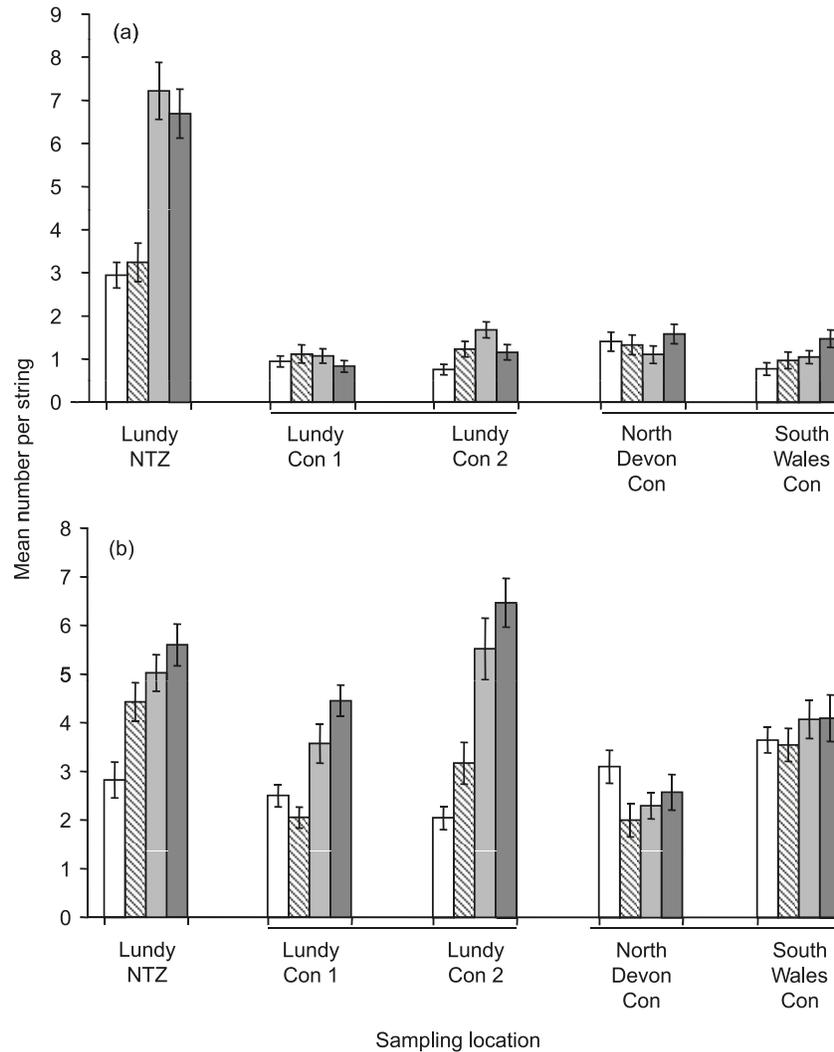
Source of variation	df	SS	MS	Denominator	Planned tests	
					F	P
<i>Location</i>	2	18.89	9.444			
Lo: NTZ vs. Far	1	18.73	18.734	Lo: Far	122.36	ns
Lo: Far	1	0.15	0.153	Site (Lo: Far)	2.56	ns
<i>Site (Location)</i>	3	0.31	0.105			
Site (Lo: NTZ)	1	0.19	0.195	Res: NTZ	1.35	ns
Site (Lo: Far)	2	0.12	0.060	Res: Far	0.69	ns
<i>Year</i>	3	2.13	0.709	Ye × Lo: Far	9.55	$P < 0.05$
<i>Year × location</i>	6	2.27	0.379			
Ye × Lo: NTZ vs. Far ^a	3	2.05	0.683	Ye × Lo: Far	9.20	ns
Ye × Lo: Far ^b	3	0.22	0.074	Ye × Si (Lo: Far)	0.62	ns
<i>Year × site (Location)^b</i>	9	0.74	0.082	Residual	0.77	ns
Ye × Si (Lo: NTZ)	3	0.02	0.007	Res: NTZ	0.05	ns
Ye × Si (Lo: Far)	6	0.72	0.119	Res: Far	1.38	ns
<i>Residual^b</i>	72	7.62	0.106			
Res: NTZ	24	3.47	0.145			
Res: Far	48	4.15	0.086			
Total	95	31.96				

Note: Far, far control. Location (Lo) was a random factor with three levels (NTZ, South Wales, and North Devon). The contrast between NTZ and Control used fixed terms. Site (Si) was a random factor to estimate spatial variance and Year (Ye) represented the 4 years of the study (fixed). Heteroscedasticity was checked by Cochran's test. Cochran's Test $C = 0.1655$ (not significant).

^aPost hoc tests: $F = 6.69$; $P < 0.001$.

^bFactors that were pooled to create the denominator for testing Ye × Lo: NTZ vs. Far.

Fig. 2. Variation in the mean abundances of lobsters (*Homarus gammarus*); (a) legal-sized lobsters (carapace length, CL \geq 90 mm) and (b) sublegal lobsters (CL $<$ 90 mm) among NTZ, Near Control (Con 1, Con 2), and Far Control (North Devon, South Wales) locations in years 2004 to 2007. Each bar represents the mean abundance (\pm SE) per string of 10 pots over 5 d of sampling. Open bars are for 2004, hatched bars 2005, light grey bars 2006, and dark grey bars are for 2007.



interaction of Ye \times Lo: NTZ vs. Far was significant (Table 4). From 2004 to 2007, the mean abundance of sublegal lobsters increased by 97% within the NTZ and by 140% in Near Control locations (Fig. 2b). The large simultaneous increases in abundance in the NTZ and Near Control locations caused a significant result for the factor Year in the ANOVA for these data (Table 3).

Because this pattern of results indicated potential spillover of sublegal lobsters from the NTZ, it was appropriate to assess the magnitude of this apparent effect by comparing trends in Near versus Far Control locations. For consistency with the preceding analyses of sublegal lobsters, data were averaged across times within each year prior to analysis, and the intended ANOVA model was modified accordingly. This analysis (specifically, the result for Distance \times Year) showed that the increase in mean abundance within Near Control locations was statistically significant (Table 5) relative to the change in mean abundance within Far Control locations (Fig. 2b).

Abundance of velvet crab

The NTZ appeared to reduce the abundance of velvet crabs. Analyses revealed a significant interaction of both Ye \times Lo: NTZ vs. NR and Ye \times Lo: NTZ vs. Far (see supplementary data,² Tables S2 and S3, respectively). From 2004 to 2007, velvet crab abundance decreased by 65% within the NTZ. The test of Ye \times Lo: NTZ vs. Nr was significant because there was an even greater decrease in abundance in Near Control locations (Fig. 3a). Conversely, the significant result for Ye \times Lo: NTZ vs. Far was due to a contrast between declining velvet crab abundance within the NTZ versus generally increasing mean abundance in Far Control locations (Fig. 3a).

Abundance of brown crab

There was no apparent effect of the NTZ on the abundance of brown crab (Fig. 3b). Neither of the critical ANOVA factors for testing potential effects of the NTZ (i.e., Ye \times Lo: NTZ vs. Nr and Ye \times Lo: NTZ vs. Far) were significant (see supplementary data,² Tables S4 and S5, respectively).

Table 3. Asymmetric analysis of variance (ANOVA) of $\ln(x+1)$ -transformed abundances of sublegal lobsters (carapace length, CL < 90 mm) per string of 10 pots for NTZ versus near control locations ($n = 4$).

Source of variation	df	SS	MS	Denominator	Planned tests	
					<i>F</i>	<i>P</i>
<i>Location</i>	2	1.27	0.633			
Lo: NTZ vs. Nr	1	0.87	0.866	Lo: Nr	2.16	ns
Lo: Nr	1	0.40	0.401	Site (Lo: Nr)	0.61	ns
<i>Site (Location)</i>	3	1.52	0.505			
Site (Lo: NTZ)	1	0.20	0.201	Res: NTZ	3.75	ns
Site (Lo: Nr)	2	1.32	0.658	Res: Nr	5.13	<0.01
<i>Year</i>	3	5.87	1.956	Ye×Lo: Nr	11.64	<0.05
<i>Year × location</i>	6	1.03	0.172			
Ye×Lo: NTZ vs. Nr ^a	3	0.53	0.177	Ye×Lo: Nr	1.05	ns
Ye×Lo: Nr	3	0.50	0.168	Ye×Si (Lo: Nr)	2.40	ns
<i>Year×site (Location)</i>	9	1.02	0.113	Residual	1.09	ns
Ye×Si (Lo: NTZ)	3	0.60	0.199	Res: NTZ	3.72	<0.05
Ye×Si (Lo: Nr)	6	0.42	0.070	Res: Nr	0.55	ns
<i>Residual</i>	72	7.44	0.103			
Res: NTZ	24	1.28	0.053			
Res: Nr	48	6.16	0.128			
Total	95	18.15				

Note: Location (Lo) was a random factor with three levels (NTZ, Near Control 1, and Near Control 2), the contrast between NTZ and Control used fixed terms. Site (Si) was a random factor to estimate spatial variance and Year (Ye) represented the 4 years of the study (fixed). Heteroscedasticity was checked by Cochran's test. Cochran's Test $C = 0.2680$ ($P < 0.01$). Largest variance = 0.665, this occurred in Near Control location 2, Site 2 in 2006.

^aPost hoc tests: None available.

Table 4. Asymmetric analysis of variance (ANOVA) of $\ln(x+1)$ -transformed abundances of sublegal lobsters (carapace length, CL < 90 mm) for NTZ versus Far Control locations per string of 10 pots ($n = 4$).

Source of variation	df	SS	MS	Denominator	Planned tests	
					<i>F</i>	<i>P</i>
<i>Location</i>	2	4.09	2.045			
Lo: NTZ vs. Far	1	2.00	2.005	Lo: Far	0.96	ns
Lo: Far	1	2.09	2.086	Site (Lo: Far)	2.12	ns
<i>Site (Location)</i>	3	2.10	0.700			
Site (Lo: NTZ)	1	0.20	0.201	Res: NTZ	3.75	ns
Site (Lo: Far)	2	1.90	0.950	Res: Far	9.70	<0.001
<i>Year</i>	3	0.45	0.151	Ye×Lo: Far	0.99	ns
<i>Year×location</i>	6	2.11	0.352			
Ye×Lo: NTZ vs. Far ^a	3	1.65	0.550	Ye×Lo: Far	3.59	ns
Ye×Lo: Far ^b	3	0.46	0.153	Ye×Si (Lo: Far)	0.32	ns
<i>Year×site (Location)^b</i>	9	3.47	0.385	Residual	4.64	<0.001
Ye×Si (Lo: NTZ)	3	0.60	0.199	Res: NTZ	3.72	<0.05
Ye×Si (Lo: Far)	6	2.87	0.478	Res: Far	4.88	<0.001
<i>Residual</i>	72	5.98	0.083			
Res: NTZ	24	1.28	0.053			
Res: Far	48	4.70	0.098			
Total	95	18.20				

Note: Location (Lo) was a random factor with three levels (NTZ, South Wales, and North Devon), the contrast between NTZ and Far Controls used fixed terms. Site (Si) was a random factor to estimate spatial variance and Year (Ye) represented the 4 years of the study (fixed). Heteroscedasticity was checked by Cochran's test. Cochran's Test $C = 0.1101$ (not significant, ns).

^aPost hoc tests: $F = 1.682$; P , ns.

^bFactors that were pooled to create the denominator for testing Ye × Lo: NTZ vs. Far.

Abundance of spider crab

Spider crab abundance varied from year to year and spatially, but not as a result of the NTZ. Analyses revealed a significant interaction of Ye × Lo: NTZ vs. Nr (see supple-

mentary data,² Table S6), but not of Ye × Lo: NTZ vs. Far (see supplementary data,² Table S7). The significant result for Ye × Lo: NTZ vs. Nr was attributable to large differences in relative abundance between the NTZ and Near Con-

Table 5. Analysis of variance (ANOVA) of $\ln(X + 1)$ -transformed abundances of sublegal lobsters (carapace length, CL < 90 mm) per string of 10 pots for Near Control locations versus Far Control locations ($n = 4$).

Source	df	SS	MS	Denominator	<i>F</i>	<i>P</i>
Distance	1	0.35	0.353	Pooled ms ^a	0.37	ns
Location (Di) ^a	2	2.49	1.244	Pooled ms ^a	1.31	ns
Site (Di×Lo) ^a	4	3.21	0.804	Res	7.11	<0.001
Year	3	2.70	0.901	Pooled ms ^b	3.81	<0.05
Distance×year	3	2.45	0.818	Pooled ms ^b	3.46	<0.05
Year×location (Di) ^b	6	0.96	0.161	Pooled ms ^b	0.68	ns
Year×site (Di×Lo) ^b	12	3.29	0.274	Res	2.42	<0.01
Residual	96	10.86	0.113			
Total	127	26.32				
Pooled ms ^a	6	5.70	0.950			
Pooled ms ^b	18	4.25	0.236			

Note: Di, distance; Lo, location. Cochran's Test $C = 0.1837$ ($P < 0.05$). Largest variance = 0.665, this occurred in Near Control location 2, Site 2, in 2006. Superscripted letters indicate factors that were pooled to create the denominators for *F* tests.

trol locations in 2006 and 2007 (Fig. 3c). Abundance was greatest in Near Control locations in both cases. Compared with the NTZ, the mean abundance of spider crabs in Near Control locations was 261% greater in 2006 and 434% greater in 2007. Whilst the relative abundance of spider crabs in Near Control locations increased from 2006 to 2007, there was a general decline in the absolute abundance in all locations at Lundy (Fig. 3c).

The sizes of lobster and crabs (Hypothesis 3)

Only lobster and brown crab showed changes in size that indicated an influence by the Lundy NTZ. In lobsters, this evidence was confined to legal-sized lobsters.

Sizes of legal-sized lobsters

There was an increase in the mean size of legal-sized lobsters in the NTZ and declining mean sizes in Near and Far Control locations (Fig. 4a). This interpretation arose from significant interactions of $Ye \times Lo$: NTZ vs. Nr (Table 6a) and $Ye \times Lo$: NTZ vs. Far (Table 6b). From 2004 to 2007, the mean size of legal-sized lobsters in the NTZ increased by 5.2%; simultaneously, mean sizes declined by 2.8% in Near Control locations and by 2.1% in Far Control locations (Fig. 4a). By 2007, legal-sized lobsters in the NTZ were on average 9.1% larger than those in Near Control locations and 9.0% larger than those in Far Control locations (Fig. 4a).

Sizes of sublegal lobsters

There was no effect of the NTZ on the sizes of sublegal lobsters (Fig. 4b). Neither of the critical factors for testing potential effects of the NTZ (i.e., $Ye \times Lo$: NTZ vs. Nr and $Ye \times Lo$: NTZ vs. Far) were significant (see supplementary data,² Table S8).

Size of velvet crabs

There was no effect of the NTZ on the sizes of velvet crabs (Fig. 5a). Neither of the critical factors for testing potential effects of the NTZ (i.e., $Ye \times Lo$: NTZ vs. Nr and $Ye \times Lo$: NTZ vs. Far) were significant (see supplementary data,² Table S9).

Size of brown crab

From 2004 to 2007, the mean size of brown crabs within the NTZ increased by 25% (Fig. 5b). There was a significant interaction of $Ye \times Lo$: NTZ vs. Nr (see supplementary data,² Table S10a), but not of $Ye \times Lo$: NTZ vs. Far (see supplementary data,² Table S10b).

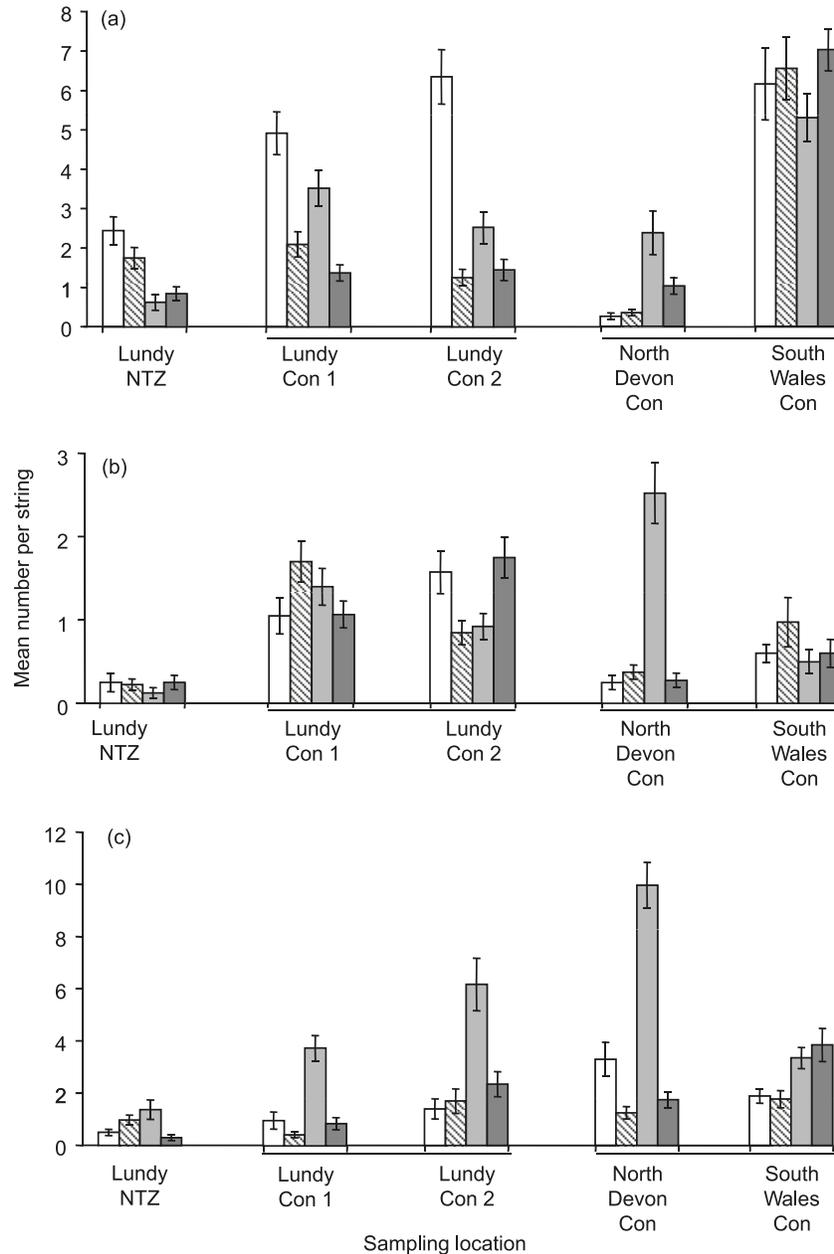
Size of spider crabs

There was no effect of the NTZ on the sizes of spider crabs (Fig. 5c). Neither of the critical factors for testing potential effects of the NTZ (i.e., $Ye \times Lo$: NTZ vs. Nr and $Ye \times Lo$: NTZ vs. Far) were significant (see supplementary data,² Table S11).

Discussion

Four years after the Lundy NTZ was implemented, three species of commercially fished crustaceans showed evidence of population change. Changes were positive in lobster and brown crab (dramatically so in lobster) and negative in velvet crab. Spider crab showed no significant changes. In many studies, lobster populations have been shown to respond rapidly to MPA/NTZ designation (e.g., Edgar and Barrett 1997; Kelly et al. 2000; Barrett et al. 2009); often, as here, in small or moderate-sized areas (1–5 km²) (Childress 1997). The large, rapid increase in lobster abundance in the Lundy NTZ (evident after only 18 months) is consistent with responses noted in Tasmania and New Zealand (Pande et al. 2008; Barrett et al. 2009). Other studies (e.g., Rowe 2002) have shown limited or no effects of MPA establishment on lobster populations. A major problem with many of these studies, however, is that they are based on single inside/outside contrasts (e.g., Follesa et al. 2008). As Barrett et al. (2009) pointed out, this weak experimental design can distort the apparent effects of MPA establishment and lead to elevated Type I or II error rates. For example, the latter may come about when the users of a marine area relinquish a less productive area (Barrett et al. 2009), and this is then compared with an area that is intrinsically more productive. Under this scenario, the tests for a control versus impact interaction will not show a significant result, even if the protected area is recovering. The only way that the re-

Fig. 3. Variation in the mean abundances of (a) velvet crab (*Necora puber*), (b) brown crab (*Cancer pagurus*), and (c) spider crab (*Maja squinado*) among NTZ, Near Control (Con 1, Con 2) and Far Control (North Devon, South Wales) locations in years 2004 to 2007. Each bar represents the mean abundance (\pm SE) per string of 10 pots over 5 days of sampling. Open bars are for 2004, hatched bars 2005, light grey 2006, and dark grey bars are for 2007.



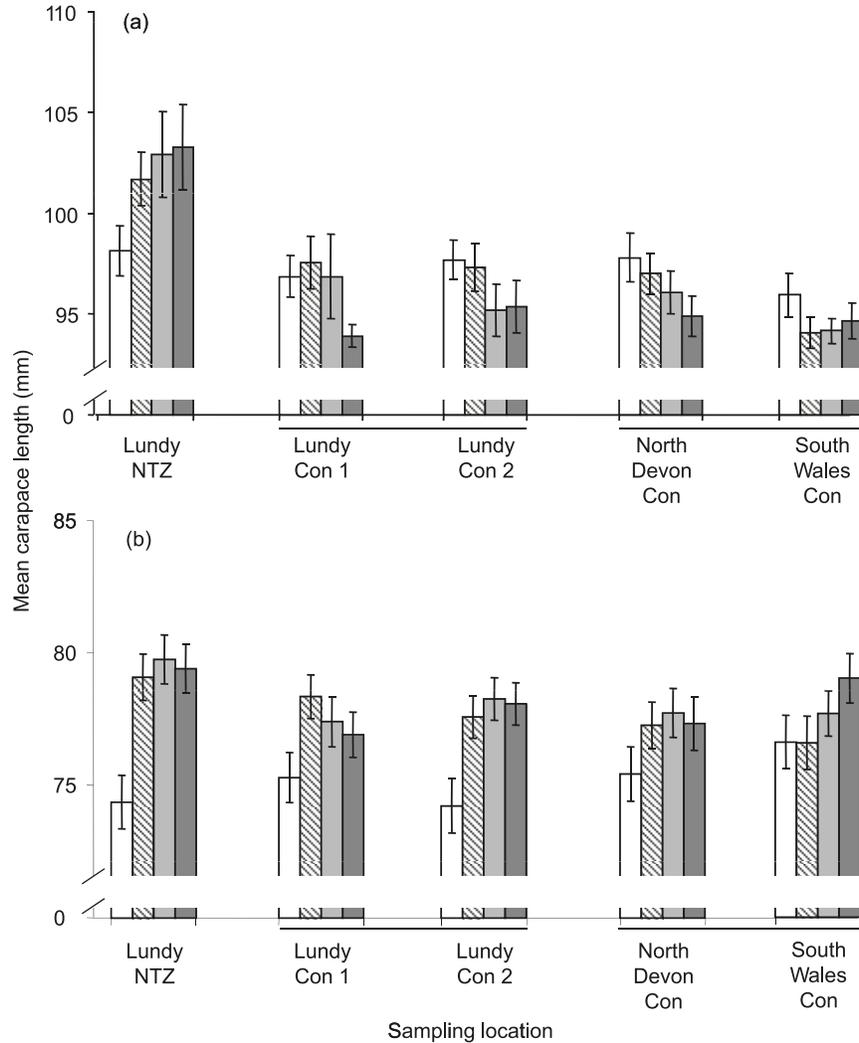
covery would be detected is if change in the protected area is tested against the average changes in a number of representative unprotected areas. Ideally, such asymmetric tests should involve a before, versus after contrast (i.e., the beyond-BACI approach; Underwood 1994), but asymmetric tests of post-impact changes can also detect recovery, as we have done here.

Abundance and size of legal-sized lobsters

The trend of increasing abundance and size of legal-sized lobsters within the Lundy NTZ is consistent with increased survivorship of resident individuals, owing to the cessation of fishing. Abundance may also have increased via large

lobsters migrating into the NTZ and accumulating in vacant territories (owing to previous fishing mortality). This is suggested on the basis that *H. gammarus* are said to be facultatively territorial or migratory according to size-related habitat requirements (Pawson 1995). We have evidence of this from a previous study of tagged adult lobsters in which some individuals stayed in the area where they were first captured for up to 1 year, whilst others moved 12.5–14 km in only 2–6 weeks (M.G. Hoskin, unpublished data). Given the large mean sizes of legal-sized lobsters in the NTZ (98.2 mm CL in 2004, increasing to 103.3 mm CL in 2007) and the growth-rate of *H. gammarus* (Bannister et al. 1994; Sheehy et al. 1999), it is unlikely that individuals arriving as

Fig. 4. Variation in the mean size of lobsters *Homarus gammarus*; (a) legal-sized lobsters (carapace length, CL ≥ 90 mm) and (b) sublegal lobsters (CL < 90 mm) among NTZ, Near Control (Con 1, Con 2), and Far Control (North Devon, South Wales) locations in years 2004 to 2007. Each bar represents mean size (\pm SE) over 5 days of sampling per year. For legal-sized lobsters, plotted means were calculated from sample sizes of $n = 31$ for NTZ and Far Control locations, and $n = 22$ for Near Control locations. For sublegal lobsters, plotted means were calculated from sample sizes of $n = 78$ for NTZ and Near Control locations, and $n = 75$ for Far Control locations. Open bars are for 2004, hatched bars 2005, light grey 2006, and dark grey bars are for 2007.



post-larvae in the NTZ after its designation contributed to increased abundance in this size-class.

Our interpretation that legal-sized lobsters exhibited an effect of the Lundy NTZ only 18 months after its designation (i.e., 205% greater abundance in the NTZ compared with fished areas in 2004) was based on there being no prior evidence from local fishermen that lobsters were naturally prolific in this area. This was one of the main reasons why they agreed to relinquish this area for the NTZ. Without “before” data, however, we cannot demonstrate conclusively that the difference we detected in 2004 was not a pre-existing natural difference.

Potential spillover of sublegal lobsters

If the increase in the abundance of sublegal lobsters within and adjacent to the Lundy NTZ represents enhancement and spillover due to the NTZ, it is not immediately obvious how this may have occurred. The usual mechanism for

spillover is that reproductive biomass increases within a no-take reserve, resulting in greater production and net export of offspring from the reserve compared with similar fished areas (Roberts and Polunin 1991; Dugan and Davis 1993; Guénette et al. 1998). Whilst there is good reason to expect increased reproductive output from the NTZ (see Tully et al. 2001 for an analysis of the positive relationship between size and fecundity in *H. gammarus*), it is unlikely that this could have produced the results seen here. This is because the enhanced population of sublegal lobsters mainly comprised individuals of a size (mean CL 77.4 ± 0.3 mm) that is appreciably larger, given typical growth rates (Bannister et al. 1994; Sheehy et al. 1999), than would be expected if they had only settled since designation.

Since enhanced larval recruitment is unlikely to have caused the increase in sublegal lobsters in the NTZ and adjacent areas, we propose an alternate model involving the indirect effect of other species negatively affected by an

Table 6. Asymmetric analysis of variance (ANOVA) of the mean sizes of legal-sized lobsters (carapace length, CL \geq 90 mm) for (a) NTZ versus Near Control locations ($n = 22$) and (b) NTZ versus Far Control locations ($n = 31$).

Source of variation	df	SS	MS	Denominator	Planned tests		Post-hoc tests	
					<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
(a) NTZ versus Near Control locations								
<i>Location</i>	2	1507.30	753.652					
Lo: NTZ vs. Nr	1	1506.94	1506.939	Lo: Nr	4144.50	<0.05	43.77	<0.001
Lo: Nr ^d	1	0.36	0.364	Res: Nr	0.01	ns		
<i>Year</i>	3	107.33	35.778	Ye \times Lo: Nr	1.73	ns		
<i>Year</i> \times <i>location</i>	6	537.94	89.657					
Ye \times Lo: NTZ vs. Nr	3	475.98	158.662	Ye \times Lo: Nr	7.68	ns	4.58	<0.01
Ye \times Lo: Nr ^{a,b}	3	61.95	20.652	Res: Nr	0.59	ns		
<i>Residual</i>	252	14217.18	56.417					
Res: NTZ	77	8116.82	105.413					
Res: Nr ^{a,b}	175	6100.36	34.859					
Total	263	16369.76						
Note: Cochran's Test $C = 0.2119$ ($P < 0.01$). Largest variance = 143.49, this occurred in the NTZ in 2006.								
(b) NTZ versus Far Control locations								
<i>Location</i>	2	3106.18	1553.089					
Lo: NTZ vs. Far	1	2916.30	2916.302	Lo: Far	15.36	ns	No test	
Lo: Far	1	189.88	189.875	Res: Far	6.72	$P < 0.05$		
<i>Year</i>	3	8.74	2.913	Ye \times Lo: Far	0.15	ns		
<i>Year</i> \times <i>location</i>	6	713.80	118.967					
Ye \times Lo: NTZ vs. Far	3	655.72	218.575	Ye \times Lo: Far	11.29	$P < 0.05$	7.76	<0.001
Ye \times Lo: Far ^c	3	58.08	19.359	Res: Far	0.68	ns		
<i>Residual</i>	360	18587.10	51.631					
Res: NTZ	113	11603.68	102.687					
Res: Far ^c	247	6983.42	28.273					
Total	371	22415.81						

Note: Cochran's Test $C = 0.2281$ ($P < 0.01$). Largest variance = 141.35, this occurred in the NTZ in 2007.

^dFactors that were pooled to create the denominator for testing Lo: NTZ vs. Nr.

^bFactors that were pooled to create the denominator for Ye \times Lo: NTZ vs. Nr.

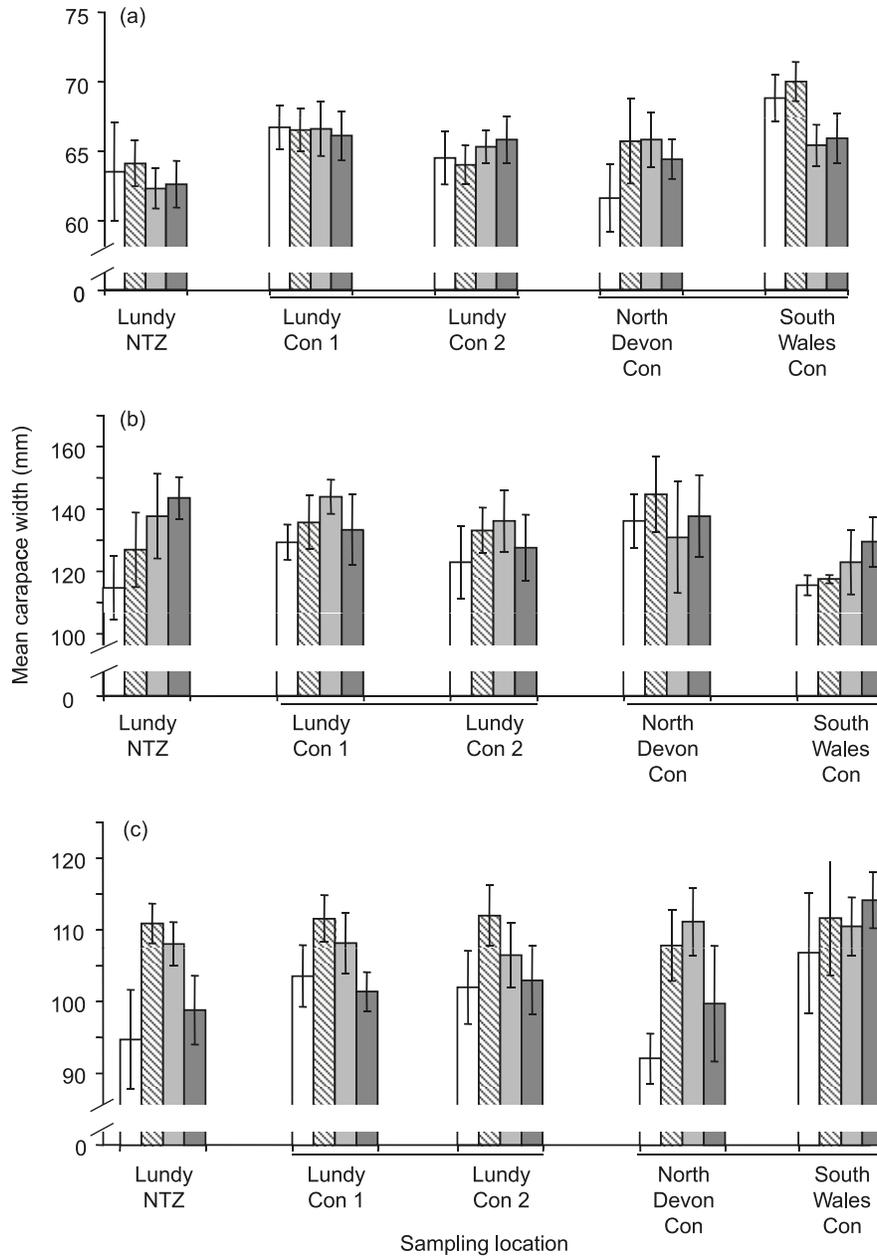
^cFactors that were pooled to create the denominator for testing Ye \times Lo: NTZ vs. Far.

increase in larger lobsters, possibly through changes in diet selection (Sainte-Marie and Chabot 2002). The other species of interest here is the velvet crab. There are two salient strands of information: (i) the increase in lobsters within and adjacent to the NTZ was accompanied by a significant decline in the abundance of velvet crabs in these areas, and (ii) both homarid lobsters and portunid crabs (including *N. puber*) include other smaller, hard-shelled crustaceans in their diet (Choy 1986; Freire et al. 1996; Cobb and Castro 2006) and may compete for food if there is no great disparity in body-size (Williams et al. 2006). In light of these facts, we propose that the general enhancement of sublegal lobsters at Lundy arose as follows: (i) increased survivorship and growth of legal-sized lobsters in the NTZ caused increased predation on velvet crabs; (ii) this reduced competition of velvet crabs with sublegal lobsters, initiating a decline in the former and an increase in the latter that, to some extent, became self-reinforcing. A predictable consequence of this would be spillover of sublegal lobsters from the NTZ into adjacent areas (and associated declines in velvet crabs in these areas). Juvenile homarid lobsters are solitary and aggressive towards each other (potentially cannibalistic), hence they require increasing amounts of space as they grow (Wahle and Fogarty 2006). Within the NTZ, growth of juveniles will also have brought them into

competition with the increasing population of legal-sized adults. An effective way for juvenile lobsters to avoid intra-specific competition would be to move to areas of progressively lower density as they grow. Consistent with the spillover model, the period of greatest increase in the abundance of sublegal lobsters in the NTZ (2004–2005) preceded that in adjacent areas (2005–2006). Some enhancement of sublegal lobsters in areas adjoining the NTZ may also have occurred via increased predation of velvet crabs in these areas by legal-sized lobsters making feeding excursions beyond the NTZ. Various tagging studies of *H. gammarus* (e.g., Bannister et al. 1994; Jensen et al. 1994; Smith et al. 1998) have shown that adult lobsters are quite capable of moving the required distance (up to 5 km) and there is some evidence of homing (van den Meeren 1997). This is unlikely to have been a significant factor, however, as legal-sized lobsters resident in the NTZ would be vulnerable to fishing during such excursions, which is not indicated by their increased abundance and size.

Finally, it must be reiterated that whilst increased abundance of sublegal lobsters within and adjacent to the NTZ is indicative of a form of spillover, it does not prove that spillover has occurred. A critical requisite of the spillover model is that populations in reserves exhibit greater net export of migrants than populations in fished areas. Until this

Fig. 5. Variation in the mean sizes (carapace width, CW) of (a) velvet crab (*Necora puber*), (b) brown crab (*Cancer pagurus*), and (c) spider crab (*Maja squinado*) among NTZ, Near Control (Con 1, Con 2), and Far Control (North Devon, South Wales) locations in years 2004 to 2007. Each bar represents the mean size (\pm SE) over 5 days of sampling per year. Plotted means were calculated from samples sizes of $n = 10$ for velvet crab, $n = 5$ for brown crab, and $n = 12$ for spider crab. Open bars are for 2004, hatched bars 2005, light grey 2006, and dark grey bars are for 2007.



has been experimentally tested for sublegal lobsters at Lundy, it cannot be concluded that spillover has occurred. Goñi et al. (2006) cautioned that researchers evaluating MPAs should not claim to have detected spillover without first having done this test. Their review of the small number of studies that have measured immigration and emigration for reserve versus nonreserve populations show that spillover is often not demonstrated.

Abundance of velvet crab

An alternative explanation for the decline of velvet crabs is the possibility of an artefact of sampling. In locations where pots were catching increasing numbers of lobsters,

fear of predation may have reduced velvet crabs' willingness to enter pots and (or) made them more likely to exit if already inside (relatively easy for velvet crabs given their swimming ability and small size). Either response would result in a false appearance of declining abundance of velvet crabs in areas with high abundance of lobsters. On balance, however, we believe that such sampling artefacts did not contribute appreciably to reduced catches of velvet crabs within and adjacent to the NTZ, mainly based on our observation that both species were frequently caught in the same pot and that evidence of lobsters eating velvet crabs within pots was rare.

Abundance and size of brown crab

Brown crab, like lobster, showed a significant increase in average size within the NTZ compared with Near- and Far-Control locations. This suggests that they were able to live longer and (or) grow larger in the NTZ than in fished areas. If that were the case, however, brown crab might also have been expected to have shown enhanced abundance in the NTZ (as did lobster), but they did not. In fact, brown crabs were typically least abundant within the NTZ. Their failure to increase within the NTZ may have been due to low levels of recruitment and (or) immigration to the NTZ during the study, or because increasing body-size within the NTZ may have suppressed positive effects on abundance by increasing the average size of territory required per individual. Brown crab may also have failed to increase in abundance within the NTZ due to competition and (or) predation of small individuals by large lobsters. *Cancer* sp. occurs in the diet of lobsters (Sainte-Marie and Chabot 2002), but may escape predation if individuals attain a certain refuge size.

On a final note of caution, it is important to recognise that the conclusion of a significant increase in the size of brown crab within the NTZ derived from an ANOVA test with a sample size (n) of only five individuals. This small sample size was attributable to the low abundance of brown crabs within the NTZ (on average, only one individual per 40 pots) and the requirement of ANOVA for equal replication for all factor levels. Given the small sample size for this test, it is quite likely that what appears to be evidence of an effect of the NTZ on the size of brown crab was actually a statistical artefact attributable to sampling variation.

Abundance and size of spider crab

Spider crabs showed no changes in abundance or size that indicated an effect of the Lundy NTZ. This is probably because of the small size of the NTZ (~ 4 km²) and the fact that spider crabs are highly migratory throughout their lives, moving between inshore and offshore areas on a seasonal basis (Pawson 1995). Thus, individual spider crabs are unlikely to have spent sufficient time within the NTZ to have gained any lasting benefit that was detectable at the population level. The common view is that fished species can only benefit from a NTZ if it is large relative to the scale of migration (Hilborn 2003; Roberts et al. 2003).

An NTZ can only induce change when the species inhabiting it satisfy two criteria: first, the local population must have been significantly impacted by fishing prior the NTZ (either directly via harvesting, or indirectly via by-catch mortality or gear-related disturbance of the environment); and second, the species must have a life history and ecology that allows the population benefits of protection (i.e., increased survival and individual growth) to accumulate within the NTZ. Based on results thus far, it would appear that these criteria were met convincingly for lobster (*H. gammarus*), but for none of the other species that were monitored. A key question arising from our work is which models may explain the increased abundance of sublegal lobsters in adjacent fished areas (potential spillover)? Research programmes examining habitat occupancy versus indirect / interspecific interactions will prove useful in this regard.

This study has clearly shown a very rapid recovery of a lobster population from fishing. The Lundy NTZ is small

by comparison with many others elsewhere in the world. Thus a key conclusion is that small reserves can have conservation benefits, and in some populations these benefits can appear rapidly. The Lundy NTZ was established for conservation purposes so the possibility that the reserve may be having fishery benefits via spillover into fished areas is an added bonus, not the primary aim of the NTZ. The results from this study are more robust than many others, since the sampling design was capable of distinguishing many different types of spatial and (or) temporal interactions, as required by the hypothesis that a NTZ promotes recovery (change in populations over time) relative to other places (spatial interactions). Thus we suggest that in monitoring the success of other unreplicated NTZs, regulatory/funding agencies require the use of asymmetrical analytical models. If this is done to test explicit, appropriate predictions of the consequences of MPA designation, then effectiveness (or otherwise) may be unambiguously determined.

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References

- Allison, G.W., Lubchenco, J., and Carr, M.H. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* **8**: S79–S92.
- Bannister, R.C.A., Addison, J.T., and Lovewell, S.R.J. 1994. Growth, movement, recapture-rate and survival of hatchery-reared lobsters (*Homarus gammarus* Linnaeus, 1758) released into the wild on the English east coast. *Crustaceana*, **67**(2): 156–172. doi:10.1163/156854094X00530.
- Barrett, N.S., Buxton, C.D., and Edgar, G.J. 2009. Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. *J. Exp. Mar. Biol. Ecol.* **370**(1–2): 104–119. doi:10.1016/j.jembe.2008.12.005.
- Bennet, D.B., and Lovewell, S.R.J. 1977. The effects of pot immersion time on catches of lobsters, *Homarus gammarus* (L.) in the Welsh coast fishery. *CEFAS Tech. Rep.* **36**: 1–4. Available from www.cefas.co.uk/publications/techrep/tech36.pdf.
- Childress, M.J. 1997. Marine reserves and their effects on lobster

- populations: report from a workshop. *Mar. Freshw. Res.* **48**(8): 1111–1114. doi:10.1071/MF97167.
- Choy, S.C. 1986. Natural diet and feeding habits of the crabs *Lio-carcinus puber* and *L. holosatus* (Decapoda, Brachyura, Portunidae). *Mar. Ecol. Prog. Ser.* **31**: 87–99. doi:10.3354/meps031087.
- Claudet, J., Osenberg, C.W., Benedetti-Cecchi, L., Domenici, P., García-Charton, J.A., Pérez-Ruzafa, A., Badalamenti, F., Bayle-Sempere, J., Brito, A., Bulleri, F., Culioli, J.M., Dimech, M., Falcón, J.M., Guala, I., Milazzo, M., Sánchez-Meca, J., Somerfield, P.J., Stobart, B., Vandeperre, F., Valle, C., and Planes, S. 2008. Marine reserves: size and age do matter. *Ecol. Lett.* **11**(5): 481–489. doi:10.1111/j.1461-0248.2008.01166.x. PMID: 18294212.
- Cobb, J.S., and Castro, K.M. 2006. *Homarus* species. In *Lobsters: biology, management, aquaculture, and fisheries*. Edited by B.F. Phillips. Blackwell Publishing Ltd., Oxford, UK. pp. 310–339.
- Dankel, D.J., Skagen, D.W., and Ulltang, O. 2008. Fisheries management in practice: review of 13 commercially important fish stocks. *Rev. Fish Biol. Fish.* **18**(2): 201–233. doi:10.1007/s11160-007-9068-4.
- Dugan, J.E., and Davis, G.E. 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* **50**(9): 2029–2042. doi:10.1139/f93-227.
- Edgar, G.J., and Barrett, N.S. 1997. Short term monitoring of biotic change in Tasmanian marine reserves. *J. Exp. Mar. Biol. Ecol.* **213**(2): 261–279. doi:10.1016/S0022-0981(96)02769-4.
- Follesa, M.C., Cuccu, D., Cannas, R., Cabiddu, S., Murenu, M., Sabatini, A., and Cau, A. 2008. Effects of marine reserve protection on spiny lobster (*Palinurus elephas* Fabr., 1787) in a central western Mediterranean area. *Hydrobiologia*, **606**(1): 63–68. doi:10.1007/s10750-008-9346-8.
- Francini-Filho, R.B., and Moura, R.L. 2008. Evidence for spillover of reef fishes from a no-take marine reserve: An evaluation using the before-after control-impact (BACI) approach. *Fish. Res.* **93**(3): 346–356. doi:10.1016/j.fishres.2008.06.011.
- Freire, J., Sampredo, M.P., and Gonzalez-Gurriaran, E. 1996. Influence of morphology and biomechanics on diet selection in three portunid crabs. *Mar. Ecol. Prog. Ser.* **137**: 111–121. doi:10.3354/meps137111.
- Glasby, T.M. 1997. Analysing data from post-impact studies using asymmetrical analyses of variance: A case study of epibiota on marinas. *Aust. J. Ecol.* **22**(4): 448–459. doi:10.1111/j.1442-9993.1997.tb00696.x.
- Goñi, R., Quetglas, A., and Reñones, O. 2006. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar. Ecol. Prog. Ser.* **308**: 207–219. doi:10.3354/meps308207.
- Guénette, S., Lauck, T., and Clark, C. 1998. Marine reserves: from Beverton and Holt to the present. *Rev. Fish Biol. Fish.* **8**(3): 251–272. doi:10.1023/A:1008859130275.
- Halpern, B.S., and Warner, R.R. 2002. Marine reserves have rapid and long lasting effects. *Ecol. Lett.* **5**(3): 361–366. doi:10.1046/j.1461-0248.2002.00326.x.
- Halpern, B.S., Gaines, S.D., and Warner, R.R. 2004. Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecol. Appl.* **14**(4): 1248–1256. doi:10.1890/03-5136.
- Hilborn, R. 2003. Marine reserves: the best option for our oceans? *Front. Ecol. Environ.* **1**: 497–498.
- Jensen, A.C., Collins, K.J., Free, E.K., and Bannister, R.C.A. 1994. Lobster (*Homarus gammarus*) movement on an artificial reef: the potential use of artificial reefs for stock enhancement. *Crustaceana*, **67**(2): 198–211. doi:10.1163/156854094X00567.
- Kelly, S., Scott, D., MacDiarmid, A.B., and Babcock, R.C. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biol. Conserv.* **92**(3): 359–369. doi:10.1016/S0006-3207(99)00109-3.
- Kinlan, B.P., and Gaines, S.D. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology*, **84**(8): 2007–2020. doi:10.1890/01-0622.
- Lovewell, S.R., Howard, A.E., and Bennett, D.B. 1988. The effectiveness of parlour pots for catching lobsters (*Homarus gammarus* L.) and crabs (*Cancer pagurus* L.). *J. Conseil Int. l'Explor. de la Mer* **44**: 247–252.
- Lubchenco, J., Palumbi, S.R., Gaines, S.D., and Andelman, S. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecol. Appl.* **13**(sp1): S3–S7. doi:10.1890/1051-0761(2003)013[0003:PAHITO]2.0.CO;2.
- Miller, R.J. 1983. Considerations for conducting field experiments with baited traps. *Fisheries*, **8**(5): 14–17. doi:10.1577/1548-8446(1983)008<0014:CFCFEW>2.0.CO;2.
- Myers, R.A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature*, **423**(6937): 280–283. doi:10.1038/nature01610. PMID:12748640.
- Narvarte, M., Gonzalez, R., and Fernandez, M. 2006. Comparison of Tehuelche octopus (*Octopus tehuelchus*) abundance between an open-access fishing ground and a marine protected area: Evidence from a direct development species. *Fish. Res.* **79**(1–2): 112–119. doi:10.1016/j.fishres.2006.02.013.
- Pande, A., MacDiarmid, A.B., Smith, P.J., Davidson, R.J., Cole, R.G., Freeman, D., Kelly, S., and Gardner, J.P.A. 2008. Marine reserves increase the abundance and size of blue cod and rock lobster. *Mar. Ecol. Prog. Ser.* **366**: 147–158. doi:10.3354/meps07494.
- Pawson, M.G. 1995. Biogeographical identification of English Channel fish and shellfish stocks. Fisheries Research Technical Report No. 99, Ministry of Agriculture, Fisheries and Food, Directorate of Fisheries Research, Lowestoft, UK.
- Roberts, C.M., and Polunin, N.V.C. 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.* **1**(1): 65–91. doi:10.1007/BF00042662.
- Roberts, C.M., and Polunin, N.V.C. 1993. Marine reserves: Simple solutions to managing complex fisheries. *Ambio*, **22**: 363–368.
- Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P., and Goodridge, R. 2001. Effects of marine reserves on adjacent fisheries. *Science*, **294**(5548): 1920–1923. doi:10.1126/science.294.5548.1920. PMID:11729316.
- Roberts, C.M., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Ruckelshaus, M., and Warner, R.R. 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecol. Appl.* **13**(sp1): S215–S228. doi:10.1890/1051-0761(2003)013[0215:AOECIS]2.0.CO;2.
- Rowe, S. 2002. Population parameters of American lobster inside and outside no-take reserves in Bonavista Bay, Newfoundland. *Fish. Res.* **56**(2): 167–175. doi:10.1016/S0165-7836(01)00321-6.
- Russ, G.R., and Alcalá, A.C. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Prog. Ser.* **132**: 1–9. doi:10.3354/meps132001.
- Sainte-Marie, B., and Chabot, D. 2002. Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands. *Fish. Bull. (Wash. D. C.)*, **100**: 106–116.
- Sheehy, M.R.J., Bannister, R.C.A., Wickins, J.F., and Shelton, P.M.J. 1999. New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). *Can. J. Fish. Aquat. Sci.* **56**(10): 1904–1915. doi:10.1139/cjfas-56-10-1904.

- Smith, I.P., Collins, K.J., and Jensen, A.C. 1998. Movement and activity patterns of the European lobster, *Homarus gammarus*, revealed by electromagnetic telemetry. *Mar. Biol. (Berl.)*, **132**(4): 611–623. doi:10.1007/s002270050426.
- Tully, O., Roantree, V., and Robinson, M. 2001. Maturity, fecundity and reproductive potential of the European lobster (*Homarus gammarus*) in Ireland. *J. Mar. Biol. Assoc. U. K.* **81**(1): 61–68. doi:10.1017/S002531540100340X.
- Underwood, A.J. 1992. Beyond BACI: The detection of environmental impacts on populations in the real, but variable, world. *J. Exp. Mar. Biol. Ecol.* **161**(2): 145–178. doi:10.1016/0022-0981(92)90094-Q.
- Underwood, A.J. 1994. On beyond BACI: sampling designs that might reliably detect environmental disturbances. *Ecol. Appl.* **4**(1): 3–15. doi:10.2307/1942110.
- Underwood, A.J. 1995. Ecological research and (and research into) environmental management. *Ecol. Appl.* **5**(1): 232–247. doi:10.2307/1942066.
- Underwood, A.J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, UK.
- Underwood, A.J. 1998. Relationships between ecological research and environmental management. *Landsc. Urban Plan.* **40**(1-3): 123–130. doi:10.1016/S0169-2046(97)00104-7.
- van den Meeren, G.I. 1997. Preliminary acoustic tracking of native and transplanted European lobsters (*Homarus gammarus*) in an open sea lagoon. *Mar. Freshw. Res.* **48**(8): 915–922. doi:10.1071/MF97126.
- Wahle, R.A., and Fogarty, M.J. 2006. Growth and development: understanding and modelling growth variability in lobsters. *In Lobsters: biology, management, aquaculture and fisheries*. Edited by B.F. Philips. Blackwell Publishing Ltd., Oxford, UK. pp. 1–44.
- Williams, P.J., Floyd, T.A., and Rosson, M.A. 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). *J. Exp. Mar. Biol. Ecol.* **329**(1): 66–74. doi:10.1016/j.jembe.2005.08.008.
- Winer, B.J., Brown, D.R., and Michels, K.M. 1991. *Statistical Principles in Experimental Design*. McGraw-Hill, New York, N.Y.