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GENERAL APPENDIX TWO

Intact ecosystems are robust to climate forcing

Mark C. Emmerson^{1,2,3}, Eoin, J. O’Gorman^{1,2,3}, Thomas F. Cross^{1,2}, Laura Lyons¹, Ruth M. O’Riordan^{1,2}, Marion Twomey^{1,2}

¹ *Department of Zoology, Ecology and Plant Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland.*

² *Environmental Research Institute, University College Cork, Lee Road, Cork, Ireland.*

³ *These authors contributed equally to this work*

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Note: Materials and Methods follow the Main Text and numbered references are also provided, following the Nature formatting style.

Abstract:

In the face of continued human impacts in the marine environment, marine protected areas are a widely implemented conservation measure worldwide¹. The natural and harvested ecosystems that these reserves protect are bewildering in their complexity. Food webs provide a framework for understanding this complexity by describing the network of feeding relationships between species in ecological communities. These trophic interactions describe the complex flows of matter and energy in a wide range of ecosystems, but despite their complexity, the dynamics of some ecosystems are dominated by just a few top-down trophic interactions^{2,3}. The role of protected areas in mediating the relative importance of predation versus climate driven ecosystem dynamics remains an unresolved and pressing question³. Here, using data from Europe's first marine nature reserve, we show that the dynamics of a key marine herbivore, sea urchins, were driven by climatic forcing prior to protection of the ecosystem. After designation of the marine reserve, we found that the threat of predation by crabs suppresses bottom-up climate driven dynamics in the system. Our results demonstrate that protected ecosystems which are trophically intact are more robust to the effects of climate change.

Keywords: marine reserve, time series, trophic cascade, omnivory, auto regressive moving average model.

Main Text:

A major challenge in ecology is to understand the relative importance of bottom-up (resource-based) and top-down (consumer-based) processes that structure communities and food webs^{4,5}. If natural ecosystems are governed by bottom-up processes then the population size of species is determined by energy and resource availability⁶. In contrast, top down processes determine species population size through the spread of indirect effects, whereby, one species has positive effects on the population size of another species occupying a non-adjacent position within a food chain or food web⁷. These indirect effects are known as trophic cascades, and can be mediated by density², or trait⁸ based effects. In marine ecosystems, cascading effects are well documented⁵, and play an important role in determining food web structure², ecosystem processes⁹, and stability¹⁰.

Climatic factors are known to drive bottom-up processes in many ecosystems¹¹, but the relative importance of climate forcing, recruitment and predation remains poorly understood¹². Marine reserves have dramatic effects on the density, biomass, size, and diversity of the species in the areas protected¹. Here, we investigated the interplay between climate and the establishment of a marine nature reserve in regulating the ecosystem-wide importance of bottom-up and top-down processes. Understanding these effects is a critical issue for ecosystem-based management and marine protection initiatives. Lough Hyne, southwest Ireland, has been intensively studied since the early 1920s, and in 1981 was designated as Europe's first marine nature reserve. We used a 49 year time series (Fig. 1a) describing the population size ($x_t = \log(N_t + 1)$) of the purple sea urchin *Paracentrotus lividus* at Lough Hyne¹³ to investigate the relationship between climate, recruitment and predation. This time series spans the period over which the reserve was established, and enables us to quantify the effects of the reserve on the population dynamics of *P. lividus*, a key herbivore in the ecosystem^{14,15}. In a wide range of marine ecosystems urchin populations are regulated by predators including fish¹⁶, lobsters⁴, and sea otters². These strong regulating effects typically manifest when human impacts in natural systems reduce the number of predators which control urchin abundance¹⁷. At Lough Hyne the role of crabs and starfish in regulating urchin populations has been recognised since the early 1960s^{14,18}.

Prior to 1981, and designation of the marine reserve, the urchin population fluctuated dramatically in size, but after 1981 the population catastrophically

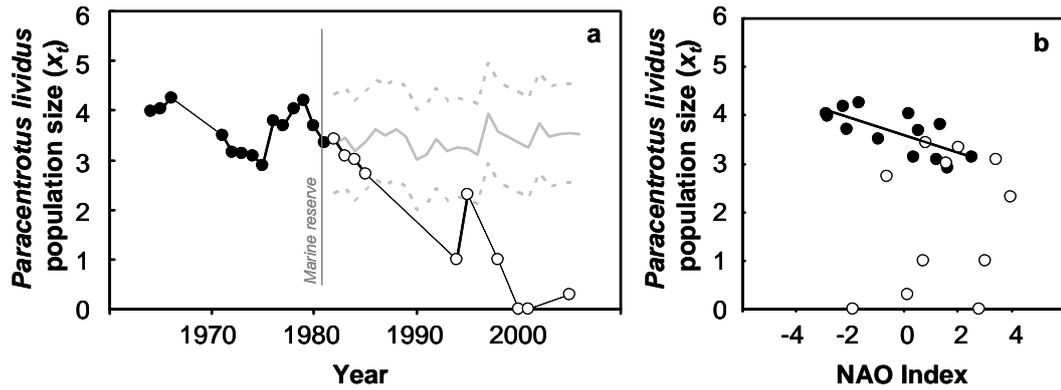


Figure 1. Urchin population changes in Lough Hyne marine reserve. (a) Total counts of *Paracentrotus lividus* ($x_t = \log_{10}(N_t+1)$) from 1963 through to 2006. Prior to 1981 (black circles) the population demonstrates dramatic fluctuations in size. In 1981 Lough Hyne was designated as Europe's first marine nature reserve. After 1981 (white circles) the population size of *P. lividus* declined dramatically. Solid grey lines correspond to the predictions of an Auto Regressive Moving Average (ARMA) model. Dashed grey lines indicate the 99% confidence intervals around the model's predictions. Post 1981 any observed data points that fall outside the dashed lines are significantly different from the model predictions ($p < 0.01$). (b) Correlation between climate (NAO) and urchin population size. Prior to 1981 (black circles) there was a strong and highly significant correlation between NAO and urchin population size (see main text; linear regression: $x_t = -0.18 \times \text{NAO} + 3.58$; $p = 0.004$). After designation of the marine reserve (white circles) this correlation is non-significant.

declined, and has not recovered¹⁹ (Fig. 1a). Before 1981, urchin population size was negatively correlated with the North Atlantic Oscillation (NAO) Index (Pearson correlation: $r = -0.73$, $p = 0.004$; black circles only in Fig. 1b). After 1981, there was no correlation between urchin population size and the NAO (Pearson correlation: $r = 0.27$, $p = 0.42$; white circles only in Fig. 1b). Hence, prior to designation of the marine reserve there is strong evidence for the climate forcing of urchin recruitment¹³, whilst post establishment of the marine reserve, factors other than climate determine urchin population size.

We studied the drivers of population change using a simple model that described the relative influence of climate (NAO) on urchin population dynamics and intrinsic density. To model the interaction between environmental noise and density dependence, we expressed population size, x_t , as a function (f) of previous population sizes and error terms, so that: $x_t = f(x_{t-1}, x_{t-2}, x_{t-3}, \dots) + f(\varepsilon_{t-1}, \varepsilon_{t-2}, \varepsilon_{t-3}, \dots) + \varepsilon_t$, where ε represents additive normally distributed noise with a mean = 0 and variance $\sigma^2 = 1$ ($\varepsilon \sim N(0, \sigma^2)$). To investigate the dependency of x_t on previous population sizes, we fitted a series of auto regressive moving average (ARMA) models²⁰⁻²¹ to the urchin time series between 1971 and 1985 (see Methods). We also included a term for climate (NAO) in the model. Using the Akaike Information Criterion (AIC) we identified the best supported model (AIC = 13.1) as:

$$x_t = a + \beta_1 x_{t-1} + \gamma \text{NAO} + \varepsilon_t.$$

This model contains an intercept (a), one auto regressive (AR) term (β_1), no moving average (MA) terms, and an NAO term (γ) (see Table S1 in Supplementary Information for details of the coefficients). Post 1981, there was a significant difference (t -test: d.f. = 4, $p < 0.01$) between model predictions and observed population counts within the marine reserve (Fig. 1a). This indicates that the decline in urchin population size, after designation of the marine reserve, is not driven by climate and that some other process may be forcing urchin recruitment in the system.

Using historical data^{14,22,23} and recent surveys (see Methods) we quantified how the abundance of key groups at different trophic levels changed over time within Lough Hyne. The velvet swimming crab, *Necora puber*, is an important omnivorous predator that feeds on the purple sea urchin^{18,22}. Since the designation of the Lough as a nature reserve, its abundance (One-sample t -test: $t = 5.02$, d.f. = 7, $p = 0.002$; Fig. 2a) and body mass (One-sample t -test: $t = 4.41$, d.f. = 32, $p < 0.001$) have increased dramatically. In parallel, the population size of purple sea urchins has

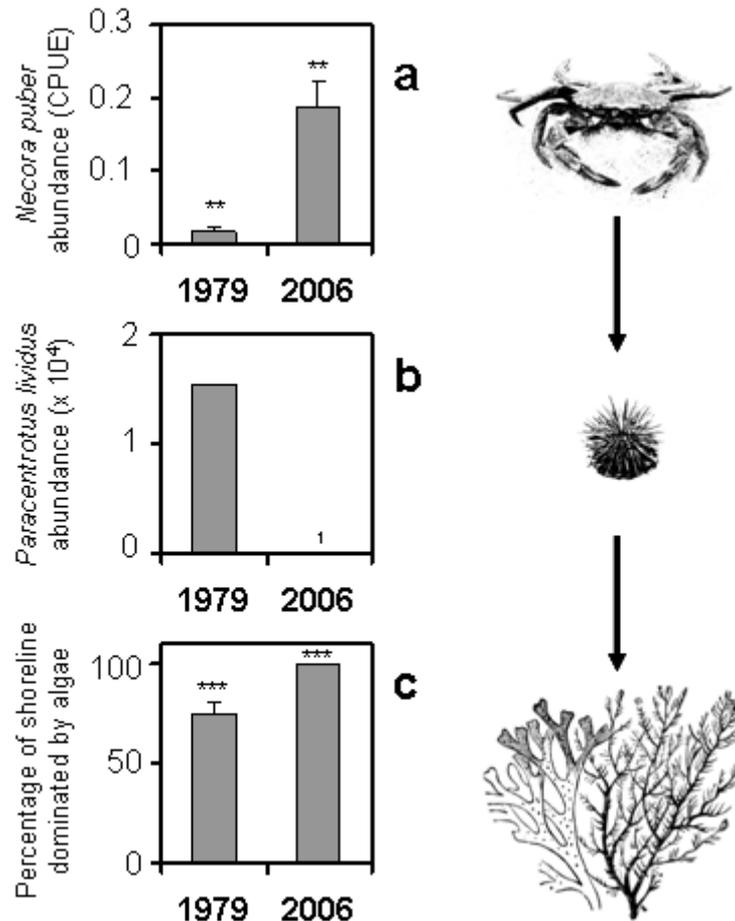


Figure 2. An ecosystem wide trophic cascade. (a) Estimates of population size (CPUE) for the omnivorous crab *Necora puber* in 1979 prior to designation of the marine reserve and in 2006, 25 years after designation of the reserve. There is a highly significant increase in population size of *N. puber* (One-sample *t*-test: $t = 5.02$, d.f. = 7, $p = 0.002$); (b) Estimates of total urchin population size in the South basin of the marine reserve. In 1979 the population was estimated at 15,530 individuals, in 2006 only 1 individual was observed (see Methods for survey design). The *t*-test reported in the main text is a comparison of population sizes before 1981 and after 1981; (c) Percentage of shoreline dominated by algae. In 1979 extensive urchin grazing barrens were observed throughout the marine reserve¹⁴, repeated surveys in 2006 showed disappearance of urchin barrens and a significant increase in the dominance of algae (Welch two-sample *t*-test: $t = 4.43$, d.f. = 44, $p < 0.001$). Error bars indicate s.e.m. ** $P < 0.01$; *** $P < 0.001$.

declined¹⁹ (Welch two sample *t*-test: $t = 4.34$, d.f. = 10.38, $p < 0.002$, Fig. 2b). The indirect effect of crabs on algal growth manifests as a significant increase in shoreline cover of algae (Welch two-sample *t*-test: $t = 4.43$, d.f. = 44, $p < 0.001$; Fig. 2c). A clear trophic cascade emerges after designation of the nature reserve, possibly as a function of increased predator abundance and biomass. In the unprotected system, the dynamics of a key herbivore, which has ecosystem-wide impacts on the structure of the community¹⁴, were driven by climate forcing. In the protected, trophically developed ecosystem, the climate effects on urchin recruitment are dampened by predation, and the community is robust to hemisphere-wide climatic changes measured using the NAO.

To investigate the mechanisms driving the trophic cascade we conducted two simple factorial experiments: an exclusion experiment under realistic environmental conditions within the reserve and a controlled laboratory experiment. Both experiments involved treatments for the presence and absence of sea urchins, refugia, and predation (with an additional treatment for the threat of predation in the laboratory experiment). Notably, the survival rate of sea urchins was mediated by the presence of a refuge (Fig. 3a). In the absence of predation, survival is maximal when a refuge is available, but declines when a refuge is not provided. In the presence of predation, survival is highest when a refuge is available, with complete mortality when no refuge is provided (Fig. 3a). This suggests a fundamental need for shelter by *P. lividus* and may indicate a behavioural change by *P. lividus* in the Lough since the designation of the marine reserve²⁴. Historically, the urchins were found grazing on the upper surface of boulders in their thousands^{14,18}. The urchins still persist in the system at very low densities, but now predominantly hide within the matrix of boulders around the shoreline of the reserve²⁴.

Under controlled laboratory conditions the urchins have an impact on algal biomass (Three-way ANOVA: $F_{1,22} = 5.714$, $p = 0.026$; Fig. 3b). Against a backdrop of natural environmental variation and other grazing pressures (e.g. from micro-gastropods that could enter exclusion cages), this impact disappears (Three-way ANOVA: $F_{1,19} = 0.103$, $p = 0.752$; Fig. 3b). This supports the hypothesis that *P. lividus* no longer plays a pivotal role in regulating algal biomass²⁵ in the system. This is further illustrated by the reduction in algal biomass observed in the presence of the omnivorous *N. puber* in both our laboratory (Three-way ANOVA: $F_{2,22} = 14.743$, $p < 0.001$; Fig. 3c) and field (Three-way ANOVA: $F_{1,19} = 7.266$, $p = 0.014$; Fig. 3c)

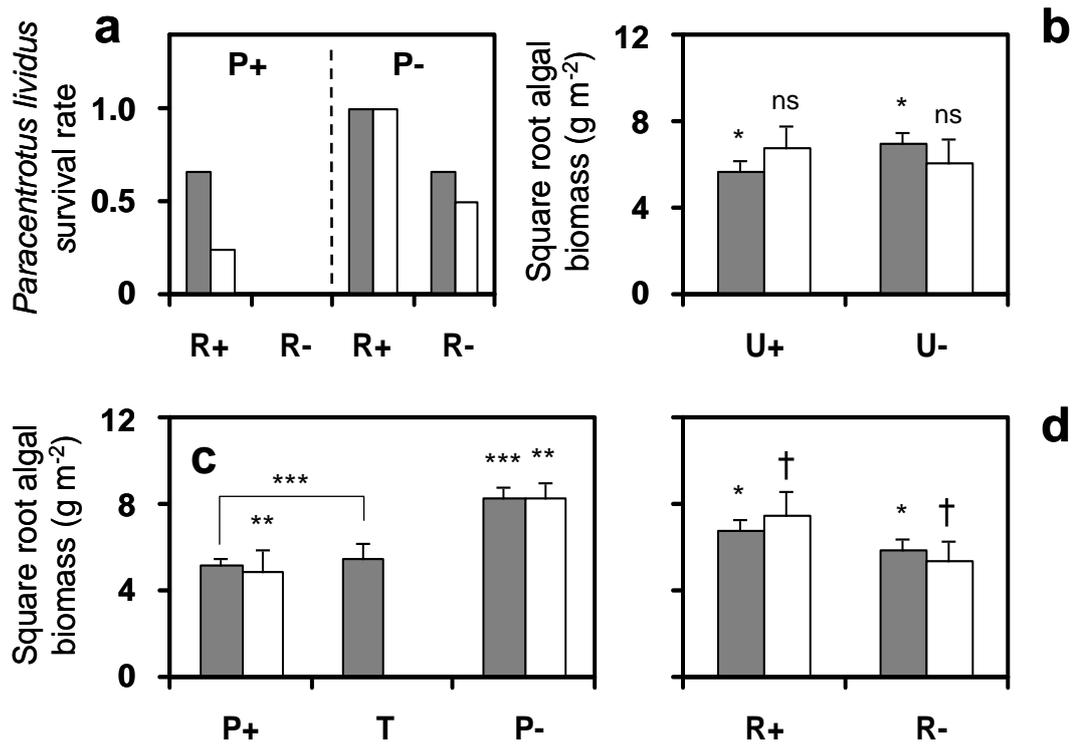


Figure 3. Survival and grazing of sea urchins in the laboratory and field experiments. (a). Survival rate of *Paracentrotus lividus* in the laboratory/field experiments (grey/white bars) is shown in the presence/absence of predation ($P+/P-$) and the presence/absence of a refuge ($R+/R-$). (b-d). Square root of algal biomass (dry weight in $g\ m^{-2}$) in the presence/absence of sea urchins ($U+/U-$), the presence/threat/absence of predation ($P+/T/P-$) and the presence/absence of a refuge ($R+/R-$). Results for the laboratory and field experiments are represented by grey and white bars respectively. In (b), (c), and (d), error bars indicate s.e.m † $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

experiments. Importantly, this suggests that in the absence of alternative prey resources, generalist omnivores such as *N. puber* can suppress algal biomass by direct herbivory²⁶.

The negative effect of refugia on sea urchin grazing is clear in our controlled laboratory experiment. When no refuge was provided, sea urchins significantly reduced algal biomass, but in the presence of a refuge, sea urchins had no impact on algal biomass (Three-way ANOVA: urchin×refuge, $F_{1,22} = 4.591$, $p = 0.043$; Fig. 4a). This experiment illustrates that the presence of disabled predators stimulates consumption by herbivores (Fig. 4b). This scenario does not occur within the marine reserve^{18,22}. When predation is possible, the crabs switch their diet from algae to sea urchins²⁵, leading to a reduction in the overall level of grazing (Three-way ANOVA: urchin×crab, $F_{2,22} = 5.568$, $p = 0.011$; Fig. 4b). These results suggest a combination of both density² and trait mediated⁸ trophic cascades within the marine reserve, resulting in a positive ecosystem wide impact on algal biomass.

Our results suggest that in the absence of protection the dynamics of the Lough Hyne marine reserve were regulated by bottom-up processes, here climate forcing. After designation of the marine reserve, the trophic structure of the system developed, with crabs becoming larger and more abundant. The predators produced a trophic cascade in the system through both a density mediated indirect interaction, suppressing urchin numbers, and a trait mediated indirect interaction, whereby urchins have changed their behaviour and now exploit refugia in the boulder matrix around the reserve. We find that, after the designation of the reserve, the intact system did not undergo dramatic fluctuations in population recruitment. The more trophically developed system is therefore more robust to the effects of climate forcing, with dampened population fluctuations of the prey species. We argue that in the face of future climate change, intact systems will have a greater ability to withstand climate forcing in the face of extreme weather events.

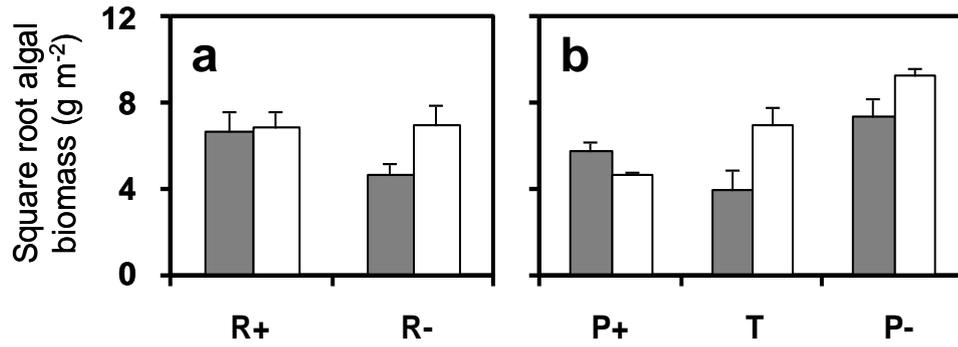


Figure 4. Interaction terms in the analysis of the laboratory experiment. (a-b). Square root of algal biomass (dry weight in g m^{-2}) in the presence/absence of a refuge ($R+$ / $R-$) and the presence/threat/absence of predation ($P+$ / T / $P-$). Presence/absence of sea urchins is indicated by grey/white bars. Error bars indicate s.e.m.

Materials and Methods:

Study site

Europe's first marine nature reserve, Lough Hyne, South West Ireland (50° 29' N, 9° 18' W) was designated in 1981. The Lough is a fully marine lake connected to the sea by a narrow channel called the Rapids. Historically the site has been intensively studied, with in excess of 300 papers published on the ecology of Lough Hyne since the late 1940s. The marine reserve is divided into two basins, North and South, by two interlinked islands. The historical time series of urchin population size within the reserve has been restricted to the South basin, although periodic observations of population size in the North basin are noted in the literature. These observations are not included in the time series detailed here.

Urchin time series

The population size of *Paracentrotus lividus* at the Lough Hyne marine nature reserve has been documented previously in a series of papers^{13,19,22,24,25}. Here we have added population census data to the time series for 2005. For continuity, the census of population size for urchins has employed the original methodology^{22,25}. A boat was rowed around the periphery of the south basin within the marine reserve with two observers at the stern; all urchins observed through a Perspex viewing box were recorded separately by the observers. These counts represent estimates of total population size for the *P. lividus* population at Lough Hyne. The time series presented here spans the periods 1963-1965, 1971-1985, 1994-1995, 1998, 2000-2001, and 2005. Dashed lines in Fig. 1a represent extrapolations between these sampling periods.

Experimental investigation of trophic cascades

To investigate the role of predation in regulating urchin grazing pressure, through changes in behaviour of urchins (trait mediated indirect interactions) or suppression of their numbers (density mediated indirect interactions), we carried out field and laboratory based experiments.

Field experiment

Field-based experimental manipulations were carried out in a small sheltered bay within Lough Hyne. The experiment employed three treatments in a fully factorial experimental design. The treatments were: presence and absence of urchins; presence and absence of refuge; and presence and absence of predators, resulting in eight combinations of urchins, refugia, and predation. Experimental manipulations were applied to 32 subtidal cages (30cm × 30cm × 10cm) arranged in a random block design (4 blocks) between 1 and 3 m depth. Each cage was made from 1cm² galvanised steel mesh. The base of each cage was covered with cleaned stones, taken from the bay in which the experiment was carried out. To provide a refuge, a section of polypropylene pipe (20cm in length × 4.5cm diameter) was fixed into each cage containing the refuge treatment. To allow predators access to cages, a partially open cage was employed that prevented escape by urchins (in laboratory trials), but enabled crabs access to the interior of the cage. For treatments that contained urchins, one individual was collected from the boulder matrix along the shore of the reserve and placed into each cage. To measure the biomass of algae a clean square ceramic tile (10cm × 10cm) was placed into each cage for colonisation by algae at the start of the experiment. There were four replicates of each treatment. The experiment ran for three months (19/07/06 to 11/10/06).

Laboratory experiment

Laboratory-based experimental manipulations were carried out in an experimental flow-through system at Lough Hyne. This system consisted of twelve separate tanks (48 × 20 × 25 cm), each of which had a constant flow and volume of natural sea water. The experimental manipulations were: presence and absence of urchins; presence and absence of a refuge; and presence and absence of predators, plus the presence of a disabled predator – providing the threat of predation. Predators were disabled by tying together the upper and lower dactylus of the chelipeds, preventing the crabs from actively preying on the urchins. The predation treatment in the laboratory experiment therefore had three factor levels. The experiment employed a fully factorial design and employed twelve different combinations of urchin, refuge and predation. The experiment ran in three separate time blocks with one replicate per block over an eight week period (blocks 1, 2, and 3 ran from 23/2/07-17/4/07, 17/4/07-14/6/07, and 14/6/07-13/8/07, respectively). Treatments

were assigned randomly to tanks in each run. At the start of each experimental run we placed one ceramic tile (10 × 10 cm) covered with periphyton (1.35 ± 0.03g dry weight), in the centre of each tank. These tiles were placed in the Lough to accumulate periphyton for a six week period prior to commencement of the experiment. One individual *Paracentrotus lividus* was added to each tank that required the presence of an urchin. One active *Necora puber* was added to each tank that required the presence of predation and one disabled *N. puber* was added to each tank requiring the threat of predation. The refuge again consisted of a polypropylene pipe (20cm in length × 4.5cm diameter). We ran the experiment in three consecutive time blocks of approximately eight weeks each (blocks 1, 2, and 3 ran from 23/2/07-17/4/07, 17/4/07-14/6/07, and 14/6/07-13/8/07, respectively). The treatments were assigned randomly to the twelve tanks at the start of each time block.

Response variables and statistical analysis

At the end of each experiment, we noted the mortality of sea urchins (all crabs survived in the laboratory experiment) and then released all animals back into the Lough. Tiles were removed and dried for 48 hours at 60°C in a drying oven. The tiles were then scraped clean and the dry weight (g) of algal biomass measured. The square root of algal biomass (for both the laboratory and field experiments) was used as the response variable to meet the assumptions of normality and homogeneity of variance. The laboratory and field experiments were analysed using a fully factorial three-way ANOVA.

Auto Regressive Moving Average (ARMA) Model

We employed a forward model selection approach using the Akaike Information Criteria (AIC) to select the best fit model describing the urchin time series as a function of past and present population size (p) and error (q) terms, plus the NAO (see Table S1 in Supplementary Information). For the sake of parsimony and ease of statistical interpretation, we restricted our analysis to simple models including $p = q = 3$ terms (see Table S2 in Supplementary Information)^{20,21}. The best fit model was an ARMA(1,0) model (AIC =13.09) containing one autoregressive term and no moving average terms, plus a term for the NAO (Table S1). Combinations of p and q led to lower AIC values, but in the forward selection process these could not be reached, e.g. the ARMA(0,3) model (Table S2) has an

AIC = 9.66, but in the forward model selection process the ARMA(1,0) has a lower AIC than the ARMA(0,1) model and hence cannot be reached by sequential model selection. All analyses were carried out in *R* (version 2.7.1). Forecasting using the ARMA(1,0) model was achieved using NAO data from 1981 to 2006. Estimates of the standard error (s.e.m) were provided for each year in the forecast. Confidence Intervals were defined as $t_{0.01, [df=4]} \times \text{SE}$ of the model prediction.

Trophic cascades

Historical data providing estimates of population size for the three trophic levels studied were obtained for 1979¹⁴ and 2006 (see below).

Algal abundance

The distribution of urchin barrens within the marine reserve in 1979 is described by Kitching and Thain¹⁴. The limited availability of survey data in this year constrained the estimates of population size for *Necora puber* and *P. lividus* to the year 1979. The shoreline of the marine reserve is divided into 108 sectors to facilitate permanent monitoring of the site. Using a digitised figure from ref.¹⁴ (Fig. 4, p. 524), we calculated the percentage of each Southern basin sector (S1-S17, W19-W25, W35-W37, I10-I19, and E11-E20) affected by urchin barrens. For each sector we then calculated the inverse area dominated by algae. To facilitate comparison, the shoreline of the southern basin was surveyed by sector for urchin grazing patches and barrens (snorkel survey) in 2006. Given the lack of homogeneity of variance between the two years, statistical comparison was made with a Welch two sample *t*-test.

Urchin abundance

Historical estimates of urchin population size are available from the time series in 1979. To facilitate comparison the survey was repeated in 2006 (see above). Because population estimates are based on whole population counts, it was not possible to carry out a formal statistical analysis to compare 1979 and 2006. However, it should be noted that in 1979 the population count was 15,530 individuals, whilst in 2006 only 1 individual was observed during the survey.

Predator abundance

Necora puber population estimates, expressed as Catch Per Unit Effort (CPUE), were obtained from previous studies at Lough Hyne from 1965 and 1971^{22,23}. These historical surveys employed baited lobster pots ($n = 8$) at nine stations in the South basin of Lough Hyne. Pots were deployed for $t = 24$ hours before retrieval. CPUE for each station was calculated as: $CPUE = C / (t \times n)$, where C is the total catch of *N. puber* from eight pots at each station. These surveys were repeated in 2004 and 2006 at the same sites using baited commercial lobster pots. CPUE for the contemporary surveys were calculated in the same way. We then fitted an exponential regression to the data describing estimates of *N. puber* population size (CPUE) as a function of time (exponential regression: $n = 4$, $p = 0.013$, $r^2 = 0.98$, $CPUE = (1.32 \times 10^{69}) \cdot e^{0.0782 \cdot \text{year}}$). Using this equation we then estimated the population size of *N. puber* in 1979 by interpolation (see ref.² for a similar approach). Statistical comparison of historical CPUE estimates and those made in 2006 was undertaken using a one sample t -test.

Using data from ref²³ reporting the size frequency distribution of *N. puber* (carapace width), we converted the mid-point of each size class to weight in grams using an unpublished length-weight relationship defined for *N. puber* at Lough Hyne ($n = 36$, $r^2 = 0.96$, $p < 0.001$, $y = 0.2247x^{3.12}$). Across size classes the mean weight of *N. puber* was calculated for 1971 and used in a one sample t -test to compare against contemporary measures of *N. puber* body mass.

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Author contributions:

M.E. and E.O.G. designed the study, analysed data, and wrote the paper. M.E. and E.O.G. collected data and carried out field and laboratory experiments. M.T. and L.L. assisted with field work. All authors discussed the results and commented on the manuscript.

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Supplementary Information:**Table S1.** Coefficients of the best fit NAO ARMA model (AIC = 13.09) to the urchin time series.

ARMA term	Coefficient	Standard Error
a (Intercept)	3.543	0.135
β_1 (AR1)	0.283	0.517
γ (NAO)	-0.107	0.112

Table S2. AIC values for the various NAO ARMA(p,q) models.

p	q			
	0	1	2	3
0	11.21	13.20	9.66	11.45
1	13.09	14.66	11.25	13.39
2	13.54	15.25	12.60	14.44
3	13.30	15.29	12.73	14.66