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Spillover and competitive exclusion in the crustacean community following the implementation of a marine reserve

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Abstract

Flamanville marine protected area (MPA) located in Normandy, France, was created in 2000 to sustain the local crustacean fishery. In 1985, an annual survey targeting crustacean populations (e.g. European lobster *Homarus gammarus*, edible crab *Cancer pagurus*, and European spider crab *Maja brachydactyla*) that include the future MPA started. The MPA implementation effects were investigated in this study. The sampling design allowed the integration of spatial and temporal covariances to estimate the MPA effects. With respect to the initial objective, the MPA significantly improves the most economically valuable species, *H. gammarus*, abundance. Lobster catch per unit effort increased by 597% in the MPA, whereas outside it only increased by 156%. The MPA creation also led to an increase in lobster size inside the protected area. Furthermore, a few years after the MPA implementation, lobster catches showed a significant non-linear decline with distance from the centre of the reserve, suggesting a spillover effect. However, the edible crab catches were halved following the MPA implementation suggesting an opposite effect. Spider crab abundance seemed unaffected. Finally, the MPA implementation had no effect on edible crab and spider crab sizes. These differential responses appear to result from these species' variable movement and competitive abilities.

Keywords: MPA; lobster; crab; BACI

Introduction

Marine protected areas (MPAs) are areas where extraction activities are banished or at least limited (OECD 2017). MPAs are expected to have benefits within their protection ranges: protected populations growing in abundance, and within these populations individuals living longer and growing larger (Hiddink et al. 2006, Leenhardt et al. 2015, Claudet et al. 2020). Consequently, the protected population's reproductive potential should increase, and juveniles may export to settle outside the boundaries of the MPA (the 'recruitment effect'). As the stocks inside the protected area get closer to the local carrying capacity, adult individuals should also migrate in the surrounding areas (the 'spillover effect') (Russ et al. 2004). Creation of MPA is thus expected to potentially promote the biodiversity inside, and sustain local populations outside of their protection range. However, performances of no-take marine reserves as fisheries management tools strongly depends on the local context and the targeted species (Hilborn et al. 2004). The spatial extent of the MPA, the time which has elapsed since the MPA creation and the complexity of the surrounding habitats (Dugan and Davis 1993, Abesamis and Russ 2005, Vandeperre et al. 2011) might impact its performances. Furthermore, mobile species can move out the reserve boundaries and be caught (Gell and Roberts 2003), so the protection that one MPA offers depends on the migratory behaviours of the species they have been designed for (Hastings and Botsford 1999 , White 2015). Moreover, beyond species specific trajectories, MPAs impacts should also be considered at the community level. Indeed, predation and competition interactions might shift following the reduction of anthropic pressure, leading to an increase of the competitive pressure for the least competitive species (Baskett et al.). An increase in species abundances will lead to the local environment carrying capacity and increased the competition for resources between individuals (Steneck 2006). As such, the positive effects expected from the MPA will be reduced (Bachet et al. 1997).

Lobsters represent an important source of income for the French artisanal fishery in the Channel. The French MPA of Flamanville was implemented in 2000 along the Normandy coast of the western channel, on the initiative of the regional fisheries committee, to preserve this species through all fishing activity ban (Delayat and Legrand 2011). The use of reserves for fishery management has already been proven successful for crustaceans in other areas (Goñi et al. 2006, Høydalsvik 2017). MPA have been shown to promote crustacean biomass enhancement (Davidson et al. 2002, Follesa et al. 2008, Follesa et al. 2011, Moland et al. 2013, 2021) as well as spill-over phenomenon (Nillos Kleiven et al. 2019), which in turn supplies benefits for adjacent fisheries (Harmelin-Vivien et al. 2008). The Flamanville MPA hosts three commercially valuable crustaceans species that are also targeted by fishermen: the European lobster (*Homarus gammarus*), the edible crab (*Cancer pagurus*), and the European spider crab (*Maja brachydactyla*). These species share common ecological

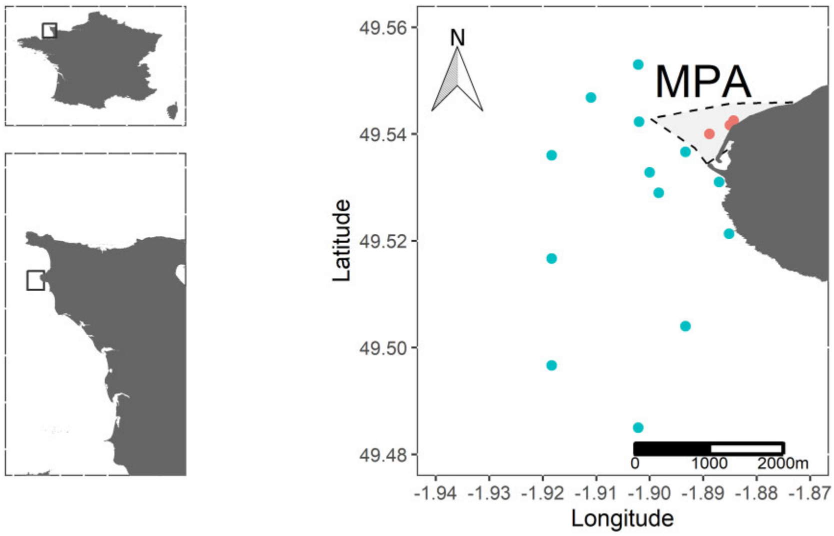

Figure 1. Map of the sampling plan.

features. Their life history includes pelagic larval stage, they have the same feeding regime, and habitat preferences. All these common characteristics imply that they compete with each other for space and food. Conversely, the characteristics of these three species regarding migratory, or sedentary, behaviour, are very different. The European spider crab is a migratory species that return year after year on the coastline (Le Foll 1993, Corgos et al. 2006), the lobster is sedentary (Smith et al. 2001) but can do short-distance seasonal movement (Campbell and Stasko 1986), whereas in edible crab, female individuals were found to carry out shorter migratory journeys than European spider crab to spawn (Hunter et al. 2013). Consequently, the implementation of an MPA might have had impacts not only on lobster, but on the entire crustacean complex.

Before-After-Control-Impact (BACI) is a recommended, yet rarely used, methodology to assess the performances of MPAs (Ojeda-Martinez et al. 2011, Moland et al. 2021). This experimental design is data-demanding, including sample points inside and outside of the MPA as well as a time series starting before and ending after the implementation of the MPA (Smith 2002). Flamanville's MPA benefits from a long-term survey since 1985 (15 years before the implementation) fulfilling these requirements.

Based on the Flamanville's MPA survey data, this paper addresses the following questions: How did the crustacean community develop, across time and space, after the creation of an MPA? Did the effect of the MPA differ between species due to competitive interactions ?

Material and method

Survey design

Sampling scheme definition

Historical time-series of crustacean abundances and sizes were collected during the 68 surveys conducted between 1985 and 2017 (Schlaich and Miossec 2003). Every year, two surveys were conducted during the neap tides occurring in June and September. The data collection continued after the MPA creation in 2000. In June, catch probability was optimal for lobsters and spider crabs, which provided good estimators of abundance for those species. In September, surveys allowed the integration of lobster summer growth and coincided with the period of optimal edible crab catch probability. However, at this period spider crabs have already started their migratory route. Consequently, the autumnal catches were not expected to be representative of spider crab abundances.

Sampling points were located along the coastline, at a distance not greater than 5 kilometres (Fig. 1). From 1985 to 2005, data were collected on 15 sampling locations overall and from 2006 onwards, a 16th point has been added which is located inside the reserve.

Biometric data collection

At each sampling location, one trap-line including 17–30 traps was soaked for 24 h during four consecutive days (Fig. 2). During the hauling of traps lobsters, edible crab and spider crab were counted to estimate a catch per unit effort (CPUE), corresponding to the number of individuals caught per species, traps and day. The length was measured for each individual (carapace length measured between the posterior end of the cephalothorax and the orbital cavity for lobster, transversal length of carapace for edible crab and carapace length measured between the posterior end of the cephalothorax and the point where the anterior spines meet for spider crab) (Schlaich and Miossec 2003).

Data analysis and representation

The survey sampling design was a variant of the Before/After and Control/Impact design (BACI) (Green 1979). Usual BACI design might not be able to account for various types of environmental variability (Underwood 1992). In this study, this limitation was overcome by the use of time and space replicates. Unlike Green's design, those replicates allowed the integration of the inter-annual variability. Furthermore, it explicitly modelled the evolution of the community after the establishment of the reserve, meeting the Underwood requirements. Spatial replication enabled to take in consideration the spatial variability, and the distance from the reserve (Ellis and Schneider 1997). The change of the crustacean community induced by reserve creation was assessed based on two estimators: (1) change in species abundances, (2) change in species

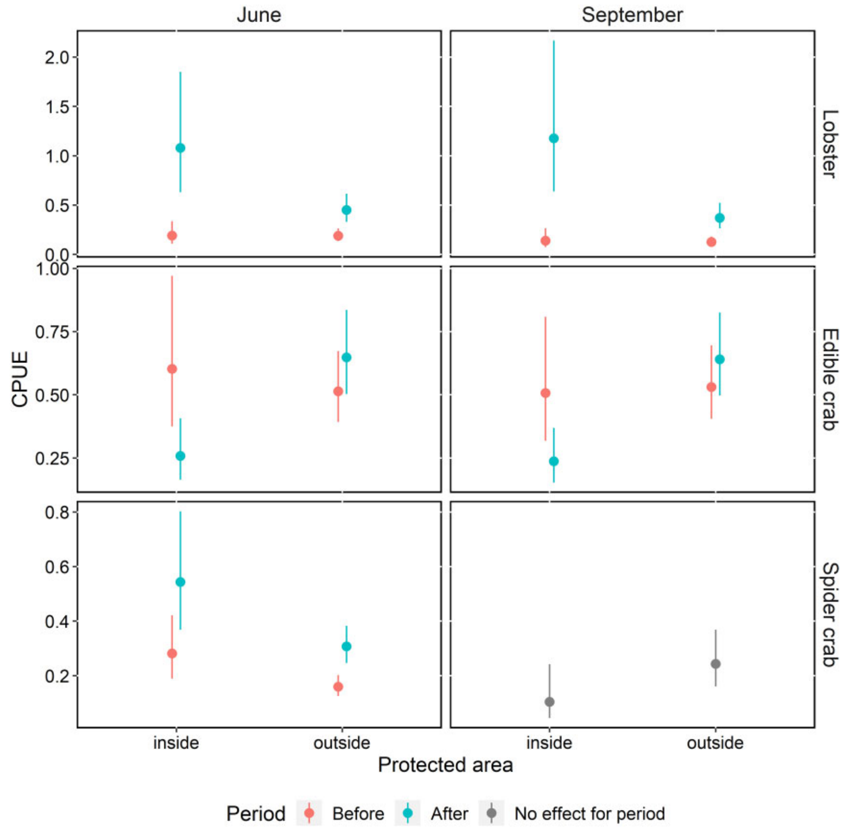

Figure 2. Predictions of fixed effects with combined confidence intervals from fixed and random parameters for CPUE.

sizes. CPUE was used as a proxy for abundance while length was used as a proxy for size.

With regard to the BACI methodology, the statistical modelling of the evolution of abundance and size across time has been first summarized into a discrete 'Period' effect, that takes only 2 levels 'Before' and 'After' the creation of the MPA. As a result, a significant 'Period' effect that affects the estimators inside and outside the MPA to the same extent may be due to an evolution of the parameter across time, but unrelated to the creation of the reserve. Conversely, the detection of a statistically significant interaction between Period effect and Area effect (inside or outside the MPA), combined with the increase of abundance or size inside the MPA, is considered as evidence for protective effect.

Thus, the hypothesis of an Area (Control/Reserve) × Period (Before/After) interaction was tested on abundance and size for lobster, edible crab, and spider crab. June and September surveys were considered separately, to avoid a 'seasonal bias' of the estimators. Spatial and temporal variability were considered as a source of unexplained, however structured, variation. Consequently, Area and Period variables were modelled as fixed effects, whereas Year and Location were declared as random effects to take into account a potential inter-annual or spatial covariance. When one fixed effect was not found significant, the model was reduced in order to improve the estimation of the effects associated with the remaining variables. In those situations, only the results of the reduced model were presented in the following sections. The unreduced mixed models equation was $Y = \text{Area} + \text{Period} + \text{Area} \times \text{Period} + (1|\text{Year}) + (1|\text{Location})$. Type II Chi^2 was used to test for fixed effects in accordance with the principle of marginality. Likelihood ratio-test was used for nested models to test for random effects. For length, mixed linear models were employed. For CPUE generalized mixed models were used, with a log-link. Because of overdispersion while modelling count data with a Poisson distribution, catches were modelled using generalized mixed models with a Negative-binomial family and a log-link function. Catch numbers were standardized as CPUEs using the fishing effort (logarithm of the number of trap), as an offset.

For model validation, we used the 'DHARMa' package that allows to create interpretable scaled residuals for fitted linear mixed models (Ellis and Schneider 1997). We paid special attention to distribution dispersion, due to the fact that we detected some overdispersion in the datasets as soon as we began the mixed-model selection process. The choice of models is therefore the result of a compromise between on one hand, the necessity to fit the data as close as possible for all the variables and the species and, on the other hand, the need to keep only one model to facilitate inter-species comparison of the outputs.

To investigate further the spatial distribution of catches around the MPA, and their putative gradual evolution over the years, the CPUE was modelled as a function of time and remoteness from the MPA, considering time and distance as continuous factors.

First, we were interested in modelling the evolution of CPUE over time, outside, and inside the MPA. We thus split the entire dataset in two distinct datasets, the first one containing the observations collected outside the MPA and the second one containing the observations collected inside the MPA. For each dataset, and each species, we adjusted a generalized additive mixed model (GAMM) with a categorical predictor for month (as a fixed effect), a non-parametric smoother for time and a random location effect. The model equation was thus Y = month + s(Year) + (1|Location).

The evolution of CPUE was modelled as a function of remoteness from the MPA before and after the implementation of the MPA, only for the sampling locations standing outside the perimeter of the reserve. Then, the dataset was split in two distinct datasets, the first one containing the observations collected before the MPA creation and the second one containing the observations collected after the MPA creation. For each dataset, and each species, a GAMM was adjusted, with a categorical predictor for month (as a fixed effect), a non-parametric smoother for space and a random year effect. The model equation was thus Y = month + s(Distance) + (1|Year).

All analyses were made using the 3.5.1 version of the R software (R Core Team R 2023), using the following libraries: ggplot2 (Wickham 2016), lme4 (Bates et al. 2014), MASS (Venables and Ripley 1999), mgcv (Wood 2004), ggeffects (Lüdecke 2018), DHARMa (Hartig 2018).

Results

CPUE before/after per species

Temporal changes in CPUE were evidenced for lobsters. The CPUE varied significantly between MPA and control (Fig. 2). Based on the GLMM results, the Area × Period was statistically significant. It meant that Period effect (before/after the reserve creation) on CPUE depended on the Area (outside/inside the reserve) for the two annual surveys (June: $Chi^2 = 75.21$; $P < 2.2e^{-16}$ and September: $Chi^2 = 69.94$; $P < 2.2e^{-16}$) (Supplementary Material, Tables S1 and S2). Before the implementation of the MPA, lobster abundance appeared to be approximately equally distributed inside and outside the perimeter of the future MPA, with a mean estimated CPUE value close to 0.175 (0.19 inside, 0.19 outside in June and 0.14 inside, 0.13 outside in September). After the MPA implementation, the mean estimated CPUE reached 1.08 in June and 1.18 in September within the MPA perimeter. During the same time period, the mean estimated CPUE was 0.45 in June and 0.37 in September outside the MPA. The estimated CPUE increase was estimated to be 597% within the MPA, whereas it only increased by 156% outside the MPA.

Mixed models also detected a significant Area × Period interaction for edible crab surveys in June ($Chi^2 = 101.18$; $P < 2.2e^{-16}$) and September ($Chi^2 = 48.44$; $P = 3.4e^{-12}$) (Fig. 2, Supplementary Material, Tables S3 and S4). However, the distribution of the edible crab population followed a distinct pattern from the one of the lobster population. Before the implementation of the MPA, distribution appeared to be homogeneous in the whole study area. The mean estimated CPUE was 0.522 outside the perimeter of the future MPA and 0.478 inside (mean number of CPUE for June and September). After the MPA implementation, the mean estimated CPUE decreased to 0.253 in June and 0.232 in September inside the MPA, meaning that edible crab abundance has been halved. Contrariwise, during the same time period the mean estimated CPUE increased by 20% outside the MPA.

Results from the GLMM suggested that MPA creation affected at best marginally the spider crab population. The Area × Period interaction was significant neither in June nor in September. In June, Area and Period effects were each significant (Area: $Chi^2 = 0.2028$; $P = 0.009$ and Period: $Chi^2 = 0.2116$; $P = 4.289e\text{-}9$) (Fig. 2, Supplementary Material, Tables S5 and S6). Spider crab abundance appeared higher inside the perimeter of the MPA. The mean estimated CPUE increased by the same proportion inside and outside the MPA after its implementation, from 0.245 to 0.533 spider crab per trap per day inside the perimeter and from 0.161 to 0.298 outside. In September, the model only detected a marginally significant Area effect. For those surveys, estimated CPUE was higher outside than inside the MPA (0.238 vs. 0.089).

Length before/after per species

Model selection supported an interaction effect between Area and Period for lobster length (June: $Chi^2 = 235.33$; $P < 2.2e^{-16}$ and September: $Chi^2 = 178.58$; $P < 2.2e^{-16}$) (Fig. 3, Supplementary Material, Tables S7 and S8). It indicated that body size evolved differently inside and outside the MPA. Inside this perimeter, estimated lengths increased from 83.12 to 92.40 mm in June and from 83.65 to 94.74 mm in September since the MPA implementation (Fig. 3). Size outside the MPA hardly changed, from 86.49 to 85.09 mm (estimated lengths) in June and from 86.01 to 85.44 mm (estimated lengths) in September.

The edible crab body size appeared to be only marginally affected by the MPA implementation. Significant interaction between Area and Period was only detected in September ($Chi^2 = 5.9572$; $P = 0.015$) (Fig. 3, Supplementary Material, Tables S9 and S10). After the MPA creation, a slight decrease of the length within the perimeter of the MPA was estimated, whereas length remained constant outside the area (Fig. 3). Inside the MPA, the mean estimated lengths decreased from 116.03 to 113.31 mm although outside the MPA, estimated lengths remained between 133.98 mm and 133.61 mm. Generally, length was significantly higher outside than inside the reserve (June: $Chi^2 = 6.3172$; $P = 0.012$ and September: $Chi^2 = 5.9572$; $P = 0.015$), with a mean estimated length of 133.34 vs. 114.92 mm.

No Area nor Period effect were found for spider crab in June (Fig. 3). In September, the interaction term was retained based on model selection ($Chi^2 = 5.1564$; $P = 0.023$, Supplementary Material, Tables S11 and S12). Indeed, the estimated lengths appeared to decrease within the MPA after its implementation, from 88.36 mm to 78.74, however it remained stable outside this area, between 96.20 and 96.61 mm (estimated lengths).

Duration since the MPA creation and distance from the MPA effects

For lobster CPUE, model showed a temporal increase over time both inside and outside the MPA (Fig. 4), although, the rise in CPUE appeared far more important for the sampling points located inside the MPA perimeter (respectively: + 1933% and + 3896% in June and September) than outside (+605% and +920%) (Table 1). Outside the protected area, CPUE remained stable until 2003 while increasing after. Inside the protected area, CPUE seems to have increased even before the MPA was created. At the end of the survey, mean CPUE had exceeded one lobster per trap per day in that area and virtually no trap were brought aboard empty from lobster.

The number of lobster catches showed no spatial trend prior to the creation of the reserve (Fig. 5). After the MPA

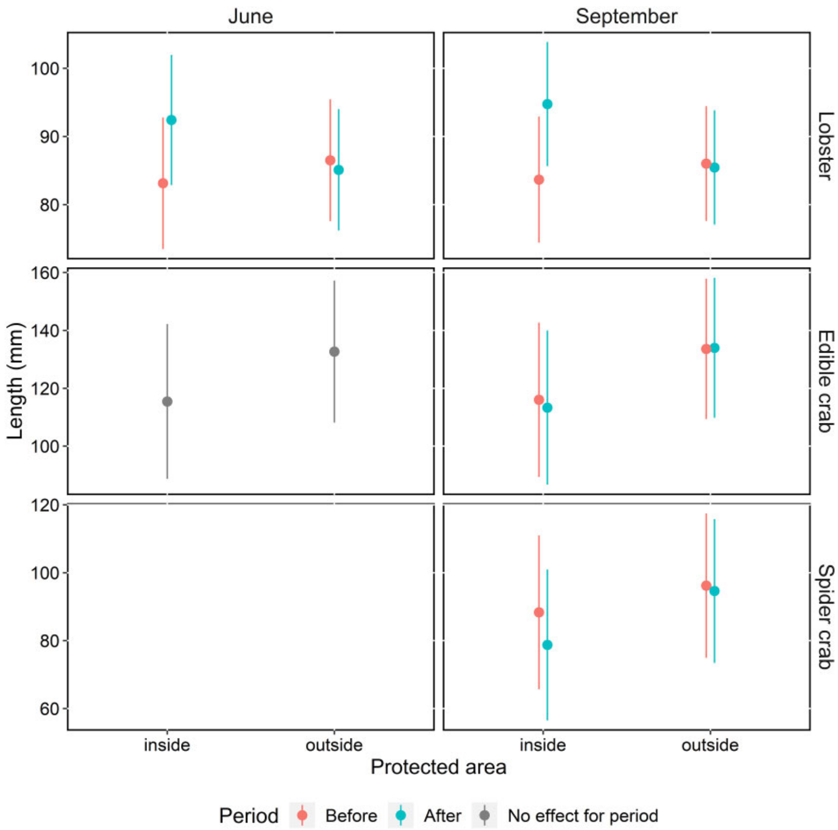

Figure 3. Predictions of fixed effects with combined confidence intervals from fixed and random parameters for cephalothorax length.

creation, the distance effect from the protected area on lobster CPUE demonstrated a downward trend with significant variations at small spatial scale (Fig. 5). The same pattern in fluctuations have been observed in both June and September, strongly supporting non random patterns.

The edible crab CPUE remained globally stable outside the MPA perimeter over time (respectively: +38% and −2% in June and September) (Table 1), occasionally reaching two local peaks in 1998 and 2012 (Fig. 4). The same pattern was observed both in June and September. Inside the MPA, the maximum number of captures was reached in 1997. Crab CPUE steadily decreased after that particular year both in June and September (−80% and −56% since the end of the survey). GAMM evidenced a slight but clear steady decrease over distance from the MPA, both before and after its creation (Fig. 5). Mean CPUE appeared superior to one individual per trap per day for the sampling point the closest to the MPA boundaries, but dropped over 0.5 individual per trap per day for points more than four kilometre away.

Spider crab CPUE exhibited a clear increase in June at the sampling stations located both outside (+168%) (Table 1) and inside (+220%) the MPA (Fig. 4). In September, estimated CPUE showed rapid fluctuations outside the MPA, with a slight general increasing trend (+ 88%).

Spider crab CPUE exhibited consistent increase related to the distance from the MPA in June and September, both before and after the MPA creation (Fig. 5). The minimal catches observed were for the points located closest to the MPA, and mean CPUE showed a slight increase with distance, reaching values superior to 0.5 individual per trap per day for the most distant points.

Discussion

MPA performances estimations

Marine protected areas restrict human activities for species conservation and biodiversity purposes, to offer refuge for animal or plant communities locally (Gaines et al. 2010). The creation of MPAs can lead to drastic decreases in fishing catches that results, in many cases, to direct increases of the abundance and the lifetime of the species (Halpern 2003). Although the principle is well-known, a lot of studies pinpointed the difficulty in evaluating the effects of the creation of one protected area implementations (Schimdt 1997, Thiault et al. 2019). The assessment protocols based on 'BACI' type methodologies are classically considered as the most suitable methods (Gell and Robert 2003, Osenberg et al. 2011).

This study first objective was to study the effect of an MPA implementation on catches. Therefore, a generalized mixed models framework was used due to non-normal distribution of CPUE data and presence of random effects (Bolker et al. 2009). These models do not account for temporal autocorrelation, as such model results probably underestimate the uncertainty caused by temporal auto-correlation. The same model was used for all BACI analysis, in order to allow result comparisons to make inferences about MPA effect. The (linear and generalized linear) model specification that were kept were those that best fit the data for all the couples of species and variables. Diagnostic tests (i.e. the Q–Q plot of scaled residuals and the tests for correct distribution) indicated that models fit the data quite well. Some significant deviations from the expected (quantile) distributions were found for spider crab CPUE in September, and more generally for

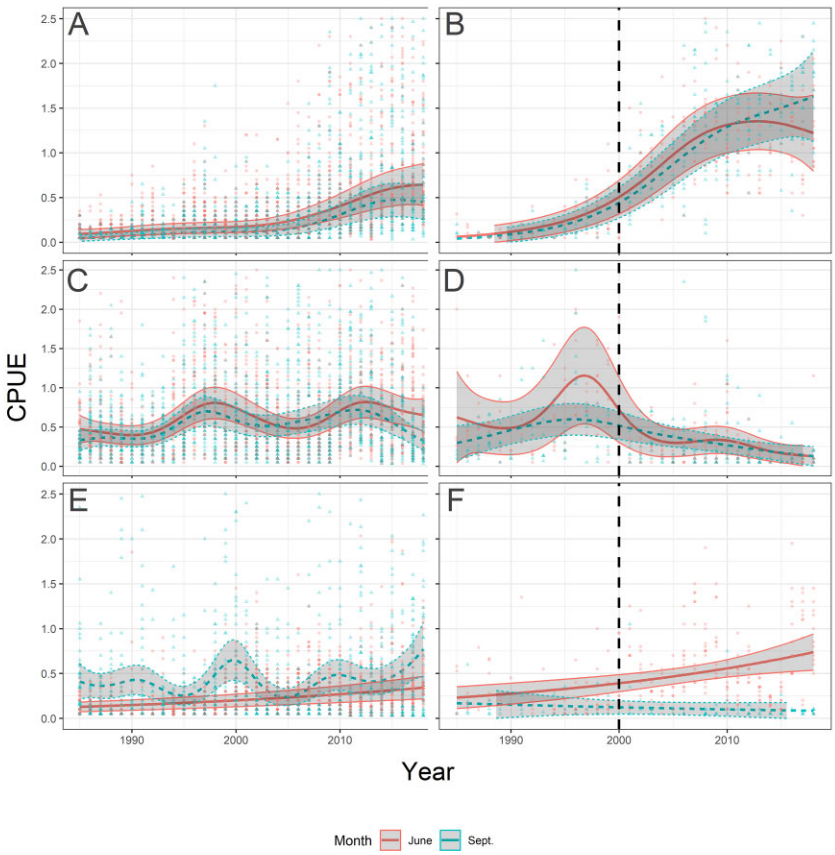

Figure 4. Generalized additive mixed model (GAMM) predicted values for CPUE as a function of year in June (continuous curve) and September (dashed curve) for lobster (A–B), edible crab (C–D), and spider crab (E–F), for the sampling points located outside the MPA perimeter (left panel) or inside the MPA perimeter (right panel). The vertical black dashed line figures the MPA creation in 2000.

Table 1. Mean CPUE evolution estimated by generalized additive mixed model (GAMM) between the beginning (1985) and the end of the survey (2018).

Species	MPA	Inside	Outside
Lobster	June	↗ +1933%	↗ +605%
Lobster	September	↗ +3896%	↗ +920%
Edible crab	June	−↘ 80%	↗ +38%
Edible crab	September	↘ −56%	↘ −2%
Spider crab	June	↗ +220%	↗ +168%
Spider crab	September	↘ −50%	↗ +88%

cephalothorax length variations analysis. In that section, we thus tried to carefully interpreted the results by paying particular attention to model adjustment.

BACI and mixed-model analysis methods can only be carried out if one has an extensive dataset at hand to characterize the initial state of the zone, and to account for the expected spatio-temporal covariance of the observations. With respect to the Flamanville MPA, the surveys began 15 years before the MPA implementation, and have continued during the 18 years following its enforcement. This time serie allowed the evaluation of the fine scale effects of the protective measure upon the crustacean community.

MPA might be designed for one or several species depending on its main objectives. In Flamanville, the main driver that led to the MPA implementation was the enhancement of the local crustacean fishery. The European lobster, as a high economical value species, was the object of a consequent fishing effort in the 1990s. In 1987, the ≪ large ≫ crustacean (i.e. Lobster, spider crab, edible crab) casey fleet numbered around 120 vessels in the Western Channel (Morizur et al. 1990). Consequently, the Flamanville MPA was designed to improve this species ecological status first and foremost, hoping that this MPA would have a cumulative effect with the other reserves previously created along the French coasts of the Western Channel.

Protective effect of the MPA for lobster

French lobster commercial catches between 2010 and 2017 increased all over the western coast of Normandy (ICES 2019). This increase results most probably from a good recruitment of juveniles over the last 10 years. The analysis carried out showed a far more important increase of lobster catches inside than outside of the protected area after its creation. From the beginning of the survey, the mean predicted CPUE has increased by 1933% and 3896% in June and September, respectively. Moland et al. (2013) evidenced an increase of 245% inside and 87% outside of a MPA in lobster CPUE 5 years after the implementation of the MPA they studied. These variations could be compared to increases, of 93% and 97% inside the MPA and 37.3% and 30% outside the MPA for June and September, respectively. These changes happened during the 5 years following the MPA implementation. This study evidenced an an increase in CPUE in the area. This increase could be related to a significant reduction of the fishing

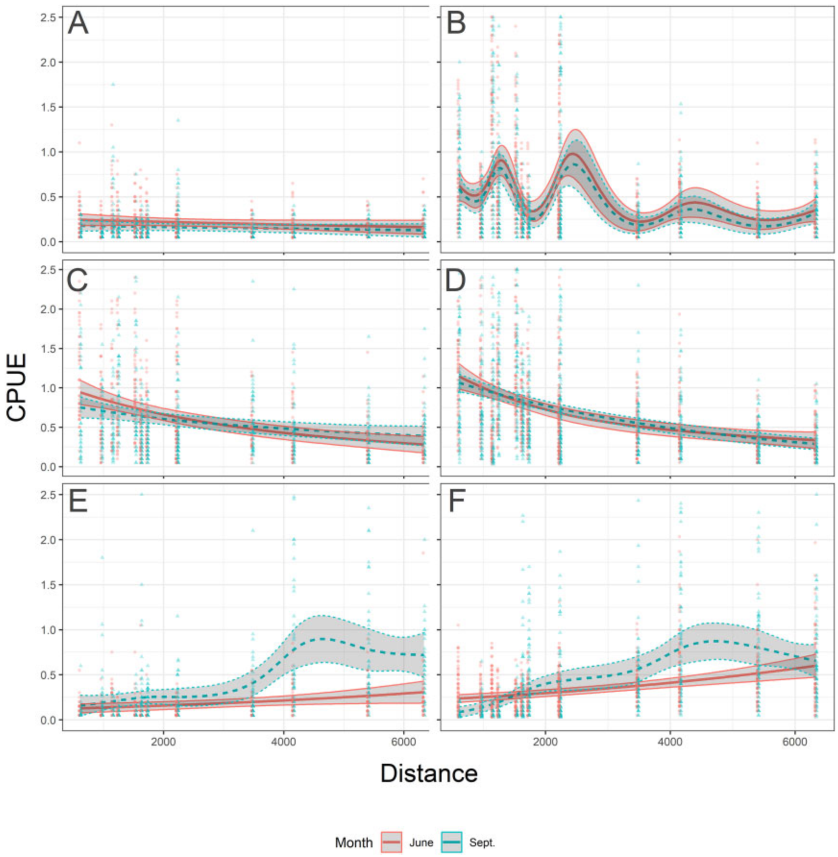

Figure 5. Generalized additive mixed model (GAMM) predicted values for CPUE as a function of distance from the MPA in June (continuous curve) and September (dashed curve) for lobster (A–B), edible crab (C–D), and spider crab (E–F), for the data collected before (left panel) and after (right panel) the MPA creation.

mortality caused by the cessation of fishing activity in the area. The MPA performances in regard to the lobster protection might be related to the sedentariness of the lobster (Smith et al. 2001). Indeed, small reserves are especially effective to protect species with limited adult mobility (Grantham et al. 2003, White 2015).

The increase in lobster size, to a lesser extent, could also be viewed as a positive effect of the MPA implementation. Indeed, bigger individuals are better breeders that more efficiently support the population's reproductive success (Campbell and Robinson 1983, Laurans et al. 2009). The increased abundance of big lobsters may have caused domino effects by increasing the intra-specific competition inside the reserve, chasing the smallest individuals outside the protected area (Goñi et al. 2014). Differences in lobster catchability-at-size by traps may also explain the increase of bigger-sized lobster's catches (Watson and Jury 2013). In examining videos, Jury et al. (2001) found that a substantial proportion of lobsters hesitate to enter the trap when another congener was already caught. Therefore, increasing the bigger lobsters' proportion in the MPA probably leads to the underestimation of the smaller-sized individuals' abundance.

If well designed and managed, the creation of a MPA may result in an increase in the abundance of the targeted species inside the no-take zone (Gell and Roberts 2003, Russ et al. 2004). The increase in densities within the MPA could also sustain exploited species populations in the surrounding areas (Di Lorenzo et al. 2016). The implementation of one MPA could result in the emergence of a decreasing density gradient from the reserve to the more remote areas This so-called 'spillover effect' have been illustrated by different case studies. Spillover is for instance documented for spiny lobster *Palinurus elephas* (Goñi et al. 2006), in the coral-reef fish *Naso vlamingii* (Abesamis and Russ 2005), in various species of Sparidae, Mullidae, Scorpaenidae, and Serranidae (Goñi et al. 2010). Two different mechanisms may drive this spillover phenomenon: (1) the net emigration of adults and juveniles from the reserve triggered by the increase of the inter and intra-specific competition inside the protected zone (Goñi et al. 2010); (2) the passive exportation of pelagic eggs and larvae that nurture the recruitment in the surroundings (Harrison et al. 2012, Hart et al. 2020).

In this study, only the lobster densities declined with distance from the MP, suggesting a spillover effect. This trend was however affected by variations that could reflect the particular affinity of this species for specific habitats occurring at very small spatial scale. Furthermore, this decrease along distance gradient is concomitant with an increase in CPUE over time, which constitutes additional support the hypothesis of a spill-over effect. It is also the same order of magnitude as the reserve effect found by Goñi et al. (2006), in the closely related spiny lobster *Palinurus elephas*. Moreover, despite the short time period since the implementation of a norwegian MPA, Nillos Kleiven et al. (2019) evidenced the existence of a comparable spill-over effect on European lobster. However, the alternative hypothesis considering that the trend was also influenced by the overall increase of lobster abundance in the Western English Channel cannot be excluded. The spatial extent of the zone is clearly smaller than the species migration ability, considering that one adult lobster could cover several kilometres in a month (Smith et al. 2001). Dispersive potential of crustaceans pelagic eggs and larvae should also be considered; for lobsters since female carries their eggs until they hatch only larval dispersal will apply. The respective shares of contribution of passive and active emigration in this area remains therefore difficult to assess. Capture–recapture studies could provide estimates of the migratory flow of lobster from the reserve to the surroundings (Smith et al. 2001).

However MPA benefits should not be considered only at the species specific level. Flamanville's MPA through the ban of all fishing activities had effects on other crustaceans species previously targeted by trap fishery, such as edible crab and spider crab. Its implementation directly impacted the fishing mortality of those species, but also might have impacted the interactions within the crustaceans complex in the area (Hoskin et al. 2011, Howart et al. 2017, Stewart et al. 2020).

MPA effects for edible and spider crabs

As a matter of fact, the Flamanville's MPA had impacted spider crab and edible crab populations. The creation of the reserve coincided with a slight increase of the spider crabs catches in June, more important in the reserve than outside, suggesting that the cessation of fishing activity significantly reduced the fishing mortality in the protected area. Contrarily, CPUE of this species appeared unaffected by the reserve creation in September. However, over this period, spider crabs have begun their annual migration to deeper waters (Le Foll 1993, Corgos et al. 2006). Consequently, abundance may be greater offshore, far from the coastline and from the protected area. This seasonal effect indicates that the protection offered by the MPA to spider crab might be only limited to the spring and summer periods when spider crabs are present in the nearshore and shallow waters.

The edible crab population does not appear to have benefited from the implementation of the protective measures. CPUE of edible crab appeared to have, on the contrary, dropped inside the reserve after its creation. Interspecific competition influences the partitioning of species across space and time (Carothers and Jaksic 1984, Chesson 2000, Rees and Hill 2001). Interspecific competition has long been recognized to be of two types: the use of the resource by one species that mechanically deprives the other (Liu et al. 2019), or the interference between species through aggression that prevents one from accessing the resource (Case and Gilpin 1974). In this crustacean community, lobster appears to be a fierce competitor. Edible and spider crabs, like lobsters, feed on molluscs bivalves, gastropods, polychaetes, and small echinoderms, and consequently compete for food. Furthermore, those species also share the same habitat. The lobster's aggressive territorial behaviour has been well documented (Karnofsky and Price 1989, Johnson and Atema 2005) and appears as a competitive advantage within this crustacean community. Furthermore, lobsters occasionally eat smaller crustaceans, among which young edible crabs, and can feed on its own congeners when resource shortfalls occur (Van Der Meerean 2005, Schmalenbach et al. 2009). It resulted in conflicting and repulsive behaviours between lobsters and edible crabs that have been observed in trap fisheries (Hoskin et al. 2011, Howart et al. 2017, Skerritt et al. 2020, Stewart et al. 2020). According to Skerrit et al. (2020), the presence of European lobster in traps subsequently reduced the CPUE of edible crab by a factor of 12.

The decrease of edible crab in the protected area, in parallel with the increase in size and abundance of lobster, was hypothesized to result from the competitive exclusion of the latter species by the former. The primary mechanism of that exclusion could be the mobilization of the resource, coupled with the territorial aggressiveness of the lobster. The fact that lobster is a very sedentary species with a long lifespan could have acted as a secondary cause, by preventing the recolonization of the protected area by species that are more mobile such as the edible crab. Although edible crab is not a migratory species, the females have been proven to undergo long distance movements (Hunter et al. 2013). The MPA creation did not seems to result in the exclusion of spider crab contrariwise to edible crab. This difference between the two species may results from the highly migratory nature of the spider crab (Corgos et al. 2006). Migratory movements renewed the population each year, making them less sensitive to the competitive pressure exerted by the lobsters.

However, the local edible crab and spider crab communities dynamics could not be investigated without considering the dynamics of the stocks they are part of. From the 2010s to the 2020s, the Western English Channel spider crab population increased (ICES 2019). This evolution might have supported the local increase in spider crab abundance. On the contrary, no external enhancement should have been expected for edible crab since the surrounding communities are expected to be decreasing as well.

Conclusion

Flamanville MPA objective was to enhance the local crustacean fishery. With respect to this objective, the implementation of the MPA was a success. However, it had a contrasting impact on the different species of the local crustacean community. It impacted positively the lobster community, which simultaneously grew in abundance and in size and seems to have the object of spillover effect. The edible crab community did suffer from the MPA implementation. Unexpected effects of the MPA impacted edible crab abundance and size as well as their spatial distribution, with the highest abundance observed outside of the MPA. Finally, the spider crabs were almost not impacted by the MPA implementation. Those dynamics were dependent on the ecological specificity of each species as well as their intra- and inter-specific competitive advantages.

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Author contributions

Morgane Amelot (supervision, writing original draft, writing review and editing), Julien Normand (data curation, formal analysis, methodology, writing original draft, writing review and editing), Ivan Schlaich (resources, data curation, methodology, writing original draft, writing review and editing), and Bruno Ernande (conceptualization, methodology, validation)

Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

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Data availability

The data underlying this article were provided by EDF by permission. Data will be shared on request to the corresponding author with permission of EDF.

References

Abesamis RA, Russ GR. Density-dependent spillover from a marine reserve: long-term evidence. *Ecol Appl* 2005;**15**:1798–812. https://doi.org/10.1890/05-0174

Bacher C, Duarte P, Ferreira JG *et al.* Assessment and comparison of the Marennes-Oléron Bay (France) and Carlingford Lough (Ireland) carrying capacity with ecosystem models. *Aquatic Ecol* 1997;**31**:379–94. https://doi.org/10.1023/A:1009925228308

Bates D, Mächler M, Bolker B *et al.* 'Fitting linear mixed-effects models using lme4'. *arXiv preprint arXiv:1406.5823*. 2014.

Bolker BM, Brooks ME, Clark CJ *et al.* Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 2009;**24**:127–35.

Campbell A Robinson AD. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. *Can J Fish AquatSci* 1983;**40**:1958–67. https://doi.org/10.1139/f83-225

Campbell A, Stasko AB. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. *Mar Biol* 1986;**92**:393–404. https://doi.org/10.1007/BF00392680

Carothers JH, Jaksić FM. Time as a niche difference: the role of interference competition. *Oikos* 1984;**42**:403–6. https://doi.org/10.2307/3544413

Case TJ, Gilpin M. Interference competition and niche theory. *Proc Natl Acad Sci* 1974;**71**:3073–7. https://doi.org/10.1073/pnas.71.8.3073

Chesson P. General theory of competitive coexistence in spatially-varying environments. *Theor Popul Biol* 2000;**58**:211–37. https://doi.org/10.1006/tpbi.2000.1486

Claudet J, Loiseau C, Sostres M *et al.* Underprotected marine protected areas in a global biodiversity hotspot. *One Earth* 2020;**2**:380–4. https://doi.org/10.1016/j.oneear.2020.03.008

Corgos A, Verisimo P, Freire J. Timing and seasonality of the terminal molt and mating migration in the spider crab, *Maja brachydactyla*: evidence of alternative mating strategies. *J Shellfish Res* 2006;**25**:577–87. https://doi.org/10.2983/0730-8000(2006)25%5b577:TASOTT%5d2.0.CO;2

Davidson RJ, Villouta E, Cole RG *et al.* Effects of marine reserve protection on spiny lobster (*Jasus edwardsii*) abundance and size at Tonga Island Marine Reserve, New Zealand. *Aquatic Conserv Mar Freshw Ecosyst* 2002;**12**:213–27. https://doi.org/10.1002/aqc.505

Delayat S, Legrand V. *Les cantonnements de pêche (1) Diagnostic général sur la façade Manche Atlantique française*. Marine Protected Areas in the Atlantic Arc—MAIA, Interreg IV B Atlantic Area Programme Scientific Report. 2011, 72.

Di Lorenzo M, Claudet J, Guidetti P. Spillover from marine protected areas to adjacent fisheries has an ecological and a fishery component. *J Nat Conserv* 2016;**32**:62–6. https://doi.org/10.1016/j.jnc.2016.04.004

Dugan JE, Davis GE. Applications of marine refugia to coastal fisheries management. *Can J Fish AquatSci* 1993;**50**:2029–42. https://doi.org/10.1139/f93-227

Ellis J, Schneider D. Evaluation of a gradient sampling design for environmental impact assessment. *Environ Monit Assess*. 1997;**48**:157–72.

Follesa MC, Cannas R, Cau A *et al.* Spillover effects of a Mediterranean marine protected area on the European spiny lobster *Palinurus elephas* (Fabricius, 1787) resource. *Aquatic Conserv Mar Freshw Ecosyst* 2011;**21**:564–72. https://doi.org/10.1002/aqc.1213

Follesa MC, Cuccu D, Cannas R *et al.* Effect of marine reserve protection on spiny lobster (*Palinurus elephas* Fabr., 1787) in a central western Mediterranean area. *Hydrobiologia* 2008;**606**:63–8. https://doi.org/10.1007/s10750-008-9346-8

Gaines SD, White C, Carr MH *et al.* Designing marine reserve networks for both conservation and fisheries management. *Proc Natl Acad Sci* 2010;**107**:18286–93. https://doi.org/10.1073/pnas.0906473107

Gell FR, Roberts CM. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol Evol* 2003;**18**:448–55.

Goñi R, Hilborn R, Díaz D *et al.* Net contribution of spillover from a marine reserve to fishery catches. *Mar Ecol Progr Ser* 2010;**400**:233–43. https://doi.org/10.3354/meps08419

Goñi R, Mallol S, Díaz Viñolas D *et al. Male Competition Propels Biomass Recovery in a New Marine Protected Area*. Gijón: XVIII Simposio Ibérico de Estudios de Biología Marina (SIEBM). 2014, 1.

Goñi R, Quetglas A, Reñones O. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Mar Ecol Progr Ser* 2006;**308**:207–19. https://doi.org/10.3354/meps308207

Grantham BA, Eckert GL, Shanks AL. Dispersal potential of marine invertebrates in diverse habitats: ecological archives. *Ecol Appl* 2003;**13**:108–16. https://doi.org/10.1890/1051-0761(2003)013%5b0108:DPOMII%5d2.0.CO;2

Green RH. *Sampling Design and Statistical Methods for Environmental Biologists*, 1st edn. New-York: John Wiley and Sons. 1979.

Halpern BS. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol Appl* 2003;**13**:117–37. https://doi.org/10.1890/1051-0761(2003)013%5b0117:TIOMRD%5d2.0.CO;2

Harmelin-Vivien M, Le Diréach L, Bayle-Sempere J *et al.* Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol Conserv* 2008;**141**:1829–39. https://doi.org/10.1016/j.biocon.2008.04.029

Harrison HB, Williamson DH, Evans RD *et al.* Larval export from marine reserves and the recruitment benefit for fish and fisheries. *Curr Biol* 2012;**22**:1023–8. https://doi.org/10.1016/j.cub.2012.04.008

Hart DR, Munroe DM, Caracappa JC *et al.* Spillover of sea scallops from rotational closures in the Mid-Atlantic Bight (United States). *ICES J Mar Sci* 2020;**77**:1992–2002. https://doi.org/10.1093/icesjms/fsaa099

Hartig F. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package version 0.4.6. 2018.

Hastings A, Botsford LW. Equivalence in yield from marine reserves and traditional fisheries management. *Science* 1999;**284**:1537–8. https://doi.org/10.1126/science.284.5419.1537

Hiddink JG, Hutton T, Jennings S *et al.* Predicting the effects of area closures and fishing effort restrictions on the production, biomass, and species richness of benthic invertebrate communities. *ICES J Mar Sci* 2006;**63**:822–30. https://doi.org/10.1016/j.icesjms.2006.02.006

Hilborn R, Stokes K, Maguire JJ *et al.* When can marine reserves improve fisheries management? *Ocean Coastal Manage* 2004;**47**:197–205.

Hoskin MG, Coleman RA, Von Carlshausen E *et al.* Variable population responses by large decapod crustaceans to the establishment of a temperate marine no-take zone. *Can J Fish AquatSci* 2011;**68**:185–200. https://doi.org/10.1139/F10-143

Howarth LM, Dubois P, Gratton P *et al.* Trade-offs in marine protection: multispecies interactions within a community-led temperate marine reserve. *ICES J Mar Sci* 2017;**74**:263–76. https://doi.org/10.1093/icesjms/fsw166

Høydalsvik MN. *Effects of Marine Protected Areas on European Lobster (Homarus gammarus) in Skagerrak, Norway*(Master's thesis, University of Oslo) 2017.

Hunter E, Eaton D, Stewart C *et al.* Edible crabs "go west": migrations and incubation cycle of *Cancer pagurus* revealed by electronic tags. *PLoS One* 2013;**8**:e63991. https://doi.org/10.1371/journal.pone.0063991

ICES. Working Group on the biology and life history of CRABs (WGCRAB). *ICES Sci Reports* 2019;**3**:74.

Johnson ME, Atema J. The olfactory pathway for individual recognition in the American lobster *Homarus americanus*. *J Exp Biol* 2005;**208**:2865–72. https://doi.org/10.1242/jeb.01707

Jury SH, Howell H, O'Grady DF *et al.* Lobster trap video: in situ video surveillance of the behaviour of *Homarus americanus* in and around traps. *Mar Freshwater Res* 2001;**52**:1125–32. https://doi.org/10.1071/MF01096

Karnofsky EB, Price HJ. Dominance, territoriality and mating in the lobster, *Homarus americanus*: a mesocosm study. *Mar Freshw Behav Phy* 1989;**15**:101–21.

Laurans M, Fifas S, Demaneche S *et al.* Modelling seasonal and annual variation in size at functional maturity in the European lobster (*Homarus gammarus*) from self-sampling data. *ICES J Mar Sci* 2009;**66**:1892–8. https://doi.org/10.1093/icesjms/fsp166

Le Foll D. Biologie et exploitation de l'araignée de mer *Maja squinado* (Herbst) en Manche Ouest. Ph.D. Thesis, University of Western Brittany, 1993.

Leenhardt P, Low N, Pascal N *et al.* The role of marine protected areas in providing ecosystem services. In: A Belgrano, G Woodward, U Jacob (eds.), *Aquatic Functional Biodiversity*, Netherlands: Academic Press, 2015, 211–39.

Liu D, Su X, Wang F *et al.* Starvation intensifies the impacts of interspecific interactions on foraging behavior of swimming crab (*Portunus trituberculatus*). *Aquaculture* 2019;**504**:22–9. https://doi.org/10.1016/j.aquaculture.2019.01.050

Lüdecke D. ggeffects: tidy data frames of marginal effects from regression models. *J Open Source Software* 2018;**3**:772. https://doi.org/10.21105/joss.00772

Moland E, Fernández-Chacón A, Sørdalen TK *et al.* Restoration of abundance and dynamics of coastal fish and lobster within northern marine protected areas across two decades. *Front Mar Sci* 2021;**8**:674756. https://doi.org/10.3389/fmars.2021.674756

Moland E, Ulmestrand M, Olsen EM *et al.* Long-term decrease in sex-specific natural mortality of European lobster within a marine protected area. *Mar Ecol Progr Ser* 2013;**491**:153–64. https://doi.org/10.3354/meps10459

Morizur Y, Berthou P, Latrouite D *et al.* *La flottille artisanale française de la Manche-Ouest : bilan des connaissances*. Scientific report from the IFREMER Living Resources Division. 1990, 189.

Nillos Kleiven PJ, Espeland SH, Olsen EM *et al.* Fishing pressure impacts the abundance gradient of European lobsters across the borders of a newly established marine protected area. *Proc R Soc B Biol Sci* 2019;**286**:20182455. https://doi.org/10.1098/rspb.2018.2455

OECD. *Marine Protected Areas: Economics, Management and Effective Policy Mixes*, OECD Publishing, Paris, 2017, 180.

Ojeda-Martínez C, Bayle-Sempere JT, Sánchez-Jerez P *et al.* Review of the effects of protection in marine protected areas: current knowledge and gaps. *Animal Biol Conserv* 2011;**34**:191–203.

Osenberg CW, Shima JS, Miller SL *et al.* Assessing effects of marine protected areas: confounding in space and possible solutions. In: J. Claudet (ed.). *Marine Protected Areas: a Multidisciplinary Approach*. United Kingdom: Cambridge University Press, 2011, 143–67.

R Core Team *R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing*, Vienna, Austria 2023.

Rees M, Hill RL. Large-scale disturbances, biological control and the dynamics of gorse populations. *J Appl Ecol* 2001;**38**:364–77. https://doi.org/10.1046/j.1365-2664.2001.00598.x

Russ GR, Alcala AC, Maypa AP *et al.* Marine reserve benefits local fisheries. *Ecol Appl* 2004;**14**:597–606. https://doi.org/10.1890/03-5076

Schlaich I, Miossec D. *Inshore crustacean fishery survey close to Flamanville nuclear power plant. CRUSTAFLAM*. Survey methodology handbook from the IFREMER Living Resources Division. 2003, 20.

Schmalenbach I, Buchholz F, Franke HD *et al.* Improvement of rearing conditions for juvenile lobsters (*Homarus gammarus*) by co-culturing with juvenile isopods (*Idotea emarginata*). *Aquaculture* 2009;**289**:297–303. https://doi.org/10.1016/j.aquaculture.2009.01.017

Schmidt KF. No-take' zones spark fisheries debate. *Science* 1997;**277**:489–91. https://doi.org/10.1126/science.277.5325.489

Skerritt DJ, Bannister RCA, Polunin NVC *et al.* Inter- and intra-specific interactions affecting crustacean trap fisheries—implications for management. *Fisher Manage Ecol* 2020;**27**:445–53. https://doi.org/10.1111/fme.12425

Smith EP. BACI design. *Encyclo Environmetric* 2002;**1**:141–8.

Smith IP, Jensen AC, Collins KJ *et al.* Movement of wild European lobsters *Homarus gammarus* in natural habitat. *Mar Ecol Progr Ser* 2001;**222**:177–86. https://doi.org/10.3354/meps222177

Steneck RS. Possible demographic consequences of intraspecific shelter competition among American lobsters. *J Crustacean Biol* 2006;**26**:628–38. https://doi.org/10.1651/S-2753.1

Stewart BD, Howarth LM, Wood H *et al.* Marine conservation begins at home: how a local community and protection of a small bay sent waves of change around the UK and beyond. *Front Mar Sci* 2020;**7**:76. https://doi.org/10.3389/fmars.2020.00076

Thiault L, Kernaléguen L, Osenberg CW *et al.* Ecological evaluation of a marine protected area network: a progressive-change BACIPS approach. *Ecosphere* 2019;**10**:e02576. https://doi.org/10.1002/ecs2.2576

Underwood AJ. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. *J Exp Mar Biol Ecol* 1992;**161**:145–78. https://doi.org/10.1016/0022-0981(92)90094-Q

Van Der Meeren GI. Potential of ecological studies to improve survival of cultivated and released European lobsters, *Homarus gammarus*. *NZ J Mar Freshw Res* 2005;**39**:399–424. https://doi.org/10.1080/00288330.2005.9517321

Vandeperre F, Higgins RM, Sánchez-Meca J *et al.* Effects of no-take area size and age of marine protected areas on fisheries yields: a meta-analytical approach. *Fish Fisher* 2011;**12**:412–26. https://doi.org/10.1111/j.1467-2979.2010.00401.x

Venables WN, Ripley BD. *Modern Applied Statistics with S-PLUS*, 3rd edn. New-York: Springer-Verlag Inc., 1999, 519.

Watson W, Jury SH. The relationship between American lobster catch, entry rate into traps and density. *Mar Biol Res* 2013;**9**:59–68. https://doi.org/10.1080/17451000.2012.727430

White JW. Marine reserve design theory for species with ontogenetic migration. *Biol Lett* 2015;**11**:20140511. https://doi.org/10.1098/rsbl.2014.0511

Wickham H. *Elegant Graphics for Data Analysis*, 1st edn. New-York: Springer-Verlag Inc., 2016, 276.

Wood SN. Stable and efficient multiple smoothing parameter estimation for generalized additive models. *J Am Statist Assoc* 2004;**99**:673–86. https://doi.org/10.1198/016214504000000980

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