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Body growth and mortality of the spiny lobster *Palinurus elephas* within and outside a small marine protected area

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ABSTRACT

Following the establishment of a small marine protected area (MPA) located off western Sardinia (Mediterranean Sea), a long-term survey was conducted on a spiny lobster (*Palinurus elephas*) population inhabiting the MPA and adjacent fishing grounds. Between 1998 and 2005, median carapace length increased by 1.9 mm year⁻¹ both within and outside the MPA. On the contrary, body size dispersion (IQR) increased by 0.9 mm year⁻¹ within the MPA and decreased by 0.6 mm year⁻¹ outside. Mark-recapture data were used to develop and calibrate a body growth model explicitly accounting for sexual dimorphism and inter-individual variability. Median asymptotic carapace length was equal to 116 mm in females and 185 mm in males. Age frequency distributions, derived from size distributions through the body growth model, were used to estimate mortality rates inside (ca. 0.41 year⁻¹, natural mortality) and outside (ca. 0.78 year⁻¹, natural + fishing mortality) the MPA. Results provide new estimates of key life history traits for this species and suggest that the MPA is effective in protecting lobsters despite its small dimensions.

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1. Introduction

A large proportion of marine stocks are currently overexploited, and fishing is considered one of the greatest threats affecting marine biodiversity and ecosystem functions and services (Pauly et al., 2002). Proper conservation measures and sustainable fishing practices can help maintain ecosystem health and related services to humans. From this perspective, marine protected areas (MPAs) have gained popularity in the last decades as a tool to ensure marine biodiversity conservation and replenishment of surrounding fishing grounds (Halpern, 2003; Stelzenmüller et al., 2007; Goñi et al., 2008). Long-term studies are fundamental to assess the effectiveness of protection measures (Russ et al., 2005). In fact, expected benefits of MPAs, including increase in stock abundance, average body size, and spillover of juveniles or reproductive adults may require several years to become evident (McClanahan et al., 2007). In addition, long-term studies provide valuable information to investigate demographic dynamics of protected stocks and derive mathematical models that can eventually be used to forecast the response of key species to different management policies.

Species with moderate mobility and subject to high levels of fishing mortality, such as most lobster species, have shown the strongest responses to protection (Micheli et al., 2004; Goñi et al.,

2008). Lobsters, which have relatively small home ranges (Smith et al., 2001; Follesa et al., 2009) and are actively pursued because of their high commercial value (Goñi and Latrouite, 2005), may greatly benefit from the establishment of even small MPAs. Edgar and Barret (1999) documented an extraordinary increase (more than an order of magnitude) of rock lobster biomass after the implementation of the Maria Island reserve, in Tasmania. Lester et al. (2009) investigated the biological effects of no-take marine reserves on different taxonomic groups and showed that lobsters were among those that experienced the most significant benefits (in terms of biomass, density and body size increase) from protection. In this respect, the spiny lobster *Palinurus elephas* is a very representative model species. *P. elephas* is intensively exploited in the Mediterranean Sea and the north-eastern Atlantic (Goñi et al., 2003). It is traditionally targeted by artisan fisheries, but the change in fishing strategy (from traps to trammel nets) that took place between the 1960s and the 1970s has severely impacted lobster populations (Hunter, 1999; Goñi and Latrouite, 2005). Consequently, lobster catches have declined in most of the distribution range during recent decades (Goñi et al., 2003; Goñi and Latrouite, 2005). Despite its high commercial value, almost no long-term surveys have been carried out on *P. elephas*, with the remarkable exception of those conducted in the Columbretas islands marine reserve (southern Spain; Goñi et al., 2003, 2006, 2010) and in Su Pallosu MPA (western Italy; Follesa et al., 2007a, 2009). Also, few studies have investigated body growth patterns and none of them has explicitly accounted for inter-individual variability. However, key demographic processes,

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such as sexual maturation, fecundity and natural mortality, are size-dependent in a number of aquatic organisms (Caswell, 1989), and a reliable mathematical description of somatic growth is crucial for population analysis, stock assessment, and fishery management (Katsanevakis and Maravelias, 2008). In particular, suitable body growth models can be used to derive information on age structure from data on body size. This allows the estimation of mortality rates also in species lacking reliable age markers, like crustaceans.

In this work we analysed a data set on *P. elephas* obtained from an 11-year long mark-recapture experiment (1997–2007) conducted within and around Su Pallosu MPA, located off Sardinian coasts, in the western Mediterranean. The objective of the work was twofold: (1) to investigate body growth in *P. elephas* and develop a stochastic model explicitly accounting for inter-individual variability; (2) to assess the effectiveness of MPA protection, by comparing body size trends inside and outside the MPA since its establishment in 1998 and by estimating and comparing mortality rates within and outside the protection range.

2. Materials and methods

2.1. The species

P. elephas is distributed throughout the Mediterranean Sea and along the Atlantic coasts between Morocco and south Norway (Hunter, 1999). The lobster inhabits rocky bottoms from near shore to 70–200 m of depth (Goñi et al., 2006). It is a long-living (maximum estimated age up to 15 year), slow-growing species reproducing once a year between July and September (Goñi and Latrouite, 2005). Adult movement is restricted within ca. 2.5 km year⁻¹ and is likely linked to reproduction and feeding, with older individuals showing higher site fidelity than juveniles (Goñi and Latrouite, 2005; Follesa et al., 2009). Fishing regulations include an annual 6-month closure from September to February and a minimum landing size that was recently increased from 80 to 90 mm carapace length (EC Regulation No. 1967/2006).

2.2. Study site and data collection

The study took place at Su Pallosu, a small MPA (ca. 4 km²) located in western Sardinia, and adjacent fishing grounds, encompassing an area of ca. 5 km radius from the MPA centre (Fig. 1). Both the MPA and fishing grounds are comprised between the 50-m and 100-m isobaths and are characterized by similar coral-ligenous habitats. A monitoring programme including a long-term mark-recapture experiment was started in the region in 1997 (see Follesa et al., 2007a for further details), before commercial fishing was banned in 1998 (Regional Decree No. 766; 6-5-1998). The MPA was established to protect the stock from overexploitation and possibly enhance nearby catches through spillover. Local fishermen have been actively involved in capturing lobsters outside the MPA. To encourage fishermen collaboration, returned individuals were valued at double their commercial price (70–90 € kg⁻¹ during the study period). Between 1998 and 2005, 3601 lobsters caught in the fishing grounds surrounding the MPA were bought from the fishermen.

Between 1997 and 2007, scientific surveys were carried out also within the MPA and 1675 lobsters were caught inside the area. Boats and fishing gears were the same as those operated by commercial fishermen, i.e. trammel nets 2.8-m high, with mesh sizes of 200 and 30 mm (inner and outer panels, respectively). Lobsters were sexed, measured (carapace length *L*, in mm), tagged with plastic T-bar-type tags inserted dorso-laterally between the first and

Fig. 1. Su Pallosu marine protected area.

second abdominal segment and eventually released in the centre of the MPA. A summary of the mark-recapture experiment is reported in Table 1. Recaptured lobsters (347 individuals) were measured to assess body growth and subsequently released in the MPA centre. Only individuals with time at liberty ≥ 1 year were considered for body growth analysis. This is a common practice in crustaceans showing periodic shedding and aims to exclude individuals captured just before a moult, avoiding a biased estimation of the growth rate (Ulmestrand and Eggert, 2001). The actual sample size used to estimate body growth was therefore reduced to 254 data matching this criterion (107 females and 147 males).

Table 1

Summary of the mark-recapture experiment performed on *Palinurus elephas* inside and outside Su Pallosu MPA (Sardinia, Italy) between 1997 and 2007.

	Location of first capture	
	Inside	Outside
Captured	1675	3601
Marked	1157	3515
Not recaptured	1068	3257
Recaptured inside (1/2/3 times)	68/8/1	114/26/4
Recaptured outside (1/2/3/4 times)	21/4/0/1	144/21/2/0

2.3. Body size trends

To assess the effect of protection on lobster size over time, we investigated the link between carapace length L and time of protection (TP), i.e. the time elapsed since the establishment of the MPA. In particular, we wanted to highlight not only possible differences in average trends, but also differences in size variability within and outside the MPA. To this end, we performed a first ANCOVA of the median L with location (in/out) as a fixed factor and TP as a covariate, and a second one with interquartile range (IQR) of L as the dependent variable. To allow the comparison of body size trends inside and outside the MPA over consistent time periods, the ANCOVA was performed only on the years in which data were collected in both locations, i.e. 1998–2002 and 2004–2005 (in 1997 and 2006–2007 sampling was conducted only within the MPA, while in 2003 no sampling was made). In order to avoid possible biases caused by their displacement, recaptured individuals (which were released in the centre of the MPA after marking) were not considered in the analysis of body size trends.

2.4. Body growth

In crustaceans, body growth is not always characterized by asymptotic patterns (Verdoit et al., 1999). To fit lobster growth in a realistic way, we used a generalized form of the classical von Bertalanffy growth model (VBGM):

$$\frac{dL}{dt} = a + bL \quad (1)$$

where a and b are parameters that can define different growth patterns. In particular, if $b < 0$ Eq. (1) is equivalent to the VBGM, where a and b can be substituted with the more familiar parameters L_∞ ($= -a/b$) and k ($= -b$); if $b = 0$, body growth is linear and characterized by a constant growth rate equal to a ; if $b > 0$, body growth follows an exponential growth pattern, with growth rate increasing linearly over time. To estimate parameters a and b from available mark-recapture data, we integrated Eq. (1) over the time interval Δt elapsed since release at marking. Thus, we obtained an estimated length at recapture $\hat{L}_r$ for each individual, to be compared with the relevant observed length at recapture L_r . By explicitly integrating Eq. (1) one obtains:

$$\hat{L}_r = -\frac{a}{b} + \left(L_m + \frac{a}{b}\right) \exp(b\Delta t) \quad (2)$$

where L_m is body length at marking.

To account for inter-individual variability, we adopted a stochastic formulation. Carapace length at recapture L_r was supposed to differ from its expected value $\hat{L}_r$ by a multiplicative error term:

$$L_r = \hat{L}_r \exp \varepsilon \quad (3)$$

where ε is a Gaussian random factor with mean zero and standard deviation $\sigma_\varepsilon \sqrt{\Delta t}$, proportional to the squared root of time elapsed since marking. This formulation assumes body growth to be affected by a lognormal noise process with variance increasing with Δt , i.e. that the following quantities

$$e_i = \frac{\ln(L_{i,r}) - \ln(\hat{L}_{i,r})}{\sqrt{\Delta t_i}} \quad (4)$$

have a Gaussian distribution with mean = 0 and standard deviation = σ_ε (an assumption that has been efficiently used for other aquatic organisms, e.g. Melià et al., 2004), where $L_{i,r}$ and $\hat{L}_{i,r}$ are observed and estimated body size at recapture of the i th individual, and Δt_i is time elapsed since release.

Model calibration was thus based on minimizing the following cost function:

$$J(a, b) = \sum_i \frac{[\ln(L_{i,r}) - \ln(\hat{L}_{i,r})]^2}{\Delta t_i} \quad (5)$$

The parameter pair (a, b) minimizing J was found with the Nelder-Mead simplex algorithm (Nelder and Mead, 1965). The relevant estimate of σ_ε was calculated as the standard deviation of vector e (Eq. (4)). Parameter uncertainty was assessed via stratified bootstrapping (Efron and Tibshirani, 1993). The original data set was subdivided into 20-mm classes, encompassing different length ranges for females (40–120 mm) and males (60–140 mm) and consisting, on average, of ca. 30 individuals per class. Data from each class were resampled 1000 times to derive empirical probability distributions for each parameter. Confidence intervals were calculated with the percentile method (Efron and Tibshirani, 1993). To account for sexual dimorphism, body growth was assessed separately for males and females.

2.5. Mortality rates

Under the assumption that a population remains stationary (i.e. there is a balance between recruitment, mortality, and immigration/emigration), mortality rate (Z) can be estimated by fitting the exponentially declining right-hand side of the age frequency curve (the well-known age frequency method; see Sparre and Venema, 1998 for details). On the other hand, if a population is increasing or decreasing with a population growth rate $r \neq 0$, the proportion of individuals in a given age class x is proportional, if the population has reached its stable age distribution, to the product $l_x \exp(-rx)$, where l_x is the proportion of survivors at age x from an original cohort (Pielou, 1977). Hence, even if the hypothesis of stationary population is relaxed and substituted with that of stable age distribution, the age frequency method can still be used. It provides the sum of mortality and population growth rate, $Z + r$, instead of Z . Data on catch per unit effort (CPUE) reported by Follesa et al. (2008) for the period 1998–2005 were used to estimate the population growth rate r inside and outside the MPA. In exploited populations, total mortality Z is the sum of natural (M) and fishing mortality (F) rates. The presence of the MPA allows the two effects to be decoupled. Within the MPA, lobsters are affected only by natural mortality, allowing the estimation of M . On the other hand, lobsters outside the MPA are subject to both mortality sources. Hence, fitting their age distribution allows the estimation of Z and (under the assumption that natural mortality does not significantly differ inside and outside the MPA) of F , which is given by the difference $Z - M$. If dispersal rates from the MPA to outside and from outside to the MPA do not balance out, the estimate of mortality rate would include also the contribution of the net emigration rate (i.e. the difference between emigration and immigration). However, available data did not allow us to discriminate between the effect of mortality and that of dispersal on the age frequency curves from inside and outside the MPA.

Due to the absence of reliable age markers in crustaceans, the age frequency method cannot be applied straightforwardly to lobster populations. However, the body growth model provides a tool to derive age distribution from the observed size distribution. According to the stochastic nature of the model, different ages can be associated to a given body length. By integrating Eq. (1) over age one can express, after some algebra, the age x of an individual with body length L as

$$x = \frac{\ln(a + bL/\exp \varepsilon) - \ln(a + bL_0)}{b} \quad (6)$$

Fig. 2. Analysis of covariance of (a) median and (b) interquartile range of carapace length for *Palinurus elephas* inside and outside Su Pallosu marine protected area, with location (in/out) as a factor and time of protection (since the establishment of the MPA) as a covariate. A single regression line is shown in panel a), indicating that the effect of location is not significant (see text for details).

where L_0 is carapace length at age 0 [here assumed to be 8.5 mm according to Marin (1985) and Diaz et al. (2001)] and ε is the multiplicative noise term, introduced in Eq. (3). To estimate mortality rates, we applied the following procedure: (1) for each individual of the sample, we extracted a value of ε from a probability distribution with mean = 0 and standard deviation = σ_ε ; (2) we used that value, together with the carapace length L of the same individual at first capture, to estimate the corresponding age x via Eq. (6); (3) after assigning an age to all individuals, we built the empirical age distribution of the sample; (4) we used that age distribution to estimate mortality with the age frequency method. We repeated steps (1)–(4) 1000× to associate a probability distribution to the estimate.

3. Results

3.1. Body size trends

When Su Pallosu MPA was established, in 1998, the body size structure of lobsters was the same inside and outside the MPA, with a median carapace length L of 64 mm and an IQR of 11 mm. Since MPA implementation, body size structure varied significantly (Fig. 2). ANCOVA of median L with location (in/out) as a factor and TP as a covariate (Fig. 2(a)) showed no significant interaction between TP and location ($F_{3,10} = 0.01$; $p > 0.20$) and no significant

Fig. 3. Comparison between observed and predicted carapace length of *Palinurus elephas* inside and outside Su Pallosu MPA.

difference in trends between locations ($F_{2,11} = 0.21$; $p > 0.20$), while the effect of TP was positive and highly significant ($F_{1,12} = 35.0$; $p < 0.01$) with median L increasing, on average, by 1.9 mm per year between 1998 and 2005. On the other hand, a significant interaction between TP and location affected body size variability in the same period (Fig. 2(b)), with carapace length IQR increasing by 0.9 mm per year inside the MPA and decreasing 0.6 mm per year in the adjacent fishing grounds ($F_{3,10} = 2.10$; $p < 0.1$). Differences between locations were also very clear with respect to the percentage of individuals larger than the minimum legal size in force during the study period ($L > 80$ mm: 33% inside and only 4% outside, where no individual > 100 mm was ever fished).

3.2. Body growth

Basic statistics for model parameters are given in Table 2. The classical VBGM provided the best match to observed length increments. Coefficient b (Eq. (1)) was indeed negative in all bootstrap iterations. Fig. 3 compares observed versus predicted L at recapture as obtained with Eq. (2) by setting model parameters to the median value of the relevant bootstrap distributions, and evidences the good predictive performances of the models ($R^2 = 0.75$ for females and $R^2 = 0.79$ for males). Estimates of σ_ε obtained from Eq. (5) are reported in Table 2 and indicate a higher inter-individual variability in males rather than females. The stochastic model (Eq. (3)) was run over 15 years to generate, through Monte Carlo simulation, the average body growth curves along with their associated probability distributions. Results are shown in Fig. 4. On average, males grow faster than females and attain a bigger body size. This is also confirmed by the growth performance index $\Phi = \log_{10} k + 2 \log_{10} L_\infty$ (Munro and Pauly, 1983), which was higher in males than in females (3.5 vs. 3.3).

3.3. Mortality rates

Age frequencies and their variability, obtained via Eq. (6), are shown in Fig. 5 along with the relevant fitting curves. Population growth rates r , estimated through log-linear regression on CPUE data, were 0.14 year^{-1} and 0.08 year^{-1} inside and outside the MPA, respectively. The resulting estimate of mortality rate within the MPA (providing an estimate of natural mortality M , inclusive of the net contribution of dispersal) was 0.27 year^{-1} (95% C.I.: $0.24\text{--}0.31 \text{ year}^{-1}$) corresponding to an annual survival probability = 76%. The estimated mortality rate outside the MPA (providing an estimate of total mortality Z , inclusive of dispersal)

Table 2

Basic statistics of *Palinurus elephas* body growth parameters (Eq. (1)), as obtained by bootstrap calibration on the 1997–2007 dataset. σ_ε : standard deviation of residuals as from Eq. (4).

Units		Exp. value $\pm$ SD	Median	Percentiles		SD of residuals
				2.5th	97.5th	
Females						
a	(mm year ⁻¹)	18.2 $\pm$ 2.1	18.2	14.4	22.3	2.2×10^{-3}
b	(year ⁻¹)	-0.16 $\pm$ 0.03	-0.16	-0.21	-0.11	
L_∞	(mm)	117 $\pm$ 7	116	106	134	
k	(year ⁻¹)	0.16 $\pm$ 0.03	0.16	0.11	0.21	
σ_ε	(year ^{-0.5})					
Males						
a	(mm year ⁻¹)	17.7 $\pm$ 1.5	17.8	14.8	20.6	2.8×10^{-3}
b	(year ⁻¹)	-0.10 $\pm$ 0.02	-0.10	-0.13	-0.06	
L_∞	(mm)	189 $\pm$ 24	185	155	247	
k	(year ⁻¹)	0.10 $\pm$ 0.02	0.10	0.06	0.13	
σ_ε	(year ^{-0.5})					

was 0.70 year⁻¹ (95% C.I.: 0.65–0.75 year⁻¹) corresponding to an annual survival probability = 50%. The resulting estimate of fishing mortality was $F = Z - M = 0.43$ year⁻¹.

4. Discussion

Our results show that lobster size structure within Su Pallosu MPA changed over time in a significantly different way from that in the adjacent fishing area, suggesting that MPA protection of larger individuals has been effective and corroborating the idea that even small MPAs can produce significant biological responses (Lester et al., 2009). Average carapace length of lobsters caught in the fishing grounds surrounding Su Pallosu (66 and 67 mm for females and males, respectively) is very close to that reported by Tidu et al. (2004) in another Mediterranean fishing area (68 and 71 mm). In contrast, sizes observed by Goñi et al. (2001) in a 14 km² MPA in the western Mediterranean were bigger (86 and 110 mm for females and males, respectively) than within Su Pallosu MPA (68 and 73 mm). Although recent studies indicate that *P. elephas* undertakes limited movements, ca. 2.5 km year⁻¹ (Goñi et al., 2006; Follesa et al., 2009), it should be noted that the maximum distance from the centre of Su Pallosu to the MPA boundary is only 1.44 km. Therefore, adult spillover favoured by the small dimensions of Su Pallosu MPA (<4 km²) might have blurred the effect of protection on body size within the MPA. Also, the increase in mean body size caused by the protection of larger individuals may have

Fig. 5. Estimated age distributions (median values and 90% confidence intervals) of *Palinurus elephas* inside and outside Su Pallosu MPA along with relevant fitting lines (y-axis in log-scale).

been reduced by the increasing presence of juveniles, as suggested by higher body size variability within the MPA. In any case, average lobster size at Su Pallosu might keep increasing in the coming years (as observed in other long-term studies on MPAs: e.g., Claudet et al.,

Fig. 4. Simulated body growth of *Palinurus elephas* obtained by Monte-Carlo simulation (1000 iterations of 15 years duration with carapace length = 8.5 mm at age 0). Thick lines: median value; thin lines: 90% confidence intervals. The small panels on the right show the size distribution at three representative ages (5, 10 and 15 years).

2008; Stobart et al., 2009) and eventually attain values similar to those observed by Goñi et al. (2001). The recovery time of protected species has important implications for the assessment of MPA efficacy and the management of surrounding fisheries (McClanahan et al., 2007). For instance, Pande et al. (2008) found that the response of rock lobster body size requires on average 8.5 year since the establishment of an MPA to become fully apparent. Our results suggest that for long-living species, such as *P. elephas*, a 10-year horizon can provide only partial evidence of the benefits of an MPA.

The long-term mark-recapture experiment provided valuable information on somatic growth in *P. elephas*. Marked individuals were always released in the MPA centre, irrespective of the capture location, with the aim to increase recapture probability. This experimental design might, in principle, have influenced vital traits such as body growth or survival, due to increased lobster density within the MPA. However, the low recapture rates observed during the study period (Table 1) suggest that the displacement of some individuals from outside to inside the MPA has likely had only a minor effect on local lobster abundance. The adequacy of the VBGM to model body growth in aquatic organisms has been questioned by several authors (Katsanevakis and Maravelias, 2008). In fact, non-asymptotic growth patterns have been observed in a number of fish (Curtis and Shima, 2005) and aquatic invertebrates (e.g. Jackson and Choat, 1992; Semmens et al., 2004). For this reason, we used a more general growth model (Eq. (1)), including the VBGM as a special case. Our results indicate that the VBGM provides a satisfactory description of body growth in *P. elephas*. As expected, the model predicts, on average, higher growth rates in males than in females. Sexual dimorphism is indeed common in lobsters (Goñi and Latrouite, 2005), as reproductive females allocate a significant amount of energy in reproduction, while males grow at a sustained rate after sexual maturity. Up to now, studies on body growth of *P. elephas* have been very few (Hepper, 1977; Marin, 1985; Follesa et al., 2007b) and none of them has explicitly considered variation among individuals. However, inter-individual variability affects a number of vital traits (including morphological, physiological and behavioural life history features), with important consequences for population dynamics, stability and persistence (Filin and Ovadia, 2007). Incorporating body growth variability into demographic models is important to provide realistic recruitment estimates and reliable MPA assessments (Pitchford et al., 2007; De Leo et al., 2009).

The method proposed here to assess mortality rates is a modification of the standard method based on age frequency distributions, which may prove particularly helpful for organisms lacking reliable age markers such as crustaceans. Combined with a non-parametric approach based on stratified bootstrapping, it provides also a powerful tool to assess the uncertainty associated to parameter estimates. Resulting estimates of natural mortality M for *P. elephas* (ranging between 0.24 and 0.31 year⁻¹) can be compared with those obtained in previous studies on other Mediterranean populations. They overlap with the range (0.15–0.30 year⁻¹) proposed by Marin (1987) on the basis of speculative arguments and, partially, with that (0.14–0.26 year⁻¹) derived by Goñi et al. (2010) through a modelling approach. In contrast, they are considerably higher than the point estimate (0.11 year⁻¹) obtained by Hepper (1977) with tag-recapture experiments in Atlantic populations. The discrepancy between those figures and ours might be due to actual differences in mortality rates between regions (Atlantic vs. Mediterranean), to differences in methodological assumptions, or to the bias caused by the effect of lobster dispersal. As for possible geographical differences, mortality rates are indeed known to increase non-linearly with water temperature in a wide range of aquatic organisms (McCoy and Gillooly, 2008; Bevacqua et al., 2010). With respect to methodology, it should be noted that our estimates have been derived under the hypothesis that the lobster population has

reached its stable age distribution. The hypothesis might be quite far from being met, because the age structure might be still shifting towards older age classes following the closure of the fishery. The transient from an age structure shaped by fishing mortality to one determined only by natural mortality is possibly further delayed by the immigration from the fishing grounds to the MPA. As for the effect of lobster dispersal, it should be noted that our estimate of M encompasses the effect of spillover from the MPA, and may therefore overestimate the actual natural mortality rate within the range of protection. On the other hand, the effect of spillover on the estimation of total mortality Z in the fishing grounds may have caused a slight underestimation of this parameter and, consequently, of fishing mortality F (calculated as the difference $Z - M$). Finally, the assumption that natural mortality is not significantly different inside and outside the MPA would be violated if a higher density of predators determined a higher rate of natural mortality within the MPA (see, e.g., Diaz et al., 2005), causing a further underestimation of fishing mortality. For these reasons, our estimate of F should be considered as a conservative evaluation of the actual pressure exerted by fishermen. Although dedicated studies focusing on the dispersal of lobsters across the MPA boundaries and on the ecological interactions involving lobsters and predatory fish species benefiting from the MPA would be highly desirable to refine the assessment of mortality rates, we are confident that the methodology proposed here represents an improvement over other techniques commonly used in stock assessment, which are often based on more stringent hypotheses (such as population stationarity).

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