Decadal trend in lobster reproductive output from a temperate marine protected area

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ABSTRACT: Increased recruitment from eggs and larvae exported from marine protected areas (MPAs) is anticipated to produce much greater benefits for exploited populations than spillover of adults. However, resolving the link between local egg production and regional recruitment is beyond current research capabilities, and quantifying the contribution of the MPA to regional reproductive output is the first step towards evaluating such potential. In this study, we assessed the egg production of spiny lobsters *Palinurus elephas* in the Columbretes MPA (western Mediterranean, Spain) and its contribution to regional reproductive output over the decade corresponding to years 10 to 19 of protection. We show that: (1) Mean female fecundity in the MPA increased by 41 % over the 10 yr of study and in recent years was more than twice the fecundity in the nearby fished areas. (2) At the end of the study, mature females were on average 20 times more abundant, and egg production per unit area was 30 times greater in the MPA than in nearby fished areas. (3) At that time, the MPA, occupying 18 % of the regional lobster habitats, was responsible for over 80 % of the regional egg production. Overall, we estimate that after nearly 2 decades of protection, regional egg production was 6 times greater than would have been without the MPA. When compared to a net benefit through biomass spillover from the MPA to the regional lobster fishery of +11 % of the annual catch, a 6-fold increase in egg production suggests that egg and larval export have far greater potential than spillover to benefit exploited populations.

KEY WORDS: Marine reserve · Mean fecundity · Reproductive contribution · Spiny lobster · *Palinurus elephas*

INTRODUCTION

Marine protected areas (MPAs) that effectively rebuild biomass of exploited species within their boundaries are expected to benefit local fisheries through biomass spillover and export of eggs and larvae (Hilborn et al. 2004). Biomass spillover of adults has now been quantified (e.g. Goñi et al. 2010) or demonstrated from tag–recapture experiments (e.g. Tupper 2007, Goñi et al. 2010) and inferred from spatial or temporal patterns of catch and effort (see review by Goñi et al. 2011). Observable adult spillover effects documented so far, even if significant, are limited to a few hundred or thousand metres from MPA boundaries (Goñi et al. 2006, 2008, Halpern et al. 2010). In contrast, egg and larvae export and their effects on recruitment are anticipated to produce much greater benefits for fisheries than spillover (e.g. Jennings 2001, Russ 2002, Moffitt et al. 2009). However, the potential effect of exported larvae on recruitment enhancement is hard to assess due to the high spatial and temporal variability of larval survival and settlement, as well as the large area over which larvae may disperse (e.g. Botsford et al. 2009). This has hampered research, and few empirical studies have addressed the recruitment effects of MPAs. At present, and despite their intuitiveness, empirical evidence of such MPA recruitment effects on exploited populations remains elusive, and most research is currently focused on unravelling larval dispersal and population connectivity patterns through genetic paternity studies (e.g. Jones et al. 2009, Planes et al. 2009).

The potential of MPAs as seeding areas of exploited species demands evaluation, despite the difficulties of

resolving the link between local egg production and regional recruitment. Differences in reproductive output of populations within and outside MPAs have been assessed in fishes (Denny et al. 2004, Evans et al. 2008) and molluscs (Manríquez & Castilla 2001), but lobsters have received the most attention. In particular, Babcock et al. (2007) found that after 17 yr without fishing, egg production of *Panulirus cygnus* per unit area in a small Western Australian MPA was 100-fold higher than in fished areas. In most cases, however, reported differences have been much less pronounced. For example, egg production of *Jasus edwardsii* was estimated to be 8 times higher in a New Zealand MPA 15 yr after fishing ceased than in exploited areas, and only 3 times higher in a newer 3 yr old MPA (Jack & Wing 2010). That greater egg production in MPAs relies on recovery of numbers and size of protected individuals was shown in a study of 3 South African MPAs that were ineffective at rebuilding lobster *J. lalandii* biomass (Mayfield et al. 2005). Most studies have been based on one-time spatial comparisons of unfished and fished areas, and temporal effects have at best been inferred indirectly by comparing MPAs of different age. Kelly et al. (2000) estimated a 6 % annual increase of lobster *J. edwardsii* egg production by combining studies from 3 New Zealand MPAs. Trends over time in a single location have not been evaluated and therefore the time dynamics of reproduction and recruitment potential are unclear.

In the Columbretes Islands MPA, the effects of the cessation of fishing on egg production of the European spiny lobster *Palinurus elephas* were studied 8 to 10 yr after its establishment (Goñi et al. 2003a). A spatial comparison indicated that egg production per unit area was 5 to 20 times greater in the MPA than in fished areas depending on the season. Monitoring was continued until 19 yr after the MPA creation, thus providing the first decade-long time series of egg production change in an MPA. This paper assesses the egg production of *P. elephas* in the MPA and its contribution to regional reproductive output between the 10th to 19th years of protection. Our goals were to estimate female fecundity and egg production in the MPA and adjacent fished areas over time to determine the fraction of regional egg production contributed by the MPA. To evaluate this, we used female lobster size, published size–fecundity relationship (Goñi et al. 2003a), and catch per unit effort (CPUE) information from fishing surveys conducted in and outside the MPA.

MATERIALS AND METHODS

Species. *Palinurus elephas* is a deep-water, temperate spiny lobster species widely distributed in the Northeast Atlantic and the Mediterranean. It inhabits rocky and coralligenous habitats from near shore to depths of 200 m; in the study area, this species reaches maximum densities at depths of 60 to 90 m, and adults are rare above 40 m depth (Goñi et al. 2003b). *P. elephas* is a long-lived (maximum estimated age 20+ yr; Díaz 2010), slow-growing species that reproduces once a year (Goñi & Latrouite 2005). In the Mediterranean, *P. elephas* matures at age 3 to 4 yr (~80 mm carapace length, CL), the egg-bearing period extends from September to February (Goñi et al. 2003a), and moulting of males (females) peaks in winter (spring) (Goñi & Latrouite 2005). Tagging studies conducted in the Atlantic and Mediterranean indicate that adult movement is restricted, with most individuals moving < 5 km, although there are occasional reports of recaptures up to 70 km away (Goñi & Latrouite 2005). Inshore–offshore migrations linked to reproduction and feeding have been reported for both Atlantic and Mediterranean populations, and have been inferred for the MPA population on the basis of seasonal bathymetric changes in size and sex structure (Goñi et al. 2001).

Study site and fishery. The study was carried out in the Columbretes Islands MPA (western Mediterranean, Spain) and surrounding fishing grounds. Situated 50 km from the coast at the edge of the continental shelf, the MPA protects 44 km^2 (expanded to 55 km^2 in 2009) of volcanic rock and coralligenous habitats (maërl beds), with patches of gravel, sand or mud extending down to 80 m depth. The regional fishing grounds near the MPA consist of patches of rock or maërl over expanses of gravel, sand and mud primarily at depths of 50 to 100 m and extending up to 30 km from the MPA limits. No lobster fishing occurs beyond those grounds, which are surrounded by sandy substrates where bottom trawl groundfish fisheries operate. The MPA harbours traditional fishing grounds of *Palinurus elephas*; legislation prohibits all commercial fisheries and all lobster fishing, and these regulations are well enforced.

Commercially, *Palinurus elephas* is the most important spiny lobster in the Mediterranean and Northeastern Atlantic. In most western Mediterranean fisheries, lobsters are caught with trammel nets set over rocky and coralligenous habitats. Trammel nets are groups of 3 rectangular nets made up of 2 outer, large-mesh panels and 1 inner, smaller-mesh panel (see Goñi et al. 2003b for further details). Northwestern Mediterranean fisheries are managed by a closed season during the egg-bearing period (September to February), a minimum landing size of 90 mm CL and the prohibition of landing berried females.

Although Mediterranean populations are highly depleted and considered overfished, they are still tar-

geted by small artisanal boats in many areas, especially around archipelagos and islands (Goñi & Latrouite 2005). The MPA was established in an offshore location, exploited by only a few boats large enough to venture that far and, after the MPA creation, the number of boats further declined. During the study period, 3 to 4 boats fished consistently through the season from 2000 to 2003, and only 2 boats operated in later years; however, increased effort per boat in recent years has maintained regional effort (Goñi et al. 2010).

Spatially, lobster fishing is distributed near the MPA (<1 km from the boundary: border zone), in adjacent grounds up to 5 km from the MPA (1 to 5 km from the boundary: adjacent zone) and in patchily distributed grounds farther away (5 to 30 km from the boundary: far zone; Fig. 1).

Data collection. Data on catch, effort and female size (CL measured from the tip of the rostral spine to the posterior edge of the carapace, in mm), were obtained from experimental and commercial fishing operations as follows:

MPA: Experimental fishing surveys inside the MPA were conducted annually since 1997, 7 yr after MPA creation. Although the timing of the survey and gear used were varied initially, standardised data all collected in June with trammel nets are available from 2000 to 2009, totalling 217 fishing sets (n = 102 at ≤50 m and 115 at >50 m). The surveys were conducted by a chartered commercial boat and crew who fished with trammel nets identical to those used in commercial operations described below and following a random sampling design over rocky and coralligenous habitats where lobsters are known to occur, and from 25 to 80 m depth (maximum depth in the MPA). See Goñi et al. (2003b) for a detailed description of the survey methods.

Adjacent fishing grounds: Data from the commercial fishery were recorded from 2000 to 2009 during the 6 mo (March to August) annual lobster fishing season. Whenever possible, sampling took place during 1 wk mo^{-1} on board one of the boats that consistently fished in the region. The observer sampled all fishing sets that were carried out in that week, recording data on net length, location, depth and lobster catch. Over the study period, 684 fishing sets (border = 266, adjacent = 187, far = 231) were recorded within 30 km of the MPA boundary (Fig. 1).

Data analysis. *Mean female fecundity:* Average female fecundity (FF, no. eggs female^{-1}) was estimated from the size composition of female lobsters in the catch using the size–fecundity (F) relationship obtained for *Palinurus elephas* in the MPA: F = 2428 × CL (mm) − 148 988, and assuming a knife-edge maturity schedule with size at maturity of 78 mm CL (Goñi et al.
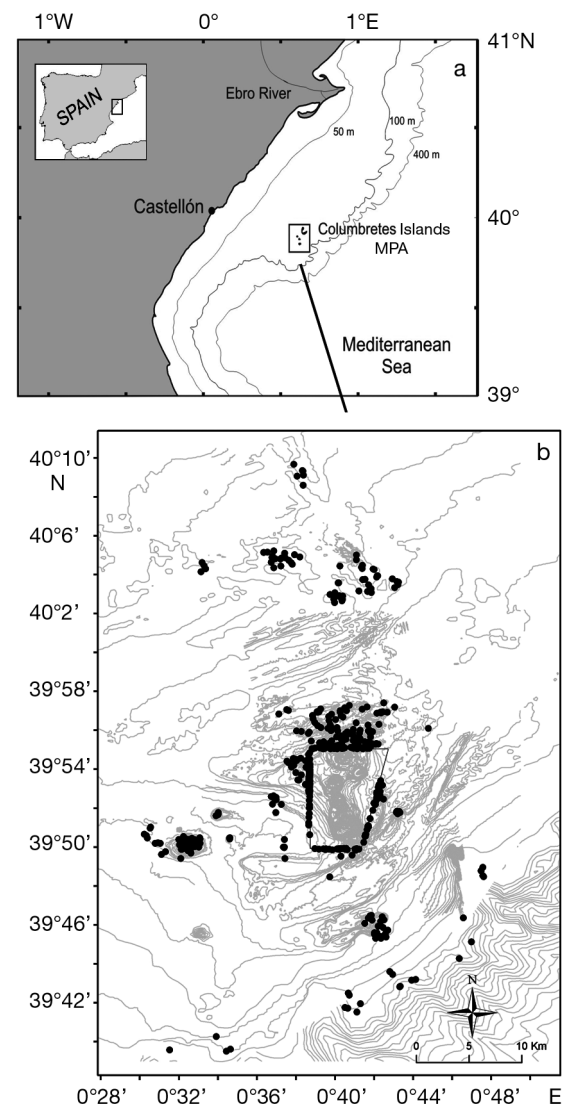

Fig. 1. Columbretes Islands marine protected area (MPA) on the continental shelf of the Iberian Peninsula (a) and bathymetric map of the region (b). Dots are commercial fishing sets sampled and illustrate the spatial distribution of lobster fishing effort in the region

2003a). Linear regression models and a power curve were fitted to average FF as a function of time (yr 2000 to 2009) to estimate trends in 2 strata within the MPA: shallow (≤50 m) and deep (>50 m), and in the fished area outside the MPA ('outside'). The significance of non-linear trends (i.e. power coefficient different than 1) was assessed by comparing the linear and power models using likelihood ratio tests. FF in the MPA and in fished areas at increasing distances from it (border, adjacent and far) were estimated for the most recent 3 yr period (2007 to 2009) and compared by 1-way analysis of variance (ANOVA). A Tukey multiple

comparison test was used after ANOVA to investigate differences between means.

Egg production per unit area: The study area was divided in 1×1 km spatial cells, and fishing sets were assigned to the corresponding cells. Female CPUE was calculated for each cell as the total number of female lobsters caught divided by the total number of nets (net length = 50 m) deployed in that cell. Egg production (number of eggs) per unit area (EPUA) was estimated from the cell mean FF multiplied by the cell CPUE. Average EPUA for the 2 depth strata (shallow: ≤50 m; deep: >50 m) was calculated as a simple average over sampled cells. The SE of the average EPUA was estimated by bootstrap in 2 steps to mimic the 2-stage sampling method used in the surveys: (1) cells were resampled with replacement and (2) females caught within each resampled cell were resampled to calculate the cell EPUA. The SD of the average EPUAs for each stratum was calculated after repeating the 2-stage resampling 1000 times.

Annual trends in average EPUA between 2000 and 2009 in the shallow and deep strata of the MPA and in the fishing grounds outside the MPA were estimated using linear regression and a power curve. Models were compared using likelihood ratio tests. Average EPUA in the MPA and in fished areas at increasing distances from it (border, adjacent and far) were estimated for the most recent 3 yr period (2007 to 2009) and compared by 1-way ANOVA. A Tukey multiple comparison test was used after ANOVA to investigate differences between means.

MPA contribution to regional egg production: To assess the MPA contribution to regional egg production ($EPUA_{MPA}$) over time, we first calculated the EPUA for the whole region ($EPUA_{tot}$) as:

$$EPUA_{tot} = \sum_i EPUA_i \times A_i \qquad (1)$$

where $EPUA_i$ is the average EPUA for zone i (i = MPA, border, adjacent, far), and A_i is the fraction of regional lobster habitat in zone i. The extension of the regional lobster grounds outside the MPA was calculated as the sum of all 1×1 km cells where at least 1 fishing set was registered since the start of the study in 1997. Within the MPA, all 1×1 km cells encompassing lobster habitats (i.e. excluding sand and mud substrate) were counted as lobster grounds. The regional lobster grounds cover 189 km^2, of which the MPA occupies 34 km^2.

The fraction of regional egg production coming from the MPA was calculated as:

$$\%MPA = EPUA_{MPA} \times A_{MPA} / EPUA_{tot} \qquad (2)$$

MPA difference in system-wide egg production: We estimated the difference in egg production attributable to the MPA by comparing the regional egg production

$EPUA_{tot}$ with and without MPA in recent years (2007 to 2009). To do this, we assumed that the mean EPUA of the system without the MPA would have been the same as the mean EPUA estimated for the fished area ($EPUA_{out}$). We then calculated $relEPUA_i$, defined as the $EPUA_i$ for each zone i relative to that baseline $EPUA_{out}$ as:

$$relEPUA_i = EPUA_i / EPUA_{out} \qquad (3)$$

The net effect of the MPA on egg production was the sum of the relative $EPUA_i$ in the 4 zones (i = MPA, border, adjacent, far) multiplied by the fraction of the regional lobster habitat in each zone (A_i):

$$\Delta relEPUA = \sum_i relEPUA_i \times A_i \qquad (4)$$

RESULTS

Mean female fecundity (FF)

Mean FF in the MPA increased by 41% over the first 8 yr of the study period, from a mean value of 92 300 eggs female^{-1} in 2000, and remained stable during the latter 3 yr ($F = 0.04$; $p > 0.99$; Tukey's multiple comparison tests $p > 0.96$; Fig. 2). Despite this recent stabilisation, the linear model was selected in favour of the power curve (likelihood ratio test = 0.65, df = 1, p = 0.42). Mean FF was greater in shallow than in deep waters within the MPA (Fig. 2; $t = 5.06$, $p < 0.000$), but the trends over time were not significantly different ($t = 1.76$, $p = 0.098$). This bathymetric difference reflected the greater proportion of large females in shallow than in deep areas of the MPA (Fig. 3a,b).
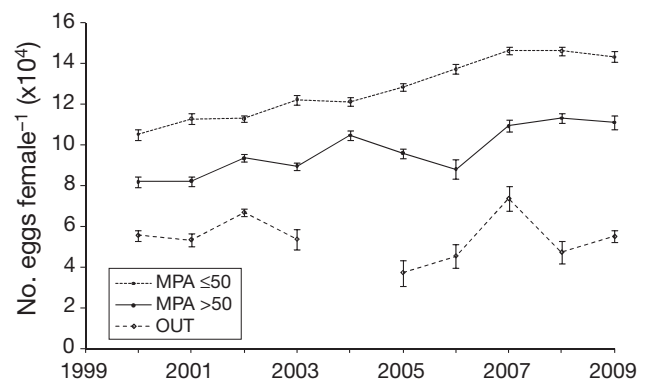

Fig. 2. *Palinurus elephas.* Trend of female fecundity (FF, number of eggs) in the shallow (MPA ≤ 50 m) and deep (MPA >50 m) strata within the marine protected area (MPA) and in the fished area outside (OUT). Means ±1 SE

In the fished area, mean FF oscillated episodically (Fig. 2, Table 1). In the latter years, mean FF in the MPA was 2.3 times greater than in the fished areas. Although FF was not significantly different among the 3 fished zones (F = 1.97, p = 0.14; Tukey's multiple com-

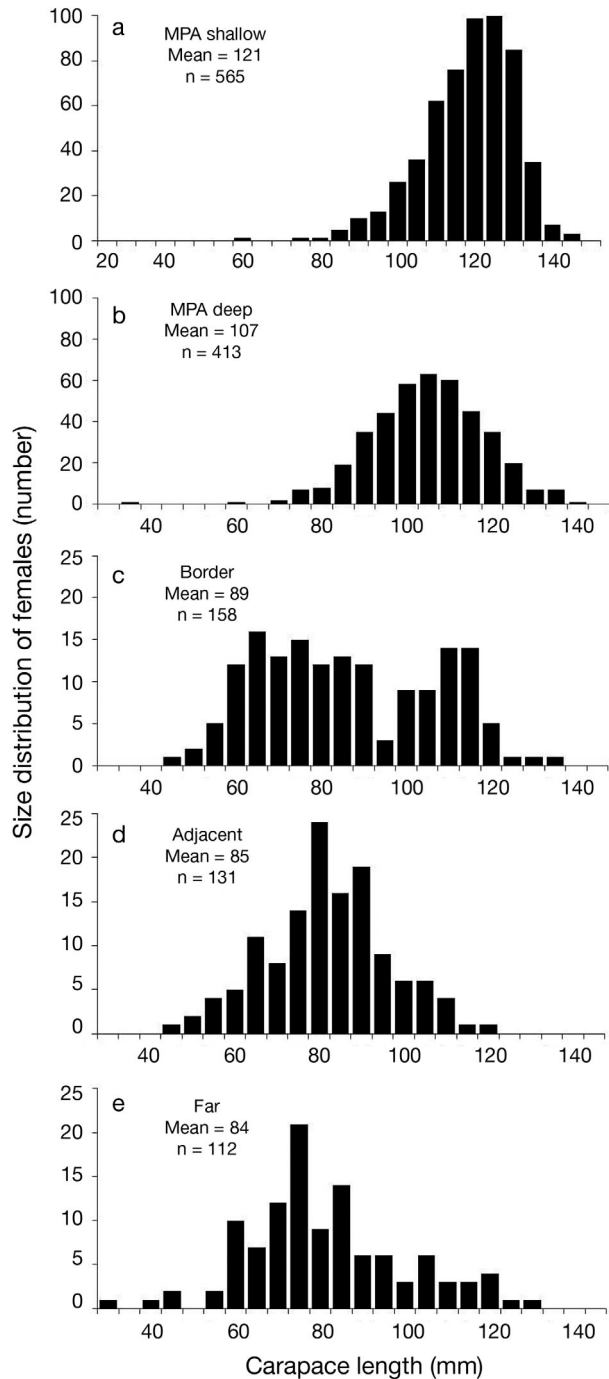parison tests p > 0.05), FF in the border area (<1 km from the MPA) was on average higher than in farther fishing grounds (Table 2), in correspondence with the greater proportion of large females in that zone (Fig. 3c–e).

Egg production per unit area (EPUA)

In the MPA, mean EPUA oscillated episodically (Fig. 4). The linear model was selected over the power curve (likelihood ratio test = 0.44; df = 1; p = 0.51), but the slope was not significantly different than 0 (Table 1). Oscillations of EPUA in the MPA were dominated by variations of mature female CPUE (not shown), which declined slightly, primarily in deep waters (Table 1). This did not translate into a significant decline of EPUA in the overall MPA (p = 0.123) due to the concomitant increase of mean female size, and therefore fecundity, particularly in shallow waters (Table 1).

In the fished area, EPUA remained stable over the study period, as did mature female CPUE (Table 1), which was on average 14 times lower than in the MPA (not shown). In recent years, mean EPUA in the MPA (Table 2) was about 30 times greater than in the fished grounds ($EPUA_{out}$ = 6.8 × 10³ eggs). During 2007 to 2009, EPUA was on average 30% higher in the border zone and 20% lower in the distant zone than the EPUA for the overall fished area $EPUA_{out}$ (Table 2).

MPA contribution to regional egg production

The fraction of regional egg production originating in the MPA increased from 0.73 to 0.87 over the study period (Fig. 5). After 17 to 19 yr of protection, regional
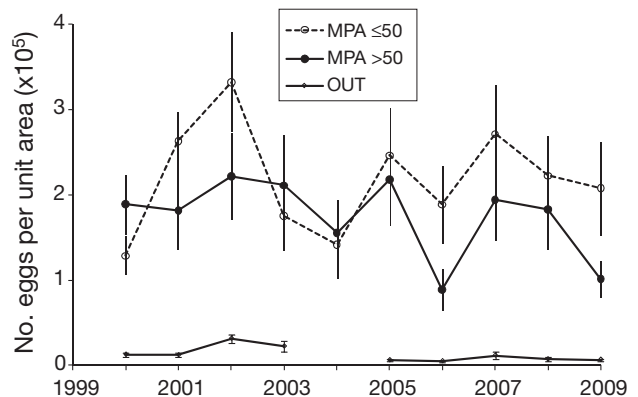

Fig. 3. *Palinurus elephas.* Size distribution of females (number) in (a) marine protected area (MPA) shallow (≤50 m) and (b) MPA deep (>50 m) strata and (c) in fished areas outside within 1 km of the MPA (Border), (d) at 1 to 5 km (Adjacent) and (e) at >5 km (Far). Data of 2007 to 2009 combined

Fig. 4. *Palinurus elephas.* Trend of egg production per unit area (EPUA, number of eggs) in the shallow (MPA ≤50 m) and deep (MPA >50 m) strata within the marine protected area (MPA) and in the fished area outside (OUT). Means ±1 SE

Table 1. *Palinurus elephas.* Linear regressions of female fecundity (FF), egg production per unit area (EPUA) and catch per unit effort (CPUE: number of lobsters net^{-1}) as a function of time in the shallow (≤50 m) and deep (>50 m) strata within the marine protected area (MPA), and in the fished area outside (OUT). SE of the parameter estimates in parentheses. Significant values (p < 0.05) in **bold**

	Intercept	Slope	t	p
FF				
MPA ≤50 m	105887 (2290)	4821 (429)	11.240	**<0.001**
MPA >50 m	82013 (3986)	3306 (747)	4.428	**0.002**
OUT	55656 (7060)	−339 (1291)	−0.263	0.800
EPUA				
MPA ≤50 m	210227 (38941)	1669 (7294)	0.229	0.825
MPA >50 m	207822 (25129)	−7424 (4707)	−1.577	0.153
OUT	19624 (4694)	−1502 (859)	−1.749	0.124
CPUE				
MPA ≤50 m	1.89 (0.32)	−0.04 (0.06)	−0.692	0.508
MPA >50 m	2.29 (0.24)	−0.12 (0.05)	−2.606	**0.031**
OUT	0.22 (0.04)	−0.02 (0.01)	−2.190	0.065

egg production in the system with the MPA was estimated to be 6 times greater than without the MPA at the latter levels of lobster depletion (Table 2).

DISCUSSION

An expected benefit of protecting overexploited populations is the enhancement of reproduction and subsequent increases in egg and larval export (Jennings 2001, Russ 2002, Moffitt et al. 2009). This study indicates that mean fecundity of *Palinurus elephas* in the Columbretes Islands MPA increased substantially over time, and after 2 decades of fisheries closure, MPA fecundity accounted for 80% of the regional egg production despite occupying only 18% of lobster habitats. As a result, the system with the MPA produced 600% more eggs than without an MPA. During the 10 yr of study, this benefit was maintained by the

growing size of mature females in the protected population rather than by their abundance, which did not increase.

Growth in size translates linearly into increased egg production due to the linear relationship between fecundity and female CL observed in *Palinurus elephas* (De Vasconcellos 1960, Goñi et al. 2003b, Galhardo et al. 2006), similarly to other *Palinurus* species (e.g. *P. gilchristi,* Groeneveld 2005). This is in contrast to spiny lobsters of the genera *Panulirus* and *Jasus*, where fecundity has been shown to increase exponentially with size (e.g. *P. marginatus*: DeMartini et al. 2003; *P. penicillatus*: Chang et al. 2007; *P. cygnus*: Babcock et al. 2007; *P. regius*: Freitas et al. 2007; *J. edwardsii*: Smith & Ritar 2007, Green et al. 2009, Linnane et al. 2009). Because of the linearity of the fecundity–size relationship, in *P. elephas* benefits of protection for egg production will not increase exponentially with time as would in other spiny lobsters, and egg production per unit biomass will decline in larger females (Goñi et al. 2003a).
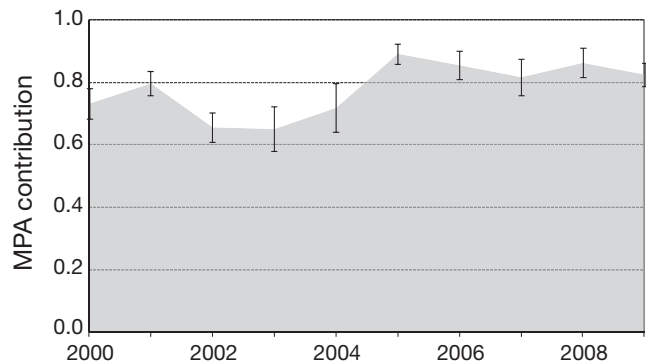

Fig. 5. *Palinurus elephas.* Fraction of regional egg production contributed by the marine protected area (MPA; grey) over time. Vertical lines represent ± 1 SE

Table 2. *Palinurus elephas.* Reproductive contribution of the marine protected area (MPA). Statistics for each zone *i* are: mean female fecundity (FF$_i$; in thousands), egg production per unit area (*EPUA$_i$*; in thousands), fraction of regional lobster habitat (*A$_i$*), mean *EPUA$_i$* relative to mean *EPUA* in the fished area (Relative *EPUA*), contribution to regional egg production (Relative *EPUA$_i$*× *A$_i$*) and relative *EPUA* weighed by the fraction of lobster habitat in each zone (% of total egg production). Zones: MPA, Border (fished area within 1 km of the MPA), Adjacent (fished area within 1 to 5 km of the MPA) and Far (fished area within >5 km of the MPA). Data are means (SE) of the period 2007 to 2009

Zone	FF$_i$	*EPUA$_i$*	Fraction of habitat (*A$_i$*)	Relative *EPUA* (*EPUA$_i$*: *EPUA$_{out}$*)	Relative *EPUA$_i$* × *A$_i$*	% of total egg production
MPA	130.9 (1.1)	202.6 (20.9)	0.18	29.66	5.34	87
Border	61.9 (4.3)	9.0 (2.4)	0.12	1.32	0.16	3
Adjacent	54.5 (3.4)	7.1 (1.5)	0.27	1.04	0.28	5
Far	50.5 (4.6)	5.5 (1.5)	0.43	0.80	0.35	5
Total	–	–	1	–	6.12	100

Mean FF in the MPA increased by 41% during the 10 yr of study and in recent years was more than twice the average FF in the fished area. A similar difference in mean fecundity between unfished and fished populations was found for *Panulirus argus* in the Dry Tortugas National Park (Florida, USA) after 20 yr of protection (Bertelsen & Matthews 2001). Interestingly, in both cases these effects were evaluated after protection periods close to the maximum life span of these species when the cohorts present had not been affected by fishing.

Although we could not reject an overall linear increase over the whole study period, mean FF in the MPA has been stable over the last 3 yr, suggesting that size and therefore potential fecundity may be approaching an asymptote. Tag–recapture data of *Palinurus elephas* in the MPA indicate a marked reduction in female growth well before they reach their potential maximum size (L_{max} = 145 mm CL; Díaz 2010). *P. elephas* is a slow-growing species with an estimated maximum age of 20+ yr (Díaz 2010). Hence, after 19 yr without fishing, the largest lobsters in the MPA should be close to L_{max}, and a limit to the contribution of female size to egg production may have been reached. Further egg production increases would depend on recruitment of young females to the brood stock.

FF in the fished area remained stable over the decade of study. Outside the MPA, female size oscillated around a mean of 84 mm CL, slightly above the size at maturity (Goñi et al. 2003b) and below the minimum landing size of 90 mm CL. Dramatic reductions of spawning potential in exploited areas associated with severely reduced abundance of large females have been also documented for *Panulirus argus* (Lyons et al. 1981) and *Jasus edwardsii* (Kelly et al. 2000). High exploitation rates characterise many spiny lobster fisheries, where few lobster in the legal size classes escape the fishery every year (e.g. Rowe 2001, Iacchei et al. 2005). Notably, mean FF near the MPA, slightly higher than in farther fishing grounds, reveals the process of spillover documented for *Palinurus elephas* whereby migrants exiting the MPA and caught in the adjacent fishery were about 30% larger than local lobsters (Goñi et al. 2010).

Our study did not account for possible changes in size-specific fecundity over time and improved egg quality produced by older females. As a result, we may be underestimating the positive impact on effective reproduction associated with demographic recovery within the MPA. FF at size was estimated based on samples collected in the MPA 10 yr ago (Goñi et al. 2003a). This relationship may underestimate present fecundity in the MPA if the increased abundance of large males within the MPA (R. Goñi et al. unpubl. data) had a positive effect on effective fecundity, as has

been shown in other spiny lobsters (MacDiarmid & Butler 1999). A second reason we may be undervaluing the reproductive benefits derived from protection is that in *Palinurus elephas* mean egg diameter increases with female size (Goñi et al. 2003b), and if large eggs hatch more competent larvae (Smith & Ritar 2007, A. MacDiarmid unpubl. data), the positive effects of increased egg production associated with demographic recovery would be amplified. On the other hand, a minor underestimation of mean fecundity in the fished area may result from the fact that a small fraction of the females collected outside were sampled before the peak spring moult.

At the end of the study, mature females were on average 20 times more abundant and EPUA was 30 times greater in the MPA than in the fished grounds. However, EPUA in the MPA did not grow despite the sustained increase in FF because the abundance of mature females declined. Goñi et al. (2010) attributed this decline of lobster abundance largely to 'dispersal imbalance' (sensu Walters et al. 2007), i.e. emigration from the MPA that is not compensated by immigration due to the high exploitation rates in the adjacent fishery. In particular, an extraordinary storm caused a massive emigration of lobsters in the winter of 2001 and a marked decline of abundance in the MPA (Goñi et al. 2010).

In our earlier study of the same population (1998–2000; Goñi et al. 2003a), greater egg production in the MPA was attributed primarily to higher female abundance (similar to present levels). At that time, when the MPA had only been closed to fishing for 10 yr (about half the maximum life span of the species), females were only slightly (4%) larger on average than those of nearby exploited populations, and had not realised their maximum lifetime reproductive potential. Now, after 10 more years without fishing, abundance has stabilised and the effect of cumulative growth is taking over. A 30% greater female size and 14 times greater mature female abundance are maintaining high levels of egg production relative to local fishing grounds. We conclude that for slow-growing species, the initial effects of protection on egg production will be mainly derived from the reduced mortality of adults, which will be gradually followed by the effects of growth on fecundity.

Overall, we estimate that after 2 decades of protection, regional egg production was over 6 times greater than would have been without the MPA. This conclusion rests on the assumption that, had the MPA not been established, EPUA in those grounds would have been similar to the EPUA that we estimated for the fished area. This in turn assumes that the displaced fishing effort has not resulted in increased exploitation rates in the grounds remaining open.

Although increased exploitation through effort displacement would be a reasonable expectation, in the particular case of Columbretes the creation of the MPA initially led to a reduction in fishing effort because it discouraged fishers coming from the most distant harbours (i.e. the Balearic Islands, >12 h sailing time). Since the beginning of monitoring in 1997, regional lobster effort has remained roughly stable (Goñi et al. 2010).

When compared to the net benefit of biomass spillover from the Columbretes MPA to the regional lobster fishery of +11% of the annual catch (Goñi et al. 2010), a 6 times greater egg production supports the contention that egg and larval export have far greater potential than spillover to benefit exploited populations. In practice this will be very difficult to determine, in particular in the case of MPAs that are small relative to the potential extent of larval dispersal. The size (44 km²) of the Columbretes MPA is well above average (Francour et al. 2001), but likely small relative to the dispersal potential of *Palinurus elephas* with a pelagic phase of 4 to 5 mo (Goñi & Latrouite 2005). Genetic studies indicate that *P. elephas* in the Western Mediterranean are interconnected (Babbucci et al. 2010), and regional populations may be linked via a common larval pool among intermediate populations (Díaz 2010). Nevertheless, although recruitment of locally spawned larvae to the MPA appears unlikely, a growing body of evidence of fish larval dispersal patterns indicates that larval retention in, or return to, parental grounds is far more important than previously believed (Jones et al. 2009).

While at present uncertainty about larval connectivity and dispersal bars further assessment of the actual impact of reproductive output from MPAs, the dominant contribution of the Columbretes MPA to the regional lobster reproduction is remarkable. In cases such as the European spiny lobster fisheries, where other means to regulate fishing pressure are largely ineffective due to poor enforcement capability, a network of interconnected MPAs seeding the exploited fishing grounds may prove to be the only way to maintain a viable metapopulation and fishery.

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