A 25-year marine reserve as proxy for the unfished condition of an exploited species

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ARTICLE INFO

ABSTRACT

In the absence of a historical baseline, long-term no-take marine reserves can provide a reference to the unfished condition in exploited species of limited mobility. This study documents the recovery of the lobster *Palinurus elephas* within a large Mediterranean no-take marine reserve (MR) and uses it as a baseline to assess stock status in exploited grounds in the region. Lobster indices of density and biomass within the MR continued to increase after 25 years of protection, a period close to the species' lifespan. Catch per unit effort (CPUE) in weight more than doubled from years 10th to 25th without fishing in the reserve while the increase of CPUE in numbers was only 20%. This faster increase in biomass reflected individual growth and spillover of predominantly smaller lobsters to adjacent grounds. A highly depleted status of exploited populations was inferred from the demographic structure and CPUEs, with fishery:MR ratios and reproductive potential indices below 0.05. In the MR the size-class of maximum egg production increased over time, in contrast to stable sizes classes in fished areas. The contribution of small lobster (<90 mm CL) to overall egg production was only 1.5% in the MR and 30% in the fished areas. Mortality estimated from recent size compositions was three to four times higher in fished areas than inside the MR, resulting in a reduction in predicted spawning potential per recruit close to 20% of the unfished level. This experiment emphasizes the value of long-term no-take areas as reference laboratories for investigating fishing effects.

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1. Introduction

Compared to large-scale fisheries, small-scale fisheries are data-limited, available studies tend to be short-term, and the status of populations they exploit is rarely assessed (Costello et al., 2012). The small-scale, multispecific, diverse and idiosyncratic nature of artisanal fisheries are not the only features that deter data collection. The close interaction of observers involved in field work with artisanal fishers means that monitoring studies will depend as much on the human component as on the technical and monetary resources available. Another difficulty is that these fisheries often have a long history, lacking a reference to the pristine or early exploitation status. This is the shifting baseline problem – where the concept of what the natural system was changes continually over time (Pauly, 1995). Well-enforced marine reserves can alleviate the problem in the case of species of limited mobility (relative to the size of the reserve), by providing a reference point that may approach the unexploited population structure (Hilborn et al., 2004).

Spiny lobsters are particularly suitable for spatial management because of their restricted adult mobility and hence propensity for depensation if populations are reduced below critical levels (Jennings,

2001). They are the subject of a number of long-term studies of marine reserves, which with limited exceptions document swift responses of abundance and body size after protection (Hoskin et al., 2011; Kelly and MacDiarmid, 2003; MacDiarmid and Breen, 1993; Pande et al., 2008; Shears et al., 2006), but see Freeman et al. (2012) and Mayfield et al. (2005).

Among the edible spiny lobsters in the Mediterranean (Holthuis, 1991), *Palinurus elephas* (Fabricius, 1787) has been historically considered an excellent food, as portrayed in a 3rd century Roman mosaic from the "House of 516 Dionysus and Ulysses" (Spanier et al., 2015). Its yields started to decrease during Roman times and deterioration of the stocks worsened in the 20th century with the intensification of effort and introduction of modern technologies (Spanier et al., 2015). Fishing techniques changed from the use of pots or diving to the use of trammel nets, which are significantly more efficient and resulted in further population declines, particularly in Atlantic populations (Goñi and Latrouite, 2005). At present, the Mediterranean population of *P. elephas* is considered overfished but it is still targeted by artisanal boats in many areas, especially in archipelagos and islands (Groeneveld et al., 2013). Published declines of catch per unit effort in Atlantic fisheries and widespread concern for the lack of proper assessment of its status led to the classification of *P. elephas* by the IUCN as Threatened Vulnerable (Goñi, 2014).

Palinurus elephas is a long-lived, slow-growing species that matures at 3–4 years and approximately 80 mm carapace length (CL) in the Mediterranean and reproduces once a year (Goñi et al., 2003a). Tagging studies indicate that adult movement is restricted with most individuals moving <5 km (Goñi and Latrouite, 2005). European fisheries are managed by a minimum landing size (90 mm CL in the Mediterranean and 95 mm CL in the Atlantic) and the prohibition of landing berried females (Goñi and Latrouite, 2005). Some fisheries (e.g., Balearic Islands NW Mediterranean) have a 7-month closed season covering the egg bearing period.

The Columbretes Islands Marine Reserve (hereafter "the MR"), located in the north-western Mediterranean (Spain), was established in 1990 as a no-take area (Fig. 1). The MR covers 55 km² and previously harboured traditional fishing grounds of *P. elephas*. Its empowering legislation prohibits all commercial fisheries and all lobster fishing, and regulations are well enforced. At present, the most traditional and profitable commercial *P. elephas* fisheries in the Mediterranean occur around archipelagos and islands, such as the Balearic Islands and around the Columbretes MR (Fig. 1). These fisheries have been used as controls in a long-term study that monitored the recovery of *P. elephas* within the MR since 2000. Although information on lobster abundance before MR implementation is not available, local fishermen corroborate that prior to MR creation catch rates were at a minimum. Density of *P. elephas* within the MR at the end of the 20th century was estimated to be 6–20 times greater than in comparable fished areas depending on the season (Goñi et al., 2001) and spillover supplied lobster to the

adjacent fishery (Goñi et al., 2006), providing a net annual benefit to the local fishery of 12% of the catch in weight (Goñi et al., 2010).

The prohibition of fishing in the MR for 25 years offers a unique opportunity to contrast the abundance and population structure in fished and unfished conditions. In this study we: 1) assess the trajectory of lobster density and biomass in the no-take MR during the period extending from years 11 to 25 since fishing ceased, and 2) evaluate the status of Western Mediterranean *P. elephas* fisheries using as reference the contemporary status of lobster in the MR. We do that in terms of density and biomass, demography, reproductive potential and mortality.

2. Material and methods

2.1. Study areas and fisheries

The study was conducted in two regions of the Spanish Mediterranean: the Columbretes Islands, where the MR is located, and the Balearic Islands (Fig. 1). Lobster fishing effort in the Columbretes Islands region is distributed in "Border" grounds surrounding the MR (<1 km from the boundary) and in contiguous and patchily distributed grounds of "Columbretes" (1–30 km from the boundary) (Goñi et al., 2010). The traditional fishing grounds of the Balearic Islands region occur around the Mallorca and Menorca Islands, 150 km away. The MR harbours volcanic rock and coralligenous habitats (maërl beds), with patches of gravel, sand, and mud extending down to 80 m depth. Fishing grounds
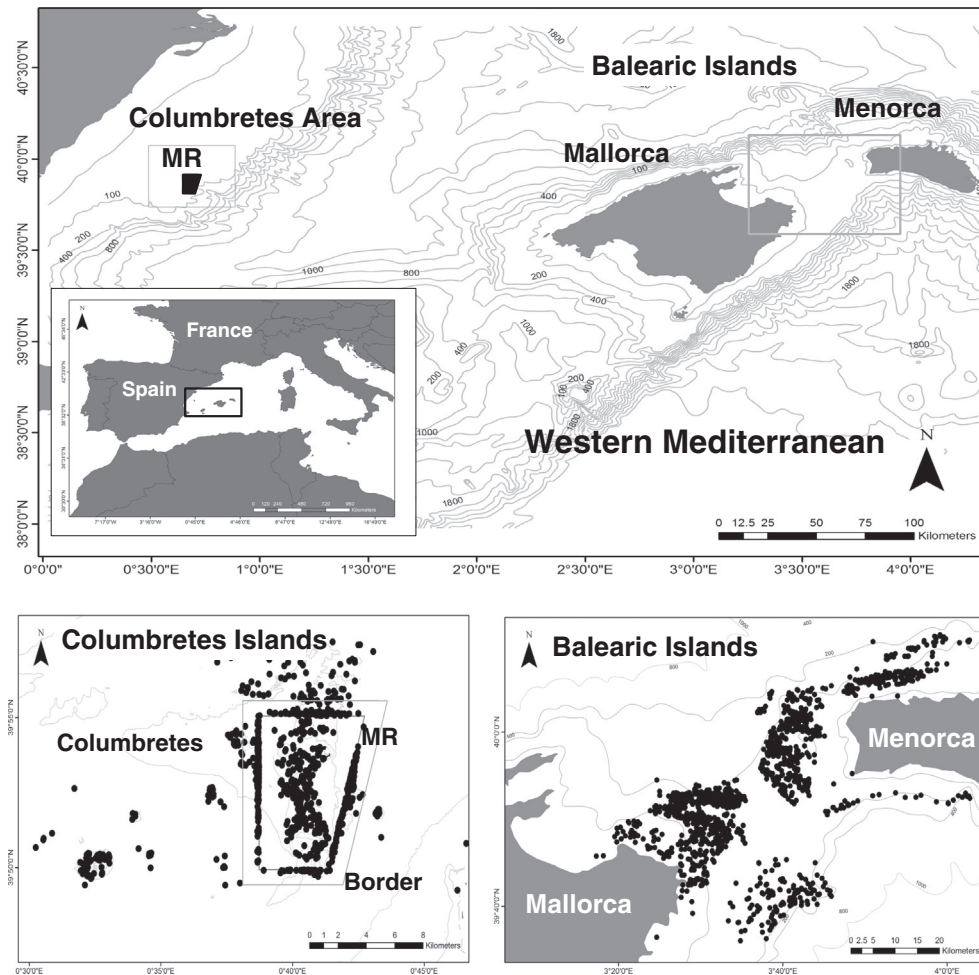

Fig. 1. Upper box: Study region in the Western Mediterranean showing the location of the study areas of Columbretes and Balearic Islands. Lower box: Experimental fishing sets in the Columbretes Islands marine reserve (MR) and commercial fishing sets in the Border (<1 km from MR boundary), Columbretes (1–30 km from MR boundary), Mallorca and Menorca fishing grounds. Fishing sets are represented by black dots.

near the MR consist of areas with patches of rock and maërl over expanses of gravel, sand, and mud at depths from 60 m to 100 m. Fishing grounds in Mallorca and Menorca harbour rocky and coralligenous habitats with maërl beds from the shore down to 100 m depth.

2.2. Data collection

2.2.1. Commercial fisheries

Catch and effort of commercial fisheries were recorded from 2000 to 2014 (years 11th to 25th without fishing in the MR) during the annual lobster fishing season (except 2004 in Border and Columbretes and 2004 and 2011 in Menorca when sampling was interrupted). Whenever possible sampling took place during one week per month on board boats that fished consistently in the region. To ensure that the data on spatial distribution of effort were representative of the true distribution, the observer sampled all the fishing sets that were carried out in that week without directing where fishing sets should be allocated. In these fisheries lobsters are caught with 600 m long trammel nets which are set over rocky and coralligenous habitats and let soak for 2–3 days; foraging lobsters become entangled in the net (details of fishing gear and operation in Goñi et al., 2003b). Data on net length, soak time, location, depth, and lobster catch of every set were recorded. Over the study period 275 fishing sets were sampled in Border, 487 in Columbretes, 1217 in Mallorca and 692 in Menorca.

2.2.2. Experimental fishing

Experimental fishing surveys inside the MR were conducted annually as part of a monitoring program that started in standardized form in 2000 (year 11th without fishing). They were conducted by experienced fishers from boats that operate regularly in the area, using the same gear as used for commercial fishing to assure comparability. Net length in the surveys was 600 m and soak time was shorter than in commercial operations (1 day) in order to minimize impacts within the MR.

Each survey consists of 18 experimental fishing sets, distributed following a stratified (by depth) random design over rocky and coralligenous habitats where lobsters are known to occur. Data available for this study, from 2000 to 2014, totalled 252 sampling sets. The surveys were carried out in the middle of the fishing season (June), prior to reproduction, when the probability of capture of females and males should be similar (Goñi et al., 2003b). Lobsters caught in the MR are tagged and released in the place of capture. They are recaptured inside the MR in subsequent experimental fishing surveys and by fishermen who report recaptures made outside the MR. Tag-recapture data have been used to characterize and estimate spillover rates from the MR (Goñi et al., 2006), as well as to estimate natural mortality (Goñi et al., 2010).

Trammel-nets are non-selective and, in the commercial fishery, are used to obtain a multispecies catch much of which is commercialized. Bycatch is composed of various species of benthic fishes (Stobart et al., 2009) which in the surveys inside the MR are usually alive due to the short soak time of the experimental fishing sets. It is extremely rare to catch birds or turtles and no seals are caught. Small sharks are occasionally entangled. Other low-impact sampling devices such as traps and underwater video have been tried but results have not been successful for the purpose of this study. Traps were used initially but they provided biased size and sex structure data (Goñi et al., 2003b). In a recent study we show that, at high densities, underwater video abundance estimates did not increase in proportion to population density (Stobart et al., 2015).

2.2.3. Longevity

To gauge the maturity of the MR in relation to *P. elephas* longevity, we estimated its maximum age (t_{max}) using values of natural mortality (M) estimated from tagging data ($M_{fem} = 0.163$ and $M_{male} = 0.199$; Goñi et al., 2010). For the purpose of this study, t_{max} was defined as the age at which 1% of a cohort of recruits survives. The estimated

$t_{max} = -\ln(0.01) / M$ was 28.3 and 23.1 years for females and males, respectively.

2.3. Data analysis

2.3.1. Density and biomass trends and ratios

Density and biomass indices for the MR and fished areas were the catch per unit effort in number (nCPUE) and weight (grams) (wCPUE) of lobsters caught in a standard fishing set (600 m long). Biomass and density ratios were calculated with data from the monitoring of the commercial fishery and from the experimental fishing conducted inside the MR.

To dampen out the variability in the ratios for a given level of monitoring effort, density and biomass ratios were calculated across multiple years (Babcock and MacCall, 2011). Upon observation of the trajectory of lobster density in the MR, three periods were distinguished: developing (years 11th to 15th without fishing: 2000–2004), intermediate (years 16th to 20th without fishing: 2005–2009) and advanced (years 21st to 25th without fishing: 2010–2014). Generalized linear models were used to assess differences in lobster abundance and biomass as a function of protection time, introducing the MR protection period as a 3-level factor (developing, intermediate and advanced), and assuming a Gamma distribution with a logarithmic-link function. When differences in density or biomass among protection periods were significant the post-hoc Tukey's test was applied to identify the periods that differed.

To assess the contemporary status of exploited *P. elephas* populations we used data from the advanced period of the MR as the best available proxy reference to unexploited conditions.

2.3.2. Mortality

Total mortality (Z) was estimated in two ways using the size compositions for the most recent period when the MR reflects unexploited conditions. The first and simplest used the length-converted catch curve (LCC) method of Pauly (1983), where N_t in Eq. (1)

$$\ln N_t = \ln No - Zt \tag{1}$$

is replaced by the frequency for size-class intervals, and t corresponds to the age a at the size interval mid-point L, calculated assuming a von Bertalanffy growth function:

$$a = -\frac{1}{K} \ln\left(1 - \frac{L}{L_\infty}\right)$$

Size classes were from 35 mm CL to 175 mm CL in females and from 35 mm CL to 195 mm CL in males, by 5 mm intervals. Only fully selected age groups, showing a linear decrease in log of abundance versus a, were used to estimate Z. Von Bertalanffy growth parameters for *P. elephas* in the MR were estimated by Díaz (2010) (females: $K = 0.108$ and $L_\infty = 145.5$ mm CL; males: $K = 0.157$ and $L_\infty = 178$ mm CL).

In the second approach, mortality and selectivity parameters were estimated by fitting the size compositions using the equilibrium recursive equations developed by Hordyk et al. (2016). This method incorporates individual variability in L_∞ (we assumed CV $L_\infty = 0.05$) and size-selective fishing mortality. It estimates the ratio of fishing mortality over natural mortality F/M and logistic selectivity parameters assuming an input value of M/K. For this application the method was modified to estimate total mortality at length, using an estimate of the von Bertalanffy K parameter as input, instead of assuming M/K known. Parameters were estimated jointly for the MR and the fished areas, assuming that natural mortality M was constant for all regions and that exploited grounds shared the same fishing selectivity parameters. A separate selectivity function was estimated for the experimental fishing conducted within the MR, even though it uses commercial fishing gear. The parameter corresponding to the length at 95% selectivity was

constrained so that it did not exceed the value of length corresponding to the first age group considered fully selected in the catch-curve analysis described earlier. The sum of multinomial log-likelihoods for the five regions was maximized using the software AD Model Builder (Fournier et al., 2012) and a code modified from one provided by A. Hordyk. A relative weight of 5 was given to the log-likelihood for the MR size frequency, while the Border and Columbretes fishing grounds were heavily down-weighted because size distributions in those areas were distorted by spillover from the MR (Goñi et al., 2010).

2.3.3. Reproductive potential

2.3.3.1. Mean size of mature lobster and mean fecundity. The mean size of mature females and males, as well as mean fecundity, were calculated for lobsters in the MR and in the fished locations for the three MR protection periods using the fecundity-size relationship in Goñi et al. (2003a) for females and assuming a knife-edge maturity schedule with size at maturity of 82.5 mm CL for males (Goñi et al., 2003a).

2.3.3.2. Female reproductive output. Three measures of female reproductive output were used. First, female relative reproductive potential (RRP_i) by size class (Goñi et al., 2003a) was calculated for each study location as:

$$RRP_i = Mat_L Fec_L C_L$$

where Mat_L is the proportion of mature females in size-class (L), Fec_L the mean fecundity and C_L the proportion of size class (L) in the sample.

Secondly, an empirical index of egg production per unit area (EPUA) (Díaz et al., 2011) was used to assess the relative reproductive potential per unit area in fished and unfished populations. The EPUA index was estimated as:

$$EPUA = F\ CPUE_{mature\ females}$$

where F is the average Fec_L of all mature females in the catch and $CPUE_{mature\ females}$ is the mean number of mature females caught in a standard fishing set, which is related to their abundance in the area fished by this standard unit of effort (assumed to be constant in all areas). While RRP_L measures the relative reproductive contribution of different size classes, EPUA depends on both the abundance and size structure of mature females. Thus, the ratio of EPUA outside:inside the MR provides an empirical measure of the impact of fishing on the reproductive output per unit area.

Finally, a model-based estimate of spawning potential ratio (SPR) was calculated as the ratio of average lifetime egg production per recruit in the unexploited and exploited populations.

$$SPR = \frac{\sum_L N_L^{exploited} Mat_L Fec_L}{\sum_L N_L^{unexploited} Mat_L Fec_L}$$

where $N_L^{unexploited}$ and $N_L^{exploited}$ are the abundances at length (for an arbitrary number of recruits) predicted under equilibrium for the unexploited and exploited populations. Equilibrium abundances were calculated using the method of Hordyk et al. (2016).

3. Results

3.1. Trajectory of lobster density and biomass indices in the MR

Lobster indices within the MR exhibited conspicuous interannual variations. Density indices declined during the developing to intermediate periods and increased during the advanced period (Fig. 2a). Mean biomass index was stable in the developing period and increased during the intermediate to advanced period, peaking at the end of the series, 25 years after fishing ceased (Fig. 2b). When data were aggregated by

protection period, only the advanced period was significantly different from the previous two.

In the fished areas lobster density and biomass indices were relatively stable and of similar magnitude in the three periods (Figs. 2a, b), except for a peak during 2002–2003 in the Border fishing grounds (Fig. 2b) corresponding to a massive spillover event from the MR occurring in the winter of 2001 (Goñi et al., 2010).

3.2. Status of lobster fisheries close and far

3.2.1. Fishery:MR density and biomass ratios

In the advanced period, when the MR biomass index was highest, fishery:MR density and biomass ratios ranged from 0.03 to 0.13 and 0.02 to 0.05, respectively (Fig. 3). The highest fishery:MR biomass ratio was recorded in the Mallorca fishing grounds followed by the Border grounds and the lowest in the Columbretes grounds (Fig. 3).

3.2.2. Size structure

In the absence of fishing mortality, old and large individuals accumulate within the MR. While female growth is slow resulting in a narrow unimodal distribution (modal sizes 110 to 130 mm CL from the developing to advanced periods; not shown), male growth is faster and the size distribution wider (modal sizes progressing from 110 up to 165 mm CL) (Fig. 4). In the advanced period, the build-up of males near the maximum size is preceded by a drop within the 120–150 mm CL size range (Fig. 4). The maximum sizes attained by lobsters in the MR in the advanced period were 172 and 190 mm CL for females and males respectively, which given the longevity of the species should be a good approximation of the maximum sizes attainable in the region.

In contrast to the MR, in the fished grounds the size structure of females and males remained comparatively stable overtime (Fig. 4; females not shown), and was truncated at about 130 mm CL for females and at 140 mm CL for males. Only in the Border fishery were a few lobsters observed that approached the maximum sizes found within the MR, this being more perceptible for males.

3.2.3. Mortality

Lobster mortality (Z) estimated from the length-based catch curve analysis was higher for males than for females and in fished areas than in the MR (Fig. 5). The slopes estimated for the different periods within the MR decreased over time as the population recovered and the size structure filled up (females Z = 0.334 to 0.166; males Z = 0.249 to 0.194) (not shown), with more uncertainty in males due to distorted size distributions associated with spillover. Estimates of mortality (Z) ranged between 0.392 and 0.433 for females and 0.683 and 0.867 for males in the Mallorca and Menorca fishing grounds, respectively. Those based on samples near the MR (Border and Columbretes) were affected by disturbances of the size structures associated with spillover, especially in males (Fig. 7). The value of CL corresponding to the first age group considered to be fully selected was much smaller in the exploited grounds (90 mm CL) than in the MR (120 mm CL).

In order to reduce statistical confounding between mortality and selectivity parameters, these same CL values were used to constrain the parameters corresponding to the size at 95% selectivity obtained with the methods of Hordyk et al. (2016). Resulting estimates of natural mortality (from the MR) for the advanced period were 0.128 for females and 0.133 for males, smaller than estimated with the previous method. The size at 95% selectivity was estimated to be very close to or at the maximum bound in both the MR and the fished areas. The fits of the size compositions for the MR and the fished regions Mallorca and Columbretes were reasonably good (Fig. 6); fits however improved when the constraints in the size at 95% selectivity were removed, allowing the selectivity to continue to increase at larger sizes. Removing the constraints resulted in higher estimates of *M* as these parameters are known to be confounded. The ratios *F/M* estimated for regions Mallorca and Menorca were 2.06 for females, and 3.87 and 3.94
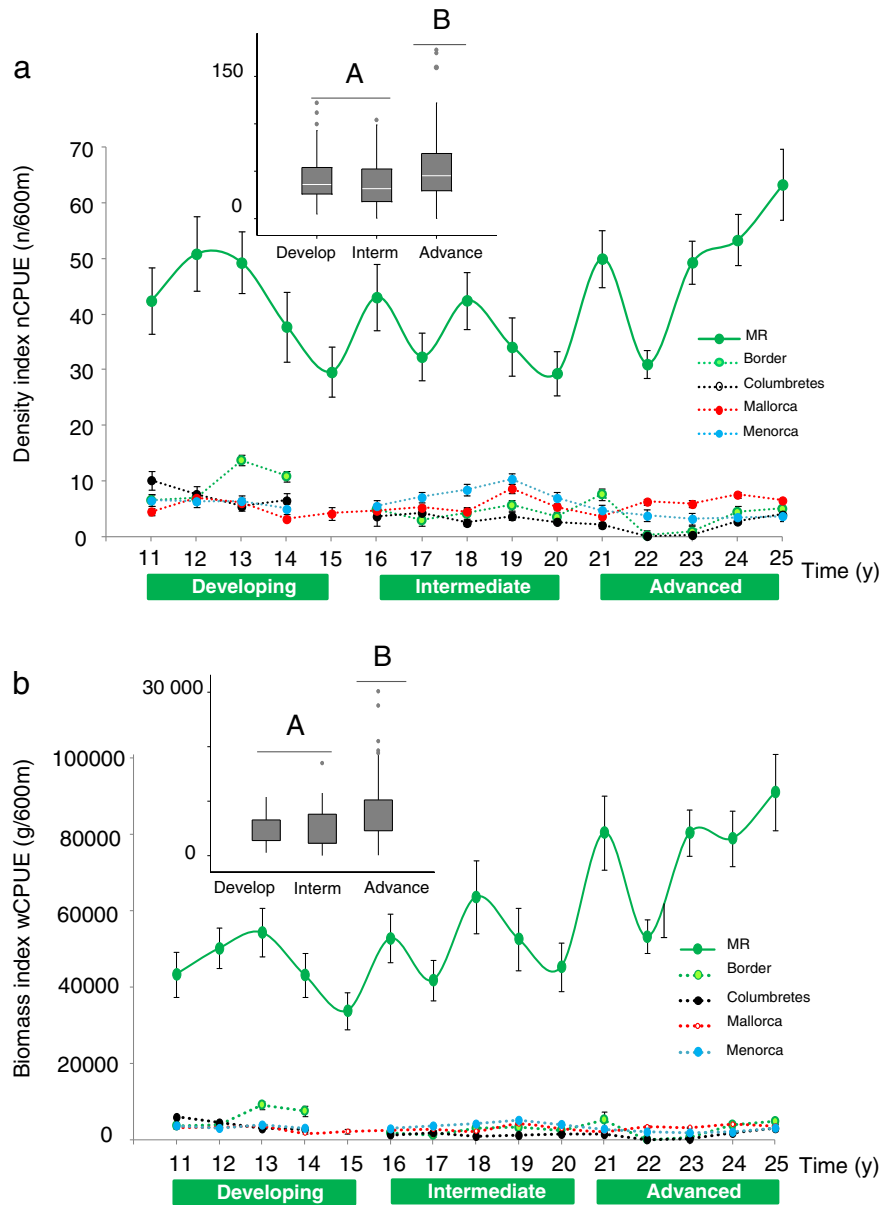
Fig. 2. Density (a) and biomass (b) indices (nCPUE and wCPUE) of *Palinurus elephas* in the study areas as a function of protection time (years without fishing) in the marine reserve (MR). Protection periods: developing (11th to 15th years without fishing), intermediate (16th to 20th years without fishing) and advanced (21st to 25th years without fishing). Boxplots in insets correspond to the MR and show the median, 25% and 75% percentiles and outliers; horizontal lines and alphanumeric labels refer to periods with significantly different indices as indicated by multiple comparisons Tukey tests.

respectively for males. Lower ratios were estimated for regions Border and Columbretes for both males and females, but the fits were poor given distortions in the size distributions caused by spillover.

3.2.4. Reproductive potential

3.2.4.1. Mean size of mature lobsters. The mean size of reproductive lobsters in the MR increased from the intermediate to the advanced protection periods (105.2 to 120.6 mm CL in females and 124.3 to 137.8 mm CL in males), while it remained roughly stable in the fished areas (90–95 and 100–105 mm CL in females and males, respectively). The Border fishery differed again, with average size of mature lobsters intermediate between those in the MR and in fished areas farther away (Fig. 7). The maximum difference in the mean size of reproductive lobsters between the protected and fished areas was attained in the advanced MR period.

3.2.4.2. Female relative reproductive potential. The size class of maximum female RRP progressed during the study period from 100 to 135 mm CL the MR and from 105 to 120 mm CL in the Border area. In the more distant fished areas the class of maximum RRP remained roughly stable around 90–105 mm CL (Fig. 8).

3.2.4.3. Egg production per unit area. During the advanced MR period, the indices of egg production per unit area (EPUA) in the fished areas ranged from 2%–4% of that in the MR. The lowest fished EPUA corresponded to the Columbretes fishing grounds (Table 1).

3.2.4.4. Spawning potential ratio. The SPR calculated based on the estimated ratios of fishing to natural mortality was 0.68 for Border, 0.28 for Columbretes and 0.23 for Mallorca and Menorca. This result based on a per-recruit calculation suggests a lower impact of fishing than the empirical EPUA index. The difference may be related to the equilibrium
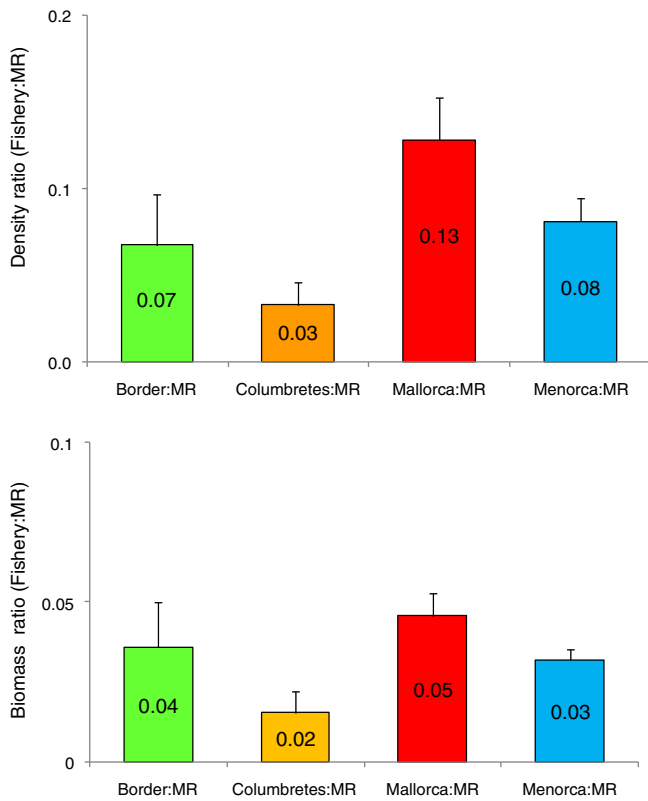
Fig. 3. Density and biomass fishery:marine reserve (MR) ratios (± SE) of *Palinurus elephas* in fished areas Border, Columbretes, Mallorca and Menorca for the advanced protection period.

Fig. 4. Male *Palinurus elephas* size frequency distributions in the marine reserve (MR) and fished areas Border, Columbretes, Mallorca and Menorca by protection period. Protection periods as described in Fig. 2.

assumptions made in the estimation of mortalities and selectivity, and the resulting shift in selectivity towards larger sizes within the MR.

4. Discussion

With acknowledged limitations due to lack of replication and plausible interferences such as environmental variability and fishing history, this experiment of unfishing the sea provides a glimpse of how far exploitation can change the demography of a exploited species. Lobsters make good models for these studies because of their high value and moderate mobility, hence heavily exploited status and swift response to fishing restrictions in marine reserves.

4.1. Trajectory of the lobster population in the MR

Indices of density and biomass of *P. elephas* in the MR continued to increase until the end of the study period, 25 years after fishing ceased, suggesting that the process of recovery is not yet fulfilled. We know from fishermen's testimonies that prior to MR implementation, the lobster population was depleted to the point of no longer being targeted (J. Navarro, pers. comm.). Although we lack data from the early years of the MR, it is expected that *P. elephas* density responded swiftly to protection, as has been documented for several decapod species in marine reserves (e.g., Freeman et al., 2012; Hoskin et al., 2011; Moland et al., 2013a). Being a site-attached species, emigration is likely to be positively density-dependent, with little emigration at low density, allowing population numbers to recover rapidly (Gårdmark et al., 2003). As abundance increases, random movements (Rakitin and Kramer, 1996), dispersion imbalance (Walters et al., 2007) or competition processes (MacDiarmid et al., 1991) trigger movements to low density areas outside the MR, as described in Goñi et al. (2010) and documented for other species (reviewed by Halpern et al., 2010; Sánchez-Lizaso et al., 2000).
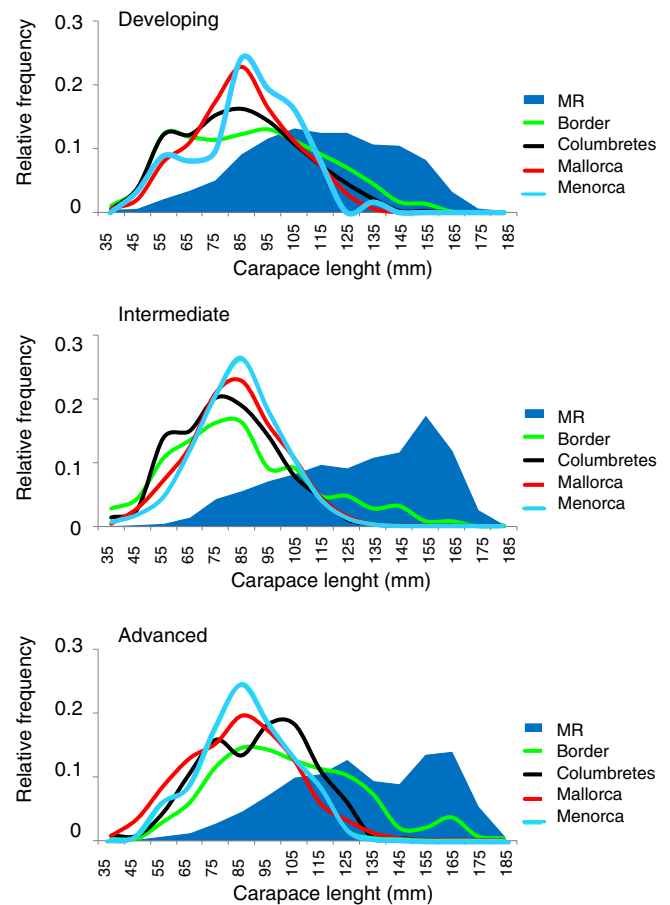
Thereafter, the relative stability of lobster density observed in this study would be modulated by the fraction that each year spills over from the MR and is caught in the fishery. Concentrated fishing effort along the MR boundaries (Goñi et al., 2006 and Fig. 1) that harvest lobsters exiting the MR could be responsible for the stabilization, or even decline, of density in the MR, as has been reported for lobster (e.g., Freeman et al., 2012) and fish (e.g., McClanahan and Mangi, 2000) in other marine reserves.

The continued growth of long-lived individuals in the MR is the most parsimonious explanation for the doubling of lobster biomass in the recent decade. The size structure with the progressive buildup of very large lobsters shows a dent at intermediate sizes likely due to the loss of medium-size individuals to spillover. The presence of increasingly large lobsters in the Border fished grounds indicates spillover. Also, the presence of large individuals in the Columbretes grounds in the advanced period supports the observation by Goñi et al. (2006) that the effects of spillover, albeit weakly, reach beyond 1 km from the boundary of the MR, an effect not perceptible in the abundance or biomass ratios. Spillover, with size-differential emigration rates, could amplify the fast increase of biomass relative to abundance inside the MR. As discussed in Goñi et al., 2010, competitive exclusion by dominant individuals, observed in male lobsters during the mating season (e.g., Frisch, 2008; MacDiarmid et al., 1991) and in fishes (e.g., Abesamis and Russ, 2005), could affect the demography of the fraction exiting the MR, which would contain a disproportionate representation of small- and medium-size individuals relative to the those remaining inside the MR. Catches in the Border grounds adjacent to the MR differ from those of fisheries further away by the presence of large lobsters. In fact, net benefits of this MR to the local fishery through spillover have been
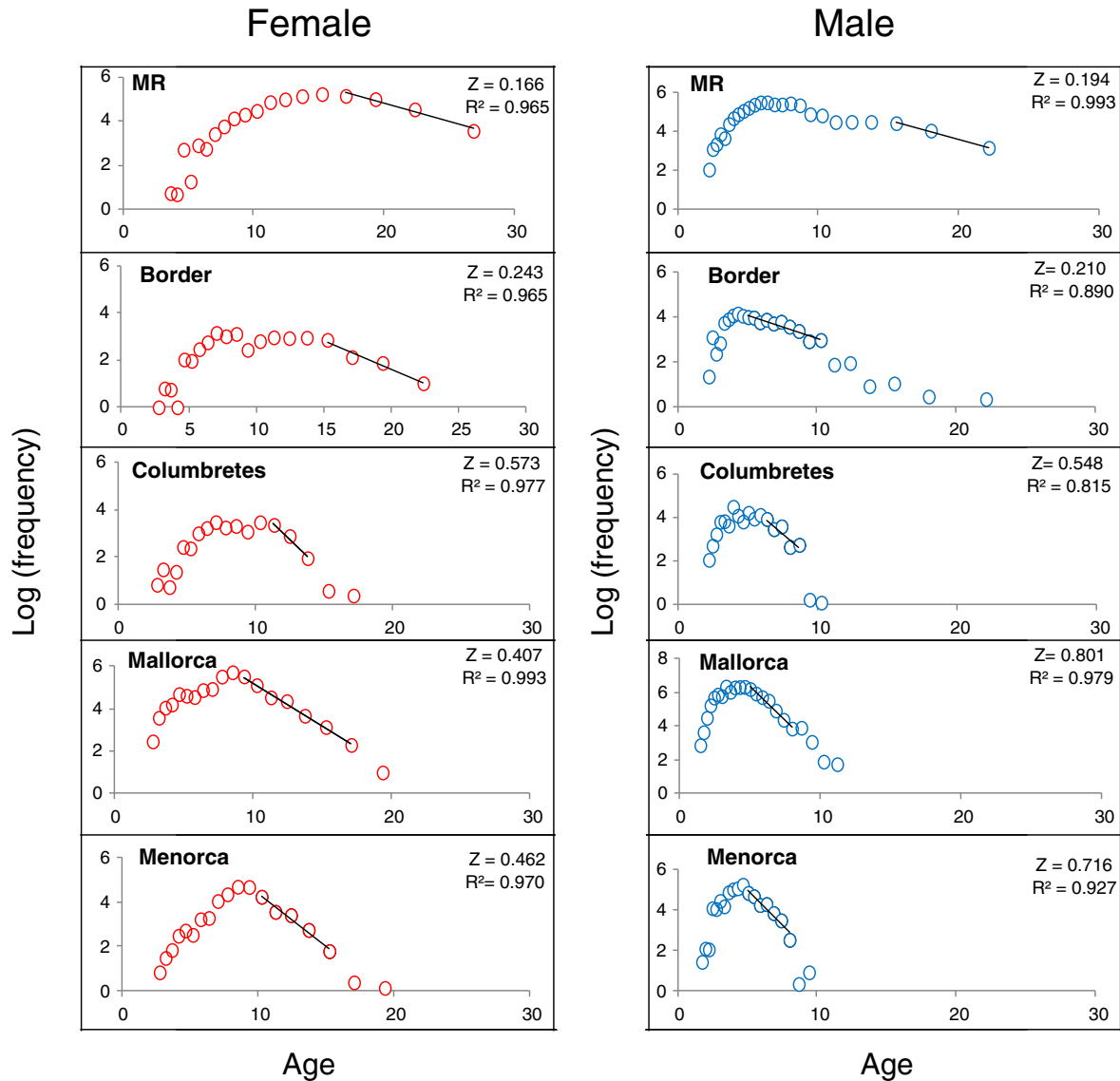
Female

Male

Fig. 5. Total mortality (Z) from linearized catch-curve (LLC) plots of female and male *Palinurus elephas* in the marine reserve (MR) and fished areas Border, Columbretes, Mallorca and Menorca for the advanced protection period.

attributed to the larger size of lobsters harvested in the vicinity of the MR rather than to their number (Goñi et al., 2010). A similar effect was documented in the temperate lobster *Jasus edwardsii* by Kelly et al. (2002) and explains why, relative to other zones, the Border:MR ratio is higher in terms of biomass than of density. Jennings (2001) noted the difficulty of empirical studies to assess performance of marine reserves when changes in behaviour, such as size- and density-dependent emigration proposed here, follow the removal of fishing mortality.

Declines or stabilization of density in marine reserves has been attributed to a variety of causes. Babcock et al. (2010) analyzed multispecies data, including lobsters, inside and outside fishery closures, and found that trajectories were variable, both increasing and decreasing. Decreases in abundance were caused by environmental fluctuations, fishing impacts outside the closures and habitat or indirect effects of increased predation. In a multi marine reserves long-term study, Freeman et al. (2012) observed declines in abundance of legal size *J. edwardsii* as a result of seasonal inshore-offshore migrations and increased fishing around the boundary of the reserve targeting lobster moving offshore (Kelly and MacDiarmid, 2003; Kelly et al., 2002). Freeman et al. (2012) pointed to settlement strength of lobster pueruli as a key factor determining the trajectory of *J. edwardsii* within marine reserves. With a

common larval pool (Hamdi et al., 2012), lobster settlement strength within the MR is close to the average level estimated for the region (Díaz et al., unpubl. data). Hence, increased survivorship in the no-take area, despite potentially greater risk of predation (Díaz et al., 2011), should lead to stable or increasing density of *P. elephas* within the MR over a period equivalent to a generation time after the closure.

4.2. Status of lobster in fished areas close and far

No-take marine reserves are useful to study the effects of fishing to the extent that they allow ecosystems to recover to pre-fishing states (Dayton et al., 2000; Eddy et al., 2014; Costello, 2014). If we assume that *P. elephas* abundance in the MR is approaching unfished conditions, the ratio of lobster density outside the MR to density inside the MR would be a proxy for population depletion (Babcock and MacCall, 2011). To avoid biases introduced by edge effects, ratios from fisheries further away from the MR should be used (Babcock and MacCall, 2011). On the other hand, and depending on the size of the protected area, the process of dispersion imbalance discussed earlier would imply that density within the MR may stabilize at a level lower than it would in an unfished population.
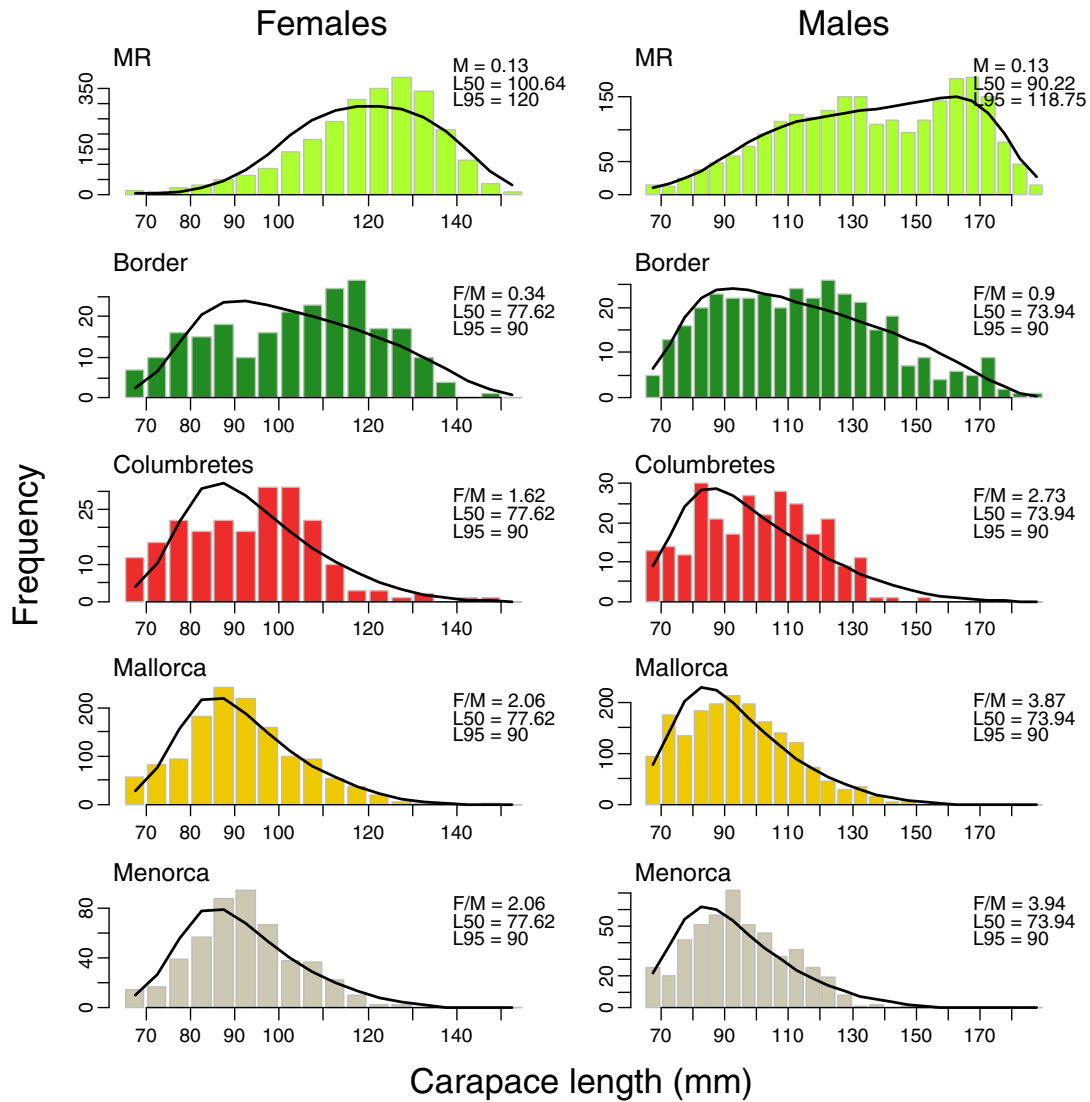
Fig. 6. Size distributions of *Palinurus elephas* in the marine reserve (MR) and Border, Columbretes, Mallorca and Menorca fished areas for the MR advanced protection period. Solid lines correspond to predicted size compositions under equilibrium assumptions, estimated using the method of Hordyk et al. (2016). Parameters L50 and L95 correspond to the size at 50% and 95% selectivity in a logistic function. M is the estimate of natural mortality and F/M the ratio of fishing rate at full selectivity to natural mortality rate.

For scenarios such as those, which include migration and post-settlement density-dependence, Babcock and MacCall (2011) recommended the use of precautionary target reference points. They proposed that a target density ratio of 0.60 of mature fish, or 0.80 of all fish, would avoid depletion for a wide range of life-history characteristics. Here mean density-ratios, either calculated across the whole study period to dampen interannual variability (0.13), or for the most recent 5-year period (0.08), are well below these proposed targets and denote a high level of depletion of *P. elephas* in the region. Ratios in terms of biomass were even lower, with the highest ratios as low as 0.05 and with the lowest ratio in the Columbretes area. This area benefited little from spillover or from the seven-month annual closed season that regulates the Balearic Islands fisheries of Mallorca and Menorca. Similar levels of depletion in lobster fisheries are common, as reported by Barrett et al. (2009) and Shears et al. (2006) for the temperate lobster *J. edwardsii*, with 7–11 and 25 times greater abundance and biomass respectively in Tasmanian and New Zealand marine reserves, and by Babcock et al. (2007) for *Panulirus cygnus* with densities up to 34 times higher in a Western Australia marine reserve than in fished areas.

The progressive expansion of the size structure observed in *P. elephas* during 25 years of protection reveals the evanescence of the footprint of fishing in the demographic structure. As a result, mortality estimates derived under assumptions of equilibrium during the recovery period are biased. However, given that a full generation period has elapsed since exploitation ceased, mortality rates estimated within the MR during the advanced period should approach the rates of natural mortality. The values estimated by the two methods are indeed close to the estimates obtained independently from tag-recapture ($M_{\text{fem}} = 0.163$ and $M_{\text{male}} = 0.199$, Goñi et al., 2010), although somewhat smaller for the method that estimates selectivity jointly with the mortality parameters. Removing the constraint in the size-at-95% parameter results in higher estimates of M.

The mortality rate estimated for the MR is markedly lower than the mortality in fished areas, where a narrow demographic structure has remained stable overtime with an absence of large individuals. Similar findings were obtained by Moland et al. (2013b) for the clawed lobster *H. gammarus* where after nearly two decades of protection, density dependence was not halting development of the population within the MR and a 14 year decline in mortality rates were observed, with lower survival of males than females. Lower survival of males, as found in this study, could be linked to boldness, i.e. a higher propensity of males to engage in potentially risky behaviours (Moland et al., 2013b) or
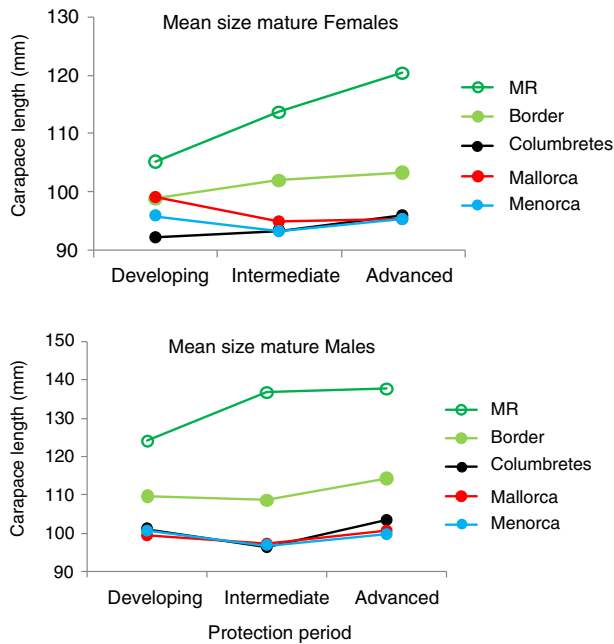
Fig. 7. Mean size (CL mm) of mature female and male *Palinurus elephas* in the marine reserve (MR) and fished areas Border, Columbretes, Mallorca and Menorca by protection period. Protection periods as described in Fig. 2.

territorial aggression (Frisch, 2008) resulting in fighting and dispersal, as proposed to underlie spillover from the MR (Goñi et al., 2010). Dramatically reduced mortality rates of female lobster *Panulirus interruptus* were documented by Kay and Wilson (2012) inside marine reserves off California. These authors found that spillover affected estimates of Z inside the reserve and concluded that *M* should be estimated using data obtained from locations at the centre of large-enough reserves, as remarked by Babcock and MacCall (2011).

With the expansion of the size structure in the MR, the average size of mature individuals of both sexes increased overtime, while it remained stable in the fished areas. The size difference was greatest in the advanced period, indicating that the process is still ongoing. The relative contribution of different size classes to reproductive potential, changes markedly as a result of exploitation due to the commercial cropping of large individuals (Kanciruck, 1980). In the MR the modal class of egg production increased over the course of the study, in contrast with the stability and smaller sizes responsible for maximum egg production in the fished areas. As a result, the contribution of the small size classes (<90 mm CL legal size) to egg production in the MR is only 1.5%, while in the fished areas approaches 30%. This stresses the importance of maintaining populations with a broad spectrum of age classes in order to buffer the impact of recruitment variability, which is notably high in *P. elephas* (Díaz, 2010) as in other lobsters (Wahle, 2003). Taking the population in the MR as a reference and assuming similar productivity in all areas, the egg production potential in the MR may have increased 10–20 times since fishing was banned 25 years ago. Based on the size-specific fecundity and the number of mature females, Davidson et al. (2002) estimated that nine times as many eggs of *J. edwardsii* were produced from a 5 year-old no-take area than an equivalent length of fished coast. Equally, studies of *Panulirus argus* by Lyons et al. (1981) and of *J. edwardsii* by Kelly et al. (2000) document dramatic reductions of spawning potential in exploited areas associated with severely reduced abundance of large females. With data from the MR 20 years after fishing ceased, Díaz et al. (2011) estimated that the MR, occupying only 18% of the fishing grounds, contributed 87% of the regional (Border + Columbretes) egg production.
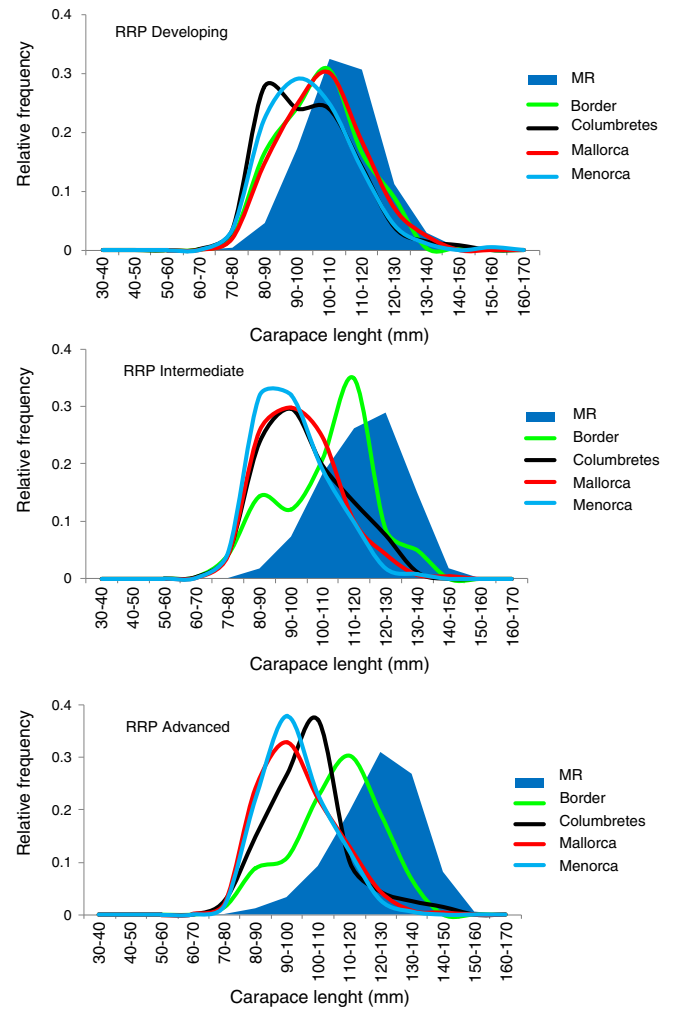

Fig. 8. Female *Palinurus elephas* reproductive potential (RRP) in the marine reserve (MR) and fished areas Border, Columbretes, Mallorca and Menorca by protection period. Protection periods as described in Fig. 2.

Our evaluation of relative egg production per unit area does not take into account possible increases in per-capita egg production associated with the greater abundance of large-size males within the MR. Laboratory experiments by MacDiarmid and Butler (1999) showed that in tropical (*P. argus*) and temperate (*J. edwardsii*) spiny lobsters egg clutches were significantly larger when eggs were fertilized by large males. Recent experiments by Butler et al. (2015) underscore the importance of maintaining large males to ensure fertilization success and caution against their overexploitation. However, assessing males' effects on lobster reproductive output is complex, as illustrated by the study by Pugh et al. (2015) where the weight of *H. americanus* ejaculate increased with male size but there was variation in the composition of ejaculates indicating that larger males may invest disproportionately more in the sperm plug (acellular component), possibly as paternal assurance. Considering that in this study males are 11 times more abundant and 30% larger in the MR, a 20 times greater EPUA in the MR relative to the fished areas is likely an underestimate of the actual reproductive benefits of protection.

4.3. Caveats

Factors other than fishing could cause the large difference of lobster density in the MR compared with customary fished areas. The MR could be a natural hotspot for *P. elephas*, leading to an over-estimation of the extent of depletion. On the other hand, population increases following

Table 1
Egg production per unit area (EPUA) of *P. elephas* from western Mediterranean fishing grounds close and far from the Columbretes Islands Marine reserve. (a) Values not corrected for egg loss (26%). nCPUE: no lobster / 600 m net. Size: Carapace length (CL mm).

	Mean size mature females	Mean fecundity (nº eggs)	Mean nCPUE mature females	EPUA (nº eggs)	EPUA (%)	Mean size mature males	Mean nCPUE mature males
Marine reserve	120.4	147,303	23.4	3,446,890	100%	139.1	22.7
Border	103.3	92,193	1.4	124,461	4%	114.2	1.9
Columbretes	96.1	71,357	1.2	84,201	2%	104.2	1.3
Mallorca	94.0	66,327	2.0	134,667	4%	101.8	2.8
Menorca	94.0	74,041	1.9	137,064	4%	100.1	2.0

protection of hot spots may be small if the habitat is highly utilized and abundance increases result in export to adjacent areas (Jennings, 2001). Empirical information provided by fishers indicates that while the Columbretes reserve was a productive lobster ground prior to protection, it shared similar habitat characteristics with the other lobster grounds in this study. Clearly, results from multiple marine reserves would be needed to provide a more robust reference to assess stock status. Also, the effects of human pressures are spatially variable and site specific; yet, our results indicate a striking similarity in the demographic parameters of separate fished subpopulations in the western Mediterranean.

Fishery:MR ratios were calculated from monitoring data where the survey gear was the same as that used commercially in order to avoid introducing changes in catchability, as recommended by Babcock and MaCCall (2011). There was however a difference that may have bearing in our results. To minimize impacts on protected benthic communities, soak time in experimental fishing surveys inside the MR was 1 day; while in the fisheries soak time is commonly 2–3 days. Because trammel net is a passive gear, shorter soak times tend to produce smaller catches so that our fishery:MR ratios may be overestimated. Changes in selectivity are also likely as soak duration may differentially affect animals with different degree of mobility. The size-based selectivity functions inferred from size distributions were shifted to the right in the MR compared to the commercial catch, implying relatively lower catchability of small and medium size lobster. Such differences in selectivity may also result from the presence of larger individuals in the MR that inhibits movement of smaller individuals. Alternatively a true deficit of small and medium size individuals in the MR (relative to equilibrium assumptions) may reflect size-dependent emigration. A more complex model that integrates tagging and size distribution data would be needed to separate these processes.

5. Conclusions

Because the MR has been in place for 25 years, a period believed to approach the maximum age of the species, the ratio of density and biomass per unit area between fished and unfished regions provides a proxy for the extent of depletion of the exploited stocks and the rebuilding of protected populations. The demographic patterns investigated here also indicate a high level of depletion of *P. elephas* in the exploited grounds relative to the no-take MR, with fishery:MR ratios of biomass and reproductive potential per unit area below 0.05. These results highlight the value of establishing no-take marine reserves as reference laboratories to investigate fishing impacts and to establish biological reference points for management.

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