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Effects of marine protected areas on fish communities in a hotspot of climate change and invasion

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Abstract

The positive ecological effect of fully protected Marine Protected Areas (MPAs) on fish populations has been widely explored. Key indicators of fully protected MPAs effectiveness include an increase in biomass, density, and body size of commercially exploited large fishes. Fully protected MPAs are also hypothesized to be more resilient to both marine invasions and ocean warming, but this has seldom been tested. The eastern Mediterranean (Levantine) basin is the warmest region in the Mediterranean. Moreover, this region is the front-line of biological invasion from the Red Sea via the Suez Canal. Thus, MPAs in this region are faced with both high numbers of exotic species and warm temperatures. Assessing the performance of MPAs in this region is important for understanding their effectiveness under adverse future conditions worldwide. The ecological effectiveness of four MPAs along the Levantine Israeli coast was followed along over five years and compared with adjacent fished control area. Sampling was conducted in both old (>20 years of enforcement) and young MPAs, which only recently became fully protected. Using SCUBA diving surveys, 978 visual transects were performed to assess fish abundance, size, and diversity. We found clear indications for the benefits of the MPAs as evident by higher numbers of large fishes and groupers within protected areas. In the largest and oldest MPA we also found higher total and commercial fish biomass. In addition, we show a clear increase in the number of groupers over time, both within and outside MPAs, that may be associated with increased fishing regulation and enforcement. We found no clear evidence for a lower number of exotic species within MPAs. Our findings suggest that restrictions on recreational and commercial fishing within MPAs benefit the recovery of fish populations even in warm waters and when faced with marine invasions, and that the effectiveness of MPAs may be evident after only a few years of protection.

Keywords: MPAs; biomass; fish; protection; invasion; Mediterranean.

Introduction

The marine realm is suffering from substantial anthropogenic stressors, such as overfishing, biological invasion, and rising sea temperatures, causing changes to species abundance and community composition (Ban, 2019; Bax *et al.*, 2003; He & Silliman, 2019). Highly enforced Marine Protected Areas (MPAs) is a key strategy to restore ecosystems and are considered a major element in marine conservation (Roberts *et al.*, 2001; Edgar *et al.*, 2014). The positive ecological effects of highly enforced MPAs on fish populations has been widely explored in both temperate and tropical regions (Edgar *et al.*, 2014; Guidetti *et al.*, 2014; Sala & Giakoumi, 2017; Giakoumi *et al.*, 2017). In addition to the benefits of highly enforced MPAs to fish populations, they are also used as an effective management tool for fisheries due to spillover of individuals beyond MPAs boundaries (Di Lorenzo *et al.*, 2020; Goñi *et al.*, 2008; Stelzenmüller *et al.*, 2008; Di Lorenzo *et al.*, 2016; Roberts *et al.*, 2001; Russ *et al.*, 2004).

Highly enforced MPAs have also been suggested as a tool to combat biological invasions (Ardura, *et al.*, 2016; Giakoumi & Pey, 2017; Giakoumi *et al.*, 2019). According to the “biotic resistance hypothesis”, diverse native communities, such as those often observed within MPAs, are more resilient to invasions (Elton, 1958). Yet, MPAs may also serve as a favorable environment for invasive species, which take advantage of protection from fishing (Lockwood *et al.*, 2013). Only few studies have examined the effectiveness of MPAs in mitigating invasive species impacts (Byers, 2005; Klinger *et al.*, 2006; Kellner & Hastings, 2009; Burfeind *et al.*, 2013; Giakoumi & Pey, 2017; Rilov *et al.*, 2018; Giakoumi *et al.*, 2019). A recent review (Giakoumi & Pey, 2017) showed that exotic species respond negatively to protection, as the density of most exotic species was found to be smaller inside protected areas than in fished grounds. Other studies show that exotic species may do equally well or better within MPAs (Giakoumi *et al.*, 2019; Klinger *et al.*, 2006; Kellner & Hastings, 2009). Finally, Ardura at al. (2016) demonstrated that exotic fish abundances are negatively correlated with the size of the MPA and the intensity of protection. Thus, whether MPAs promote or hamper the establishment of exotic species is still under debate (Burfeind *et al.*, 2013, Giakoumi & Pey, 2017).

MPAs effectiveness strongly depends on the level of protection and enforcement (Edgar *et al.*, 2014; Grorud-Colvert *et al.*, 2021) yet only 6% of the world's marine protected areas are currently managed and enforced as no-take zones (Costello & Ballantine, 2015). It is still unclear how long it takes for protection and enforcement measures to have a biological signal, as monitoring of MPAs since their establishment is uncommon (Giakoumi *et al.*, 2017; Claudet *et al.*, 2006). Some studies suggest that substantial increases in densities and biomass of commercially valuable species occur within 1-5 years from enforcement initiation (Roberts *et al.*, 2001, Halpern & Warner, 2002, Russ *et al.*, 2004 , Rife *et al.*, 2013). However, other studies suggest that it takes much longer to observe MPA benefits (Aburto-Oropeza *et al.*, 2011). No information on the temporal duration of recovery is available from regions suffering from multiple stressors such as rapidly increasing water temperatures and a high rate of invasion, in addition to fishing.

The Eastern Mediterranean (Levantine) basin is located on the front-line of an extensive invasion via the Suez Canal (Buba & Belmaker, 2019, Givan *et al.*, 2018, Edelist *et al.*, 2013, Galil, 2007). In addition, this region is the hottest and most saline region in the Mediterranean Sea , and is rapidly warming (Coll *et al.*, 2012, Rilov *et al.*, 2018, Ozer *et al.*, 2017). These conditions benefit thermophilic exotic species of Red Sea origin (Galil, 2007, Givan *et al.*, 2018), turning the Levantine basin fish communities into a unique blend of native and exotic species.

In Israel, only a very small portion of the Mediterranean coast is protected (2.5%). Most of the protected area were established only recently (Israel Nature and Parks Authority, unpublished data). An exception is Rosh Hanikra – Achziv MPA which has been established 30 years ago and regulation has been well enforced. Other, younger declared, MPAs in Israel were mainly '*Paper parks* 'and were very loosely enforced and illegally fished (Goren *et al.*, 2013). Nevertheless, over the past few years, enforcement measures have changed drastically both within and outside the MPAs. First, nation-wide fishing regulations were updated in 2016, incorporating species-specific catch size limitation and fishing bans in breeding and recruitment seasons. Second, the Israel Nature and Park Authority (INPA) was given the authority and the means to enforce fishing regulations. Intensive enforcement began in July 2018, after recruiting and training 12 new marine rangers. Since then, all reserves in Israel are actively enforced.

Data from these newly enforced MPAs provide important baseline information on the effects of MPAs in a region impacted by multiple stressors. In this study, the change in fish populations were examined within and outside Israeli MPAs during a period characterized by increased enforcement. Specifically, we examined: (1) Recovery of fish populations within MPAs, (2) Changes in fish populations both within and outside MPAs, potentially as a result of the new fishing regulations, and (3) the number and diversity of exotic species relative to native species. We anticipate that the results will have important implications for the management of MPAs, especially in a region dominated by rapid climate change and accelerating biological invasion.

Methods

MPAs

Underwater visual SCUBA surveys were performed between 2015-2021 to characterize fish assemblages within four MPAs within the northern Israeli Mediterranean coast: Rosh Hanikra – Achziv, Shikmona, Dor-Habonim, and Gdor (Fig. 1). Also unprotected, adjacent areas were surveyed, and served as control sites (Fig. 2). We describe the physical characteristics of each MPA and classify the protection level according to the regulation-based classification system for MPAs by Costa *et al.* (2016).

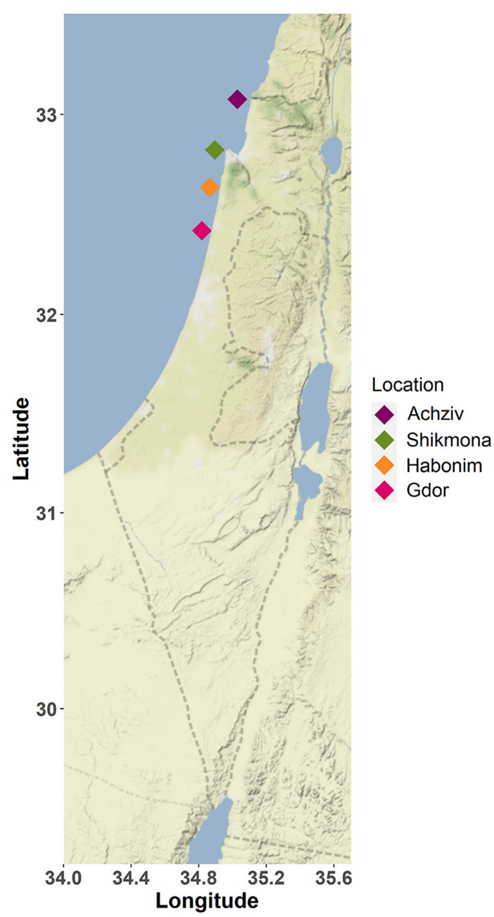

Fig. 1: Sampling locations along the northern Israeli coast.

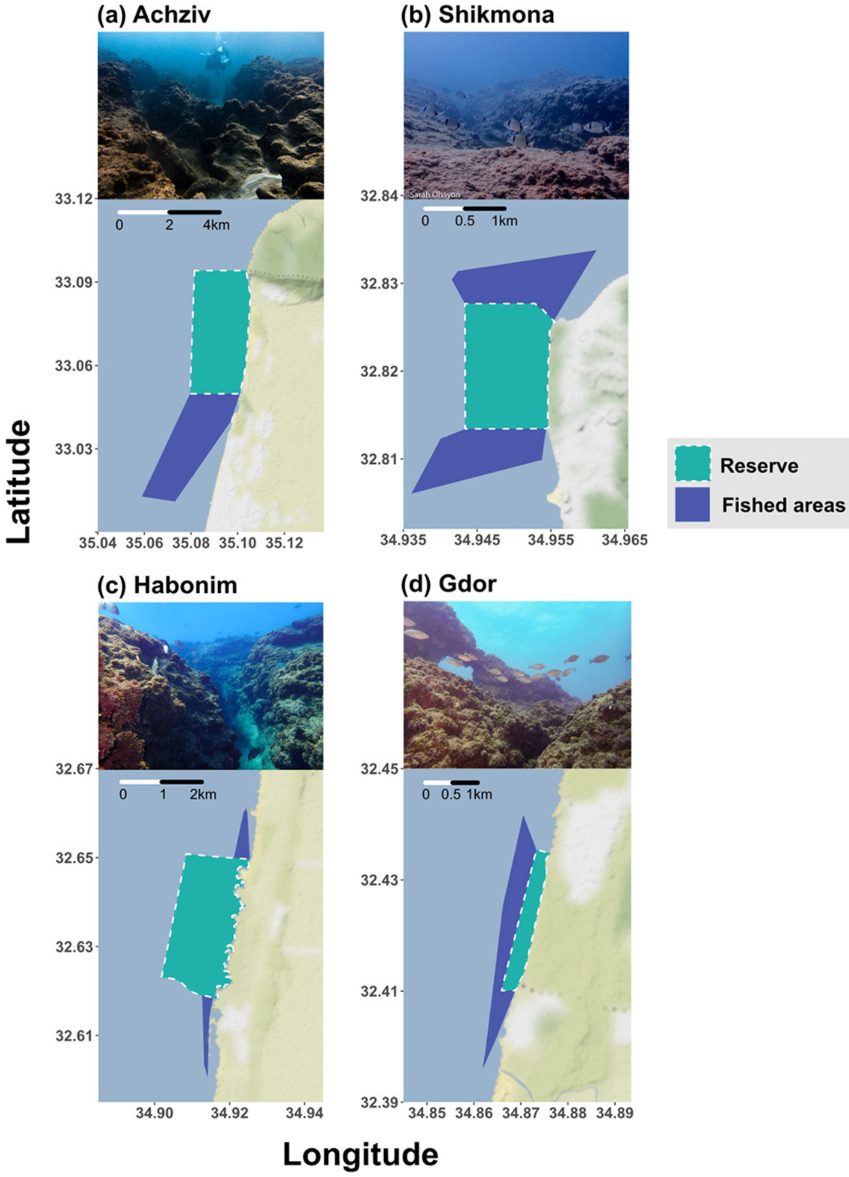

Fig. 2: MPAs borders (light blue) and adjacent control sites areas (dark blue) in which sampling was performed. Adjacent photos illustrate the characterizing rocky habitat within these locations (photos credits: (a) Shevy Rothman, (b) Sara Ohayon, (c-d) Shahar Chaikin). Produces using the *ggmap* package (R software, version 3.6.3).

The **Rosh-Hanikra Achziv** MPA ('Achziv') is located at the Israeli extreme north (Fig. 2a). This MPA is the largest and most consistently enforced MPA in Israel, extending over 10 km^2 and up to 45m deep. It protects the richest and most diverse fish and invertebrate communities along the Israeli Mediterranean coast (Frid & Yahel, 2017; Lazarus & Yahel, unpublished data). It consists of varied habitats: abrasion tables bordering the shoreline, sandy bottom, submerged eolianite Kurkar ridges (a unique endemic structure of lithification of ancient dunes which were formed along the Israeli shoreline; Rilov *et al.*, 2018), which also include steep, complex rocky formations. The bedrock is covered by complex biogenic structures made of organism shells and macroalgal crust (see representative seascape in Fig. 2a). Commercial artisanal and recreational fishing is forbidden within MPA boundaries since the early 80's, excluding beach angling, which has only been forbidden since 2017. However, hook and line fishing is permitted in the first 660 m of the southernmost part of the MPAs shoreline. Thus, we classified this MPA as level *4* – "*highly regulated extraction*". Control sites were confined to rocky areas of similar depths and similar seascape complexity characteristics as sampling sites in the MPA, as much as possible (see appendix, Table A1). A distinct rocky structure in the form of a ~20m drop is found only within the MPA but only minority of sites in this area were sampled; 9 out of 42 sampling sites within the MPA between 2017-2021 (georeferenced data from surveys conducted in 2015 within the MPA is unavailable).

The **Shikmona** MPA is much smaller than Achziv and extends over 1.7 km^2 with a maximal depth of 15m (Fig. 2b). The MPA is part of the Carmel Head submerged limestone headland. Like in Achziv complex biogenic structures cover the bedrock (Rilov *et al.*, 2018). Generally, seascape complexity is much lower compared to

Achziv. The shallow depth substrate is relatively devoid of invertebrates and algae cover and characterized by relatively low relief crevices (see representative seascape in Fig. 2b). Fishing was illegal in Shikmona since the establishment of the MPA in 2008, except for angling from the shore. However, enforcement only began in mid-2016. Thus, this MPA was classified as level *8 – "unregulated extraction"* in 2015 and since 2016 the entire MPA is classified as level *4* – "*highly regulated extraction"*. Control sites were confined to rocky areas of similar depths and similar seascape complexity (see appendix, Table A1) as sampling sites within the MPA.

Dor-Habonim ('Habonim') is the second largest MPA in Israel, extending over 5.2 km^2, and with a maximal depth of 21m (Fig. 2c). This reserve's shoreline is characterized by broad, developed abrasion tables continued by the underwater rocky habitat - the submerged eolianite Kurkar ridges, as in Achziv (see representative seascape in Figure 2c). However, the submerged rocky habitat area within Habonim is shallow, reaching a depth of approximately 6m. Beyond this depth the MPA mostly consists of a sandy substrate. Thus, we sampled only in the shallow hard-bottom area. The seascape complexity of the rocky substrate is characterized by many concave and convex configurations. Fishing regulations in Habonim are different from other MPAs due to fishing permits given to 11 artisanal fishers using set nets and long-lines. However, recreational fishing is illegal except for angling from the shore. Enforcement began in this MPA in mid-2016, reducing recreational fishing, although the 11 artisanal fishers still operate. Thus, until 2016 the MPA was classified as level *8 – "Unregulated extraction"* and since 2016 as level *5 – "Moderately regulated extraction"*. Control sites were confined to rocky areas of similar depths and similar seascape complexity (see appendix, Table A1) as sampling sites within the MPA.

The smallest, southernmost MPA surveyed is the **Gdor** MPA which extends over only 0.85 km^2 and reaches a maximal depth of ~6 m (Fig. 2d). The MPA consists of varied habitats: detached abrasion tables, shallow sandy lagoons, a submerged Kurkar rocky bottom (like in Achziv and Habonim), and patches of a sandy bottom among the rocky substrate. The seascape complexity of the rocky substrate is characterized by many concave and convex configurations, including prominent overhangs, burrows and crevices (see representative seascape in Fig. 2d). Since the MPA's establishment in 2004, all fishing practices are illegal, except for angling from the shore. However, enforcement was partial, and improved only in mid-2018, from which it includes fishing bans (excluding angling from the shore) on illegal commercial artisanal fishing and recreational fishing (spear fishing and angling from a vessel). Thus, until 2017 we classified the MPA as level *5 – "Moderately regulated"* and since 2018 as level *4 – "highly regulated extraction"*. Control sites were confined to rocky areas of similar depths and similar seascape complexity as much as possible as sampling sites within the MPA. However, we found that the complexity of the area within the MPA is higher compared to the control sites (Appendix, Table A1).

Sampling

At each location, both MPAs and control sites were sampled by skilled SCUBA divers using a visual census. Sampling sites were confined to rocky reef habitats. Surveys depths differed in accordance with rocky reefs depth ranges within each location (3-24.6m in Achziv, 2-17.3 m in Shikmona, 2-6m in Habonim, and 1.8-6 m in Gdor) and were matched between MPAs and control areas. The number of potential control sites with habitats similar to the ones found within the MPA is limited. Thus, control sites were planned so they will include a habitat as similar as possible to the habitat of the MPA. These were set within distances of 160 to 4,000 m from the MPAs' borders (appendix Table A2). Sampling campaigns were conducted bi-annually during 2015 (April & November), 2017 (June & October), 2019 (April & November) and 2021 (April).

Within each sampling campaign we sampled in 24 (± 3 SD) sites within and 19 (± 3 SD) sites outside the MPAs (appendix Table A3). Sampling effort was set to approximately represent the habitat within each MPA so larger MPAs with more diverse depths received higher sampling intensity. In each site, between 2-8 belt transects were performed. A total of 978 transects were performed across all locations and sampling campaigns. To create a balanced data set, we randomly sampled 2 transects at each site and summed the observations. In each transect, fish were recorded along 25X6m belt transects, up to a height of approx. 5m above the substrate. As two transects were combined in each site the actual area sampled was 300 m^2.

For each transect we used the following protocol: After descending along a rope tied to a pre-deployed buoy, the divers attached a measuring tape to the rope and started swimming. The documentation of the fish started only after 5m of swimming to reduce the interruption caused by the diver descent and preparations for sampling. The two divers documented fish identity and abundance, and estimated fish total length. An underwater calibration of length estimation showed a correlation of 0.97 (± 0.01 SD, averaged across surveyors) between actual size of fish to its estimated length. Fish were identified to species level (excluding Mugilidae and Atherinidae, which are difficult to identify to species level underwater). Although species from the families Gobiidae, Blenniidae and Tripterygiidae are common on rocky substrate they are underestimated in visual surveys and thus omitted from analyses (for the full species list, see appendix Table A4).

Once completing the transect, a measurement of the seascape complexity was conducted. The shape of the seascape was quantified using the contour of the seabed along a transect estimated from a digital water level data logger (Onset HOBO). We followed the protocol suggested by (Dustan *et al.*, 2013) with slight changes: The diver held the device as close as possible to the bottom while swimming along the transect indicated by the pre-laid tape measure. The target swimming velocity was constant and slow (~0.2m/sec). Pressure measurements were recorded at 1 second intervals (0.41 cm resolution). These data were converted to a bottom profile contour assuming swimming speed was constant. Bottom profiles with <80 and >250 measurements (i.e., very slow/fast sampled transects) were excluded from analyses.

To quantify seascape complexity for each transect we calculated the Vertical Relief index (Luckhurst & Luckhurst, 1978) a measure for the depth range along the profile that displayed high performance in a recent study (Lazarus & Belmaker, 2021). Due to technical limitations, complexity was measured in only a subset of transects (196 transects, ~20% of data), and hence is used here only to compare MPA and control sites, and not as part of the analyses. Using a simple linear model, we found that seascape complexity is similar between MPAs and their corresponding control sites, excluding Gdor, in which the complexity was significantly higher within the MPA (see appendix, Table A1). The eastern Levantine basin is characterized by low cover of macroalgal vegetation (Giakoumi *et al.*, 2019). This is due to the invasion of the Siganus species which inhibit shallow rocky reefs)Rilov *et al.*, 2018). Hence, we did not quantify macroalgal abundance or diversity.

Response variables

We examined the effect of protection on total biomass, biomass of commercially valuable species (species which are regularly fished along the Mediterranean Israeli coast and regularly consumed by the Israeli public, appendix Table A4), and exotic species biomass. Biomass was calculated using the parameters of the length-weight relationship ($W=aL^b$), where a and b were extracted from studies in Fishbase website (Froese & Pauly, 2000), using studies conducted as close as possible to the study area, with a preference for Eastern Mediterranean values (for the full species list, see appendix Table A4). Biomass was log transformed before used as a response variable. In addition, we quantified the effect of protection on the abundance (number of individuals) of all large individuals (>20cm) which is considered a key indicator to assess the overall impact of fishing (Edgar *et al.*, 2014).

Groupers are considered indicator species for examining the performance of protection on MPAs (Hackradt *et al.*, 2014). Thus, we examined the total number of groupers and the number of groupers which reached size of first maturity. The number of groupers that reached size at first maturity was analyzed for the two most common species: *Mycteroperca rubra* and *Epinephelus marginatus.* These species are both protogenic hermaphrodites (Aronov & Goren, 2008); for an individual to mature as a male, it must first mature as a female. Thus, male length at first maturity values were used (53.9 cm for *E. marginatus* and 35.5 cm *M. rubra).*

Analyses

Due to the large difference in MPA size, enforcement duration and habitat analyses, models were performed for each MPA separately in relation to both the control location and over time. GLMs (Generalized Linear Models) were used to related total biomass, commercial biomass, exotic biomass; abundance of large individuals, groupers abundance; and number of groupers above length of first maturity to the predictors. GLMs used Gaussian error distribution, apart from abundance models, in which a Poisson regression (suitable for count data) was used. To quantify the MPA effect in a way comparable with other studies we also included an ANOVA table (appendix Table 5A) for total biomass.

The main predictors tested were time (continues), MPA (categorical; in, out) and their interaction. In all models we also used season (categorical; Spring, Fall), and depth (continues, used only for the deeper MPAs Achziv and Shikmona). As complexity estimates were not available for all sites these were not added to the analyses.

To control for the potential for spillover to mask the effect of protection, we performed a separate analysis removing control sites that were located <300m of MPA borders (where spillover effect should be less dominant; Di Lorenzo *et al.,* 2020).

Finally, we examined which species are most affected by protection by calculating the log-ratio of the mean biomass per site within and outside the MPA for each species. A bias-corrected confidence interval was calculated using the '*batch_calc_ES'* function in 'SingleCaseES' package (Pustejovsky, 2015; Pustejovsky & Swan, 2021), as log-response ratios are sensitive to sample size. All analyses were performed using R (Software R Core Team, 2020).

Results

In the oldest and largest MPA, Achziv, total and commercial biomass was significantly higher within the MPA than in adjacent control areas: 178% higher total biomass (25.3 ± 43.8 SD within the MPA and 9.1 ± 9.6 SD outside of MPA borders, appendix Table A5), and 250% higher commercial biomass (21.1 ± 41.1 SD (kg/300 m^2) within the MPA and 6 ± 9.6 SD outside of MPA borders (appendix Fig. A1, Table A5). Due to the high impact of protection in this MPA, we also examined the long-term effect of protection on specific species for this MPA. A variable response of biomass to protection was found among different species (Fig. 3)." In Shikmona, total biomass was found to be significantly higher within the MPA compared to control sites (12 % higher; appendix Table A5). In the other two MPAs (Habonim and Gdor) no consistence difference was found between the MPAs to the fished areas in either total biomass nor commercial species biomass. In all MPAs, we found no interaction between time and protection for biomass (Appendix Fig. A1; Table A5).

The number of large individuals was significantly

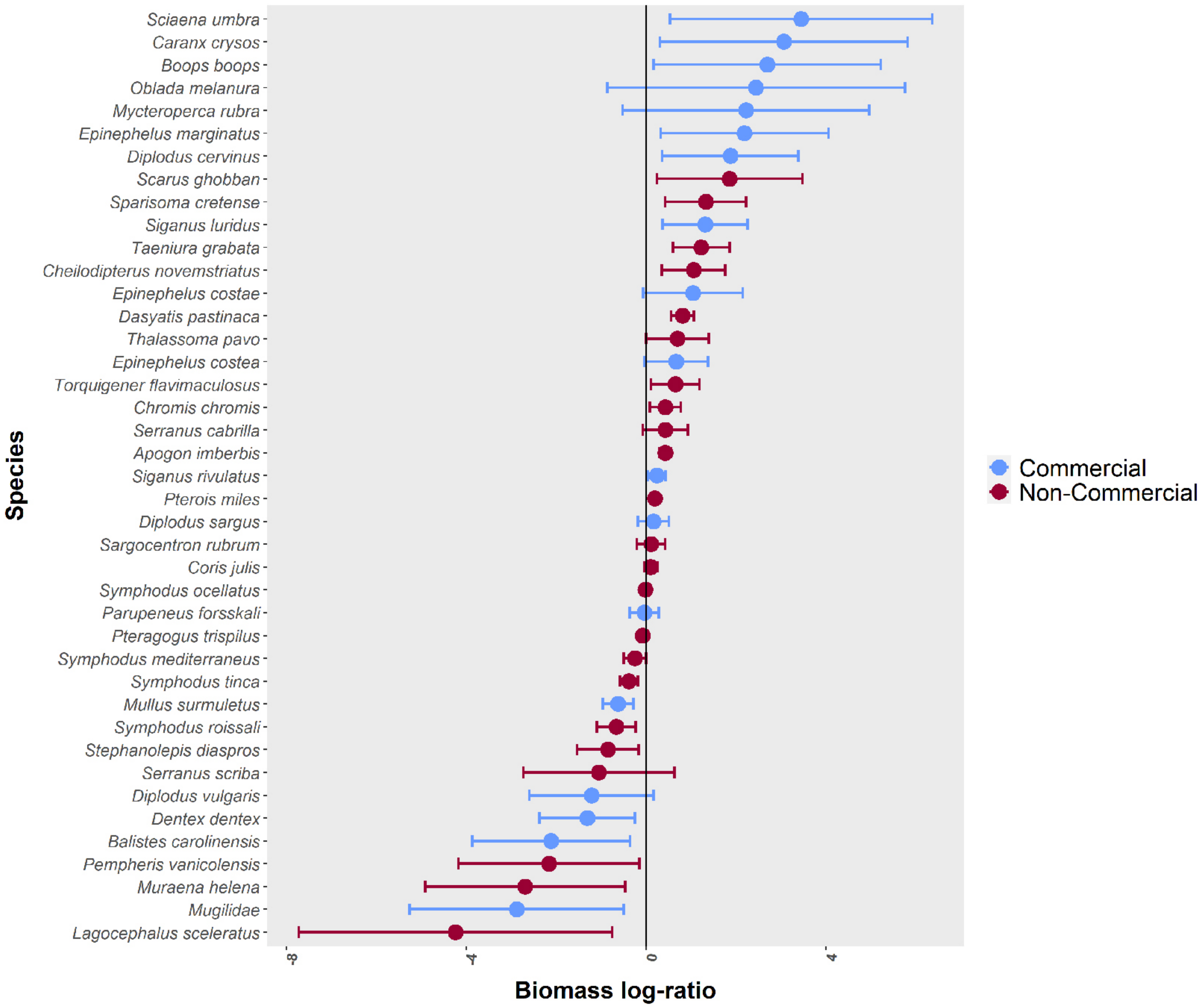

Fig. 3: **Log ratio of species level biomass density within to outside of the Achziv MPA.** Positive values show the species that gaining increased in abundance within the MPA relative to control area. Error bars represent 95% confidence intervals of the biomass ratio.

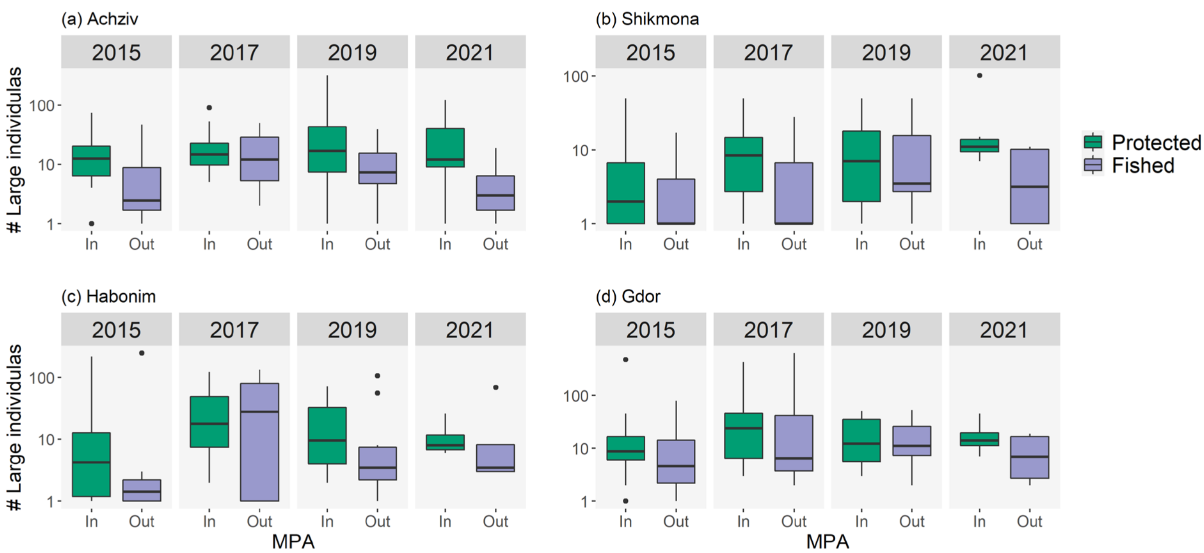

Fig. 4: **The number of large individuals observed in each MPA across the four years of survey.** We tested how the number of large individuals changed with season, year, protection. Protection (in/out) was significant for Achziv (a; $p<0.001$) and Habonim (c; $p<0.05$). Colors represent sampling within or outside of MPAs. Note the Y axis log scale. Box plots display the 25% and 75% quartiles, and lines within boxes represents the median. Dots represent points 1.5 times outside the interquartile range.

higher in MPA sites compared to control sites in all MPAs. An interaction between protection and time was found in Achziv and Habonim (Fig. 4; Appendix Table A6). Within Achziv, large-individual abundance increased faster over time in the MPA than outside the MPA. In Habonim, the abundance of large individuals decreased over time both within and outside the MPA, but the decrease was larger outside the MPA. The results of the models above did not qualitatively change when exotic species, such as *Siganus rivulatus*, were excluded from the analyses.

Exotic species biomass was significantly higher within Achziv than in unprotected fished areas (112% higher). However, for the other MPAs, exotic biomass was similar within and outside the MPAs (appendix Fig. A2 and Table A7). No interactions were found between time and protection for exotics in all MPAs.

We found both temporal and MPA effects on grouper abundance. We observed significantly higher grouper abundance within MPAs compared to adjacent fishing grounds in Achziv (182%), Habonim (13%) and Gdor (28%). In Shikmona, we did not find such difference. Over time (year), a significant increase in groupers abundance was observed in all areas, protected as well as fished. A significant interaction between protection and time was found in Achziv and Habonim, with a sharper increase in grouper abundance over time within protected areas (Fig. 5; Appendix Table A8).

The number of grouper individuals above size of first maturity was significantly higher within Achziv MPA compared to adjacent control sites (264.7%, Fig. 6; Appendix Table A9). In Shikmona, the number of grouper individuals above size of first maturity within MPA was similar to the number in adjacent unprotected areas. No interactions were found between MPA and time. In the two other MPAs the numbers were too small for analyses (only 1 mature individual found in Habonim, and 7 in Gdor). Even though the number of groupers significantly increased within all four MPAs as well as in adjacent fishing grounds we found no significant trend in the number of individuals above size of first maturity (Appendix Table A9).

When testing models including only control sites located >300m from MPAs borders, all model results were similar apart from the small following differences: The direction of the interaction between grouper abundance and time in Achziv, indicated on a sharper increase with time in the control area compared to the MPA. The opposite was observed for Shikmona, Habonim and Gdor, where a sharper increase in grouper abundance with time was observed within the MPAs.

Discussion

We present clear indications for the effectiveness of MPAs under extreme environmental conditions and an extensive biological invasion. Specifically, within Achziv, the oldest and largest MPA in our study, we found multiple indicators for the ecological effectiveness of the MPA. These indicators included: higher total biomass and commercial biomass (250% and 178%, respectively, Appendix Fig. A1 and Table A5), higher overall grouper abundance (182%, Fig. 5 and Table A8) and more groupers larger than the size of first maturity (166% higher for *M. rubra*, for *E. marginatus,* mature individuals were found only within the MPA) in the MPA when compared to control sites. This provides strong evidence for the effect of enforced MPAs on fish populations (Sala & Giakoumi, 2017), maintained in a region characterized by large numbers of exotic species and extreme climatic conditions.

Other than Achziv, the three MPAs studied reflect a transition stage between "Unregulated extraction" MPA to "Moderately regulated extraction" (Habonim) and "Highly regulated extraction" MPAs (Gdor and Shikmona) (classified following Costa *et al.*, 2016, see Methods).

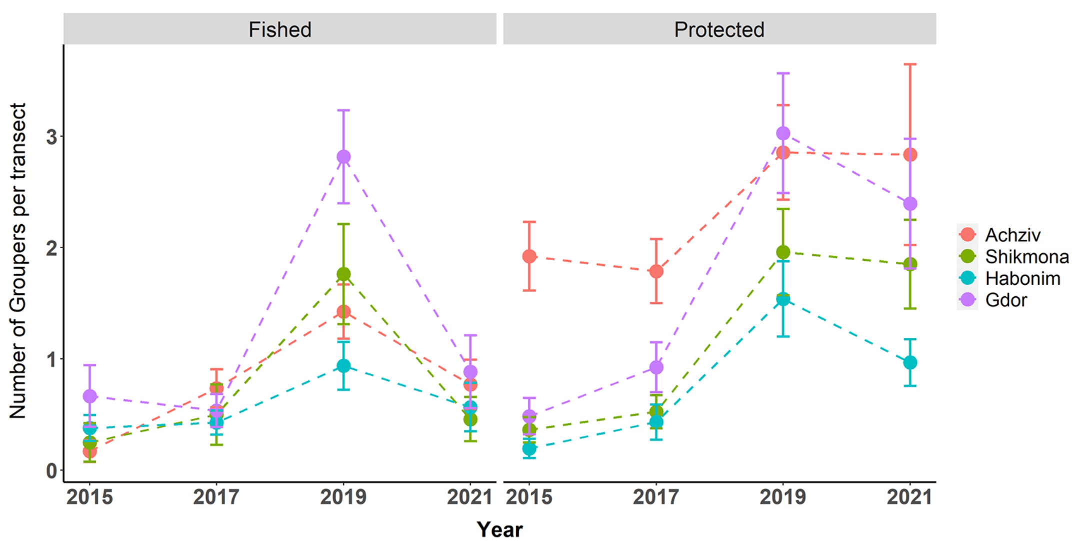

Fig. 5: **Mean grouper abundance (*Epinephelus marginatus* and *Mycteroperca rubra*).** The number of groupers was examined with respect to the effect of protection (in/out), year, season, and depth (fixed effect). The number of groupers in 2019 was significantly higher than in 2015 and 2017 in all locations. Colors represent the different MPAs and error bars represent standard errors (model results shown in appendix Table 7).

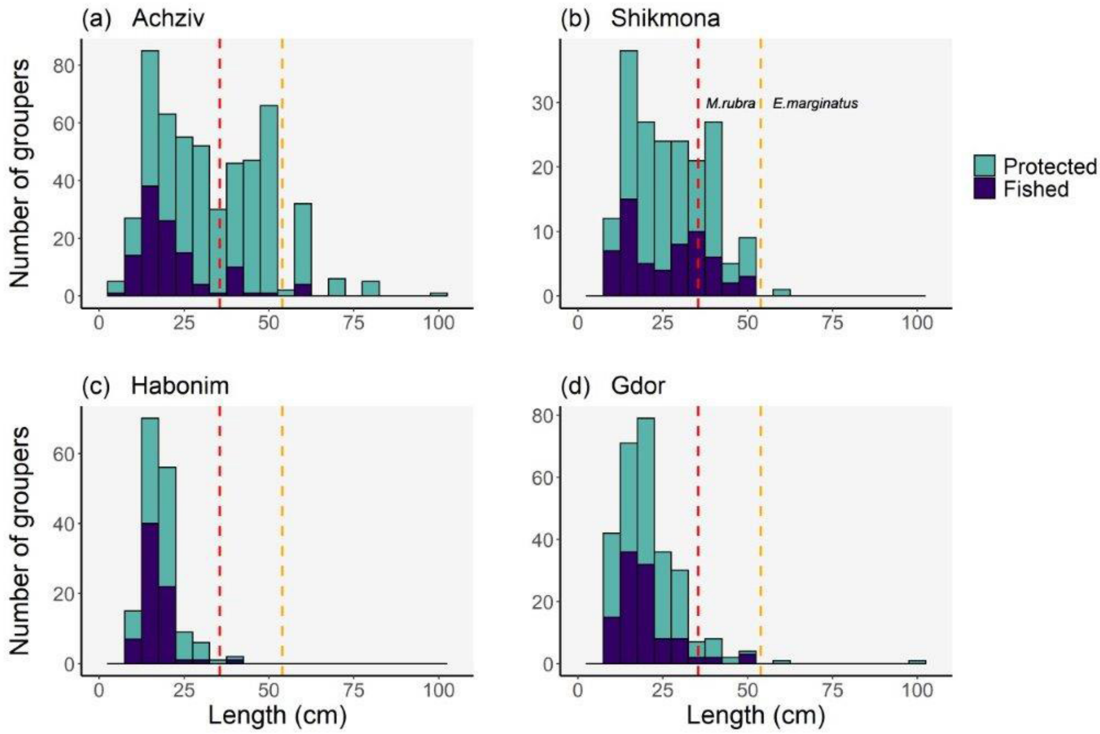

Fig. 6: **Length (TL) distributions of the groupers *Mycteroperca rubra* and *Epinephelus marginatus*.** Dashed red line present maturity length of *M. rubra* and orange dashed line presents maturity length of *E. marginatus*. Within the Achziv MPA the number of mature individuals is significantly higher than in adjacent fished areas (p=0.045). Histograms represent the total across all sampling.

Monitoring of reserves since their establishment is uncommon (Claudet *et al.*, 2006). Here, we show that during a period of 5 years, there is a measurable effect of MPAs on indices such as the number of large individuals (excluding Habonim, appendix Table A6) and the abundance of groupers (excluding Shikmona; Appendix Table A8). However, other measures such as total biomass and the number of mature groupers displayed little change.

Thus, the differences observed in these MPAs are much smaller than in Achziv, and in addition are more variable (as some indices show change and other do not). Nevertheless, these three MPAs show improvement in some indices despite their small sizes and the short time since their enforcement began. The observed changes are compatible with some studies that found rapid MPA recovery after protection (for example, Halpern & Warner, 2002) and with a recent meta-analysis pointing to the benefit of smaller but well enforced MPAs in the Mediterranean region (Giakoumi *et al.*, 2017).

At the same time, the small differences between MPA and control sites are also in line with other studies that find measurable MPA effects only after longer periods of time since the initiation of enforcement (Aburto-Oropeza *et al.*, 2011). As MPAs typically protect multiple habitats and species with varying life history, the reaction to protection is also likely to be variable. This might be the reason for the lack of signal in total biomass increase in the newly enforced MPAs, for which additional time may be needed to detect a measurable buildup of populations for long-lived species such as grouper. Alternatively, the inherently less complex physical characteristics of Habonim, Gdor and Shikmona compared to Achziv (see Methods) and the shallower nature of Habonim and Gdor may limit recovery potential. Finally, edge effects may have eroded these small MPA performance (Ohayon *et al.,* 2021). It is currently unclear if given sufficient time the performance of these three MPAs will increase to be comparable to that of Achziv.

When comparing MPAs and fished control areas, sampling habitats were matched to be as similar as possible. As a result, the distance of the control sites from MPA boundaries was sometimes small (appendix Table A2). Thus, control sites might contain individuals originating from the MPA that appear in adjacent areas due to spillover (Di Lorenzo *et al.*, 2016; Di Lorenzo *et al.*, 2020). Therefore, MPA success may be somewhat masked by the presence of dispersing individuals, reducing our ability to identify differences between MPAs and control areas. This may explain the lack of a signal for total and commercial biomass between the MPAs and control sites (appendix Table A5 and A6). Nevertheless, even when controlling for the potential effect of spillover by only accounting for sites sampled farther than 300m out of MPAs borders, we still could not find an effect of the MPAs on total and commercial biomass (appendix Table A12).

Groupers are a *bona fide* indicator species for examining MPAs success in the Mediterranean Sea (Hackradt *et al.*, 2014, Anderson *et al.*, 2014, Koeck *et al.*, 2014), and the importance of mature individuals for maintaining a sustainable reproductive population is well established (Vasilakopoulos *et al.*, 2011, Berkeley *et al.*, 2004, Froese, 2004). Changes in grouper abundances within and outside MPAs occurred against a backdrop of increasing number of groupers over time in all MPAs (including the small MPAs) and in adjacent fishing grounds (Fig. 5). This increase coincides with the enforcement of new fishing regulations (since 2016), such as species-specific catch size limitations (fishing of juveniles is banned), breeding season fishing bans (grouper fishing bans vary somewhat by year, between April and June), and the ban on the use of SCUBA for spear fishing. The increase in grouper abundance in unprotected areas suggests that the increase in grouper abundance was not related solely to MPAs *per se*, but also to improved nation-wide fishing regulations.

For grouper abundance, we could find an interaction between protection and time in Achziv and Habonim, and for all MPAs when accounting only for sampling sites > 300m from MPAs borders. Interestingly, while in Shikmona, Habonim and Gdor, a sharper increase in groupers abundance over time was found within MPAs, in Achziv we observed a sharper increase over time in the control area. This difference may imply that Achziv MPA is close to its carrying capacity in terms of supporting groupers, while for the younger MPAs, groupers populations are still building up within MPAs. This is further supported for other indices in Achziv, including commercial biomass, total biomass and mature groupers, where no temporal trends were visible despite a clear MPA effect (appendix Tables A5 and A9).

The increase in groupers abundance over time was not paralleled by an increase in the number of individuals above size of first maturity. Thus, the increase in grouper abundance is mainly attributed to juvenile individuals. Large breeding groupers ("mega-spawners") were found mainly within the MPA boundaries of Achziv and are only rarely observed in fished areas. These large-sized individuals have likely survived stress and their offspring may be more resistant and have higher survival rates (Venturelli *et al.*, 2009, Froese, 2004). The absence of mature individuals in fished areas suggests that population in these areas may depend on juvenile and larvae originating from within MPAs.

One reason for the lack of mature groupers in Habonim and Gdor is that these MPAs contain habitats of lower quality, as rocky reefs are present only in shallow depths, which may be unsuitable to support larger individuals of these species (Dimitriadis *et al.*, 2018; Bodilis *et al.*, 2003) (in support, depth had a positive effect on groupers size in Achziv, appendix Table A9). In addition, artisanal fishing in Habonim may also limit recovery of large mature groupers. Nevertheless, we note that recreational fishing bans, and especially spearfishing which is known to target groupers (Sbragaglia *et al.*, 2021), are being strictly enforced. Over time, the number of fishers in Habonim is expected to slowly decrease as no additional permits are granted. Additional time is required to test if the increase in juvenile abundance will manifest as larger grouper breeding populations within these MPAs (Hackradt *et al.*, 2014; Mitcheson *et al.*, 2013).

Even though we found a clear MPA effect and a clear temporal effect, for most indices we found no interaction between MPA and time. The lack of interaction means we cannot unambiguously link the increase in performance over time to the effect of the MPAs. This may mean MPA effects are occurring in tandem with a general improvement in the fisheries condition in the Levantine basin. However, spillover and edge effects (Ohayon *et al.*, 2021) may erode our ability to detect such interactions. In addition, statistical power is lower for detecting interactions compared to main effects. Hence, interactions may be present but only detected after a few more years of sampling.

The highly invaded Levantine basin is a suitable location to examine the biotic resistance hypothesis, suggesting that MPAs buffer exotic species establishment (Ardura *et al.*, 2016; Giakoumi & Pey, 2017; Giakoumi *et al.*, 2019). In this study we found that the exotic species *Pterois miles* and *Scarus ghobban* benefit from MPA protection, while the biomass of the exotic *Lagocephalus sceleratus* was higher in fished areas (Fig. 3). However, overall, higher or similar biomass of exotic species was found within MPAs compared to control fished regions (Fig. A2, Appendix Table A7), suggesting that MPAs do not provide strong biotic resistance. Similar results were observed in Achziv in a different study (Rilov *et al.*, 2018), showing higher abundances of the exotic species *Siganus rivulatus* within MPA boundaries and at a broader Mediterranean scale, where higher biomass of exotic species was found in the South and Eastern Mediterranean MPAs than in adjacent unprotected areas (Giakoumi *et al.*, 2019). The results suggest that MPAs are not an effective management tool to combat exotic species. However, MPAs may still be effective in modifying species behaviors or specific species. For example, the presence of more predators such as groupers may change grazing activity of herbivores (Laundre *et al.*, 2010) such as the exotic *Siganus rivulatus* (Rilov *et al.*, 2018, Shapiro Goldberg *et al.*, 2021), reducing their impact within MPAs. However, more research is needed to validate this hypothesis.

In this study, MPA performance is examined in the highly disturbed Levantine basin, exposed to a rapid increase in water temperatures as well as an influx of exotic species. The studied period covers the transition from poorly enforced to strongly enforced MPAs, and thus provides an important baseline against which to compare future changes. Clear indications for the benefits of MPAs were found and as time from enforcement increases, enforcement effects may accumulate. These benefits of MPA co-occur with an increase in the number of groupers over time both within and outside MPAs, which coincides with enforcement of restrictions on recreational and commercial fishing. The number and area of highly enforced MPAs in the Levantine basin are the lowest in the Mediterranean sea (Claudet *et al.*, 2020). This study suggests that the continual embellishment of well enforced MPAs may have a strong beneficial impact on fish populations even in a region suffering from warming waters and a substantial impact of exotic species.

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Author contributions:

Conceptualization: OF, ML, JB, RY**; Data providers**: OF, ML, SM, RY, JB; **Original Draft Preparation:** OF, ML, JB; **Final Review & Editing: all authors.**

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Appendix

Table A1. LM results for the difference in seascape complexity between MPA and control areas in each location. The response variable was vertical relief while the explanatory variable was protection (categorical; in, out). *n* represents the number of transects within the MPA and in the control sites. *VerRelief MPA* represents the mean values and standard deviation of complexity in transects within MPAs and *VerRelief Control* represents the mean values and standard deviation of complexity in transects outside MPAs.

Location	*Variable*	*Estimate*	*Std. Error*	*P-value*	*n*	*VerRelief MPA*	*VerRelief Control*
Achziv	*Protection*	0.31422	0.16046	0.0549	MPA - 35, control - 27	1.72 ± 1.12	1.17 ± 0.59
Shikmona	*Protection*	0.1036	0.1392	0.4612	MPA - 25, control - 18	0.97 ± 0.38	0.94 ± 0.54
Habonim	*Protection*	0.2049	0.2248	0.3702	MPA - 13, control - 17	1.94 ± 0.64	1.73 ± 0.58
Gdor	*Protection*	0.6631	0.1530	<0.001	MPA - 33, control - 28	2.25 ± 0.59	1.59 ± 0.59

Table A2. Mean distance of the control sites from each of the MPA borders.

MPA	**Mean distance (m)**	**SD**
Achziv	381.8	793.3
Shikmona	228.3	330.1
Habonim	400.5	619.1
Gdor	325.6	487.3

Table A3. Sampling effort (sites) across locations, years, and within/outside MPAs.

MPA	year	Fall		Spring		
		In	**Out**	**In**	**Out**	
Achziv'	2015	8	6	6	6	
	2017	9	6	7	5	
	2019	9	10	8	6	107
	2021	-	-	9	12	
Total		26	22	30	29	
Gdor'	2015	6	4	4	2	
	2017	6	5	9	3	
	2019	4	4	4	3	62
	2021	-	-	4	4	
Total		16	13	21	12	
Habonim'	2015	6	4	4	4	
	2017	4	4	6	4	
	2019	6	6	6	4	66
	2021	-	-	4	4	
Total		16	14	20	16	
Shikmona'	2015	6	3	5	6	
	2017	6	4	6	4	
	2019	6	4	6	4	70
	2021	-	-	6	4	
Total		18	11	23	18	
Total		76	60	94	75	305

Table A4. Mean species abundance and biomass per site (a sum of two transects, 300m^2). *Native* indicates whether species are native to the Mediterranean (+) or exotics (-), *commercially valuable* indicates whether species are of commercial value (+) or not (-), and *a* and *b* represents species' length-weight conversion factors. *Mean abundance* represents the number of individuals observed from each species at a site, and *Mean biomass* represents the biomass of each species in a site, calculated using the length-weight formula. Identifying species from the Clupeidae family is difficult in underwater visual surveys, thus we only categorize to native or exotic.

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m^2)	SD (abundance)	Mean biomass per site (gr per 300m^2)	SD (biomass)
Abudefduf saxatilis	+	-	0.0209	3.12	2015	0.000	0.0	0.0	0.0
			0.0209	3.12	2017	0.000	0.1	0.3	2.9
			0.0209	3.12	2019	0.011	0.0	0.0	0.0
			0.0209	3.12	2021	0.000	0.0	0.0	0.0
Apogon imberbis	+	-	0.114	2.117	2015	0.020	0.2	0.2	1.1
			0.114	2.117	2017	0.057	0.3	0.6	3.1
			0.114	2.117	2019	0.088	0.4	1.0	4.8
			0.114	2.117	2021	0.025	0.1	0.3	2.1
Apogonichthyoides pharaonis	+	-	0.01096	3.1	2015	0.000	0.0	0.0	0.0
			0.01096	3.1	2017	0.011	0.0	0.0	0.0
			0.01096	3.1	2019	0.000	0.1	0.2	1.4
			0.01096	3.1	2021	0.000	0.0	0.0	0.0
Atherinomorus forskalii	+	+	0.01122	3.04	2015	0.000	0.0	0.0	0.0
			0.01122	3.04	2017	71.364	542.4	29.7	187.3
			0.01122	3.04	2019	0.000	0.0	0.0	0.0
			0.01122	3.04	2021	0.000	0.0	0.0	0.0
Balistes carolinensis	+	+	0.0678	2.429	2015	0.000	0.4	0.4	3.4
			0.0678	2.429	2017	0.050	0.5	10.7	80.0
			0.0678	2.429	2019	0.068	0.1	2.9	27.5
			0.0678	2.429	2021	0.011	0.0	0.0	0.0
Belone belone	+	+	0.00093	3.05	2015	0.000	0.0	0.0	0.0
			0.00093	3.05	2017	0.000	1.7	25.7	241.1
			0.00093	3.05	2019	0.182	0.0	0.0	0.0
			0.00093	3.05	2021	0.000	0.0	0.0	0.0
Boops boops	+	+	0.01467	2.877	2015	156.667	26.8	20.1	179.9
			0.01467	2.877	2017	14.857	45.9	195.9	811.3
			0.01467	2.877	2019	11.125	136.3	106.5	958.3
			0.01467	2.877	2021	3.000	635.0	27.3	121.6

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m²)	SD (abundance)	Mean biomass per site (gr per 300m²)	SD (biomass)
Caranx crysos	+	+	0.01	3	2015	0.659	4.1	10.0	59.5
			0.01	3	2017	1.080	5.8	185.8	1123.7
			0.01	3	2019	4.471	2.2	107.5	547.4
			0.01	3	2021	0.575	28.0	512.6	3312.3
Cheilodipterus novemstriatus	-	-	0.01047	3.08	2015	1.033	6.4	4.7	30.1
			0.01047	3.08	2017	0.020	17.2	6.3	33.9
			0.01047	3.08	2019	3.682	8.1	1.6	11.2
			0.01047	3.08	2021	0.975	0.1	0.2	1.8
Chromis chromis	+	-	0.0275	2.703	2015	66.955	91.9	742.4	1443.8
			0.0275	2.703	2017	57.471	130.8	623.9	1412.0
			0.0275	2.703	2019	58.863	315.6	810.6	1598.7
			0.0275	2.703	2021	134.462	102.8	457.5	912.1
Clupeidae sp.	***	+	0.00741	3.03	2015	0.000	0.0	0.0	0.0
			0.00741	3.03	2017	263.187	0.0	0.0	0.0
			0.00741	3.03	2019	0.000	2106.0	118.9	906.6
			0.00741	3.03	2021	0.000	0.0	0.0	0.0
Coris julis	+	-	0.0082	3.054	2015	15.175	36.0	96.1	197.9
			0.0082	3.054	2017	14.250	31.8	113.0	206.2
			0.0082	3.054	2019	10.000	24.2	86.8	123.0
			0.0082	3.054	2021	13.923	14.7	68.6	97.3
Dasyatis pastinaca	+	-	0.0149	2.81	2015	0.039	0.2	19.3	122.7
			0.0149	2.81	2017	0.025	0.6	182.8	531.4
			0.0149	2.81	2019	0.022	0.1	10.4	69.7
			0.0149	2.81	2021	0.216	0.3	18.6	132.5
Dentex dentex	+	+	0.013	2.987	2015	0.080	0.0	0.0	0.0
			0.013	2.987	2017	0.000	0.5	11.4	70.6
			0.013	2.987	2019	0.000	0.0	0.0	0.0
			0.013	2.987	2021	0.000	0.0	0.0	0.0
Diplodus annularis	+	+	0.0123	3.13	2015	0.261	0.9	14.1	98.7
			0.0123	3.13	2017	0.163	1.3	7.1	30.7
			0.0123	3.13	2019	0.099	0.8	1.7	11.6
			0.0123	3.13	2021	0.020	0.1	0.9	6.7

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m²)	SD (abundance)	Mean biomass per site (gr per 300m²)	SD (biomass)
Diplodus cervinus	+	+	0.0116	3.14	2015	1.235	3.5	87.9	329.3
			0.0116	3.14	2017	1.231	1.5	120.7	333.0
			0.0116	3.14	2019	0.727	3.0	137.9	441.7
			0.0116	3.14	2021	1.188	2.4	188.9	472.4
Diplodus puntazzo	+	+	0.0044	2.662	2015	0.011	0.1	0.1	0.6
			0.0044	2.662	2017	0.013	0.1	0.1	0.9
			0.0044	2.662	2019	0.011	0.1	0.1	0.5
			0.0044	2.662	2021	0.000	0.0	0.0	0.0
Diplodus sargus	+	+	0.0608	2.5	2015	48.451	63.7	1322.1	4638.5
			0.0608	2.5	2017	45.627	149.0	2450.8	4410.9
			0.0608	2.5	2019	31.925	67.5	2159.0	2850.9
			0.0608	2.5	2021	69.795	77.1	2299.6	3890.4
Diplodus vulgaris	+	+	0.0194	2.93	2015	22.055	88.5	317.0	710.9
			0.0194	2.93	2017	24.175	28.3	318.0	1080.4
			0.0194	2.93	2019	10.409	99.2	307.1	549.4
			0.0194	2.93	2021	8.745	15.1	395.1	800.3
Echeneis naucrates	+	-	0.127	2.113	2015	0.011	0.0	0.0	0.0
			0.127	2.113	2017	0.000	0.0	0.0	0.0
			0.127	2.113	2019	0.000	0.1	1.4	13.0
			0.127	2.113	2021	0.000	0.0	0.0	0.0
Epinephelus aeneus	+	+	0.012	2.987	2015	0.011	0.0	0.0	0.0
			0.012	2.987	2017	0.057	0.2	13.2	56.1
			0.012	2.987	2019	0.000	0.1	0.3	3.3
			0.012	2.987	2021	0.000	0.0	0.0	0.0
Epinephelus costae	+	+	0.0176	2.885	2015	0.000	0.2	2.5	15.7
			0.0176	2.885	2017	1.118	0.4	34.6	142.9
			0.0176	2.885	2019	0.000	2.6	345.7	1116.1
			0.0176	2.885	2021	0.000	2.1	361.7	1019.1
Epinephelus marginatus	+	+	0.0127	3.085	2015	0.000	1.6	838.6	3891.1
			0.0127	3.085	2017	1.352	1.3	574.3	2443.4
			0.0127	3.085	2019	0.091	4.5	1274.1	2437.5
			0.0127	3.085	2021	0.025	4.3	2094.0	4339.0

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m²)	SD (abundance)	Mean biomass per site (gr per 300m²)	SD (biomass)
Fistularia commersonii	-	-	0.0112	2.54	2015	2.978	3.0	139.7	1249.7
			0.0112	2.54	2017	2.922	2.7	39.9	350.1
			0.0112	2.54	2019	0.773	0.3	10.3	58.9
			0.0112	2.54	2021	0.788	0.0	0.0	0.0
Herklotsichthys punctatus	-	+	0.00933	3.04	2015	0.000	0.0	0.0	0.0
			0.00933	3.04	2017	0.338	319.8	348.8	3271.6
			0.00933	3.04	2019	0.055	158.7	23.3	197.1
			0.00933	3.04	2021	0.330	0.0	0.0	0.0
Himantura uarnak	+	+	0.01698	3.17	2015	34.091	0.0	0.0	0.0
			0.01698	3.17	2017	18.901	0.1	23.1	216.9
			0.01698	3.17	2019	0.000	0.0	0.0	0.0
			0.01698	3.17	2021	0.000	0.0	0.0	0.0
Lagocephalus sceleratus	-	-	0.013	2.933	2015	0.000	0.3	57.9	518.2
			0.013	2.933	2017	0.000	1.6	214.9	1986.1
			0.013	2.933	2019	0.077	0.5	138.7	802.4
			0.013	2.933	2021	0.038	1.1	168.0	940.4
Lithognathus mormyrus	+	+	0.0192	2.83	2015	0.077	1.3	91.9	565.1
			0.0192	2.83	2017	0.182	9.1	54.7	243.7
			0.0192	2.83	2019	0.038	9.3	75.0	494.6
			0.0192	2.83	2021	0.196	0.0	0.0	0.0
Mugilidae sp.	+	+	0.0104	2.964	2015	0.250	4.3	346.4	1965.6
			0.0104	2.964	2017	1.352	7.4	349.7	1147.8
			0.0104	2.964	2019	0.000	16.8	813.5	2850.3
			0.0104	2.964	2021	1.705	2.1	142.1	596.7
Mullus surmuletus	+	+	0.0083	3.15	2015	4.538	0.4	4.6	19.3
			0.0083	3.15	2017	2.148	1.3	4.9	17.3
			0.0083	3.15	2019	0.950	0.0	0.0	0.0
			0.0083	3.15	2021	0.000	0.0	0.0	0.0
Muraena helena	+	-	0.0056	2.776	2015	0.000	0.3	31.3	190.5
			0.0056	2.776	2017	0.569	0.0	0.0	0.0
			0.0056	2.776	2019	0.000	0.1	11.8	112.6
			0.0056	2.776	2021	0.000	0.0	0.0	0.0

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m²)	SD (abundance)	Mean biomass per site (gr per 300m²)	SD (biomass)
Mycteroperca rubra	+	+	0.008	3.065	2015	0.000	3.5	758.7	3268.0
			0.008	3.065	2017	0.000	2.3	590.2	1072.7
			0.008	3.065	2019	0.352	6.1	1596.4	3868.8
			0.008	3.065	2021	0.088	13.6	3245.7	17698.3
Oblada melanura	+	+	0.017	2.934	2015	0.011	67.3	710.8	4076.6
			0.017	2.934	2017	0.000	68.3	866.7	2571.0
			0.017	2.934	2019	0.000	532.5	5892.5	24409.4
			0.017	2.934	2021	0.063	52.4	578.3	1401.1
Pagellus acarne	+	+	0.0186	2.841	2015	5.538	0.0	0.0	0.0
			0.0186	2.841	2017	2.000	16.0	7.3	68.7
			0.0186	2.841	2019	5.333	0.0	0.0	0.0
			0.0186	2.841	2021	1.950	0.0	0.0	0.0
Pagrus auriga	+	+	0.01905	3	2015	19.500	0.0	0.0	0.0
			0.01905	3	2017	203.110	0.0	0.0	0.0
			0.01905	3	2019	16.980	0.2	18.0	171.2
			0.01905	3	2021	25.636	0.0	0.0	0.0
Pagrus caeruleostictus	+	+	0.0125	2.995	2015	0.000	0.0	0.0	0.0
			0.0125	2.995	2017	0.011	0.0	0.0	0.0
			0.0125	2.995	2019	0.020	0.1	14.4	112.4
			0.0125	2.995	2021	0.000	0.1	10.3	73.7
Pagrus pagrus	+	+	0.0138	3.03	2015	0.000	0.0	0.0	0.0
			0.0138	3.03	2017	1.705	0.0	0.0	0.0
			0.0138	3.03	2019	0.000	0.2	0.2	1.6
			0.0138	3.03	2021	0.000	0.0	0.0	0.0
Parupeneus forsskali	-	+	0.0037	3.381	2015	0.022	0.2	0.1	0.9
			0.0037	3.381	2017	0.000	4.9	28.9	88.0
			0.0037	3.381	2019	0.000	9.3	243.8	496.1
			0.0037	3.381	2021	0.000	3.1	78.4	159.7
Pempheris vanicolensis	-	-	0.0119	3.026	2015	0.000	22.5	180.7	879.3
			0.0119	3.026	2017	0.000	4.0	43.6	167.5
			0.0119	3.026	2019	0.000	5.6	64.7	200.9
			0.0119	3.026	2021	0.022	2.2	27.5	96.1

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m^2)	SD (abundance)	Mean biomass per site (gr per 300m^2)	SD (biomass)
Plotosus lineatus	-	-	0.008	2.95	2015	0.022	12.1	28.9	148.5
			0.008	2.95	2017	0.000	0.0	0.0	0.0
			0.008	2.95	2019	0.000	0.0	0.0	0.0
			0.008	2.95	2021	0.000	0.0	0.0	0.0
Pomadasys incisus	+	+	0.0199	2.834	2015	1.529	18.3	43.2	386.5
			0.0199	2.834	2017	5.615	0.0	0.0	0.0
			0.0199	2.834	2019	0.025	0.7	9.8	67.2
			0.0199	2.834	2021	1.693	0.3	2.3	16.7
Pseudocaranx dentex	+	+	0.131	2.51	2015	1.529	0.0	0.0	0.0
			0.131	2.51	2017	5.615	2.5	365.8	3229.9
			0.131	2.51	2019	0.025	1.1	68.8	519.6
			0.131	2.51	2021	1.693	0.0	0.0	0.0
Pteragogus trispilus	-	-	0.02042	2.99	2015	1.901	0.0	0.0	0.0
			0.02042	2.99	2017	1.261	0.0	0.0	0.0
			0.02042	2.99	2019	0.745	0.4	0.3	1.9
			0.02042	2.99	2021	6.050	0.4	0.5	1.7
Pterois miles	-	-	0.01023	3.1	2015	0.000	0.0	0.0	0.0
			0.01023	3.1	2017	2.025	0.0	0.0	0.0
			0.01023	3.1	2019	0.000	0.3	10.3	62.2
			0.01023	3.1	2021	0.000	0.3	34.8	153.6
Sardina pilchardus	-	+	0.00688	3.05	2015	2.050	0.0	0.0	0.0
			0.00688	3.05	2017	0.000	0.9	4.7	43.9
			0.00688	3.05	2019	0.039	0.0	0.0	0.0
			0.00688	3.05	2021	0.088	0.0	0.0	0.0
Sargocentron rubrum	-	-	0.0571	2.658	2015	0.000	8.1	483.0	1065.0
			0.0571	2.658	2017	0.198	10.2	701.4	1458.9
			0.0571	2.658	2019	0.341	10.2	627.7	1177.1
			0.0571	2.658	2021	0.000	16.1	580.4	1637.4
Sarpa salpa	+	+	0.0087	3.134	2015	0.137	0.0	0.0	0.0
			0.0087	3.134	2017	0.000	0.0	0.0	0.0
			0.0087	3.134	2019	0.000	0.2	0.9	9.0
			0.0087	3.134	2021	0.066	0.6	4.9	35.0

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m²)	SD (abundance)	Mean biomass per site (gr per 300m²)	SD (biomass)
Scarus ghobban	-	-	0.0233	2.919	2015	0.000	1.7	302.5	1943.2
			0.0233	2.919	2017	0.044	0.6	67.5	305.5
			0.0233	2.919	2019	0.078	0.9	168.6	521.6
			0.0233	2.919	2021	0.000	0.5	109.9	665.5
Sciaena umbra	+	+	0.0069	3.159	2015	0.000	0.1	1.1	9.9
			0.0069	3.159	2017	0.000	0.3	13.4	125.5
			0.0069	3.159	2019	0.091	0.2	16.2	154.3
			0.0069	3.159	2021	0.000	0.3	45.2	322.5
Scomberomorus commerson	-	+	0.012	2.812	2015	5.549	0.1	0.7	6.1
			0.012	2.812	2017	6.148	0.0	0.0	0.0
			0.012	2.812	2019	5.396	0.1	29.6	282.6
			0.012	2.812	2021	4.425	0.0	0.0	0.0
Seriola dumerili	+	+	0.0199	2.964	2015	0.078	0.1	0.4	3.5
			0.0199	2.964	2017	0.022	0.0	0.0	0.0
			0.0199	2.964	2019	0.000	0.2	21.2	202.5
			0.0199	2.964	2021	0.000	0.0	0.0	0.0
Serranus cabrilla	+	-	0.0174	2.85	2015	0.098	1.4	18.2	53.1
			0.0174	2.85	2017	0.253	1.0	12.7	44.8
			0.0174	2.85	2019	0.125	1.0	10.8	39.8
			0.0174	2.85	2021	0.288	0.4	3.0	10.6
Serranus hepatus	+	-	0.0151	3.04	2015	0.039	0.1	0.2	1.9
			0.0151	3.04	2017	0.022	0.0	0.0	0.0
			0.0151	3.04	2019	0.034	0.0	0.0	0.0
			0.0151	3.04	2021	0.013	0.0	0.0	0.0
Serranus scriba	+	-	0.0044	3.409	2015	0.000	0.7	30.2	96.0
			0.0044	3.409	2017	0.011	0.8	92.9	544.6
			0.0044	3.409	2019	0.013	2.6	52.5	154.2
			0.0044	3.409	2021	0.000	2.2	61.9	140.5
Siganus luridus	-	+	0.011	3.04	2015	0.000	66.1	1352.8	4030.2
			0.011	3.04	2017	0.022	38.8	631.7	2297.0
			0.011	3.04	2019	0.013	123.7	907.9	2035.7
			0.011	3.04	2021	0.000	60.2	1095.7	2443.2

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m²)	SD (abundance)	Mean biomass per site (gr per 300m²)	SD (biomass)
Siganus rivulatus	-	+	0.022	2.82	2015	0.488	519.6	8623.0	22974.1
			0.022	2.82	2017	0.330	662.0	11068.5	20321.4
			0.022	2.82	2019	0.363	438.4	5961.8	14421.7
			0.022	2.82	2021	0.098	57.4	1596.1	2957.3
Sparisoma cretense	+	-	0.01127	3.052	2015	0.000	3.6	33.2	194.0
			0.01127	3.052	2017	0.000	0.3	11.4	67.3
			0.01127	3.052	2019	0.000	3.1	6.7	28.1
			0.01127	3.052	2021	0.013	5.2	58.3	125.2
Sparus aurata	+	+	0.0266	2.736	2015	0.275	0.6	18.3	96.5
			0.0266	2.736	2017	0.307	1.1	25.8	85.2
			0.0266	2.736	2019	1.039	0.9	18.0	79.3
			0.0266	2.736	2021	0.879	0.4	9.4	67.3
Sphyraena chrysotaenia	-	+	0.012	2.73	2015	26.216	0.0	0.0	0.0
			0.012	2.73	2017	23.088	0.1	3.2	30.2
			0.012	2.73	2019	25.462	0.0	0.0	0.0
			0.012	2.73	2021	9.955	0.0	0.0	0.0
Spicara maena	+	-	0.0089	3.1	2015	31.275	1.7	0.7	6.2
			0.0089	3.1	2017	235.525	0.3	0.5	4.2
			0.0089	3.1	2019	469.375	209.7	262.3	2502.1
			0.0089	3.1	2021	177.681	0.0	0.0	0.0
Spicara smaris	+	-	0.0105	2.97	2015	2.333	0.0	0.0	0.0
			0.0105	2.97	2017	0.080	1.6	1.7	15.7
			0.0105	2.97	2019	0.703	1.0	1.9	17.7
			0.0105	2.97	2021	0.813	0.0	0.0	0.0
Stephanolepis diaspros	-	-	0.0162	3.03	2015	0.176	0.2	1.8	9.6
			0.0162	3.03	2017	0.295	0.0	0.0	0.0
			0.0162	3.03	2019	0.059	0.3	5.5	34.7
			0.0162	3.03	2021	0.113	0.3	2.3	16.6
Symphodus cinereus	+	-	0.01148	3.06	2015	0.000	0.0	0.0	0.0
			0.01148	3.06	2017	0.000	0.0	0.0	0.0
			0.01148	3.06	2019	0.000	0.1	0.1	0.7
			0.01148	3.06	2021	0.011	0.0	0.0	0.0

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m^2)	SD (abundance)	Mean biomass per site (gr per 300m^2)	SD (biomass)
Symphodus mediterraneus	+	-	0.0173	2.902	2015	21.978	1.0	2.3	9.3
			0.0173	2.902	2017	0.045	0.5	2.2	12.1
			0.0173	2.902	2019	0.188	2.2	4.0	8.6
			0.0173	2.902	2021	0.000	0.9	3.2	8.3
Symphodus ocellatus	+	-	0.0123	3.13	2015	0.000	0.0	0.0	0.0
			0.0123	3.13	2017	0.000	0.0	0.0	0.0
			0.0123	3.13	2019	0.170	0.2	0.0	0.3
			0.0123	3.13	2021	0.110	0.0	0.0	0.0
Symphodus roissali	+	-	0.0069	3.386	2015	0.055	0.7	6.2	25.2
			0.0069	3.386	2017	0.000	1.5	1.8	6.1
			0.0069	3.386	2019	0.050	1.9	6.4	18.9
			0.0069	3.386	2021	0.039	0.8	7.0	26.0
Symphodus tinca	+	-	0.02782	2.733	2015	0.000	1.4	20.1	61.5
			0.02782	2.733	2017	0.000	1.9	30.1	64.5
			0.02782	2.733	2019	0.000	8.6	60.3	107.8
			0.02782	2.733	2021	0.011	2.1	60.2	168.6
Taeniura grabata	+	-	0.00869	3	2015	0.114	0.2	169.3	1319.0
			0.00869	3	2017	0.294	0.1	98.8	926.4
			0.00869	3	2019	0.300	0.1	128.2	959.8
			0.00869	3	2021	0.967	0.6	579.5	2926.7
Thalassoma pavo	+	-	0.0092	3.111	2015	0.000	138.0	1264.4	1536.4
			0.0092	3.111	2017	0.000	55.9	745.8	811.7
			0.0092	3.111	2019	0.000	67.0	956.5	861.3
			0.0092	3.111	2021	0.022	248.7	1195.7	2007.1
Torpedo marmorata	+	-	0.0579	2.733	2015	0.560	0.0	0.0	0.0
			0.0579	2.733	2017	0.314	0.0	0.0	0.0
			0.0579	2.733	2019	0.175	0.0	0.0	0.0
			0.0579	2.733	2021	0.341	0.1	14.7	105.3
Torpedo torpedo	+	-	0.04544	2.689	2015	0.795	0.0	0.0	0.0
			0.04544	2.689	2017	0.563	0.0	0.0	0.0
			0.04544	2.689	2019	1.020	0.0	0.0	0.0
			0.04544	2.689	2021	3.110	0.3	31.6	185.2

Continued

Table A4 continued

Species	Native	Commercially valuable	a	b	Year	Mean abundance per site (300m²)	SD (abundance)	Mean biomass per site (gr per 300m²)	SD (biomass)
Torquigener flavimaculosus	-	-	0.0403	2.902	2015	0.137	7.9	8.8	42.8
			0.0403	2.902	2017	0.038	2.2	31.5	127.2
			0.03761	2.8363	2019	0.022	11.0	277.0	799.8
			0.0403	2.902	2021	0.011	0.5	6.8	21.3
Trachinotus ovatus	+	+	0.022	2.73	2015	65.648	0.6	4.9	43.8
			0.022	2.73	2017	76.714	0.0	0.0	0.0
			0.022	2.73	2019	120.150	0.1	0.7	7.1
			0.022	2.73	2021	146.627	0.0	0.0	0.0
Trachurus mediterraneus	+	+	0.0128	2.81	2015	0.000	0.0	0.0	0.0
			0.0128	2.81	2017	0.000	0.0	0.0	0.0
			0.0128	2.81	2019	0.000	0.1	0.0	0.1
			0.0128	2.81	2021	0.020	0.0	0.0	0.0
Upeneus pori	-	+	0.0095	3.02	2015	0.059	0.0	0.0	0.0
			0.0095	3.02	2017	0.000	0.0	0.0	0.0
			0.0095	3.02	2019	0.000	0.2	0.5	4.6
			0.0095	3.02	2021	0.000	0.0	0.0	0.0
Xyrichtys novacula	+	-	0.01288	2.89	2015	0.196	0.0	0.0	0.0
			0.01288	2.89	2017	4.857	0.0	0.0	0.0
			0.01288	2.89	2019	0.523	0.1	0.1	0.5
			0.01288	2.89	2021	1.013	0.0	0.0	0.0

Table A5. GLM results for total and commercial biomass and ANOV results for total biomass, shown for each MPAs. We tested how log (biomass, kg/300m^2) changed with season, year and protection. Depth was also included for the deeper MPAs Achziv and Shikmona. We also tested the interaction between year (time) and MPA in a separate model to identify whether the effect of protection changed over time.

'Achziv' - Total biomass					'Achziv' - Commercial biomass			
Variable	*Estimate*	*Std. Error*	*P-value*		*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.104	0.101	0.307		*Year*	0.258	0.143	0.074
MPA	-0.861	0.211	<0.001		*MPA*	-1.400	0.292	<0.001
Season	-0.611	0.225	0.008		*Season*	-0.818	0.311	0.010
Depth	-0.033	0.017	0.056		*Depth*	-0.074	0.024	0.002
Interaction model					**Interaction model**			
Year	0.168	0.146	0.253		*Year*	0.128	0.201	0.524
MPA	-0.925	0.537	0.088		*MPA*	-2.034	0.747	0.008
Season	-0.724	0.228	0.002		*Season*	-0.826	0.312	0.009
Depth	-0.043	0.017	0.015		*Depth*	-0.074	0.024	0.002
Year : Reserve Interaction	-0.037	0.194	0.850		*Year: Reserve Interaction*	0.249	0.270	0.358
ANOVA model results for total biomass	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*P-value*			
MPA	1	23.9	23.898	17.39	<0.001			
Residuals	99	136.1	1.375					
Shikmona' - Total biomass					Shikmona'- Commercial biomass			
Variable	*Estimate*	*Std. Error*	*P-value*		*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.575	0.136	<0.001		*Year*	0.645	0.189	0.001
MPA	-0.593	0.276	0.035		*MPA*	-0.501	0.390	0.204
Season	-1.021	0.276	<0.001		*Season*	-1.646	0.388	<0.001
Depth	0.032	0.030	0.288		*Depth*	0.038	0.043	0.373
Interaction model					**Interaction model**			
Year	0.379	0.175	0.034		*Year*	0.502	0.223	0.028
MPA	-1.647	0.660	0.015		*MPA*	-0.079	0.815	0.923
Season	-0.982	0.272	0.001		*Season*	-1.769	0.327	<0.001
Depth	0.032	0.029	0.288		*Depth*	0.043	0.043	0.319
Year: Reserve Interaction	0.471	0.269	0.085		*Year: Reserve Interaction*	-0.141	0.320	0.661
ANOVA model results for total biomass	*Df*	*Sum Sq*	***Mean Sq***	*F value*	*P-value*			
MPA	1	8.87	8.874	4.953	0.030			
Residuals	66	118.24	1.792					

Continued

Table A5 continued

'Achziv' - Total biomass					'Achziv' - Commercial biomass			
Habonim' - Total biomass					Habonim'- Commercial biomass			
Variable	*Estimate*	*Std. Error*	*P-value*		*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.320	0.127	0.014		*Year*	0.466	0.156	0.004
MPA	-0.370	0.246	0.137		*MPA*	-0.499	0.299	0.101
Season	-1.420	0.250	<0.001		*Season*	-1.742	0.309	<0.001
Interaction model					**Interaction model**			
Year	0.330	0.170	0.057		*Year*	0.504	0.212	0.021
MPA	-0.322	0.625	0.608		*MPA*	-0.304	0.777	0.697
Season	-1.421	0.253	<0.001		*Season*	-1.745	0.312	<0.001
Year: Reserve Interaction	-0.021	0.252	0.933		*Year: Reserve Interaction*	-0.083	0.305	0.786
ANOVA model results for total biomass	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*P-value*			
MPA	1	2.12	2.119	1.547	0.219			
Residuals	53	72.6	1.37					
Gdor' - Total biomass					Gdor'- Commercial biomass			
Variable	*Estimate*	*Std. Error*	*P-value*		*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.132	0.128	0.305		*Year*	0.189	0.142	0.189
MPA	-0.245	0.244	0.320		*MPA*	-0.402	0.271	0.144
Season	-1.403	0.250	<0.001		*Season*	-1.695	0.278	<0.001
Interaction model					**Interaction model**			
Year	0.212	0.166	0.208		*Year*	0.241	0.186	0.200
MPA	0.177	0.611	0.774		*MPA*	-0.128	0.682	0.852
Season	-1.395	0.251	<0.001		*Season*	-1.689	0.280	<0.001
Year: Reserve Interaction	-0.185	0.246	0.455		*Year: Reserve Interaction*	-0.120	0.274	0.663
ANOVA model results for total biomass	*Df*	*Sum Sq*	*Mean Sq*	*F value*	*P-value*			
MPA	1	0.53	0.5287	0.469	0.496			
Residuals	54	60.85	1.1269					

Table A6. GLM results for the number of large individuals, shown for each MPAs. We tested how the number of large individuals changed with season, year and protection. Depth was also included for the deeper MPAs Achziv and Shikmona. We also tested the interaction between year (time) and MPA in a separate model to identify whether the effect of protection changed over time.

'Achziv' - Number of large individuals							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.067	0.017	<0.001	*Year*	0.148	0.019	<0.001
MPA	-1.474	0.043	<0.001	*MPA*	-0.542	0.101	<0.001
Season	0.087	0.036	0.015	*Season*	0.082	0.036	0.022
Depth	-0.039	0.003	<0.001	*Depth*	-0.039	0.003	<0.001
				Year: Reserve Interaction	-0.358	0.037	<0.001

'Shikmona'- Number of large individuals							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.528	0.042	<0.001	*Year*	0.478	0.050	<0.001
MPA	-0.339	0.080	<0.001	*MPA*	-0.757	0.247	0.002
Season	-0.538	0.080	<0.001	*Season*	-0.531	0.080	<0.001
Depth	0.036	0.008	<0.001	*Depth*	0.037	0.009	<0.001
				Year: Reserve Interaction	0.151	0.083	0.071

'Habonim'- Number of large individuals							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	-0.310	0.024	<0.001	*Year*	-0.096	0.034	0.005
MPA	0.292	0.043	<0.001	*MPA*	1.084	0.102	<0.001
Season	-1.420	0.053	<0.001	*Season*	-1.450	0.054	<0.001
				Year: Reserve Interaction	-0.414	0.048	<0.001

'Gdor'- Number of large individuals							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	-0.019	0.022	0.381	*Year*	-0.042	0.027	0.122
MPA	-0.318	0.038	<0.001	*MPA*	-0.443	0.096	<0.001
Season	-1.747	0.050	<0.001	*Season*	-1.748	0.050	<0.001
				Year: Reserve Interaction	0.061	0.043	0.156

Table A7. GLM results for biomass of exotic species, shown for each MPAs. We examined how exotic species biomass (kg/300m^2) changed with protection and season. Depth was also included for the deeper MPAs Achziv and Shikmona. We also tested the interaction between year (time) and MPA in a separate model to identify whether the effect of protection changed over time.

'Achziv'-Exotic biomass

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	-0.169	0.192	0.380	*Year*	-0.118	0.273	0.667
MPA	-0.832	0.408	0.044	*MPA*	-0.594	0.992	0.550
Depth	-0.025	0.033	0.442	*Depth*	-0.025	0.033	0.444
Season	-1.599	0.437	< 0.001	*Season*	-1.597	0.439	< 0.001
				Year: Reserve Interaction	-0.095	0.362	0.793

'Shikmona'-Exotic biomass

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.719	0.272	0.010	*Year*	0.517	0.359	0.155
MPA	-1.051	0.568	0.069	*MPA*	-2.110	1.349	0.123
Depth	0.074	0.062	0.235	*Depth*	0.073	0.062	0.247
Season	-2.214	0.575	< 0.001	*Season*	-2.171	0.578	< 0.001
				Year: Reserve Interaction	0.470	0.542	0.390

'Habonim'- Exotic biomass

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.609	0.330	0.073	*Year*	0.994	0.434	0.028
MPA	0.275	0.709	0.700	*MPA*	2.046	1.492	0.179
Season	-4.425	0.785	< 0.001	*Season*	-4.491	0.778	< 0.001
				Year: Reserve Interaction	-0.802	0.596	0.187

'Gdor' -Exotic biomass

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.047	0.322	0.885	*Year*	-0.073	0.408	0.858
MPA	-1.129	0.588	0.061	*MPA*	-1.753	1.416	0.222
Season	-3.256	0.606	< 0.001	*Season*	-3.264	0.611	< 0.001
				Year: Reserve Interaction	0.271	0.558	0.630

Table A8. GLM results for groupers abundance, shown for each MPAs. We tested how the number of groupers changed with year, protection, and season. Depth was also included for the deeper MPAs Achziv and Shikmona. We also tested the interaction between year (time) and MPA in a separate model to identify whether the effect of protection changed over time.

‘Achziv’ – Grouper’s abundance

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.327	0.050	< 0.001	*Year*	-1.793	0.319	< 0.001
MPA	-0.909	0.099	< 0.001	*MPA*	0.207	0.057	< 0.001
Depth	-0.024	0.007	0.001	*Depth*	-0.024	0.007	0.001
Season	-0.396	0.100	< 0.001	*Season*	-0.419	0.100	< 0.001
				Year: Reserve Interaction	0.323	0.101	0.001

‘Shikmona’– Grouper’s abundance

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.742	0.088	< 0.001	*Year*	0.862	0.110	< 0.001
MPA	-0.280	0.149	0.061	*MPA*	0.627	0.491	0.201
Depth	0.098	0.017	< 0.001	*Depth*	0.096	0.017	< 0.001
Season	-0.766	0.155	< 0.001	*Season*	-0.796	0.156	< 0.001
				Year: Reserve Interaction	-0.318	0.166	0.055

‘Habonim’– Grouper’s abundance

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.956	0.113	< 0.001	*Year*	1.145	0.148	< 0.001
MPA	-0.327	0.160	0.040	*MPA*	0.950	0.599	0.112
Season	-1.754	0.195	< 0.001	*Season*	-1.772	0.197	< 0.001
				Year: Reserve Interaction	-0.452	0.206	0.028

‘Gdor’– Grouper’s abundance

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.996	0.077	< 0.001	*Year*	1.060	0.090	< 0.001
MPA	-0.460	0.115	< 0.001	*MPA*	0.069	0.395	0.861
Season	-1.889	0.143	< 0.001	*Season*	-1.882	0.143	< 0.001
				Year: Reserve Interaction	-0.191	0.138	0.165

Table A9. GLM results for the total number of mature groupers (per 300 m^2), shown for each MPA. We tested how the number of mature individuals changed with season, year, protection, depth. Notice that the number of mature individuals was too small for analyses in Habonim and Gdor (1 and 7 mature individuals only, respectively).

'Achziv' - Grouper's maturity

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.148	0.099	0.140	*Year*	0.184	0.108	0.093
MPA	-0.953	0.409	0.022	*MPA*	352.856	422.027	0.406
Depth	0.058	0.028	0.040	*Depth*	0.057	0.028	0.044
Season	-0.616	0.381	0.109	*Season*	-0.590	0.380	0.124
				Year: Reserve Interaction	-0.175	0.209	0.404

'Shikmona' - Grouper's maturity

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.173	0.175	0.328	*Year*	0.114	0.200	0.574
MPA	-0.209	0.685	0.762	*MPA*	-468.358	788.013	0.556
Depth	0.104	0.081	0.205	*Depth*	0.107	0.085	0.216
Season	-0.187	0.666	0.780	*Season*	-0.178	0.687	0.797
				Year: Reserve Interaction	0.232	0.390	0.556

Table A10. GLM results for number of groupers, shown for each MPAs. Models include only sites sampled within the MPA and at distance of >300m from MPA boarder. We tested how the number of groupers changed with year, protection, and season. Depth was also included for the deeper MPAs Achziv and Shikmona. We also tested the interaction between year (time) and MPA in a separate model to identify whether the effect of protection changed over time.

Achziv' - Grouper's abundance (transects >300 m from MPA border)							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.327	0.054	< 0.001	*Year*	0.209	0.057	< 0.001
MPA	-1.010	0.126	< 0.001	*MPA*	-3.979	0.694	< 0.001
Depth	-0.018	0.008	0.026	*Depth*	-0.018	0.008	0.019
Season	-0.444	0.105	< 0.001	*Season*	-0.359	0.105	0.001
				Year: Reserve Interaction	1.131	0.244	< 0.001

Shikmona'- Grouper's abundance (transects >300 m from MPA border)							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.631	0.091	< 0.001	*Year*	0.798	0.112	< 0.001
MPA	-0.145	0.186	0.434	*MPA*	1.276	0.528	0.016
Depth	-0.664	0.170	< 0.001	*Depth*	-0.722	0.170	< 0.001
Season	0.104	0.020	< 0.001	*Season*	0.109	0.019	< 0.001
				Year: Reserve Interaction	-0.509	0.184	0.006

Habonim'- Grouper's abundance (transects >300 m from MPA border)							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.836	0.119	< 0.001	*Year*	1.034	0.155	< 0.001
MPA	0.070	0.246	0.775	*MPA*	1.326	0.580	0.022
Season	-1.693	0.255	< 0.001	*Season*	-1.667	0.250	< 0.001
				Year: Reserve Interaction	-0.467	0.200	0.019

Gdor'- Grouper's abundance (transects >300 m from MPA border)							
				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.985	0.092	< 0.001	*Year*	1.055	0.097	< 0.001
MPA	-0.672	0.176	< 0.001	*MPA*	0.263	0.423	0.534
Season	-1.833	0.166	< 0.001	*Season*	-1.780	0.165	< 0.001
				Year: Reserve Interaction	-0.354	0.152	0.020

Table A11. GLM results for the number of large individuals, shown for each MPAs. Models include only sites sampled within the MPA and at distance of >300m from MPA boarder. We tested how the number of large individuals changed with season, year and protection. Depth was also included for the deeper MPAs Achziv and Shikmona. We also tested the interaction between year (time) and MPA in a separate model to identify whether the effect of protection changed over time.

Achziv' -Number of large individuals (transects >300 m from MPA border)

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.216	0.018	<0.001	*Year*	0.089	0.024	<0.001
MPA	-1.179	0.049	<0.001	*MPA*	-0.436	0.117	<0.001
Season	0.090	0.037	0.015	*Season*	-0.626	0.044	<0.001
Depth	-0.037	0.003	<0.001	*Depth*	-0.046	0.003	<0.001
				Year: Reserve Interaction	-0.262	0.046	<0.001

Shikmona'-Number of large individuals (transects >300 m from MPA border)

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.362	0.042	<0.001	*Year*	0.382	0.050	<0.001
MPA	-0.183	0.096	0.059	*MPA*	-0.006	0.247	0.981
Season	-0.356	0.085	<0.001	*Season*	-0.362	0.086	<0.001
Depth	0.040	0.010	<0.001	*Depth*	0.040	0.010	<0.001
				Year: Reserve Interaction	-0.068	0.089	0.441

Habonim'-Number of large individuals (transects >300 m from MPA border)

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	-0.201	0.027	<0.001	*Year*	-0.048	0.035	0.166
MPA	0.721	0.044	<0.001	*MPA*	1.398	0.106	<0.001
Season	-1.424	0.055	<0.001	*Season*	-1.385	0.054	<0.001
				Year: Reserve Interaction	-0.392	0.056	<0.001

Gdor' - Number of large individuals (transects >300 m from MPA border)

				Interaction model			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	-0.031	0.024	0.194	*Year*	-0.024	0.026	0.354
MPA	-1.103	0.053	<0.001	*MPA*	-1.041	0.128	<0.001
Season	-1.520	0.051	<0.001	*Season*	-1.520	0.051	<0.001
				Year: Reserve Interaction	-0.030	0.056	0.594

Table A12. GLM results for total and commercial biomass, shown for each MPAs. Models include only sites sampled within the MPA and at distance of >300m from MPA boarder. We tested how log (biomass, kg/300m^2) changed with season, year, protection (fixed effects). Depth was also included for the deeper MPAs Achziv and Shikmona. We also tested the interaction between year (time) and MPA in a separate model to identify whether the effect of protection changed over time. These results did not change our main conclusions.

Biomass (transects >300 m from MPA border)							
Achziv' - Commercial biomass				**Achziv' -Total biomass**			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.145	0.14	0.303	*Year*	0.124	0.105	0.241
MPA	-1.321	0.286	<0.001	*MPA*	-0.958	0.217	<0.001
Season	-0.789	0.305	0.011	*Season*	-0.8	0.229	0.001
Depth	-0.072	0.023	0.003	*Depth*	-0.041	0.017	0.022
Interaction model				**Interaction model**			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.068	0.197	0.731	*Year*	0.208	0.146	0.159
MPA	-1.698	0.734	0.023	*MPA*	-0.546	0.544	0.318
Season	-0.794	0.306	0.011	*Season*	-0.803	0.23	0.001
Depth	-0.072	0.023	0.003	*Depth*	-0.04	0.017	0.023
Year : Reserve Interaction	0.148	0.265	0.577	*Year: Reserve Interaction*	-0.165	0.2	0.411
Shikmona- Commercial biomass				**Shikmona- Total biomass**			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.668	0.188	0.001	*Year*	0.505	0.14	0.001
MPA	-0.553	0.386	0.158	*MPA*	-0.527	0.282	0.066
Season	-1.597	0.385	<0.001	*Season*	-1.115	0.282	<0.001
Depth	0.036	0.042	0.398	*Depth*	0.039	0.031	0.202
Interaction model				**Interaction model**			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.706	0.241	0.005	*Year*	0.277	0.178	0.124
MPA	-0.328	0.984	0.74	*MPA*	-1.754	0.671	0.011
Season	-1.605	0.389	<0.001	*Season*	-1.069	0.277	<0.001
Depth	0.036	0.043	0.396	*Depth*	0.039	0.03	0.198
Year: Reserve Interaction	-0.095	0.38	0.804	*Year: Reserve Interaction*	0.548	0.273	0.049
Habonim- Commercial biomass				**Habonim- Total biomass**			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.46	0.159	0.005	*Year*	0.348	0.129	0.009
MPA	-0.47	0.305	0.129	*MPA*	-0.303	0.25	0.231
Season	-1.693	0.315	<0.001	*Season*	-1.332	0.255	<0.001
Interaction model				**Interaction model**			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.513	0.217	0.021	*Year*	0.409	0.173	0.021
MPA	-0.208	0.792	0.794	*MPA*	0.005	0.635	0.994
Season	-1.697	0.318	<0.001	*Season*	-1.34	0.257	<0.001
Year: Reserve Interaction	-0.112	0.311	0.721	*Year: Reserve Interaction*	-0.135	0.256	0.6

Continued

Table A12 continued

Gdor- Commercial biomass				Gdor - Total biomass			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.241	0.141	0.092	*Year*	0.136	0.131	0.305
MPA	-0.425	0.269	0.12	*MPA*	-0.11	0.246	0.657
Season	-1.709	0.276	<0.001	*Season*	-1.364	0.251	<0.001
Interaction model				**Interaction model**			
Variable	*Estimate*	*Std. Error*	*P-value*	*Variable*	*Estimate*	*Std. Error*	*P-value*
Year	0.254	0.184	0.174	*Year*	0.115	0.176	0.517
MPA	-0.359	0.678	0.599	*MPA*	-0.213	0.623	0.734
Season	-1.708	0.279	<0.001	*Season*	-1.366	0.253	<0.001
Year: Reserve Interaction	-0.029	0.273	0.916	*Year: Reserve Interaction*	0.046	0.254	0.857

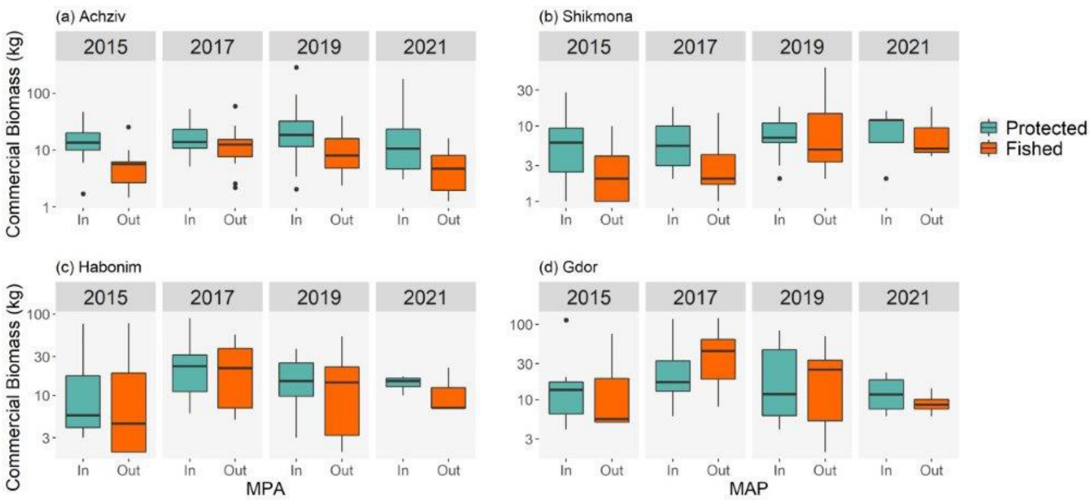

***Fig. A1:* The temporal difference in commercial biomass density (kg/300m^2) per site for each MPA.** Log (biomass) was tested against season, year, and protection. Protection (in/out) was only significant for Achziv (a; p<0.001). No interaction was found between time and protection. Colors represent sampling within (light blue) or outside of MPAs (orange). Notice the different Y axis scale for each MPA. Box plots display the 25% and 75% quartiles, and lines within the boxes represents the median (model results in appendix Table 3). Dots represent points 1.5 times outside the interquartile range.

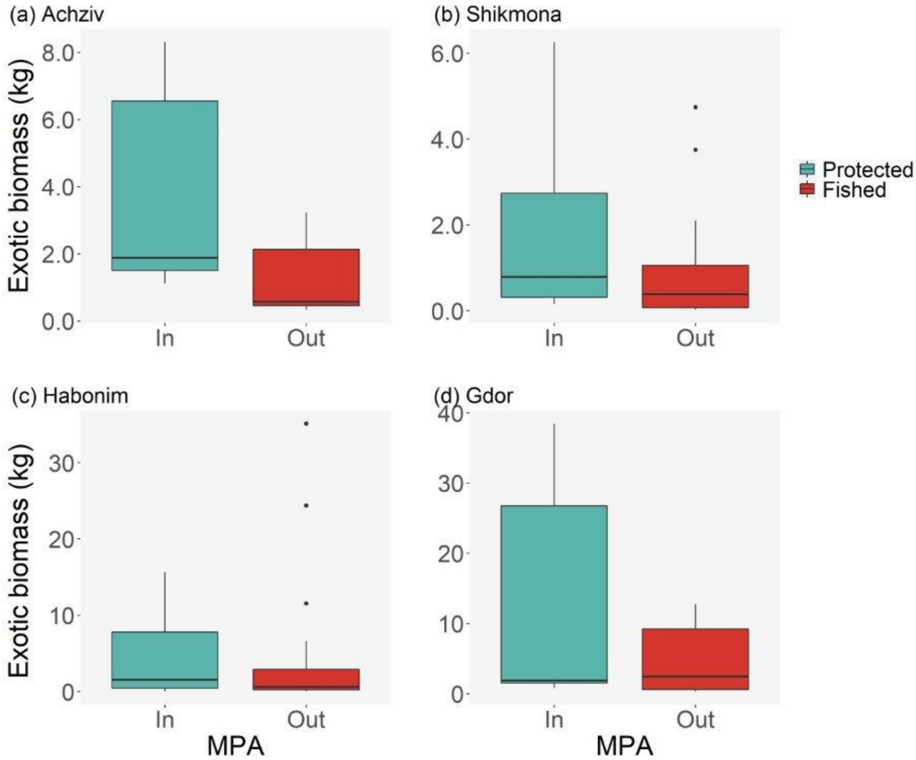

Fig. A2: **The biomass per site of exotic species within reserves and their adjacent fishing grounds.** We examined how exotic species biomass (kg/300m^2) changed with protection, depth, and season. Exotic biomass was significantly higher within MPAs for Achziv (A; $p < 0.01$). Colors represent sampling within or outside of MPAs. Box plots display the 25% and 75% quartiles, and lines within boxes represents the median. Dots represent points 1.5 times outside the interquartile range. Note the different Y axis scale for each MPA.