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1 Marine protected areas' positive effect on fish biomass persists across
2 the steep climatic gradient of the Mediterranean Sea

3

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37 **Abstract**

- 38 1. The positive effect of fully protected Marine Protected Areas (MPAs) on marine
39 biodiversity, and specifically on fishes, has been widely documented. In contrast, the
40 potential of MPAs to mitigate the impact of adverse climatic conditions has seldom
41 been tested.
- 42 2. Here, we test the effectiveness of MPAs, quantified as increasing fish biomass, across
43 wide geographic and environmental gradients across the Mediterranean Sea. For this,
44 we performed underwater visual surveys within and outside MPAs to characterize fish
45 assemblages in 52 rocky reef sites across an extent of over 3,300 km. We further use
46 the steep spatial temperature gradient across the Mediterranean as a ‘space-for-time’
47 substitution to infer climate-driven temporal changes.
- 48 3. We find that, as expected, Mediterranean MPAs increased fish biomass. At the same
49 time, higher seawater temperatures are associated with decreased fish biomass,
50 changes in species composition and shifts towards more thermophilic species.
51 Importantly, we also found that the rate of decrease in fish biomass with temperature
52 was similar in protected and fished sites.
- 53 4. Taken together, these results suggest that the capacity of MPAs to harbor higher fish
54 biomass compared to surrounding areas is maintained across a broad temperature
55 range. At the same time, MPAs will not be able to offset larger-scale biotic alterations
56 associated with climate.
- 57 5. Policy implications. Our results suggest that sustained warming will likely reduce fish
58 biomass in the Mediterranean Sea and shift community structure. At the same time,
59 protection from fishing should remain an important management tool even with future
60 high water temperatures, and MPAs will continue to provide local-scale benefits to
61 conservation, and fisheries.

62 **Key words:** MPAs, Fish, biomass, Mediterranean Sea, warm waters, effectiveness

63 **Introduction**

64 Climate change has substantial implications for biodiversity, ecosystem functioning, and
65 human wellbeing (He & Silliman, 2019; Pinsky et al., 2020). Ocean warming is causing
66 changes in fish size, species distributions, and community composition, as well as declines in
67 fish biomass (Lotze et al. 2019; Cheung et al. 2012; Van Rijn et al. 2017; Pinsky et al., 2020).
68 Marine Protected Areas (MPAs) can help recover and sustain marine life (Edgar et al., 2014;
69 Reimer,et al 2021; Sala & Giakoumi, 2017; Grorud-colvert et al., 2021) and continue to be
70 advocated under climate change as they have been suggested to increase ecosystem resilience
71 and resistance (Rilov et al., 2019; Roberts, et al., 2017; Wilson et al., 2020). However,
72 empirical evidence regarding MPAs ability to mitigate climate associated changes is limited
73 (Freedman et al., 2020; Bruno et al., 2019; Bates et al., 2019; Mellin et al., 2016; Bates et al.,
74 2014). Thus, it remains unclear how climate interacts with MPAs to impact fish biomass, and
75 whether MPAs can remain a valid conservation tool in the future.

76
77 There are a variety of hypotheses that might explain how MPA impact on fish biomass would
78 change with increasing sea temperatures. Starting with a single species, we expect higher
79 abundance and biomass under moderate temperatures, where thermal conditions are
80 favorable, and decreases in abundance towards more extreme conditions towards the range
81 edge (Waldock et al., 2019; Yancovitch Shalom et al., 2020). The mechanisms leading to this
82 decrease in abundance towards the warm edge of species ranges may stem from thermal
83 limitation on growth, survival, and fecundity, but also from altered biotic interactions such as
84 higher predation rates or more severe competition (Paquette and Hargreaves 2021).

85 We outline three potential scenarios on how a gradient in thermal conditions may interact
86 with protections from fishing:

87

88 (1) MPAs are less effective at warmer temperatures (Fig. 1A). While inside MPAs we may
89 observe biomass decreases as water temperature increases, outside of MPAs fishing may
90 consistently reduce fish biomass. This may lead to low biomass outside of MPAs regardless
91 of temperature. Hence, the difference between fished and non-fished sites will decrease as
92 water temperature increases (Fig. 1A). Note, that this scenario is dependent on high fishing
93 pressure outside of the MPAs but is independent of the exact mechanisms leading to reduced
94 biomass with higher temperature inside MPAs.

95 (2) MPAs are more effective at warmer temperatures. MPAs are hypothesized to may support
96 both resistance and recovery from disturbances (Roberts et al., 2017; Wilson et al., 2020;
97 Duffy et al., 2016). Warming waters is a major disturbance impacting marine systems, and
98 its impact can be associated with acute heat waves (Bosch et al., 2021, Garrabou et al., 2022)
99 but also with persistently warm water placing individuals under constant thermal stress.
100 Higher resilience within MPAs in face of waring could be due to many processes within
101 MPAs including the presences of older, bigger and less sensitive individuals, more intact
102 trophic food webs influencing the strength of trophic cascades or increased in ecosystem
103 function via increased diversity (Bates et al., 2019; Bruno et al., 2019, Brandel et al., 2019,
104 Lefcheck1 et al., 2019). All these mechanisms will cause higher relative increase in biomass
105 within MPAs compared to fished areas in regions that are already subject to high water
106 temperatures compared to more moderate conditions where fishing is the only stressor (Fig.
107 1B).

108 (3) Biomass decreases with warming water at similar rates both in MPAs and in fished areas
109 (Fig. 1C). This would happen if the physiological or biotic constraints limiting biomass with
110 warming do not interact with the effects of fishing. The relative support for these hypotheses
111 has never, to the best of our knowledge, been tested.

112

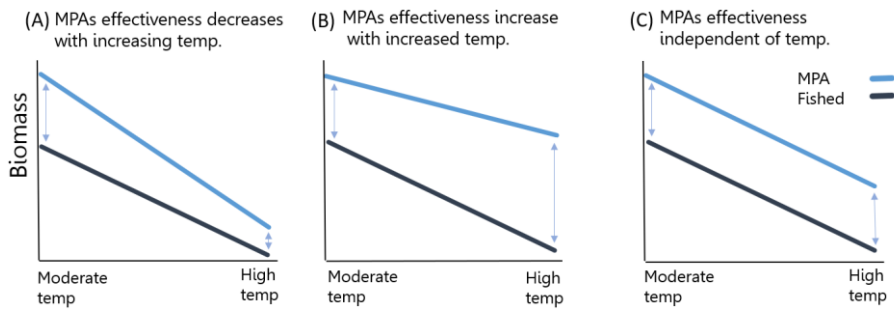
113 The scenarios outlined above are formulated at the species-level and extending these to the
114 community- level, adds another level of complexity. Even across the same temperature

115 gradient different species may have divergent thermal preferences and different range
116 dynamics, leading to multiple community level patterns. Thus, total community level biomass
117 may either decline or increase with temperature, depending on species identity and species
118 turnover (Free et al., 2019, Lotze et al., 2019; Cheung et al., 2013; Tittensor et al., 2021;
119 Duffy et al., 2016; Moullec et al. 2019). Moreover, it is clear that different species display
120 different sensitivity to fishing (Cheung et al. 2005). If, across species, the traits related to
121 fishing sensitivity and those related to warm-water resilience are independent (Bates et al.,
122 2019) we may expect scenario C in which biomass changes with warming at similar rates
123 both in MPAs and in fished areas. However, covariation between these traits may lead to
124 alternative scenarios. Thus, when species most sensitive to warming are also most sensitive to
125 fishing, we will observe scenario A (MPAs are less effective at warmer temperatures) and
126 when species most sensitive to warming are least sensitive to fishing, we will observe
127 scenario B (MPAs are more effective at warmer temperatures). Elucidating both the species-
128 and community-level patterns is critical for understanding how protection and temperature
129 gradients interact.

130 In this study, we examined these three scenarios using extensive fish surveys carried out
131 within and outside Mediterranean MPAs. The Mediterranean Sea is particularly relevant to
132 study the effects of climate on marine species. Many Mediterranean fishes are of North
133 Atlantic origin, and hence adapted to temperate climates which puts them under elevated risk
134 from climate change (Pita et al., 2021; Marbà et al., 2015; Albouy et al., 2013; Coll et al.,
135 2012; Givan et al., 2018; Guidetti et al., 2014). In addition, the Mediterranean Sea has a large
136 range of sea temperatures, with a high of 28C° (annual average) at its easternmost basin (El-
137 geziry, 2021) (Fig. 2). This unique blend of mostly cold-water species across a steep climatic
138 gradient allows us to examine the variation in fish biomass gains associated with MPAs
139 across multiple seawater temperatures. The results can help us understand whether MPAs can

140 offset the impacts of climate on fish biomass and thus continue to be an important
141 management tool in future oceans.

142



143

144

145 **Fig. 1. Schematic representation of three potential scenarios of Marine Protected Area**

146 **(MPA) effectiveness, in terms of relative fish biomass gains, across a temperature**

147 **gradient: (A)** MPA effectiveness decreases when water temperature increases. **(B)** MPA

148 effectiveness increases when water temperature increases. **(C)** No change in MPA

149 effectiveness across a temperature gradient. In all scenarios we assume that total fish biomass

150 decreases with increased temperatures. Arrows within plots illustrate the difference between

151 MPA and fished areas, representing MPA effectiveness.

152

153 **Methods**

154 **Study sites**

155 We sampled fish assemblages in 52 rocky reef sites across the Mediterranean Sea (Fig. 2).

156 The data was aggregated across three main survey teams (Fig. A1) using similar methods (see

157 expansion on survey methods in Supplementary material). Importantly, as sampling by each

158 team was geographically dispersed (Fig. A1) we do not expect geographic biases related to

159 sampling. Sampling sites were confined to rocky reef habitats and fished and MPA sites

160 covered similar habitats and depths. MPAs ranged in size between 84 and 50,000 ha (mean

161 8520 ha) and MPA age ranged between 1 and 57 years (mean 21 years). For a complete
162 description of the sampling sites see Supplementary material.

163

164 Sites were initially classified as either ‘fully protected’ MPAs (all fishing activities forbidden
165 and enforced, n=9), ‘intermediate protection’ MPAs (most fishing activities regulated and
166 enforced, n=10), ‘non-enforced’ MPAs (n=8), or ‘fished’ (n=25). However, we did not find a
167 significant difference in biomass between ‘intermediate protection’ and ‘fully protected’
168 MPAs, so we combined and re-classified them as ‘Protected’ (Fig. A2). While we did not
169 find significant differences between full and intermediate protection, fully protected MPAs
170 do appear to have higher biomass as found in other studies (Sala & Giakoumi, 2017).

171 Therefore, this re-classification was only done to increase sample size and, thus, the power of
172 the analyses. Using only fully protected MPAs did not change the main results (i.e., we still
173 could not find an interaction between temperature and protection, see below). ‘Non-enforced’
174 MPAs (n=8) are regularly fished. Thus ‘Non-enforced’ MPAs and fished areas (n=25) were
175 re-classified as ‘Fished’.

176

177 Size and age of MPAs are known to significantly affect MPA in terms of safeguarding fish
178 biomass (Edgar et al., 2014, Claudet et al., 2008) and were used as covariates in the analyses
179 (see below). Importantly, neither MPA size nor age displayed clear gradients across the
180 Mediterranean or with mean temperature (correlations between MPA size and age to
181 temperature were $r = 0.118$ and $r = -0.07$, respectively). We note that our goal was not to
182 explore these patterns in depth, but rather to assure that the results are not an artifact of
183 hidden gradients in MPA size or age across the Mediterranean that may be mistakenly
184 interpreted as associated with climatic gradients.

185 **Sampling**

186 We performed underwater visual surveys to characterize fish assemblages using 25 x 5m belt
187 transects and documenting fish identity, abundance, and size. Sampling was conducted in
188 seasons where temperatures are suitable for diving, mostly summer. A total of 1,891 transects
189 were sampled; the number of transects within each site varied between 9 and 138. We
190 account for the unbalanced sampling design in the analyses (see below). Size was later
191 converted to biomass using species-specific Mediterranean-based length-weight relationships
192 ($W = aL^b$) gathered from FishBase (Froese and Pauly 2021). We included all species
193 identified to species level (with the exception of Mugilidae and Atherinidae which are
194 difficult to identify to species level underwater) and excluded cryptic species such as families
195 Gobidae and Blennidae that are generally underestimated by visual censuses. Transects took
196 place along rocky substrate at depths of 3-30m.

197

198 Although the Mediterranean Sea suffers from a high number of non-indigenous species, their
199 abundance in our data was extremely low (8%). Moreover, these non-indigenous species are
200 concentrated in the Levantine Basin which comprise only a small fraction of the area
201 surveyed, and their community level impacts have been shown to be small (Buba &
202 Belmaker, 2019, Arndt et al., 2018; Givan et al., 2018; Buba et al., 2017). Finally, all
203 observed patterns were robust to inclusion or exclusion of these species.

204

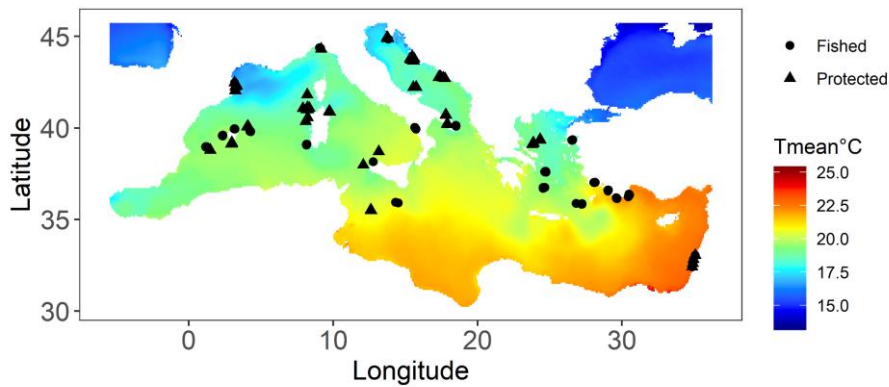
205 **Broad scale environmental data**

206 For each site we extracted the following environmental variables: minimum annual
207 temperature (C° , T_{min}), mean annual temperature (C° , T_{mean}), maximum annual
208 temperature (C° , T_{max}), *Primary Production* ($mgC \cdot m^{-2} / day / cell$), and *Chlorophyll-a*
209 concentration (mg/m^3). We downloaded environmental data from GMED

210 (<http://gmed.auckland.ac.nz/>). This site provides sea surface temperature of the topmost m
211 of the ocean water column, collected by remote sensing and at a resolution of 9.2 km.
212 To reduce potential small spatial-scale variability bias, we used average values within a
213 radius of 15km from the site center. We used current values of these environmental variables
214 and did not attempt to match values to the time of sampling as temporal changes over the
215 time period examined are small relative to the large variability in these values across the
216 Mediterranean (e.g., *Tmean* range was 6 °C, compared to maximal change of 0.32 C° over
217 time within the range of periods examined (2003 to 2019; García-Monteiro et al., 2022).

218

219 We examined which environmental variables (*Chlorophyll –a Primary Production*, *Tmin*,
220 *Tmax*, and *Tmean*) best explained transect-level biomass using Generalized Linear Models
221 (GLMs) using fish biomass as a response, followed by calculating variable relative
222 importance (“relaimpo” package in R). To identify the prime environmental variables for
223 species-level occurrence we used ‘MaxEnt’ (Maximum Entropy) based species-distribution
224 models, and then compared the relative importance of the environmental variables. With both
225 methods, and across all species, temperature predictors (*Tmin*, *Tmean* and *Tmax*) contributed
226 most to the explained variation. To avoid co-linearity, we used *Tmean* as our main
227 temperature predictor in further analyses (Fig. A3).



228
 229 **Fig.2. Sampling sites across the Mediterranean Sea.** Colors represent mean annual
 230 temperatures (Tmean, °C) Circles represent fished sites and triangles protected sites (MPAs).

231
 232

233 **Fishing pressure**

234 Direct fishing pressure is hard to quantify, thus we estimated it using three different methods:
 235 (1) First, we calculated the Gravity index, which was recently shown to be a reliable predictor
 236 of fishing pressure (Cinner et al., 2018). To do so we downloaded human population density
 237 maps from NEO–NASA earth observation (<https://neo.sci.gsfc.nasa.gov/about/>; pixel
 238 resolution 1 km²). We divided the value of all pixels within a 150-km radius from each
 239 sampling point (a realistic travel distance for coastal fishers) by the squared distance to the
 240 point. Other radii gave similar results (50, 100, and 500 km). (2) Second, we calculated *Catch*
 241 *per Km Coastline* by extracting total fished tonnage of ‘perch-likes’ fish (most species in our
 242 data) by country along the Mediterranean coast. As this index is based on actual fish
 243 removed, albeit at coarse resolution, this is the only index directly related to catch and not to
 244 effort. Data were based on The Sea Around Us project
 245 (www.seaaroundus.org/data/#/topic/biodiversity), and are composed of catch reported to the

246 UN Food and Agriculture Organization (FAO) operated by GFCM (General Fisheries
247 Commission for the Mediterranean). GFCM has the biggest and most reliable fishing data
248 repository available for the Mediterranean Sea that includes data from all countries included
249 in our analysis. We then compiled data on Mediterranean coastlines from the (FAO)
250 (www.fao.org), the CIA World Factbook (www.cia.gov/library/publications/the-world-
251 factbook), and Google Maps. We divided the tonnage fished in each country by their
252 Mediterranean coastline to create an index of *Catch per km Coastline* (Shapiro Goldberg et
253 al., 2019). (3) Third, we used *Distance from Port*, downloaded from GMED and based on
254 data from the National Geospatial intelligence Agency
255 (<https://msi.nga.mil/Publications/WPI>). This data includes both large and small ports. Small
256 ports were important to include in this indicator of fishing pressure as the sites surveyed in
257 this study are mostly impacted by local coastal fishers, who often operate from very small
258 ports.

259

260 **Species-level traits**

261 *Climatic Affinity* indicates the environmental conditions most suitable for each species. These
262 values are based on the preferred temperature of the species which was estimated using
263 species distribution models (including depth, salinity, temperature, and primary production).
264 We base our estimates on the Climatic Affinity values extracted from FishBase (Froese and
265 Pauly 2021).

266 *Sensitivity to fishing* may explain species response to protection, with sensitive species
267 displaying higher benefits. Intrinsic sensitivity to fishing was based on the vulnerability index
268 (extracted from FishBase). This index is calculated using fuzzy logic, integrating life history
269 and ecological characteristics of marine fishes including intrinsic rate of increase, longevity,
270 age at first maturity, fecundity, and the von Bertalanffy growth parameter, K (Cheung et al.
271 2005).

272 **Statistical analyses**

273 **Community level analyses**

274 We first tested how assemblage-level biomass changes with protection (binary, yes/ no),
275 depth, fishing pressure indices (*Gravity*, *Catch per Km Coastline*, *Distance from Port*), and
276 across environmental gradients. To avoid over parametrized models, we considered each of
277 the three fishing pressure indices separately. We did not include MPA age and size in these
278 analyses as these values are not available outside MPAs. However, these were included in
279 other analyses (see cross-species analysis below).

280

281 Our focus was on detecting to what extent temperature (*Tmean*) interacts with protection, to
282 determine if protection influences fish assemblages differently at different locations along the
283 temperature gradient (Fig. 1A and B). We used GLMMs (generalized linear mixed-effect
284 models) using transect-level total biomass (log transformed) as a response. *Site* was included
285 as a random effect to account for non-independence of transects within each site. Thus, the
286 full model formula was as follows:

287 $\log(\text{Biomass}) \sim \text{protection} \times \text{Tmean} + \text{depth} + \text{primary production} + \text{fishing pressure index}$
288 $+ \text{random}(\text{site})$

289 While linear models are generally robust, highly uneven sampling designs may still bias
290 results. In our case, we sampled many more transects along the Israeli coast than in other
291 locations. Thus, we randomly sampled nine transects (the lowest number of transects in a
292 site) in each site to create a new data set with a balanced sampling design. We then ran
293 transect level analyses (see below) on 1,000 random iterations of the balanced data and
294 presented the average values across these iterations.

295

296 We further tested spatial simultaneous autoregression (SAR) models at the site level to
297 account for spatial proximity (function *spautolm* from the “spdep” R package). We examined
298 a range of possible neighborhood sizes (400–2000 km) and chose the neighborhood size with

299 the lowest AIC score (2000 km). However, adding the SAR component did not change the
300 results (Table A1).

301
302 We also calculated weighted climatic affinity (Cheung et al., 2013), which represents the
303 mean temperature preferences of the entire assemblage, by taking the *Climatic Affinity*
304 weighted by the biomass of the species within the transect. Weighted climatic affinity is used
305 to estimate changes in community composition associated with altered thermal preferences.
306 Model structure and statistical tests were similar to those used for biomass, and the focus was
307 on estimating whether the effect of *Tmean* on weighted climatic affinity changes with
308 protection.

309

310 **Species level analyses**

311 We repeated the community-level GLMM analyses at a species level, using transect-level
312 biomass for each species. Tweedie models were used to deal with the zero inflated data
313 (Shono 2008). We also estimated variable relative importance, quantified as the contribution
314 of each variable to the R^2 of the model (*calc.relimp* function from the “relaimpo” R package).
315 This analysis does not support random effects; thus, we could not include site in the relative
316 importance models. The full model formula was as follows:

317 $\log(\text{Species level biomass}) \sim \text{protection} \times \text{Tmean} + \text{depth} + \text{primary production} + \text{fishing}$
318 pressure index

319

320 **Cross-species analysis**

321 We were interested in understanding what explains both species- and site-level responses to
322 protection. Thus, we separated the data into paired protected and fished sites, then calculated
323 the log-ratio of biomass in protected vs. fished sites as a species-specific and site-specific
324 effect size. This was done only for common species (>30 observations) (Table A2). We
325 paired protected and fished sites by country, similar habitat, sampling procedures, and

326 locations within 400 km of each other ($88\text{km} \pm 103$, mean \pm SD). Not all sites had such
327 pairs, so we restricted our analyses to 17 paired sites (Fig. A1B). As the number of transects
328 varied in both protected and fished sites, we calculated the pooled standard deviation of the
329 log-ratio (S_{pooled}) based on the sampling effort. The reciprocal of S_{pooled} was used as a
330 weighting factor.

331
332 We used GLMMs to investigate whether log-ratio values were affected by T_{mean} and
333 species-level traits. Under the scenarios of higher biomass in MPAs in either moderate (Fig.
334 1A) or extreme conditions (Fig. 1B), we would expect an interaction between T_{mean} and
335 species-level *Climatic Affinity*. As the effect of protection is expected to vary across species,
336 we added *Sensitivity to Fishing* as an additional species-level predictor. Site level predictors
337 included one of the three fishing pressure indices (*Gravity*, *Catch per Km Coastline*, *Distance*
338 *from Port*), *MPA area* (log transformed), *MPA age*, and *Primary Production*. Species (as
339 they appear multiple times at different sites) and *site-pair* (as multiple species are examined
340 in each) were modeled as random effects. The full model formula was as follows:

341 $\text{Log-ratio} \sim T_{\text{mean}} \times \text{climatic affinity} + \text{Sensitivity to Fishing} + \text{Fishing pressure index} +$
342 $\text{MPA area} + \text{MPA age} + \text{Primary Production} + \text{random (species)} + \text{random (site)}$

343

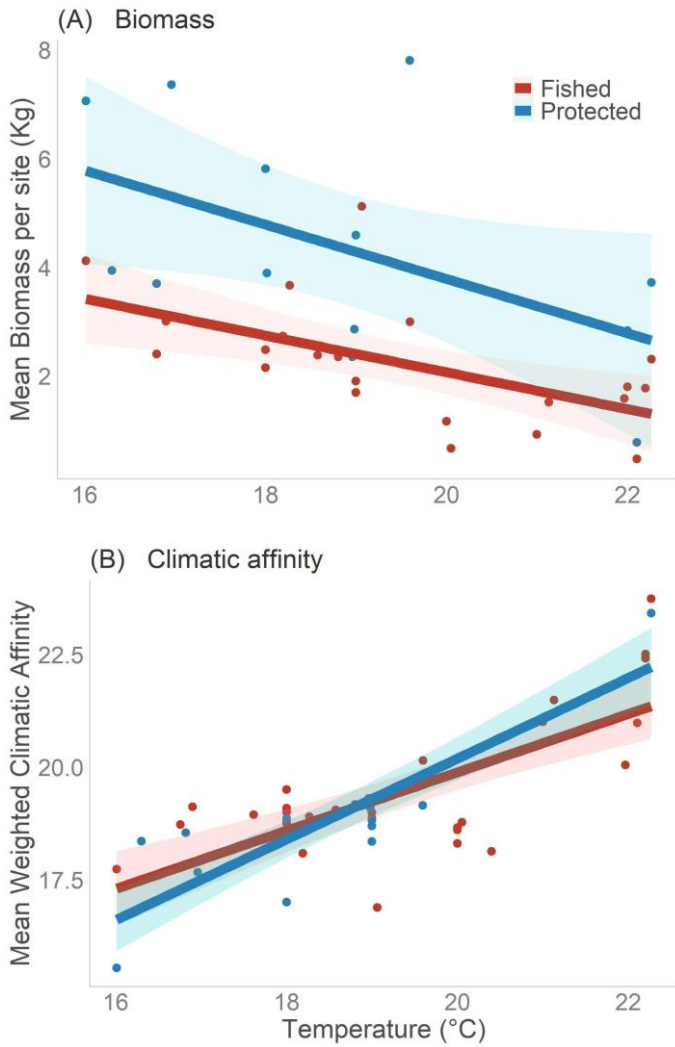
344 **Results**

345 We surveyed a total of 1,891 transects over rocky habitats along 52 protected and fished sites.
346 Our first aim was to detect whether and to what extent seawater temperature (mean annual
347 temperature; C° , T_{mean}) interacts with protection when explaining assemblage-level biomass
348 (Fig. 1). We found that both T_{mean} and protection had a significant effect ($p < 0.05$) on
349 overall community-level biomass. Biomass decreased with higher T_{mean} and was higher in
350 protected compared to fished sites (Fig. 3A). Across the Mediterranean, the overall change in
351 biomass associated with protection (37% higher biomass in protected relative to fished areas,
352 on average) was similar to that of temperature (27% higher biomass at $16^{\circ}C$ compared to

353 22°C, the lowest and highest *Tmean* across the gradient). However, the interaction between
354 protection and *Tmean* was non-significant. These patterns remained even when fishing
355 pressure (using the indices *Catch per km Coastline*, *Distance from Port*, and *Gravity*),
356 productivity (*Primary Production*), and spatial autocorrelation were accounted for (Tables
357 A1, A3). We did not find clear evidence of an interaction between protection and temperature
358 suggesting that MPA effectiveness, in relation to increasing overall fish biomass, remains
359 constant across the temperature gradient examined (scenario C; Fig. 1).

360

361 Second, we assessed how different seawater temperatures could impact the fish community
362 composition, and whether this changed in response to protection. To test for a thermal
363 signature at the community level, we calculated a weighted climatic affinity index based on
364 the estimated thermal preference of each species (*'Climatic Affinity'*) weighted by the species
365 relative abundance. It is possible that protection leads to increased overall biomass but does
366 not buffer against unfavorable climate change. In this case, we expected MPAs to have little
367 impact on community composition in terms of weighted climatic affinity. On the other hand,
368 if protection also acts as a climate refuge, MPAs may disproportionately support species with
369 lower climatic affinity compared to fished sites. This could be observed as a significant
370 interaction between protection and temperature. We found support for the former pattern;
371 although temperature had a clear effect on weighted climatic affinity, and hence species
372 composition, we found no interaction with protection (Fig 3B). Thus, protection does not
373 appear to alter the relative thermal preferences of constituent species (Tables A4).



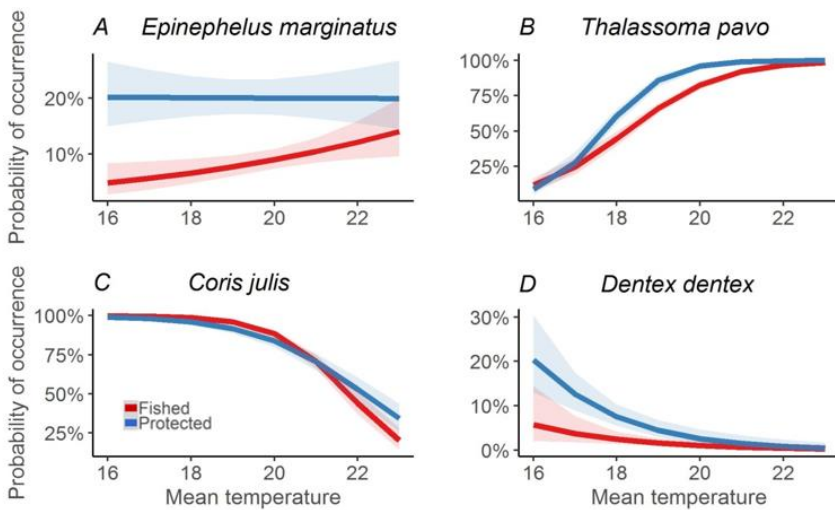
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375

376

377 **Fig. 3. Change in (A) biomass (kg) and (B) weighted climatic affinity (°C) for the entire**
 378 **fish community with mean temperature (T_{mean} , °C) and protection. (A) Temperature**
 379 **and protection had independent, significant effects on biomass, but no significant interaction**
 380 **was found between temperature and protection. (B) Weighted climatic affinity increased with**
 381 **temperature regardless of protection level. Shaded areas represent 95% confidence intervals.**

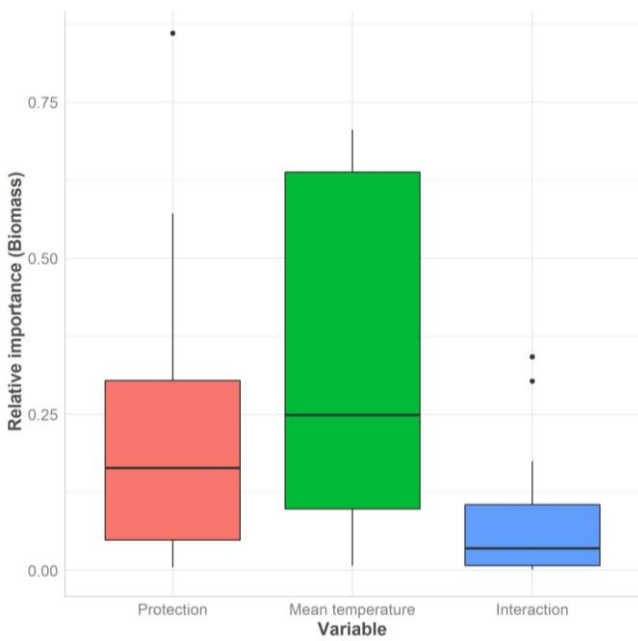
382 Third, we analyzed the change in biomass of 39 species, and found that many species
383 displayed strong responses to temperature (significant for 20 of the 39 species) and protection
384 (significant for 15 species; Table A5). For most species, we observed a decline in biomass
385 with increased T_{mean} , as observed for *Coris julis* and *Dentex dentex*, but some species, such
386 as *Epinephelus marginatus* or *Thalassoma pavo*, actually benefit from higher T_{mean} (Fig. 4).
387 Interactions between temperature and protection (T_{mean} -protection interaction; Table A5)
388 varied among species and did not consistently support any specific scenario. Ten species
389 supported scenario A (biomass changes with increased temperature are steeper in protected
390 sites), 5 scenario B (biomass changes with increased temperature are steeper in fished sites),
391 and 24 species scenario C (protection and temperature effects are additive). Importantly, even
392 when an interaction was present, most variation in biomass was explained by T_{mean} ; the
393 interaction between T_{mean} and protection explained only a small amount of the variation in
394 the data (Fig. 5). Thus, also at the species level, protection did not have a consistently
395 stronger effect in warm or cold waters.



396

397

398 **Fig. 4. Select species' response to temperature and protection.** Models represent the
399 species' probability of occurrence. Temperature has a strong effect on species occurrence, but
400 in different directions. Protection usually increased species occurrence probability, especially
401 for targeted species such as *Epinephelus marginatus* (A). However, across species, protection
402 did not consistently increase probability of occurrence more at cold or warm temperatures.
403 Shaded areas represent 95% confidence intervals.



404
405
406 **Fig. 5. Mean relative importance across species (N=15) for which the interaction**
407 **between temperature and protection was significant.** Temperature has the highest effect
408 on species biomass, while the interaction between protection and temperature has the lowest
409 importance. Box plots display the 25% and 75% quartiles, and lines within boxes represents
410 the median. Dots represent points 1.5 times outside the interquartile range.

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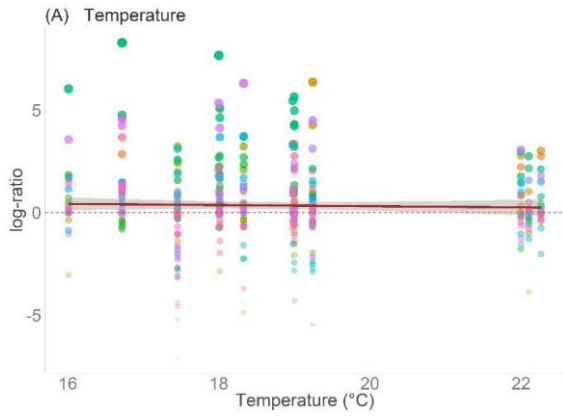
414 Finally, we were interested in understanding why some species responded to protection
415 differently on different sides of the environmental gradient. For example, we expected that
416 MPAs would enhance biomass more at cold temperatures for species with cold-water affinity,
417 and at warm temperatures for species with warm-water affinity. We used the log-ratio of
418 biomass between protected and fished sites as an effect size. This log ratio was not
419 significantly affected by Tmean (Fig. 6A). This means that across all fish species, protection
420 had a similar effect in the warmer and colder areas of the Mediterranean, consistent with the
421 species and community level analyses reported above. Importantly, we did not detect an
422 interaction between Tmean and species-level Climatic Affinity, and thus we find that MPAs
423 benefit both warm and cold-water species similarly across temperatures. Sensitivity to
424 Fishing was the only variable that had a positive significant effect on the log-ratio, indicating
425 that species that are more sensitive to fishing tend to benefit more from protection (Fig. 6B,
426 Table A6). Results were similar when we took Gravity, Catch per km Coastline, Distance
427 from Port, Primary Production, and the size and age of MPAs into account (Table A6).

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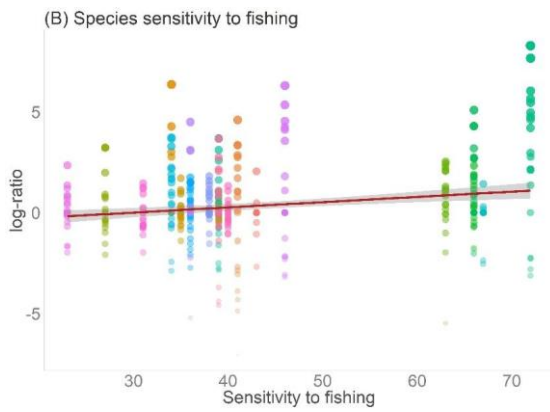
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- *Atherina boyeri* • *Diplodus annularis* • *Mullus surmuletus* • *Serranus scriba* • *Symphodus tinca*
- *Boops boops* • *Diplodus sargus* • *Mycteroperca rubra* • *Sparisoma cretense* • *Thalassoma pavo*
- *Caranx crysos* • *Diplodus vulgaris* • *Oblada melanura* • *Sparus aurata*
- *Chromis chromis* • *Epinephelus costae* • *Scorpaena maderensis* • *Symphodus mediterraneus*
- *Coris julis* • *Epinephelus marginatus* • *Serranus cabrilla* • *Symphodus roissali*

435

436 **Fig. 6. Change in log-ratio of mean biomass of protected to fished sites across (A) mean**

437 **temperature (T_{mean} , °C) and (B) species sensitivity to fishing. Size of circles and**

438 **transparency represent the magnitude of the log-ratio. (A) No change in log-ratio is found**

439 **across the temperature gradient. (B) Species more sensitive to fishing benefit more from**

440 **protection. Shaded areas around the line in both plots present 95% confidence intervals.**

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445 **Discussion**

446 We found that protection is associated with an increase in fish biomass, particularly for
447 fishing-sensitive species. This result is intuitive and expected (Edgar et al., 2014, Micheli et
448 al., 2004). In addition, higher temperatures had a strong negative effect on fish biomass, both
449 at species and community levels. Importantly, we also found that when the community was
450 considered as a whole, the rate of decrease in fish biomass with temperature was similar in
451 protected and fished sites. This suggests that the effect of temperature and protection are
452 additive (scenario C; Fig. 1), and thus that MPA effectiveness does not change with varying
453 climate.

454 A decline in abundance along the temperature gradient is expected for a number of species
455 (Azzurro et al., 2022) and at the species level, we found a variable response of species to
456 increased temperature and MPAs (Fig. 4). Nevertheless, here we observed that the most of
457 species declined in biomass in warmer waters, and species sensitive to fishing were
458 positively impacted by MPAs. At the same time, most species did not show a significant
459 interaction between temperature and protection (Fig. 5), and we could not find species-level
460 traits that explain why specific species follow each scenario. Hence, despite highly
461 idiosyncratic species-level effects we find little support for the idea that MPAs can buffer
462 against the impacts of warming.

463 Local decision makers and conservationists have limited management tools since climate
464 change can only be effectively addressed on a global scale. One major management option is
465 to increase the number and size of MPAs (Sala & Giakoumi, 2017). However, uncertainty is
466 high around the ability of MPAs to continue to perform as expected under changing climatic
467 conditions (Bates et al., 2019; Wilson et al., 2020). We show here that extreme temperatures
468 do not undermine the capacity of MPAs to sustain larger fish biomass than fished sites (Fig.

Commenté [EA1]: Azzurro, E., Ballerini, T., Antoniadou, C., Aversa, G.D., Souissi, J.B., Blašković, A., Cappanera, V., Chiappi, M., Cinti, M.F., Colloca, F. and Cvitković, I., 2022. ClimateFish: A Collaborative Database to Track the Abundance of Selected Coastal Fish Species as Candidate Indicators of Climate Change in the Mediterranean Sea. *Frontiers in Marine Science*, 9, p.910887.

Commenté [EA2]: Bipmass or abundance?

469 3A). Hence, even when faced with challenging extreme climates, managers can still rely on
470 MPAs as a local management tool for reducing the damage caused by fishing.

471
472 While these results are encouraging, we did not find broad evidence that MPAs can offset the
473 relative decrease in fish biomass associated with warmer seawater. Consequently, increasing
474 water temperatures will likely result in an overall decrease in fish biomass, even within
475 MPAs. Further support for the inability of MPAs to mitigate warming is evident from the
476 weighted climatic affinity analysis, as we found similar increases in weighted climatic
477 affinity with increased temperature in fished and protected sites (Fig. 3B). Thus, higher water
478 temperatures lead to species turnover and changes in species composition, the replacement of
479 cold water species by warm water species, independent of protection levels. This implies that
480 thermophilic species will become a more dominant part of fish communities under future
481 seawater warming both within and outside MPAs, as recently illustrated for invasive fishes of
482 tropical origin (D'Amen and Azzurro, 2020). At the same time, the lack of interaction at the
483 community-level between the effect of MPA and temperature suggests that, across species,
484 the traits related to fishing sensitivity and those related to warm-water preferences are
485 independent (Bates et al., 2019). Consequently, although MPAs may maintain higher local
486 biomass of exploited species, they will not be able to offset larger-scale biotic alterations
487 associated with climate.

488 Marine ecological systems are predicted to suffer from warming water, especially in the
489 Mediterranean Sea (Albouy et al., 2013; Giakoumi et al., 2017; Van Rijn et al., 2017; Pita et
490 al., 2021). With business-as-usual emissions, sea-surface temperatures within MPAs are
491 projected to increase 2.8 °C by 2100 (Bruno et al., 2018) and Mediterranean MPAs are
492 particularly vulnerable to warming (Kyprioti et al., 2021, Garrabou et al., 2022). We show
493 here that at the community level fish biomass strongly decreases with temperature.
494 Extrapolating this pattern through time, we may expect dramatic declines in fish biomass in
495 the Mediterranean with additional warming. This is consistent with models predicting

Commenté [EA3]: D'Amen, M. and Azzurro, E., 2020. Lessepsian fish invasion in Mediterranean marine protected areas: a risk assessment under climate change scenarios. *ICES Journal of Marine Science*, 77(1), pp.388-397.

496 significant decreased catch in the Mediterranean under IPCC warming scenarios (Cheung et
497 al. 2010; Lotze et al., 2019).

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501 We note that while some studies predict biomass declines with warming (Free et al., 2019,
502 Lotze et al., 2019; Cheung et al., 2013; Tittensor et al., 2021) other studies have found fish
503 biomass to be positively related to temperature (Duffy et al., 2016; Moullec et al. 2019). This
504 apparent contradiction with our results may stem from three main factors. First, the
505 Mediterranean Sea, where we performed our study, contains mostly cold-water species,
506 which may be particularly sensitive to warm waters (Albouy et al., 2013; Giakoumi & Pey,
507 2017; Givan et al., 2018). Second, the temperatures within the Mediterranean Sea, especially
508 towards the Eastern Mediterranean, are amongst the warmest in the world (Ozer et al., 2017)
509 likely reaching the upper thermal threshold for many species (Rilov, 2016). These warm
510 waters may lead to declines in fish biomass along the progressive loss of climatically suitable
511 habitats, with species living in suboptimal conditions, reaching their physiological limits.
512 Finally, even within the Mediterranean Sea warming may produce different patterns for
513 different regions and different species groups where large bodies species decline, and small
514 bodies species increase in abundance (Moullec et al. 2019).

515 The steep spatial temperature gradient across the Mediterranean can be used as a ‘space-for-
516 time’ substitution to infer climate-driven temporal changes in fish biomass. If the observed
517 links between temperature and fish biomass are causal, then the results can be used to predict
518 temporal changes associated with warming. Indeed, empirical assessments suggest that such
519 an approach produces reliable results (Algar et al., 2009; Blois et al., 2013; White & Kerr,
520 2006). One limitation of this approach is that the spatial patterns explored here focus on
521 mean temperatures and long temporal scales, and do not quantify extreme climatic events at
522 finer temporal scales. This prevented us to consider the effect of marine heat waves (MHW),

523 that In the last 20 years, have globally doubled in frequency and have become more intense,
524 longer-lasting and geographically extended (Frölicher et al 2018; Collins et al., 2019;
525 Laufkötter et al., 2020). These extreme events are associated with increasing events of mass
526 mortalities all over the world and in the Mediterranean Sea (Garrabou et al., 2022), with
527 cascade effects, which are expected to affect a large number of marine organisms, including
528 fish species. Another limitation is that adaptive responses by species to changing
529 environmental conditions may differ across space and across time.

530 We also note that dispersal limitations and emergent species interactions may make temporal
531 patterns differ from spatial patterns. However, the limited spatial extent of the Mediterranean,
532 meaning that most species can be found throughout the entire study range, and the strong
533 dispersal ability of marine fish larvae, make these less of a concern.

534
535 Our results suggest that protection from fishing should remain an important management tool
536 even at high water temperatures. In addition to increasing fish biomass within their
537 boundaries, MPAs provide additional population-level advantages such as protecting
538 individuals of high reproductive potential (Marshall et al. 2019; Micheli et al. 2012;
539 Venturelli et al. 2009) and increased ecosystem resilience (Bates et al., 2014; Mellin, et al.,
540 2016). However, as protection does not offset the changes in biomass associated with
541 warming, local conservation efforts and regular monitoring (Garrabou et al., 2022) should be
542 accompanied by global efforts to limit climate change. Different MPAs protect different
543 species (Blowes et al., 2020). Hence a regionally planned network of MPAs, covering large
544 climatic gradients (Kyprioti et al., 2021; Meehan et al., 2020; Claudet et al., 2020; Rilov et
545 al., 2019), is vital to assure the regional conservation of fish and the ecosystem services they
546 deliver to our societies.

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Commenté [EA6]: Garrabou J., Bensoussan N., Di Franco A., Boada J., Cebrian E., Santamaria J., Guala I., Grech D., Cerrano C., Pulido T., Jou M., Marambio M. & Azzurro E., 2022. Monitoring Climate-related responses in Mediterranean Marine Protected Areas and beyond: ELEVEN STANDARD PROTOCOLS. 74 pp. Edited by: Institute of Marine Sciences, Spanish Research Council ICM-CSIC, Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain.

Commenté [EA7]: I wouldn't use the term 'assure' in the conclusion. Maybe is better to say something like 'manage Mediterranean fish populations'

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556 **Author contributions:**

557 **Conceptualization:** OF, JB; **Data providers:** OF, SM, ADF, PG, EA, JC, FM, RY, JB;

558 **Original Draft Preparation:** OF, JB; **Final Review & Editing:** all authors.

559 All of the data is available in the Belmaker lab Githb repository.

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