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Evaluating the long term effectiveness of a Mediterranean marine protected area to tackle the effects of invasive and range expanding herbivorous fish on rocky reefs

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Abstract

Here we provide evidence, along an 8-year period time-series based on multifaceted data from a Mediterranean marine protected area (MPA), whether protection can tackle invasive and range expanding herbivore fishes, and their effects on the algal resource availability, taking into account the population trends of predatory fishes, fisheries catches of herbivore fishes and sea surface temperature (SST) through time. Our findings pointed out that an ineffective in restoring top-down control process MPA may facilitate, rather than alleviate, the sudden and enduring population burst of invasive and range-expanding herbivorous fishes at tipping points of abrupt change. This subsequently results in the deterioration of rocky reef habitats and the depletion of algal resources, with the tipping points of abrupt change for algal and herbivore fish species not overlapping chronologically. As sea temperature increases, ineffective or recently established MPAs may inadvertently facilitate the proliferation of invasive and range-expanding species, posing a significant challenge to management effectiveness and conservation objectives.

Key-words: marine parks, ecosystem management, exotic species, Ionian Sea, marine invasions

1. Introduction

Climate change affects species distribution, modifying the community structure and dynamics, as well as the interspecific relationships and the functioning of ecosystems in complex ways, which are often hard to predict (Simberloff et al., 2013; Gallardo et al., 2016; Santana-Garcon et al., 2023). The Mediterranean Sea is a hotspot of climate change and biological invasions (Katsanevakis et al., 2014a, b; Costello et al., 2021; Zenetos et al., 2022). Impacts of biological invasions in this region have been associated to harsh alterations of the structure of native communities and to degradation of ecosystem functioning, thus impairing the provision of nature's contributions to people (Tsirintanis et al., 2022). Currently, the Mediterranean Sea hosts at least 173 non-indigenous fish species, the vast majority of which are of tropical origin and have entered the Mediterranean Sea through the Suez Canal (Zenetos et al., 2022). Although most of the invasive fishes have been recorded in the Eastern Mediterranean Sea (e.g. Kalogirou et al., 2012; Katsanevakis et al., 2014a), predictive models using different climatic scenarios suggest that by the end of the 21st century the most invasive species will spread throughout the Mediterranean basin (Schickele et al., 2021). Such climate-induced range shifts, of both invasive and native species (including many of commercial importance), are likely to cause in the future deep ecological and socio-economic consequences throughout the Mediterranean Sea (Farahmand et al., 2023).

Reef systems are characterized by transitions between alternate states and phase shifts due to intense herbivory or other stressors, with abrupt changes at certain tipping points being more common than a linear response to incremental change of the stressor (Baskett and Salomon, 2010; Donovan et al., 2018). Evidence on the impacts of warm-affiliated non-native herbivorous fish on temperate rocky reefs increases over time and mainly suggests the decline or even loss of habitat-forming macroalgae, and their associated biota (Bennett et al., 2015; Zarco-Perello et al., 2017; Santana-Garcon et al., 2023). Yet, high impact invasive herbivores may compete for resources with their native counterparts, thus challenging the persistence and reproduction potential of the native herbivores, while the thermal stress induced by the ongoing sea warming (especially in shallow stands) can further reduce the fitness of both native herbivores (Simberloff et al., 2005; Yeruham et al., 2015; 2020) and algal resources (e.g. Mulas et al., 2022). One of the most documented and profound impacts of biological invasions on Mediterranean ecosystems is the deforestation of algal forests from rocky reefs and the creation of extended barrens by the overgrazing activity of two high impact invasive herbivores, the rabbitfishes *Siganus luridus* (Rüppell, 1829) and *S. rivulatus* Forsskål & Niebuhr, 1775 (Sala et al., 2011; Giakoumi, 2014; Vergés et al., 2014; Roy et al., 2019). These two species of Siganidae find a favorable habitat in the Mediterranean Sea, where shallow reefs are algae-dominated and host only two potential herbivore fish competitors, the European parrotfish *Sparisoma cretense* (Linnaeus, 1758) and the salema *Sarpa salpa* (Linnaeus, 1758). Both *S. cretense* and *S. salpa* are major grazers of marine vegetation at rocky reefs across their distributional range (Franco et al. 2015; Del Moral et al., 2016). However, the competitive dominance of Siganidae (particularly *Siganus rivulatus*) against the native *Sarpa salpa* has been postulated (Bariche et al., 2004; Verges et al., 2014), while the high persistence of the native but range expanding *Sparisoma cretense* populations in certain areas of the Eastern Mediterranean, has been ascribed to resource partitioning with rabbitfishes (Azzurro et al., 2007; Verges et al., 2014). Yet, as the sea is getting warmer under the effect of climate change, a reduced performance and thermal suitability for the native herbivores is anticipated, further exacerbating the competition for resources with existing or upcoming warmer-affiliated herbivores (Yeruham et al., 2020). Overall, rabbitfishes cause ecosystem-wide changes by creating and maintaining areas void of canopy algae with dramatic reduction in biodiversity, overall biomass, and algal growth, which in turn provoke cascading effects that propagate through the food web and influence local fisheries (Sala et al., 2011; Giakoumi et al., 2019; Dimitriadis et al., 2021). Yet, the high presence of rabbitfishes in the eastern Mediterranean has been linked to very low density or even exclusion of native sea urchins (e.g. *Paracentrotus lividus,* and *Arbacia lixula*) (Giakoumi et al., 2019a; Nikolaou et al., 2023), which are the most important invertebrate grazers of macroalgae at Mediterranean rocky reefs (Guidetti & Dulčić, 2007; Bonaviri et al., 2011; Agnetta et al., 2015; Tsirintanis et al., 2018).

Worldwide and particularly in the Mediterranean Sea, there is little and contradicting evidence on the effect of protection offered by Marine Protected Areas (MPAs) on invasive fishes. In theory, MPAs can either limit, facilitate or have no effect on the persistence of invasive species based on major hypotheses in invasion biology and mechanisms related to effects of MPAs on ecosystems (see Burfeind et al., 2013; Giakoumi and Pey, 2017 for a review). Empirical evidence in this region, albeit restricted, suggests that invasive and native range expanding species perform equally well or better within the Mediterranean MPAs than in unprotected sites (Rilov et al., 2018; Giakoumi et al., 2019a; Frid et al., 2022; Ohayon et al., 2023). Yet, evidence for the performance of marine invasions in MPAs through time lacks from scientific literature (Dimitriadis et al., 2021; Tsirintanis et al., 2022). This knowledge gap, impedes to unveil the processes driving the final observed effects, and therefore poses significant constrains to MPA managers to plan and implement adaptive and cost - effective management measures towards the mitigation of invasive species effects in the face of climate change.

The aim of this study was to explore along an 8-years' time-series, whether protection offered by a Mediterranean MPA can shape population trends of invasive, range expanding and native herbivore fishes, and their effects on the algal resource availability, taking into account the population trends of predatory fishes, fisheries catches of herbivore fishes and increasing sea temperature due to climate change. To this end, we hypothesized that protection offered by the MPA has a significant effect in: (i) controlling the population of the invasive and range expanding herbivore fishes through time and (ii) safeguarding algal resources against overgrazing. Our ability to understand such processes can lead to realistic and targeted conservation efforts enhancing the resilience of Mediterranean MPAs to climate change and biological invasions.

2. Material and methods

2.1. Study area

The study was conducted in Zakynthos Island, Eastern Ionian Sea, Greece, including the marine protected area (MPA) of Zakynthos National Marine Park (APPENDIX 1) which is officially established since 1999. The MPA is located in the south part of Zakynthos Island, embodying 89 km^2 of marine area. According to the protection level offered by the MPA relevant to fish fauna and benthic habitats, the MPA is divided into two main protection zones (P1 and P2). More specifically, zone P1 (highest protection level) is a seasonal (May to October) fully protected (no take / no boating) area, while zone P2 (moderate protection level) is a permanent partially protected areas, with only small-scale fishery (mainly using trammel nets and long-lines) allowed, as an extractive activity, all year round (Dimitriadis et al., 2018). From November to April, regulations in zone P1 are lifted, and this zone is subjected to the rules applied in zone P2. Still, the MPA lacks of any other fisheries-related regulations regarding the number of fishers that can fish in the MPA, the gears used, the fishing effort or the maximum allowed catches. The marine area which corresponds to unprotected areas, outside the MPA, is herein coded as zone OUT. The MPA has been reported to host 15 impactful invasive species (Ragkousis et al., 2023; Dimitriadis et al., 2023).

2.2. Data collection

The dataset considered in this study was derived from a compilation of data obtained during different research projects conducted from 2012 to 2019 (MEDPAN NORTH, FISHMPABLUE 2, PAVIS, OP Environment & Sustainable Development) within the MPA and in adjacent areas. The dataset includes data on: (a) fish biomass calculated from size and density estimates obtained via Underwater Visual Census (UVC) on rocky reefs; (b) percentage of macroalgae area cover estimated from photo-quadrats on rocky reefs; (c) biomass per unit effort (1000 m of net length, BPUE) of small-scale fishery catches; and (d) sea surface temperature from 1987 to 2019 (Clementi et al., 2021).

2.2.1. Fish biomass from UVC

UVC was used to estimate the density and individual size of fish along 125 m^2 transect lines (depth range: 5-15 m) (diver swam at constant speed, identifying, counting, and estimating the size of all individuals within 2.5 m on either side of the transect line – Giakoumi et al., 2019a) within each zone (P1, P2, OUT). Length estimate of each fish encountered was then transformed into biomass through length-weight relationships (Giakoumi et al., 2012; Froese et al., 2021). Data were obtained in 2012 and from 2015 to 2019 (n = 168 replicate transects) during summer months, retaining the same sampling sites through years as much as possible (not all sampling sites were used across all years) (Table 1). In order to examine the long-term dynamics of herbivorous fishes, in relation to their origin, distribution, and potential range expansion, we used the biomass data of the following species per protection zone: (a) invasive: *Siganus luridus* and *S. rivulatus*; (b) range expanding: *Sparisoma cretense*; and (c) native: *Sarpa salpa*. The ratio of invasive versus native and range-expanding herbivorous fish was calculated as an index of their relative co-variance through time and protection level. Biomass of piscivorous fish was used as a proxy of higher level predator population. Piscivorous fish were defined here as carnivores with a preference for fish and a fractional trophic level – TROPH – higher than 4.0 (Karachle & Stergiou, 2017; Froese et al. 2021). Piscivorous species used were: *Caranx crysos* (Mitchill, 1815), *Dentex dentex* (Linnaeus, 1758), *Epinephelus marginatus* (Lowe, 1834), *Euthynnus alletteratus* (Rafinesque, 1810), *Muraena helena* Linnaeus, 1758, *Mycteroperca rubra* (Bloch, 1793), *Pomatomus saltatrix* (Linnaeus, 1766), *Seriola dumerili* (Risso, 1810), *Scorpaena scrofa* Linnaeus, 1758, and *Sphyraena viridensis* Cuvier, 1829. None of the aforementioned predators were invasive species. To identify the overall fish assemblage response to protection level and variation through time, we estimated the biomass of all species, excluding herbivores (avoiding masking the response of other species when collectively analyzed due to their high dominance in overall biomass).

Table 1. Sampling design in the study area for underwater visual census (fish biomass) (P1: highest protection zone, P2: moderate protection zone, OUT: no protection), photoquadrats (benthic algal coverage) (P1: highest protection zone, P2: moderate protection zone, OUT: no protection), and small scale fishery catches (IN: P1 and P2, OUT: P3) (n/a: not available).

Sampling method	**Zone**	**Year**						
		2012	**2013**	**2015**	**2016**	**2017**	**2018**	**2019**

Under water visual census - number of sites (number of 125m^2 transects)	P1	4 (12)	n/a	4 (12)	4 (12)	2 (6)	2 (6)	2 (6)
	P2	5 (15)	n/a	6 (18)	4 (12)	2 (6)	2 (6)	2 (6)
	OUT	3 (9)	n/a	4 (12)	4 (12)	2 (6)	2 (6)	2 (6)
Photoquadrats – number of sites (number of 50x50cm quadrats)	P1	n/a	n/a	4 (20)	2 (10)	2 (10)	2 (10)	2 (10)
	P2	n/a	n/a	4 (20)	2 (10)	2 (10)	2 (10)	2 (10)
	OUT	n/a	n/a	4 (20)	2 (10)	2 (10)	2 (10)	2 (10)
Small-scale fishery operations (number of fishing operations)	IN	n/a	10	10	n/a	15	20	n/a
	OUT	n/a	17	10	n/a	17	15	n/a

2.2.2. Benthic algal coverage

Algal coverage was estimated at the same sites (and surveys) of UCV sampling (3-15 m depth) using photoquadrats (50 x 50 cm). Algae were identified down to species level when possible, and the percent cover within each quadrat was calculated using the PhotoQuad software (Trygonis and Sini, 2012). Data were available for the years 2015, 2016, 2017 and 2019 in all zones (P1, P2, OUT) (Table 1). Algal taxa were assigned to morphological groups according to Sala et al. (2012) and Giakoumi et al. (2019a): (a) canopy, representing "bush"-forming algae (e.g., *Cystoseira sensu lato* spp.); (b) coralline, articulated calcareous algae (coral-like formations) (e.g., *Amphiroa* spp.); (c) encrusting, calcareous algae with moss-like formations and/or prostrate growth (e.g., *Peyssonnelia* spp.); (d) erect, standing up-right algae (e.g., *Dictyota* spp.); (e) turf, algae with soft/pulp formations (low-lying, several mm to cm tall, layer of algae e.g., *Enteromorpha* spp.). Hard substrate not covered by algae, was coded as barrens (bare rock).

2.2.3. Catch per unit effort from small-scale fisheries and fishers' perception

Catch (gr) per unit of effort (CPUE) was assessed by the researchers of this study for small-scale fishery (SSF) operations using trammel nets in collaboration with local fishers. Net length of each fishing set varied from 500 to 6000 m, while inner mesh size of the nets ranged from 21 to 36 mm. Fishing activity took place at depths ranging from 15 to 60 m with an average fishing duration of 6 hours. The dataset includes fish biomass derived from 114 fishing operations held from 2013 to 2018 inside (zones P1 and P2) and outside (zone OUT) the MPA. The CPUE of *S. luridus*, *S. rivulatus*, *S. cretense* and *S. salpa* was calculated per fishing operation throughout the years and standardized to 1 Km as an indication of herbivores biomass export due to fisheries per net length. The ratio of CPUE for invasive herbivores to other herbivores, as well as of herbivores to total catch, were calculated as an indication of their relative importance in the catches over time. The CPUE for predators was not calculated here as trammel net is not an effective fishing gear for several predators such as *Epinephelus marginatus* and *Mycteroperca rubra*; these species are mainly targeted by long-lines. In 2020, 13 small-scale artisanal fishers operating both inside and outside the MPA were interviewed in order to: (a) assess if Siganidae represent SSF target species, and (b) capture fishers' perceptions on population trends of *S. salpa* through years.

2.2.4. Sea surface temperature

Sea surface temperature (SST) data were obtained from Copernicus EMS – Mapping Service (CMEMS). The acquired data consist of the average monthly SST (1 m depth) inside (37.68B°N, 20.92°E) and outside (37.77B°N, 20.96°E) the MPA from 1985 to 2019 (Clementi et al., 2021). For the monthly SST data, the average maximum and minimum temperature per year were calculated, as well as the average of the warmer summer (June-August) and colder winter (December-February) months.

2.3. Statistical analyses

We used linear mixed-effects models (LMMs) and generalized linear mixed-effects models (GLMMs) (Bates et al., 2015) to test the effect of "year" (treated as random component) and "protection level" (treated as fixed component), on the formulated response variables at each section of the dataset (i.e., biomass from UVC – 7 variables; benthic algal coverage – 6 variables; and species CPUE from fisheries – 6 variables; Table 2, Table 3, Table 4). In more details, LMMs for the response variables related to biomass from UVC and species CPUE from fisheries were fitted using restricted maximum likelihood method and Satterthwaite approximation for testing the significance of fixed effects as the optimal setting for the model being neither anti-conservative nor overly sensitive to sample size (Luke, 2017). As regards variables linked to benthic algal coverage, we used GLMMs with Gaussian errors and identity link function performing the lowest AIC score. Spearman's rank order correlation coefficient, followed by a permutational significance test, was employed to seek for possible relations between the biomass of the herbivores under scrutiny. Regarding the SST data analysis, Ordinary Least Squares (OLS) regression models with the temperature-related variables as dependent and "year" as independent variable, were employed to identify temperature trends inside and outside the MPA. A Mann-Kendall trend Test was also used, to determine if these trends exhibit monotonic upward or downward tendencies.

3. Results

3.1. Temporal and spatial trends of fish herbivores – UVC dataset

A significant effect of the factors "year" and "protection" was detected for the biomass of the invasive fish *Siganus luridus*, with both zones inside the MPA exhibiting significantly higher biomass than outside (P1 exhibited two time more biomass than outside) (Table 2, Figure 1a). A significant and abrupt increase of *S. luridus* biomass was recorded from 2017 onwards (Table 1- Figure 1a), with almost 33% of the total fish biomass corresponding to this species in 2017 (average±SE of 7704±1030 gr/125m^2 in 2017) (Figure 1c). As for the case of the range expanding *Sparisoma cretense* (significant effect of the factors "year" and "protection", Table 2, Figure 1a), a profound burst of biomass was detected from 2017 onwards (average±SE of 4189±1408 gr/125m^2 during 2017), while areas inside the MPA consistently presented higher average biomass than unprotected areas through time (P1 exhibited two time more biomass than outside). Almost 24% of the total fish biomass belonged to *S. cretense* in 2017 (Figure 1c). The change of *S. luridus* and *S. cretense* biomass through time was highly correlated (Spearman rho = 0.7, $p < 0.001$). Both protection level and year did not have a significant effect on the biomass of *Siganus rivulatus* and *Sarpa salpa*, with the average biomass of the latter species being remarkably low (less than 40 gr/125 m^2) throughout the study period and across protection zones (Table 2, Figure 1a).

The biomass ratio of invasive to other herbivore fishes indicates a clear prevalence of invasive species, exhibiting no significant response in relation to year or the protection status (Table 2, Figure 1d). Siganidae (mainly *S. luridus*) displayed approximately a biomass that was twice that of *S. cretense* and *S. salpa* (Figure 1d). Likewise, no significant effect of the examined factors was detected, on predators' biomass (Table 2), which was overall low (minimum value: 86 gr/ 125 m^2 in 2016, maximum value:

2,182 gr/125 m^2 in 2019), and on the total fish assemblage biomass, excluding herbivores (Table 2; Figure 1 b).

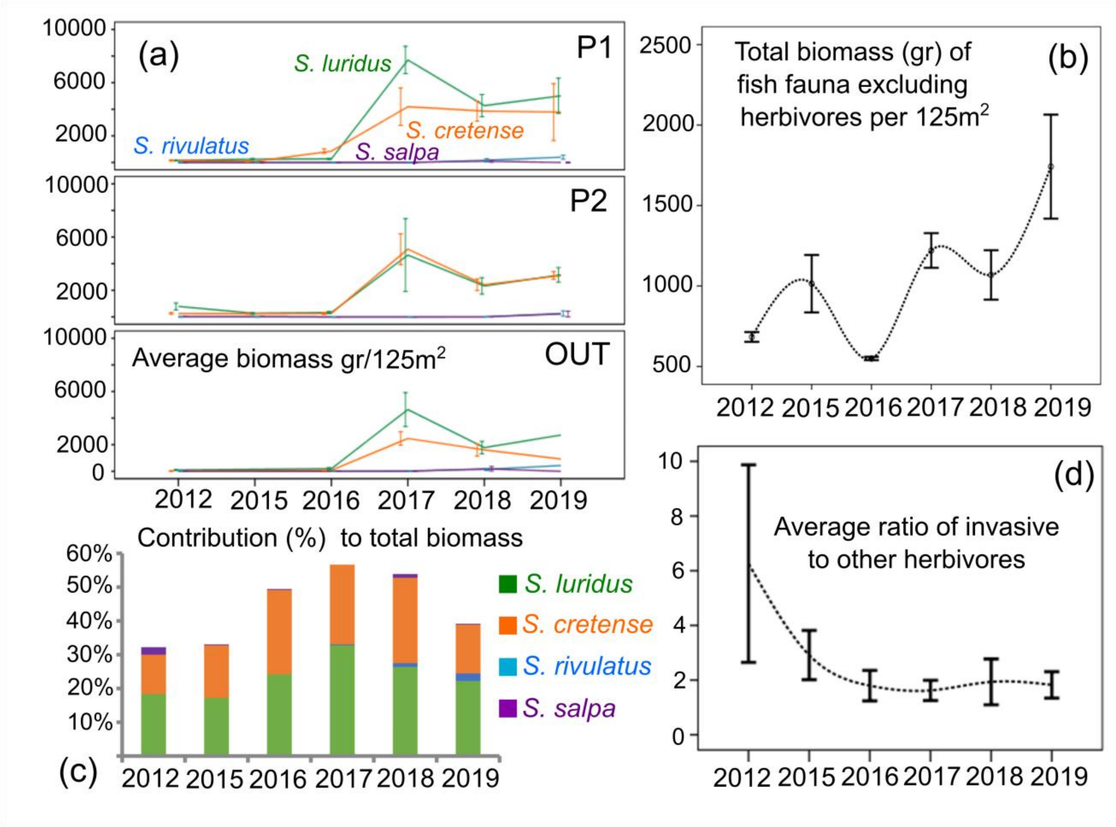

Figure 1. (a) Biomass variation of herbivores by year and protection level (P1 = highest protection, P2 = medium protection, OUT = no protection), (b) biomass variation of total fish assemblage (excluding herbivores) per year (spline line interpolation is also shown), (c) contribution of herbivore fishes to the overall fish biomass per year and (d) average biomass ratio of invasive (*Siganus luridus* and *S. rivulatus*) to other herbivores (*Sparisoma cretense* and *Sarpa salpa*) through time (spline line interpolation is also shown). Error bars represent standard error of mean.

Table 2. Results of linear mixed models including post hoc pairwise comparison of fixed effects levels, and modeled group means for variables derived by UVC data set. Significant p-values (< 0.05) in bold (P1: highest protection zone, P2: moderate protection zone, OUT: no protection)

Response Variable	Random component – Year		Fixed component – Protection		Estimated marginal means – fixed component				Post-hoc comparisons (p values)
Biomass from UVC	X^2	p	X^2	p	Level	Mean	SE	95% CI's	
Siganus luridus	6.31	**0.03**	5.91	**0.04**	P1	2947.32	1212.57	-29.51; 5923.90	P1vsP2: 0.13
					P2	1892.47	647.92	282.25; 3502.69	**P1vsOUT: 0.04**
					OUT	1529.34	653.96	-96.82; 3155.50	**P2vsOUT: 0.04**
Sparisoma cretense	8.06	**0.01**	5.90	**0.01**	P1	2160.88	762.66	289.36; 4032.41	P1vsP2: 0.29
					P2	1840.27	74.60	95.43; 3585.11	**P1vsOUT: 0.02**
					OUT	912.01	406.22	-101.33; 1925.37	**P2vsOUT: 0.04**
Sarpa salpa	0.45	0.39	0.34	0.84	P1	19.12	19.42	-26.94; 65.19	P1vsP2: 0.85
					P2	15.01	15.08	-07.07; 55.01	P1vsOUT: 0.59
					OUT	37.15	35.58	-51.84; 126.15	P2vsOUT: 0.75
Siganus rivulatus	0.41	0.67	2.18	0.33	P1	92.87	61.09	-60.71; 246.45	P1vsP2: 0.20
					P2	39.30	31.70	-47.99; 126.60	P1vsOUT: 0.21

					OUT	96.98	63.87	-67.99; 261.97	P2vsOUT: 0.83
Invasive/other Herbivores	0.62	0.33	2.85	0.24	P1	1.86	1.83	-1.98; 5.71	P1vsP2: 0.10
					P2	2.58	1.58	-0.59; 5.76	P1vsOUT: 0.09
					OUT	7.84	2.44	2.59; 13.08	P2vsOUT: 0.76
Epenephelus marginatus	0.53	0.29	1.86	0.39	P1	917.62	487.37	-393.39;2228.63	P1vsP2: 0.71
					P2	729.68	360.28	-161.20; 1620.56	P1vsOUT: 0.23
					OUT	133.38	381.38	-623.64; 890.16	P2vsOUT: 0.26
Total fish biomass excluding herbivores	0.62	0.53	5.54	0.06	P1	10974.26	3512.84	2225.22; 19723.30	P1vsP2: 0.45
					P2	9909.47	2960.23	2322.66; 17496.29	P1vsOUT: 0.06
					OUT	5355.24	1973.31	311.18; 10399.31	P2vsOUT: 0.06

3.2. Spatial and temporal trends of benthic algal coverage

The factor "year" had a significant effect on algal coverage for the morphological categories of turf and erect algae, and the barrens substrate category, irrespectively of the protection status (GLMMs results; Table 3, Figure 2). For turf algae, a sharp increase was detected from 2016 onwards (Figure 2), as their coverage values rose from 20% in 2015 to approximately 80% in 2016, and remained at high levels (>60%) during 2017-2019. On the contrary, erect algae coverage presented a six-fold decrease from 2015 (30%) to 2016 (5%), and its coverage remained at very low values up to 2019 (less than 8%) (Figure 2). An abrupt increase of barrens was also evidenced from 2016 onwards (Figure 2).

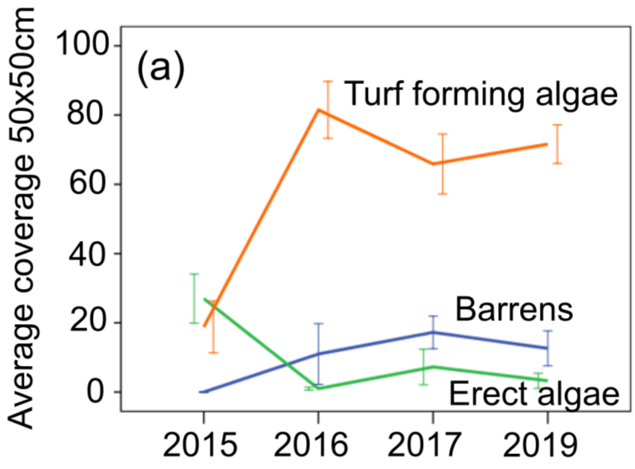

Figure 2. Temporal trends of algae morphological groups coverage (%) for which a significant effect of the factor "year" was evidenced. Error bars represent standard error.

Table 3. Results of generalized linear mixed models including post hoc pairwise comparison of fixed effects levels, and modeled group means for variables related to benthic algal coverage. Significant p-values (< 0.05) in bold (P1: highest protection zone, P2: moderate protection zone, OUT: no protection)

Response Variable	Random component – Year		Fixed component – Protection		Estimated marginal means – fixed component				Post-hoc comparisons (p values)
Algae/substrate coverage	X^2	p	X^2	p	Level	Mean	SE	95% CI's	
Barren	2.55	**0.01**	0.67	0.71	P1	12.28	7.45	-2.37; 26.82	P1vsP2: 0.43
					P2	8.14	5.04	-1.74; 18.03	P1vsOUT: 0.73
					P3	8.19	7.14	-5.81; 22.19	P2vsOUT: 0.99

Canopy	0.56	0.57	1.22	0.54	P1	0.17	3.16	-6.02; 6.38	P1vsP2: 0.30
					P2	9.40	8.39	-7.05; 25.8	P1vsOUT: 0.89
					P3	0.83	3.62	-6.26; 7.92	P2vsOUT: 0.31
Coralline	1.11	0.27	0.94	0.62	P1	2.54	3.79	-4.88;9.97	P1vsP2: 0.74
					P2	1.02	3.37	-5.60; 7.64	P1vsOUT: 0.39
					P3	9.04	8.91	-8.42; 26.50	P2vsOUT: 0.36
Encrusting	1.31	0.31	0.81	0.66	P1	3.13	3.04	-2.82;9.09	P1vsP2: 0.39
					P2	0.08	1.95	-3.75;3.91	P1vsOUT: 0.58
					P3	1.45	2.35	-3.16;6.08	P2vsOUT: 0.65
Erect	3.30	**0.03**	1.23	0.53	P1	7.04	5.16	-2.72; 17.52	P1vsP2: 0.37
					P2	15.29	9.94	-4.19; 34.78	P1vsOUT: 0.96
					P3	7.63	8.27	-8.58; 23.85	P2vsOUT: 0.28
Turf	4.25	**0.01**	0.60	0.74	P1	61.81	14.06	34.25; 89.38	P1vsP2: 0.45
					P2	54.17	18.38	18.13; 90.20	P1vsOUT: 0.98
					P3	61.53	15.34	31.45; 91.60	P2vsOUT: 0.57

3.3. Catch per unit effort from small-scale fisheries

LMMs revealed statistically significant effects of the factors ‘year’ and ‘protection’ on the CPUE of *Sparisoma cretense*, and herbivore to total CPUE ratio (Table 4). Average CPUE of *S. cretense* was significantly higher (i.e. six times higher) inside than outside the MPA (Table 4; Figure 3a). Herbivores’ contribution to CPUE of the total catch varied considerably through time, showing the lowest value in 2018 (3%) and highest in 2015 (40%), across the study area (Figure 3b). Interviews with fishers suggested that 12 out of the 13 respondents consistently avoid targeting Siganidae, mainly due to the low market price and demand, as well as to the heavy labor of extracting big schools of Siganidae from their nets. All the fishers highlighted a remarkable decline of *Sarpa salpa* in their catches from 2010 onwards, and since 2015 catches of this species became very rare both inside and outside the MPA.

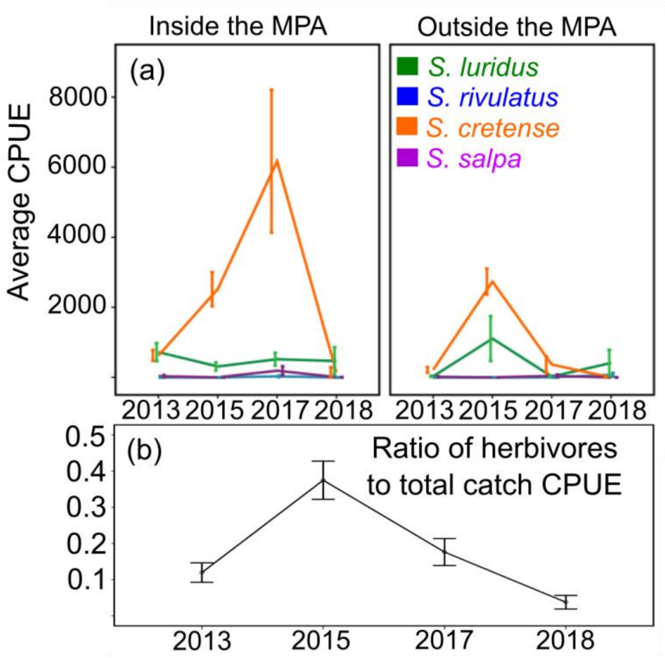

Figure 3. Average CPUE (gr/1km of net length) variation of the herbivore species by (a) protection level (inside, including P1 and P2, and outside, OUT, the MPA) across years, and (b) average CPUE ratio of herbivores to the total catch. Error bars represent standard error.

Table 4. Results of linear mixed models including post hoc pairwise comparison of fixed effects levels, and modeled group means for variables related to small scale fishery catches CPUE. Significant p-values (< 0.05) in bold (IN: includes P1- highest protection zone and P2- moderate protection zone, OUT: no protection – outside the MPA)

Response Variable	Random component – Year		Fixed component – Protection		Estimated marginal means – fixed component				Post-hoc comparisons (p values)
CPUE from fisheries	X^2	p	X^2	p	Level	Mean	SE	95% CI's	
Siganus luridus	0.43	0.51	1.60	0.20	P1	478.20	127.17	226.26; 730.14	INvsOUT: 0.14
					P3	138.86	138.86	-74.48; 475.70	
Sparisoma cretense	7.48	**0.01**	9.13	**0.01**	P1	2331.14	438.46	1462,38; 3199.89	**INvsOUT: 0.01**
					P3	347.56	478.86	-601,06; 1296,17	
Sarpa salpa	0.35	0.49	0.73	0.39	P1	53.99	25.79	2.89; 105.10	INvsOUT: 0.36
					P3	19.54	28.16	-36.26; 75.34	
Siganus rivulatus	0.41	0.67	0.27	0.60	P1	7.18	10.62	-13.85; 28.31	INvsOUT: 0.48
					P3	22.07	17.17	-26.42; 70.57	
Invasive/other Herbivores	0.06	0.90	0.04	0.94	P1	0.15	0.05	0.07; 0.21	INvsOUT:0.95
					P3	0.15	0.04	0.06; 0.22	
Herbivores/total catch	**5.59**	**0.03**	9.72	**0.01**	P1	0.22	0.05	0.06; 0.38	**INvsOUT: 0.01**
					P3	0.10	0.09	-0.14;0.46	

3.4. Sea surface temperature

The minimum and maximum SST per year, for the warmer and colder months, revealed an increasing trend both inside and outside the MPA ($p_{MK} < 0.05$, OLS slope test $p < 0.05$ in all cases) from 1985 onwards (Figure 5). Within the time frame of this study (2012-2019), the warmer seasons maintained an average SST at approximately 25ºC, and the colder seasons at around 17.4 ºC across the study area, while the warmest temperature was 27.7 ºC in 2015. Average SST of the warmer months was 24.7 ºC and 25.2 ºC for the time periods 2012-2016 and 2017-2019, respectively.

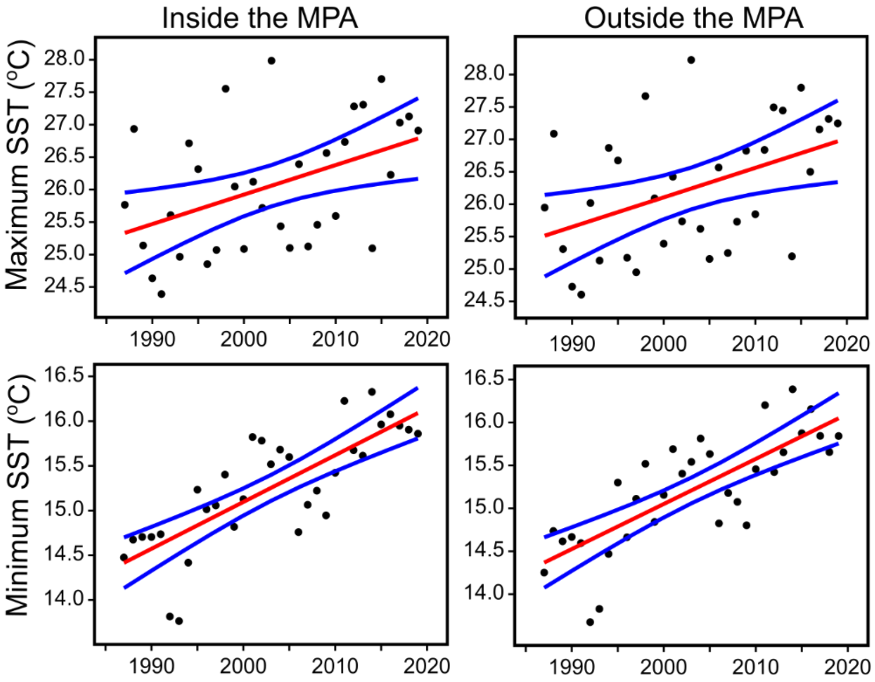

Figure 4. Temporal trends of the maximum and minimum recorded sea surface temperature (SST) during the warmest and coldest months, from 1985 to 2019, inside and outside the MPA (95% confidence intervals of the regression are shown in blue).

4. Discussion

MPAs, and especially those that include no-take marine reserves, have been proven to be highly effective in increasing fish biomass, restoring top and high-level predator populations, safeguarding biodiversity from human stressors, and enhancing important ecosystem functions (Giakoumi et al., 2017; Sala & Giakoumi 2018; Topor et al., 2019, Grorud-Colvert et al., 2021). However, despite being in the frontline of effective marine conservation management, MPAs are vulnerable to climate change effects, and especially to biological invasions (Burfeind et al., 2013; Giakoumi & Pey, 2017; Giakoumi et al., 2019a). Regarding the invasive herbivorous rabbitfishes *S. luridus* and *S. rivulatus*, empirical evidence (albeit restricted) suggests that they have been benefited by the protection offered in Mediterranean MPAs (Rilov et al., 2018; Giakoumi et al., 2019a,b; Frid et al., 2022; Ohayon et al., 2023). This was also confirmed by the findings of this study which, unlike other studies, explored the effects of protection on invasive herbivores not only spatially, but also temporarily along an 8-year period. The invasive *S. luridus* and the native range expanding *Sparisoma cretense* presented abrupt population burst within the MPA in a co-varying manner over time. The high performance and competitive dominance of these invasive and range expanding species against their temperate native herbivore competitor, *S. salpa*, have been attributed to their increased temperature tolerance (Marras et al., 2015), higher dietary plasticity (Verges et al., 2014; Santana-Garcon et al., 2023) and historical over-harvesting of *S. salpa* (Dimitriadis et al., 2018). If optimal temperatures differ between the competitors, then a mismatch in their comparative performance could be in place. In Zakynthos MPA, the maximum summer temperature was well above the optimal thermal limit for *S. salpa* (21.8 ºC) throughout the time frame of the study, while it progressively reaches its critical temperature threshold (28.7 ºC), beyond which the physiological performance (i.e., aerobic activities, such as swimming, feeding or growth) are expected to cease (Marras et al., 2015). On the contrary, the optimal thermal conditions for the Siganidae (29.1 ºC) are about to be met in the MPA. Therefore, as SST increases due to climate change, native herbivorous species are expected to be highly impacted, further allowing their invasive counterparts to thrive (Fodrie et al., 2010; Eger et al., 2020). On top of that, *S. luridus* and *S. salpa*, both feed primarily on adult macrophytes, acting as browsers (Yeruham et al., 2020), while *S. rivulatus* and *S. cretense* feed on earlier life stages through consumption of the epilithic algal matrix, acting as grazers (Azzurro et al., 2007; Bariche et al., 2014; Verges et al., 2014). Therefore, their populations can co-exist through niche partitioning, as is case for species-rich communities of herbivorous fishes in coral reefs (Topor et al., 2019). Yet, seaweeds are also susceptible to sea warming and thermal stress which are challenging their survivorship, growth rate and performance (Bennett et al., 2022; Mulas et al., 2022). Thus, further research is needed for the identification of recovery potential and resistance of seaweeds to herbivory at rocky reefs as sea temperature is rising.

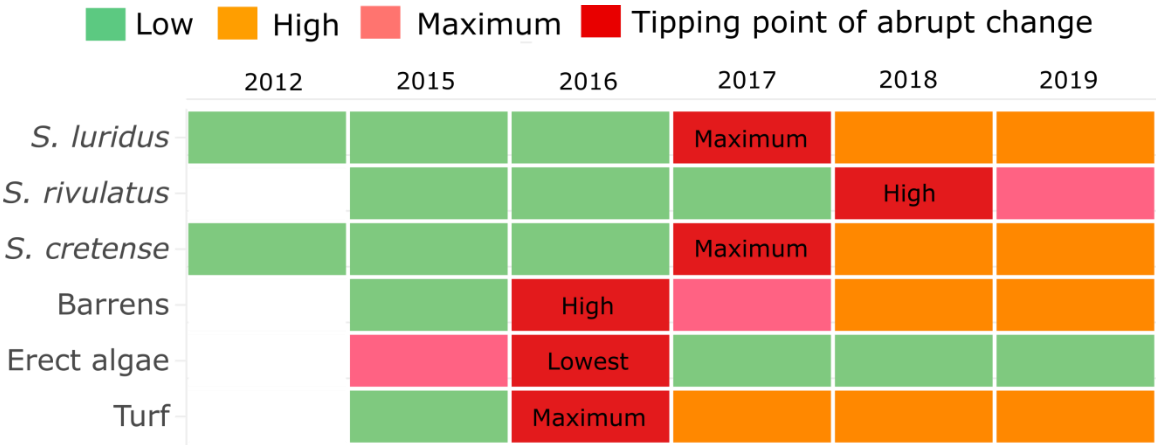

Figure 5. Summary of results regarding the tipping points of abrupt change of herbivorous fish biomass and algal/substrate categories coverage (marked in red, the text inside those boxes indicates the level biomass or coverage for fish and algal category) over time (low biomass of herbivorous fish and algal coverage is marked in green and high or maximum levels are marked in orange and pink, respectively).

The implied functional complementarity amongst herbivorous fish species leads to a more effective utilization of algal resources, which provokes the observed deforestation of rocky reefs. In the current study, turf algae and rocky barrens appeared to increase abruptly from 2016 onwards regardless the protection zone, while erect algae generally presented low area cover. Previous research regarding the status of macroalgae of rocky reefs in the MPA, before the establishment of invasive and range expanding fish herbivores (prior to 2004), highlighted the important presence of well-developed erect algae, as well as species rich and healthy macroalgae communities (Tsirika & Haritonidis, 2005). The current replacement of erect macroalgae by turf-dominated habitats and barrens due to overgrazing by Siganidae, has also been reported from unprotected rocky reefs of the Eastern Mediterranean (Sala et al., 2011; Verges et al., 2014; Yeruham et al., 2019; Santana-Garcon et al., 2023; Nikolaou et al., 2023). Still, as sea warming prevails and invasive herbivorous fish are rapidly spreading in the Mediterranean, it is expected that the degraded reef state will gradually advance westward (Rilov et al., 2018; Schickele et al., 2021; Azzurro et al., 2022).

Understanding the relationship and interaction strength between herbivores and primary producers in the long-term, especially within MPAs, can facilitate the design of suitable and adaptive management measures aiming to sustain ecosystem functioning (Poore et al., 2012). This information is crucial for the identification of priority sites for restoration of canopy algae in the Mediterranean Sea (Fabbrizzi et al., 2023), especially in the face of climate change. Yet, recognizing the tipping points where the structure and composition of ecosystems undergo a shift due to a significant change in the abundance and composition of herbivorous fishes may contribute to improving the recovery potential of algae assemblages on rocky reefs through timely and targeted interventions (Bosch et al., 2022). This study hints towards the notion that population evolution of range expanding and invasive herbivorous fishes and macroalgae coverage through time can be described by non-linear trends and tipping points of abrupt change, with the latter not necessarily overlapping chronologically. The time lag between the tipping point of population boom of the co-varying *S. luridus* and *S. cretense*, and the tipping points of abrupt increase of barrens and turf-forming algae, and decrease of erect algae was one year (Figure 5). As for the more recently established *S. rivulatus* (since 2014, Dimitriadis et al., 2021), the time lag was found to be two years, as the biomass of this species gradually advanced, although it was still considerably lower than that of *S. luridus* and *S. cretense* (both established around 2004, Dimitriadis et al., 2021). Holbrook et al. (2016) showed that even a small amount of herbivory is able to suppress macroalgae and create sharp transitions in algal coverage in coral reef ecosystems. In this context, it is possible that the surplus of herbivory across rocky reefs may lead to sudden shifts in algal coverage preceding the tipping point of abrupt increase of invasive and range expanding herbivorous fish species. In any case, the initial population boom phase of invasive and range expanding herbivores (collectively covering almost 60% of total fish biomass in 2017) appears to reach a more stationary stage, in which biomass of herbivores stabilizes to high levels. At the same time, erect macroalgae coverage remains low, whereas turf-forming algae and barrens prevail, thus probably indicating low recovery potential of the formerly dominant foundational species as has also been shown at other temperate reef system (Bosch et al., 2022). Time-lagged relationships and disproportionate changes between consumer population size and resource availability have been highlighted as possible mechanisms driving the long-term interactions between invaders and their ecosystems (Strayer et al., 2017; Zarco-Perello et al., 2017; Eger and Baum, 2020). Still, despite sea urchins being key invertebrate herbivores at temperate rocky reefs (Agnetta et al., 2015; Piazzi & Ceccherelli, 2019; Pinna et al., 2020), their contribution to grazing pressure on macroalgae resources across the study area is probably limited since they have become very rare from 2014 onwards (Dimitriadis et al., 2021).

After eighteen years of its establishment, Zakynthos MPA still falls short in maintaining sufficient protection for the recovery of high-level predators (due to inadequate spatial and temporal regulations for fisheries, habitat suitability for large predators and historical overfishing), and thus top-down population control of herbivorous fish species through predation is not very likely (Dimitriadis et al., 2018; 2021). This may also be relevant for new or recently established MPAs which, may appear as non-effective in restoring top-down predation processes for the regulation of invasive or range expanding herbivores, given that rebuilding of top predator populations may take decades (Di Franco et al., 2009; Frid et al., 2022), whereas the populations of invasive and range expanding herbivorous fish need only a couple years to burst as demonstrated herein. Thus, both non-effective or recently established MPAs may act as highways for the proliferation of invasive and range expanding species, subsequently challenging the success of achieving the sustainable development goal 14 (conserve and sustainably use oceans, seas, and marine resources) of UN 2030 Agenda which promotes the establishment of new MPAs for the effective management, protection and restoration of marine and coastal ecosystems.

We recognize that our study findings are subjected to limitations mainly linked to the consideration of a single MPA, albeit situated on the forefront of marine invasions in the Mediterranean Sea (D'Amen and Azzurro, 2020). Additionally constraints stem from the relatively restricted timeframe (i.e. eight years) of available data and the absence of direct measurements for the intensity of pertinent ecological processes (e.g. herbivory rate). Consequently, additional research conducted on a broader spatial and temporal scale is essential to enhance the robustness of our conclusions.

Controlling the spread and population size of the invasive species is a challenging task since they are usually well-established prior to the identification of their impacts and population trends in the recipient ecosystems. However, management measures, such as early eradication, may be unachievable and costly (Giakoumi et al., 2019c), subjected also to legislative and practical limitations (Ulman et al., 2021). Alternatively, targeted harvesting of invasive species within MPAs through fisheries, and protection of overfished predators and key habitats have been put forward as more feasible options for the management of invasive species (Kleitou et al., 2020; Eger et al., 2020). Within Zakynthos MPA: (a) top-down regulation of invasive and range expanding fish herbivores by native predators is unlikely due to poor design and historical overfishing in and around the MPA (Dimitriadis et al., 2018); (b) fishers are consistently avoiding targeting Siganidae due to their low market price and demand; (c) the range expanding herbivore *S. cretense* constitutes an important part of the catches, especially in the MPA; and (d) recreational fishing is not allowed in the MPA. Based on the above-mentioned facts, we propose to: (1) promote targeted removal of fish herbivores, and especially Siganidae, through fisheries and fishery-related tourism; (2) improve the market potential of low-value Siganidae by marketing the species consumption, and generate additional motivation for small-scale fishers to target these species and overcome the cost associated with the extraction of big schools of Siganidae from their nets; (3) improve public awareness on the effects of Siganidae on the marine ecosystem, and promote their consumption; (4) enhance the effectiveness of high-level predator restoration through the establishment of adequate year round no-take marine reserve(s) identified through effective conservation objectives and planning; and (5) maintain or even improve the monitoring of invasive and range expanding fish species.

The systematic and targeted promotion of Siganidae in the local market may possibly contribute to obtain commercial interest, increase the retail price, reduce their populations and enhance the income of the fishers. The rabbitfishes *S. luridus* and *S. rivulatus* are the species with the greater catches and value of the total catch in the Levantine basin (Michailidis et al., 2020). Regulation of herbivore fish populations in Zakynthos Island, and more broadly in the Ionian Sea, could generate significant benefits for the recovery of the impoverished rocky reefs and the associated benthic invertebrates (e.g. *Arbacia lixula*, *Paracentrotus lividus*, *Echinaster sepositus*, *Ophidiaster ophidianus*, *Hacelia attenuata*), that have recently declined in the MPA and beyond (Dimitriadis et al., 2021), and for the biodiversity conservation in the region.

5. Conclusions

Our study represents a good showcase of how an MPA may facilitate rather than mitigate the sudden and persistent population burst of invasive and range expanding herbivorous fishes at tipping points of abrupt change. This subsequently leads to the degradation of rocky reef habitats and depletion of algal resources, with their tipping points of abrupt change not necessarily occurring in chronological alignment with those related to invasive and range expanding herbivores. The native herbivore *S. sarpa* was very rare throughout the time frame of the study, likely attributed to historical overfishing. This rarity may have been further facilitated by the increasing SST, posing a challenge to the thermal suitability of this species. Challenges linked to thermal suitability could also be relevant for algal species. Therefore, as the sea is getting warmer, non-effective in restoring fish communities and lost top-down control process or recently established MPAs in historically overexploited and degraded areas may act as highways for the proliferation of invasive and range expanding species, subsequently challenging management effectiveness and conservation goals.

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CRediT authorship contribution statement

Charalampos Dimitriadis: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft, Visualization. **Christina Marampouti**: Methodology, Formal analysis, Writing - Review & Editing. **Antonio Calò**: Conceptualization, Methodology, Investigation, Writing - Review & Editing. **Antonio Di Franco**: Conceptualization, Methodology, Investigation, Writing - Review & Editing. **Sylvain Giakoumi**: Conceptualization, Methodology, Investigation, Writing - Review & Editing. **Eugenio Di Franco**: Investigation, Writing - Review & Editing. **Manfredi Di Lorenzo**: Investigation, Writing - Review & Editing. **Vasilis Gerovasileiou**: Investigation, Writing - Review & Editing. **Paolo Guidetti**: Conceptualization, Methodology, Investigation, Writing - Review & Editing, Supervision. **Alexis Pey**: Investigation, Writing - Review & Editing. **Maria Sini**: Investigation, Writing - Review & Editing. **Laurent Sourbès**: Conceptualization, Writing - Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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