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Trophic group responses to marine reserve protection in temperate and tropical reefs: a systematic review and meta-analysis

Mariana Cardoso-Andrade[1,2] ✉, **Bárbara Horta e Costa**[2], **Andreia Hall**[3], **Jorge M. S. Gonçalves**[2] & **Henrique Queiroga**[1]

Marine reserves impact not only exploited species but also other groups, highlighting broader ecological effects within marine communities. While some of these effects are well documented, comprehensive assessments of overall reserve impacts on functional guilds and community structure remain limited. Our systematic review and meta-analyses used structural metrics to test global patterns across 138 tropical and temperate reef reserves, covering seven fish and invertebrate trophic groups and 11 macroalgae and coral morphological groups (99 studies, 679 response-ratio values). In tropical reserves, herbivorous fish presented the highest positive response, followed by carnivores. Potential indirect negative effects may result from predatory fish reducing herbivorous invertebrates and herbivorous fish decreasing macroalgae. Coral cover was higher inside reserves, while algal cover declined. In temperate reserves, herbivorous invertebrate declines did not appear to consistently affect macroalgae, indicating context-dependent outcomes. These results suggest both direct and indirect effects of protection, contributing to valuable insights for ecosystem-based management.

The Kunming-Montreal Global Biodiversity Framework's 30 by 30 target—to conserve at least 30% of the planet by 2030[1]—, has become more central than ever in the international environmental policy agenda. Aligned with this global objective, the European Biodiversity Strategy for 2030 establishes the commitment to protect 30% of the European Union's land and sea, with at least 10% under strict protection[2]. The Nature Restoration Law also sets a binding target to restore at least 20% of the EU's land and marine areas by 2030, and all ecosystems in need of restoration by 2050, through effective area-based measures[3]. In the ocean, research has shown that strongly regulated, well-implemented, and actively managed marine protected areas (MPAs) can protect and restore marine biological communities and achieve healthy marine ecosystems[4–6]. It is also well established that the combination of five key MPA features—no-take, well-enforced, old, large, and isolated—greatly improves their conservation benefits, including the recovery of highly fished species[7].

During MPA design and management processes, participatory approaches are desirable, with marine conservation science playing a critical role in informing policymakers and ocean stakeholders and supporting evidence-based decision-making[8–10]. In these dialogs, conveying the importance of ecosystem-based conservation and that fishing impacts are likely to extend beyond target species may be challenging. This challenge underscores the importance of studying the potential effects of marine reserve protection on non-targeted groups and of testing the consistency of these effects across different contexts.

There is extensive evidence that no-take MPAs (hereinafter marine reserves) can recover species targeted by fishing, especially those of high trophic level[11–17]. Direct effects of fishing prohibition and other habitat protection measures (e.g., ban on anchoring) can also cause indirect effects that extend to the whole reef community through top-down and bottom-up interactions[18]. Top-down interactions are typically observed due to recovered predators exerting top-down control on mid-level consumers, thereafter affecting smaller prey or primary producers and, ultimately, changing habitat structure[19,20]. Bottom-up interactions can occur from the recovery of habitat-forming species (e.g., corals, kelps), improving habitat complexity

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[1]Departamento de Biologia and Centro de Estudos do Ambiente e do Mar (CESAM), Universidade de Aveiro, Campus Universitário de Santiago, Aveiro, Portugal. [2]Centro de Ciências do Mar do Algarve (CCMAR /CIMAR LA), Universidade do Algarve, Campus de Gambelas, Faro, Portugal. [3]Centro de Investigação e Desenvolvimento em Matemática e Aplicações (CIDMA), Departamento de Matemática, Universidade de Aveiro, Campus Universitário de Santiago, Aveiro, Portugal. ✉e-mail: mariana.andrade@ua.pt

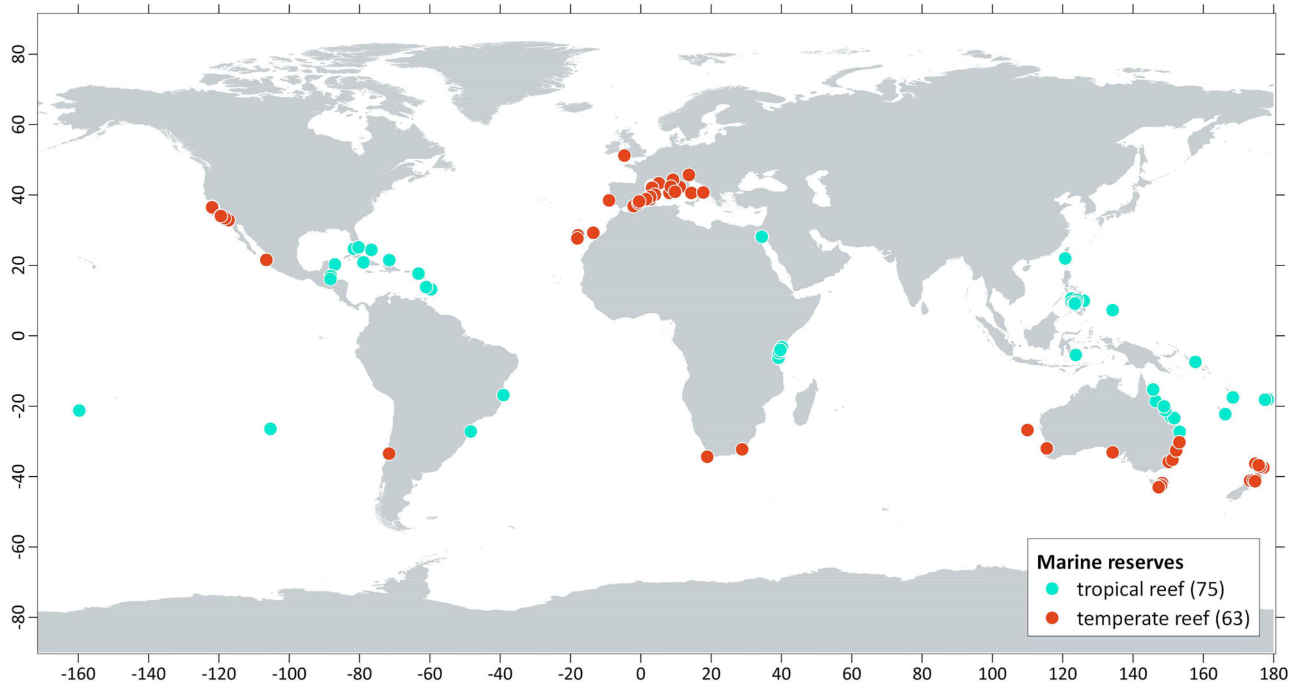

Fig. 1 | Marine reserves ($n = 138$) from 32 countries for which peer-reviewed data were retrieved.

and enabling key ecological processes–such as primary productivity, feeding, resting, reproduction, juveniles' development and recruitment—thereby increasing the biomass, abundance and diversity of fish and invertebrates[19,21].

Depending on the climatic region and reef type, marine reserve effects on the trophic structure vary. In tropical coral reefs the most reported effects are the recovery of predatory and herbivorous fish populations, macroalgae cover reduction due to increased herbivory, and the recovery of coral cover due to decreased spatial competition with macroalgae[11,22–24]. In temperate rocky reef reserves the main effects described are the recovery of predatory fish, the decline of grazing sea urchin populations, and the promotion of macroalgae growth[11,25–27]. Temperate rocky reefs' structures depend on the substrate's complexity and engineering species such as kelp, corals and sponges, whose conservation contributes to the passive restoration of the ecosystem. Tropical coral reefs are formed by a complex biogenic substrate that fundamentally shapes ecological communities' structure and functioning[28].

However, studies on monitoring and evaluation of MPA effects still largely focus on a few target species, or key species, instead of addressing the reef community and its various trophic levels[18,22,29].

Marine reserves can restore ecological processes by influencing the trophic structure of marine biological communities[12,22], but protection effects vary between taxonomic groups and trophic levels[29]. Understanding patterns across functional groups is therefore important[24,30], as it provides insight into potential community-level responses to protection and the broader ecological role of marine reserves in supporting ecosystem health and resilience[31]. This is especially important in a climate transition period, which is driving biodiversity and habitat loss, shifting species distributions and disturbing ecosystem structure and functioning through ocean warming, acidification and deoxygenation[23,32]. Climate change impacts include habitat loss (e.g., marine heatwaves devastating kelp forests and coral reefs), decreased habitat complexity and biodiversity, declines of top predators and collapsed food webs[32,33]. These impacts challenge the conservation objectives of MPAs and, if not considered in their design and management, may undermine their effectiveness[34–36]. Better understanding of ecological processes, and distinction between climate change and biotic drivers of change, is crucial to find strategies to enhance the adaptation and mitigation capacity of MPAs under climate change[33,37].

While previous individual studies and a few systematic reviews and meta-analyses have laid important groundwork regarding the effects of marine reserves on trophic structure[11,22,25–27,38], further work is still necessary to identify consistent global patterns across temperate and tropical systems in various trophic groups. This study aims to contribute to this knowledge gap through a quantitative systematic review of the effects of marine reserves on seven trophic groups for fish and invertebrates and 11 morpho-functional groups for macroalgae and corals, separately, using available data on structural metrics. With this robust statistical approach, we aimed to evaluate, across global studies, the existing hypotheses of effects from marine reserve protection with broader and more updated evidence. Further, where local information is not yet available, identifying patterns across multiple contexts with a geographically comprehensive MPA sample can provide insights until the knowledge gap at the local level is filled.

We computed the log-transformed response ratios (an effect size measure) of abundance, biomass, and individual size for each functional group and for community species richness. Given that after-control-impact (ACI) and before-after (BA) designs can potentially confound reserve effects with spatial and temporal variability independent of the reserve—variability that is minimized in before-after-control-impact (BACI) designs—effect sizes were analyzed separately for each monitoring design[39]. The database included 679 response-ratio values measured in 138 marine reserves of 99 different studies from 32 countries in tropical and temperate reefs (Fig. 1; Results). This dataset provides broader functional and geographic coverage compared to earlier syntheses (e.g. [22,25,26]), enabling us to test the consistency of marine reserve effects across ecosystems while also detecting system-specific responses. The separation of tropical and temperate reefs allowed us to account for ecologically meaningful differences driven by environmental factors such as substrate type, and differences in fishing targets, while the separation of monitoring designs reduced potential bias associated with spatial and temporal variability. By adhering to PRISMA guidelines and predefined eligibility criteria, this study ensured transparency, replicability, and minimized selection bias. Together, these steps strengthened the robustness of our analyses and the generality of the patterns identified.

Meta-analyses returned significant effects for 10 out of 18 functional groups, of which carnivorous and herbivorous fishes shared positive effects for both reef types. Tropical and temperate reef marine reserves also shared negative effects for herbivorous invertebrates potentially associated with top-down control by predators. Impacts detected on other functional groups were unique to each reef type. The findings of this quantitative review inform researchers and policymakers about the overall effectiveness of marine reserves in protecting different functional groups and contributing to ecosystem-based conservation. It also shows what data (quantity and quality) have been reported on marine reserve effectiveness in different environmental conditions. This information is critical to assessing how key environmental monitoring questions are being answered worldwide.

Results

Of the 3108 papers reviewed, 588 were considered for potential inclusion. Of these, 99 papers satisfied all the criteria for inclusion in the meta-analyses (see the process flow and list of included papers in Fig. S1 and Data S1, respectively). Marine reserves included in the data set ($n = 138$) were well distributed around the globe with their latitudes ranging between –43.0 and 51.2 decimal degrees (WGS84) (Fig. 1, Table S1). Data were available mainly for small marine reserves[40] ($\bar{X} = 1249\text{Km}^2$, median=3.5 Km^2, 3rd quartile=12.1 Km^2), whose mean age was 11 years old. We computed 79 independent random-effects meta-analyses (see Tables S2–S12) using log-response ratios (679 response-ratio values extracted or derived from the literature; see Table S13), separately for each combination of indicator (see Table 1) and monitoring design: After-Control-Impact (ACI: 571 response-ratio values), Before-After (BA: 63 response-ratio values), and Before-After-Control-Impact (BACI: 45 response-ratio values). Among the indicators, 31 were functional group indicators, i.e., a combination of variable, organism type, and functional group, and 3 were community indicators that evaluated species richness for the three organism types included, i.e., fishes, invertebrates, and macroalgae (Table 1). Marine reserves that shared the same control site (2 tropical reef and 3 temperate reef marine reserves), were analyzed as independent studies. However, as this choice could incur data dependency, we also analyzed these marine reserves as one "merged" study for each reef type. We pooled their treatment data (weighted average; see Section "Data processing" for further details on variance calculation) to see how integrating these marine reserves' effect sizes affected results independently.

Table 1 | Community indicators (organism type + variable) and functional group indicators (organism type + variable + functional group) assessed for each reef type

Organism type	Community variables		Functional group variables	Functional groups	
	Tropical reefs	*Temperate reefs*		*Tropical reefs*	*Temperate reefs*
Macroalgae		species richness (3)	percent cover	macroalgae (32)	macroalgae (5)
				calcified-encrusting algae (8)	calcified-encrusting algae (9)
				calcified-erect algae (3)	erect non-calcified algae (6)
				erect non-calcified algae (13)	leathery macrophytes (16)
				leathery macrophytes (5)	turf algae (11)
				corticated macrophytes (4)	foliose & corticated foliose (8)
				turf algae (10)	filamentous (5)
				foliose & corticated foliose (7)	
			abundance		macroalgae (5)
					calcified-encrusting algae (5)
					leathery macrophytes (4)
Coral			percent cover	hard coral (36)	
				soft coral (22)	
Invertebrates		species richness (3)	abundance	filter-feeders (8)	carnivores (16)
				herbivores(11)	filter-feeders (18)
					herbivores (34)
					omnivores (3)
			biomass	herbivores (4)	herbivores (6)
			percent cover	filter-feeders (13)	filter-feeders (4)
			size of the organism	herbivores (3)	herbivores (7)
Fish	species richness (18)	species richness (31)	abundance	carnivores (21)	carnivores (46)
				corallivores (5)	herbivores (23)
				detritivores (6)	omnivores (3)
				herbivores(18)	planktivores (9)
				omnivores (8)	
				planktivores (9)	
			biomass	carnivores (31)	carnivores (37)
				herbivores (40)	herbivores (14)
					planktivores (8)
			size of the organism		carnivores (5)

In parentheses, the number of response ratios for community and functional group indicators for all designs. Community indicators are independent by nature. Functional group indicators are independent by design, i.e., there are no common species among functional categories.

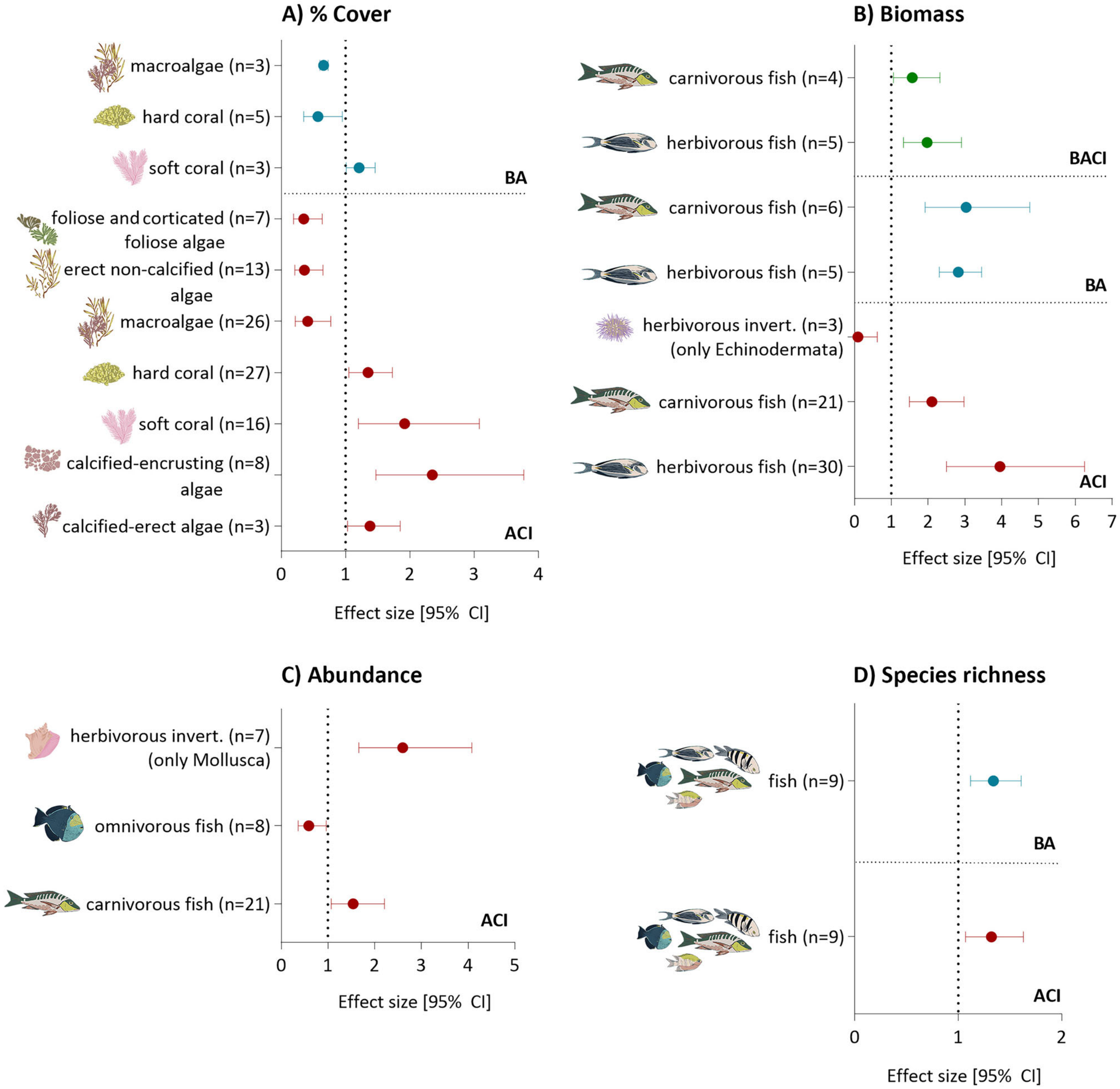

Fig. 2 | Tropical reefs' significant outcomes. Back-transformed (exp) mean effect-sizes (lnRR) and 95% confidence intervals for each functional group and variable (**A–D**). The vertical dotted line at 1 represents no significant difference. Values above and under 1 indicate higher and lower values in the treatment group (protected site) than in the control group (unprotected site), respectively. ACI: After-Control-Impact (red); BA: Before-After (blue); BACI Before-After-Control-Impact (green). See Tables S2–S5 for the complete set of results.

Tropical reefs

Hard coral cover response to protection was positive and significant for ACI ($\overline{RR} = 0.30, p = 0.02$), meaning higher values inside the MPA compared to outside, and negative and significant for BA studies ($\overline{RR} = -0.55, p = 0.03$), meaning lower values after the establishment of the MPA compared to before (Fig. 2, panel A)). Soft coral cover response to protection was positive and significant for ACI ($\overline{RR} = 0.65, p < 0.01$) and BA ($\overline{RR} = 0.19, p = 0.04$) studies. Calcified and non-calcified algae cover showed mixed results. Calcified-encrusting (ACI: $\overline{RR} = 0.86, p < 0.001$) and calcified-erect algae (ACI: $\overline{RR} = 0.32, p = 0.03$) cover were higher at protected sites, whereas erect non-calcified algae cover ($\mathrm{ACI} : \overline{RR} = -1.01, p < 0.001$) was significantly lower. Results for the group of foliose and corticated foliose algae were also negative and significant ($\mathrm{ACI} : \overline{RR} = -0.74, p = 0.04$). The result for macroalgae, with no distinction between morpho-functional groups, was also negative and significant across space ($\mathrm{ACI} : \overline{RR} = -0.88, p < 0.01$) and time ($\mathrm{BA} : \overline{RR} = -0.41, p < 0.001$).

Herbivorous and carnivorous fish biomass were significantly higher for all designs (ACI, BA, BACI), pointing to higher biomass inside compared to outside, as well as after compared to before (Fig. 2, panel B)). Herbivorous fishes benefited the most, almost quadrupling their biomass for ACI studies ($\overline{RR} = 1.37, p < 0.001$) and tripling it for BA studies ($\overline{RR} = 1.04, p < 0.001$). Carnivorous fish biomass was two times higher inside marine reserves than outside ($\mathrm{ACI} : \overline{RR} = 0.74, p < 0.001$) and three times higher inside marine reserves compared to its reference condition ($\mathrm{BA} : \overline{RR} = 1.11, p < 0.001$). Carnivorous fish abundance was also positive and significant but only for the ACI design ($\overline{RR} = 0.43, p = 0.02$), whereas omnivorous fish abundance was negative and significant ($\mathrm{ACI} : \overline{RR} = -0.53, p = 0.03$) (Fig. 2, panel C)). Herbivorous invertebrate biomass showed no significant responses to protection

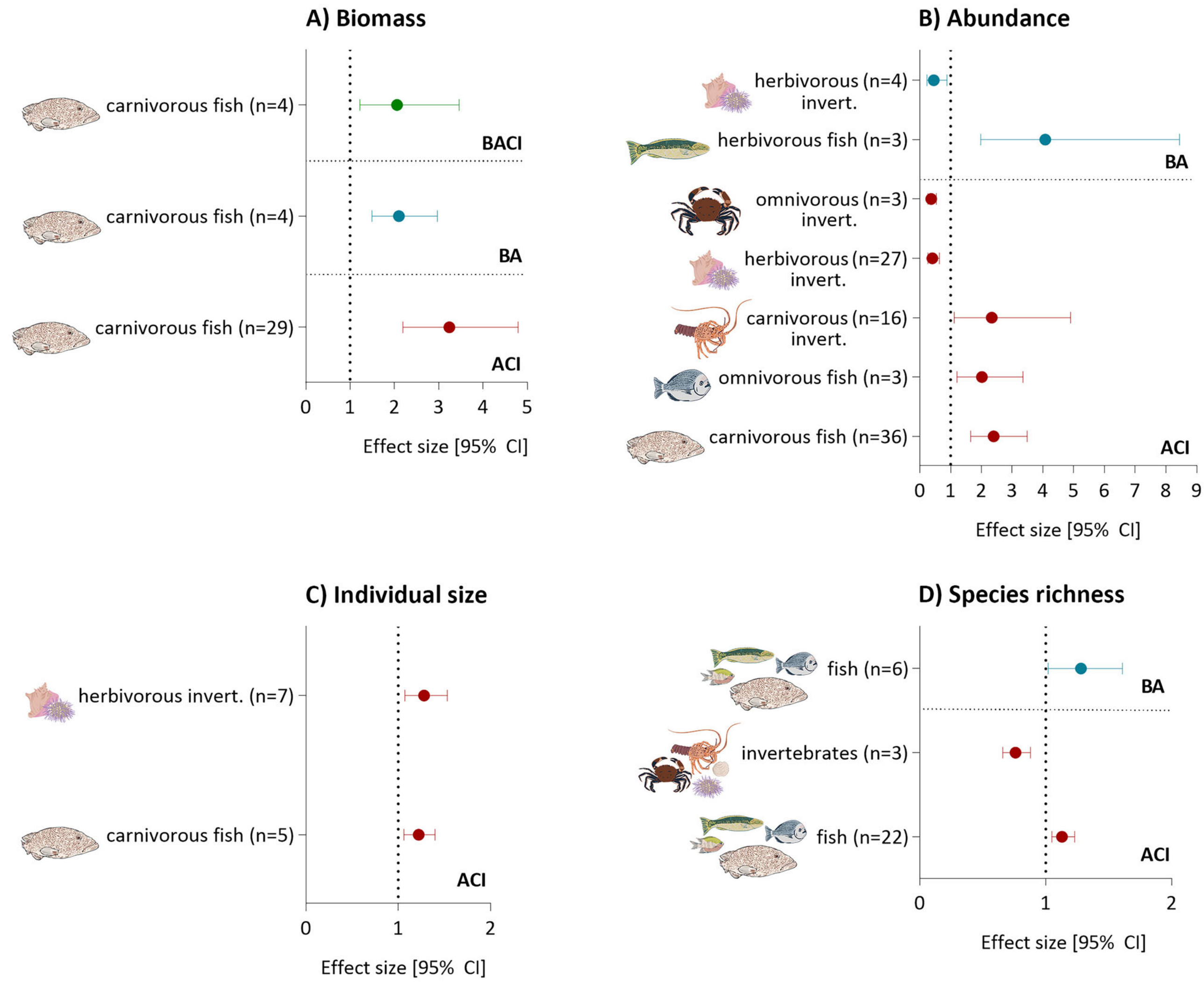

Fig. 3 | Temperate reefs' significant outcomes. Back-transformed (exp) mean effect-sizes (lnRR) and 95% confidence intervals for each functional group and variable (**A–D**). The vertical dotted line at 1 represents no significant difference. Values above and under 1 represent higher and lower values in the treatment group (protected site) than in the control group (unprotected site), respectively. ACI After-Control-Impact (red), BA Before-After (blue), BACI Before-After-Control-Impact (green). See Tables S8–S11 for the complete set of results.

(ACI : $\overline{RR} = -1.72, p = 0.09$). However, after selecting only Echinodermata studies from that group (which included Mollusca), herbivore biomass was significantly lower inside marine reserves than outside (ACI : $\overline{RR} = -2.43, p = 0.01$). Herbivorous invertebrates' abundance also did not show significant results (ACI : $\overline{RR} = 0.14, p = 0.75$). Nevertheless, if one were to select only Mollusca studies, the result would become positive and significant (ACI : $\overline{RR} = 0.96, p < 0.001$).

Size data were possible to assess only for herbivorous invertebrates, with no significant results ($\overline{RR} = 0.07, p = 0.40$). Community-level species richness was possible to assess only for fishes and revealed positive and significant responses to protection, though with small effect sizes, for ACI ($\overline{RR} = 0.28, p = 0.01$) and BA studies ($\overline{RR} = 0.30, p < 0.01$)(Fig. 2, panel D)).

Temperate reefs

All macroalgae morpho-functional groups had neutral responses to protection. As with tropical coral reef marine reserves, we observed significant positive responses of carnivorous fish biomass for all sampling designs (ACI, BA, and BACI) (Fig. 3, panel A)). Carnivorous fish biomass more than tripled inside marine reserves compared to outside (ACI : $\overline{RR} = 1.18, p < 0.001$) and followed the same trend over time (BA : $\overline{RR} = 1.02, p < 0.001$). Predators were 22% larger inside marine reserves compared to outside (ACI : $\overline{RR} = 0.20, p < 0.01$) (Fig. 3, panel C)). Omnivorous fish were also more abundant inside marine reserves than in fished sites (ACI : $\overline{RR} = 0.70, p < 0.01$) (Fig. 3, panel B)).

In contrast to tropical reef marine reserves, we found no significant differences of herbivorous fish biomass and abundance between temperate reef marine reserves and fished sites (ACI : $\overline{RR} = 0.80, p = 0.09$ and $\overline{RR} = 0.49, p = 0.08$, respectively). However, the result for abundance over time indicates the recovery of herbivorous fishes since the marine reserves' implementation year (BA : $\overline{RR} = 1.41, p < 0.001$). The abundance of herbivorous and omnivorous invertebrates was lower inside marine reserves (ACI : $\overline{RR} = -0.90, p < 0.001$ and $\overline{RR} = -0.98, p < 0.001$, respectively), with herbivores also showing this trend compared to the marine reserves' baseline condition (BA : $\overline{RR} = -0.81, p = 0.02$). Conversely, the outcome for abundance of carnivorous invertebrates was positive and significant ($\overline{RR} = 0.85, p = 0.02$). Nevertheless, herbivorous invertebrates were larger inside marine reserves than outside (ACI : $\overline{RR} = 0.24, p < 0.01$).

Community-level species richness was assessed for fish, invertebrates, and macroalgae, but only fish and invertebrates' species richness changed significantly (Fig. 3, panel D)). Fish species richness was greater inside marine reserves for ACI ($\overline{RR} = 0.12, p < 0.01$) and BA ($\overline{RR} = 0.25, p = 0.03$) treatments, while invertebrate species richness was lower for the ACI ($\overline{RR} = -0.27, p < 0.001$).

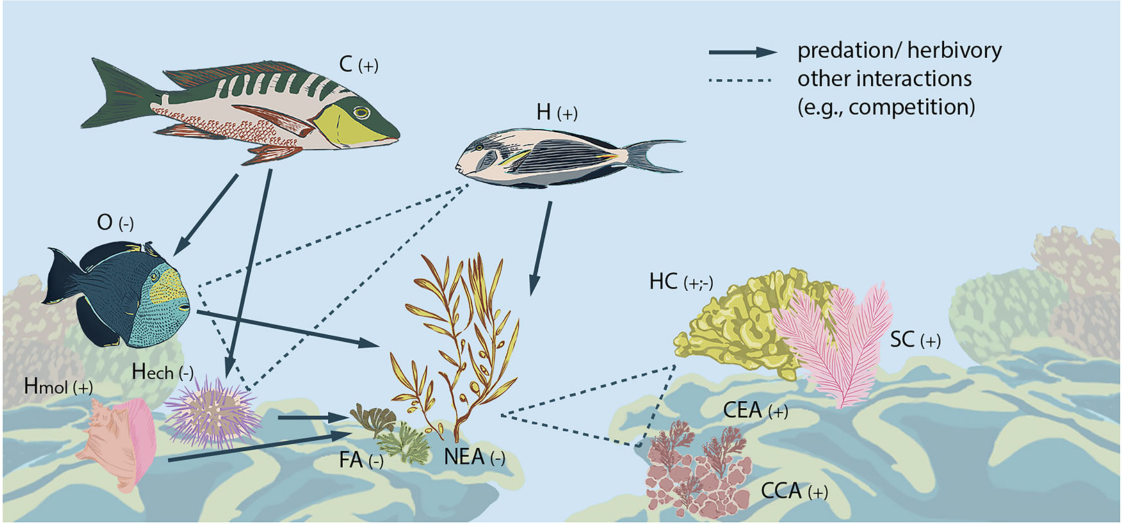

Fig. 4 | Possible interactions explaining the meta-analyses results on tropical reef marine reserves. Notes: C carnivorous fish, H herbivorous fish, Hech herbivorous echinoderms, Hmol herbivorous mollusks, O omnivorous fish, FA foliose and corticated foliose algae, NEA non-calcified erect algae, HC hard coral, SC soft coral, CEA calcified-erect algae, CCA calcified-encrusting algae. Plus (+) and minus (−) symbols mean positive or negative effects. Hard coral had both positive and negative effects for ACI and BA treatments, respectively.

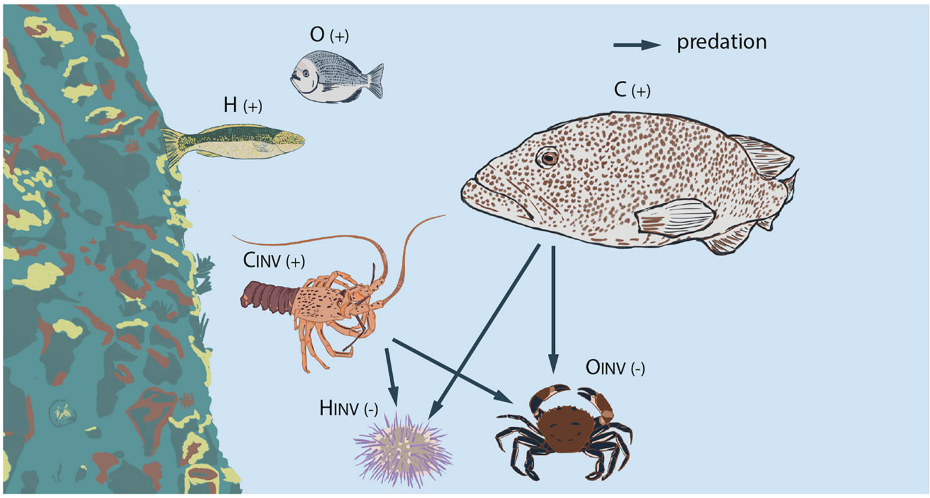

Fig. 5 | Possible interactions explaining the meta-analyses results on temperate reef marine reserves. Notes: C carnivorous fish, H herbivorous fish, O omnivorous fish, HINV herbivorous invertebrates, OINV – omnivorous invertebrates. Plus (+) and minus (−) symbols mean positive or negative effects.

Heterogeneity and publication bias

Considerable variation of biological responses among studies was expected due to marine reserves' different geographical, ecological, biological, and socioeconomic conditions, as well as different approaches in the sampling design and the way that treatment effects were measured. Therefore, we used a random-effects statistical model to consider this heterogeneity (see Section 4.4.3 and Note S1). In general, responses were variable across studies with few exceptions pertaining to meta-analyses with a small number of studies (see results of Q-statistics in Tables S2–S5 and S8–S11).

Egger's regression test indicated funnel plot asymmetry and, therefore, apparent publication bias in the studies included in the meta-analyses assessing several functional categories: hard coral (BA), macroalgae (ACI, BA), foliose and corticated foliose algae (ACI) percent cover, and fish species richness (ACI), for tropical reef marine reserves; and carnivorous fish abundance (ACI) for temperate reef marine reserves (Tables S6, S7 and S12 for tropical and temperate meta-analyses, respectively; further explanations in Section 4.4.2). It should be noted that data asymmetry in funnel plots may also be related to the heterogeneity among effects or even to randomness[41]. Nevertheless, the apparent influence of publication bias in the observed mean effects of original studies with small sample sizes is acknowledged here.

Discussion

This study tested the impact of marine reserve protection in 7 trophic groups and 11 morphological groups of reef communities, of which 10 out of the 18 returned significant effects.

The outcomes of this study highlight the complexity of community responses to full protection by marine reserves (Figs. 4 and 5). Our results suggest, alongside established knowledge on trophic interactions, the presence of top-down effects and competitive mediation between macroalgae and corals. The majority of positive functional group responses to protection coincides with the inclusion of commercially exploited species (i.e., direct reserve effects). This pattern of improved condition of harvested trophic groups was consistent across multiple trophic levels, including predatory fish, predatory invertebrates in temperate reefs, herbivorous fish in tropical reefs, and herbivorous mollusks in tropical reefs. However, our analyses focused on functional groups irrespective of whether the species included were targeted or non-targeted, so distinctions between targeted and non-targeted species were not explicitly tested. Some groups, such as carnivorous fishes, generally include more targeted species than others, and this was considered qualitatively when interpreting results.

In a typical trophic cascade, top predators exert top-down control over smaller prey, such as herbivorous fishes, resulting in increased coverage of primary producers[20]. However, in this study, direct positive effects are also observed for intermediate or lower trophic levels, which may obscure potential indirect effects[19]. This may be due to marine reserves being insufficiently old or large enough for observing this top-down control by carnivores[24]. Nevertheless, this pattern likely reflects a combination of ecological context, species-specific traits (determining susceptibility to predation), behaviors and predator-prey interactions[19].

Our findings show similar trends to both reef types across the globe, as well as distinct responses, reinforcing the understanding that tropical and temperate reef food webs differ in structure and function.

In tropical reefs, fish and invertebrate groups more targeted for human consumption (predatory fish and herbivorous fish and mollusks) responded positively to full protection, regardless of their trophic level. Predatory fish biomass was twice as great inside marine reserves as it was outside, and three-fold compared to the marine reserves' baseline situation, indicating a restoration of top-down control of the ecosystems, which is one of the critical goals of marine reserves[42]. Yet, the recovery of herbivorous fishes was even more remarkable, increasing their biomass by a factor of four within marine reserves relative to fishing grounds and mirroring carnivores in their positive change over time. Both groups are targeted by fishing, which justifies the positive effect in no-take areas, but this does not explain why herbivorous fishes show the strongest response.

One possible explanation found in previous literature is that few reserves are sufficiently large or old to verify a mitigation or reversal of this effect through top-down control by carnivores[24]. In fact, marine reserves with reported biomass measurements for carnivorous and herbivorous fish ($n = 36$), tend to be relatively young and very small (age in years: $\bar{X} = 11.4$, median=7; size in Km^2: $\bar{X} = 23.9$, but median=0.6). Another possibility not confirmed by the studied dataset is that herbivorous fishes may reach larger body sizes inside MPAs than outside, potentially increasing their chances of size refuge from predators, and thereby influencing population dynamics and trophic interactions. Moreover, a recent study on the effects of marine reserves in the Seychelles before and after coral bleaching events[23] found that biomass increases were greater for carnivores prior to the events, whereas herbivores showed greater increases afterward. The authors hypothesized that this shift was related to the colonization of bleached corals by photoautotrophic organisms, which provided a food source for herbivores, while the reduced structural complexity of the reef remained insufficient to support the recovery of carnivores. These hypotheses are not mutually exclusive and may interact to explain the greater recovery of herbivorous fishes within marine reserves compared to carnivores.

Despite extensive local evidence supporting the rapid recovery of herbivorous fishes in tropical reef marine reserves, this is, to our knowledge, the first meta-analysis to reveal this trend at a global scale–showing a biomass increase for herbivorous fishes that is notably greater than that observed for predatory fishes. Previous meta-analyses[22,25,26] assessing marine reserve effects on the abundance or biomass of trophic groups, or on trophic interactions such as herbivory and predation, did not detect this pattern. This may be due to a greater focus on herbivorous invertebrates[25] or the use of density instead of biomass[22,26]. In our study, by segregating the effects by organism type–herbivorous fishes and herbivorous invertebrates–we identified a strong positive effect on the biomass of herbivorous fishes, in contrast to a negative effect for herbivorous invertebrates, namely echinoderms.

The abundance of targeted groups also showed significant positive responses, although these were less significant than those observed for biomass indicators. This may be because increases in biomass can be observed within a single generation – protected individuals would survive longer and grow larger following a fishing ban – whereas increases in abundance typically require longer timeframes, as they depend on reproductive success over several generations[19].

The increase in biomass and abundance of predatory fish may have directly contributed to the observed decrease in the biomass of grazing echinoderms and in the abundance of omnivorous fish (mostly omnivorous pomacentrids), their known prey[43,44]. This association is supported by 10 studies (i.e., marine reserves) assessed here, reporting both predator and prey measurements – three including predator-echinoderm data and seven including predator-omnivore data. Subsequently, these prey groups likely compete with the growing population of herbivorous fish for a decreasing cover of erect non-calcified algae[45].

Different response directions within the invertebrate herbivores group suggest that some indirect effects should be confirmed at the taxonomic level. In contrast to the negative response observed in echinoderms, molluscan herbivores (which include commercial species such as the queen conch, *Aliger gigas*, and *Trochus*) more than doubled their abundance inside marine reserves compared to fished sites. This group should complement the removal of macroalgae by grazing the sporelings of erect algae, which are too small to be consumed by other herbivores and omnivores[46].

Although marine reserve effects were found in tropical and temperate reefs, significant changes in habitat structure, potentially reflecting indirect effects, were observed exclusively in tropical reef marine reserves, with differing responses between coral and macroalgae groups. Presumably, the intensified herbivory by a notable increase of herbivorous fish biomass helped control erect non-calcified macroalgae growth in coral reefs[22]. In turn, decreased coverage of non-calcified macroalgae inside marine reserves promoted coral and calcified algae dominance, probably due to decreased spatial[47] and light[28] competition. Therefore, reserve effects can be observed across three trophic levels as identified by this analysis.

Although this study's findings show robust evidence that hard coral cover was greater inside marine reserves than outside (despite high variability among studies), they also reveal that it diminished over time. This observation is consistent with case studies reporting increased coral bleaching and extreme weather events affecting the most sensitive hard coral species[48,49]. The low number of reported BA and BACI studies may have over-represented sites where extreme conditions prevailed more recently, precluding the recovery of such sensitive species[49]. Only recently have experts started to investigate the potential role of MPAs in increasing ecosystem resilience to climate change[50–53]. Conclusions drawn on their effectiveness in building the resilience of corals to bleaching events are mixed[54–56].

Finally, fish species richness response was positive and significant for ACI and BA studies, reinforcing the broader conclusion that tropical reef marine reserves are fulfilling their purpose of reestablishing marine biodiversity for this group. This finding substantiates a general pattern previously observed, confirming that marine reserve protection often results in higher species richness compared to fished areas. This effect is often linked to the removal of destructive fishing gear and bycatch, alongside the recovery of harvested populations, which can shift community structure in ways that promote greater diversity, depending on species-specific life histories, previous fishing pressure, and trophic interactions across protected and fished areas[19].

In temperate reef marine reserves, top-down interactions were restricted to two consecutive trophic levels. The abundance, biomass, and size of predatory fish increased significantly. Recovered populations of carnivorous fishes usually exert greater pressure on their prey, regardless of the latitude[22], with sea urchins being the prey most affected according to reports. Two prey groups, small omnivorous and herbivorous invertebrates, were consistently less abundant inside marine reserves than outside, differing from the divergent responses found for herbivorous invertebrates in tropical systems. This negative effect was possibly due to higher levels of predation, as suggested by several of the studies reviewed[27,57,58]. Nevertheless, herbivorous invertebrates were larger inside marine reserves[59,60]. The sea urchin *Paracentrotus lividus* (one of the reported species in the studies analyzed) has been harvested in the Mediterranean, which might have contributed to this effect due to size-selective harvest[61]. Studies also pointed to a negative relationship between invertebrate size and density[58] and suggested that smaller individuals are more subject to higher predation rates compared to larger individuals inside reserves[60]. Other included studies covered mollusks of commercial interest[59,62], also contributing to this positive effect.

Predatory invertebrates (mainly commercial arthropods) were also more abundant inside temperate reef marine reserves. These were reported to prey on small invertebrates, and their increase is therefore likely to introduce greater pressure on small invertebrate populations[63,64], contributing to their reduced abundance. Herbivorous fishes also showed a significant positive response over time inside marine reserves, but not when compared to adjacent fished areas. This temporal effect was observed in temperate reef marine reserves in Australia and New Zealand for species targeted by fishing, mostly attributed to sporadic events of strong recruitment pulses[65]. Although some species in this group have commercial value, herbivorous fish did not exhibit a significant positive response in comparisons between marine reserves and fished sites, as in tropical regions. This difference may be attributed to the variable fishing pressure on herbivorous species among temperate reef studies – some were reported as exploited by commercial or recreational fisheries[66,67], while others as rarely targeted or of lower commercial value[27,66,68]. Omnivorous fish abundance returned a positive response inside marine reserves compared to outside. Typically, the species included in this group are not commercial. Whether they benefit directly from protection (bycatch and recreational fisheries) and habitat integrity inside marine reserves or indirectly through trophic interactions therefore depends on the morphological and behavioral idiosyncrasies of the species observed[69].

Macroalgae morphological groups did not respond significantly to protection in temperate reefs. Although the number of studies was lower compared to the most representative trophic groups, some macroalgal functional groups were fairly represented in studies using the ACI design—namely turf algae ($n = 11$), leathery macrophytes ($n = 10$); calcified-encrusting algae ($n = 9$), and foliose and corticated foliose algae ($n = 8$). While the sample size in these meta-analyses does not fully justify the absence of an effect, as proposed in another meta-analytic study[22]— but restricted geographic representation is noted (mainland Australia and Tasmania)— there are various biotic and abiotic factors that could contribute to the lack of statistical evidence. Some sites documented increases in leathery macrophyte species within reserves, while others reported non-reserve related declines or no change. The studies included in our analysis described natural variability, episodes of thermal stress, grazing pressure by range-expanding tropical herbivores[57,70]. These factors suggest that ecological and environmental dynamics can mediate or mask reserve effects on macroalgae, helping to explain the overall inconclusive pattern detected in our analysis. Other factors such as depth and season of data collection[71], increased nutrients at disturbed sites[25,72], and sedimentation[73], have been reported in other studies. Moreover, less abundance and diversity of herbivorous fish compared to tropical reefs and greater dominance of macroalgae cover could result in more selective herbivory in temperate reefs[74–76]. Nevertheless, the abundance of leathery macrophytes is one of the leading indicators of ecological status in temperate reef ecosystems[77], and the outcome of this meta-analysis was close to a positive and significant response. A greater availability of studies on this group might have provided confirmation.

Finally, fish species richness was positive and significant for ACI and BA studies on temperate reef marine reserves, mirroring the pattern observed in tropical marine reserves. Conversely, ACI studies reported lower invertebrates' species richness inside than outside reserves. As for abundance and biomass indicators, we found that an increase in biodiversity following marine reserve protection may not be consistently observed for all organisms and trophic levels. In fact, this reinforces the suggestion that predators' top-down control can potentially lead to lower species richness at lower trophic levels[57].

Meta-analyses require careful interpretation of results due to different sources of bias. In the present study a few meta-analyses (6 in 37) indicated apparent publication bias toward positive (direct effects) and negative (indirect effects) results. Another source of potential bias is that some marine reserves could have been designed and located at healthier sites than their unprotected counterparts, possibly exerting even greater pressure on adjacent unprotected areas that may already be impaired, thereby enhancing their difference[5,78,79]. Therefore, more BA and BACI studies are urgently needed to clarify true protection effects[80], which requires considerable planning and funding.

Our findings are based on a wide spectrum of quantitative studies that report the effectiveness of marine reserves in promoting marine ecosystems' health. This exercise is naturally carried out with heterogeneous representation of the different functional groups, which is inherent to the gaps to be filled in by individual studies. Species representation in the selected studies depended mostly on their commercial interest, or on their role in top-down interactions impacting the food web, as in the case of sea urchin predation by benthic carnivores. The marine reserve effects reported on trophic groups need to be better documented compared to species-level studies, which focus mostly on commercial species of high trophic level. Invertebrates are key for interpreting changes in the ecosystem structure, as they have a place in and interact with various trophic groups[81]. Despite their importance, they are often overlooked in the literature. In tropical reef marine reserves, herbivorous shell-forming mollusks and sea urchins had mixed responses to protection, showcasing the complexity of morphologies and functional roles of invertebrates and the importance of improving data coverage for these organisms. Increasing attention to groups representing lower trophic levels (e.g., filter-feeders) is desirable to capture other relevant dynamics from the complex food webs[82]. Moreover, this study does not directly examine trophic interactions. Consequently, interpretations regarding marine reserve effects on trophic interactions were based on previous studies, especially those included in the meta-analyses. Finally, open data would be critical for the development of high-quality meta-analyses and more profound and substantiated reviews on this matter.

Our findings add new layers of knowledge over previous studies[12,16,22,83], providing a more comprehensive review of trophic and morpho-functional groups' responses to marine reserve protection and straightforward and unambiguous interpretations of the reported effects on reef communities and habitat structure. As marine ecosystems' structure and functions are upstream of ecosystem services[22], this study also provides a clearer vision of how marine reserves contribute to the enhancement of ecosystem services.

The primary objectives of marine reserves are to restore biodiversity and recover commercial fish populations in abundance, biomass, and individual size. Nevertheless, other natural, socioeconomic, and cultural values are now receiving increased consideration, especially as diverse groups of MPA stakeholders are being invited to the table in MPA design and management processes[10,84,85].

Effective marine reserves restore biodiversity and biomass and reestablish interactions and functions across trophic levels, keeping food webs robust and contributing to a healthier and more productive environment[22]. According to the effects studied, marine reserves in tropical and temperate reefs ensure the long-term continuity of ecosystem services, such as: food provision (increased abundance, biomass, individual size and, thus, greater reproductive capacity and recruitment of commercial groups[86]); diversification of food resources (increased species richness and the restoration of habitats and upper trophic levels enhancing the complexity of food webs[87]); coastal protection and refugia (coral reef recovery by maintaining habitat integrity and top-down control of macroalgae growth[28,74,88]); "blue carbon" storage and sequestration (recovery of calcifying organisms, namely increased hard coral cover); and opportunities for enhancing livelihoods and economies (e.g., improved fishing and marine tourism revenues) as well as recreation, cultural heritage and sense of place (e.g., increased species richness and individual size of iconic predatory fishes and intact coral reefs)[86,89,90].

Coral reefs were reported to be in better condition inside marine reserves than outside, offering more complex, biodiverse, and resilient ecosystems. Marine reserves have the potential to mitigate and promote adaptation to climate change[88]. However, despite protection efforts, hard coral cover seems to be diminishing over time.

With climate change hampering to some degree the effectiveness of marine reserves, studies on the resilience/ vulnerability of ecosystems to climate change are increasingly important[23,91]. Combining climate data with historical and current monitoring data and understanding marine reserves' effects on the marine communities' trophic structure is critical to informing the future design and management of marine reserves, as interactions within food webs determine how ecosystems react to both the loss of biodiversity and climate change[92]. This information contributes to evidence-based decision-making on conservation strategies, providing the tools to foresee chain reactions that may arise from human impacts or climate change and identify management priorities[93]. Though the impacts of climate change are global and impossible to manage directly[94], actions for their mitigation and adaptation can be delivered locally[88].

Marine reserves' conservation objectives extend beyond the protection of biodiversity and commercial species populations. Their objectives now include restoring ecosystem functions and services[95], and more recently, climate mitigation and adaptation. In this sense, it is important to assess biological communities as a whole and evaluate the impact on food webs and the stability of ecosystems. The use of functional groups allows a clear interpretation of the dynamics between trophic levels and the impacts of conservation on their structure. MPA monitoring research would therefore benefit from more integrated and holistic approaches to generate more robust and consistent evidence for the various functional groups. Naturally, this means more investment in monitoring to assess and guarantee MPA effectiveness.

Methods

Selection of studies

We conducted a systematic review considering the PRISMA reporting guidelines (see Tables S15, S16)[96,97]. Reviewed papers had to report on biological effects of marine reserves in reef ecosystems for different trophic groups of fish and invertebrates, and morpho-functional groups of algae and corals. We searched for relevant key terms to obtain and refine a comprehensive and significant sample of studies on the topic[98]. In order to ensure quality, only peer-reviewed studies were considered. The online search was performed on 13 May 2020 in the Web of Science database. Searches for topic (TS =) terms were done in the title, abstract, and keywords, using the following research keys:

1. TS = (marine reserve* OR no-take OR no-go OR sanctuar* OR refugia) AND TS = (reef*) AND TS= (fish* OR invertebrate* OR *alga*) AND TS = (effect* OR change*) NOT TS = (freshwater OR estuar* OR river* Or mangrove*). [$n = 1943$]
2. TS= (marine reserve* OR no-take or no-go OR sanctuar* OR refugia) AND TS= (trophic OR cascade) AND TS= (effect* OR change*) NOT TS= (freshwater OR estuar* OR river* OR mangrove*). [$n = 1407$]

To avoid the repetition of studies, we used the Boolean operator "OR" between the selected research keys and searched them together, returning 3108 papers. One author (M.C-A) screened these papers' titles and abstracts. Based on Lester et al.[11] and Sciberras et al.[15], we used the following 8 eligibility criteria to retain studies:

1. Studies should compare marine reserves (no-take MPAs) to fished sites (areas open to fishing or general use zones/buffer zones exposed to intensive fishing activities) or time series inside marine reserves if reference data were available close to the implementation year (up to one year after the reserve implementation date mentioned in the studies, sometimes different from its establishment date).
2. Assess protection effects on reef communities—species or groups of species of macroalgae, coral, and other invertebrates, and fishes.
3. Provide data on at least one of the following variables: abundance (density or MaxN for studies using BUV/BRUV sampling method), biomass, size, or species richness.
4. Make complete data available—means, sample sizes, and error measures (standard deviation, standard error, or 95% confidence intervals) —in the text, tables, or graphics[99].
5. When different studies were reported for the same MPA, the one with the most recent survey data was selected. If these were surveyed in the same year, results were averaged following the rules explained in Section "Data processing".
6. If a study presented more than one sampling event after MPA implementation, only the most recent event was retained, in order to account for the longest protection period. When the most recent sampling event was during or shortly after some extreme weather event (e.g., typhoon), data were from the year before that event.
7. Studies assessing multiple marine reserves or MPA networks were considered if data were detailed for each marine reserve; if these studies reported only aggregated data they were excluded. The Great Barrier Reef Marine Park (GBRMP) was an exception because it is managed through a zoning plan in which no-take reefs are numerous and is thus often assessed by island groups (e.g., Keppel, Palm, and Whitsunday Island groups).
8. Data from only unmanipulated environments were extracted from studies conducting experiments.

The screening of titles and abstracts resulted in the selection of 588 studies (ca. 19%) as potentially relevant. The studies' full texts were read to ensure they met all the eligibility criteria, resulting in a sample of 99 studies (ca. 3% of the studies returned by the search strings). The process is reported in a PRISMA diagram in Fig. S1.

Data collection

One author (M.C-A) collected data from graphs (68%, using the GetData Graph Digitizer Version 2.26), tables (29%), and the main text (3%). If studies did not identify the taxa's corresponding trophic groups, the information was searched for in papers focused on diet tracing or biodiversity online datasets, such as "FishBase"[100], "SeaLifeBase"[101], and "AnimalDiversity"[102]. Algae's functional groups were the ones proposed by Steneck and Dethier[103], based on anatomical and morphological characteristics that influence productivity and disturbance (herbivory) sensitivity.

Sampling designs employed to test MPA effects include After-Control-Impact (ACI), Before-After (BA), and Before-After-Control-Impact (BACI) designs. ACI designs are the most commonly employed because they are the least subjected to planning, funding, and effort constraints, but provide a lower capacity to detect true reserve effects because of pre-existing ecological differences between the protected and the control areas. Both BA and BACI designs can detect ecological changes in the designated sites through time, which are essential to distinguish between naturally induced changes and protection effects[104], but BACI designs analyze ecological response variables considering both temporal and spatial variability and are considered the most informative analytical approach to assess MPA effectiveness[15].

Data processing

Because studies directly assessing marine reserve effects on functional groups were limited, we included studies focusing on individual species and subsequently classified them into functional groups.

When each individual study provided abundance or biomass for different taxa, genera, or size classes belonging to the same functional group, the means for the indicator were summed to provide the mean effect on that functional group. In these cases the variance was obtained as the sum of the variances for each taxa, genera, or size class, except when it was possible to compute the correlation coefficients, in which case the more precise Eq. (1)[105] was used:

$$Var\left[x_1 + \ldots + x_k\right] = \sum_{i=1}^{k} \sigma_i^2 + 2\sum_{i<j}\sum \rho_{i,j}\sigma_i\sigma_j \tag{1}$$

where σ_i^2 are the variances for each species or size class, etc., $\rho_{i,j}$ are the correlation coefficients, and $\sigma_i \sigma_j$ the product of the standard deviations of each possible pair.

If data in individual studies were for different sampling events (e.g., different sites, depths, or seasons), we computed the weighted average of their means. When the data were on organism size, unweighted averages of the means were calculated. In these cases we used Eq. (2), derived from the definition of variance[105], $Var[x] = E[x^2] - (E[x])^2$, to compute the total variance:

$$\sigma_T^2 = \frac{1}{n_T}\left(\sum_{k=1}^{N}\left(\left(n_k - 1\right)\sigma_k^2 + n_k \bar{x}_k^2\right) - n_T \bar{x}_T^2\right) \tag{2}$$

where n_T is the sum of the sample sizes of each sampling event (n_k) and $\bar{x}_T$ is the weighted average of the means of each sampling event ($\bar{x}_k$).

Meta-analyses

Meta-analysis is a statistical method used to combine evidence of treatment across studies[96,106]. It allows for estimating an average treatment effect size and testing the variation of effect magnitudes obtained by each analysis[107]. Marine reserve effects were assessed separately for tropical and temperate reef marine reserves[11]. Doing so, accounts for possible latitudinal variation in food web structure resulting from different levels of diversity and complexity of food webs, energy levels, inert (rocky) versus biogenic (coral) substrates, and sources of anthropic pressure.

For the ACI and BA designs, effect sizes were computed using the log-response ratio and the effect size variance formulas in Eqs. (3) and (4), provided by Hedges et al.[108]:

$$RR_{ijk} = \ln \frac{X_{ijk}{}^{\mathrm{T}}}{X_{ijk}{}^{\mathrm{C}}} \tag{3}$$

$$\sigma_{ijk}^2 = \frac{\left(\sigma_{ijk}^T\right)^2}{n_{ijk}^T\left(\bar{x}_{ijk}^T\right)^2} + \frac{\left(\sigma_{ijk}^C\right)^2}{n_{ijk}^C\left(\bar{x}_{ijk}^C\right)^2} \tag{4}$$

where RR_{ijk} is the log-response ratio for study i (i.e., marine reserve), functional group j (trophic or morphological) and organism k (fish, invertebrate, or macroalgae), $X_{ijk}{}^{\mathrm{T}}$ is the mean of the treatment group (i.e., after the marine reserve implementation for the BA design; and inside the marine reserve for the ACI design), $X_{ijk}{}^{\mathrm{C}}$ is the mean of the control group (i.e., before the marine reserve implementation for the BA design; and outside the marine reserve for the ACI design), σ_{ijk}^2 is the variance of RR_{ijk}, n_{ijk}^T and n_{ijk}^C are the sample sizes of the treatment and control groups, and σ_{ijk}^T and σ_{ijk}^C the error measures (standard deviations).

For the BACI design we used the response ratio proposed by Lester et al.[11], in which the BA ratio inside is divided by the BA ratio outside the marine reserve (Eq. (5)). The BACI's effect size variance was the sum of the nominator and denominator ratios' variances, computed using Eq. (6).

$$RR_{ijk,BACI} = \ln\left(\frac{\dfrac{X_{ijk}{}^{after-inside}}{X_{ijk}{}^{\mathrm{before-inside}}}}{\dfrac{X_{ijk}{}^{\mathrm{after-outside}}}{X_{ijk}{}^{\mathrm{before-outside}}}}\right) \tag{5}$$

$$\begin{aligned}\sigma_{ijk,BACI}^2 = {} & \frac{\left(\sigma_{ijk}^{after-inside}\right)^2}{n_{ijk}^{after-inside}\left(\bar{x}_{ijk}^{after-inside}\right)^2} + \frac{\left(\sigma_{ijk}^{before-inside}\right)^2}{n_{ijk}^{before-inside}\left(\bar{x}_{ijk}^{before-inside}\right)^2} \\ & + \frac{\left(\sigma_{ijk}^{after-outside}\right)^2}{n_{ijk}^{after-outside}\left(\bar{x}_{ijk}^{after-outside}\right)^2} + \frac{\left(\sigma_{ijk}^{before-outside}\right)^2}{n_{ijk}^{before-outside}\left(\bar{x}_{ijk}^{before-outside}\right)^2}\end{aligned} \tag{6}$$

Random-effects meta-analyses were computed individually for each combination of indicator (i.e., combination of variable, organism, and functional group) and monitoring design using the weighted mean effect size formula (Eq. (7)[108,109]):

$$\overline{RR}_{jk} = \frac{\sum_{i=1}^{mjk} w_{ijk} RR_{ijk}}{\sum_{i=1}^{mjk} w_{ijk}} \tag{7}$$

where mjk is the number of studies included for functional group j of organism k, and w_{ijk} is the weight of each study. The weight of each study (w_{ijk}) is determined by Eq. (8)[108,110]:

$$w_{ijk} = \frac{1}{\sigma_{ijk}^2 + \sigma_{among}^2} \tag{8}$$

where σ_{ijk}^2 is the within-study variance (Eq. (4)) and σ_{among}^2 is the among-study variance, estimated using the Restricted Maximum Likelihood (REML) method.

Total heterogeneity was calculated using the Cochran's generalized Q-statistic (Eq. (9)[111]), following an χ^2 distribution with $mjk - 1$ degrees of freedom. Among-studies variance was estimated using the Restricted Maximum Likelihood (REML) method, the most consensual in simulation studies[112–114].

$$Q_t = \sum_{i=1}^{mjk} w_{ijk}\left(RR_{ijk} - \overline{RR}_{jk}\right)^2 \tag{9}$$

All meta-analyses were computed using R package 'metafor'[114,115]. The reasoning behind the choices of this meta-analysis is explained in detail in Note S1.

Assumptions regarding species interactions, interpreted from the responses of functional groups to protection, were based on evidence from peer-reviewed studies identified during the systematic review, ensuring that only well-supported ecological relationships were considered.

A meta-analysis is a statistical method that combines several treatment results – in this study, the results of published peer-reviewed papers. Because of this, in addition to the various forms of bias that can be introduced during the meta-analysis process (including the search, selection, and combination of studies[31]), publication bias will likely interfere with the results[116]. Publication bias arises from studies presenting significant and "positive" (or desirable) results being submitted and accepted for publication more often[117]. To assess the risk of publication bias, we (1) used contour funnel plots[118], i.e., scatter plots of effect sizes (X-axis) against the standard errors (Y-axis with values displayed in descending order), for a visual assessment and (2) the Egger's regression test for a quantitative assessment of funnel plot asymmetry (regtest {metafor}[116,119]).

Non-independence of data is a common issue when dealing with ecological data[110]. We avoided some potential forms of non-independence originated from within-study data correlation by aggregating into one effect-size estimate when a set of replicates was presented. However, we chose to accept other sources of non-independence affecting between-study variability to avoid rejecting sources of relevant information that were already scarce for some functional groups. This occurred when papers presented results for more than one marine reserve, i.e., observations on different reserves were made by the same research team and entered into the dataset as different studies.

Moreover, although rare in the dataset (ca. 4% of the studies included), papers comparing more than one marine reserve to the same unprotected site (control) were included, and each comparison treated as an independent study. Otherwise, limiting each study to one treatment-control comparison would result in a loss of information and statistical power[120]. It would also require the selection of one of the reported marine reserves, which could introduce bias into the meta-analysis[121]. On the other hand, averaging these marine reserves' treatment data (as described in Section 4.3 Data Processing) would assure the independence of effect-size measures but remove valuable information, as different marine reserves represent distinct environmental, social, and cultural conditions. Nevertheless, in order to test how choosing to pool these marine reserves' effect sizes affected the results[122], we also used this last method (as described in Section 4.3 Data Processing)[76]. Meta-analyses with pooled reserves (Table S14) presented effects and conclusions similar to those using the option of treating the data as separate independent observations. The only exceptions were for the percent cover of foliose and corticated foliose algae (tropical reefs) and the size of herbivorous invertebrates (temperate reefs), which became not significant (ACI: $\overline{RR}_{pooled} = -0.69, p = 0.06, \overline{RR}_{pooled} = 0.22, p = 0.09$, respectively).

Data availability

The dataset generated for all meta-analyses in this study are available in the DUnAs data repository from the University of Aveiro under https://doi.org/10.48527/FGRRCE and is publicly available as of the publication date. [https://dunas.ua.pt/privateurl.xhtml?token=5f3a288e-60df-4eb0-bdb3-f50b61e5071d].

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Author contributions

M.C-A. contributed to this paper's conception, design, methodology, data analysis, and writing (original draft, review, and editing); B.H.C. contributed to the conception, design, methodology, data analysis, and writing (review and editing); A.H. contributed to data analysis; J.M.S.G. contributed to the conception, design, methodology, and writing (review and editing); and H.Q. contributed to the conception, design, methodology, data analysis, and writing (original draft, review, and editing).

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Mariana Cardoso-Andrade.