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Kelp forests as nursery and foundational habitat for reef fishes

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Abstract

Conservation of marine biodiversity requires an understanding of the habitats needed to support and replenish species of interest. It also requires knowledge about the abundance and diversity of multispecies assemblages. Variation in the distribution and composition of kelp forests, one of the most productive marine coastal habitats globally, can have major influences on reef fishes—a group of ecologically and socioeconomically important species. In the face of widespread and escalating loss of kelp forests, quantification of these effects is urgently needed to assess and project cascading impacts on biodiversity. Here, we evaluate relationships between kelp forests and associated reef fish populations using a global meta-analysis of experimental kelp removals and comparative surveys of kelp and adjacent non-kelp habitats. These analyses show that kelp forests increase the abundance of reef fishes, though the significance of this effect varied depending on the structural complexity of kelp forests. In experimental

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studies, kelp forests have a significant positive effect on fish species richness, revealing that kelp act as true foundation species by supporting the diversity of associated multispecies assemblages. Importantly, regardless of kelp forest morphology and type of study (observational or experimental studies), kelp forests enhance the recruitment of early life history stages suggesting they are nursery habitats for many reef fish taxa. Lastly, kelp forests differentially affected species with different functional traits; small body size fishes from low trophic levels (e.g., herbivore and detritivores, micropredators, and mesopredators) and large body size fish from higher trophic level (e.g., piscivores, general carnivores) were both facilitated by kelp forests. Taken together, these results indicate that the loss of kelp forest, particularly those with more complex morphology, can reduce total abundance and diversity of fish, with possible cascading consequences for coastal ecosystem function.

KEYWORDS

global change, habitat complexity, kelp beds, recruitment temperate reefs

INTRODUCTION

The importance of biodiversity for humanity is irrefutable in the Anthropocene (Cardinale et al., 2012; Mace et al., 2012). Foundational habitats—species that create biogenic structure—such as coral reefs, seagrass beds, and algal forests, support whole assemblages and ecosystem function, making their conservation a priority for broader biodiversity conservation (Ellison et al., 2005). However, our understanding of the dynamics and function of foundation species is still limited (Edgar et al., 2023; Wernberg et al., 2016). Increasing our knowledge of how the loss of foundation species may influence the diversity and functioning of coastal assemblages is particularly critical in temperate marine environments due to a persistent lack of monitoring programs that identify causes of variation at spatial and temporal scales relevant to management and conservation, despite tremendous advances made in recent times (Edgar et al., 2023). Habitat loss is one of main drivers of marine species extinction (Crain et al., 2008; Lotze, 2021). Recent reports revealed that 67% of wetlands, 65% of seagrasses, and 48% of other habitat-forming aquatic vegetation have been lost over the past decades. The loss of important foundation species can have major ecosystem-level consequences and is associated with regime shifts from complex, productive, and highly diverse habitats to simpler, less productive and diverse ones (Folke et al., 2004; Hughes et al., 2003). These shifts occur because suitable habitat is essential to the ecological and evolutionary success of most organisms (Airoldi et al., 2008; Fulton et al., 2020; Kramer & Chapman, 1999).

Of the nearly 22,000 known species of marine fishes, many are of critical ecological and/or of are economic importance. In general, habitat attributes can shape local population densities (Choat et al., 1988; Curley et al., 2002; Tuya et al., 2009), survival rates (Anderson & Underwood, 1994; Tolimieri, 1995), dispersal patterns, and recruitment dynamics (Anderson, 1994; Carr, 1989, 1991, 1994; Jones, 1984; White & Caselle, 2008). Biogenic habitats such as macroalgal forests can provide refuge from predators and food, either directly or indirectly, by supporting high local productivity and/or concentrating prey (e.g., Edgar, Barrett, & Morton, 2004; Edgar, Barrett, Morton, & Samson, 2004; Norderhaug et al., 2007; Taylor, 1997, 1998; Winkler et al., 2017). Similarly, positive links and feedback loops from fishes to habitat-forming organisms (e.g., kelp) have been described, as some fishes may facilitate the persistence of marine vegetation via consumption of macroalgal grazers (Cowen, 1983; Davenport & Anderson, 2007; Pérez-Matus & Shima, 2010a) and some species of herbivores can act as potential kelp zoospore disperser (Ruz et al., 2018). In contrast, many fishes utilize complex habitat but do not provide benefits to habitat-forming species (Taylor & Schiel, 2010).

Understanding the processes that maintain reef fish populations and assemblages, and their interactions with different foundation species such as coral, seagrass, and kelp, is critically needed in the context of assessing, anticipating, and mitigating the impacts of global change (Bosch et al., 2022). Given that the distribution and local abundances of ecologically and/or economically important fish species may depend upon suitable habitat, a mechanistic understanding of the effects of different

habitat components on population demography and fish assemblages is essential for predicting the impacts of habitat loss and informing the management and/or conservation of coastal fish species and communities (Bosch et al., 2022). Large brown seaweeds are conspicuous inhabitants of most temperate rocky coasts that can dominate reef scapes to form kelp forests (Dayton, 1985; Wernberg et al., 2019; Wernberg & Filbee-Dexter, 2019). While “kelp” technically refers to species of the order Laminariales, we use the term “kelp forests” to encompass marine macroalgal forests comprised of species within the orders Laminariales and Fucales (Wernberg & Filbee-Dexter, 2019). In total, with more than a dozen of forest-forming species, which vary in size, morphology, and life span (Wernberg & Filbee-Dexter, 2019). These species are particularly abundant where the water temperature is generally lower than 20°C, often forming dense stands, with individuals of some species reaching more than 30 m in length (Schiel & Foster, 2006). Laminarian forests are estimated to cover 36% of the world's coastlines (Jayatilake & Costello, 2021).

Kelp forests provide an important three-dimensional habitat structure in subtidal environments and are typically highly productive (Pessarrodona et al., 2022) and sustain some of the most diverse and dynamic ecosystems on earth (Miller et al., 2018; Teagle et al., 2017). Their holdfasts represent areas for feeding, refuges from predators, and settlement habitats for a variety of organisms (Schuster & Konar, 2014; Teagle et al., 2017; Vasquez & Buschmann, 1997; Winkler et al., 2017) and numerous epifauna occur in their fronds and stipes, which collectively provide a link to higher trophic level species such as fishes (Kingsford & Choat, 1985). Kelp also contributes to the multiple vertical layers of structure (surface canopy, sub-canopy, understory) in a forest, exerting differential influences on species within the reef fish assemblages (Holbrook et al., 1990). The varying heights and densities of kelp create microhabitats that cater to the specific needs of different fish species, thereby impacting their distribution, behavior, and ultimately their abundance and diversity within the ecosystem (Holbrook et al., 1990; Villegas et al., 2018).

Underwater grasses and mangroves significantly enhance the density and growth of juvenile reef fishes compared with other structured habitats (Lefcheck et al., 2019). Recent reviews emphasize the importance of underwater vegetation, not only as nurseries but also as mosaic habitats that enhance fisheries (Fulton et al., 2020; Lefcheck et al., 2019). However, there is a notable lack of evidence from various other systems, such as kelp forests, and for responses beyond the density of reef associated fishes. In kelp ecosystems, the relationship between the number of stipes/fronds (multi vs. single stipes) and the

height of a kelp species plays a crucial role in conferring structural complexity (Norderhaug et al., 2007). This complexity affects the forest environment by influencing factors like light availability and water flow and provides nursery habitat for certain fish species. For instance, studies investigating the effects of tall surface canopy-forming kelps (e.g., *Macrocystis*) on fish recruitment have shown that these kelps offer not only structural refuge from predators but also spatial refuge allowing juvenile fish to grow and reduce their vulnerability based on size before transitioning to the reef surface (Love et al., 1991).

Specific macroalgal features and their role as habitat for associated reef fish vary over small spatial scales (Connell & Irving, 2008; Graham, 2004), depending on local environmental conditions (e.g., degree of wave exposure), herbivory, competition, or may be a function of the phenotypic traits of the macroalgae themselves (e.g., the number of stipes or fronds, and whether individual seaweeds occur in monospecific or mixed canopy stands) (Goodsell et al., 2004). Specific macroalgal traits may act in synergy to shape patterns of fish distribution and abundance but the global context is not well understood (Wernberg, 2005). Consequently, macroalgae likely offer multiple functions that combine to determine overall “habitat quality,” which may affect fish species depending on foraging mode (collectively known as trophic level) and ontogeny (Mulders et al., 2022; Tuya et al., 2009). While some species may be uniquely linked to a certain habitat type, such as many coral reef associated species, habitat-associations may also vary with life cycle stage, with planktonic larvae settling into an initial habitat before migrating to different habitats as juveniles and/or adults (Wilson et al., 2022). Evaluating the role of kelp forests as nurseries—where density, growth, survival, and/or movement are on average greater than other habitats (Beck et al., 2001; Lefcheck et al., 2019)—is crucial, especially in light of potential loss of this foundational species.

For temperate rocky reefs, the loss of kelp species has become increasingly common, including in Western Australia, Tasmania, Japan, USA, and Europe (Beas-Luna et al., 2020; Bosch et al., 2022; Edwards et al., 2020; Krumhansl et al., 2016; Verges et al., 2014; Wernberg et al., 2019). The ecosystem-wide consequences of kelp loss are not well understood, despite their value for biodiversity and provision of ecosystem services (Eger et al., 2023). Community structure and function may change drastically following foundation species loss (Graham, 2004; Metzger et al., 2019; Smith et al., 2024; Srednick & Steele, 2022; Wernberg et al., 2016). However, once foundation species are lost, fish assemblages could shift and compensate as new formerly outcompeted species begin to create new habitats (also helped by habitat determiners such as sea urchins; see Ling et al., 2015).

Therefore, here we ask how will communities shift if the current dominant foundation species decline in abundance? Niche requirements in the use of macroalgal stands, variation in the distribution and abundance of food (associated macroalgal epifauna) among algal elements, and different types of refugia provided from predators (particularly for recently recruited fish) vary as a consequence of complexity of the habitat utilized by different fish species (Bosch et al., 2022; Deza & Anderson, 2010; Norderhaug et al., 2005; Pérez-Matus & Shima, 2010a, 2010b). Determining which habitats can sustain the diversity of fish species, their abundance, trophic groups, and how this function may vary during ontogeny is poorly understood. A comprehensive understanding of fish-kelp associations is crucial to inform management and prioritize kelp forests species and characteristics in conservation planning.

To fill this knowledge gap, we conducted a meta-analysis of published studies to define relationships between kelp forests and reef fish diversity, abundance, juvenile density, structural complexity influences, and the specific impacts on different size and trophic groups of reef fishes. Specifically, we addressed the following questions: (1) does the presence of kelp forests increase total reef fish species richness and/or abundance? (2) Do kelp forests influence the density of reef fish fishes at juvenile stages? (3) How does the structural complexity within kelp forests influence these patterns? (4) Which size classes and trophic groups of reef fishes are facilitated by kelp forests?

MATERIALS AND METHODS

Review methods

We searched multiple electronic bibliographic databases (web of Science, ASFA, Google Scholar), with the following terms: “macroalga(e)” and “fish(es),” “seaweed(s),” and “fish(es),” “kelp” and fish(es), “kelp forests (and beds) and fish(es).” The last search was conducted on 2 December 2022. We divided the records identified through database searches and records from other sources including references from the studies identified through the database searches. Personal reference collections and colleagues with active research interests in these areas were also included. We recorded the total number of studies for screening (>100 studies). We reviewed studies that manipulated habitat and subsequently sampled fish that were published to the end of 2020. In addition to manipulative experiments, we also reviewed observational studies that measured and compared the natural variability in fish(es) metrics

(abundance, species richness, and functional diversity) in kelp and non-kelp forests (i.e., urchin barrens, sponge gardens, turf algae, and sand).

Data extraction

For articles that met selection criteria (Appendix S1: Table S1), we recorded type of study (experimental or observational), mean species richness, total species abundance, and/or abundances of single species in either treatments (kelp control versus removal) or habitat type (kelp forest versus non-kelp forest), sample size of groups, and variance in order to estimate the effect of kelp on fish. Where possible, we noted the ontogenetic state of fish assemblages or single species assessed (e.g., young of the year [YoY] or settlement phase, juveniles and/or adults). Individual values from most articles were found in graphs such as scatterplots and bar plots in which case webplotdigitizer was used for translation of plots into numerical values (Rohatgi, 2020). Articles that did not provide relevant means, measures of variance, or other values in tables, means plots, boxplots, or scatterplots were not used in this meta-analysis (Appendix S1: Table S1).

Fish and kelp trait data

Where possible, we recorded information about fish trophic groups and size to assess the variability of the effects of fish on kelp. The functional roles of reef fish species may be described using broad trophic groups or exploring more detailed information on traits (Micheli & Halpern, 2005; Mouillot et al., 2007, 2014; Pérez-Matus et al., 2022). We extracted trait data for individual fish species from FishBase using rFishBase (Boettiger et al., 2012; Froese & Pauly, 2014) (Appendix S1: Table S2). We categorized species into the following trophic groups: planktivores, herbivores and detritivores, omnivores, benthic microcarnivores (feeding predominantly on small epifauna), benthic macroinvertebrates, and general carnivores (including piscivores). These groupings were applied broadly to ensure compatibility across studies and were based on available dietary information for all taxa, irrespective of their taxonomic resolution. To simplify comparisons, we grouped species into broader categories: herbivores, mesopredators (including benthic microcarnivores, macroinvertebrates, and omnivores), and top predators (representing general carnivores, including piscivores). These classifications reflect trophic-level distinctions relevant to ecological analyses and comparisons across different datasets. We also recorded maximum total length (TL) and a continuous measure of fish trophic level.

To assess the effects of kelp structural complexity on fish, we grouped kelp according to their numbers of stipes as single (i.e., *Ecklonia*) or multi-stipe (i.e., *Macrocystis pyrifera*) (Appendix S1: Table S3). Studies spanned a total of 17 different kelp species: 13 Laminarian species (*M. pyrifera*, *Ecklonia radiata*, *Saccharina latissima*, *Laminaria digitata*, *L. farlowii*, *Eisenia arborea*, *Egregia menziesii*, *Nereocystis luetkeana*, *Pterygophora californica*, *Lessonia trabeculata*, *Undaria pinnatifida*) and 4 Furoid species (*Carpophyllum maschalocarpum*, *Carpophyllum flexuosum*, *Cystophora racemosa*, *Cystophora retroflexa*). Some studies (experimental and/or observational) have compared a complex set of kelp species against habitats devoid of kelp forests. When two kelp species with different morphologies were studied, we categorized the study using the species that was more structurally complex (see Appendix S1: Table S3).

Effect size calculation and analysis

For each study that provided the needed data, we calculated Hedges' g (Hedges, 1981) using the following formula:

$$\text{Hedges}'g = \frac{\text{Fish}_{+ \text{ kelp}} - \text{Fish}_{- \text{ kelp}}}{\text{Pooled } \sigma},$$

where $\text{Fish}_{(+ \text{ or } -) \text{ kelp}}$ is the mean of the treatment group (either observational or experimental) and σ is the pooled variance (SD). Effect sizes were corrected for small sample sizes according to Hedges and Olkin (1985). Therefore, a smaller sample size moderates the estimated effect size aiding the control for different sample sizes across observational and experimental studies.

Statistical analysis

For all analyses, we fit variance weighted mixed meta-regression models with the relevant Hedges' g , as our response and a set of predictors depending on the question being answered. Models were fit using the metafor package (Viechtbauer, 2010) in R 4.2.3 (R Core Team, 2024). For all analyses, we fit models with random effects of study and site within study to adjust for nonindependence of having multiple measurements per study. We used a heterogeneous compound symmetric approach to variation within these groups (e.g., in addition to residual variance between studies, we also modeled variance within studies with measurements

assumed to be correlated). For the individual species model, we assumed a variance component due to species rather than site. The calculation of the standardized mean difference (SMD) is a measure used in meta-analyses and other contexts to quantify the size of the difference between two groups: Group 1 (e.g., kelp) with $n1_i$ subjects, mean $m1_i$, and SD $sd1_i$. Group 2 (e.g., non-kelp) with $n2_i$ subjects, mean $m2_i$, and SD $sd2_i$. The difference in means between the two groups is $(m1_i - m2_i)$. The pooled variance (SD) was calculated based on

$$\text{Pooled } \sigma = \sqrt{\frac{(n1_i - 1) \times sd1_i^2 + (n2_i - 1) \times sd2_i^2}{n1_i + n2_i - 2}}.$$

To determine the effect of kelp on the measure of effect size for (1) total adult reef fish abundance, (2) species richness of adult fish, and (3) total abundance of juvenile or YOY fish, we ran three models for each group. We first examined whether total effect size differed between experimental versus observational studies. We then looked at whether effect size differed between single versus multi-stipe, and multiple kelp species for experimental data only. We then did the same kelp morphology analysis for observational data only. To assess whether spatial scale of a study mattered for these metrics, we evaluated each category of response variable to see if clearing or patch size created additional heterogeneity. Additional predictors (regarding blade width, surface vs. subsurface canopy, ecoregion, etc.) were not included in the analyses as were either too collinear with single versus multi-stipe or have too small of a sample size to produce meaningful results.

For analysis of the abundances of adult individual species, we carried out a meta-regression using only data from experiments with trophic level and fish maximum length as predictors of effect size to assess the causal effects of kelp on these traits within fish assemblages. Visually, we present this below by binning fish into trophic groups for ease of understanding. To explore whether the effects of kelp removal (or addition) on fish species richness and abundance change over time, we performed an analysis using experimental data, with the duration between kelp removal (or addition) and subsequent fish censuses as primary predictor variables. Specifically, we evaluated whether "Time Until Resampling" influenced effect sizes for fish species richness, total abundance, and juvenile abundance. This allowed us to assess whether the time elapsed after a habitat disturbance (kelp removal/addition) had any measurable impact on fish assemblage response.

RESULTS

Literature search and study selection

The different internet searches and initial searches resulted in 32,000 independent studies from 1960 to 2020. All of these were reviewed and resulted in 90 studies that evaluated fish species richness and/or abundance and/or single species abundance under the presence of kelp forests. To conduct the quantitative meta-analysis we considered irrelevant studies that (1) lacked replication (in both experimental or observational experimental designs), (2) lacked reported variation and effect sizes, and/or (3) compared fishes between kelp forests and partially forested areas (i.e., thinning, removal, artificial reefs with canopy cover, urchin barrens with patches of kelp).

Using these criteria, a total of 23 observational and 20 experimental studies were included in this meta-analysis (Appendix S1: Table S1, Figure S1). The maximum number of studies per year was 4, and there were some years without any studies to report in this meta-analysis (Appendix S1: Figure S1). These 43 studies yielded 1131 data points. From these, subsets of 12, 21, and 24 studies yielded 86, 92, 958 data points to examine variations in fish species richness, total abundance, and single species abundance, respectively (Appendix S1: Table S1). Selected studies encompassed primarily 19 ecoregions. Of these, Northeastern New Zealand, Southern California Bight, Manning-Hawkesbury, New South Wales, Central New Zealand, Gulf of Maine, and Humboldtian accounted for 90% of the data points (Figure 1).

A total of 24 studies (experimental and observational) met the criteria for determining the effect of kelp on a single fish species abundance in kelp and non-kelp forests. From these studies, 146 reef fish species from 52 different Families were included; max length (TL) ranged from 2.6 to

200 cm; trophic groups included planktivores, herbivores and detritivores, omnivores, mobile and sessile invertivores (benthic microcarnivores and macroinvertivores), and general carnivores (including piscivores). We simplified these groups into broader categories: herbivores (including detritivores), mesopredators (representing omnivores and invertivores), and top predators (representing general carnivores and piscivores). Lastly, the trophic level ranged from 2 to 4.35 (Appendix S1: Table S2).

Kelp influence on total reef fish abundance and species richness

Overall, the mean effect of kelp on total fish abundance was not significant for both experimental (estimate = 0.35; SE = 0.26; 95% CI: -0.17, 0.88; $p = 0.19$; Figure 2A) and observational studies (estimate = 0.16; SE = 0.22; 95% CI: -0.27, 0.59, $p = 0.46$, Figure 2A). However, there were significant differences in the ecological roles of kelp species with different morphologies. The categorization of kelps by their structural complexity, which accounts for multi-stipe species and mixed kelp species having different architectural complexity than single stipe kelp species, revealed a significant positive effect of multi-stipe kelp on total reef fish abundance in observational studies (mainly *Lessonia*, *Macrocystis*, and *Carpophyllum*, Appendix S1: Table S3) (estimate = 1.4; SE = 0.26; 95% CI: 0.86, 1.88; $p = 0.0001$; Figure 2B). However, this effect was not evident based on the experimental studies (Figure 2C).

The effect of kelp on reef fish species richness (number of species) was significant for experimental studies (estimate = 0.58; SE = 0.12; 95% CI: 0.34, 0.82; $p = 0.001$; Figure 3A); the total number of fish species was greater in kelp-dominated habitat as opposed to

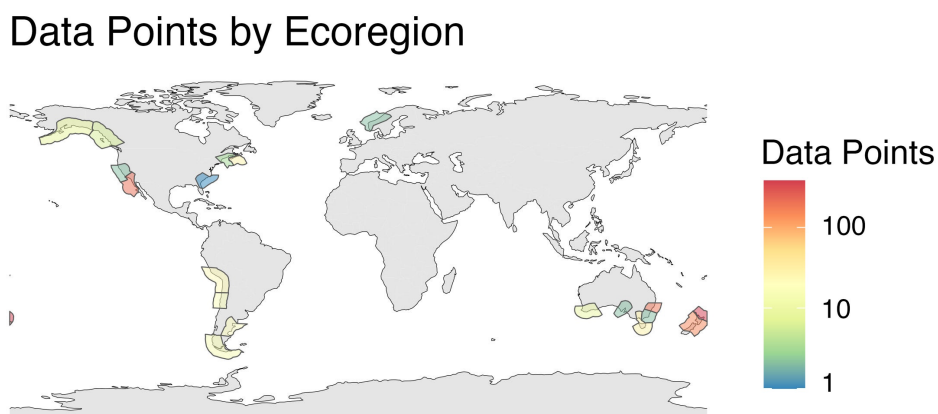


FIGURE 1 Map of the study sites that have conducted observational and manipulative experiments comparing the total abundance of fish assemblages, single species abundance, and/or species richness in kelp and non-kelp-dominated habitats.

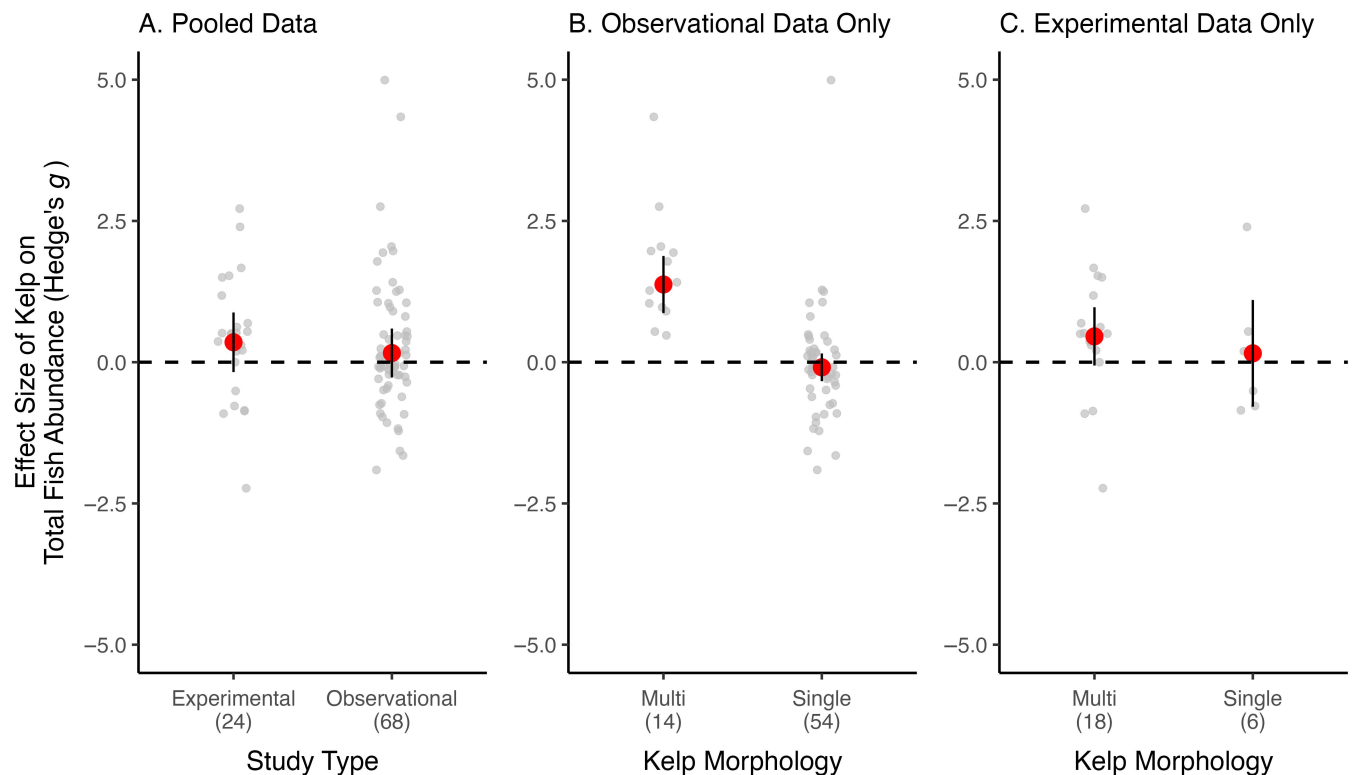


FIGURE 2 Effect size of kelp on total fish abundance (Hedges' g) in both experimental and observational studies is presented in (A) the effect size of kelp on total fish abundance (Hedges' g) considering kelp morphology (single or multiple stipes) is illustrated in (B) for observational studies and (C) for experimental studies. The numbers above each study type represent the corresponding data points. Positive values above zero, including the 95% CI, indicate a positive effect of kelp on total fish abundance.

non-kelp habitats. Kelp with different architectural complexity had a significant positive effect on total reef fish species richness in experimental studies (estimate = 0.6; SE = 0.12; 95% CI: 0.35, 0.83; $p = 0.0001$; Figure 3C). This pattern was variable across observational studies that evaluated the mean number of fish species and overall, was not significant (estimate = -0.11 ; SE = 0.16; 95% CI: -0.43 , 0.19; $p = 0.47$; Figure 3A,B).

Influence of spatial scales on reef fish species richness and abundance

At local scales, the effect of clearing size and/or addition of kelp (for experimental studies) and total area sampled did not influence the observed patterns. There was no relationship between reef fish species richness effect size (Hedges' g) and spatial scale (i.e., clearing size in experimental studies or total area sampled in observational studies) in experimental (estimate = 0.35; SE = 0.005; 95% CI: -1.83 , 0.87; $p = 0.4$) or observational studies (estimate = 0.00; SE = 0.004; 95% CI: -0.001 , 0.02; $p = 0.09$). Similarly, there was no relationship between

pooled effect size (Hedges' g) for total reef fish abundance and spatial scale in experimental (estimate = 0.00; SE = 0.0001; 95% CI: -0.0001 , 0.0002; $p = 0.65$) and in observational studies (estimate = 0.003; SE = 0.002; 95% CI: -0.0006 , 0.006; $p = 0.1$).

Kelp as nursery habitats

Kelp had a positive and significant effect on reef fishes at juveniles and YoY stages in observational (estimate = 1.27; SE = 0.09; 95% CI: 1.1, 1.46; $p = 0.0001$; Figure 4A) and experimental studies (estimate = 0.35; SE = 0.07; 95% CI: 0.2, 0.49; $p = 0.0001$; Figure 4A). In observational studies, kelp had a positive effect in all types of kelp forests, both multiple or mixed kelp (estimate = 0.67; SE = 0.18; 95% CI: 0.31, 1.04; $p = 0.0001$; Figure 4B) or single stipe kelp (estimate = 0.65; SE = 0.23; 95% CI: 0.005, 0.19; $p = 0.001$; Figure 4B). In experimental studies, only multi-stipe kelp forests exhibited a positive effect on juvenile reef fish abundance (estimate = 0.35; SE = 0.07; 95% CI: 0.19, 0.50; $p = 0.001$; Figure 4C).

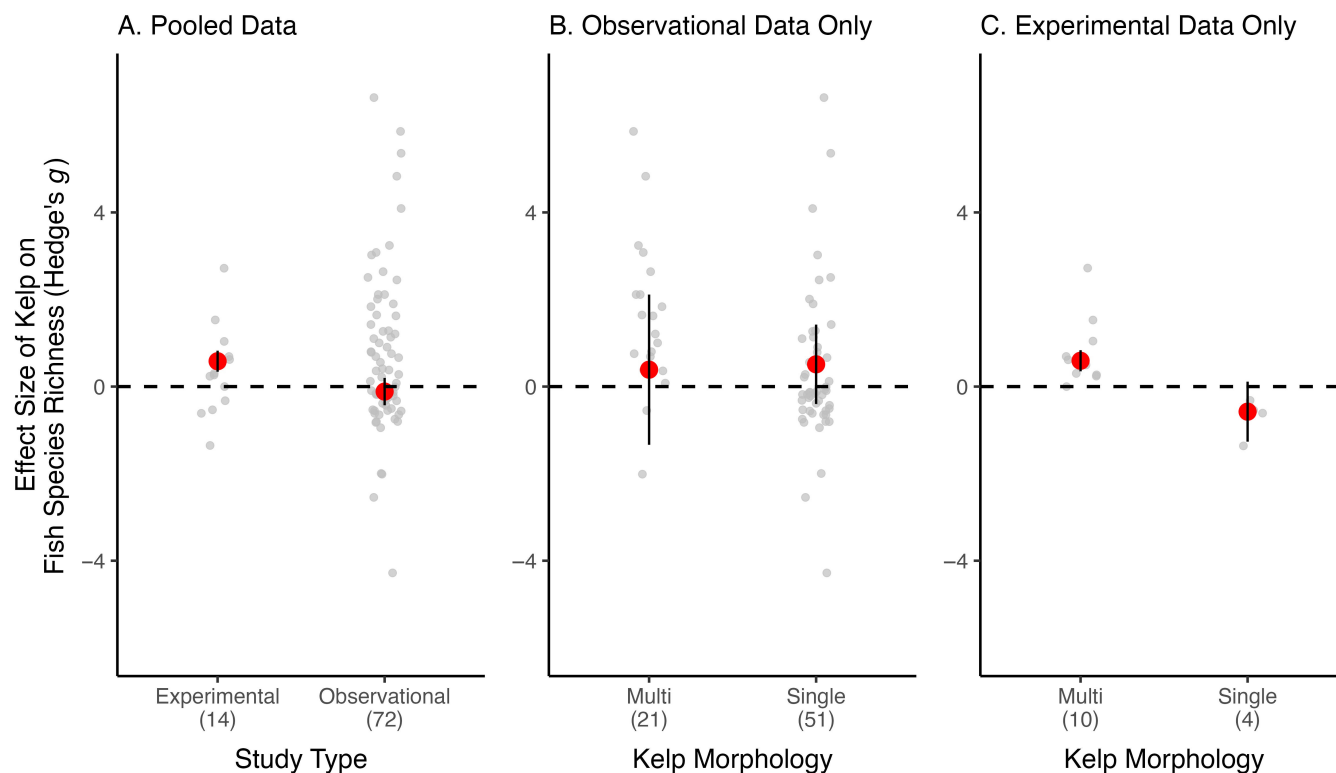


FIGURE 3 Effect size of kelp on total fish species richness or number of species (Hedges' g) in both experimental and observational studies is presented in (A) the effect size of kelp on total fish abundance (Hedges' g) considering kelp morphology (single or multiple stipes) is illustrated in (B) for observational studies and (C) for experimental studies. The numbers above each study type represent the corresponding data points. Positive values above zero, including the 95% CI, indicate a positive effect of kelp on number of species.

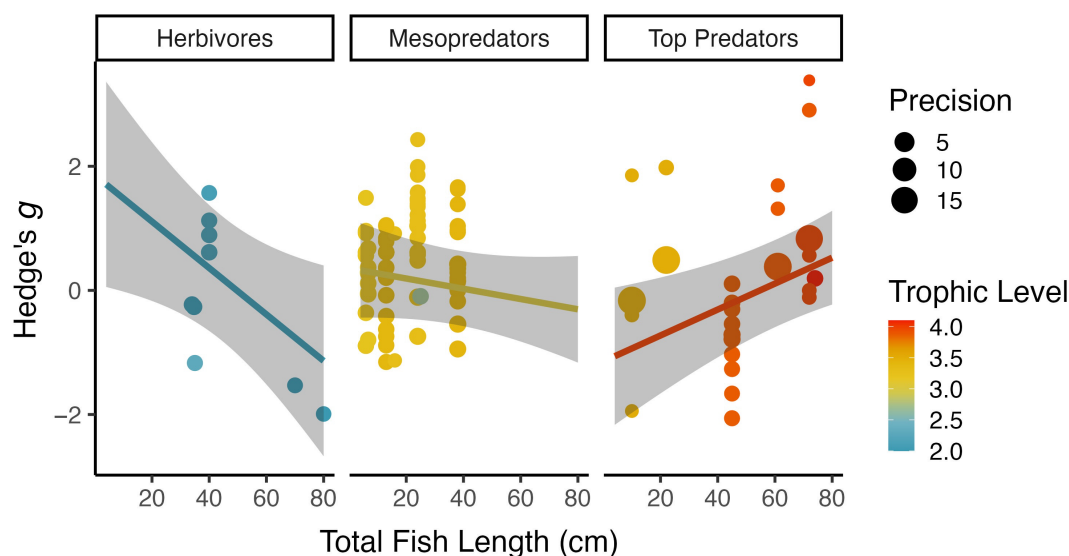


FIGURE 4 Effect size of kelp reef fish abundance at juvenile (or young of the year) stages (Hedges' g) in both experimental and observational studies is presented in (A) the effect size of kelp on total fish abundance (Hedges' g) considering kelp morphology (single or multiple stipes) is illustrated in (B) for observational studies and (C) for experimental studies. The numbers above each study type represent the corresponding data points. Positive values above zero, including the 95% CI, indicate a positive effect of kelp on abundance of juvenile species.

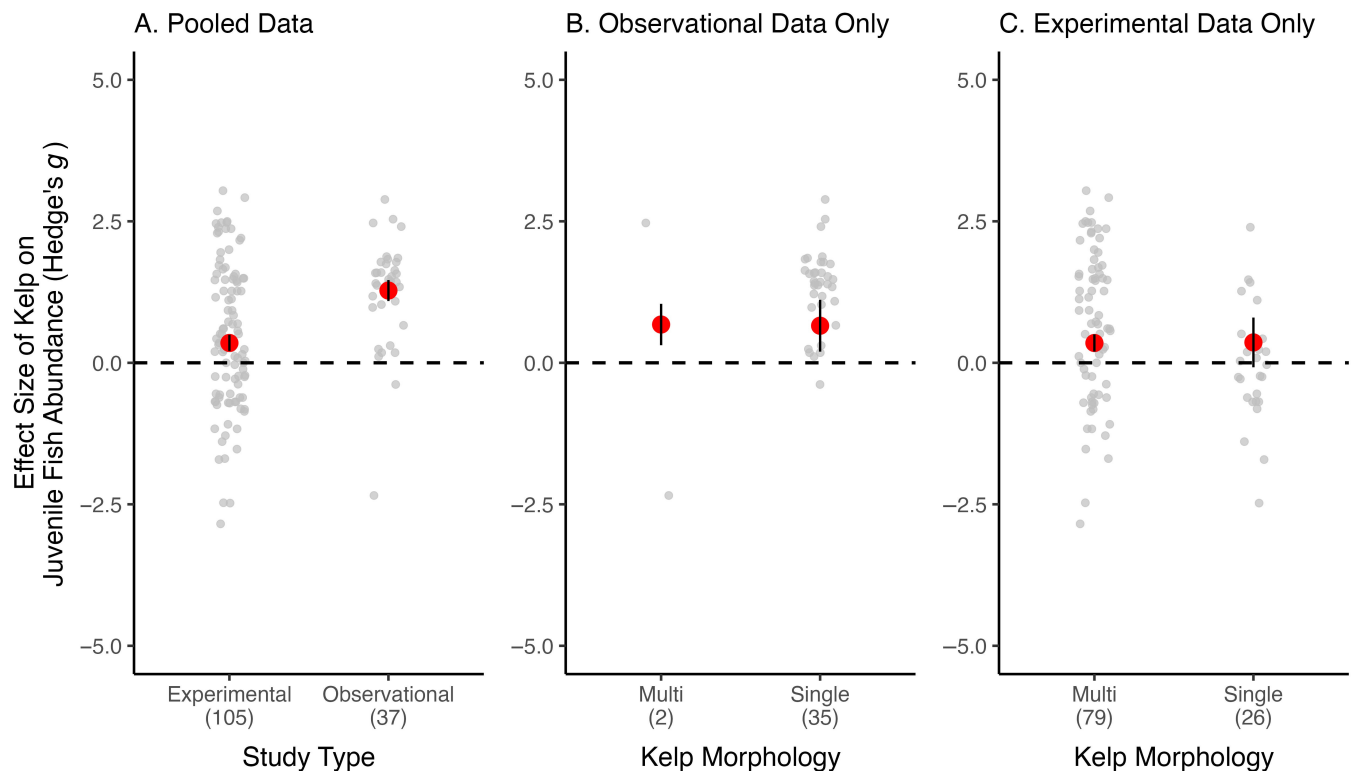


FIGURE 5 Interaction between effect size (Hedges' g) with reef fish body size (maximum body size in TL, in centimeters) and trophic level (i.e., coarse trophic categories such as herbivores, mesopredators, top-generalized fish predators). Gray area is represented by 95% CI and precision of the effect size (Hedges' g). Positive values above zero indicate a positive effect of kelp on abundance of species.

Effects across trophic levels and size classes

In analyses of traits data for reef fish species (body size, trophic level, and trophic groups), the correlation between Hedges' g with the interaction between trophic level and body size was positive (estimate = 0.0292; SE = 0.1; 95% CI: 0.007, 0.05, $p = 0.05$) suggesting that small (<40 cm in TL) herbivores and mesopredators (species that consume mobile and sessile invertebrates) increase in abundance in kelp forests but have the opposite trend with larger (>40 cm in TL) reef fishes belonging to these trophic groups (herbivores, slope = -0.0374, CI: -0.011, -0.064; mesopredators, slope = -0.008, CI: 0.001, -0.01). Kelp forests have a positive effect on larger (>50 cm in TL) generalized carnivore (top predators, slope 0.021, CI: 0.033, 0.009) reef fishes (Figure 5).

The analysis of the influence of time since kelp removal/addition on fish juveniles, total abundance, and species richness showed no significant effect of time on effect sizes ($p > 0.05$; Appendix S1: Table S4). While the null hypothesis was not rejected, this result is likely due to the limited number of long-term studies (only five studies exceeding three months; Appendix S1: Figures S2 and S3), which reduces the statistical power to detect potential time-dependent effects of kelp removal/addition.

Additional analyses considering variations by kelp morphology similarly yielded inconclusive results due to insufficient sample size.

DISCUSSION

Our meta-analysis shows positive effects of kelp forests on several attributes of reef fish populations and assemblages. We found evidence of significant ecological roles that kelp forests play in shaping reef fish populations and assemblages. Specifically, we found that not all kelp forests significantly enhance the abundance of reef fishes, but kelp act as ecosystem engineers and represent a nursery habitat for many reef fishes. Lastly, we found interactions between trophic level and fish body size, indicating that kelp forests facilitate smaller reef fish from low trophic levels (i.e., herbivores and mesopredators) (Figure 6). However, we found that higher trophic level species with longer bodies are facilitated in kelp forests suggesting important ecosystem functions of this habitat in supporting food web structures. Although our results reveal high variability in patterns of abundance and reef fish species richness across independent studies, we conclude that structural complexity of kelp forests underpins complex interactions between reef fish size and trophic



FIGURE 6 Underwater photographs highlighting the crucial role of kelp forests and their complexity for reef fishes, depicting (A) nursery habitats (photo credit: D. Okamoto), (B) reef fish abundance (photo credit: C. Ruz), and (C) large generalist carnivores or reef fish top predators (photo credit: A. Pérez-Matus).

level irrespective of geographic region of the temperate reef.

We found that the structural complexity of kelp forests is one of the main factors that contributed to the variable effect of kelp forests on reef fish abundance. Structural complexity is an important component of reef ecosystems, as this complexity supports a wide variety of niches and functional strategies (Bosch et al., 2022). Our meta-analysis showed that kelp forests comprised of species with multi-stipe morphologies or mixed kelp species facilitate reef fish species diversity and higher abundance (Pérez-Matus & Shima, 2010b). The complex physical structure of kelp forests provide food (or feeding areas), refuge from predators, and mating sites for a wide variety of fishes (Koenigs et al., 2015). Kelp forest structural complexity may also influence several of the factors that have been found to explain variability in organization of macroalgal communities, including (1) competitive interactions (within and between species); (2) herbivory, particularly dislodgement by grazing sea urchins and consumption by mesograzers; and (3) physical factors (i. e., variation in temperature, nutrient levels, light, degree of exposure to wave action, and bottom relief) (for reviews see: Graham et al., 2007; Krumhansl et al., 2016; North, 1994; Wernberg et al., 2019).

The high variability in effect sizes of kelp forest impacts on reef fish abundance in experimental and observational studies might be driven by factors other than kelp forest presence and quality, which are not reported or quantified in the studies we examined. Direct human impacts (e.g., harvest) on reef fishes, levels of recruitment, and variation in the physical environment could be important potential drivers to consider and are often overlooked (Claudet et al., 2010, 2011; Januchowski-Hartley et al., 2011, 2012). Kelp forests typify a patchy habitat having different edges (including edge effects) and variable in size with numerous understory foundation species (Deza & Anderson, 2010; Efrid

& Konar, 2014). The variability in these components is determined by depth, and substrate slope and rugosity, which, together, may structure fish assemblages (Hamilton & Konar, 2007; Villegas et al., 2018). Substantial and historic removal of large benthic carnivorous and herbivorous fishes by humans from kelp forests may also explain variability observed in many observational studies (Caselle et al., 2011; Dayton et al., 1998; Hamilton et al., 2007; Perez Matus et al., 2017). The wariness of fish in heavily fished kelp forests may represent another source of variability not measured in our selected studies (Goetze et al., 2017).

Numerous studies have contributed to our understanding of the importance of kelp for reef fish abundance; such studies covered a large spatial scale but had low replication (mainly due to logistical constraints), which limited our ability to include them in this study (Angel & Ojeda, 2001; DeMartini & Roberts, 1989, 1990). A review by Witman et al. (2015) found that many older experimental studies were complex in spatial scales but had low replication, whereas today many experimental studies are highly replicated but, due to logistical issues, small in spatial scales (Ebeling & Laur, 1985). The lack of significant effect sizes in reef fish abundance in many experimental studies could be attributed to the small sizes of the experimental manipulations. For species with high mobility and large home ranges, kelp forests may represent one habitat within a larger seascape (Lowe et al., 2003; Topping et al., 2005, 2006). The experimental size of highly replicated (5 or more replicates) studies may not capture all reef fish fauna. On the other hand, observational studies using 40–50-m-long belt transects may be more effective in capturing both small and large home range species (Edgar et al., 2011; Edgar, Barrett, & Morton, 2004; Edgar, Barrett, Morton, & Samson, 2004).

Kelp forests have been studied extensively to understand their role as nursery habitats that support the early growth stages of reef fishes (Anderson, 1994; Carr, 1989,

1991; Caselle & Warner, 1996; White & Caselle, 2008). Kelp forests are important because they provide areas for fish to settle and grow, acting as either initial or backup recruitment zones for many fish species (Jones, 1984). In certain regions where kelp forests are prevalent, the recruitment and survival rates of early juvenile reef fishes are observed to rise significantly with the presence of both the kelp canopy and subcanopy species (Anderson, 1994). In a recent review, Fulton et al. (2020) suggested that large macroalgal canopies enhance productivity in tropical reef systems by generating a primary or secondary habitat for multiple reef fish species. From the perspective of an individual fish, the decision to move from one patch to another may depend upon a range of (potentially conflicting) drivers that, for example, may include the use of food resources and/or mating opportunities and minimization of risk from predators and/or competitors (Holbrook & Schmitt, 1988).

Our study revealed complex ecological interactions between kelp forests and reef fishes. Through analysis of trait data, we found that reef fish from all trophic levels increase their abundance in kelp forests as opposed to barren or non-kelp-dominated habitat (Galaiduk et al., 2013). Kelp may reduce density-dependent competition by increasing habitat refuges and food availability particularly for small fish herbivores and mesopredators that can find refuge and at the same time consume the numerous epifaunal species that kelp provide (Carabajal et al., 2021; Johnson, 2006a, 2006b; Teagle et al., 2017). There are few herbivores fishes that consume kelp, but in some regions fish can impact kelp distribution and abundance (Barrientos et al., 2022; Taylor & Schiel, 2010), and also maintain foraging algal areas at small scales (Andrew & Jones, 1990). Large-bodied herbivores in temperate reefs tend to forage on turf or green algae that in general occur in the understory or in sympatry with kelp forest seascapes (Sievers et al., 2016). Small-bodied fish tend to co-occur in kelp forests (hence the “kelpfishes” of the family Clinidae) and in other vegetative habitats where they have restricted home ranges (Mensink & Shima, 2015; Tuya et al., 2009). However, a trade-off may offset this due to the presence of large piscivorous and carnivorous fish, as kelp forest facilitate larger-bodied fish at high trophic level. The notable rise in the diversity and abundance of juvenile fishes (prey) likely plays a crucial role in driving the positive impact of kelp on the abundance of this trophic group of large carnivores. Adult piscivores heavily rely on juvenile fishes as a substantial subsidy to reef fish assemblages (Hallacher & Roberts, 1985; Zuercher & Galloway, 2019).

This study aimed to delve into the implications of kelp forest loss on fish assemblages. Kelp forests are under increasing threat from multiple sources and

drivers, with climate change and the subsequent rise in sea surface temperature (SST) being one of the most significant (Reed et al., 2016; Smale & Moore, 2017; Wernberg et al., 2013). Heatwaves, intensified by higher temperatures, can severely damage kelp by affecting its reproductive capacity, settlement, and growth (Straub et al., 2019), which in turn disrupts associated species (Beas-Luna et al., 2020). Kelp forests play a pivotal role in marine ecosystems (Eger et al., 2023), particularly in shaping the diversity and abundance of reef fishes. The analyses reveal several key insights about the relationship between kelp forests and reef fish populations by enhancing the abundance of reef fishes. However, the degree of this effect is influenced by different structures of kelp forest. This implies that not just the presence, but the intricate structures and layers within the kelp forests, can be determinants of how many fish they can support. Importantly, kelp forests significantly elevate fish species richness. This underlines the foundational role of kelp, not just as a habitat, but as a pillar that upholds the diversity of multiple species in their vicinity or in adjacent habitats. Kelp forests facilitate the early life stages of fish, emphasizing their role in the life cycle of many species. Lastly, the influence of these forests varies depending on the functional traits and body size of the fish species. This differential effect indicates that while kelp forests are beneficial for many, their benefits are tailor-made to suit the needs and characteristics of specific fish species. In synthesis, kelp forests are not just passive underwater structures but dynamic ecosystems that actively shape the life, abundance, and diversity of reef fishes (Duffy et al., 2016). Many reef fish are facing threats from fishing activities, leading to dwindling populations in several temperate regions (Godoy et al., 2010). Populations of reef fishes are under threat from overfishing, underscoring the importance of investigating the consequences of kelp loss. Kelp forests worldwide harbor diverse reef fish assemblages that play crucial ecological roles and provide essential ecosystem services (Eger et al., 2023). To grasp the full extent of climate-induced kelp decline, we must dig into how the loss of kelp affects the multitude of functions and services delivered by reef fishes.

Our study highlights the intricate relationships between kelp ecosystems and reef fishes while also highlighting several important considerations that emerged in this meta-analysis (Figure 6). One of the key challenges we identify lies in the potential biases associated with removal experiments and underwater visual counts. In particular, removal experiments that focus on short-term outcomes may fail to capture the delayed responses of species to habitat alteration phenomenon known as extinction debt (Kuussaari et al., 2009). This

occurs when species initially survive habitat loss but eventually decline and disappear over time, pointing the need for the long-term monitoring (Witman et al., 2023). While our analysis examined the role of time as a factor in the few studies that included multiple post-disturbance surveys, we found no significant legacy effects or time-dependent changes in species richness or abundance. However, this lack of significance may reflect the limited number of long-term studies in our dataset rather than the absence of actual ecological impacts.

Another important caveat involves the methodology used to assess fish populations. Visual counts, particularly in kelp-dominated environments, can introduce bias by underestimating abundance of certain species (Edgar, Barrett, & Morton, 2004; Edgar, Barrett, Morton, & Samson, 2004). Small cryptic reef fishes may be undercounted in areas with extensive algal cover lacking canopy-forming species (Bernard et al., 2013). Given these challenges, future research must adopt comprehensive approaches to monitoring reef fish assemblages in kelp ecosystems. Complementary methods, such as the use of underwater cameras, diver-operated video systems, and environmental DNA (eDNA), can help overcome the limitations of visual surveys and provide a more accurate picture of community dynamics. Integrating these techniques with longer-term experimental designs will improve our understanding of how kelp ecosystems influence reef fish populations, enabling us to better predict and mitigate the consequences of habitat loss and fragmentation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Pérez-Matus & Byrnes, 2024) are available in the Environmental Data Initiative Data Portal at <https://doi.org/10.6073/pasta/2c6e5c63bf01432e39414bb9dc1e787a>. Code (Byrnes, 2024) is available on Zenodo at <https://doi.org/10.5281/zenodo.12406302>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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