**To be submitted to *Ecology or Fish and Fisheries or MEPS***

**Title**

**Kelp forests enhance reef fish species richness and facilitate large top predators: a global metanalysis**

Authors

Alejandro Pérez-Matus\*1,2, Fiorenza Micheli3, Brenda Konar3, Nick Shears5, Natalie H.N. Low2, Daniel K. Okamoto4, Thomas Wernberg5, Kira Krumhansl6, Scott Ling7, Michael Kingsford8, Teresa Navarrete-Fernandez1, Catalina S. Ruz1, Jarrett E. K. Byrnes10

1. Subtidal Ecology Laboratory, Estación Costera de Investigaciones Marinas, Facultad de Ciencias Biológicas, Departamento de Ecología, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile.
2. Millennium Nucleus for the Ecology and Conservation of Temperate Mesophotic reef ecosystem, Las Cruces, Valparaiso, Chile.
3. Hopkins Marine Station and Stanford Center for Ocean Solutions, Stanford University, Pacific Grove, CA 93950, USA.

\*Corresponding Author: aperez@bio.puc.cl

**Abstract**

Conservation and management of marine biodiversity requires an understanding of the habitats needed to support and replenish all the species in a region of interest. Variation in the presence, density, and composition of kelp forests, one of the most a diverse and productive marine coastal habitat found throughout temperate regions around the world, can have large influences on the abundance, diversity, and interactions of associated organisms. However, the generality of these effects has not been quantified across multiple species, communities and geographic regions. Here, we evaluate the effects of kelp forests on populations and communities of reef fishes. We examine ecosystem impacts of kelp forests over fish population and functional attributes in a global meta-analysis of experimental kelp removals and comparative surveys of kelp and adjacent non-kelp habitats. These analyses show that removal of kelps impacts fish community structure by both reducing top trophic level fish abundance and small and juvenile fish. We found that kelp loss has overall significant effect on species richness. Moreover, In some ecoregions, the presence of kelps significantly increases the abundance of reef fish; for instance in five of 13 evaluated ecoregions kelp have positive effects on reef fish abundance but in none non-kelp habitat sustain larger abundance of reef fish assemblages. Kelp loss or removals generally result in shifts in fish community structure, reducing the abundances of fish that are either at high trophic levels or small in size. Taken together, these results indicate that the loss or removal of foundation species may not always cause large changes in total abundance or species richness, but rather shifts in community composition that can have cascading consequences for ecosystem function.

**Keywords: barren grounds, kelp beds, nursery habitats, global review, global change**

**Introduction**

Suitable habitat is essential to the ecological and evolutionary success of most organisms (Kramer and Chapman 1979, Airoldi et al. 2008, Fulton et al. 2020). For marine fishes, a group of critical ecological and economic importance comprising nearly 28,000 known species, particular habitat attributes may shape local population densities (Choat et al. 1988), survival rates (Anderson and Underwood 1994, Tolimieri 1995), dispersal patterns of adults, and recruitment dynamics (Carr 1989, 1991, 1994). Biotic habitats such as macroalgal forests are often important for reef fishes, providing refuge from predators and food, either directly or indirectly, by concentrating prey (e.g., Taylor 1997, 1998, Edgar et al. 2004, 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 vegetative structures via consumption of macroalgal grazers (Cowen 1983, Davenport and Anderson 2008, Pérez-Matus and Shima 2010a) and some species of herbivores can act as potential kelp zoospore disperser (Ruz et al. 2018). Given that the distributions 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 collective fish communities is essential for the successful management and/or conservation of many species.

Large brown seaweeds are among the best-known forms of macroalgae. They inhabit nearshore environments of most temperate coasts (Dayton 1985). Two orders comprise the assemblage of large brown algae: the Laminariales and Fucales (Schiel and Foster 2006, Wernberg et al. 2018). There are around 30 genera, which vary in size, morphology, and life span. They 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 and Foster 2006). Attached to the substratum by a holdfast, stands of large brown macroalgae often provide important three-dimensional structure in subtidal environments (Miller et al. 2018). Communities of large brown macroalgae are typically highly productive and sustain some of the most diverse and dynamic ecosystems on earth (Graham et al. 2007, Teagle et al. 2017). Their holdfasts represent areas for feeding, refuges from predators and settlement habitats for a variety of organisms (Vasquez and Buschmann 1997, Teagle et al. 2017, Winkler et al. 2017) and numerous meso epifauna occur in their fronds and stipes, which collectively provide a link to higher trophic level species such as fishes.

Specific macroalgal features and their role for the associated fauna vary over short distances (Graham 2004). This variation may depend upon local environmental conditions (e.g., degree of wave exposure), herbivory, competition, or 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) (Norderhaug et al. 2007). Specific macroalgal traits may act in synergy to shape patterns of distribution and abundance of fishes but our understanding in the global context is not well understood. Consequently, macroalgal habitats likely offer multiple sources of environmental variation that combine to determine overall “habitat quality” which may affect species depending on the foraging mode (collectively known as trophic level) and when during the ontogeny in which individuals demands and the so called quality may differ depending on the age, sex, and maturity. While some species may be uniquely linked to a certain habitat type and this has been reported in many coral reef associated species we have improve our knowledge that many fish taxa follow a triphasic life cycle, where planktonic larvae settle into an initial habitat before migrating to different habitats as juveniles and/or adults. Whether large brown macroalgae enhance the abundance of any particular stages is not universal.

Considerable variation has been documented for the effects of habitat on reef fish (Syms 1995, 1998, Syms and Jones 1999, Valesini et al. 2004). Other authors have noted that fishes may be responding to spatial variation in habitat (e.g., Öhman et al. 1997, Valesini et al. 2004, Pérez-Matus et al. 2007, Wellenreuther et al. 2007, Williams et al. 2008). Generally speaking a consensus exists regarding the positive effect of complex habitat on fishes, particularly early in their life-history, e.g., at recruitment and for subsequent juvenile-adult stages, although much of this evidence comes from studies that were conducted at small spatial scales (McDermott and Shima 2006). These observations made at small spatial scales may not be sufficient to predict abundance at larger-scales, where, in general, oceanographic processes appear to play a greater role in demographic patterns (Caselle and Warner 1996b, White and Caselle 2008). Contrary examples suggesting reasonable relationships between observations from small- to large scales are limited, and appear to be species dependent (but see, Munday 2002).

Disturbances are changes in the biotic and/or abiotic environment that modify the structure and dynamics of ecosystems and communities (Donohue et al. 2016). Kelp forests are highly variable in over temporal and spatial scales (Reed et al. 2008, Reed et al. 2009, Mora-Soto et al. 2020), displaying a range of resistance to and recovery from natural and anthropogenic disturbances. Disturbances are numerous and operate at multiple scales such as heat waves, contamination, sedimentation, eutrophication, harvesting, and habitat loss and degradation (Edwards and Richardson 2004, Halpern et al. 2008, Airoldi et al. 2009, Wernberg et al. 2011, Wernberg et al. 2013). Kelp populations in general are showing decreases in local abundances, contractions in distributional ranges and local extinctions, mainly due to anthropogenic disturbances and global warming (Wernberg et al. 2010, Smale and Moore 2017) and kelp-harvesting (Vásquez et al. 2013). Kelps are key structural and functional organisms within marine ecosystems (Krumhansl et al. 2016), their local removal, loss or extinction can strongly affect the composition and stability of coastal ecosystems.

The ecosystem wide consequences of kelp loss are not well understood. Community structure could change drastically following foundation species loss (e.g. Graham 2004). However, once foundation species are lost, communities can shift and compensate as new formerly outcompeted space-holding species begin to create new habitats. How will communities shift if the current dominant foundation species declines in abundance? In temperate marine ecosystems dominated by kelps – a key foundation species – this issue has become increasingly important as areas such as Western Australia, Tasmania, Japan, and Europe witness changes in kelp abundance (Krumhansl et al. 2016, Wernberg et al. 2018). Niche requirements in the use of macroalgal stand, variation in the distributions and abundance of food (associated epifauna to macroalgae) 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 which collectively can be identified as the provision of the different “services” to reef fishes (Deza and Anderson 2010, Pérez-Matus and Shima 2010b, Pérez-Matus and Shima 2010a). Determine which habitats are capable of sustaining more fish species, abundance, trophic groups and how this change during the ontogeny has not been consistently understand.

Here, we conducted a meta-analysis of published studies to answer the following questions: (1) does the structural complexity within kelp forests enhance total reef fish abundance and species richness; if so it does occur during juvenile or adult stages? (2) does spatial scale influence any observed influence on species richness and abundance?; (3) do kelp forests enhance local predator abundance, by facilitating large body size and higher trophic level species?; and lastly (3) does the presence of kelp forests increases the total reef fish species richness and/or abundance?

**Materials and Methods**

*Review methods*

Multiple electronic databases and the internet were explored. Specifically, we searched 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)”. Last search was December 2022. We also searched the references in the studies identified through the database searches. Personal reference collections and colleagues with active research interests in these areas were also included. 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) metric (abundance, species richness, functional diversity) in kelp and non-kelp forests (i.e., urchin barrens, sponge gardens, turf algae, sand). We selected studies that have explicitly compared via observational (i.e., observational studies) or manipulative experiments the difference in mean (and estimation of variance) over a) single reef fish species abundance, b) total abundance of reef fish assemblage, and/or c) reef fish species richness.

*Data Extraction*

All data and effect sizes were independently extracted, and sample sizes were extracted from relevant studies (Table 1). Individual values from most articles were represented in graphs such as scatterplots and barplots in which case a web plot digitizer was used for translation of plots into numerical values (Rohatgi 2020). Articles that did not provide relevant effect sizes, individual values in tables, or barplots and scatterplots were not used in this meta-analysis. We also included independent unpublished data sets from Tasmania (~41º SL) and New South Wales (~33ºSL) Australia, authors of such data were contacted and asked to provide effect sizes (Table 1).

*Fish and kelp traits data*

The functional roles of reef fish species may be described using broad trophic groups or using more detailed information on traits (Micheli and Halpern 2005, Mouillot et al. 2007, Mouillot et al. 2014). For this meta-analysis, we explored the differences in mean abundance in kelp and non-kelp habitats of single species abundance and the functional trends using broad trophic groups based on their trophic level. We categorized species as planktivores, herbivores, omnivores, benthic carnivores (invertivores), and general carnivores (including piscivores). These groupings are available for all taxa, regardless of taxonomic resolution. We also used maximum total length and trophic level which are non-categorical traits that are known to reflect the role of a species within the ecosystem. This type of traits data was readily available and we downloaded from FishBase using rFishBase (Boettiger et al. 2012, Froese and Pauly 2014) (ESM, Table S2).

Finally, a total of 16 different kelp species were included in this meta-analysis where 12 from the order Laminareales (*Macrocystis pyrifera, Ecklonia radiata, Laminaria longicruris, L. digitata, Saccharina latissima, L. farlowii, Eisenia arborea, Egregia menziesii, Nereocystis luetkeana, Pterygophora californica, Lessonia trabeculata, Undaria pinnatifida*) while 4 species in the order Fucales (*Carpophyllum maschalocarpum, C. flexuosum, Cystophora racemosa, C. retroflexa*). We grouped kelp according to their numbers of stipes as single (i.e., *Ecklonia spp*) or multi-stipe (i.e., *Macrocystis pyrifera*). Therefore, the morphological characteristics of kelp were also described in this meta-analysis by dividing kelp maximum size and number of stipes as categorical variables such single or multiple stipes.

*Effect size calculation*

Studies with multiple outcomes were categorized either a) total reef fish abundance (accounting for reef fish abundance of entire assemblages), b) species richness (i.e., number of reef fish species), and c) single species abundance and then combined within each domain as experimental and/or observational (observational) studies. When the necessary data were available, all effect sizes were calculated directly using the following formula:

where is the mean of the treatment group (either observational or experimental),  is the pooled standard deviation or variance. If these data were not provided, *g* was not estimated. All 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. Effect sizes were calculated with both fixed and random effects models. The fixed effects analysis estimates the exact effect size based on all studies and the random effects analysis estimates the overall effect size assuming the studies included are only a sample of the entire population of studies (i.e., data points). We report Hedge's *g* (to control for sample number size).

**Results**

*Literature search and study selection*

The total number of studies that resulted from different searches in the internet and initial searches resulted in 32,000 independent studies from 1960-2020. All of these were examined pre-screened and resulted in 90 studies which evaluated fish species richness and/or abundance and/or single species abundance under the presence of kelp forests (Laminareales) (Table s1). To conduct the quantitative metanalysis, from these studies we considered irrelevant reference studies those that: a) lack of experimental replication (in both experimental or observational experimental designs), b) lack of reported variation and effect sizes, and/or c) comparison between kelp forest(s) fishes with partially forested areas (i.e., thinning, removal, artificial reefs with canopy cover, urchin barrens with patches of kelp).

A total of 23 observational and 17 experimental studies were included in this analysis (Table 1, Fig S1). The maximum number of studies per year were 4 and since 1984 at least one study per year were included except in 2016/7 (Fig S1). These 40 studies yielded 1131 data points and were included in this meta-analysis. From these, 12, 21, and 24 studies yielded 86, 92, 958 data points were allocated to understand variations in fish species richness, total abundance, and single species abundance, respectively (Table 1). All the selected studies encompassed 19 ecoregions. Northearstern New Zealand, followed by Southern California Bight, Manning-Hawkesbury, Central New Zealand, Gulf of Maine and Humboldtian ecoregions accounted for 90% of the data points (Fig. 1).

A total of 24 studies (experimental and observational) were selected for determining the effect of kelp on single species abundance in kelp and non-kelp forests. From these studies, 146 reef fish species from 48 different Families were included, max length (total length, TL) range from 2.6 to 200 cm in body size (total length, TL); trophic groups included planktivores, herbivores and detritivores, omnivores, mobile and sessile invertivores, general carnivores; and trophic level ranged from 2 to 4.35 of diet trophic level (ESM, Table S2).

*Kelp forests influences total reef fishes abundance and species richness*

The effect of kelp on total abundance of reef fish assemblage on effect size was significant in 5 (Central Chile: S.E. =0.92; 95% CI: 1.28, 4.90; p = 0.0001, Carolinian: S.E. = 1.09; 95% CI: 0.73, 5.03; p = 0.001, Humboldtian: S.E. = 0.85; 95% CI: 0.60, 3.94; p = 0.001, Southern California Bight: S.E. = 0.94; 95% CI: 0.5, 4.23; p = 0.01 and Norway: S.E. = 1.08; 95% CI: 0.09, 4.35; p = 0.04) of the 13 ecoregions (Fig 2). This means that kelp enhance total reef fish abundance in these 5 ecoregions. Moreover, no significant negative effect sizes were present in the 5 ecoregions, suggesting that in non-kelp habitats the total reef fish abundance is variable as in kelp habitats (Fig 2).

When evaluating separate effect of experimental and observational studies. The analysis of the effect kelp on total abundance on effect sizes was not significant for both experimental (S.E. = 0.26; 95% CI: -0.17, 0.85; p = 0.19; Fig 3a) and observational studies (S.E. = 0.22; 95%, CI: -0.27, 0.59, p = 0.46, Fig 3a). The nonsignificant overall effect of kelp masks an important difference in the ecological roles of kelp species with different morphologies. Categorization of kelps by their structural complexity, to separate multi stipe species that have greater architectural complexity from single stipe kelp species, revealed that total reef fish abundance is greater in kelp forests dominated by multi-stipes species (S.E. = 0.19; 95% CI: 0.33, 1.11; p = 0.0001; Fig 3b).

The analysis of the effect of kelp on reef fish species richness (number of species) was significant for experimental studies (S.E. = 0.12; 95% CI: 0.34 , 0.82; p = 0.001; Fig 4) meaning that in most experimental studies included in this metanalysis, the total number of fish species increases in kelp-dominated as opposed to non-kelp habitats. This pattern was variable for most observational studies (S.E. = 0.16; 95%, CI: -0.42, 0.16; p = 0.47; Fig 4).

*Influence of spatial scale on patterns in species richness and abundance*

The effect of spatial scales (i.e., clearing size in experimental studies or total area sampled in observational studies) over the effect size (Hedges’ g) was not significant for reef fish species richness in experimental (S.E. = 0.001; 95% CI: -2.03, 0.01; p = 0.1) and observational studies (S.E. = 0.002; 95% CI: -0.001, 0.003; p = 0.91). Similarly, the influence of spatial scale over pooled effect size (Hedges’ g) for total reef fish abundance was not significant in experimental (S.E. = 0.0001; 95% CI: -0.0001, 0.0002 ; p = 0.44) and in observational studies (S.E. = 0.0002; 95% CI: -0.0001, 0.0005 ; p = 0.15). These mean that at local scale, the effect of size of clearing/and or addition of kelp (for experimental studies) and total area sampled (i.e, patch size) did not influence the observed patterns herein. However, the effect of spatial scale was significant for single species abundance (S.E. = 0.001; 95% CI: 0.0009, 0.002; p < 0.001) in observational studies only, meaning that the total area sampled influence positively patterns of abundance of a particular reef fish species. The size of the experimental set up revealed no overall evidence over the abundance of single species (S.E. = - 0.001; 95% CI: -0.003, 0.0009, 0.001; p = 0.25).

*Effects across trophic levels and size classes*

For experimental studies of single species abundance, we found an overall negative correlation between Hedges’ g and body size (S.E. = - 0.1; 95% CI: -0.17, -0.03; p = 0.01) meaning that small sized fishes increase in abundance in the presence of kelp. This relationship with size however, varies with trophic level (i.e., there is a significant size and trophic position interaction) both in experimental (S.E. = 0.01; 95% CI: 0.01, 0.04; p = 0.01). Lastly, a negative relationship between Hedges’ g and trophic level (S.E. = 0.05; 95% CI: -2.57, -0.38; p = 0.01), meaning that higher trophic level species are facilitated in kelp ecosystems (Fig 5).

**Discussion**

Our metanalysis of 38 published studies and 2 unpublished studies from multiple temperate reefs on the effect of kelp forests on reef fish total reef fish assemblage abundance, species richness, and single species abundance partly supports our hypothesized positive effect of large brown macroalgal on several attributes of reef fish populations and communities. We found evidence of significant ecological roles that kelp forests play in shaping reef fish communities: a) the presence of kelp forests enhances the abundance of reef fishes in a third of the ecoregions analyzed, confirming the importance of kelp ecosystem, b) structural complexity associated with multi-stipe kelp morphologies (i.e., more complex macroalgal forests) supports greater fish abundance in temperate reefs; and lastly, c) in experimental studies, fish species richness increased within kelp-dominated habitats, and lastly d) we found interactions between trophic position and fish body size, indicating that kelp forests facilitate small sized reef fish at low trophic levels (i.e., herbivores and mesopredators), as well as higher trophic level species which are, in general, larger in body size. Although our results present a high variability in patterns of abundance and reef fish species richness which may mimic many isolated studies, we concluded that kelp architectural heterogeneity underpin complex interaction between reef fish size and trophic level irrespective of the temperate reef.

The effect of kelp forests as nursery habitats enhancing early life stages of reef fishes overall has been experimentally tested in many studies (Carr 1989, 1991, Anderson 1994, Caselle and Warner 1996a). The choice of an appropriate spawning site is one of the fundamental processes that affect offspring success (Hastings and Botsford 2006) and kelp forest represents a settlement habitat for numerous fish species or at least a secondary habitat. This view is becoming also relevant in tropical environments. In a recent review Fulton et al. (2020) suggested that large macroalgae canopies enhance productivity in tropical reef systems by generating a primary or secondary habitat to multiple reef fish species. From the perspective of an individual of a given fish species, the decision to move from one patch to another may depend upon a range of (potentially conflicting) motives that, for example, may include the use of food resources and/or mating opportunities, minimization of risk from predators and/or competitors (Connell and Kingsford 1998, Kramer and Chapman 1999, Pérez-Matus et al. 2016). At juvenile stages, reef fish species from all trophic levels increase their abundance in kelp forests as opposed to barren or non-kelp dominated habitat. Kelp may reduce density dependence competition by increase habitat refuges and food availability. However, trade off may be offset this by the presence of large piscivore fishes (since large size higher trophic level are facilitated in this habitats). This may be the link, small juveniles increase in abundance due to a reduce intraspecific competition (cryptic density dependence, see (Shima and Osenberg 2003) and spill-over is taken by larger piscivore species (Abesamis and Russ 2005). These dynamic processes are one of the fundamental findings of this global review.

We found that structural complexity is one of the main factors that contributed to the differences in reef fish abundance. Complex kelp forests sustain more reef fishes. The factors that explain changes in organization of macroalgal communities include: (a) variable life-histories (e.g., annual vs perennial species); (2) competitive interactions (within and between species); (c) herbivory, particularly dislodgement by grazing sea urchins and consumption by mesograzers; and (d) physical factors (i.e., variation in temperature, nutrient levels, light, degree of exposure to wave action and bottom relief) (for reviews see:(North 1994, Graham et al. 2007, Krumhansl et al. 2016, Wernberg et al. 2018). The physical structure of large brown macroalgae may provide food (or feeding areas), refuge from predators, and mating sites for a wide variety of fishes (Miller et al. 2018). Associated fauna may use the same structures of a macroalgae for different purposes, or they may partition their activities among different components of an individual seaweed (e.g., fronds may be used for refuge/shelter, holdfasts for feeding sites) (Steneck et al. 2002; Christie et al. 2007). More niches may be available for multiple demands in highly complex kelp forests habitats.

The limited number of experimental studies that met our criteria, as well as low replication may explain these results. There were numerous studies that have contributed to our understanding of the importance of kelp over reef fish faunas, such studies were consistent with large spatial scale but low sample replication (mainly due to logistical issues) which limited our options to include them in this study (i.e., DeMartini and Roberts 1989, DeMartini and Roberts 1990, Angel and Ojeda 2001). In a recent review, Witman et al. (2015) found that many experimental studies were complex in spatial scales but low replicated in the past studies whereas today, many experimental studies are highly replicated but, due to logistical issues small in spatial scales. The lack of effects sizes in many experimental studies could be attributed to the size of scale of experimental manipulation. For species with a variable mobility, and large home ranges, kelp forests may represent one habitat within the seascape encountered by fish species with large home ranges (Topping et al. 2005, Topping et al. 2006). The experimental size of highly replicated studies may not capture all reef fish fauna. On other hand the observational studies using belt, 40-50 m transects are good for capturing both small and large home range species (Edgar et al. 2004, Edgar et al. 2011).

The high variability in effect sizes of kelp impacts on abundance and richness in observational studies might be driven by factors other than kelp forest which are either not reported or not quantified in all the studies. The physical environment and human impacts on reef fishes could be important parameters to consider and are often overlooked (Claudet et al. 2010, Claudet et al. 2011, Januchowski-Hartley et al. 2011, Januchowski-Hartley et al. 2012). In terms of habitat characteristics, kelp forest typifies a patchy habitat having different edges and variable in size with numerous understory foundation species. The variability in this components is determined by depth, slope, substratum rugosity which in synergy may structure fish assemblages (Efird and Konar 2013). On the other hand, substantial removal of large benthic carnivorous and herbivorous fishes from kelp forests in non-protected areas may provide insights of the variability observed in many observational studies (Hamilton et al. 2007, Caselle et al. 2011). The fish wariness in heavily fished kelp forests may represent another source of variability not measured in our selected studies (Goetze et al. 2017).

In conclusion, kelp represent a resource for many species, influencing directly other species that find refuge by the shaped root haptera that holds the kelp to the rocks (or any hard-bottom substrate) and fronds. Indirectly, kelp control the amount of light under their canopy which can reduce the cover of competing macroalgae whilst enhancing sessile invertebrates abundance (Arkema et al. 2009, Teagle et al. 2017) and reef fishes (PALMA and Ojeda 2002, Perez Matus et al. 2016). Threats on kelp are increasing from number of sources and drivers. Drivers can differ in magnitude and direction, and large-scale drivers can work antagonistically or synergistically with local drivers to influence the survival and growth of kelps forests (Araujo et al. 2013, Araújo et al. 2016, Hamilton et al. 2020). One of the biggest threats to kelp forests is climate change and especially, the rise in sea surface temperature (SST) (Wernberg et al. 2013, Reed et al. 2016, Smale and Moore 2017). High temperatures occurring with heatwaves can decimate complete kelp, impairing reproduction fertility, settlement and growth. In addition to such detrimental short-term events, long-term climatic events, like the El Niño–Southern Oscillation (ENSO), also pose significant threats (Dayton et al. 1999).. ENSO, for example, causes elevated ocean temperatures, which have had destructive effects on Pacific kelp forests (Edwards 2019). Furthermore, increases in storm frequency and intensity can lead to the dislodgement or breaking of individuals or complete stands of kelp (Reed et al. 2006). On the hand, kelp are harvested for their alginates or as food, and they have been harvested for over 16,000 years (Erlandson et al. 2007). Currently, harvesting effort is intensifying and the amount of kelp taken from the oceans increases (Vásquez and Santelices 1990, Vásquez 2008). Over one million tons wet weight of kelp are pulled from the ocean annually. Therefore, understanding the effect of such loss over important components of reef systems represents a moral responsibility in this changing world.

**Acknowledgements**

NERC-PCI ANID grant to APM; NCEAS Working Group

FONDECYT 1210216. ICM NCN19\_056 Granted to APM

**References**

Abesamis, R. A., and G. R. Russ. 2005. Density-dependent spillover from a marine reserve: long-term evidence. Ecological Applications **15**:1798-1812.

Airoldi, L., D. Balata, and M. W. Beck. 2008. The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. Journal of Experimental Marine Biology and Ecology **366**:8-15.

Airoldi, L., S. D. Connell, and M. W. Beck. 2009. The loss of natural habitats and the addition of artificial substrata.269-280.

Anderson, M. J., and A. Underwood. 1994. Effects of substratum on the recruitment and development of an intertidal estuarine fouling assemblage. Journal of Experimental Marine Biology and Ecology **184**:217-236.

Anderson, T. W. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. MARINE ECOLOGY-PROGRESS SERIES- **113**:279-290.

Angel, A., and F. P. Ojeda. 2001. Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. Marine Ecology Progress Series **217**:81-91.

Araújo, R. M., J. Assis, R. Aguillar, L. Airoldi, I. Bárbara, I. Bartsch, T. Bekkby, H. Christie, D. Davoult, S. Derrien-Courtel, C. Fernandez, S. Fredriksen, F. Gevaert, H. Gundersen, A. Le Gal, L. Lévêque, N. Mieszkowska, K. M. Norderhaug, P. Oliveira, A. Puente, J. M. Rico, E. Rinde, H. Schubert, E. M. Strain, M. Valero, F. Viard, and I. Sousa-Pinto. 2016. Status, trends and drivers of kelp forests in Europe: an expert assessment. Biodiversity and Conservation **25**:1319-1348.

Araujo, R. M., I. Bartsch, T. Bekkby, K. Erzini, and I. Sousa-Pinto. 2013. What is the impact of kelp forest density and/or area on fisheries? Environmental Evidence **2**.

Arkema, K., D. Reed, and S. Schroeter. 2009. Direct and indirect effects of giant kelp determine benthic community structure and dynamics. Ecology **90**:3126-3137.

Boettiger, C. D., D. T. Lang, and P. Wainwright. 2012. Rfishbase: Exploring, manipulating and visualizing FishBase data from R. Journal of Fish Biology **81**:2030-2039.

Carr, M. H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes\* 1. Journal of Experimental Marine Biology and Ecology **126**:59-76.

Carr, M. H. 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. Journal of Experimental Marine Biology and Ecology.

Carr, M. H. 1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology:1320-1333.

Caselle, J. E., S. L. Hamilton, D. M. Schroeder, M. S. Love, J. D. Standish, J. A. Rosales-Casián, and O. Sosa-Nishizaki. 2011. Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. Canadian Journal of Fisheries and Aquatic Sciences **68**:288-303.

Caselle, J. E., and R. Warner. 1996a. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. Ecology **77**:2488-2504.

Caselle, J. E., and R. R. Warner. 1996b. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. Ecology **77**:2488-2504.

Choat, J., A. Ayling, and D. R. Schiel. 1988. Temporal and spatial variation in an island fish fauna. Journal of Experimental Marine Biology and Ecology **121**:91-111.

Claudet, J., J. A. Garcia-Charton, and P. Lenfant. 2011. Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area. Conserv Biol **25**:105-114.

Claudet, J., C. W. Osenberg, P. Domenici, F. Badalamenti, M. Milazzo, J. M. Falcón, I. Bertocci, L. Benedetti-Cecchi, J. A. García-Charton, R. Goñi, J. A. Borg, A. Forcada, G. A. De Lucia, A. Perez-Ruzafa, P. Afonso, A. Brito, I. Guala, L. Le Diréach, P. Sanchez-Jerez, P. J. Somerfield, and S. Planes. 2010. Marine reserves: fish life history and ecological traits matter. Ecological Applications **20**:830-839.

Connell, S. D., and M. Kingsford. 1998. Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. Coral Reefs.

Cowen, R. K. 1983. The effects of sheephead (Semicossyphus pulcher) predation on red sea urchin (Strongylocentrotus franciscanus) populations: an experimental analysis. Oecologia **58**:249-255.

Davenport, A., and T. W. Anderson. 2008. Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers.

Dayton, P., M. Tegner, P. Edwards, and K. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecological Monographs **69**:219-250.

Dayton, P. K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics:215-245.

DeMartini, E. E., and D. Roberts. 1990. Effects of Giant Kelp (Macrocystis) on the Density and Abundance of Flshes in a Cobble-Bottom Kelp Forest. Bulletin of Marine Science **46**:287-300.

DeMartini, E. E., and D. A. Roberts. 1989. Contrasting patterns of fish density and abundance at an artificial rock reef and a cobble-bottom kelp forest. Bulletin of Marine Science **44**:881-892.

Deza, A. A., and T. W. Anderson. 2010. Habitat fragmentation, patch size, and the recruitment and abundance of kelp forest fishes. MARINE ECOLOGY-PROGRESS SERIES- **416**:229-240.

Donohue, I., H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L. Jackson, M. Lurgi, D. McClean, N. E. O'Connor, E. J. O'Gorman, and Q. Yang. 2016. Navigating the complexity of ecological stability. Ecol Lett **19**:1172-1185.

Edgar, G., N. Barrett, A. Morton, and C. Samson. 2004. Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. Journal of Experimental Marine Biology and Ecology **312**:67-87.

Edgar, G. J., S. A. Banks, S. Bessudo, J. Cortés, H. M. Guzman, S. Henderson, C. Martinez, F. Rivera, G. Soler, D. Ruiz, and F. A. Zapata. 2011. Variation in reef fish and invertebrate communities with level of protection from fishing across the Eastern Tropical Pacific seascape. Global Ecology and Biogeography **20**:730-743.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature **430**:881-884.

Edwards, M. S. 2019. Comparing the impacts of four ENSO events on giant kelp (Macrocystis pyrifera) in the northeast Pacific Ocean. Algae **34**:141-151.

Efird, T. P., and B. Konar. 2013. Habitat characteristics can influence fish assemblages in high latitude kelp forests. Environmental Biology of Fishes **97**:1253-1263.

Erlandson, J. M., M. H. Graham, B. J. Bourque, D. Corbett, J. A. Estes, and R. S. Steneck. 2007. The Kelp Highway Hypothesis: Marine Ecology, the Coastal Migration Theory, and the Peopling of the Americas. The Journal of Island and Coastal Archaeology **2**:161-174.

Froese, R., and D. Pauly. 2014. Fishbase. [www.fishbase.org](file:///Users/ale/Dropbox/Papers&%20Manuscripts/FIsh_kelp_Metaanalysis/www.fishbase.org).

Fulton, C. J., C. Berkström, S. K. Wilson, R. A. Abesamis, M. Bradley, C. Åkerlund, L. T. Barrett, A. A. Bucol, D. H. Chacin, K. M. Chong‐Seng, D. J. Coker, M. Depczynski, L. Eggertsen, M. Eggertsen, D. Ellis, R. D. Evans, N. A. J. Graham, A. S. Hoey, T. H. Holmes, M. Kulbicki, P. T. Y. Leung, P. K. S. Lam, J. Lier, P. A. Matis, M. M. Noble, A. Pérez‐Matus, C. Piggott, B. T. Radford, S. Tano, and P. Tinkler. 2020. Macroalgal meadow habitats support fish and fisheries in diverse tropical seascapes. Fish and Fisheries.

Goetze, J. S., F. A. Januchowski-Hartley, J. Claudet, T. J. Langlois, S. K. Wilson, and S. D. Jupiter. 2017. Fish wariness is a more sensitive indicator to changes in fishing pressure than abundance, length or biomass. Ecological Applicatios **27**:1178-1189.

Graham, M. 2004. Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. Ecosystems **7**:341-357.

Graham, M., J. Vasquez, and A. H. Buschmann. 2007. Global ecology of the giant kelp Macrocystis: from ecotypes to ecosystems. Oceanography and Marine Biology: An Annual Review **45**:39-88.

Halpern, B., S. Walbridge, K. A. Selkoe, C. Kappel, F. Micheli, C. D&apos;Agrosa, J. Bruno, K. Casey, C. Ebert, and H. Fox. 2008. A global map of human impact on marine ecosystems. Science **319**:948.

Hamilton, S. L., T. W. Bell, J. R. Watson, K. A. Grorud-Colvert, and B. A. Menge. 2020. Remote sensing: generation of long-term kelp bed data sets for evaluation of impacts of climatic variation. Ecology **101**:e03031.

Hamilton, S. L., J. E. Caselle, J. D. Standish, D. M. Schoeder, M. S. Love, J. A. Rosales-Casián, and O. Sosa-Nishizaki. 2007. Size-selecive harvesting alters life history of a temperate sex-changing fish Ecological Applicatios **17**:2268-2280.

Hastings, A., and L. Botsford. 2006. Persistence of spatial populations depends on returning home. Proceedings of the National Academy of Sciences **103**:6067.

Januchowski-Hartley, F. A., N. A. Graham, D. A. Feary, T. Morove, and J. E. Cinner. 2011. Fear of fishers: human predation explains behavioral changes in coral reef fishes. PLoS One **6**:e22761.

Januchowski-Hartley, F. A., K. L. Nash, and R. J. Lawton. 2012. Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. Marine Ecology Progress Series **469**:113-119.

Kramer, D., and M. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. Environmental Biology of Fishes **55**:65-79.

Kramer, D. L., and M. R. Chapman. 1979. Implications of fish home range size and relocation for marine reserve function - Springer. Environmental Biology of Fishes:1-15.

Krumhansl, K. A., D. K. Okamoto, A. Rassweiler, M. Novak, J. J. Bolton, K. C. Cavanaugh, S. D. Connell, C. R. Johnson, B. Konar, S. D. Ling, F. Micheli, K. M. Norderhaug, A. Perez-Matus, I. Sousa-Pinto, D. C. Reed, A. K. Salomon, N. T. Shears, T. Wernberg, R. J. Anderson, N. S. Barrett, A. H. Buschmann, M. H. Carr, J. E. Caselle, S. Derrien-Courtel, G. J. Edgar, M. Edwards, J. A. Estes, C. Goodwin, M. C. Kenner, D. J. Kushner, F. E. Moy, J. Nunn, R. S. Steneck, J. Vasquez, J. Watson, J. D. Witman, and J. E. Byrnes. 2016. Global patterns of kelp forest change over the past half-century. Proc Natl Acad Sci U S A **113**:13785-13790.

McDermott, C. J., and J. S. Shima. 2006. Ontogenetic shifts in microhabitat preference of the temperate reef fish *Forsterygion lapillum*:

implications for population limitation. Marine Ecology Progress Series **320**:259-266.

Micheli, F., and B. S. Halpern. 2005. Low functional redundancy in coastal marine assemblages. Ecology Letters **8**:391-400.

Miller, R. J., K. D. Lafferty, T. Lamy, L. Kui, A. Rassweiler, and D. C. Reed. 2018. Giant kelp, Macrocystis pyrifera, increases faunal diversity through physical engineering. Proc Biol Sci **285**.

Mora-Soto, A., M. Palacios, E. C. Macaya, I. Gómez, P. Huovinen, A. Pérez-Matus, M. Young, N. Golding, M. Toro, M. Yaqub, and M. Macias-Fauria. 2020. A High-Resolution Global Map of Giant Kelp (Macrocystis pyrifera) Forests and Intertidal Green Algae (Ulvophyceae) with Sentinel-2 Imagery. Remote Sensing **12**.

Mouillot, D., N. W. H. Mason, and J. B. Wilson. 2007. Is the abundance of species determined by their functional traits? A new method with a test using plant communities. Oecologia **152**:729-737.

Mouillot, D., S. Villéger, V. Parravicini, M. Kulbicki, J. E. Arias-Gonzalez, M. Bender, P. Chabanet, S. R. Floeter, E. B. J. E. C. C. F. G. A. T. P. I. P. E. V. A. M. W. E. S. Alan M Friedlander, L. Vigliola, and D. R. Bellwood. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proceedings of the National Academy of Sciences **111**:13757-13762.

Munday, P. L. 2002. Does habitat availability determine geographical-scale abundances of coral-dwelling fishes? Coral Reefs **21**:205-116.

Norderhaug, K., H. Christie, and S. Fredriksen. 2007. Is habitat size an important factor for faunal abundances on kelp (Laminaria hyperborea)? Journal of Sea Research **58**:120-124.

North, W. 1994. Review of Macrocystis Biology. Biology of Economic Algae:447-527.

Öhman, M. C., A. Rajasuriya, and E. Ólafsson. 1997. Reef fish assemblages in north-western Sri Lanka: distribution patterns and influences of fishing practises. Environmental Biology of Fishes **49**:46-61.

PALMA, Á., and F. P. Ojeda. 2002. Abundance, distribution and feeding patterns of a temperate reef fish in subtidal environments of the Chilean coast: the importance of understory algal turf. Revista Chilena de Historia Natural **75**:189-200.

Perez Matus, A., F. Sánchez, J. C. González-But, and R. W. Lamb. 2016. Understory algae associations and predation risk influence broad-scale kelp habitat use in a temperate reef fish. Marine Ecology Progress Series **559**:147-158.

Pérez-Matus, A., L. A. Ferry-Graham, A. Cea, and J. A. Vásquez. 2007. Community structure of temperate reef fishes in kelp dominated subtidal habitats of northern Chile. Marine and Freshwater Research **58**:1069-1085.

Pérez-Matus, A., F. Sánchez, J. C. González-But, and R. W. Lamb. 2016. Understory algae associations and predation risk influence broad-scale kelp habitat use in a temperate reef fish. Marine Ecology Progress Series **559**:147-158.

Pérez-Matus, A., and J. S. Shima. 2010a. Density- and trait-mediated effects of fish predators on amphipod grazers: potential indirect benefits for the giant kelp Macrocystis pyrifera. Marine Ecology Progress Series **417**:151-158.

Pérez-Matus, A., and J. S. Shima. 2010b. Disentangling the effects of macroalgae on the abundance of temperate reef fishes. Journal of Experimental Marine Biology and Ecology **388**:1-10.

Reed, D., B. Kinlan, P. Raimondi, L. Washburn, B. Gaylord, and P. Drake. 2006. A metapopulation perspective on the patch dynamics of giant kelp in Southern California. Marine metapopulations:353–386.

Reed, D., A. Rassweiler, and K. Arkema. 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology **89**:2493-2505.

Reed, D., A. Rassweiler, and K. Arkema. 2009. Density derived estimates of standing crop and net primary production in the giant kelp Macrocystis pyrifera. Marine Biology **156**:2077-2083.

Reed, D., L. Washburn, A. Rassweiler, R. Miller, T. Bell, and S. Harrer. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. Nature Communications **7**:13757.

Rohatgi, A. 2020. WebPlotDigitizer. <https://automeris.io/WebPlotDigitizer>, Pacifica, California, USA.

Ruz, C. S., A. F. Muth, F. Tala, and A. Pérez-Matus. 2018. The herbivorous fish, Aplodactylus punctatus , as a potential facilitator of dispersal of kelp, Lessonia trabeculata , in Chile. Journal of Experimental Marine Biology and Ecology **500**:112-119.

Schiel, D. R., and M. S. Foster. 2006. The population biology of large brown seaweeds: Ecological consequences of multiphase life histories in dynamic coastal environments. Annual Review Of Ecology Evolution And Systematics **37**:343-372.

Shima, J. S., and C. Osenberg. 2003. Cryptic density dependence: effects of covariation between density and site quality in reef fish. Ecology **84**:46-52.

Smale, D. A., and P. J. Moore. 2017. Variability in kelp forest structure along a latitudinal gradient in ocean temperature. Journal of Experimental Marine Biology and Ecology **486**:255-264.

Syms, C. 1995. Multi-scale analysis of habitat association in a guild of blennioid fishes. Marine ecology progress series. Oldendorf **125**:31-43.

Syms, C. 1998. Disturbance and the structure of coral reef fish communities on the reef slope. Journal of Experimental Marine Biology and Ecology **230**:151-167.

Syms, C., and G. P. Jones. 1999. Scale of disturbance and the structure of a temperate fish guild. Ecology **80**:921-940.

Taylor, R. 1997. Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. Hydrobiologia **361**:25-35.

Taylor, R. 1998. Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. MARINE ECOLOGY-PROGRESS SERIES- **172**:37-51.

Teagle, H., S. J. Hawkins, P. J. Moore, and D. A. Smale. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. Journal of Experimental Marine Biology and Ecology **492**:81-98.

Tolimieri, N. 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia **102**:52-63.

Topping, D. T., C. Lowe, and J. E. Caselle. 2006. Site fidelity and seasonal movement patterns of adult California sheephead Semicossyphus pulcher (Labridae): an acoustic monitoring study. MARINE ECOLOGY-PROGRESS SERIES- **326**:257-267.

Topping, D. T., C. G. Lowe, and J. E. Caselle. 2005. Home range and habitat utilization of adult California sheephead, Semicossyphus pulcher (Labridae), in a temperate no-take marine reserve. Marine Biology **147**:301-311.

Valesini, F. J., I. C. Potter, and K. R. Clarke. 2004. To what extent are the fish composition at nearshore sites along a heterogeneous coast related to habitat type? Estuarine Coastal and Shelf Science **60**:737-754.

Vasquez, J., and A. H. Buschmann. 1997. Herbivore-kelp interactions in Chilean subtidal communities: a review. Revista Chilena de Historia Natural **70**:41-52.

Vásquez, J. A. 2008. Production, use and fate of Chilean brown seaweeds: re-sources for a sustainable fishery. Journal of Applied Phycology **20**:457-467.

Vásquez, J. A., and B. Santelices. 1990. Ecological effects of harvesting Lessonia (Laminariales, Phaeophyta) in central Chile. Hydrobiologia **204**:41-47.

Vásquez, J. A., S. Zuñiga, F. Tala, N. Piaget, D. C. Rodríguez, and J. M. A. Vega. 2013. Economic valuation of kelp forests in northern Chile: values of goods and services of the ecosystem. Journal of Applied Phycology **26**:1081-1088.

Wellenreuther, M., P. T. Barret, and K. D. Clements. 2007. Ecological diversification in habitat use by subtidal triplefin fishes (Tripterygiidae). Marine Ecology Progress Series **330**:235-246.

Wernberg, T., K. A. Krumhansl, K. Filbee-Dexter, and M. F. Pedersen. 2018. Status and trends of the world's kelp forests.

Wernberg, T., B. D. Russell, P. J. Moore, S. D. Ling, D. A. Smale, A. Campbell, M. A. Coleman, P. D. Steinberg, G. A. Kendrick, and S. D. Connell. 2011. Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. Journal of Experimental Marine Biology and Ecology **400**:7-16.

Wernberg, T., D. A. Smale, F. Tuya, M. S. Thomsen, T. J. Langlois, T. de Bettignies, S. Bennett, and C. S. Rousseaux. 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nature Climate Change **3**:78-82.

Wernberg, T., M. S. Thomsen, F. Tuya, G. A. Kendrick, P. A. Staehr, and B. D. Toohey. 2010. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecology Letters **13**:685-694.

White, J. W., and J. E. Caselle. 2008. Scale-dependent changes in the importance of larval supply and habitat to abundance of a reef fish. Ecology **89**:1323-1333.

Williams, G. J., M. J. Cameron, J. R. Turner, and R. B. Ford. 2008. Quantitative characterisation of reef fish diversity among nearshore habitats in a northeastern New Zealand marine reserve. New Zealand Journal of Marine and Freshwater Research **42**:33-46.

Winkler, N. S., A. Pérez-Matus, Á. A. Villena, and M. Thiel. 2017. Seasonal variation in epifaunal communities associated with giant kelp (Macrocystis pyrifera) at an upwelling-dominated site. Austral Ecology **42**:132-144.

Witman, J. D., J. E. Byrnes, and R. W. Lamb. 2015. Towards an integration of scale and complexity in marine ecology. Ecological Monographs **85**:475–504.

**Tables**

Table 1. Total number of studies included in this review, given by the author(s) year, response variable measured included such as species richness, total abundance of reef fish assemblage and/or abundance of a single species. Refer to methods for more details \*denotes for unpublished data sets.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| N | Author | Species Richness | Total Abundance | Single Species | Type of Study |
| 1 | Anderson (1994) |  |  | Yes | Observational |
| 2 | Anderson and Millar (2004) | Yes | Yes |  | Observational |
| 3 | Black and Miller (1991) | Yes | Yes |  | Experimental |
| 4 | Bodkin (1988) |  | Yes | Yes | Experimental |
| 5 | Carr (1989) |  |  | Yes | Experimental |
| 6 | Carr (1991) |  | Yes | Yes | Experimental |
| 7 | Carr (1994) |  |  | Yes | Observational |
| 8 | Choat and Ayling (1987) |  | Yes |  | Observational |
| 9 | Cole et al. (2012) |  | Yes | Yes | Experimental |
| 10 | Curley et al. (2002) |  |  | Yes | Observational |
| 11 | Dean et al. (2000) |  | Yes |  | Observational |
| 12 | De Martini and Roberts (1990) |  | Yes |  | Observational |
| 13 | De Martini et al. (1989) |  |  | Yes | Observational |
| 14 | Ebeling and Laur (1985) |  |  | Yes | Experimental |
| 15 | Edgar et al. (2004) |  |  | Yes | Experimental |
| 16 | Feary and Clements (2006) |  |  | Yes | Observational |
| 17 | Gillanders and Kingford (1998) |  |  | Yes | Observational |
| 18 | Graves et al. 2006 |  |  | Yes | Observational |
| 19 | Holbrook et al. (1990) |  |  | Yes | Observational |
| 20 | Holbrook et al. (1994) |  |  | Yes | Observational |
| 21 | Irigoyen et al. (2011) |  | Yes |  | Observational |
| 22 | Jones (1984) |  |  | Yes | Observational |
| 23 | Kingsford (2011)\* | Yes | Yes |  | Observational |
| 24 | Krumhansl et al. (2015) | Yes | Yes |  | Experimental |
| 25 | Levin (1993) |  |  | Yes | Experimental |
| 26 | Levin and Hay (1996) |  |  | Yes | Experimental |
| 27 | Levin and Hay (2002) |  |  | Yes | Experimental |
| 28 | Ling (2014)\* | Yes |  |  | Observational |
| 29 | Lorentsen et al. (2010) |  | Yes | Yes | Experimental |
| 30 | McDermott and Shima (2006) |  |  | Yes | Experimental |
| 31 | Moreno and Jara (1984) |  |  | Yes | Experimental |
| 32 | Morton and Gladstone (2011) | Yes | Yes | Yes | Observational |
| 33 | O'Connor and Anderson (2010) |  | Yes |  | Experimental |
| 34 | Perez-Matus and Shima (2010) |  | Yes | Yes | Experimental |
| 35 | Perez-Matus et al. (2007) |  | Yes | Yes | Observational |
| 36 | Salter et al (2010) |  |  | Yes | Experimental |
| 37 | Schmidt and Scheibling (2007) |  |  | Yes | Experimental |
| 38 | Smith et al. (2014) | Yes | Yes | Yes | Observational |
| 39 | Steele et al. (2002) |  | Yes | Yes | Observational |
| 40 | Syms and Jones (1999) |  |  | Yes | Experimental |
| 41 | Villegas et al. (2019) | Yes | Yes |  | Experimental |
| 42 | Williams et al. (2008) |  | Yes | Yes | Observational |
| 43 | Willis and Anderson (2003) | Yes | Yes |  | Observational |
| 44 |  |  |  |  |  |

**Figure Captions**

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. Ecoregion

Figure 3. Effect size (Hedges’ g) of a) total reef fish abundance and b) reef fish species richness meta-analysis in both experimental and observational (i.e., observational) studies. Number above each study type indicates the data points.

Figure 4. Effect size (Hedges’ g) of kelp architectural complexity (single, multiple stipes or both single and multiple stipes) on a) total reef fish abundance and b) species richness.

Figure 5. Interaction between trophic level (i.e., course trophic categories such as herbivores, mesopredators, top predators) and total fish length (Maximum size in TL, cm) over the effect size (Hedges’ g) of single species abundance. Grey area is represented by confidence interval (CI) and precision of the effect size (Hedges’ g). Trendline represented by correlation between Hedges’ g and max fish size at each trophic course category.

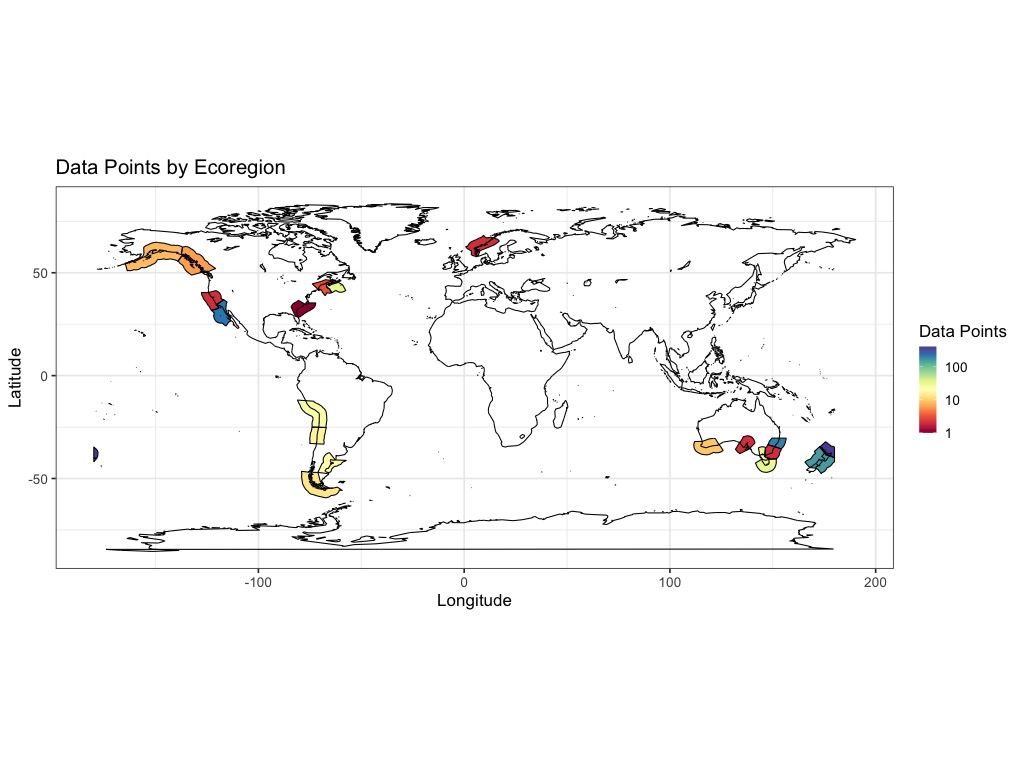
****

Figure1.,

Chart, box and whisker chart

Description automatically generated

Figure 2.,

Chart, scatter chart

Description automatically generated

Figure 3.,

Chart, line chart, scatter chart

Description automatically generated

Figure 4,

Chart, scatter chart

Description automatically generated

Figure 5.,