The role of predators and species diversity in structuring marine ecosystems

by

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Abstract

Marine ecosystems contain both highly abundant and diverse communities of vertebrates and invertebrates; however anthropogenic activity has drastically altered the species composition and diversity of these ecosystems. Specifically, human activity has targeted high trophic level species and degraded much of the biogenic habitat that faunal communities rely upon. These alterations have resulted in the loss of many marine predators and overall declines of marine biodiversity. To investigate the consequences of marine predator loss and community level species decline, I use a combination of large-scale data synthesis and in situ field observations of marine fish communities. I first use a meta-analysis approach to synthesize the consequences of marine predator loss in benthic marine ecosystems worldwide. From this synthesis, I was able to determine some of the biotic and abiotic factors that regulate the response of marine herbivores and primary producers to predator loss. Specifically, I show that marine predators have the strongest effect on populations of marine herbivores when predators and herbivores were similar in size and when larger herbivores were involved. Conversely the factors that best explained the response of the primary producer populations were related to the abiotic environment. The results show that primary producers respond the most positively to the presence of predators in high nutrient environments. While I found no link between the magnitude of change in the herbivore population and the magnitude of change in the producer population, I was able to demonstrate that primary producers are under the strongest top-down controls when nutrient concentrations are high, sea surface temperatures are low, and when the predator is larger in size than the herbivore. Finally, I use the data related to marine reserves to show that reserves are an effective tool to help reverse the trophic consequences of marine predator loss and that they are most effective when they are older in age. The third chapter examines the links between community diversity and community biomass within fish communities in eelgrass ecosystems in Northern British Columbia. After controlling for environmental variation, I found that it was the dominance of certain species within a community that resulted in the highest ecosystem function. This finding was demonstrated by both the taxonomic and functional metrics of diversity used. While previous work on this topic has shown that richness is positively correlated to function, my results are to the contrary, and suggest that further investigation into which aspects of community diversity drive ecosystem function is required. In conclusion, my results provide a new synthesis of the consequences of marine predator loss across the world and show how species diversity is linked to ecosystem function in local eelgrass fish communities.

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Acknowledgments

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Chapter 1 - Introduction

Coastal marine ecosystems cover a fraction of the earth but contain an extraordinarily high diversity of marine flora and fauna (Gray 1997). The diversity of fauna within these ecosystems ranges from the microscopic base of the food web to marine mammals and predatory fish at the top. Such biodiversity consists of hundreds of thousands of invertebrates (Mora et al. 2011), tens of thousands of fish species (Gray 1997), and numerous biogenic habitats such as kelp forests and seagrass meadows (Barbier et al. 2011). This biodiversity is tightly linked to the goods and services provided by coastal ecosystems. In fact, coastal ecosystems are of enormous economic importance and are estimated to provide 43% of the world's ecosystems goods and services (Costanza et al. 1997).

As the human footprint continues to expand, ocean ecosystems across the world are being altered in substantial ways. Activities such as industrial fishing, shoreline modification, warming ocean temperatures, and marine pollutants have had significant effects on the biotic composition and condition of marine ecosystems (Hoegh-Guldberg and Bruno 2010, Halpern et al. 2015). These changes are most typically realized as declines in faunal species richness and abundance (Dulvy et al. 2006) as well as declines in habitat-forming producer species (Lotze et al. 2006). Such changes have been shown to have negative impacts on the different ecosystem services and functions provided by marine fauna (Worm et al. 2006) and habitats (Costanza et al. 1997). Of the aspects of the ocean being affected, predatory species (Heithaus et al. 2008) and seagrass ecosystems (Waycott et al. 2009) have been notably impacted. Given their immense economic value and vulnerable status, there is a strong interest in better understanding how these changes are occurring, and how to make predictions about when they will occur (Palumbi et al. 2009).

Within marine biodiversity, marine predators are a numerous and diverse group of species, ranging from smaller crustaceans (Elner and Jamieson 1979) to large chondrichthyans, osteichthyans (Sibert et al. 2006), and mammalian species (Estes et al. 1998). Such predatory species are essential to fisheries and extractive harvest industries across the world (Smith and Addison 2003, Myers and Worm 2005) and provide both a crucial food source to billions of people across the globe as well as a source of local income (Allison et al. 2009). Beyond their economic value, marine predators play an influential role in shaping the biotic composition of their communities (Shurin et al. 2010). In a three-level food web, marine predators exert predation pressure on the herbivore community that helps mitigate the negative pressure from the herbivores on the primary producers; such an interaction has been termed a trophic cascade. If the predators are removed from the system, the predation pressure on the herbivores is eased and their populations increase. As a result of the herbivore increase, the predation pressure on the primary producers is increased as well. Consequently, the decrease of predators from an ecosystem can result in the decline of the primary producers of that ecosystem (Pinnegar et al. 2000). Trophic cascades are not exclusive to marine systems, but are currently thought to play a particularly strong role in shaping benthic marine systems (Shurin et al. 2002, Shurin et al. 2010).

As a result of their economic value, marine predators have faced particularly strong harvest pressures and subsequent declines. Most notably, large predatory fish have declined 66% over the last 100 years (Christensen et al. 2014). Three-quarters of pelagic shark species have been classified as threatened or near threatened (Dulvy et al. 2008). Crustacean fisheries have shown repeated crashes (Armstrong et al. 1998). Furthermore, species such as the sea otter (*Enhydra lutris*) have been extirpated from much of their home range (Larson et al. 2002). These declines have had extraordinary economic and ecological consequences (Jackson et al. 2001, Hutchings and Reynolds 2004) and while it is accepted that these loses impact the community, further work is required to understand the context dependencies of these losses.

Seagrass ecosystems are of similar importance to the marine seascape and are classified as the third most valuable ecosystem per hectare (Costanza et al. 1997). Specifically they are known to be a critically important habitat, especially for juvenile fishes and invertebrates which grow faster and to higher densities in seagrass meadows than in alternate habitats (McDevitt-Irwin et al. 2016). Consequently, seagrass ecosystems support many different fishery species across the world (Unsworth and Cullen 2010). In addition to fishery species, seagrass ecosystems provide habitat to numerous other taxa that are both residential and transient within the meadows, as a result seagrass ecosystems are of vital importance to marine food webs within the seagrass itself and habitat in proximity to the seagrass (Phillips 1984, Heck et al. 2008).

Given their importance to marine ecosystems, it is all the more alarming that seagrasses have declined by over 30% since the 1890s and that the median rate of loss has accelerated to 7% per year since 1990 (Waycott et al. 2009). These losses are also largely anthropogenic in nature, with habitat destruction, eutrophication, and increased sedimentation being some of the largest factors responsible for their decline (Waycott et al. 2009). Concurrent with the loss of the seagrass, is the loss of biodiversity, specifically, that which resides within or relies upon seagrass habitat at some point during its life stage (Barbier et al. 2011). The loss of this biodiversity consequently negatively impacts a variety of ecosystem services and functions that are crucial to human and non-human well being (Hooper et al. 2012).

Marine biodiversity loss, whether it is marine predators or community diversity, is expected to be an ongoing issue in marine conservation for years to come (Tanzer et al. 2015). It is therefore of high importance that we work to better understand how these two different types of biodiversity-loss, predator removal and general diversity declines- impact overall ecosystem functioning. This thesis seeks to address these questions by making use of synthetic data and *in situ* community observations. First, this thesis uses a meta-analysis approach to ask how biotic and abiotic factors influence the degree to which marine predator loss drives changes in marine herbivore and primary producer populations. Secondly, this thesis uses observational community level data to assess the influence of fish biodiversity in real-world eelgrass ecosystems in Northern British Columbia, Canada.

Trophic cascades within marine benthic ecosystems have provided some of the best-known examples of trophic cascades in nature, but they have also demonstrated considerable variability in strength. Because only a few studies have been synthesized, there is little research into what drives this variability. As a result, there is an incomplete understanding of when to expect cascades to be strongest or weakest in benthic marine systems; a serious limitation given that cascades have become well integrated into both ecological theory and management policies. To better understand the determinants, management impacts, and strengths of trophic cascades in marine benthic ecosystems, the second chapter synthesizes 57 independent data points, and 129 measurements using a synthetic meta-analysis approach.

Marine reserves are a popular management tool in marine conservation and several stand-alone studies have demonstrated how marine reserves can help reverse the effects of marine predator loss. However, no study has synthesized the existing data to determine the overall size effect of marine reserves in a trophic cascade context. Consequently, we are unsure about the overall influence of reserves on food web dynamics and which aspects of a marine reserve might influence a reserve's ability to restore predators, reduce herbivores, and benefit primary producers. I use this same data set to explore the answers these questions and provide a more thorough understanding of the links between marine reserves and trophic cascades.

Finally, it is currently believed that trophic cascades are stronger in benthic marine systems compared to terrestrial ecosystems. I take advantage of an updated sample size to re-examine this notion. By doing so, I provide a more up to date and thorough understanding of the strength of trophic cascades in marine systems and how they compare to past work in other systems.

Taken all together, this work strengthens our understanding of the drivers of benthic marine cascades, highlights the use of reserves to induce cascades, and establishes a new baseline of trophic controls and cascades in benthic marine systems.

The third chapter seeks to investigate the link between biodiversity and ecosystem function within fish communities in eelgrass meadows (genus: *Zostera*) in Northern British Columbia, Canada. The two main mechanisms that are thought to link BEF are the complementarity hypothesis, where all species contribute to ecosystem function, or the selection hypothesis where only particular species are needed to sustain ecosystem function. The selection hypothesis can also be extended to determine if it is the presence or the relative abundance (dominance) of particular species that drives function. My work builds on several recent studies that have tested the relationship between richness diversity metrics in large-scale marine systems while also adding new analysis related to species trait and taxonomic dominance.

To investigate the link between biodiversity and ecosystem function, I ask how the taxonomic and functional diversity of fishes influence community standing stock biomass in 14 eelgrass meadows in the Northeast Pacific. To achieve this, I combine taxonomic and functional measures of diversity to investigate if it is the diversity of species within an ecosystem that drive function (complementarity hypothesis) or if it is the presence and-or dominance of particularly important species that drive function (selection and dominance hypotheses).

In conclusion, this thesis first tests the biotic and abiotic drivers of food web perturbations following marine predator loss and second determines whether the complementarity, selection, or dominance hypothesis describe the relationship between biodiversity and ecosystem function within a near shore marine ecosystem. As a result, this work allows researchers and managers to more accurately predict the consequences of marine predator loss and removal, as well as to better understand which aspects of biodiversity are driving ecosystem function within eelgrass ecosystems in Northern British Columbia. This work substantially updates our understanding of trophic cascades in marine systems and helps explain the links between biodiversity and ecosystem function at the ecosystem level.

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Chapter 2 - Trophic cascades in benthic marine ecosystems: a meta analysis of experimental and observational research

2.1. Introduction

Trophic cascades (defined as a predator population positively influencing a producer population by controlling a herbivore population) in benthic marine ecosystems are well established in many contexts and include textbook cases (Duggins 1980), experimental studies (Bruno and O'Connor 2005), and management induced cascades whereby management action allows for the return of predators whose effects than cascade to producers (Shears and Babcock 2002). As a result, trophic cascades have become a paradigm of marine ecology as well as a tangible management action for marine conservation (Halpern 2003, Estes et al. 2011). However, within all these studies there is a demonstrated variation in the response of herbivore and producer populations to predator presence and absence (herein, "cascade strength"; Shurin et al. 2002, Borer et al. 2005). Moreso, very little work has been conducted that explains this observed variation (Hessen and Kaartvedt 2014, though see elements in: He and Silliman 2016, Östman et al. 2016). As a result we are restricted in our ability to predict when marine benthic cascades should be strongest or weakest, which translates into an inability to predict the potential ecosystem consequences of marine predator loss or restoration, issues that are highly germane as ocean predators continue to decline (Christensen et al. 2014) and as the oceans become more managed and more protected (Edgar et al. 2014).

While the determinants of benthic marine cascades have yet to be deeply explored, we can devise a number of hypotheses based on the findings of prior work in alternate systems. Specifically, we can expect the strength of a cascade to vary based on the abiotic, biotic, or methodological contexts in which they occur (Shurin et al. 2002, Borer et al. 2006, Rodríguez-Castañeda 2013).

The key abiotic hypotheses relate sea surface temperature and nutrient availability to cascade strength. It is thought cascades are strongest in environments with higher levels of nutrients because these systems are not nutrient limited and should instead be controlled by top-down forces (Oksanen et al. 1981, Jeppesen et al. 2003, Östman et al. 2016). Stronger cascades could also be expected in areas with higher sea surface temperatures, as metabolic rates and energy demands are typically higher resulting in higher predation and grazing rates (Bruno et al. 2015). However, these predictions are expected to be mutually exclusive as lower sea surface temperatures were correlated with higher nutrient levels.

The leading biological hypotheses focus on species sizes and the connectivity between trophic levels. The strongest cascades are expected when the predators and herbivores are similar in size, which facilitates prey matching (Vucic-Pestic et al. 2010) and when larger predators and herbivores are involved as they have higher consumption rates (DeLong et al. 2015). Following from the predator-herbivore interaction, we expect that changes in the producer population will be negatively correlated with the predator-induced changes in the herbivore population (Shurin et al. 2002). Furthermore, we hypothesize that we can use this relationship between the change in herbivore populations and the change in the producer populations to infer when systems are top-down controlled as opposed to bottom-up, a central question in ecology (Hunter and Price 1992). Specifically, we predict that producers will respond more strongly to changes in herbivore populations when systems are not nutrient limited and are thus more likely to be top-down controlled (Oskanen et al. 1981, Jeppesen et al. 2003, Östman et al. 2016, see methods for further details).

The other biological hypotheses are linked to species life history traits and are as follows. Cascades should be strongest when the producers have longer generation times, as they are less able to rebound from the effects of grazing over the time span of the study (Shurin et al. 2006, Poore et al. 2012). Moving up a trophic level, it is reasoned that invertebrates have higher grazing efficiencies and susceptibility to predators, both factors that should lead to stronger cascades (Polis and Strong 1996, Borer et al. 2005) compared to cascades involving vertebrate herbivores. With regard to predators, vertebrate predators have been hypothesized to be involved in the strongest cascades due to their higher predation rates (Borer et al. 2005). By better understanding the mechanisms of cascade strength, we can better predict the consequences of predator loss and introduction in a variety of circumstances.

While trophic cascades have traditionally been tested at the experimental plot level (Terborgh et al. 2010), marine reserves in which predators are able to re-establish have provided an opportunity to test trophic cascades at the ecosystem level (Shears et al. 2008, McClanahan et al. 2011). Because they are not directly manipulated, we expect that cascades will not be as strong in the protected area studies as they are in controlled, experimental research (Hillebrand 2009), but will never-the-less prove to be a viable management option for reversing the trophic effects of marine predator decline. Within reserves, it is also expected that cascade strength will amplify with reserve age as the predators have had longer to recover from harvest pressure (Molloy et al. 2009), but not size, as has been previously found with predator return (Lester et al. 2009).

Finally, it has been previously noted that cascades are strongest in aquatic and specifically marine benthic ecosystems (Strong 1992, Polis 1999, Halaj and Wise 2001, Shurin et al. 2002, Shurin et al. 2010), but these conclusions have been made based on postulations and limited sample sizes. This research takes the opportunity presented by the updated sample size to retest this notion and provide a new baseline for cascade strength in benthic marine ecosystems. Furthermore, this work aims to highlight existing data gaps in cascade research as to encourage future research to fill those gaps and continue to develop our knowledge base.

By bringing all of these concepts together into one study, this research aims to: (i) quantify the direction and strength of trophic cascades in marine benthic ecosystems, (ii) identify the relationships of trophic cascade strength with abiotic (environmental conditions, marine reserve characteristics) and biotic (body size, species type) factors, (iii) examine the management implications of marine reserve characteristics for trophic cascades and (iv) compare the results from the new data to previous meta analysis results. To achieve these goals, this study is global in extent (Appendix A Fig. A1), contains 57 independent data points comprising 129 measurements and focuses on near shore benthic marine ecosystems.

2.2. Methods

2.2.1. Literature search and study selection

First off, I conducted a literature review using SCOPUS Web of Science (WOS) and Google Scholar for two separate searches. The first search looked for studies that examined trophic cascades using experimental methods. The search terms were as follows: ("top down" or trop* or cascad* or contr* or indirect*) AND (exclus* or enclos* or remov* or cage* or fenc* or mesocosm) AND (marine or sea or ocean) AND (pred* or prey) AND (primary or producer or *grass or *phyte or alga* or seaweed). The second search targeted studies that examined natural experiments and observations, primarily the establishment of marine reserves and used the search terms: ("top down" or trop* or cascad* or contr* or indirect*) AND TOPIC: (reserve* or MPA or park or protect*) AND TOPIC: (marine or sea or ocean) AND TOPIC: (pred* or prey) AND TOPIC: (primary or producer or *grass or *phyte or alga* or seaweed). The WOS search was restricted to ecological and environmental science categories. The original WOS search resulted in 735 and 1789 studies for the first and second search respectively and Google scholar was used to verify the thoroughness of the first search.

After reading the abstracts and titles, I examined the bodies of text for 208 selected studies to determine if they met the inclusion criteria. A study was included if it occurred in a photic benthic marine environment and measured the mean and variance of herbivore and producer populations with and without predators present. To be included, the primary producer metric had to be measured in one of the following units: biomass, density, percent cover, or chlorophyll a concentration in the water column. The herbivore metric had to be recorded using density, biomass, or abundance measurements. I extracted the data from the qualifying studies using graphClick 3.0.3 (Arizona Software Inc., USA).

I excluded a study if it only examined an omnivorous predator (Heck et al. 2000), only reported values for grazing rate or tissue damage (Shurin et al. 2002, Borer et al. 2005), only recorded the predator effect when mixed with another treatment (e.g. nutrient addition), used cages that excluded both herbivorous and predatory species, or only provided modeled results. I also excluded studies if they recorded predator, herbivore, or producer populations greater than one month apart from each other. Specific to marine reserves, I excluded studies that used fisheries landings as a proxy for biomass or if the study reported herbivores that were part of an active fishery, as they too would directly benefit from the protection of the reserve.

This study had several other criteria for data point selection. For instance, if a study had multiple time points, the point at the end of the study was used because this point should be the closest to population equilbrium. If a study manipulated a predator and recorded more than one herbivore or primary producer, each species response was considered individually while acknowledging that they are not independent events - see effect size calculation. If a study recorded both biomass and abundance, biomass was used as the metric of measurement. If zero values were present in either the herbivore or the producer metric, the lowest reasonable value that could have been recorded was substituted (e.g. 1 if abundance was measured or 1% if percent cover was measured, as suggested by Poore et al. 2012).

2.2.2. Calculation and analysis of the effect sizes

This work used a meta-analysis approach to examine the effect size -direction and -magnitude of the herbivore and primary producer metrics with and without predators. I opted to use the log-response ratio as the measure of effect size (Borenstein et al. 2009) as to facilitate comparison with past studies on this subject (Shurin et al. 2002, Borer et al. 2005, Poore et al. 2012). However, I diverged from the two major prior studies (Shurin et al. 2002, Borer et al. 2005), and included measures of variance while calculating the effect size. The prior reasoning was that there were more studies without variance than those with. This is no longer the case, as only 24 (out of 153) data points had to be removed due to a lack of variance data. I used the R programming environment 3.3.3 (R Core Team 2015), the package *metafor (*Viechtbauer 2010) to calculate the effect sizes, and the package *ggplot2* (Wickham 2016).

A positive herbivore or producer effect size indicates an increase in the population in the presence of the predator and a negative effect size indicates a decrease. A significant herbivore effect size had a 95% CI less than 0 and a significant producer effect size had a 95% CI greater than 0. The overall 95% confidence interval (CI) and the CI for the subfactors within: study type, study method, predator type, herbivore type, and primary producer type were calculated to determine if the presence of a predator had an effect on the herbivore or primary producer population.

2.2.3. Predictor variables of trophic cascade strength

Once a data point was marked for inclusion, I collected a variety of factors, both quantitative and qualitative (Appendix A Table A1). Specifically, I used the world ocean atlas dataset (Levitus et al. 2013) and the site's geographic coordinates (atlas resolution 1˚ x 1˚) to extract Sea surface temperature (SST), nitrate concentrations, and phosphate concentrations for each data point. Mesocosm studies were excluded from this analysis because these field variables, SST, nitrate concentration, and phosphate concentration, would not necessarily be representative of the conditions in the mesocosm. The body size of predators and herbivores was measured in centimeters as the maximum length in any dimension and were either taken from the study or extracted from the online sources. If multiple species were present, I used the mean body size. I calculated the marine reserve age as the year the work was conducted minus the year the reserve was founded and the reserve size data was sourced from the publication or extracted from the web (see supplement for sources). Finally, the categorical factors that I recorded were, predator type (invertebrate, vertebrate), herbivore type (invertebrate, vertebrate), and primary producer type (macro algae, micro algae, epiphytic algae, seagrass).

I analyzed the statistical significance of the predictor variables (Appendix A Table A1) using linear mixed effects models that were developed using the *rma.mv* function, which is also found in the *metafor* package. During these calculations, location ID was considered as the random effect. I chose mixed effects models to account for the number of repeated measures used in the analysis (e.g. same study, different species considered). If a factor had a P value < 0.05, it was tested for significant within-group differences using a Tukey Honest Significance test with a Bonferroni correction by using the R package *multcomp* (Hothorn et al. 2008). No statistical difference was found between the effect sizes of the observational studies and the experimental studies so I analyzed all studies together.

2.2.4. Trophic connection between herbivores and producers

I determined the strength of the trophic connection to be the relative change in the producer population given a change in the herbivore population. I calculated this metric by taking the residuals of a 1:1 regression line with the producer effect sizes greater than zero on the y-axis and the herbivore effect sizes less than zero on the x-axis. A value of 0 indicates that for every unit change in the herbivore metric, there was a proportional change in the producer metric. A negative residual signifies a smaller increase in the producer metric than in the herbivore and a positive value indicates the opposite. These values were then tested for significance using the same methods as above except that the *nlme* package (Pinheiro et al. 2014) in R was used.

Similarly, I used the *nlme* package in R to test whether the effect sizes from this study are significantly different than those found in Shurin et al. (2002) and Borer et al.'s (2005) work across alternate terrestrial and aquatic systems.

2.3. Results

The presence of predators had significant negative impacts on herbivore populations and significant positive impacts on primary producer populations. Herbivores decreased an average of 3.52 times (95% CI, 2.25 – 5.58, Fig. 2.1.) in the presence of predators while producers increased an average of 2.27 times (95% CI, 1.66 – 3.13, Fig. 2.1., Appendix A Table A2). However, no significant difference ($P > 0.05$, Appendix A Table A3) was found between experimental and observational studies for either effect size.

2.3.1. Within group effect sizes

The presence of a predator on the herbivore and producer populations was found to have a significant effect compared to treatments with no predator in most of the categories considered. The exception was for studies that used a study design with an enclosure approach; here it was found that both the herbivore (95% CI > 0) and producer effect sizes (95% CI < 0) were non-significant (Appendix A Table A2). The only other non-significant herbivore effect size was found for studies that contained herbivores with vertebrae (Appendix A Table A2). Finally, the only non-significant producer effect sizes were found for studies where the primary producers were either epiphytes or seagrass (Appendix A Table A2).

2.3.2. Predictors of the herbivore effect size

Four factors were significant predictors of the herbivore effect size. First, studies occurring in higher temperatures were found to have greater reductions in herbivores when predators were present ($P = 0.04$, $N = 94$, Fig. 2.2., Appendix A Table A3). Second, the reduction in herbivores was greatest when predators were more similar in size to the herbivores, as indicated by a low predator to herbivore size ratio ($P < 0.01$, $N = 129$, Fig. 2.2., Appendix A Table A3). Third, the reduction in herbivores was found to be greatest when larger herbivores were involved in the study ($P < 0.01$, $N = 129$, Fig. 2.2., Appendix A Table A3). Fourth and finally, the study method was found to be a significant categorical predictor ($P = 0.01$, $N = 129$, Appendix A Table A3), but there were no significance within group differences ($P > 0.05$, Appendix A Table A4).

2.3.3. Predictors of the producer effect size

The key significant predictors of the producer effect size were abiotic. Studies that had higher phosphate and nitrate levels had larger increases in producer populations when predators were present ($P = 0.04$ and $P = 0.02$, respectively, $N = 94$, Fig. 2.2., Appendix A Table A3). It was also found that the producer category was a significant predictor ($P < 0.01$, $N = 94$) but the only within group difference was that studies using micro algae had significantly larger effect sizes than those examining epiphytic algae ($P < 0.01$, Appendix A Table A4).

2.3.4. Strength of trophic connection

The strength of the trophic connection, defined as the change in the producer population given a change in the herbivore population, was found to be highest in low temperature environments ($P = 0.02$, $N = 82$, Fig. 2.3., Appendix A Table A5), when predators were larger than herbivores ($P = 0.03$, $N = 82$, Fig. 2.3., Appendix A Table A5) and in high phosphate and nitrate systems ($P = 0.02$, $N = 82$, Fig. 2.3., Appendix A Table A5). Trophic connectivity was also significantly weaker when the producer was seagrass compared to either epiphytic- or micro-alga ($P < 0.01$, Appendix A Table A4).

2.3.5. Influence of marine reserve design

The size of a marine reserve had no influence on the herbivore or producer effect size, whereas older marine reserves had greater reductions in herbivores compared to non-reserve areas ($P < 0.01$, $N = 50$, Fig. 2.4., Appendix A Table A3) but no effect on the change in the producer population.

2.3.6. Comparison to past studies and systems

The updated dataset contained over 16 times as many data points as the studies conducted by Shurin et al. (2002) and Borer et al. (2005). Therefore these results pertain to trophic cascades from a variety of habitats (Coral reef, kelp, mudflat, rocky intertidal saltmarsh, seagrass, and shallow benthic), a wide range of geographic locations (Appendix A Fig. A1), and a mix of observational and experimental research ($N = 71$ and $N = 58$, respectively). Neither the herbivore nor the producer effect sizes were found to be significantly different ($P > 0.05$, Appendix A Table A6) than those found using data from benthic marine ecosystems by Shurin et al. (2002) and Borer et al. (2005). When comparing the effect sizes from this study to the effect sizes from other systems, a similar result was found. There were no significant differences ($P > 0.05$) for the producer effect size. However, the herbivore effect was significantly stronger in marine benthic than in lentic benthic ecosystems ($P = 0.04$, $N = 12$) and significantly weaker than in stream ecosystems ($P = 0.01$, $N = 33$, Appendix A Table A6).

2.4. Discussion

2.4.1. Determinants of the herbivore effect size

The best predictors of herbivore effect size were the biotic as opposed to the abiotic factors measured, specifically those relating to the size of the species involved. As herbivore size increased, so did the magnitude of their reduction in the presence of a predator. These results could be reflective of the fact that larger organisms have longer generation times (Fenchel 1974) and may be unable to replenish reduced population numbers over the duration of a study. A more methodological explanation is that larger individuals remove more biomass in a single predation event and as a result the effect size is larger. As the predator to herbivore size ratio is also a predictive factor, but not absolute predator size, there is support for both the biological and methodological mechanisms. The predator-herbivore size ratio indicates that herbivore reductions are greatest when the herbivore and predator are similar in size. This suggests the presence of prey matching and that organism size is an important determinant of trophic control (Vucic-Pestic et al. 2010). Counter to this conclusion, predator size, a component of the ratio, has no significant influence on the herbivore effect size, suggesting the influence is mainly due to the size of the herbivores. Therefore it is still unclear if the importance of size is an inherent biological mechanism or a result of how effect sizes are calculated. Work going forward could attempt to clarify this by standardizing the effect size by the mass of the organisms involved. Unfortunately, the required organism mass data were not available to test this theory in the current study.

The only abiotic factor to significantly influence the herbivore effect size was temperature. Temperature was positively correlated; suggesting that predator control of herbivores is strongest in warmer water ecosystems where there are higher metabolic rates, energy demands, and resultant consumption rates (Bruno et al. 2015).

Past studies (Griffin et al. 2013, Gamfeldt et al. 2015) found predator species richness in a community to be a good predictor of the effect size of the predator-herbivore connection, but did not describe any other significant abiotic predictors. Taking these results in concert with this study’s findings, we can infer that biological factors are likely more influential in determining the strength of herbivore reduction by predators than abiotic factors. In particular, metrics linked to body size, temperature, and consequently metabolism, appear to be of particular importance, though more work needs to be done to identify the causal mechanism within the context of cascades.

2.4.2. Determinants of the producer effect size

Contrary to the herbivore effect size, abiotic factors were the best predictors of the producer effect size. As expected (Oksanen et al. 1981, Jeppesen et al. 2003, Östman et al. 2016), the increase in the producer population, given the presence of a predator, was strongest in environments with high nitrate or phosphate levels, where nutrients are not limiting and producer populations are more likely top down controlled. More over, these conditions tend to be found in ecosystems with fewer trophic connections and the manipulation of a single species in these systems should have larger impacts (Rodríguez-Castañeda 2013). Poore et al. (2012) found the same result for the herbivore-producer trophic link and hypothesized that it was due to greater primary productivity and higher standing stock producer biomass. As a result, there would be a greater contrast between the grazed and un-grazed plots. These explanations are not mutually exclusive but future research should seek to standardize measures of producer populations, as was previously noted for herbivores. As a consequence, particular attention should be paid to marine predator loss in high nutrient environments (e.g. coastal upwelling zones), as these are the most likely to have negative consequences for primary producers. This result is particularly important because these high nutrient areas are also home to substantial fisheries that are likely to target marine predators (Hartline 1980).

2.4.3. Strength of the trophic connection

When examined across all studies, and against expectations, the strength of herbivore suppression had no influence on the strength of the producer response to predator presence. However individual studies show that even minor modifications to food webs and ecosystems can have large reverberations. Conversely, other studies show that large shifts in one trophic level do not always translate into shifts at other levels. This lack of relationship shifts the question from what determines the strength of a trophic cascade to what determines the strength of the trophic connections, and provides the grounds for a great deal of future research.

The residuals of a 1:1 regression line between the significant herbivore and producer effect sizes were used to quantify how a change in the herbivore population translated to a change in the producer population. These values were considered a proxy for the trophic connectivity of the species interactions and differed from the cascade effect size as they related the change in producer population to that in the herbivore population while the effect size only measures these changes in relation to predator presence and absence. To the author's knowledge, this method has not been used for this purpose before and provides a potential new tool for investigating the strength of trophic cascades and connections.

Four continuous variables were found to be significant in predicting the previously mentioned residuals: temperature, the predator-herbivore size ratio, and the two nutrient concentrations. Higher temperatures were negatively correlated with these residuals and thus weaker trophic connections. This suggests that a large amount of change is needed in the herbivore population to produce a resulting change in the producer population. The predator-herbivore body size ratio, nitrate concentration, and phosphate concentration were positively correlated with positive residuals suggesting that trophic connections are stronger in these conditions.

These residuals may also provide insight into the relative importance of top-down and bottom up controls in these systems. If the residual is positive and the producer responds in greater proportion than the herbivore reduction, the producer is most likely limited by top down forces, as even a small change in the grazer population equates to a significant release for the producer. Likewise, a negative residual indicates a nutrient limited system, as changes in herbivores do not equate to changes in the producer system. These inferences are supported by the results above high nutrients are associated with more positive residuals and fall in line with prior reasoning that high nutrient environments are top down controlled, not bottom up (Oskanen et al. 1981, Jeppesen et al. 2003, Östman et al. 2016). Such results provide grounds to apply this approach in other systems and discern potential for cross-system applicability.

The degree to which the herbivore effect size predicts the producer effect size is likely dictated by the strength of the trophic connection between these two levels (van Veen and Sanders 2013, Heath et al. 2014). Notably, past work on the subject (Duffy et al. 2007, Griffin et al. 2013, Katano et al. 2015) has highlighted species diversity at both the higher and lower trophic levels, as either a potential amplifier (more efficient resource use by predators) or mitigator (antagonistic interactions at the predator level) of consumption pressure between trophic levels and these results are likely to extend to trophic connectivity. While this study did not measure trophic complexity or species diversity, food webs closer to the poles are known to be simpler and contain lower levels of richness (Rodríguez-Castañeda 2013) and there was a negative correlation between trophic connectivity and sea surface temperature. While acknowledging that high nutrient concentrations are also correlated with low sea surface temperatures and could thus be the potential driver, this result provides preliminary evidence that trophic connectivity is stronger in food webs with lower levels of diversity. Future work could use the trophic connectivity metric in combination with varying levels of predator, herbivore, or producer diversity to better investigate the role that diversity, temperature, and nutrients play in determining trophic connectivity.

The predator-herbivore size ratio was positively correlated with trophic connectivity, whereas the same ratio was negatively correlated with the strength of herbivore reduction. This contradiction suggests that herbivores are most reduced when the predator and herbivore are similar in size but the reduction is more likely to propagate to changes in producer populations when the predator is larger than the herbivore. Furthermore, herbivore size was negatively correlated with the trophic connection metric, suggesting that the key aspect of this ratio is the herbivores. Specifically, producers are more likely to positively respond to herbivore declines when there is a large predator-herbivore ratio, as facilitated by a smaller herbivore species being involved.

Lastly, it was found that the trophic connectivity of studies involving seagrass was weaker than those involving epiphytic and micro-algae. Seagrass is known to be less nutritious (Cebrian et al. 2009) and therefore less desirable as a food item for most grazers. It is therefore logical that the strength of the trophic connection between herbivore and producer is weaker when seagrass is involved. A possible exception is when mega-marine herbivores such as turtles or manatees are involved (Burkholder et al. 2013). These large herbivores specialize on seagrass and their high grazing rate significantly reduces the producer population. Regardless, further work is required for trophic cascades involving seagrass, as only three seagrass studies were found for this synthesis.

2.4.4. Marine reserves and trophic cascades

Though there have been several studies reporting the ability of marine reserves to restore predator populations and thus have indirect benefits on producer populations (e.g. those included in this meta-analysis), this work is the first quantitative review on the subject. There was an average 3.35 times decrease in herbivore metrics and an average 1.97 times increase in primary producer metrics when comparing populations within and outside the marine reserve, numbers that are comparable or stronger than the other methods analyzed. If we consider the possible confounding variables, such as spill over benefits to herbivore populations (e.g. higher habitat quality or lower pollution levels, Jamieson and Levings 2001) and illegal poaching from the reserve (Byers and Noonburg 2007), it is all the more remarkable that reserves have such a significant effect. These results provide quantitative evidence of the effectiveness of marine reserves in restoring shifts in community trophic structure and further the evidence for their use as an effective marine management tool.

The mechanism that makes a marine reserve effective in restoring populations is a subject of much ongoing research (Lester et al. 2009, Molloy et al. 2009, Di Franco et al. 2016) and this work provides some insight into what outcome to expect given the characteristics of a reserve. I found that reserve size had no influence on effect size, while reserve age was significantly and positively correlated with the herbivore effect size. Therein when looking to restore predator-herbivore dynamics via the use of marine reserves, bigger is not necessarily better. Immediate effects should not be expected as results in herbivore reduction are realized over time. Given that no link was found between changes in herbivore population versus the producer population, it is not as surprising that the herbivore link with reserve age did not extend to the producer effect size.

2.4.5. Trophic Cascades in Benthic Marine Systems

In agreement with previous synthesis studies (Shurin et al. 2002, Borer et al. 2005, Poore et al. 2012, Griffin et al. 2013), there is consistent evidence for trophic controls and cascades in marine ecosystems. This study shows an average 3.52 times decrease in herbivores and a 2.27 times increase in producers populations when predators present in benthic marine systems. There is however, very little significant differentiation amongst the different categories examined. Very few sub-factors have non-significant effect sizes (producer effect size 95% CI < 0 or herbivore effect size 95% CI > 0) and categorical factors were poor predictors of cascade strength. This lack of differentiation indicates that cascades are generally prevalent in all the marine benthic systems that have been tested thus far. Additionally, there should be little reason to expect cascade strength to be significantly different under one factor or another. Past work found differences between categories such as predator or herbivore type (e.g. Borer et al. 2005), but this could possibly stem from an unbalanced data set, and stands to be reconsidered in other systems as well.

If we revisit the cross system comparison using the updated sample size, there is no longer a statistical difference between the effect sizes in benthic marine systems and nearly all other ecosystems considered (lake benthic, lake plankton, marine plankton, streams, and terrestrial). The only differences that exist are found when comparing the new results to herbivore effect sizes previously found in stream ($P = 0.04$) and lentic benthic ($P = 0.01$) ecosystems (Shurin et al. 2002). It would thus appear that trophic cascades in benthic marine systems are not inherently stronger than in others as previously suggested (Shurin et al. 2010). This lack of differentiation appears to be driven by an increased number of studies that report null or negative results and as a result a lower average effect size (Appendix A Fig. A2). Based on this pattern, we can infer there is potential for strong trophic cascades in benthic marine systems, but that they are not guaranteed and can indeed have counter-intuitive results, e.g. a decrease in producers when predators are present. Such results update our baseline understanding of trophic cascades in benthic marine systems and stress the importance of revisiting landmark findings in ecology as additional work becomes available, especially when the original conclusions are drawn with small samples sizes.

2.4.6. Influence of the study method

No significant difference was found between experimental and observational studies for the herbivore effect size (P = 0.97) or the producer effect size (P = 0.49). These results counter the belief that observational studies are too complex or contain too many confounding variables to allow for robust testing of theoretical principles (Sagarin and Pauchard 2010). This shows that using natural experiments and observations can result in similar conclusions as those obtained by more traditional experimental methods. Such findings should provide greater incentive for ecologists to empirically test theoretical predictions at larger scales and with less direct manipulation.

The only study method that was noticeably different was the enclosure method sub-factor. It was the only method to have a 95% confidence interval below and above zero for the herbivore and producer effect sizes. This result indicates that adding a predator can increase the size of the herbivore population and decrease the producer population. If future studies choose to employ enclosure methods, caution should be taken in selecting appropriate species to be enclosed in the experiment.

2.4.7. Data gaps

Despite synthesizing the results from 129 data points, there still remain significant gaps in multiple data categories that prevent the synthesis of a truly balanced dataset. The experimental study locations were all located in Europe and the United States of America (USA). Interestingly, a vast majority of the observational studies occurred in other regions of the world (namely the Caribbean, SE Australasia, and select parts of Africa). Therefore, future experimental studies should seek to expand beyond Europe and the United States of America, whereas future observational studies should look to occur within these same regions. Of final geographic note, no studies at all were conducted in South America, Antarctica, or Asia (Appendix A Fig. A1). Naturally, these geographic biases also extend to the abiotic variables associated with those regions. In particular, more work should be conducted in regions with high nutrient concentrations and sea surface temperatures (Fig. 2.2.). Two notable biotic gaps exist as well. First, as was the case in the Borer et al.'s (2005) analysis, very few vertebrate herbivores were examined in this study (5 / 129) and the majority of the studies looked at macro algae as the producer (109 / 129), with seagrass and micro algae in particular being under-examined (3 and 4 / 129 respectively, see Appendix A Table A3 for all sample sizes). Given these gaps, I present these results as an update of our understanding of cascades in benthic marine systems and by no means a definitive answer applicable to every system.

2.4.8. Conclusion

I found consistent evidence for trophic cascades in benthic marine systems regardless of the study method, species involved, or abiotic environment. The determinants of the strength of the predator control on herbivores were primarily biotic and related to herbivore size. The determinants of the predator induced herbivore release of producers were primarily abiotic and related to the nutrient levels of the system. Though there was no relationship between the strength of the herbivore reduction and the strength of the producer response, I used the residuals of a 1:1 regression of the two variables to glean further insights. This provided evidence that top-down control and trophic connectivity are stronger in high nutrient, low temperature environments, and with larger predator-herbivore size ratios. As such, particular attention should be paid to predator loss in said types of marine ecosystems. This study also quantifies the ability of marine reserves to reduce herbivore populations as facilitated by the restoration of predator populations, subsequently aiding to restore producer populations within reserves. The older a reserve was, the greater the reduction in herbivores; however, this did not translate to the producer population. However, the strength of these cascades calls into question the previously held belief that cascades are strongest in benthic marine environments and highlights the importance of revisiting ecological paradigms with updated study sizes. Through this study we, are better able to predict the consequences of marine predator loss and addition, have an improved understanding of the context specifics of top-down control, have illustrated the efficacy of marine reserves in reversing the impacts of marine predator loss, updated the cross ecosystem baseline of trophic cascades, and suggested areas for future research to address data gaps.

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Tables

Table 2.1. Predicted relationship between explanatory variables and the herbivore and producer effect sizes.

Factor	Herbivore	Producer
Temperature	╱	╲
Nutrient concentration	╱	╱
Predator size	╱	╱
Herbivore size	╱	╱
Predator-herbivore Size ratio	╲	╲
Herbivore effect size	NA	╱
Marine reserve age	╱	╱
Marine reserve size	╱	╱

Figures

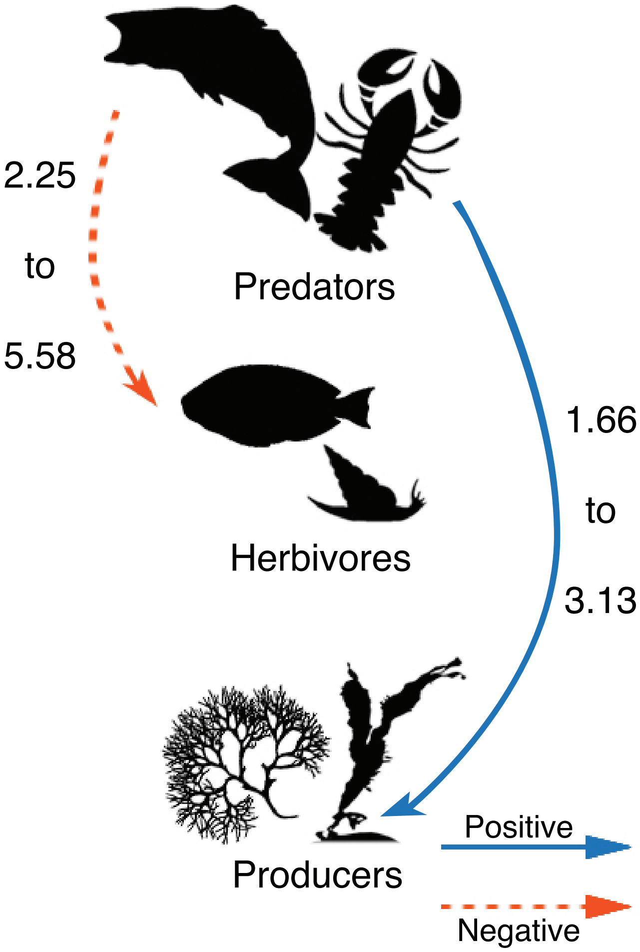

Figure 2.1. The 95% confidence intervals of the overall population fold increase (blue-solid) or decrease (red-dashed) in the presence of a predator.

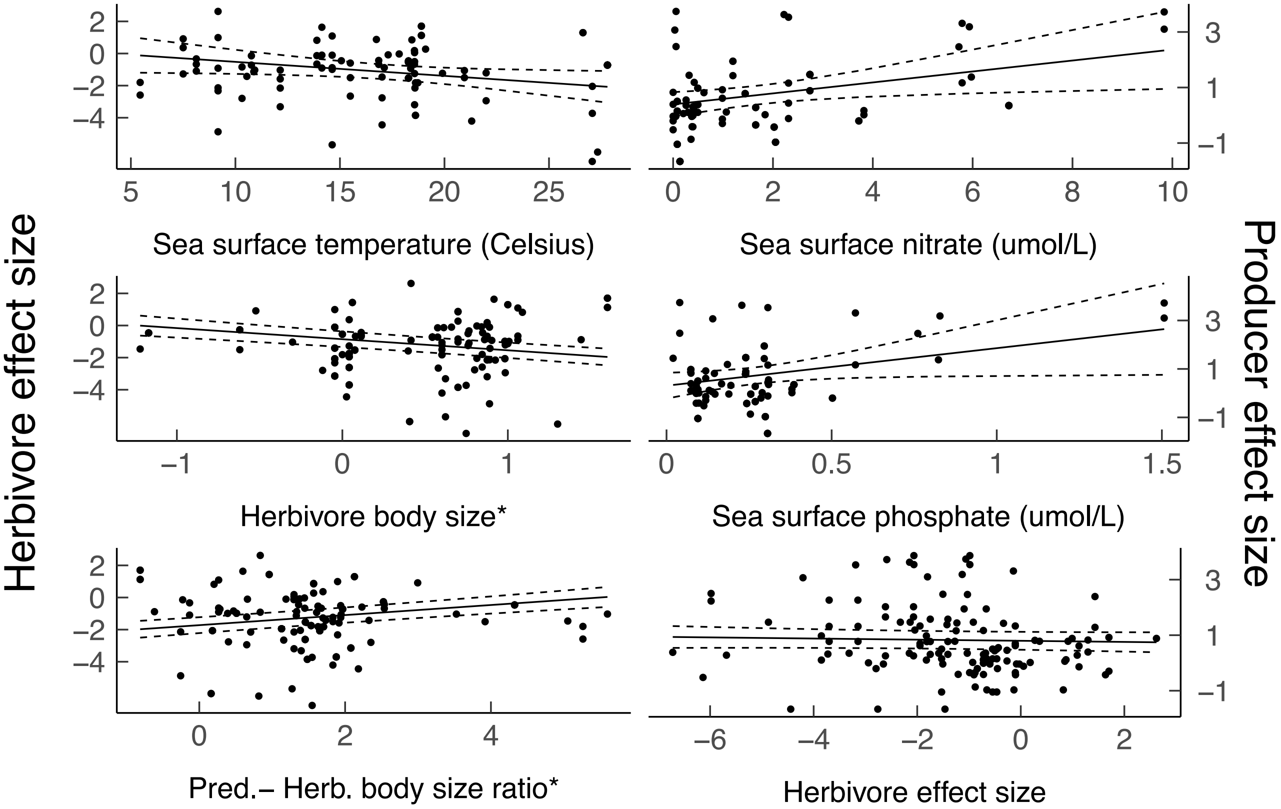

Figure 2.2. Herbivore (left) and producer (right) effect sizes versus significant (save for herbivore effect size – bottom right) explanatory variables. The solid line is the predicted value and the dashed lines are twice the standard error. *Indicates a variable that was log transformed for analysis.

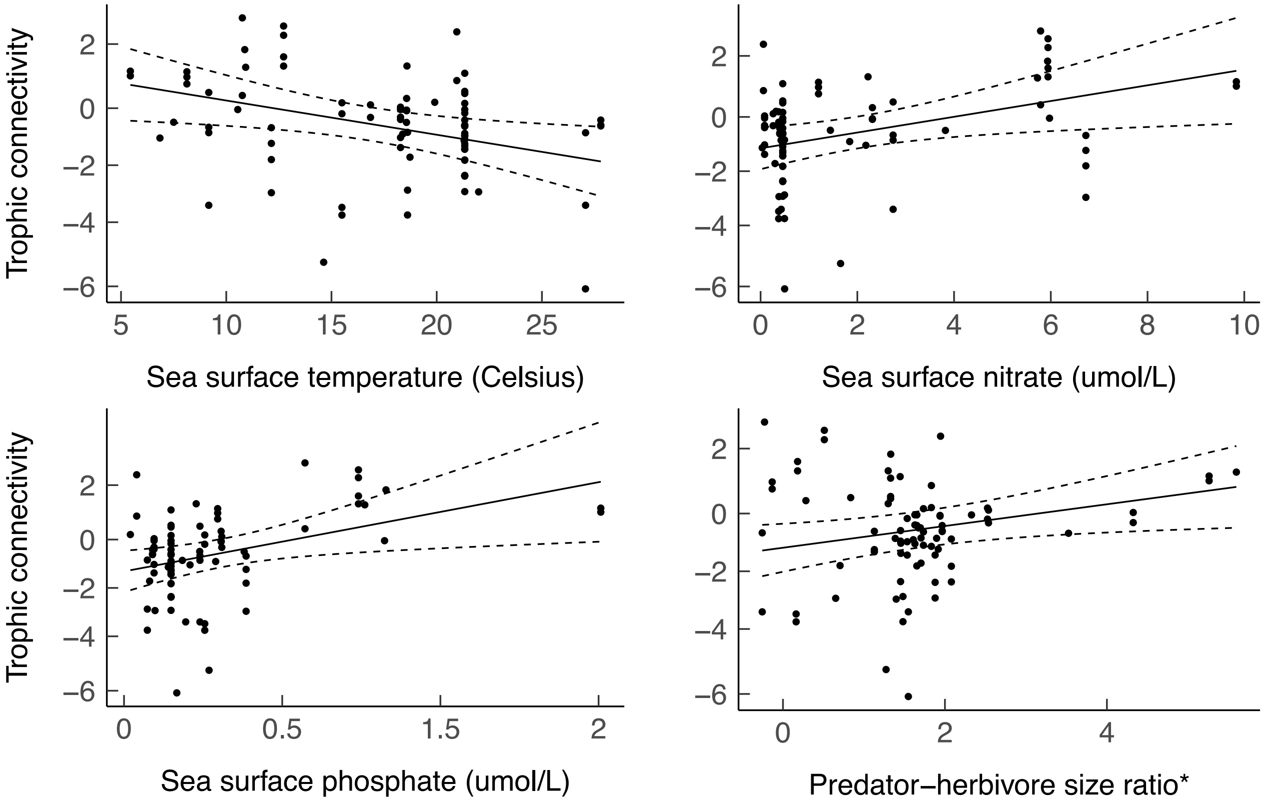

Figure 2.3. The strength of the trophic connectivity versus significant explanatory variables. Trophic connectivity relates to relative change in the producer population given the predator induced change in the herbivore population. The solid line is the predicted value and the dashed lines are twice the standard error. *Indicates a variable that was log transformed for analysis.

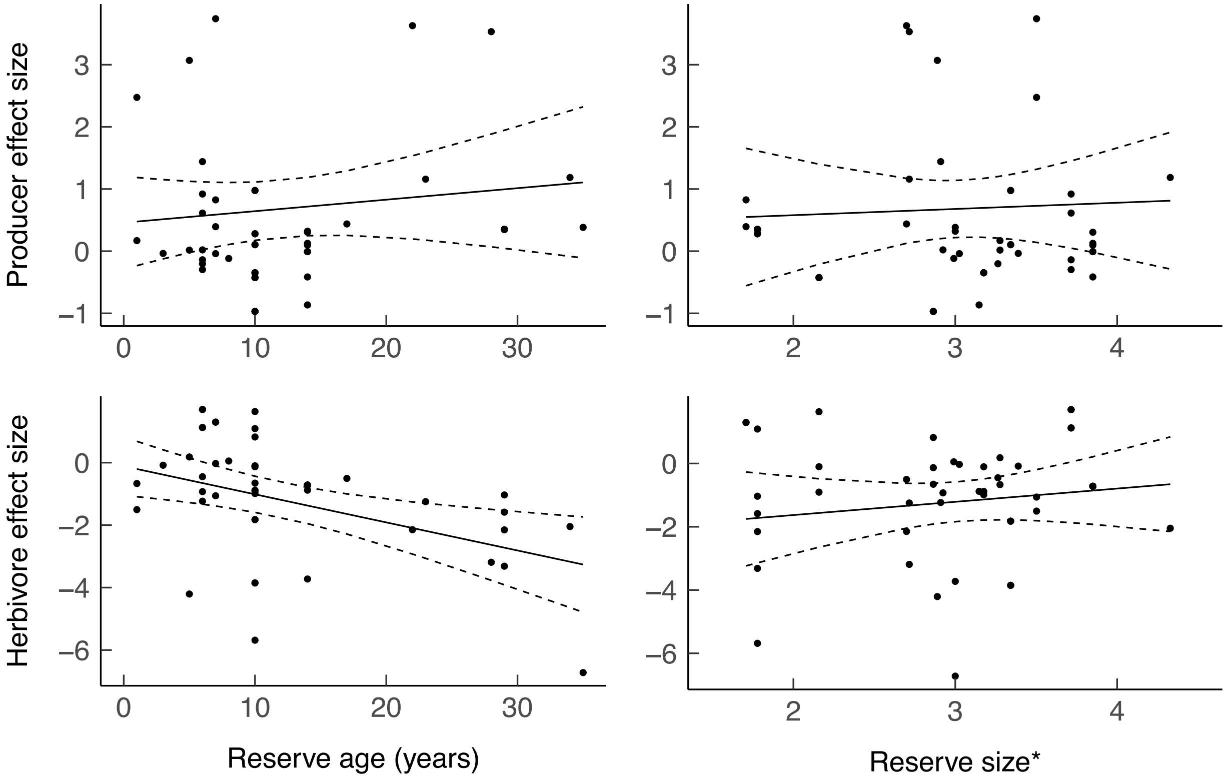

Figure 2.4. The producer (top) and herbivore (bottom) effect sizes versus marine reserve size and age. The solid line is the predicted value and the dashed lines are twice the standard error. *Indicates a variable that was log transformed for analysis.

Chapter 3 - Dominance of key species drives fish community biomass in a temperate seagrass ecosystem

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3.1. Introduction

The two main mechanisms thought to explain the link between the diversity of the species in an ecosystem and the function of that system are the complementarity and the selection hypothesis. The niche complementarity hypothesis (Tilman et al. 2001) posits that more species within a system will occupy more niche space, resulting in a greater range of functions performed or more biomass present (Davies et al. 2011, Jenkins 2015). Alternatively, the selection hypothesis (Loreau and Hector 2001) suggests that increased species richness only results in greater function by increasing the probability that a system will contain one or several highly productive species. Under this hypothesis it is a select few species whose presence drives the functioning of the system, and additional species contribute only marginal gains in ecosystem function. The selection hypothesis can also be broken down to consider whether it is not just the presence of certain species but the high relative population abundance of high functioning species that drives ecosystem function (EF), but so far this distinction is rarely investigated (Hillebrand et al. 2008).

These hypotheses have drastically different implications for the “value” of species diversity to an ecosystem. In cases where complementarity is important, the loss of any single species has realized negative impacts on an ecosystem’s function; under the selection and dominance hypothesis, only losses of particular species will impact functioning. By better understanding the mechanisms linking biodiversity and ecosystem function, we can more accurately quantify previous loses of ecosystem function, prioritize future conservation efforts as biodiversity loss accelerates across the globe

(Steffen et al. 2007, Cardinale et al. 2012), and more carefully consider which types of ecosystem functions might be best conserved with a biodiversity and ecosystem function first (BEF) approach vs. species-specific targets.

Both presence-absence and abundance weighted measures of taxonomic and functional diversity can be used to test for the selection, dominance, or complementarity hypotheses within a community (Table 3.1.). Taxonomic richness measures the number of taxonomically unique species there are in a community and does not consider the abundance or composition of those species. Taxonomic diversity, in this case, Fisher's alpha, measures how many taxonomic species there are in a community and how evenly their abundances are distributed. Functional diversity metrics can be calculated based on one or several traits, and these metrics include functional richness and evenness (Villéger et al. 2008), and functional dispersion (Laliberté and Legendre 2010). Functional richness measures how wide a range of traits are in a community, functional evenness measures the evenness of those traits, and functional dispersion measures the dissimilarity of trait values as well as their evenness. In addition, the community weighted mean (CWM) value of a single trait (Swenson 2014) gives the average value of that trait across all individuals in that community.

We determine whether complementarity, selection, or dominance is the key mechanism within our system by assessing the shape of the relationship between diversity and function. These relationships are based on the first principles that have been put forward in the literature, not previously described patterns in nature. If ecosystem function (EF) is driven by the complementarity effect, we expect that more diversity (taxonomic or functional) will always result in greater functioning and that more evenly distributed communities will have higher functioning than highly dominated communities. As such, under the complementarity hypothesis we expect to see positive, non-saturating relationships between EF and both taxonomic and functional richness (Mora et al. 2014), as well as positive relationships between EF and taxonomic diversity (Cavanaugh et al. 2014), functional dispersion (Chiang et al. 2016), and functional evenness (Mason et al. 2005). If EF is instead driven only by the presence of select species, diversity will only result in substantial gains in ecosystem function if that diversity performs a high level of ecosystem function on its own. Therefore we expect positive but saturating relationships between EF and functional and taxonomic richness, the taxonomic diversity and functional dispersion metrics (Mora et al. 2014), and no relationships with EF and the evenness measures. Finally, if it is the dominance of certain species that drives EF, we expect to that, communities with low levels of evenness and communities dominated by certain trait values will have the highest ecosystem function. Therefore the we expect negative relationships between EF and the multi and one-dimensional functional evenness metrics (Grime 1998), negative relationships between EF and the taxonomic diversity and functional dispersion, as well as strong relationships between EF and the associated CWM values, i.e. the “biomass ratio hypothesis” (Finegan et al. 2015, Zhu et al. 2016). We include both multi and one-dimensional measures of functional trait metrics because it is possible that ecosystem functions are mostly impacted by a select few traits as opposed to a composite measurement of all traits (Butterfield and Suding 2013) or it is also possible that different traits have different directionality and these directionalities are obscured by composite traits. Lastly, there is no expected directionality to the relationship with the CWM values but we can use any emergent directionality to make inferences about which community trait values lead to highly functioning communities.

Extensive research has analyzed the evidence for BEF mechanisms in controlled experimental settings (Hooper et al. 2012) and increased focus is being directed towards observational tests of BEF (Duffy et al. 2017). However, the majority of the work has been conducted with terrestrial primary producers (though see work by O'Connor et al. 2017 and Duffy et al. 2017) and therefore further analysis is required for higher trophic levels, which have important roles in extractive industries (USDOI 2011, FAO 2016) and in shaping the ecosystem itself (Duffy 2002). More so, the research has primarily used taxonomic metrics of biodiversity and has therefore often overlooked the intricacies of species' functional trait metrics and their plausible impact on function. In particular, the CWM has primarily only been used to examine the BEF relationship in plant communities (e.g. Chanteloup and Bonis 2013, Finegan et al. 2015, Zhu et al. 2016) and not vertebrates and there is thus significant potential to apply single trait based ecological approaches to investigate the underlying mechanisms of vertebrate ecosystem function.

Though first proposed during the nascent periods of BEF research, the biomass ratio hypothesis (Grime 1998) has not been as deeply explored, as have other BEF theories. There is however some recent work that links the various function of a system to the dominance of certain species. Terrestrial work has demonstrated the role of dominant species in dictating colonization in forest understory plants (Gilbert et al. 2009), pollination in bee communities (Winfree et al. 2015), and decomposition rates in leaf litter (Tardif and Shipley 2012). Within marine systems previous work has focused on testing the selection hypothesis in marine invertebrates. For example, studies have demonstrated that dominance drives redox potential discontinuity in bivalves (Clare et al. 2016), feeding rates in echinoderms (Godbold et al. 2009), and secondary production in benthic systems (Dolbeth et al. 2015). Given that most natural communities possess steep rank abundance curves (Ulrich et al. 2010), it seems plausible that strong relationships with dominance exist elsewhere and they need to be tested and accounted for.

Given the established research on the link between taxonomic and functional richness metrics and emerging interest in the role of dominance in determining ecosystem function, this work looks to progress the understanding of the mechanisms underlying the marine fish community biomass by applying both multi- and unidimensional trait approaches. We do this by assessing the relationship between multiple metrics of taxonomic and functional diversity within fish communities in eelgrass (genus: *Zostera*) ecosystems in the Canadian pacific. Specifically, we evaluate and compare the relationships between our function of interest, standing stock community biomass (SSBM) and species richness and functional richness, as well as the measures of functional trait diversity, functional dispersion, functional evenness, and the community average trait value (CWM).

3.2. Methods

3.2.1. Fish community surveys

We surveyed the fish communities in fourteen subtidal eelgrass meadows in Northern British Columbia (Fig. 3.1.) between July 1 and August 5, 2017. To access the subtidal portion of meadows, we surveyed each meadow at the day’s low-low tide and only on days with a tidal height of less than 1-meter depth as measured by chart datum at mean low-low water. Surveying consisted of duplicate beach seines (Guest et al. 2003) using a seine that measured 10 m in length, 3 m deep at the center, tapered to 1 meter deep at each end, and had a mesh size of 6 mm as measured along the diagonal. After each seine haul, we collected the fish in totes on shore, but to avoid recounting released individuals we conducted both hauls before any identification. Once both sets were conducted, we measured the fork length (to the nearest millimeter) of the first 20 individuals of each species at each site. We photographed representative individuals of each species (although not every species was photographed at every site). We recorded temperature and pH at each site using a Hanna HI® meter, extracted salinity measurements from a GIS layer at a 500 x 500 m spatial resolution (Foreman et al. 2008), and collected five 0.25 x 0.25 m quadrats to sample to eelgrass length and density.

3.2.2. Functional trait measures

We used the species photos and the image processing software ImageJ to measure morphometric traits for each species (Villéger et al. 2010, Fig. 3.2.) and then used these to calculate seven size-standardized functional traits: body length, mouth length, oral gape position, eye size, eye position, pectoral fin position, and caudal peduncle throttling (Fig. 3.2.). We chose these specific traits because of their influence towards a species' resource acquisition, either through size, visual acuity, mobility, or position in the water column, and hence their presumed relationship with each species' niche and its function within the community (Villéger et al. 2010). Species-level functional trait values were obtained by taking the mean of each trait value across all individuals measured for each species. Unlike the other species *Cymatogaster aggregata* occurred in both juvenile and adult populations, therefore we considered these two groups as functionally different species and separate morphological metrics were computed for the juveniles and adults.

Photos and trait measures were not available for five very rare species (*Myoxocephalus polyacanthocephalus* (n = 3)*, Rimicola muscarum* (n = 1), *Ascelichthys rhodorus* (n = 1), *Sebastes miniatus* (n = 1)*,* and *Rhacochilus vacca* (n = 1), so they were dropped from both the taxonomic and functional analysis.

3.2.3. Functional diversity

We quantified multidimensional functional diversity using the seven functional traits described above for three indices (functional richness, evenness, and dispersion, as defined by Villéger et al. 2008, Laliberté and Legendre 2010). To understand impacts of individual traits, we then calculated both the one-dimensional CWM (Swenson 2014), and functional evenness of each trait considered separately. Functional evenness was considered as a multi and one-dimensional trait as it was specific to our dominance hypothesis, whereas richness is not; furthermore past work has shown that multidimensional metrics can obscure the importance of single traits within a community (Butterfield and Suding 2013). All of the functional trait values, except the CWM, are obtained by first performing a Principal Coordinates Analysis (PCoA). Functional richness is the convex hull volume of this transformation. Functional evenness is a measure of how regularly traits are distributed throughout the trait space and how even this distribution is; functional evenness is independent of functional richness. Functional dispersion is calculated as the average distance to the abundance weighted centroid with the traits represented in n-dimensional space. Finally, the community weighted mean trait values (CWM) are calculated by taking the abundance-weighted average of each morphological trait at each site. We did all functional diversity calculations in the *FD* package (Laliberté and Legendre 2010) in R (R Core Team 2015, V 3.3.3). The calculations were done using an abundance weighted Gower's dissimilarity measure and included six of the seven traits; "caudal peduncle throttling" was dropped from the functional richness calculation as it was found to be redundant in the principle coordinate analysis. In these calculations (except for the CWM traits metrics), we standardized the morphometric traits to a mean of zero and standard deviation of one and gave all traits equal weighting. Finally, the quality of the 6 dimensional reduced space representation was found to be 0.90.

3.2.4. Taxonomic diversity

We assessed taxonomic diversity using two metrics, species richness and Fisher's alpha diversity, which relies on the log-series rank abundance curve of each community and accounts for the relative dominance of species (Fisher et al. 1943), therefore it should be best related to our hypothesis about dominance. We calculated both metrics using the *vegan* (Oksanen et al. 2007) package in R (R Core Team 2015, V 3.3.3).

3.2.5. Ecosystem function

Following Mora et al. (2011) and Duffy et al. (2016) we used community standing stock biomass (SSBM) as our measure of ecosystem function, because fisheries landings are viewed as a type of ecosystem function or service (Holmlund and Hammer 1999) and because the biomass of an individual frequently predicts its contribution to a range of other ecosystem functions such as and suspension feeding, nutrient uptake, and gross productivity (Davies et al. 2011, Jenkins 2015). We estimated each individual's mass using its recorded length and established length-weight relationships. The majority of the length-weight relationships were specific to fishes in eelgrass meadows in British Columbia (Siegle et al. 2014), but five species' weight-length relationships were not available and were obtained from Fishbase.org (Froese and Pauly 2012). We measured individual lengths for 21% of all the fish surveyed and then used these distributions to estimate the lengths of the remaining individuals on a per site basis. To estimate the remaining fishes' lengths, we used truncated density distributions based on maximum and minimum observed fish lengths were created using the *fitdistrplus* package in R (Delignette-Muller and Dutang 2015) and we then sampled individual lengths from these using base R (R Core Team 2015, V 3.3.3). Finally, we summed biomass at each site and logged it to reduce its variance.

3.2.6. Statistical analyses

We developed generalized linear models fit with a gamma distribution to examine the relationships between fish community biomass and each of our selected measures of taxonomic and functional biodiversity in turn. To account for potential environmental influences on fish biomass, we included the geographic location (longitude) of the survey sites as a second fixed effect in each model. Longitude was chosen as the fixed effect because it had a strong correlation with the abiotic variables temperature and salinity as well as the distance of each site from human activity and the date of sampling; more so we did not want to over-parameterize our model by including multiple correlated fixed effects (Appendix B Fig. B1). Similarly, we found no significant relationship between community biomass and eelgrass density or blade length and did not include it in our models. We also tested for spatial autocorrelation amongst the surveyed sites using the Durbin-Watson test, but found no significant effects for our predictor variables. We then evaluated the models for relative fit using the proportion of the deviance explained (D^2)

using the R package *modEvA* (Márcia Barbosa et al. 2016) and we assessed variables for statistical significance based on their P value ($P < 0.05$).

3.3. Results

3.3.1. Survey results

Species richness and community biomass both varied significantly across study sites. Taxonomic richness ranged from 7 to 23 species per site, with a regional pool of 34 species. Of these 34 species, 26 were found at more than one site within the region. Community biomass ranged from 1 216 to 12 774 grams (logged, 3.08 to 4.10) per site (approximately 60 m^2). All sites were dominated (50% of abundance) by three or fewer species (Appendix B Fig. B2) and only 16 of the 34 species had median site biomass proportion values above 0.01 (Appendix B Table B1). Of these 16 species, the two with the highest median proportion of site biomass were *Cymatogaster aggregata* followed by *Leptocottus armatus* (0.34 and 0.21 respectively, Appendix B Table B1).

3.3.2. Diversity metrics and ecosystem function

We found that the sites with the lowest taxonomic diversity had the highest site biomass ($P = 0.04$, Fig. 3.3.) and that taxonomic diversity explained the most deviance of the diversity and richness metrics considered ($D^2 = 0.41$, Fig. 3.3.). Conversely, functional dispersion, taxonomic richness, and functional richness were not significant predictors of site biomass ($P = 0.74$, $P = 0.59$, and $P = 0.30$ respectively, Fig. 3.3.) and explained little deviance ($D^2 = 0.12$, $D^2 = 0.13$, and $D^2 = 0.20$, Fig. 3.3.).

Sites with the lowest values for functional evenness were also found to have the highest standing stock biomass ($P = 0.01$, Fig. 3.4.) and functional evenness explained the most deviance of any metric considered ($D^2 = 0.51$, Fig. 3.4.). Of the seven traits considered for evenness individually, eye position and oral gape position were found to be significant predictors of SSBM (P = 0.04 for both, Fig. 3.4.) and explained the same amount of deviance ($D^2 = 0.40$, Fig. 3.4.).

As with the measures of functional evenness, the CWM for eye position and oral gape position were both found to be significant predictors of SSBM (P = 0.02, Fig. 3.5.) and both explained high levels of deviance ($D^2 = 0.46$ and $D^2 = 0.47$, respectively, Fig. 3.5.). Both of these traits had negative relationships suggesting that communities composed of more benthic-adapted species (Gatz 1979) had higher SSBM.

3.4. Discussion

We found that the dominance of particular species and their traits best explained the relationship between biodiversity and ecosystem function in fish communities within eelgrass ecosystems in Northern British Columbia. This conclusion was supported by the negative relationships between EF and the following metrics: taxonomic diversity, multidimensional functional evenness, two one-dimensional measures of functional evenness, and by strong relationships with two CWM trait measures. These results are contrary to similar studies of fishes in marine environments and provide support for testing alternative relationships between biodiversity and ecosystem function in large ecosystem scale studies and for considering additional metrics of biodiversity in these analyses.

3.4.1. Dominance drives ecosystem function

Communities with low levels of taxonomic diversity, which are characterized by high levels of dominance and lower numbers of taxonomic richness, were found to have to highest levels of ecosystem function in our communities (negative relationship with taxonomic diversity, $P = 0.04$, $D^2 = 0.41$). This result provides support for the dominance hypothesis whereby high functioning communities contain low diversity. In fact, the abundance and distribution of particularly important species (contributing a high proportion of community biomass) played a critical role at two spatial scales. First, under the selection hypothesis we would have predicted a limited increase in biomass with increased species richness, due to the increased chances of including those species. However, the particularly important species, namely *C. aggregata and Leptocottus armatus*, had a very high degree of regional occupancy (A1 Table 1), meaning that additional species richness at the community level largely corresponded to adding low biomas species. Second, at the level of an individual community, the highest functioning communities in our study system had the highest relative abundances locally of these high-contributing species.

In agreement with the taxonomic results, we found that it was the dominance of both multidimensional and one-dimensional functional trait values at a site, not the functional trait richness that best explained SSBM. Multidimensional functional evenness was the best predictor variable in this study ($P = 0.01$, $D^2 = 0.51$) and suggested that the sites with the lowest levels of trait evenness had the highest SSBM. When considering the evenness of the seven traits individually, two traits related to a species position in the water column (Gatz 1979, Karpouzi and Stergiou 2003) proved to be influential in determining SSBM. Both of the evenness values for the eye position and oral gape position traits were significant predictors of SSBM and showed the same relationship as the multidimensional measure of evenness. As before, these results provide support for the dominance effect, i.e. the biomass-ratio hypothesis, whereby communities have higher function when they are dominated by species with particular functional traits. As mentioned, two CWM trait values also explained high levels of variance in models for SSBM. These results are in line with the abundance weighted diversity results and subsequently support the biomass ratio hypothesis. This mechanism has been documented with producers and invertebrates (Dolbeth et al. 2015, Finegan et al. 2015, Zhu et al. 2016) but has never been shown before with fish. Based on these results, we can infer that there is an optimal trait space in these systems for high fish biomass. The communities that have traits best suited for occupying these niches are consistently the most productive, whereas communities that possess traits far from the optima, contribute little to the function of the ecosystem at the community scale.

There is emergent support for the role of dominant species in driving ecosystem function across systems (Gilbert et al. 2009, Tardif and Shipley 2012, Winfree et al. 2015). Given the predominance of steep rank abundance curves in nature (Ulrich et al. 2010) these results are perhaps not surprising, but relatively little focus has been spent on these effects of taxonomic and functional dominance in BEF research to date. As we move forward in our efforts to prioritize our management and conservation efforts, this topic deserves further attention.

Both the taxonomic and functional (except for dispersion) measures of diversity that incorporated abundance explained much more deviance in the community biomass than did their count based counterparts. These results suggest that it is not the absolute number of species in a system that drives function in this instance, but rather their abundance and subsequently their distribution. Given that communities are far more liable to change in relative abundances as opposed to absolute richness (Ceballos et al. 2017), further work into the consequences of those changes is required. As such, we suggest an increased value be placed on studying and maintaining species abundances within a community as opposed to species richness alone. This line of reasoning is also much more tractable for management as it is simpler to track relative declines in species populations compared to exhaustively surveying an area to prove a species extinction (Boakes et al. 2015) and even more so for mobile species.

3.4.2. Multi versus one-dimensional measures of functional diversity

It is interesting to note that only two of the seven functional traits were found to be significant when considered separately for the functional evenness measure and the CWM metrics. These results suggest that only a subset of traits is driving local community biomass in these species and that information would have been overlooked had we only relied on the multidimensional measures of functional diversity. Whether ecosystem function is driven by similar traits in other fish communities is unknown but we highly recommend the inclusion of one-dimensional measures of functional diversity is similar future analyses. By better understanding exactly which traits are structuring the community and its function, we can move toward testing mechanistic hypotheses linking the ecologies of individual species to ecosystem processes. We can also work to make predictions about how disturbance events will select for species given their trait values and possibly devise management plans to protect for communities containing certain trait values.

In this case we found that the two traits related to the species' position in the water column were influential in determining the biomass of a community. Both the eye position and oral gape position were negatively correlated with community biomass suggesting that the optimal community within eelgrass meadows tends toward species that are more adapted for a benthic environment. Fish with high values for the eye position metric have more dorsally located eyes and are adapted to capturing prey from the pelagic environment, whereas fish with low scores for eye position have more laterally located eyes and are more adapted for capturing prey from the benthic environment (Gatz 1979). Similarly, fish with high gape position scores have dorsally located mouths and those with low scores have ventrally located mouths and are best adapted to capturing prey from the benthic environment (Karpouzi and Stergiou 2003). The lack of a relationship with body length is important to note because it demonstrates that it is not simply the larger bodied communities that contain more biomass and that it is rather ecologically relevant traits that determine this relationship. While we chose to focus on traits related to a species' feeding ability, it is possible that other traits related to other life history characteristics could influence a species' dominance within a community (e.g. metabolic rate, parental care habits, pollution tolerance) and this provides grounds as an area for further research.

Because the optimal trait of a species is likely to change depending on the local environmental conditions, it is important to consider which of our results are widely applicable and which are likely restricted to application within similar, coastal, temperate aquatic ecosystems. Prey in eelgrass systems are known to be benthic and epifanual (Phillips 1984) which corresponds with our findings that communities with trait values associated with more benthic prey capture were found to contain the highest SSBM. If prey were to be distributed higher in the water column, alternative eye and oral gape positions would likely be favoured. Therefore our findings with regards to eye and oral gape positions are most likely translatable into systems with similar prey distributions. Future studies could use this finding to question if these same trait values structure communities within different habitats or at different scales.

3.4.3. Comparisons to past results

Taxonomic richness was the second worst predictor of SSBM ($D^2 = 0.13$) and had no significant relationship with SSBM. This is contrary to past work in marine systems that suggested that more species should equate to more biomass (Danovaro et al. 2008, Mora et al. 2011, Duffy et al. 2016). These results are particularly surprising because the synthesis by Duffy et al. (2016) found the strongest relationship between fish richness and community biomass to be in temperate regions such as ours. We put forward three main differences between the two studies that may explain the divergent conclusions. First, Duffy et al.'s (2016) paper was based on the Reef Life Survey which counts species at a scale of 500 m^2 for a given site, whereas our sampling occurs at a scale of approximately 150 m^2 and scale has been shown to have a positive effect on the BEF relationship (Brose and Hillebrand 2016). Second, our sampling method employed beach seines, which are more likely to detect rare, singleton species than surveys conducted by visual surveys (Baker et al. 2016). These rare, singleton species contributed very little biomass while driving up the species count and thus possibly negating a relationship between species richness and community biomass. Third, the range in species richness was quite different, Duffy et al.'s (2016) surveys in temperate regions ranged from ~ 1 to 10 species whereas our surveys ranged from 7 to 23 species. Therein Duffy et al. (2016) might have found such a steep result because they were considering communities with very few species and the addition of even a single extra species in those systems results in a substantial fulfillment of niche space. This could occur if species that are important contributors to community biomass are not regionally well distributed and reliably found in almost all communities at minimum species richness levels, as is the case in our system. Because our study contained species rich ecosystems (i.e. *Zostera marina*), we might have been past the saturation point on the richness-function curve that is often seen in BEF relationships (Mora et al. 2011). Other lower diversity temperate marine ecosystems may therefore find alternative results such as complementarity.

3.4.4. Implications

The importance of a select few species within a community has significant implications for the conservation priorities of these systems. If we wish to prioritize the preservation of biomass as a function within these systems, it appears we need only focus on a few species that constitute the majority of that biomass. Such an optimization simplifies the conservation process, but raises important questions about employing a BEF approach to conservation. Under such an approach, many rare, low biomass species would be deemed expendable, as their "ecosystem function" is low. It is also important to consider how we might manage for only one or a few species all sharing the same habitat. If it were more resource intensive to work to only protect these highly functional species, a more prudent approach might be to simply protect the habitat and protect all species. How we value the intrinsic and utilitarian existence of species as well as how we apply that value will be important questions in future conservation of these systems, especially as the BEF approach becomes more popular (Granek et al. 2010).

Though fish considered in this study are largely outside of an extractive fishery, it is possible to see how these results might translate onto fisheries management. Based on these results it is tempting to target communities that have the highly productive CWM values but more nuance is required. Because we only considered SSBM and not production rate, we cannot say for certain that these trait values are the most desirable form a fisheries viewpoint; for this we would need to consider production and the specific locations where that production occurs (e.g., nursery vs. adult habitats). However it is probable that a similar trait based approach could be applied with production rates on the Y-axis and thus the needed information obtained.

3.4.5. Limitations

Given the observational, landscape level design to our research, there are several inherent limitations to this research. The primary limitation is the number of confounding variables that potentially influence the fish diversity metrics themselves as well as the fish community biomass at each site. This said, we did not find the variables: temperature, salinity, pH, site remoteness, eelgrass meadow area, eelgrass density, and eelgrass blade length to be significant predictors of fish biomass and we partially accounted for their influence by including longitude, which itself was correlated with the abiotic variables, as a fixed effect in our models. The previously discussed diversity metrics were found to still be significant predictors of fish biomass after allowing for this control. Our second main limitation was the lack of full balance in our predictor variables as the extreme values of diversity were under sampled for species and functional richness as well as species diversity. Because of this undersampling, the certainty of our results is limited at this time and the addition of further data points could alter the conclusions drawn by this work. Finally, changes in species communities over time, either yearly, seasonally, and daily, could be considered another limitation if the community composition is shifting significantly. Robinson and Yakimishyn (2013) have carried out extensive research on this subject and found that eelgrass fish communities in British Columbia had stable species presence-absence and total abundance across the years but that they demonstrated variability in relative abundances. However, Robinson and Yakimishyn (2013) also showed that the dominant species remained dominant within 1-3 ranks over the years, which lends support to the possibility that our findings related to dominance and ecosystem would be replicated in years to come or years gone by. Seasonal and diel variation have been found to be much higher (Yakimishyn et al. 2004) and therefore could limit our findings to the season (summer) and diurnal time (day) at which they were sampled. Therefore, further testing is required to see if the same patterns are demonstrated nocturnally and in alternate seasons. As a result, we might expect similar results related to dominance but with different species compositions depending on the season and diel period. Finally it should be noted that these results are specific to the ecosystem function that we defined (community biomass) and do not give concrete information on other ecosystem functions that maybe measured.

3.4.6. Conclusion

We have highlighted the importance of dominant species, their traits, and their distribution within a community for driving ecosystem function in a real world ecosystem. While a significant amount of past research has focused on species richness measures, we stress the importance of considering the above metrics in addition to taxonomic richness when considering the link between biodiversity and ecosystem function. In particular, we recommend the inclusion of both richness based and abundance weighted measures of biodiversity in future studies as to better investigate the role of dominance in determining EF. With regards to functional diversity metrics we have also shown the potential uses of the currently under utilized one-dimensional functional evenness CWM metric and how it can be used to understand which functional traits and which values of those traits best explain ecosystem function. Finally, given the importance of dominant species in determining overall ecosystem function in our system, we conclude that a BEF approach to conservation may not always maximize diversity, and a greater understanding of how different dimensions of diversity contribute to different dimensions of ecosystem functioning and value is needed.

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Tables

Table 3.2. Predicted relationship between diversity metrics and ecosystem function under each hypothesis.

		Selection	
Metric	Complementarity	Presence	Dominance (Mass Ratio)
Taxonomic richness	╱	╭	—
Taxonomic diversity	╱	╭	╲
Functional richness	╱	╭	—
Functional dispersion	╱	╭	╲
Functional evenness (multi- or one-dimensional)	╱	—	╲
CWM traits	—	—	+/-

Figures

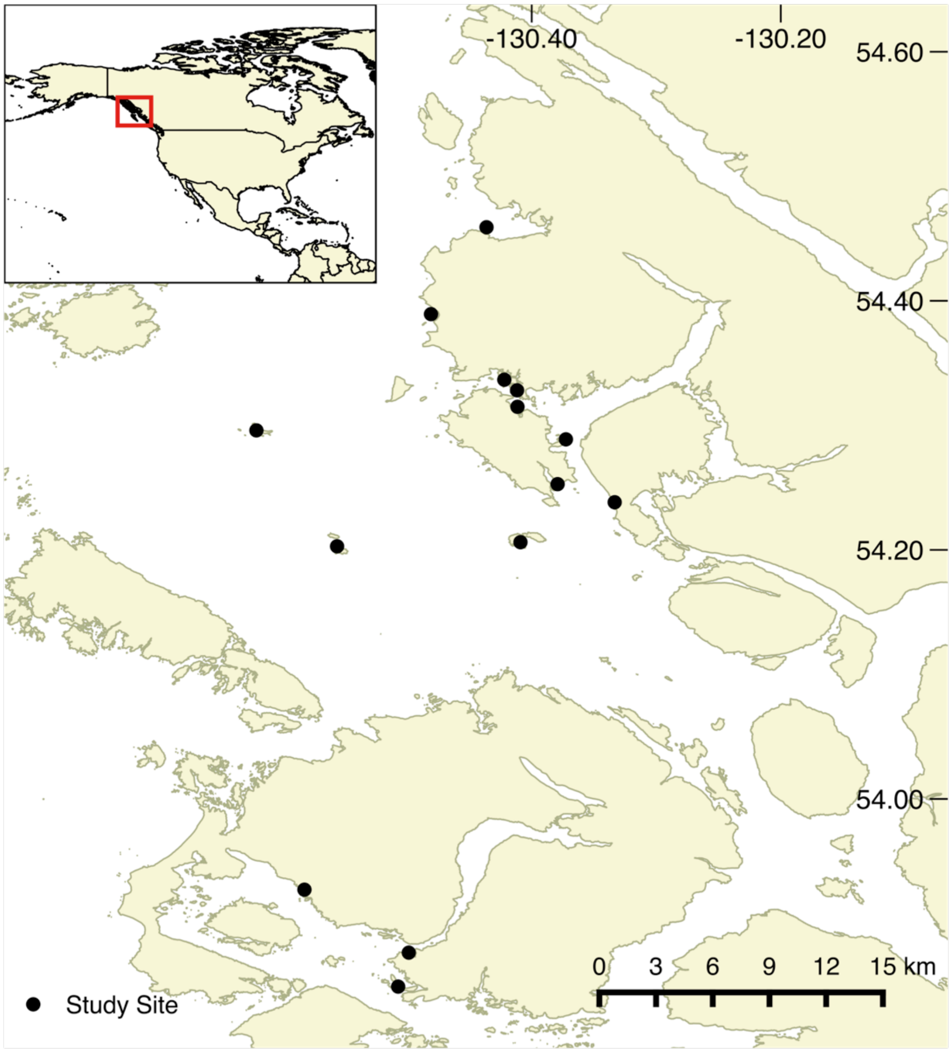
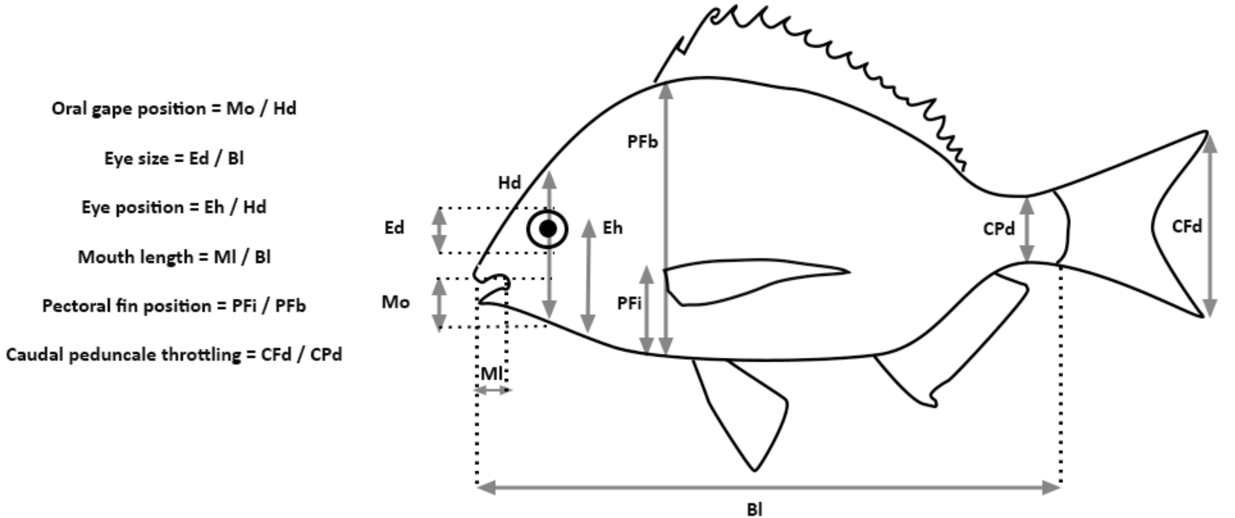


Figure 3.1. Map of study area and sampling sites



Adapted from Villéger et al. 201

Figure 3.2. Morphometric traits measured from photographs of individuals from each of the 34 species. All traits are expressed relative to total head or body size, and are therefore independent of variation in total size. Trait abbreviations are as follows: Ed: Eye depth Mo: Mouth opening Ml: Mouth length Hd: Head depth Eh: Eye height PFb: Body depth at pectoral fin PFi: Height of pectoral fin Cpd: Caudal peduncale depth CFd: Caudal fin depth Bl: Body length

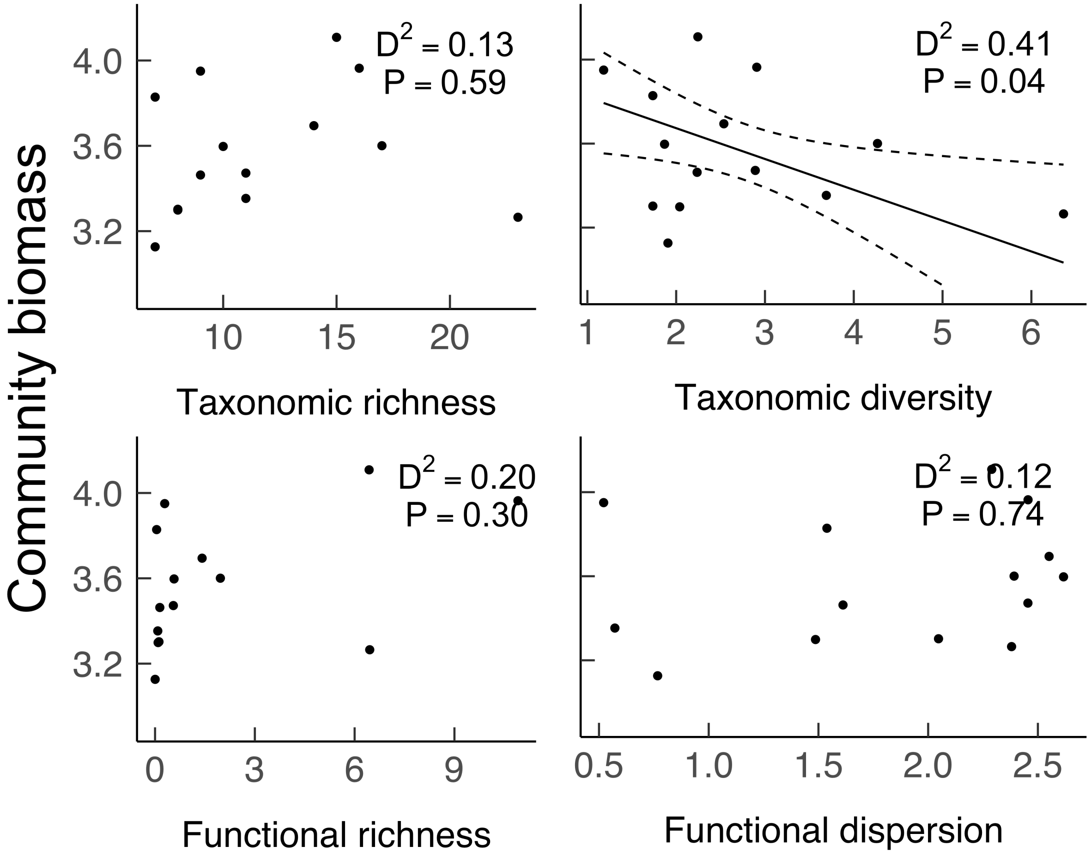


Figure 3.3. The relationships between fish community biomass and the community diversity metrics. D^2 is the deviance explained in comparison to a null model with no deviance explained. The solid line is the regression line and the dashed lines are twice the standard error.

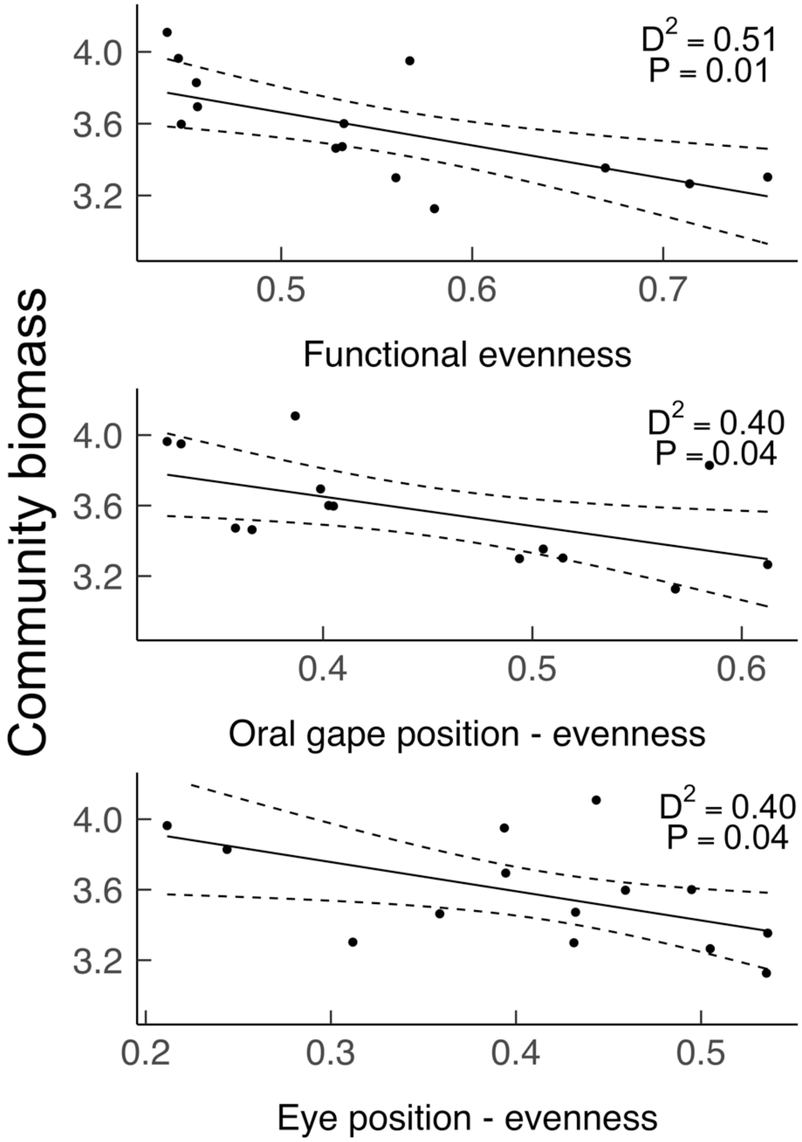


Figure 3.4. The relationships between community biomass and the multi and one-dimensional functional evenness metrics. D^2 is the deviance explained in comparison to a null model with no deviance explained. The solid line is the regression line and the dashed lines are twice the standard error.

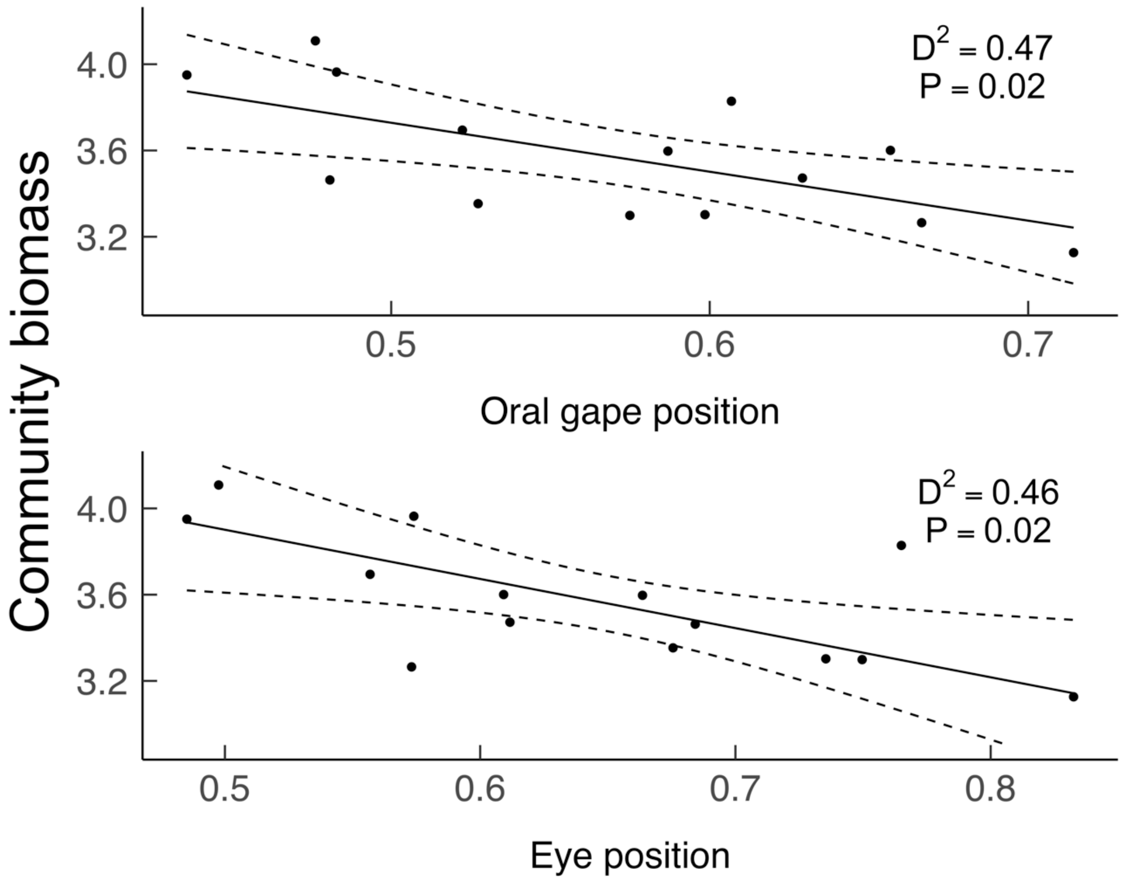


Figure 3.5. The relationships between fish community biomass and the community weighted average of two trait values. D^2 is the deviance explained in comparison to a null model with no deviance explained. The solid line is the regression line and the dashed lines are twice the standard error.

Appendix A

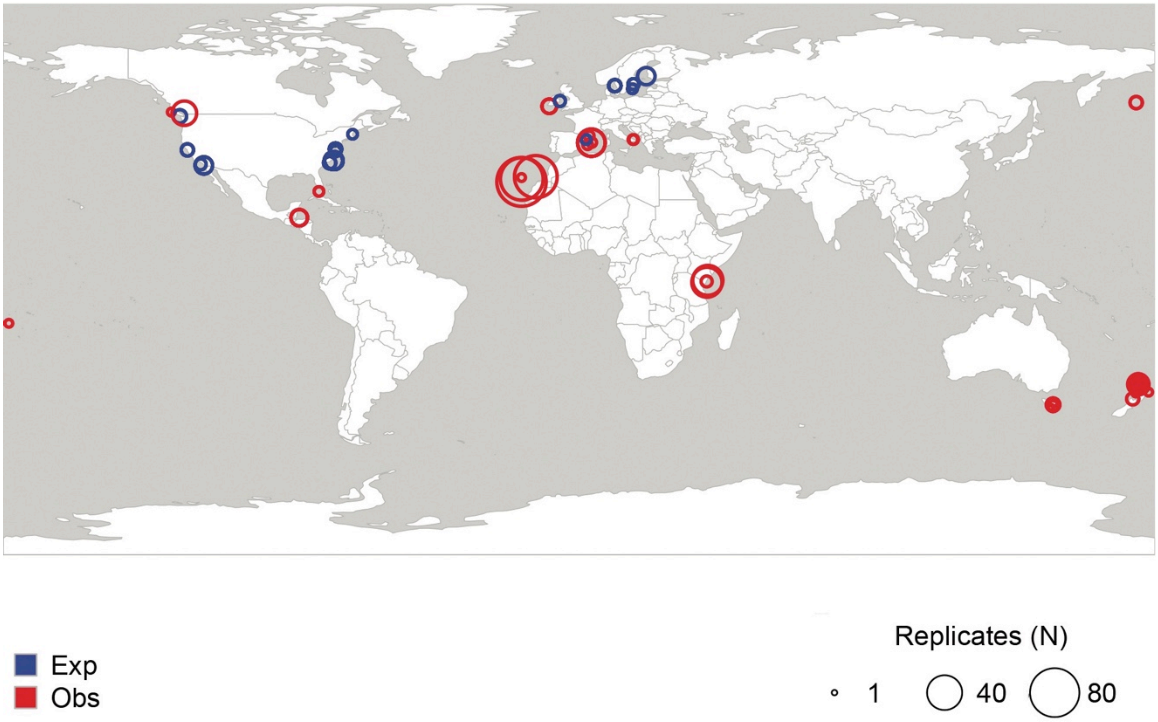


Figure A.1. Location of the studies included in this analysis. The size of the circles represents the number of study replicates and the colour represents the study type.

Table A.1. List of predictor variables, units, and their ranges. *Indicates a variable that was log transformed for analysis.

Predictor variable	**Type**	**Range and units**
Study type	Categorical	Exclusion, enclosure, mesocosm, marine reserve, observational
Predator	Categorical	Vertebrate, invertebrate
Herbivore	Categorical	Vertebrate, invertebrate
Primary producer	Categorical	Mirco algae, macro algae, epiphytic algae, seagrass
Sea surface temperature	Continuous	5.44 – 27.80 ˚C
Nitrate levels	Continuous	0.01 – 9.83 *u*mol/L
Phosphate levels	Continuous	0.02 – 1.51 *u*mol/L
Study length (experimental only)*	Continuous	15 - 730 Days
Predator size*	Continuous	3 – 1350 cm
Herbivore size*	Continuous	0.06 - 40 cm
Predator-herbivore ratio*	Continuous	0.44 - 270
Marine reserve size*	Continuous	51 – 21300 hectares
Marine reserve age	Continuous	1 – 35 years

Table A.2. The various mean effect sizes (herbivore and producer) with the upper (Ub) and lower (Lb) boundaries of 95% confidence intervals as broken down by category. An italicized value indicates a non-significant effect size.

	Producer effect size			Herbivore effect size		
Factor	Mean	Ub	Lb	Mean	Ub	Lb
Predator: invertebrate	0.83	1.43	0.23	-1.50	-0.66	-2.34
Predator: vertebrate	0.82	1.21	0.44	-1.16	-0.62	-1.71
Herbivore: Invertebrate	0.82	1.14	0.51	-1.28	-0.82	-1.74
Herbivore: vertebrate	0.83	1.18	0.49	*-0.88*	*0.73*	*-2.49*
Producer: epiphyte	*0.40*	*1.14*	*-0.35*	-1.27	-0.71	-1.82
Producer: macro	0.88	1.21	0.55	-1.26	-0.80	-1.71
Producer: micro	1.20	1.55	0.86	-1.25	-0.67	-1.84
Producer: seagrass	*0.58*	*1.79*	*-0.64*	-1.36	-0.74	-1.99
Enclosure	*0.55*	*1.28*	*-0.18*	*-0.06*	*1.06*	*-1.17*
Exclusion	0.93	1.68	0.18	-1.98	-0.78	-3.18
Marine reserve	0.68	1.13	0.23	-1.21	-0.54	-1.88
Mesocosm	1.31	2.11	0.51	-1.80	-0.64	-2.96
Observation	0.99	1.95	0.03	-1.46	0.00	-2.92
Experimental	0.98	1.50	0.45	-1.27	-0.54	-2.01
Observational	0.74	1.14	0.33	-1.25	-0.66	-1.84
Overall	0.83	1.14	0.51	-1.26	-0.81	-1.72

Table A.3. Results of the linear mixed effects models between the various predictor variables and the herbivore and producer effect sizes. Bolded entries are statistically significant (P < 0.05), SE = standard error, "Int." indicates the model intercept.

		Producer effect size			Herbivore effect size		
Factor	*N*	Estimate	SE	P value	Estimate	SE	P value
Herbivore: invertebrate (Int.)	129	0.82	0.16	0.90	-1.28	0.23	0.63
Herbivore: vertebrate	7	0.01	0.07	0.90	0.39	0.82	0.63
Herbivore size	129	0.01	0.04	0.91	**-0.69**	**0.12**	**< 0.01**
Nitrate	94	**0.20**	**0.08**	**0.02**	< 0.001	0.12	1.00
Phosphate	94	**1.55**	**0.77**	**0.04**	-0.502	0.99	0.61
Predator-herbivore size ratio	129	0.00	0.00	0.77	**0.01**	**0.00**	**< 0.01**
Predator: invertebrate (Int.)	43	0.83	0.30	0.98	-1.50	0.43	0.51
Predator: vertebrate	86	-0.01	0.36	0.98	0.34	0.51	0.51
Predator size	129	0.23	0.28	0.41	0.10	0.48	0.84
Producer: epiphyte (Int.)	13	**0.40**	**0.38**	**< 0.01**	-1.27	0.28	0.97
Producer: macro	109	**0.48**	**0.38**	**< 0.01**	0.01	0.18	0.97
Producer: micro	4	**0.80**	**0.41**	**< 0.01**	0.01	0.21	0.97
Producer: seagrass	3	**0.18**	**0.72**	**< 0.01**	-0.10	0.30	0.97
Study duration	69	0.07	0.59	0.91	0.53	0.74	0.47
Temperature	94	-0.04	0.03	0.21	**-0.09**	**0.04**	**0.04**
Enclosure (Int.)	24	0.55	0.37	0.39	**-0.06**	**0.57**	**0.01**
Exclusion	12	0.38	0.26	0.39	**-1.92**	**0.57**	**0.01**
Marine reserve	50	0.13	0.43	0.39	**-1.15**	**0.66**	**0.01**
Mesocosm	35	0.76	0.55	0.39	**-1.74**	**0.82**	**0.01**
Observation	8	0.44	0.61	0.39	**-1.41**	**0.94**	**0.01**
Experimental	71	0.98	0.27	0.49	-1.27	0.38	0.97
Observational	58	-0.24	*0.34*	0.49	0.02	0.48	0.97
Reserve age	50	0.02	0.03	0.46	**-0.09**	**0.03**	**< 0.01**
Reserve size	50	0.10	0.39	0.80	0.42	0.53	0.43

Table A.4. Results of the Tukey honest significant difference tests performed on the different significant categorical variables.

Producer effect size			Estimate	SE	P value
Micro	-	Macro	0.09	0.75	1.00
Epiphyte	-	Macro	0.41	0.75	1.00
Seagrass	-	Macro	-0.22	0.97	1.00
Epiphyte	**-**	**Micro**	**0.32**	**0.06**	**< 0.01**
Seagrass	-	Micro	-0.30	0.62	1.00
Seagrass	-	Epiphyte	-0.63	0.62	1.00

Herbivore effect size			Estimate	SE	P value
Exclusion	-	Enclosure	-1.87	0.96	0.51
Marine reserve	-	Enclosure	-1.10	1.19	1.00
Mesocosm	-	Enclosure	-1.68	1.29	1.00
Observation	-	Enclosure	-1.35	1.36	1.00
Marine reserve	-	Exclusion	0.77	0.70	1.00
Mesocosm	-	Exclusion	0.18	0.85	1.00
Observation	-	Exclusion	0.52	0.96	1.00
Mesocosm	-	Marine reserve	-0.59	0.68	1.00
Observation	-	Marine reserve	-0.25	0.82	1.00
Observation	-	Mesocosm	0.34	0.95	1.00

Trophic connectivity			Estimate	SE	P value
Micro	-	Macro	1.59	1.41	1.00
Epiphyte	-	Macro	2.12	1.54	1.00
Seagrass	-	Macro	-2.95	1.88	0.70
Epiphyte	-	Micro	0.53	0.63	1.00
Seagrass	**-**	**Micro**	**-4.54**	**1.24**	**< 0.01**
Seagrass	**-**	**Epiphyte**	**-5.07**	**1.37**	**< 0.01**

Table A.5. Results of the linear mixed effects models between the various predictor variables and the trophic connectivity metric. Bolded entries are statistically significant ($P < 0.05$), SE = standard error, "Int." indicates the model intercept.

	Trophic connectivity			
Factor	Estimate	SE	P value	N
Exp. type: enclosure (Int.)	0.31	0.76	0.69	11
Exp. type: exclusion	-0.41	0.83	0.62	9
Exp. type: marine reserve	-1.36	0.89	0.14	25
Exp. type: mesocosm	-1.12	0.99	0.27	33
Exp. type: obersvation	0.58	1.34	0.67	4
Herbivore: invertebrate (Int.)	-0.58	0.31	0.07	77
Herbivore: vertebrate	0.46	0.94	0.62	5
Herbivore size	-0.68	0.40	0.10	82
Nitrate	**0.29**	**0.12**	**0.02**	82
Phosphate	**2.42**	**1.00**	**0.02**	82
Predator-herbivore size ratio	**0.01**	**0.01**	**0.02**	82
Predator: invertebrate (Int.)	-0.93	0.60	0.13	26
Predator: vertebrate	0.51	0.70	0.47	56
Predator size	0.26	0.67	0.70	82
Producer: epiphyte (Int.)	-0.93	0.72	0.19	4
Producer: macro	0.64	0.72	0.39	74
Producer: micro	1.37	0.94	0.22	2
Producer: seagrass	**-3.94**	**1.41**	**0.01**	2
Temperature	**-0.12**	**0.05**	**0.02**	82

Table A.6. Results of the Tukey honest significant difference tests performed between the current study and the effect sizes of the Shurin et al.'s (2002) and Borer et al.'s (2005) work. Bolded values are significant, SE = standard error.

Herbivore effect size		Borer et al. 2005 system	Estimate	SE	P value	N
Updated marine benthic	-	**Lentic benthic**	**1.57**	**0.47**	**0.01**	12
	-	Lakes	-0.44	0.36	0.88	22
	-	Marine benthic	0.56	0.56	0.95	8
	-	Marine pelagic	-0.30	0.53	1.00	9
	-	**Stream**	**-0.94**	**0.31**	**0.04**	33
	-	Terrestrial	-0.84	0.39	0.32	18

Producer effect size		Shurin et al. 2002 system	Estimate	SE	P value	N
Updated marine benthic	-	Lentic benthic	-0.14	0.40	1.00	16
	-	Lakes	0.00	0.27	1.00	30
	-	Marine benthic	-0.71	0.38	0.48	18
	-	Marine pelagic	0.67	0.36	0.50	14
	-	Stream	0.36	0.24	0.74	35
	-	Terrestrial	0.67	0.25	0.09	97

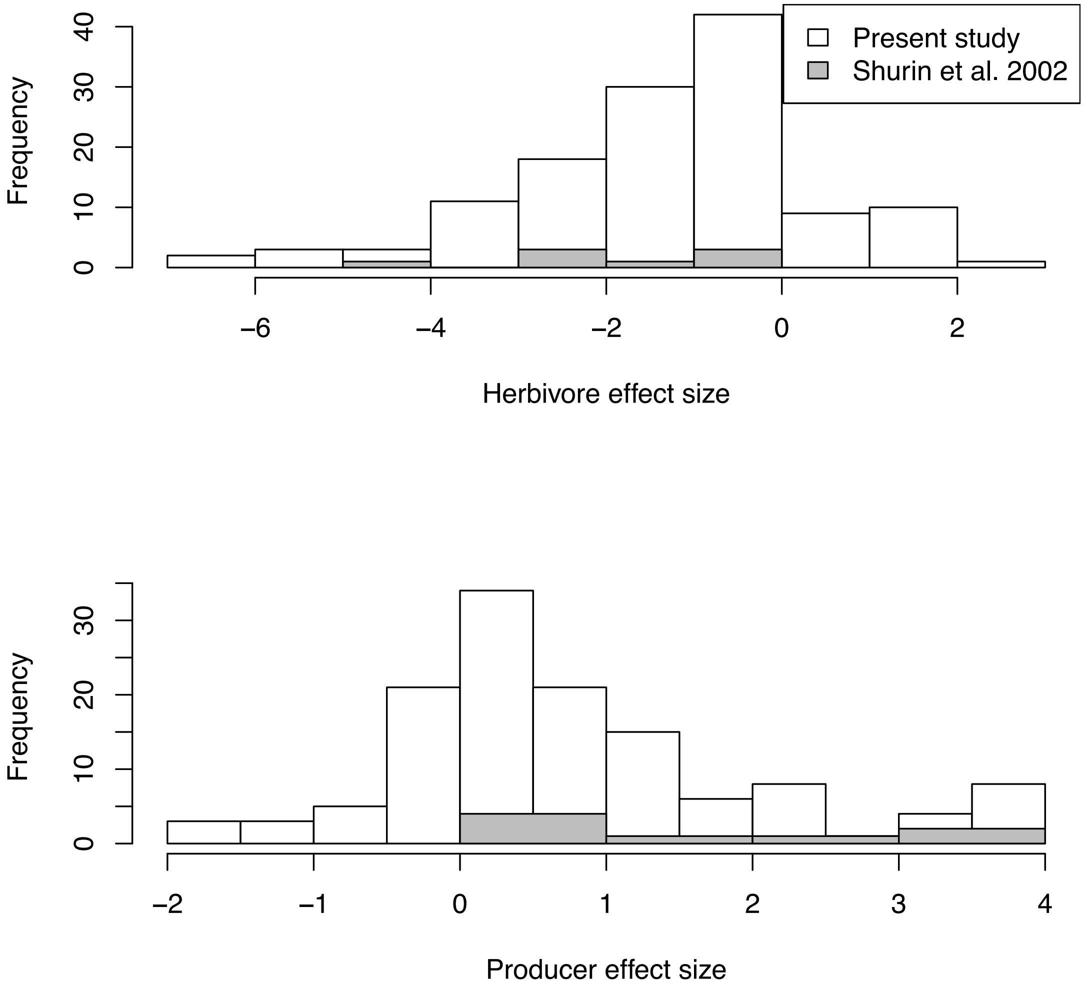
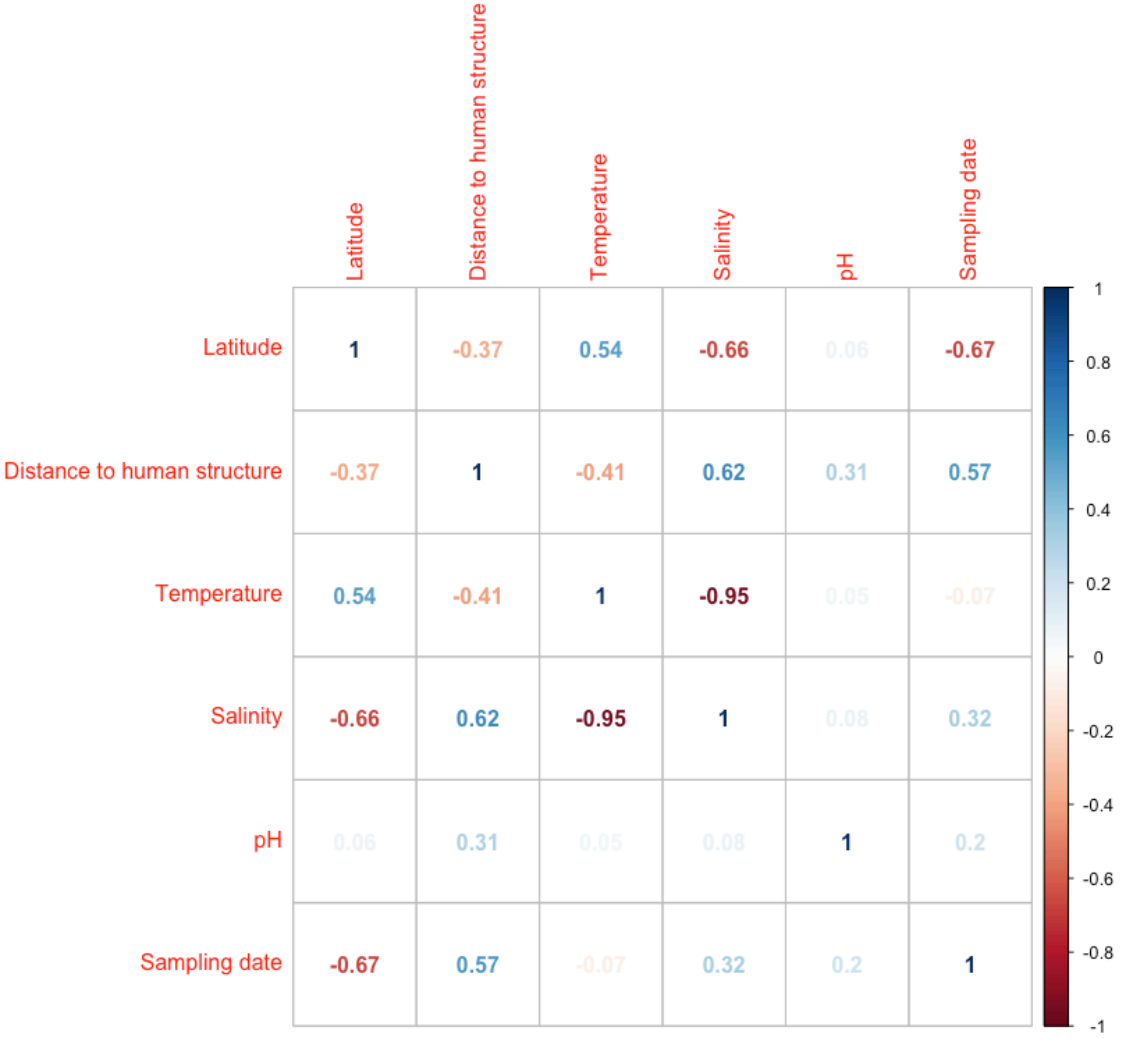


Figure A.2. Histogram of the effect sizes from the current study and the effect sizes of the benthic marine studies used in Shurin et al.'s (2002) and Borer et al.'s (2005) work.

Appendix B



	Latitude	Distance to human structure	Temperature	Salinity	pH	Sampling date
Latitude	1	-0.37	0.54	-0.66	0.06	-0.67
Distance to human structure	-0.37	1	-0.41	0.62	0.31	0.57
Temperature	0.54	-0.41	1	-0.95	0.05	-0.07
Salinity	-0.66	0.62	-0.95	1	0.08	0.32
pH	0.06	0.31	0.05	0.08	1	0.2
Sampling date	-0.67	0.57	-0.07	0.32	0.2	1

Figure B.1. Correlation values (Pearson's R) between latitude and the abiotic and variables and sampling date for each site.

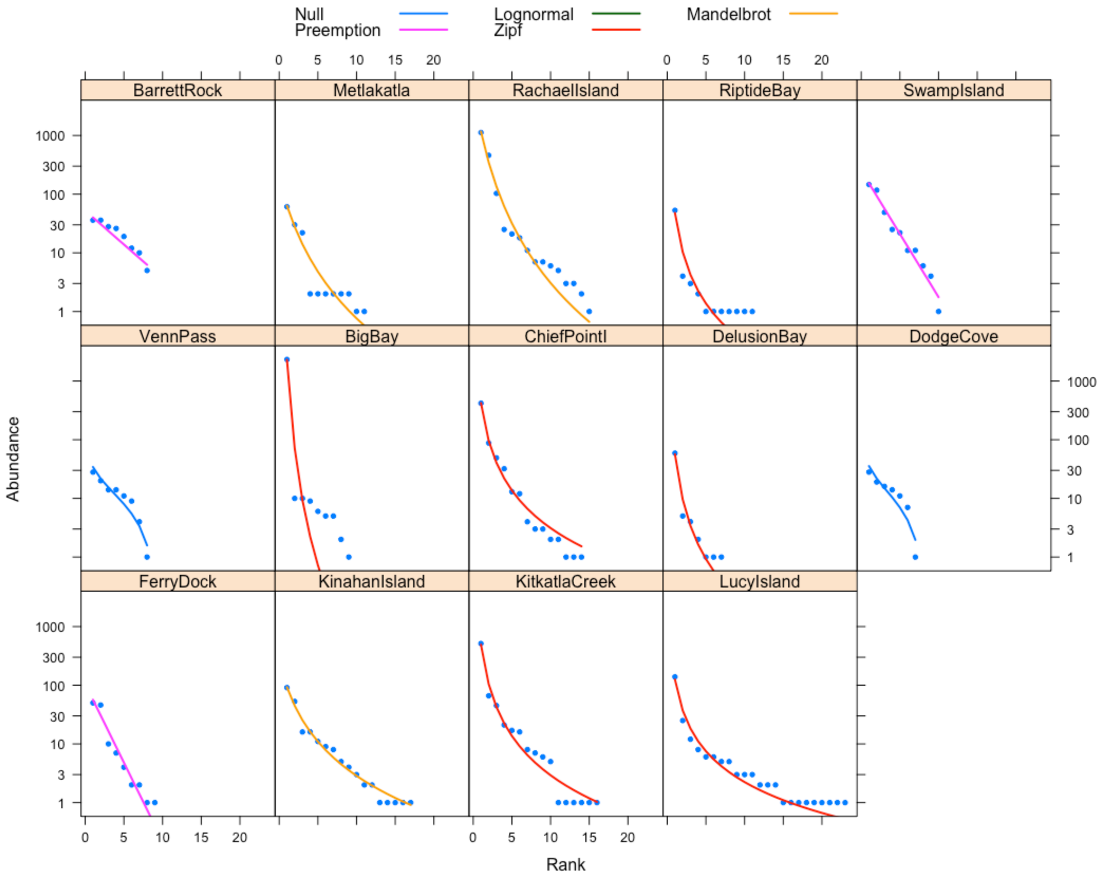


Figure B.2. Species rank abundance plots for the survey sites. Different coloured lines represent the different models used to fit the curves; the fits were done using the radfit function in the *vegan* package in R.

Table B.1. All species caught and photographed along with the number of sites where species was observed (Regional occupancy, maximum of 14), the median proportion that species contributed to a site's biomass, and the species' morphological measurements used to calculate trait values. Trait abbreviations are as follows: Bl: Body length Cpd: Caudal peduncale depth CFd: Caudal fin depth PFi: Height of pectoral fin PFb: Body depth at pectoral fin PFl: Pectoral fin length Hd: Head depth Ed: Eye depth Eh: Eye height Mo: Mouth opening Ml: Mouth length

Latin name	**Common name**	**Regional occupancy**	**Median proportion of site biomass**	**Bl**	**CPd**	**CFd**	**PF_i**	**PFb**	**PFl**	**Hd**	**Ed**	**Eh**	**Mo**	**Ml**
Cymatogaster aggregata	Shiner surfperch-A	14	0.320	10.87	0.47	0.95	1.15	3.49	0.78	1.91	0.87	1.25	1.03	0.27
Leptocottus armatus	Staghorn sculpin	13	0.208	13.75	1.31	0.81	0.36	0.80	3.31	0.65	0.31	0.48	0.28	0.32
Platichthys stellatus	Starry flounder	10	0.071	15.07	0.33	0.84	3.20	7.16	2.50	2.28	0.71	1.83	1.65	0.56
Hypomesus pretiosus	Surf smelt	1	0.069	5.50	0.17	0.50	0.67	0.73	0.15	0.46	0.25	0.19	0.19	0.38
Lepidopsetta bilineata	Rock sole	2	0.044	12.10	0.17	1.43	1.84	4.42	1.59	1.44	0.56	0.94	1.05	0.39
Scorpaenichthys marmoratus	Cabezon	2	0.038	10.51	0.71	1.86	1.02	2.51	3.29	1.79	0.66	1.72	0.55	0.94
Lumpenus sagitta	Snake prickleback	7	0.034	16.20	0.85	3.20	0.52	1.22	1.85	0.94	0.46	0.63	0.26	0.38
Parophrys vetulus	English sole	11	0.033	9.20	0.39	1.40	1.28	2.80	1.10	1.09	0.42	0.94	0.84	0.34
Hemilepidotus hemilepidotus	Red Irish lord	2	0.020	12.60	1.36	1.04	1.18	2.53	2.93	1.71	0.70	1.26	0.64	0.87
Cymatogaster aggregata	Shiner surfperch-J	14	0.020	4.17	0.12	1.48	0.40	1.29	0.33	0.86	0.45	0.41	0.37	0.14
Pholis ornata	Crescent gunnel	13	0.019	13.62	0.75	0.39	0.42	1.27	0.60	0.74	0.28	0.55	0.38	0.28
Citharichthys stigmaeus	Speckled sanddab	8	0.018	8.45	0.26	1.09	1.30	2.78	1.37	1.27	0.39	0.95	0.89	0.56
Microgadus tomcod	Pacific tomcod	1	0.012	15.88	0.42	1.33	1.17	2.97	2.12	1.70	0.79	1.16	0.60	1.25
Citharichthys sordidus	Pacific sanddab	6	0.012	9.12	0.84	0.97	1.37	2.66	1.25	1.15	0.41	0.86	0.91	0.46
Artedius fenestralis	Padded sculpin	7	0.012	7.62	0.86	2.66	0.58	1.49	1.96	1.12	0.52	0.77	0.45	0.76
Pleuronichthys coenosus	CO sole	1	0.011	12.10	0.47	1.39	2.14	3.91	1.34	1.57	0.64	0.99	0.96	0.48
Sebastes paucispinis	Bocaccio	1	0.008	9.73	0.77	2.19	0.88	2.71	1.79	1.96	0.76	1.35	0.58	1.24
Sebastes caurinus	Copper rockfish	1	0.008	8.42	0.88	0.95	0.91	2.71	2.27	1.65	0.89	1.25	0.98	0.84
Enophrys bison	Buffalo sculpin	6	0.006	7.24	0.40	1.48	0.61	1.57	1.69	1.16	0.46	0.88	0.17	0.11
Syngnathus leptorhynchus	Bay pipefish	13	0.005	17.14	0.12	0.58	0.28	0.42	0.33	0.35	0.22	0.26	0.28	0.14
Ophiodon elongatus	Lingcod	4	0.005	13.39	0.83	1.29	0.72	1.98	2.06	1.29	0.63	0.96	0.48	0.88
Apodichthys flavidus	Penpoint gunnel	8	0.005	11.74	0.71	0.76	0.33	1.01	0.32	0.50	0.17	0.35	0.29	0.13
Aulorhynchus flavidus	Tubesnout	7	0.005	6.89	0.26	1.84	0.14	0.36	0.68	0.33	0.24	0.15	0.25	0.39
Artedius lateralis	Smoothhead sculpin	5	0.005	9.27	0.52	0.84	0.73	1.65	2.16	1.28	0.56	1.05	0.42	0.47
Hemilepidotus spinosus	Brown Irish lord	1	0.004	4.58	0.26	0.95	0.41	0.97	1.27	0.83	0.35	0.48	0.26	0.25
Oligocottus snyderi	Fluffy sculpin	2	0.003	5.19	0.66	1.54	0.51	1.16	1.62	0.80	0.35	0.60	0.37	0.30
Oncorhynchus kisutch	Coho salmon	1	0.002	10.79	0.90	1.43	0.29	2.07	1.36	1.39	0.72	0.79	0.72	0.85
Blepsias cirrhosus	Silverspotted sculpin	4	0.002	6.01	0.55	1.39	0.52	1.37	2.07	0.91	0.41	0.63	0.40	0.41
Oncorhynchus keta	Chum salmon	1	0.002	9.19	0.72	2.19	0.10	1.66	1.44	1.14	0.65	0.48	0.52	0.60
Gasterosteus wheatlandi	Threespine stickleback	4	0.002	5.04	0.39	0.56	0.45	0.89	0.71	0.56	0.32	0.36	0.32	0.14
Tilesina gibbosa	Tubenose poacher	1	0.001	6.34	0.09	0.50	0.23	0.42	1.02	0.42	0.26	0.83	0.36	0.15
Oligocottus maculosus	Tidepool sculpin	3	0.001	6.13	0.09	0.93	0.44	1.31	1.92	1.03	0.42	0.48	0.24	0.36
Artedius harringtoni	Scalyhead sculpin	2	0.001	4.49	0.33	1.09	0.70	1.10	1.59	0.89	0.39	0.73	0.32	0.34
Ammodytes personatus	Sandlance	2	0.001	6.22	0.35	1.52	0.26	0.52	0.49	0.36	0.22	0.30	0.28	0.22
Gadus macrocephalus	Walleye pollock	1	0.001	5.47	1.17	2.19	0.55	0.97	2.53	0.81	0.41	0.58	0.38	0.51
	Max trait value			17.14	1.36	3.20	3.20	7.16	3.31	2.28	0.89	1.83	1.65	1.25
	Min trait value			4.17	0.09	0.39	0.10	0.36	0.15	0.33	0.17	0.15	0.17	0.11