

TRAIT-BASED ASSEMBLY ACROSS TIME AND LATITUDE
IN MARINE COMMUNITIES

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ABSTRACT

One of the central questions of ecology aims to understand the mechanisms that maintain patterns of species coexistence. Community assembly, the process of structuring communities, occurs in ecological time, is influenced by biotic interactions at local scales, and is thought to help maintain diversity patterns. Species invasions, however, as a result of globalization and intense marine trade, are common in coastal ecosystems, and have the potential to change the outcome of biotic interactions and community structure. Human-induced disturbance also disrupts community structure and coastal habitats are at greater risk due to encroachment of human populations near coasts. Changes in community structure are usually quantified as the number and distribution of species, however, the processes that shape communities act on the traits that allow and optimize species survival. Recently, ecological questions aiming to understand changes in community structure, invasion dynamics, and responses to disturbance are using measures that reflect species' ecological functions (i.e., traits) and describe the trait composition of communities (i.e., functional structure and diversity).

The objectives of my dissertation are to use functional diversity and structure to 1) determine trait responses from predation across latitude while considering interaction histories between native and introduced species with local predators, 2) use functional diversity patterns and changes in functional structure to infer the relative influence of predation and competition on community assembly through time and across latitude, and 3) assess trait responses to physical disturbance, also, through time and across latitude while considering the trait diversity of the system. To achieve these objectives, I used

field experiments to grow coastal sessile marine invertebrate communities in treatments that test the influence of biotic interactions or disturbance. Experiments ran for three or twelve months at 12 sites in four regions of the Pacific Coast: Alaska, California, Mexico, and Panama.

For my first objective, I found predation driven trait responses mainly occurred at lower latitudes where biotic interactions are expected to be stronger. Additionally, the native and introduced species of focal communities showed opposite trait responses to predation at lower latitudes with traits related to palatability and parental investment being primarily influenced. For my second objective, I found strong competition influenced late-stage assembly across the latitudinal gradient, while predation had a greater influence during early assembly in the tropics. Thus, the relative strength of biotic interactions changes with time and latitude and either predation or competition may serve as primary filters of community assembly. For my third objective, I found fast colonization and regeneration abilities help communities recover from intense disturbance, but only at lower latitudes where communities were most impacted by disturbance. In plant communities, functional traits have been studied quite extensively for several years and have set the stage for exploration in other ecosystems. In marine systems, the link between traits and ecological processes that influence community structure are mostly understudied, and my dissertation is contributing to close this knowledge gap about nearshore communities from across 47 degrees of latitude.

DEDICATION

I dedicate my dissertation to the love of my life, Nicolas Bernal, who has been calling me “doctora” before I had decided to become one. A special feeling of gratitude to my loving parents Carlos López and Amparo Lozano whose words of encouragement and vivid example of hard work resonate in my daily life. My sisters Karol, Aleja and Lulu who despite the distance have never left my side. I also dedicate this dissertation to my many friends who have supported me throughout the process. I will always appreciate all they have done, especially Jenny Paredes for diving into this PhD journey besides me and being the encouragement I needed. Los amo.

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CHAPTER 1

INTRODUCTION

1.1 Trait-based ecology

A primary objective of community ecology is to disentangle the complex dynamics that contribute to the structuring of communities, and further reveal how such dynamics change along spatial and temporal gradients (Hairston et al. 1960, Agrawal et al. 2007). While much work has focused on exploring assembly from a taxonomic perspective, the mechanisms that influence communities act on traits of individuals (Díaz and Cabido 2001). The match between an individual's trait and the environment at a particular time and space as a result of evolutionary processes and ecological sorting would dictate membership in a community (Webb et al. 2010, Enquist et al. 2015). In recent decades, the search to understand assembly processes now includes accounting for intrinsic trait differences and/or similarities between community members and among communities (Webb et al. 2010, Cadotte et al. 2013). Therefore, trait-based assembly offers a mechanistic alternative to traditional taxonomic approaches to describe and assess the influence of the varying forces that shape communities.

Nowadays, to examine coexistence and assembly, additional factors that impact community structure need to be considered. For example, as a consequence of globalization, including marine trade, species invasions are changing the taxonomic, phylogenetic, and functional identity of communities (Ruiz et al. 2000, Li et al. 2020), and invasions can modify species interactions and the organization of communities (Franklin et al. 2016, Wong et al. 2017). The outcome of novel interactions between

native and introduced species may depend on trait mechanisms that deal with predators and/or competitors, and both trait mismatches or non-coevolved trait strategies would determine interaction outcomes (Verhoeven et al. 2009). Trait-based approaches, then, are well suited to determine how communities may respond to rapid changes in community structure such as species invasions.

Other anthropogenic induced changes also impact community structure. Altered disturbance regimes from climate change and human activities such as agriculture, logging, pollution, and fishing, among many others, cause mass mortality, biomass loss, and disruption of community structure (Lenihan and Oliver 1995, Stark et al. 2014, Franklin et al. 2016). Short and long-term responses to disturbance may differ as more immediate responses may be observed from direct human interventions than from climate change related disturbances (Franklin et al. 2016). Moreover, a community's response and recovery from disturbances may depend on multiple factors including the stability of the system as well as their taxonomic and functional diversity (Hillebrand and Kunze 2020). Disturbed communities often respond with trait trade-offs related to reproductive, growth, and recolonization strategies (Seifan et al. 2013, Rodman et al. 2020) and a reduction of trait profiles tends to occur (Mouillot et al. 2013). Trait-based approaches, thus, capture changes in community structure from disturbances and provide more in depth information than taxonomic approaches, but multiple factors can influence the extent of the impact and potential for recovery. With anthropogenic disturbance on the rise, there is an ever growing need to test disturbance regimes in natural communities

from broad spatial and temporal scales, specially from understudied regions like the tropics (Hillebrand and Kunze 2020).

1.2 Ecological processes varying across time and latitude

Many ecological processes known to influence assembly are hypothesized to vary with latitude. At local scales, biotic interactions are believed to have a greater influence in assembly than abiotic filters (Pearson et al. 2018), and according to the biotic interaction hypothesis, interaction strength increases towards the equator (Schemske et al. 2009). While much evidence supports the prediction that predation is stronger at lower latitudes (Freestone et al. 2011, 2020, Roslin et al. 2017, Hargreaves et al. 2019), a latitudinal gradient of competitive strength is still debated (Barnes 2002, Henriques-Silva et al. 2019). Changes in trait diversity as result of either predation and/or competition may help explore trait-based assembly (Götzenberger et al. 2012, Obertegger and Flaim 2015), and whether strong interactions have a greater impact on the trait architecture of communities from different latitudes.

Primary filters of assembly may change through time as communities develop (Spasojevic et al. 2014, Peralta et al. 2019). Competition, for example, becomes more relevant later in development as resources become limited (Martorell and Freckleton 2014), while predation may act as a continuous disturbance regardless of the age of the community (Repetto et al. *in prep*). In sessile communities, space is an important limiting factor and pulse disturbances that open up space may weaken competitive dynamics (Chase et al. 2002) and can have a greater impact in mature communities (Cornell and Lawton 1992). Shifting patterns of trait diversity through time may signal

changes in assembly filters and/or when disturbance has a greater impact on community structure. Few studies have measured the impact of biotic interactions or disturbance on trait diversity through time despite ontogeny being a source of variation in community assembly.

Examining how ecological processes influence communities across time and latitude is greatly understudied despite decades of research looking to understand how communities form in nature. In my dissertation, I used in situ experimental approaches to reveal the importance of species interactions and human-induced disturbance in the assembly of communities while considering additional factors that can influence these dynamics. In my first chapter, I use the native and introduced status of prey species as a proxy of interaction history with predators to assess trait responses from predation. In my second chapter, I use two community development stages to assess the relative influence of predation and competition on the trait distribution of communities from different latitudes. Likewise, in my third chapter, I use two community development stages to assess trait responses to repeated physical disturbance (i.e., biomass removals) on focal communities. These stressors act upon functional traits of organisms, thus trait-mediated responses can reveal the strategies that communities use to cope, but responses may depend on latitude and/or the assembly stage of the community.

1.3 Trait selection

A successful assessment of ecological processes with trait-based approaches depends on a meaningful selection of traits. Using traits unrelated to the assembly mechanisms in question can confound results (Spasojevic and Suding 2012, Gianuca et al. 2017), and

using too few traits can reduce the power to detect the processes influencing assembly (Kraft et al. 2015). Although, it is difficult to determine how many traits are needed to define an optimum functional space (Maire et al. 2015), multi-trait approaches are important as species differences are best described with a variety of traits (de Bello et al. 2017). I therefore created a functional trait table that defined the functional space associated with the ability of species to gain resources, reproduce, and survive under biotic interactions and disturbances (Table 1.1). For each chapter, I used both multi- and single-trait measures to determine the influence of species interactions or disturbance on the trait-based assembly of sessile marine invertebrate communities. A list of literature sources is available in the appendix.

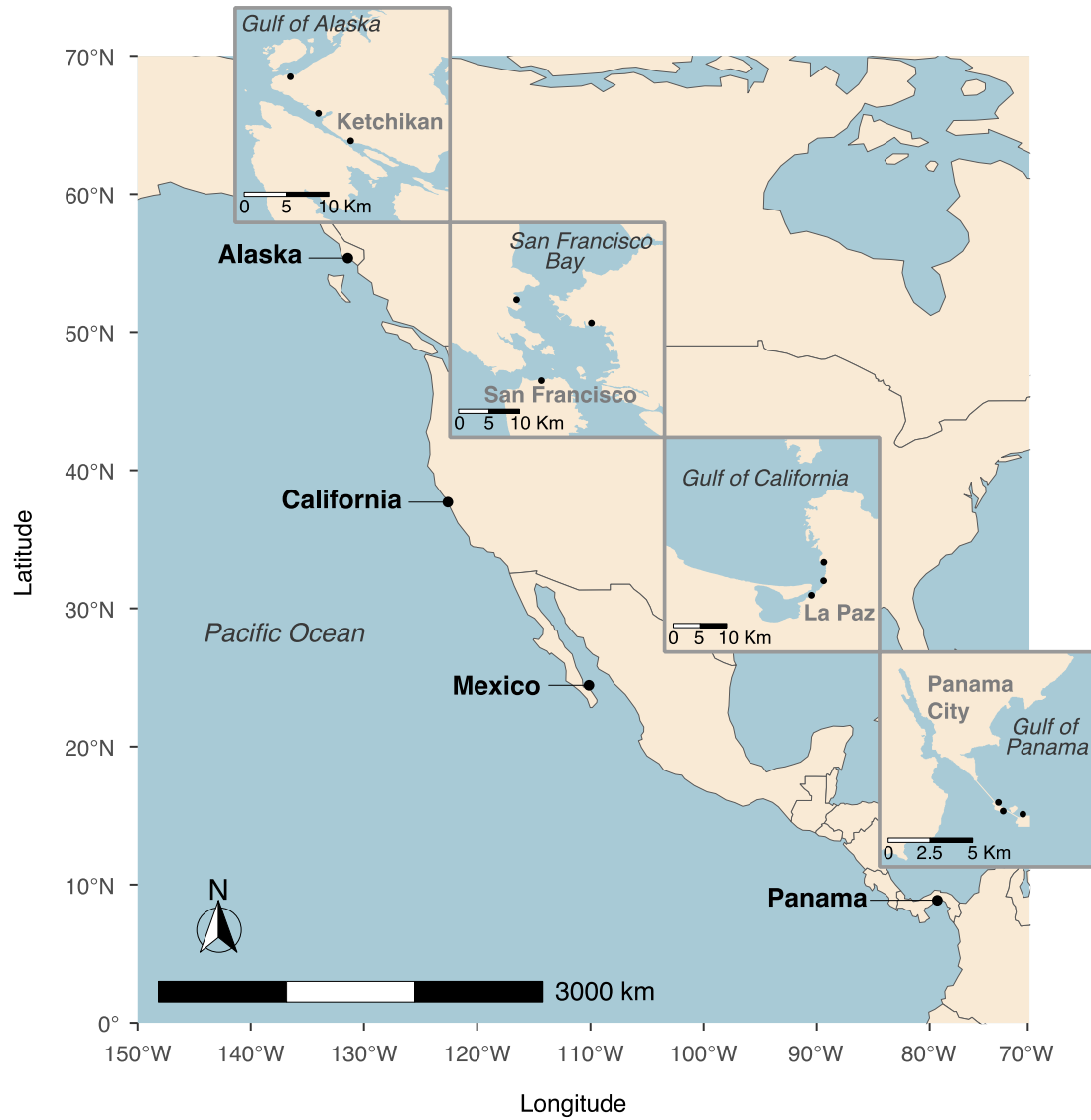
Table 1.1 List of traits considered in this study with their surrogate function and corresponding reference. For categorical traits, each category included more than one taxonomic group (e.g., with feeding appendages: bryozoans, barnacles, polychaetes, etc.).

Trait	Category	Data Type	Source	Function	Reference
Organic content		Continuous	Field/laboratory	Palatability, growth	(Tarjuelo et al. 2002, Lippert and Iken 2003)
Water Content		Continuous	Field/laboratory		
Color	Bright, dull, dark, transparent, white	Categorical	Field/laboratory	Defense	(Stoecker 1980, Wicksten 1989)
Structural defense	Calcified structure, uncalcified structure, no structure	Categorical	Field/observation		(Dyrynda 1986, Kicklighter and Hay 2006, Buckeridge and Reeves 2009)
Sociability	Colonial, solitary	Binary	Literature	Competition, defense, resource acquisition	(Hiebert et al. 2019)
Growth form	Encrusting, erect, arborescent, massive, runner, stolonate	Categorical	Literature/observation	Resource acquisition, competition, growth	(Svensson and Marshall 2015)
Feeding Structure	With feeding appendages, without feeding appendages	Binary	Field/observation	Competition, defense, resource acquisition	(Palmer et al. 1982, Shea 2002, Fleming et al. 2007, Riisgård and Larsen 2010, Thompson et al. 2015)
Asexual reproduction	Yes/no	Binary	Literature	Competition, resource acquisition, colonization	(Stocker and Underwood 1991)
Sexual reproduction	Hermaphroditic, gonochoristic, simultaneous	Categorical	Literature		(Crombie 1947)
Larval duration (max hours)		Continuous	Literature	Dispersal, competition	(Sams et al. 2015)
Egg size (μm)		Continuous	Literature	Competition, colonization/dispersal, predation	(Vance 1973, Mukherjee et al. 2014)
# eggs per individual		Discrete	Literature		
Larval development	Simultaneous lecithotrophic, planktotrophic	Categorical	Literature		
Fertilization type	Oviparous, ovoviviparous, viviparous	Categorical	Literature		

1.4 Experimental approach

For all chapters, I used field experiments deployed at twelve sites from four regions along the Pacific Coast of North and Central America (Fig 1.1). In each region, I grew sessile marine invertebrate communities on settlement panels deployed for three or twelve months in treatments that capture ambient and reduced predation pressure or disturbed and undisturbed regimes. In predation treatments, caging was used to keep macropredators from disturbing communities during assembly, and regular maintenance was necessary to keep invertebrates from settling and blocking the flow of water. Upon experimental panel retrieval, community composition data was captured from all treatments and was used in all chapters along trait data. More specific information about each experiment is available in the following three chapters.

Figure 1.1 Field sites shown as black dots in insets in each of four regions, for 12 study sites across the latitudinal gradient.



CHAPTER 2

HISTORY OF CO-OCCURRENCE SHAPES PREDATION EFFECTS ON FUNCTIONAL DIVERSITY AND STRUCTURE AT LOW LATITUDES

2.1 Abstract

1. The intensity of biotic interactions is hypothesized to increase towards the equator. Predation can have a stronger effect on prey composition, biomass, and taxonomic diversity in tropical regions compared to higher latitudes. Whether predation also shapes patterns of functional diversity and structure of prey communities, however, has rarely been explored across a latitudinal gradient. History of co-occurrence between predators and prey may also shape the outcome of the interaction, and increased novelty of introduced prey may lead to stronger trait responses.
2. I investigated the influence of predation on trait responses of prey communities across 12 sites in four regions, from the sub-arctic to the tropics, using a field experiment in invaded coastal habitats. Prey communities experienced ambient or reduced predation pressure during assembly, and the effect of predation on functional diversity and structure of whole communities as well as their native and introduced components was assessed.
3. Overall, predation increased functional diversity in the tropics, but effects were evident for introduced species only. Predation also shaped functional structure of low latitude communities, but effects were strongest for native species in subtropical Mexico and introduced species in tropical Panama.

4. Key traits driving shifts in functional structure were related to palatability and reproduction. In the tropics, the strong predation present under ambient conditions reduced the abundance of palatable traits in introduced prey relative to low predation treatments, while in the subtropics, ambient predation increased the abundance of palatable traits in native prey. Reproductive traits that require high parental or energetic investment were favored in low predation treatments at both low latitude regions.
5. In summary, predation had a stronger influence on trait responses of prey communities at lower latitudes where biotic interactions are expected to be more intense, but changes in functional diversity and structure hinged on co-occurrence histories of local predators with native or introduced prey. This study provides one of the first examinations of the effects of predation on functional trait responses of prey communities across a latitudinal gradient.

2.2 Introduction

Biotic interactions are hypothesized to be more intense at lower relative to higher latitudes (Schemske et al. 2009), and predation in particular can shape patterns of prey taxonomic diversity, composition, and biomass more strongly in the tropics (Freestone et al. 2011, Lavender et al. 2017, Hargreaves et al. 2019, Hiebert et al. 2019). Despite the likelihood that these large-scale patterns emerge due to strong biotic filters on functional traits of prey, or the characteristics relevant to an individual's response to the environment or species interactions, functional trait responses of prey communities to predation across latitude have rarely been explored. Functional diversity (i.e., degree of

trait diversity in a community) and structure (i.e., mean trait value in a community) can indeed change in response to disturbance (Boersma et al., 2016; Carmona, Mason, Azcárate, & Peco, 2015; Laliberté, Norton, & Scott, 2013; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013), and the magnitude of these changes could therefore vary with predation intensity across latitude. Moreover, shifts in the functional structure of prey communities due to predation can identify trait strategies that govern prey survival (Díaz et al. 2007). Therefore, understanding functional trait responses, including both functional diversity and structure, of prey communities to predation across latitude can provide a novel and mechanistic understanding of how local predator-prey interactions unfold across biogeographic scales.

Furthermore, prior research examining the effect of consumer pressure on functional trait responses has largely been done in terrestrial plant assemblages (Carmona et al., 2012; de Bello, Lepš, & Sebastià, 2006; Díaz et al., 2007; Laliberté & Tylianakis, 2012), and trait responses to consumers in other systems remains largely unexplored (Ceulemans et al. 2019). In plant communities, consumer pressure is hypothesized to increase functional diversity by reducing competitive dominance and promoting trait dissimilarity (Grime, 2006; Laliberté et al., 2013; Sasaki et al., 2009), but additional factors such as habitat type, productivity, and environmental gradients coupled with intense grazing can influence functional diversity (Carmona et al., 2012; de Bello et al., 2006; Laliberté et al., 2013; Laliberté & Tylianakis, 2012). Further, grazing can alter the functional structure of plant communities favoring certain life histories, growth forms, or palatabilities (sensu Díaz et al. 2007). While plant-herbivore interactions can inform expectations for

predator-prey dynamics, studied plant communities are often more phylogenetically restricted (e.g., single phyla communities: Laliberté et al., 2013; Sasaki et al., 2009) than other types of prey communities. Further study is needed to understand how consumers, and predators in particular, shape functional trait responses in other systems that encompass greater functional and phylogenetic diversity. In this study, I explore these questions using marine invertebrate communities, in which community membership can span seven phyla even across relatively small spatial scales (tens of centimeters), providing a novel opportunity to test the generality of these functional trait responses in a very diverse system.

The history of predator-prey co-occurrence can also impact functional responses of prey. Models predict weaker trait responses to grazing the longer plant-herbivore interactions have occurred in evolutionary time (Milchunas et al. 1988). In practice, consumer-prey evolutionary history is difficult to assess, and empirical studies have used historical accounts of the introduction of grazers by humans (e.g., wild versus domesticated) to attribute length of interaction history (Adler et al. 2004, Díaz et al. 2007). Evidence to date suggests that interaction history may be particularly important to life history trait responses in plant communities. At a global scale, a meta-analysis showed increased dominance of fast life histories with intense and short grazing histories, while phenotypic traits shifted in response to grazing regardless of interaction history (Díaz et al. 2007). In invaded communities, interaction histories with consumers are longer for native than introduced prey species, and functional responses of prey communities may hinge on their native or introduced status. Studies that determine the

influence of grazing on functional diversity often overlook the co-occurrence history of herbivores and plants despite the presence of introduced plant species (Laliberté et al., 2013; Laliberté & Tylianakis, 2012). Therefore, while there is some evidence that the co-occurrence history of grazers can influence the functional structure of plants, the effect of predator-prey co-occurrence histories on functional trait responses in invaded prey communities is still unknown.

Using a predator exclusion experiment on nearshore marine invertebrate communities replicated across four regions and 47-degrees latitude, I tested the hypothesis that predation would shape the functional diversity and structure of prey communities more strongly at low latitudes and the effect would further hinge on interaction history. Specifically, I hypothesized that at low latitudes, predation would both increase functional diversity by expanding trait dissimilarity and influence functional structure by selecting traits related to low palatability and enhanced defense mechanisms. I also expected these shifts in functional diversity and structure to be stronger for the introduced than the native components of low latitude prey communities due to shorter interaction histories between predators and prey. The model prey community represents a functionally and phylogenetically broad suite of taxa, including multiple phyla and both native and introduced species, which provide a unique opportunity for testing the effect of predation and predation histories on the functional diversity and structure of communities. To my knowledge this study, novel in its scale and scope, is the first to uncover trait-based responses to predation in invaded prey communities across a continental scale.

2.3 Materials and methods

2.3.1 Study system

Sessile marine invertebrate communities are functionally and phylogenetically diverse, are present in coastal habitats across the globe, and can be shaped by interactions with local predators (Freestone et al. 2011, Hiebert et al. 2019), making them an ideal model prey. The functional diversity of these communities is striking, as constituent species span multiple phyla, including Chordata, Bryozoa, Annelida, Porifera, Mollusca, Arthropoda, and Cnidaria, encompassing a broad spectrum of functional traits related to life history, predator defense, among others. Further, introduced species are now common as a result of intense marine traffic from global trade (Carlton and Geller 1993, Grosholz 2002, Ruiz et al. 2009), providing an opportunity to compare functional responses to predation of both native and introduced species across continental scales. The predator community associated with the focal prey communities is mainly composed of native fish (Freestone et al., *unpublished data*). Thus, lacking an evolutionary history with co-occurring organisms, introduced species must overcome local predation pressure, and consequently traits associated with predator defense, palatability, and reproductive strategies may dictate their abundances under strong predation. I therefore used native and introduced components of sessile marine invertebrate communities, representing different interaction histories with local predators, to assess trait responses to predation across a latitudinal gradient.

2.3.2 Predation experiments

I conducted a large-scale predator enclosure experiment comparing sessile marine invertebrate communities that assembled under ambient and reduced predation pressure across three sites in each of four regions (12 sites in total), along the Pacific Coast of North and Central America. I compared communities from southeast Alaska, USA (Ketchikan; 55° N, 131° W), California, USA (San Francisco; 37° N, 122° W), Baja California, Mexico (La Paz; 24°N, 110° W), and Panama (Panama City; 8° N, 79° W). Each sampling site was located in a recreational boat marina in close proximity to commercial ports to maximize the presence of introduced invertebrates. I used settlement panels as standardized model habitat for invertebrates, on which they can undergo natural dynamics of recruitment and growth. Settlement panels are widely used to control community development time and substrate type (Newcomer et al. 2019), and facilitate comparison of invertebrate communities across large biogeographic gradients (Freestone and Osman 2011, Freestone et al. 2011). At each site, I deployed 14 x 14 cm polyvinyl chloride (PVC) settlement panels hung horizontally one meter below the water surface from floating docks. The side of the panel facing the seafloor was abraded to facilitate invertebrate settlement and served as the focal substrate for prey community development.

Panels were assigned at random to three treatments: (1) cage enclosure (i.e., reduced predation), (2) partial cage (i.e., procedural cage control; ambient predation), and (3) open (i.e., ambient predation). All caging material had a mesh size of 0.635cm. Cages of this mesh size allow for the recruitment and growth of sessile invertebrate prey, while

reducing predation by large predators (Freestone et al. 2011). Partial cages had mesh on four sides, but no top (facing the seafloor when deployed), thereby providing a procedural control for physical changes due to mesh cages while allowing full access to predators.

Prey communities assembled in the three treatments for three months (Alaska: June to September, 2015; California: May to August, 2016; Mexico: June to September, 2017; Panama: December 2015 to March 2016), during periods of high recruitment and productivity across the latitudinal gradient (Bonfim et al., unpublished data; Freestone and Inouye 2015). Following assembly, I retrieved five panels of each treatment at each site for a total of 180 experimental communities. Upon retrieval, I identified invertebrates on a 50-point grid using a stereoscope to generate a measure of percent cover by taxa. Individuals were identified to the lowest taxonomic resolution possible and were assigned a species or a consistent morphospecies identifier. Identifications were confirmed by taxonomic experts and DNA barcodes wherever possible. While species composition of communities changed across the gradient, I found representatives of at least seven phyla in each region (i.e., Chordata [i.e., ascidians], Bryozoa, Annelida [e.g., tube-building polychaetes], Porifera [i.e., sponges], Mollusca [e.g., bivalves], Arthropoda [i.e., barnacles], and Cnidaria [e.g., hydroids]), with 60 taxa found in Alaska, 55 in California, 99 in Mexico and 94 in Panama (Freestone et al. *unpublished data*). Chordata and Bryozoa were the most abundant phyla in all regions. Additionally, I used the National Exotic Marine and Estuarine Species Information System (NEMESIS; Fofonoff et al. 2018) to assign status to confirmed species and complemented status

information with published literature. Status designations were native, introduced, and cryptogenic (species of unknown origin, Carlton 1996).

2.3.3 Functional characterization & functional indices

The ability to quantify a functional response from consumer pressure depends on the trait choice that define the functional space (Vesk et al. 2004). In the focal communities, sessile invertebrates rely on a variety of defense mechanisms to increase survival against predation. For example, some tube-forming polychaetes, barnacles, and bivalves have calcified outer shells hard enough to deter predators (Dyrynda 1986, Kicklighter and Hay 2006, Buckeridge and Reeves 2009), while toxic prey may use color to warn predators (Stoecker 1980, Wicksten 1989). Predation itself modifies the competition and recolonization dynamics of sessile communities by removing organisms and opening up space, a limiting resource for sessile invertebrates (Chase et al. 2002). Moreover, reproductive traits are known to respond to different levels of predation pressure (Magnhagen 1991). I therefore used traits related to defense, palatability, competition, and reproduction to define the functional space and examine prey community trait responses (Table 1.1).

To characterize function, I collected information on 14 functional traits for 109 taxa identified to genus or species and 28 taxa assigned to family or class. From this data, 81 species representing all taxonomic groups except sponges and hydroids were assigned status information and used in analyses of communities separated by status. Trait data were categorical, binary, discrete, or continuous and were collected through direct observation, measurements, or from literature sources (Table 1.1; List of sources

available in the Appendix). For categorical data, each taxa was assigned a single trait category, and each trait category included representatives from multiple taxonomic groups to avoid trait clustering within taxa (Table 1.1). When taxa-specific data was unavailable in the literature, I used values from the closest taxonomic level (Weigel et al. 2016).

For field measurements, an average of five individuals per taxa were photographed for color, structural defense, and growth form determination. Then, each specimen was blotted dry and weighed to obtain wet weights (WW), dried for approximately 48 hours at 60°C to obtain constant dry weights (DW), and placed in a muffle furnace at 500°C for four hours to obtain ash free dry weights (AFDW). For each sample, I calculated water content as $[(1-(DW/WW)) \times 100]$ (Reed et al. 2016) and organic content as $[(1-(AFDW/DW)) \times 100]$ (Widbom 1984). I then calculated a single mean trait value per taxa to be included in the species \times trait matrix to compute functional indices (Nogueira et al., 2018).

To test the hypothesis that predation would increase functional diversity and structure at low latitudes, particularly for species with short predation histories, I calculated functional divergence (FDiv) and community weighted means (CWM) for each prey community. FDiv is a trait similarity measure weighted by species abundance that represents the mean distance of the trait composition of a community to the centroid of its functional space (Villéger et al. 2008). Values of FDiv range from zero (i.e., high similarity) to one (i.e., high dissimilarity) when abundant species are closer to or further from the centroid, respectively. Community weighted means (CWM) represent the

average trait value or the highest proportion of a category (Nogueira et al., 2018), and I used these values to infer trait strategies that optimize survival or increased vulnerability to predation (Butterfield & Suding, 2013). I built separate functional diversity and functional structure indices for (a) all species (i.e., whole communities), (b) introduced species, and (c) native species (including species designated as cryptogenic to ensure a conservative estimate of the origin of these species, as in Gestoso et al. 2018), and tested for the effect of predation on each grouping separately.

2.3.4 Data analyses

I tested the hypothesis that predation would increase trait dissimilarity (e.g., FDiv) in low latitude communities, and that results would hinge on predation history, by examining FDiv patterns (1) for whole communities without regard for predation history, and (2) with explicit consideration of predation history of native and introduced components of the community. First, to test the effect of predation pressure on FDiv across latitude for whole communities, I used a linear mixed model (LMM) with region (Alaska, California, Mexico, Panama), treatment, and their interaction as fixed factors and site nested within region and its interaction with treatment as a random factor to account for multiple replicates being sampled from each site. I then employed contrasts to test for treatment effects in each region. Second, to test for the influence of predation history, I built a LMM with region, status, treatment, and their interaction as fixed factors and corresponding random factors of site nested within region and its interaction with treatment, status, and community ID. Presence of introduced or native species were too low in Alaska and California, respectively, to calculate FDiv for those region/status

combinations (Villéger et al. 2008). I therefore grouped Alaska (native) and California (introduced) components of the data as a single “high-latitude” region to ensure that all regions had indices for native and introduced species for a balanced statistical design. I again used planned contrasts to compare treatment responses for native and introduced assemblages in each region, which also enabled us to decompose treatment effects in the combined high latitude region into Alaska native and California introduced components.

I then examined whether individual traits had a disproportionate influence on model performance using a jackknife approach (Gagic et al. 2015) to overcome known limitations of interpreting the contribution of individual traits using multivariate functional diversity indices (Butterfield & Suding, 2013). I built LMMs with FDiv indices that included all traits, sequentially removed one trait, and then calculated the difference in explanatory power (i.e., marginal R^2 ; Nakagawa and Schielzeth 2013) between the model using FDiv with all traits and models with FDiv without a given trait. Negative differences in explanatory power (ΔR^2) indicate traits capable of decreasing model fit, while positive ΔR^2 show traits that improve model performance.

To test the hypothesis that functional structure will shift more strongly at low latitudes and for introduced species, I built PERMANOVAs (Permutational Multivariate ANOVA) (Anderson, 2001) on the Gower dissimilarity matrix of all CWMs for whole communities as well as separated by species status (Liebergesell et al. 2016, Weigel et al. 2016). I tested differences between treatments in each region and region/status combinations by including region and treatment as fixed factors for whole communities, and region, status, and treatment for communities separated by invasion status. Site

nested within region was included as a random factor for both designs. For each PERMANOVA, I used unrestricted permutations of raw data, 9999 permutations, and type III sums of squares for the most conservative approach for unbalanced designs (Anderson, Gorley, & Clarke, 2008). To identify differences among treatments, I then performed pairwise tests of treatment within region for whole communities, and treatment within region and status (Weigel et al. 2016). In cases where I found significant pairwise tests for specific region/status combinations, I then built generalized linear mixed models (GLMM) for categorical/binary CWMs and LMMs for continuous CWMs to infer trait strategies that may increase the survival or vulnerability of introduced or native prey. For each model, I used region, treatment, and their interaction as fixed factors, and the interaction between site (nested within region) and treatment as a random factor, followed by region \times treatment interaction contrasts with a Holm correction to account for multiple model comparisons (Nogueira et al., 2018). To satisfy normality assumptions, I used log or square root transformations (Gagic et al. 2015).

Preliminary analyses demonstrated no compositional differences between the cage control and ambient predation treatments (Freestone et al. *unpublished data*). I, thus, performed all aforementioned analyses comparing the ambient and reduced predation treatments only, to focus the analyses more squarely on the comparison of interest. I used PRIMER 7 with the PERMANOVA+ add on to build PERMANOVAs (Anderson, Gorley, & Clarke, 2008; Clarke & Gorley, 2015), and the FD (Laliberté, Legendre, & Shipley, 2014), lme4 (Bates et al. 2015), emmeans (Lenth 2019), MuMIn (Barton 2019),

and car (Fox and Weisberg 2019) packages under the R statistical environment for all other analyses (R Development Core Team 2019).

2.4 Results

2.4.1 Predation and functional diversity

Predation increased functional diversity, but only in the tropics and for the introduced components of the community. In Panama, differences in FDiv between communities exposed to ambient and reduced predation pressure were only evident when the status of prey species was considered (Figs 2.1 and 2.2). In Panama, FDiv of introduced species was higher under ambient ($0.896 \pm \text{SE } 0.052$) than reduced predation ($0.757 \pm \text{SE } 0.051$; $t = 2.291$, $P = 0.042$), and no effect between treatments was evident for native species ($P > 0.05$) (Fig 2.2). No individual traits were identified as having a strong influence on model performance in that marginal changes in R^2 were small ($< \pm 0.1$) and mainly negative (Supporting Information Fig 2.4) (sensu Gagic et al. 2015), suggesting the diversity of traits collectively contributed to model fit. Despite introduced species being common in all regions except Alaska, these results suggest predation had a stronger effect on functional diversity of the introduced than the native components of prey communities in the tropics, where predation is expected to be most intense.

Figure 2.1 Functional diversity (i.e., FDiv) for whole communities by region grouped by treatment; *reduced predation* ($N = 60$), and *ambient predation* ($N = 60$). Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles. Data from three sites per region are pooled for visual comparison. LMM results: all fixed factors $P > 0.05$.

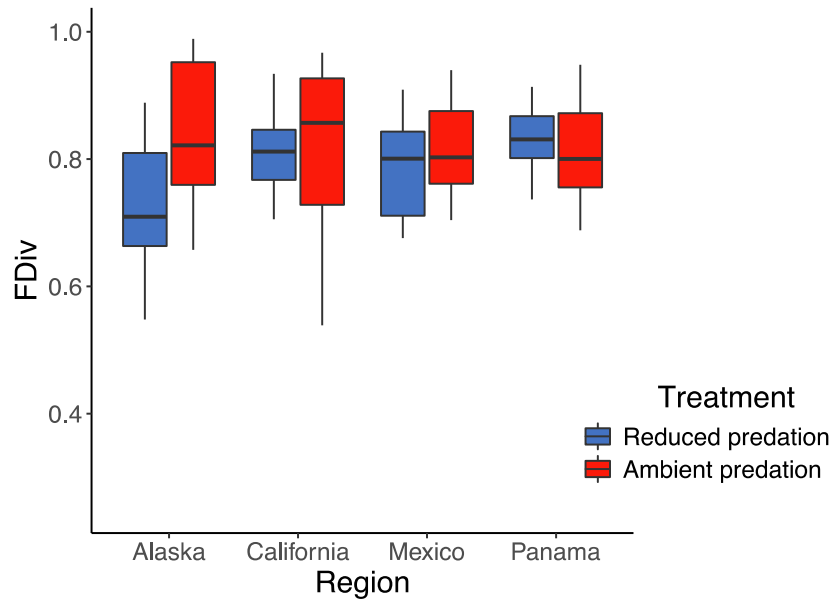
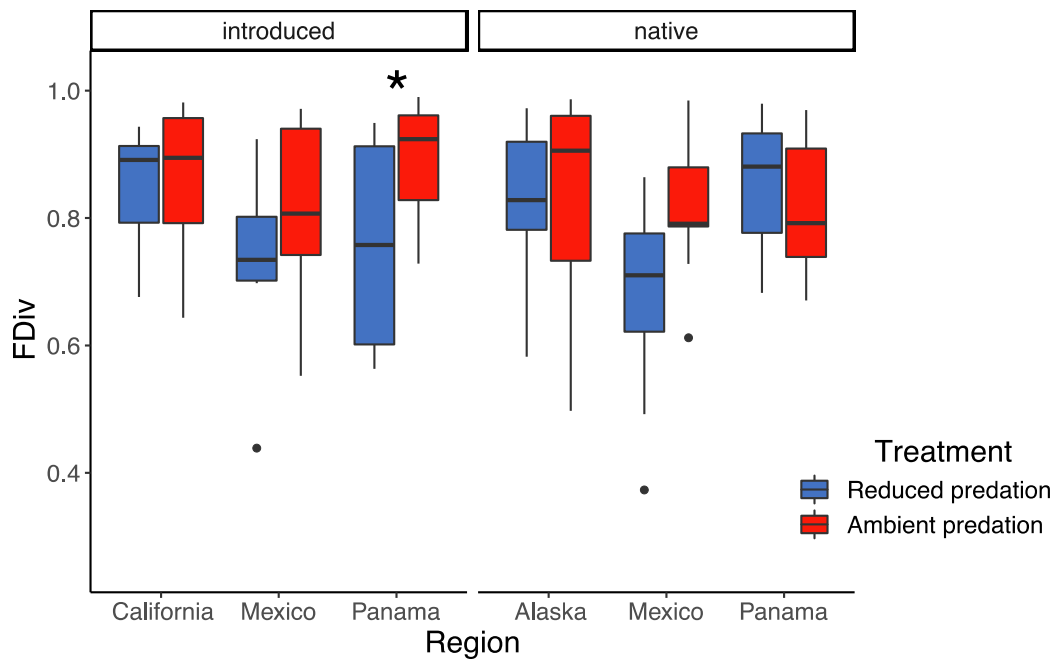


Figure 2.2 Functional diversity (i.e., FDiv) by region separated by species status and treatment: *ambient predation* (N=75) and *reduced predation* (N=73). Insufficient occurrences of native species in California and introduced species in Alaska prohibited the calculation of FDiv for those status: region combinations. Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles, and dots represent outliers. Data are pooled among three sites for each region: status: treatment combination. LMM results: region*status*treatment, $F_{2,47} = 3.422$, $P = 0.041$; all other fixed factors $P > 0.05$. Planned contrast * $P < 0.05$.

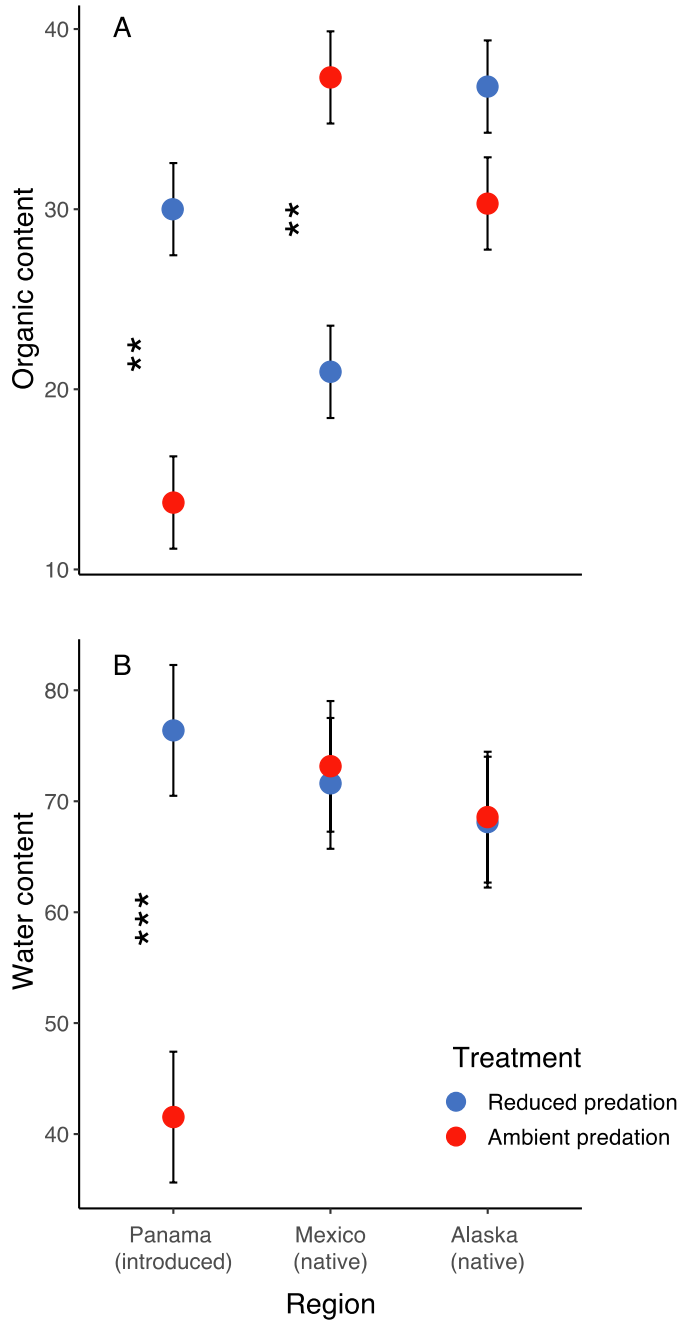


2.4.2 Predation and functional structure

Predation more strongly shaped functional structure of prey communities at low latitudes for whole communities, as well as introduced and native components (Supporting Information Table 2.1). Trait structure (CWM) of whole communities differed between ambient and reduced predation treatments, but only in Panama ($t = 2.810$, $P = 0.048$). When separating communities by species status, differences between treatments emerged for introduced species in Panama ($t = 5.074$, $P = 0.007$), and native species in Mexico ($t = 3.740$, $P = 0.017$) and Alaska ($t = 3.710$, $P = 0.012$). Of these comparisons by invasion status, the strongest effects of predation treatment on trait structure were observed at low latitudes, with the effect in Panama being twice as strong as in Alaska (estimated variance component [EVC, effect size] for Panama = 0.30; Mexico, EVC = 0.21; Alaska, EVC = 0.14) (Anderson, Diebel, Blom, & Landers, 2005).

Differences in functional structure of native and introduced assemblages between predation treatments at low latitudes were driven by the dominance of different trait strategies related to palatability and reproduction. For introduced species in Panama, ambient predation reduced organic and water content mean trait values (Figs 2.3a and 2.3b) and decreased three-fold the abundance of invertebrates with non-feeding (lecithotrophic) larvae ($0.3 \pm \text{SE } 0.2$) relative to reduced predation ($0.9 \pm \text{SE } 0.1$; $z = -2.83$, $P = 0.01$). For native species in Mexico, ambient predation increased organic content (Fig 2.3a) and the abundance of prey with an ovoviviparous (internal egg development and fertilization) reproductive strategy (ambient: $0.9 \pm \text{SE } 0.07$; reduced predation: $0.3 \pm \text{SE } 0.12$; $z = 2.84$, $P = 0.01$), and decreased the abundance of prey with

oviparous (egg hatching and external fertilization) reproduction (ambient: $0.07 \pm \text{SE}$ 0.002; reduced predation: $0.66 \pm \text{SE}$ 0.02; $z = -2.85$, $P = 0.01$) relative to reduced predation. In Alaska, no differences in CWM between predation treatments were



observed.

Figure 2.3. Estimated marginal means (\pm SE) of CWMs of A) organic content and B) water content for the region and status combinations with a significant pairwise PERMANOVA (see Supplementary Information Table 2.1). Asterisks show significant differences between treatments after a Holm correction adjusting for multiple comparisons was applied. ** $P < 0.01$; *** $P < 0.001$

2.5 Discussion

Functional diversity and structure of marine communities were shaped by predation more strongly at low than high latitudes, but results hinged on interaction history among local predators and prey. While predation increased functional diversity in the tropics, this shift was only observed for introduced species, demonstrating the importance of co-occurrence histories predicting functional trait responses. I also found a stronger shift in functional structure at low latitudes, with traits related to palatability and reproductive strategies driving key differences. Species interactions, and predation in particular, are thought to be stronger at lower latitude (Schemske et al. 2009), and my results support this hypothesis. Furthermore, beyond the functional responses documented here, predation on the focal prey communities also shaped patterns of biomass and composition more strongly at lower relative to higher latitudes. A parallel experiment also revealed predation rates (i.e., fish strikes/hr.) that were more than an order of magnitude higher, a predator community that was over three times more diverse, and predator body sizes that were up to four times larger, in Panama than in California or Alaska, showing direct evidence of increased predation intensity in the tropics (Freestone et al. *unpublished data*). With my results here, I provide novel evidence that stronger impacts of predation at low latitude also manifest in meaningful functional trait responses of these communities.

Strong predation increased functional diversity, or dissimilarity in trait combinations, in the tropics, but only for introduced species with shorter predation histories with local predators. In the system, direct observations of the predator communities suggest that

predation effects are driven largely by native predators (Freestone et al., *unpublished data*). Under ambient predation conditions, some introduced prey species in the tropics were vulnerable to native predators with which they did not share a long history of co-occurrence. Under low-predation conditions, introduced prey species with similar traits became dominant, resulting in a homogenized trait space. Predation, as a selective disturbance, modified the communities and increased functional diversity by allowing for the coexistence of more variable trait combinations (Laliberté & Tylianakis, 2012). This result provides new evidence that strong predation and interaction histories determine functional diversity of prey (Adler et al. 2004), and aligns both with theoretical predictions and empirical findings for grazing in high-productivity grassland systems (Grime 2006, Carmona et al. 2012). While studies on herbivory provide critical insight into how consumer pressure can shape patterns of functional diversity, this study provides some of the first evidence that strong predation, as a core component of consumer pressure, can produce similar effects in a phylogenetically diverse system.

Predation further influenced the functional structure of both native and introduced assemblages at low latitudes. Strong predation in tropical Panama restricted introduced prey community membership to those taxa that were less palatable, resulting in a lower abundance of palatable traits (i.e., organic/water content). This biotic filter was weakened under reduced predation conditions, which allowed introduced taxa with more palatable traits to dominate. Indeed, Panama had the strongest shift in taxonomic composition as well, with communities that assembled under ambient predation being dominated by barnacles, while reduced predation communities harbored more soft-bodied

ascidians, with Bryozoa being common in both treatments. Low palatability may serve as a relic survival strategy of introduced species that also co-evolved under strong predation, while high palatability may indicate a trait mismatch that increased the vulnerability of introduced species to native predators (Verhoeven et al. 2009). Conversely in subtropical Mexico, where predation pressure was observed to be weaker than in Panama (Freestone et al., *unpublished data*), native species that were exposed to ambient predation were characterized by high organic content. Weaker predation likely explains the lack of an effect on functional structure of introduced species in Mexico and may produce less predictable ecological and evolutionary trade-offs for native species as other assembly processes may be more important at local scales (López and Freestone, *unpublished data*). Other co-evolved defense mechanisms, however, may also be present but not captured in this assessment. For example, secondary compounds serve as defense strategies in many sessile organisms (Lindquist et al. 1992, Kicklighter and Hay 2006, Lopanik 2014), but are difficult to assess for a broad range of taxonomic groups (Ritson-Williams and Paul 2007). Nonetheless, these results demonstrate that at low latitudes, consumer pressure shapes patterns of prey palatability, with predation histories driving the directionality of trait responses.

In addition to palatability, reproductive traits were also influenced by predation. For introduced species in Panama, species with non-feeding larvae (i.e., lecithotrophic) were more abundant in communities protected from predators. Lecithotrophic species invest substantial energy in the production of large yolky eggs, and may be at greater risk of predation than species with other life histories (e.g., Mukherjee et al. 2014). For native

species in Mexico, I found the dominance of contrasting reproductive strategies, ovoviviparity (i.e., internal fertilization and egg development) and oviparity (i.e., egg hatching and external fertilization), to be higher in communities experiencing reduced and ambient predation, respectively. Ovoviviparous reproduction, which requires significant energy investment but increases the likelihood of successful larval survival (Jablonski and Lutz 1983), can pose an increased predation risk for some small marine invertebrates (Logerwell and Ohman 1999). Predators, having an evolutionary history with native prey, may select brooders for the high nutritional value of eggs (Priori et al. 2015), thereby reducing the abundance of this trait under ambient predation conditions. These results show that strong predation at low latitudes shaped the functional structure of sessile communities by selecting against reproductive strategies that invest high energy in the production of large eggs or parental care.

The observed functional responses of native and introduced prey at low latitudes could be related to differences in diet preferences and metabolic demands of the predator communities. Specifically, generalist predators may be better able to recognize and utilize novel resources than specialist predators (Shea 2002). Fish are important predators in this system, and I observed a greater proportion of juvenile reef fish to be present in Mexico than in Panama (López, *personal observation*). Indeed, coastal habitats from the Gulf of California, near my study sites in Mexico, are an important nursery for reef fish (Aburto-Oropeza et al. 2009). While the degree of diet specificity of fish in the predator communities is an active area of research, juvenile reef fish have been documented to have narrow diet niche breadths (Wilson et al. 2008, Vázquez et al. 2008),

and may more readily consume native species than introduced. The more diverse predatory fish fauna, larger-bodied individuals, and more intense predation pressure observed in this system in Panama (Freestone et al. *unpublished data*) may contain predators that more readily impact introduced prey species. Moreover, warmer temperatures in tropical waters can increase metabolic demands and consumption rates of predators (Brown et al. 2004), resulting in increased consumer pressure at low latitudes (Reynolds et al. 2018) for either native or introduced species. Therefore, geographic differences in the age structure and diet specialization of predator communities, but also metabolic demands of predators at warmer temperatures, may contribute to patterns of prey consumption and therefore trait profiles.

Coastal marine invasions are exponentially increasing in many regions (Ruiz et al. 2000), and uncovering the underlying mechanisms has become an urgent challenge. Commercial shipping is the primary vector of marine invasions, and with expanding global trade, increased propagule supply and the timing and source of those introductions in many regions will likely shape invasion dynamics (Verling et al. 2005). These results, however, highlight the importance of local scale interactions in shaping post-introduction invasion success. For example, biotic resistance by predators, where native species reduce the abundance of introduced species (deRivera et al. 2005), likely acts on particular traits of introduced prey. In contrast, while some invasive species may persist in a novel habitat due to release from natural enemies (Colautti et al. 2004), defense strategies that evolved in a species' native range may also provide protection against predators in their introduced range, a mechanism that may be more likely to occur if the

functional traits of predators in the native and introduced ranges are similar. Further, functional differences between competing native and introduced species can also influence the successful establishment and persistence of invaders (Gross et al. 2013), and may further constrain trait structure. Therefore, employing trait-based approaches will likely continue to inform the mechanisms that underlie invasion dynamics (Conti et al. 2018).

This study represents one of the first investigations of prey trait responses to predation across a large biogeographic gradient. Strong predation at low latitudes drove shifts in functional measures of prey communities, but co-occurrence histories defined the functional strategies that optimize survival. Changes in functional diversity were only evident for introduced species in the tropics, but the functional structure of native and introduced components of communities shifted with strong predation at low latitudes. Specifically, traits related to palatability showed opposite patterns for native and introduced prey species, while reproductive strategies that confer low energetic cost facilitated survival of prey species with either short or long interaction history with predators. Studies that reveal trait outcomes from biotic interactions between species with different co-occurring histories across continental scales remain rare, but should further be explored as invasions are reshaping communities and will continue to be a consequence of anthropogenic induced global change (Lenzner et al. 2019).

2.6 Supporting information

Figure 2.4 Difference in explanatory power between LMM models using FDiv indices with all traits and without a given trait. The shaded region corresponds to changes in R^2 that are considered small and that result in a fairly equal contribution to model performance (sensu Gagic et al. 2015).

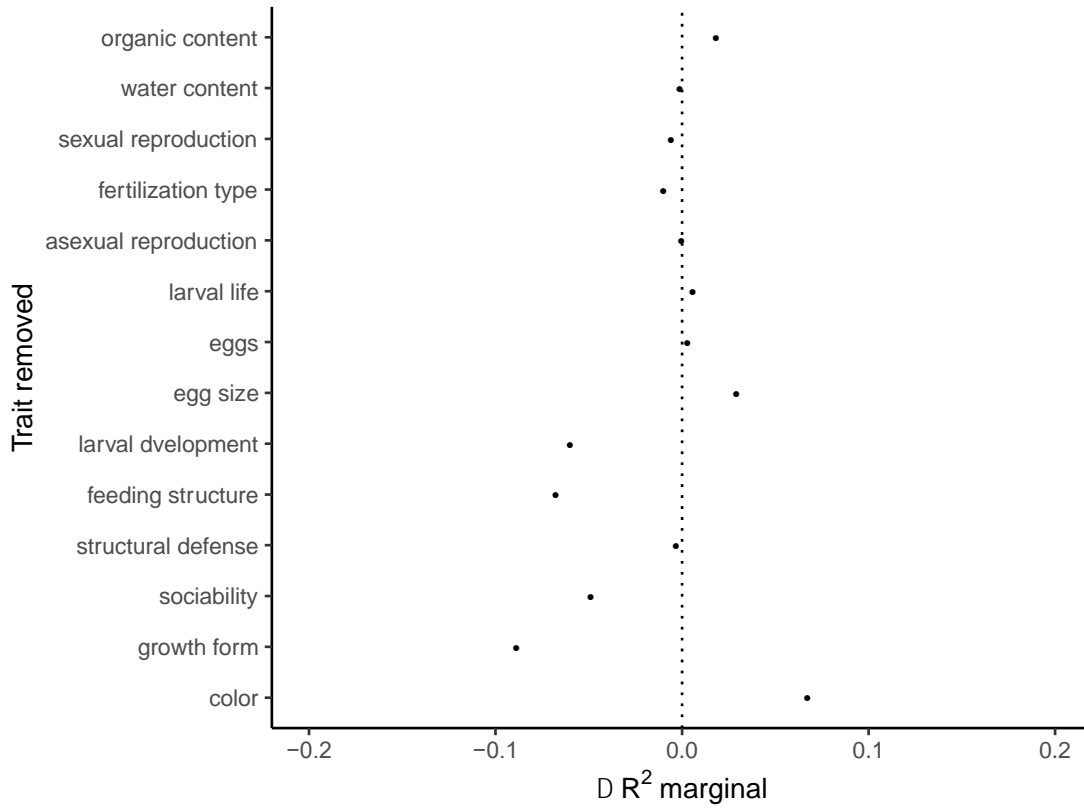


Table 2.1 Differences in functional trait structure (CWM) among regions and treatments for a) whole communities ($N = 120$) and b) communities separated by status ($N = 178$). Results generated from PERMANOVAs based on the Gower dissimilarity of all CWMs. Terms of interest (bolded) are the interaction between region and treatment (for whole communities) and the interaction between region, status and treatment (for communities separated by status). Significant differences are indicated with p-values drawn from Monte-Carlo samplings (P -MC). ‡Indicates random factors.

Source of variation	df	SS	MS	Pseudo- F	P (MC)
<i>(a) Whole communities</i>					
Region	3	1.501	0.500	2.778	0.030
Treatment	1	0.284	0.284	2.729	0.075
Site (Region)‡	8	1.441	0.180	6.221	0.0001
Region*<i>Treatment</i>	3	1.096	0.365	3.509	0.001
Treatment*Site(Region)‡	8	0.832	0.104	2.594	0.0001
Residual	96	2.780	0.029		
Total	119	7.934			
Pairwise comparisons: Region* <i>Treatment</i>					
	Alaska	California	Mexico	Panama	
Full cage vs. Open	$t = 1.079,$ $P = 0.400$	$t = 1.756,$ $P = 0.160$	$t = 2.067,$ $P = 0.107$	$t = 2.810,$ $P = \mathbf{0.048}$	
<i>(b) Separated communities</i>					
Region	3	2.695	0.898	5.359	0.001
Status	1	1.270	1.271	15.805	0.001
Treatment	1	0.177	0.177	3.600	0.030
Site(Region)‡	8	1.477	0.185	5.900	0.0001
Region* <i>Status</i>	1	1.433	1.433	17.821	0.001
Region* <i>Treatment</i>	3	0.622	0.207	4.233	0.003
Status* <i>Treatment</i>	1	0.594	0.594	14.098	0.001
Status*Site(Region)‡	4	0.322	0.080	2.569	0.005
Treatment*Site(Region)‡	8	0.410	0.051	1.637	0.036
Region*<i>Status*<i>Treatment</i></i>	1	0.277	0.277	6.563	0.013
Status* <i>Treatment*<i>Site(Region)</i></i> ‡	4	0.169	0.042	1.347	0.195
Residual	142	4.444	0.031		
Total	177	13.391			
Pairwise comparisons: Region* <i>Status*<i>Treatment</i></i>					
	Alaska	California	Mexico	Panama	
Full cage vs. Open Native	$t = 3.710,$ $P = \mathbf{0.012}$	NA	$t = 3.740,$ $P = \mathbf{0.017}$	$t = 2.703,$ $P = 0.054$	
Introduced	NA	$t = 1.770,$ $P = 0.146$	$t = 0.543,$ $P = 0.757$	$t = 5.074,$ $P = \mathbf{0.007}$	

CHAPTER 3

**BIOTIC INTERACTIONS SHAPE FUNCTIONAL DIVERSITY, STRUCTURE,
AND ASSEMBLY ACROSS TIME AND LATITUDE
IN MARINE COMMUNITIES**

3.1 Abstract

Assembly processes are highly dynamic shifting with time, scale, latitude, or environmental gradients. Biotic filters operate more intensely at local scales, and the strength of biotic interactions is hypothesized to vary across time and latitude. Predation, for example, can be stronger at lower latitudes, while competition intensifies at later stages of community assembly due to resource limitation. Since biotic filters act upon functional traits of organisms, I explored trait-mediated community assembly using patterns of trait convergence, divergence, and shifts in trait strategies in functionally diverse marine assemblages. I examined the effects of predation and competition on trait distribution across latitude in four regions along the Pacific coast of North and Central America using predator exclusion experiments and two assembly stages up to one year. I hypothesized non-random trait patterns would emerge from competition during late assembly across latitudes and from predation at low latitudes regardless of assembly stage. As expected, trait divergence occurred later in assembly across the gradient and was driven by competitive traits. In the tropics, predation caused trait convergence early in assembly and non-palatable traits were favored under ambient predation. Therefore, community assembly was differentially influenced by the strongest biotic interaction across time and latitude.

3.2 Introduction

Biotic interactions, as primary assembly filters, gain greater relevance at local scales (McGill 2010), but their strength is hypothesized to vary with latitude (Schemske et al. 2009). Predation has greater influence on community dynamics such as biomass, composition, and taxonomic diversity in tropical areas (Freestone et al. 2011, 2020), and opposing evidence suggests stronger competition can occur at either high or low latitudes (Barnes 2002, Buzzard et al. 2016). Many studies consider competition as the only relevant biotic filter (Götzenberger et al. 2012), and only a few have investigated the influence of multiple biotic interactions in the assembly of communities across latitude (e.g., Giam and Olden 2016). Yet, at local scales, the strongest biotic interaction should surface as a primary filter (Menge and Sutherland 1987), and both predation and competition should be considered relevant in the assembly of communities.

Competitive strength is believed to increase with later development stages (Martorell and Freckleton 2014, Bracewell et al. 2017). In sessile communities, for example, initial assembly may be random and only when resources such as space become scarce deterministic processes operate (Stokes and Archer 2010). Depending on the rate of community development, space saturation and the onset of competition can shift with time (Menge and Sutherland 1987, Bracewell et al. 2017). Therefore, the influence of biotic interactions in the assembly of communities could become relevant at different stages of community development.

The non-random distribution of traits within local assemblages indicate biotic processes are operating (Kohli et al. 2018). Trait divergence, for example, is expected under strong resource competition as niche differentiation allows greater coexistence (Götzenberger et al. 2012). Alternatively, trait convergence can occur when shared traits optimize survival under strong predation pressure (Obertegger and Flaim 2015), or when competitive exclusion ensues (Mayfield and Levine 2010). To confirm biotic processes are operating, the functional structure of communities provide information on survival strategies and predation susceptibility (López and Freestone, *in prep*), but also reflect optimal trait strategies in a given scenario (Muscarella and Uriarte 2016). Therefore, non-random trait distributions coupled with changes in trait strategies would help disentangle the influence of predation or competition at a given region and stage of community development.

I hypothesized non-random trait patterns would emerge at lower latitudes regardless of assembly stage due to strong predation and during late assembly across latitudes due to competition. To test these hypotheses, I assessed functional diversity of sessile marine invertebrate communities that developed for three (i.e., early assembly) and twelve (i.e., late assembly) months under ambient or reduced predation across a latitudinal gradient. Experiments were conducted in four regions, from the sub-arctic to the tropics, along the Pacific coast of North and Central America. I tested for non-random patterns of trait convergence and divergence, and further explored changes in functional structure to understand the optimal trait strategies that underlie non-random community assembly.

To my knowledge, this study is the first to explore multiple biotic filters at local scales while considering interaction strength across time and latitude.

3.3 Materials and methods

3.3.1 Study system

Sessile marine invertebrate communities are a tractable system to examine fundamental assembly processes at local scales and across continental ranges (Freestone and Inouye 2015). These communities have a global distribution in nearshore habitats which facilitate latitudinal comparisons (Freestone et al. 2011), and their fast growth help evaluate assembly at multiple assembly stages (Barnes 2002, Bracewell et al. 2017). Bryozoans, ascidians, bivalves, cirripeds, hydroids, sponges, and tube-forming polychaetes are present in these communities, and their wide array of traits reflecting competitive abilities and defense strategies can contribute to our understanding of trait-mediated assembly (Table 1.1). I thus used functional traits to study the influence of biotic interactions on the assembly of sessile communities from four regions along the Pacific coast: Ketchikan, Alaska, USA (55° N); San Francisco, California, USA (37° N); La Paz, Baja California, Mexico (24°N); and Panama City, Panama (8° N).

I used polyvinyl chloride (PVC) settlement panels (14 x 14 cm) to grow communities in three treatments; open (ambient predation), caged (reduced predation; mesh size 0.635cm²), and partial caged (cage control). I hung experimental panels one meter below the water surface from floating docks at three sites in each region (i.e., 12 sites total) where communities developed facing the seafloor for three or twelve months (Supporting information Table 3.1). In Panama, experimental panels for the 12-month experiment

from one site were re-deployed at a later time due to losses to wave action and storms. Additionally, caged and partial caged treatments were not available for the 12-month growth interval in Mexico. At each sampling interval, I retrieved five panels per site per treatment for a total of 330 experimental communities. I assessed communities with a stereoscope by identifying individuals to the lowest taxonomic level to record taxonomic richness and percent cover from a 50-point grid. I sampled individuals of all morphospecies and confirmed field identifications with the help of taxonomic experts.

3.3.2 Functional diversity

I defined the functional space of 179 taxa (genus/species 149; family/class 30) with traits associated with competitive abilities, defense mechanisms, and reproduction (Table 1.1). These traits directly relate to coexistence abilities under biotic interactions and appropriately test for biotic filters (Kohli et al. 2018, López and Freestone, *in review*). Taxa specific traits were collected through field measurements, observations, or from literature, and when unavailable, I used values from the closest taxonomic level (López and Freestone, *in review*). The taxonomic richness of each community was converted into a presence-absence matrix per site, and together with the trait matrix, I calculated functional diversity using the pairwise similarity index, Rao's quadratic entropy (RaoQ) (Botta-Dukát 2005). Use of the RaoQ functional diversity index is a preferred approach for detecting community assembly (Mouchet et al. 2010).

3.3.3 Functional structure

Community Weighed Means (CWM) were used to assess trait structure. The CWMs from categorical or binary traits become percentages of trait affinity for each category,

while those from continuous traits represent the mean value weighted by their abundance. Prior to analysis, I standardized CWMs of continuous traits to values ranging from 0-100 by obtaining percentages out of the maximum mean trait value and multiplied by 100. For each region, I generated a community \times CWM matrix with 34 corresponding traits for subsequent analysis.

3.3.4 Statistical analyses

To explore the effect of predation and/or assembly time on the observed functional diversity (RaoQ) of communities across latitude, I built a linear mixed model (LMM) with region, assembly time, treatment, and their interaction as fixed factors and corresponding random factors of site nested within region interacting with the fixed components. I tested regional variation of functional diversity with groups identified *a priori* using planned contrasts comparing RaoQ from predation treatments as well as each assembly time regardless of predation treatments. For this analysis, I excluded Mexico to obtain a balanced statistical design.

To explore non-random trait patterns driven by either predation or competition, I compared the observed functional diversity (RaoQ) to null expectations derived for each site (i.e., 12 sites) and included the species pool from both assembly stages to include some “dark diversity” (de Bello et al. 2012). Focusing on local-scale (i.e., site) dynamics is preferred for explicitly testing biotic filters independent of confounding abiotic filters (Götzenberger et al. 2012). I randomized the community matrix constraining the richness of each community and the frequency of all species per site (Götzenberger et al. 2012) with the *independentswap* algorithm from the *picante* package (Kembel et al. 2010b).

For each community, I re-sampled the species matrix 999 times and re-calculated RaoQ. I then compared the observed versus the simulated functional diversity with standardized effect size (SES) as follow: $SES = \frac{FD_{\text{observed}} - FD_{\text{mean(random)}}}{FD_{\text{sd (random)}}$, and used Wilcoxon signed-rank tests to find significant departure from zero of SES values pooled by region (Zhang et al. 2018). I performed all statistical analyses using the ambient and reduced predation treatments, to avoid randomization biases towards one treatment. For Mexico, I performed a second round of randomizations that excluded the 12-month communities as I had an uncomplete set of treatments, but I found similar patterns and show only one set of results.

To explore shifts in CWMs from predation and/or assembly time, I used a multivariate generalized linear model with region, assembly time, treatment, and their interactions as predictors while accounting for correlation between response variables. I found the negative-binomial error distribution as most appropriate, and checked assumptions of normality and homoscedasticity of residuals. Predictor significance was tested with Wald tests from a PIT-trap resampling blocked by site with 999 iterations. Model results include tests for the whole CWMs matrix and univariate tests for each CWM. Pairwise comparisons were used to examine the significance of interactions of interest (i.e., region \times assembly time; region \times assembly time \times treatment) using likelihood ratio tests (LRT) and adjusted *p-values*. For this analysis, I only assessed regions with non-random trait distributions (i.e., Alaska, California, and Panama).

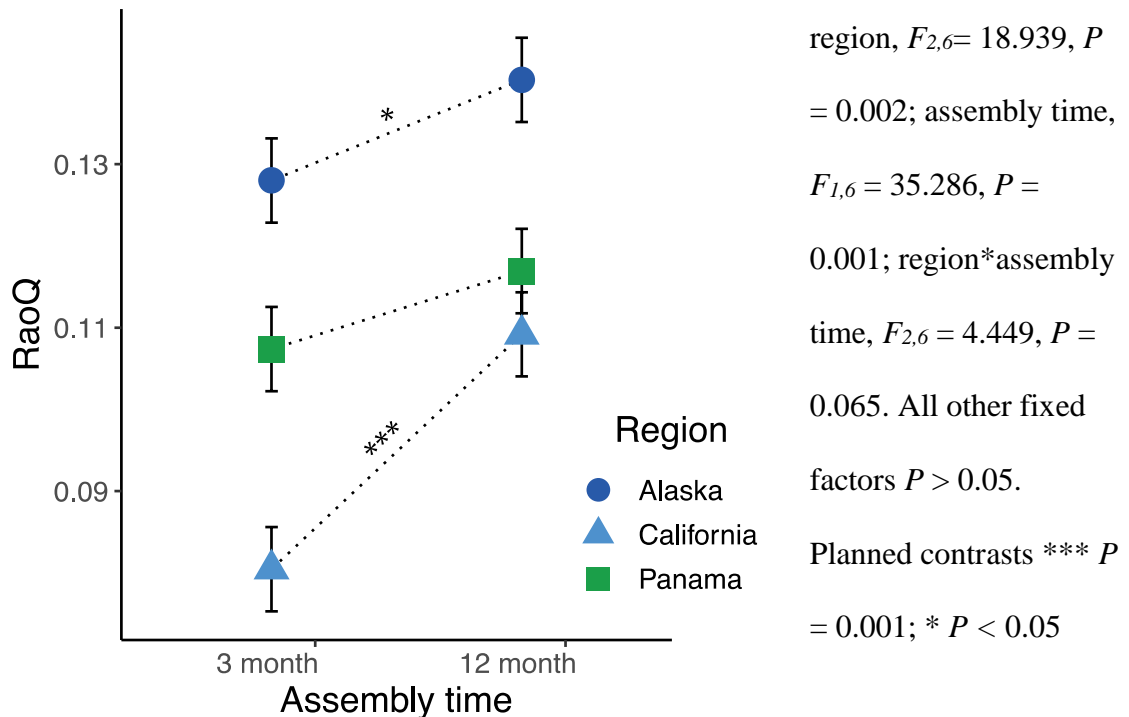
I determined environmental heterogeneity by evaluating the coefficient of variation (CV) for temperature and salinity within sites, among sites within regions, and among all

regions. Environmental variables were recorded every other week at one-meter depth from four opposite corners at each site. All analyses were completed in R (R Development Core Team 2019) with the FD (Laliberté et al. 2014), lme4 (Bates et al. 2015), emmeans (Lenth 2019), and mvabund (Wang et al. 2012) packages.

3.4 Results

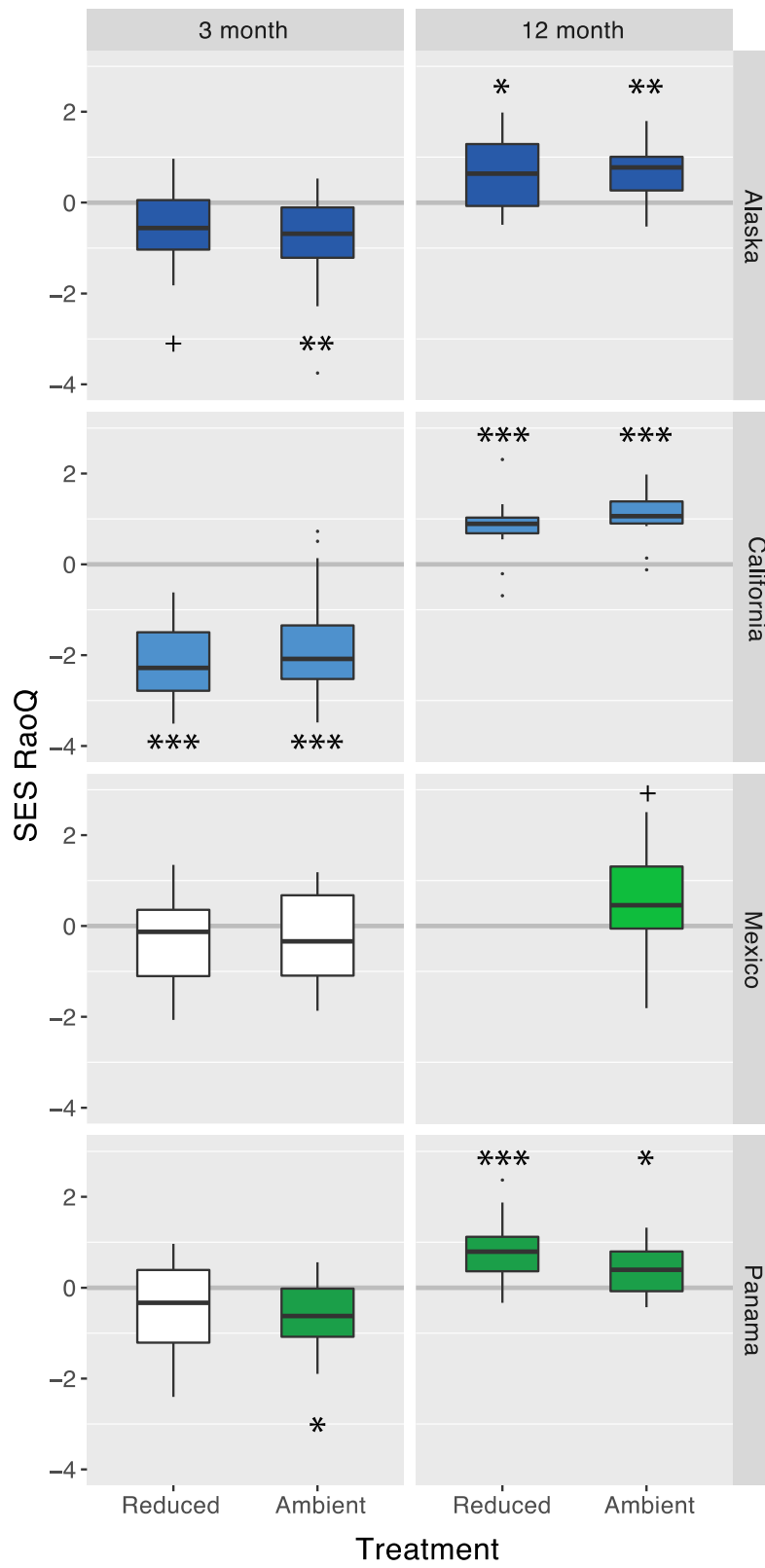
Assembly time shaped the observed functional diversity (RaoQ) at high latitudes. Lower functional diversity occurred during early versus late assembly in Alaska ($t = -2.506$, $P = 0.046$) and California ($t = -5.847$, $P = 0.001$) regardless of predation, and no effect was evident in Panama ($P > 0.05$) (Fig 3.1). Predation did not shape RaoQ in any region (Supporting information Fig 3.4).

Figure 3.1 Effect of assembly time on the *observed* functional diversity defined with RaoQ and shown as estimated marginal means (\pm SE) of the region assembly time interaction from the linear mixed model (LMM) ($N = 180$) with the following results:



During early assembly, communities in Alaska and California showed non-random trait convergence (negative SES values), while later in assembly, high latitude communities showed opposite non-random trait divergence (positive SES values) (Fig. 3.2). In tropical Panama and during early assembly, ambient predation resulted in non-random convergence, but under relaxed predation random patterns emerged. During late assembly, however, trait divergence occurred in both treatments in Panama (Fig. 3.2). Moreover, in Mexico, early assembly was randomly structured while late assembly had a divergent trend (Fig. 3.2).

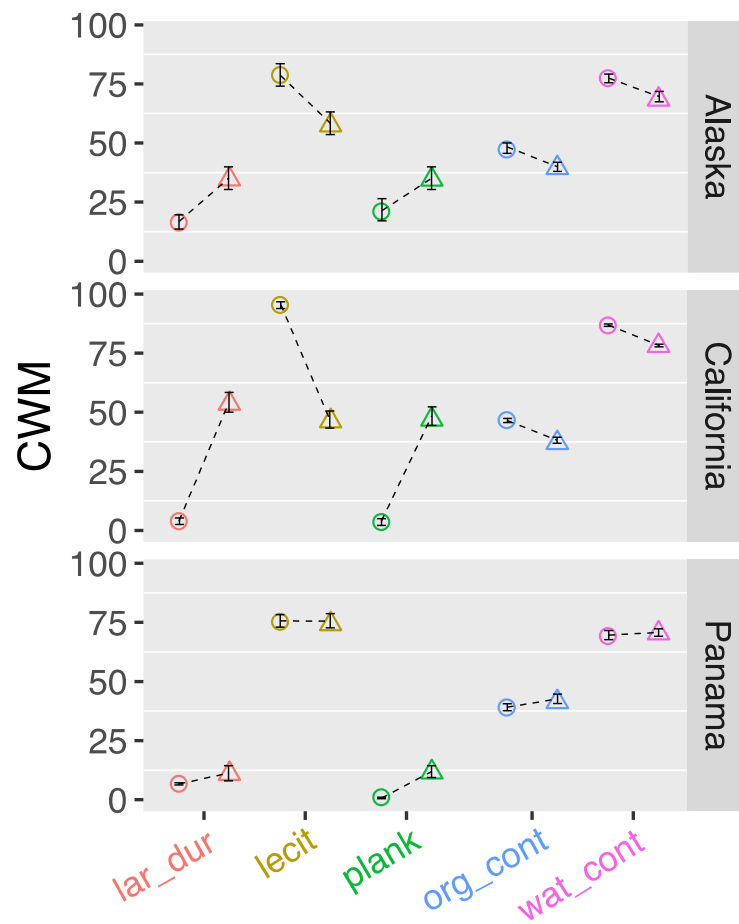
Figure 3.2 The distributions of standard effect size (SES) for each region, treatment (i.e., reduced and ambient predation), and assembly interval shown with box-plots. Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles, and dots represent outliers. Non-random trait distributions correspond to solid colored box-plots, random distributions are white box-plots. SES significantly greater or smaller than zero are based on Wilcoxon signed-rank tests. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; + $P < 0.1$



Assembly time had an effect on functional structure (CWMs) in Alaska (LRT = 149, $P = 0.005$), California (LRT = 696.1, $P = 0.005$), and Panama (LRT = 207.2, $P = 0.005$), while predation influenced the functional structure of Panama during both assembly stages (early assembly: LRT = 407.1, $P = 0.005$; late assembly: LRT = 206.8, $P = 0.005$) and Alaska during late assembly (LRT = 205.4, $P = 0.005$). CWMs influenced by assembly time include larval duration ($p = 0.005$), larvae development type (lecithotrophic and planktotrophic, $p = 0.005$), organic ($p = 0.005$) and water content ($p = 0.02$) (Fig. 3.3). At high latitudes, organisms with shorter larval duration and lecithotrophic (non-feeding) versus planktotrophic development (feeding larvae) were favored during early versus late assembly, respectively (Fig. 3.3). In addition, higher organic and water content were also observed between early and late assembly in Alaska and California (Fig. 3.3). Predation changed the mean water content ($p = 0.01$) of communities and survival of calcified organisms ($p = 0.005$) in Panama. Calcified taxa that retain little water were more prevalent in the presence of predators (Supporting information Fig 3.5). In Alaska, a lower proportion of solitary organisms were found on caged treatments during late assembly (Supporting information Fig 3.5), however, a caging artifact may have caused the observed pattern as bivalves mainly recruited on cages and were removed during maintenance every two weeks. All traits with significant univariate tests from the region*assembly time*treatment and region*assembly time interactions are shown in Supporting information Fig 3.5 and Fig 3.6, respectively.

Figure 3.3 Effect of assembly time on functional structure defined with CWMs and shown as mean and standard deviation with significant (adjusted $P < 0.05$) univariate tests (*manyglm*) from region*assembly time . Selected traits shown here, all others available in Supporting information Fig 3.6.

○ = 3-month; △ = 12-month. Abbreviations on x-axis defined in Table 1.1.



Most sites had low variation in abiotic conditions during sampling. Within each site, the CV for temperature was ≤ 0.1 and even among all sites within a region temperature variation remained low (< 0.2). The range of salinity variation was slightly broader. Some sites had negligible salinity variation (< 0.01) and few others, mainly in California and Panama, reached up to ~ 0.2 . Overall, variation in temperature and salinity within most sites was at least three orders of magnitude lower than among regions (Supporting information Table 3.2).

3.5 Discussion

Biotic interactions played a primary role in deterministic assembly of nearshore communities at local scales across latitude, but assembly time played a key role in capturing changes in assembly patterns across the gradient. Trait divergence was observed at later assembly stages when competition is expected to be stronger, while predation mainly influenced trait patterns in tropical Panama earlier in assembly. Shifts in the individual trait structure of communities confirmed these assembly patterns. Specifically, multiple trait trade-offs were evident between early and late assembly at higher latitudes and traits related to low palatability and structural defense increased predation survival in the tropics.

Across the studied gradient, an increase in trait differentiation was observed with later assembly, perhaps to limit resource use overlap as competition intensifies (Götzenberger et al. 2012). Competitive dynamics are reported to gain relevance later in development (Bracewell et al. 2017), and strong competitors can be late-successional in sessile communities (Chang and Marshall 2016). Competitive exclusion, however, may lead to

trait similarity or convergence (Mayfield and Levine 2010). Although, I found convergence during early assembly in Alaska and California, I suspect competitive exclusion was unlikely, since space, an important limiting resource, was readily available (Bonfim and Freestone, *in prep*). Instead, colonizers with faster establishment strategies (i.e., lecithotrophic development and shorter larval duration) dominated the substrate and reduced trait diversity early in assembly, while stronger competition resulted in trait differentiation later in development. Therefore, a competition-colonization (CC) tradeoff (Cadotte et al. 2006) may have influenced assembly at high latitudes. The timing of the CC tradeoff depends on the rate of community development and in warmer regions like the tropics communities can grow faster (Bracewell et al. 2017). Therefore, the CC tradeoff was not evident at all latitudes, but niche differentiation through competition may have influenced later assembly across latitudes.

Life-history trade-offs are documented as mechanisms that drive stable coexistence in competitive scenarios (D'Andrea et al. 2013). At higher latitudes, trait structure changed from fast settlers (i.e., non-feeding and shorter larval life) with high organic content to slower settlers (i.e., feeding and longer larval life) with less organic content between early and late assembly. Short planktonic stages may facilitate rapid colonization, but may be competitively inferior compared to species with planktotrophic development (feeding larvae) that are capable of re-settling to avoid non-optimal substrate (Palmer et al. 1996). Additionally, low acquisition of organic content is hypothesized to facilitate faster growth (Thresher 2009), which could enhance overgrowth and competitive abilities

of sessile organisms (Sebens 1982). These ontogenic shifts in life-history may represent trade-offs driven by colonizing versus competitive dynamics.

In Panama, trait convergence evident during early assembly and driven by predation could result from similar traits that optimize survival (Obertegger and Flaim 2015). Functional diversity, however, can also increase under consumer pressure and often depends on additional factors such as interaction history (Milchunas et al. 1988). In a parallel study, I found increased functional diversity in response to predation for a fraction of *introduced* species in focal communities (López and Freestone, *in review*), and the novelty of the interaction between *introduced* prey and local predators may have contributed to the observed patterns (Milchunas et al. 1988). Nevertheless, predation shaped non-random trait patterns and shifted trait strategies in Panama during early assembly. Calcified structures provided protection (Dyrynda 1986) and low water content decreased palatability to increase survival (López and Freestone, *in review*). During later assembly, a shift to trait divergence could result from stronger competition, and a temporal shift of biotic filters may have influenced community assembly in Panama.

Through time, a shift from random to deterministic assembly may occur (Stokes and Archer 2010). Random assembly is expected when resources are widely available, species interactions are weak to non-existent, or random colonization prevails (Bracewell et al. 2017, Zhang et al. 2018). In Mexico, a shift from random to divergent patterns was observed with time and may result from weaker species interactions. In subtropical regions, predation can have an intermediate effect on prey when compared to higher and

lower latitude (Freestone et al. 2020, Freestone et al. *in review*). Subtropical regions may be a transition zone between tropical and temperate dynamics (Freestone and Inouye 2015) and fit the expectation of a latitudinal gradient in the strength of species interactions (Schemske et al. 2009).

Temporal shifts help disentangle the complex dynamics that govern coexistence across spatial (Peralta et al. 2019), environmental (Spasojevic et al. 2014), and in this study, a latitudinal gradient. By focusing on small scale dynamics, I assessed the influence of species interactions on the distribution of traits across time and latitude. Early assembly was influenced by different dynamics across latitude with predation being more important in the tropics and good colonization abilities highlighted at higher latitudes. During late assembly, divergence prevailed across latitude as competition influenced mature communities (Martorell and Freckleton 2014). The temporal assessment of trait patterns at local scales may serve as a tool to detect trait-based assembly across biogeographic gradients.

3.6 Supporting information

Table 3.1 Summary of field deployment of experimental panels. Treatments: open (ambient predation), caged (reduced predation), and partial cage (cage control).

Region (Site)	Duration	Deployment date	Treatment	<i>N</i>
Alaska	3 and 12 months	June 2015	all	90
California	3 and 12 months	May 2016	all	90
Mexico	3 months	June 2017	all	45
Mexico	12 months	June 2017	open	15
Panama	3 and 12 months	December 2015	all	90
Panama (Naos)	12 months	April 2016	all	45

Figure 3.4 Effect of predation on the *observed* functional diversity measured with the RaoQ similarity index shown with box plots. Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles, and dots represent outliers. No difference between treatments were found for any region. Planned contrasts $P > 0.05$

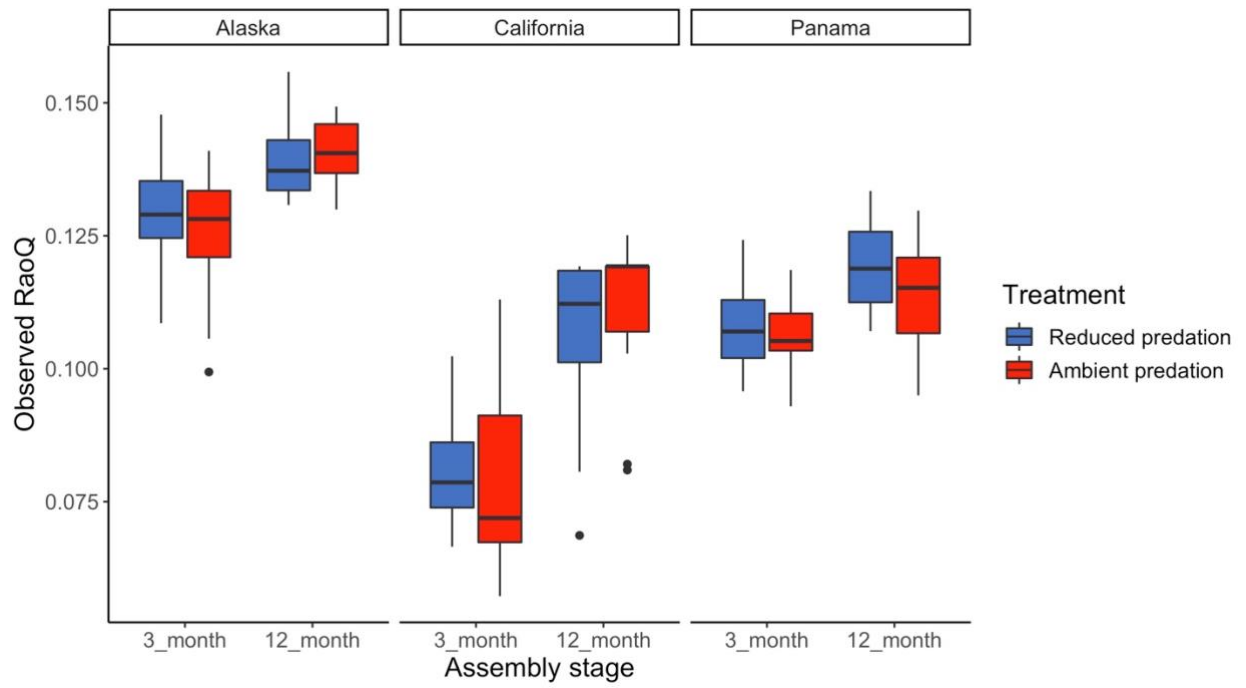


Figure 3.5 Effect of predation on CWMs captured with univariate tests from the manyglm interaction between region*assembly time*treatment. CWMs shown were significant under adjusted P -values (<0.05). Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles, and dots represent outliers.

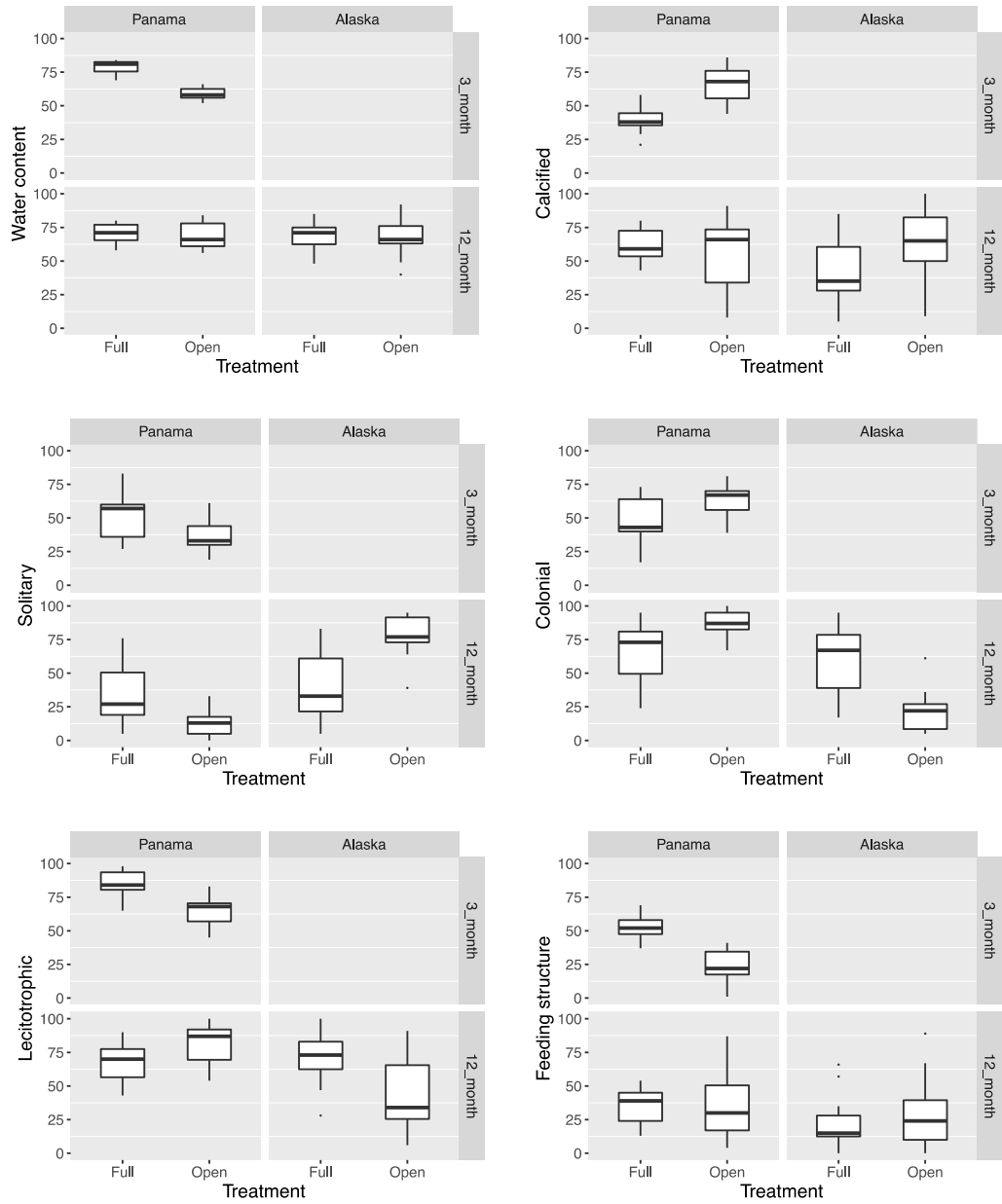


Figure 3.6 Effect of assembly time on CWMs and shown as mean and standard deviation with significant (adjusted $P < 0.05$) univariate tests from the manyglm interaction between region*assembly time. \circ = 3-month; \triangle = 12-month.

Abbreviations on x-axis are defined in Table 1.1.

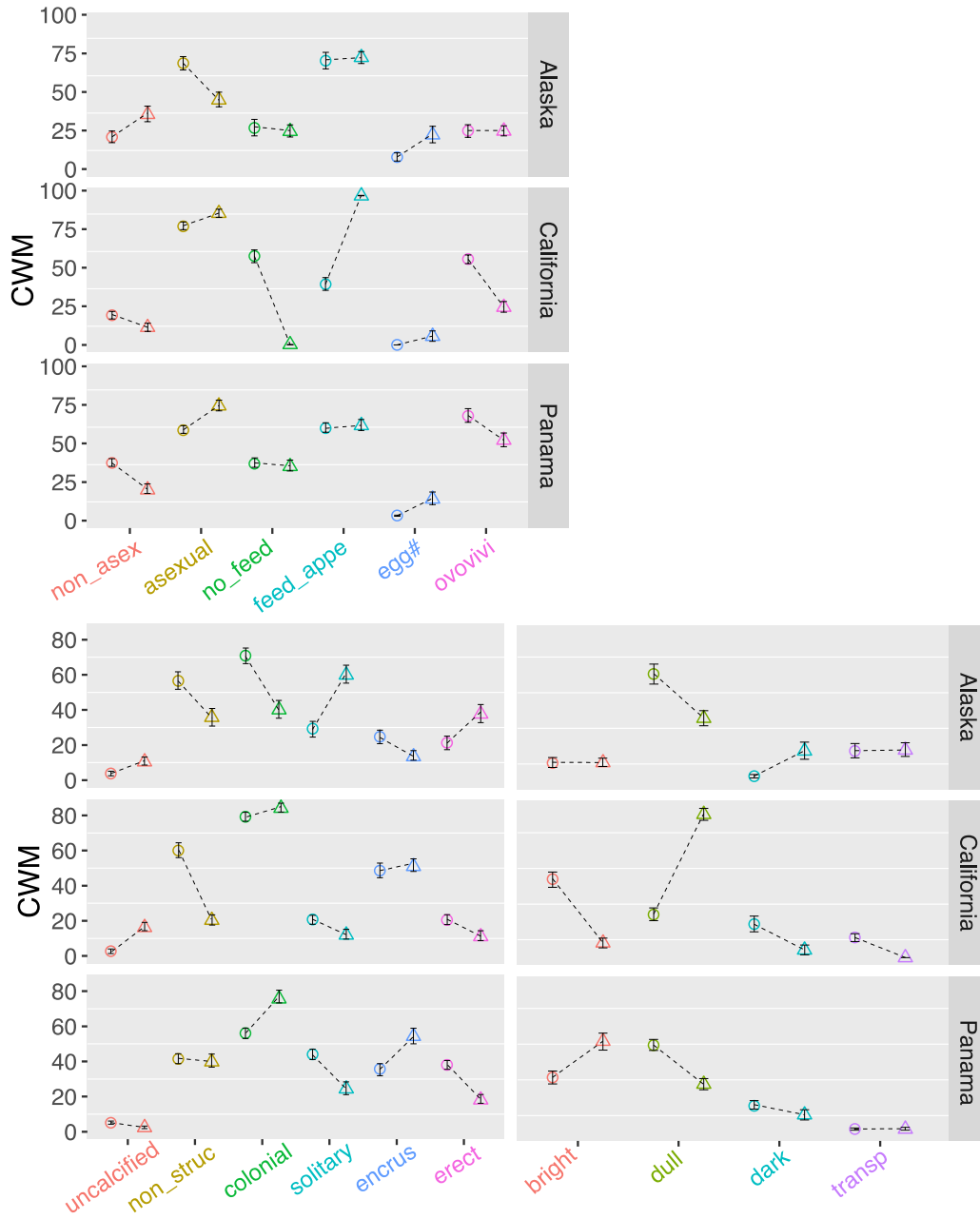


Table 3.2 Mean and variation (coefficient of variation - CV) of environmental variables within sites in each region, within a single region, and among all regions. Environmental variables include temperature (T) and salinity (Sal). Data from the 3 & 12-month sampling intervals are shown.

Region	Site	Mean T (°C)		Mean Sal (ppt)		CV T		CV Sal	
		3 month	12 month	3 month	12 month	3 month	12 month	3 month	12 month
<i>Within site</i>									
Alaska	Bar Harbor	12.06	13.04	20.90	22.41	0.015	0.073	0.073	0.062
Alaska	Knudson Cove	12.15	14.98	21.89	21.56	0.029	0.101	0.071	0.073
Alaska	Refuge Cove	11.99	14.30	21.50	22.90	0.022	0.074	0.034	0.020
California	Loch Lomond	20.89	19.01	29.25	12.70	0.026	0.091	0.004	0.234
California	Richmond	19.14	19.03	31.74	16.71	0.017	0.058	0.002	0.100
California	San Francisco Marina	17.24	13.61	32.78	24.69	0.011	0.056	0.009	0.064
Mexico	Marina Costa Baja	29.91	25.13	35.38	34.07	0.003	0.004	0.011	0.021
Mexico	Marina La Paz	29.10	24.75	36.44	34.95	0.040	0.002	0.005	0.011
Mexico	Marina Palmira	29.98	25.98	35.48	34.84	0.020	0.002	0.008	0.005
Panama	Flamenco	23.40	27.61	32.49	21.08	0.023	0.006	0.004	0.212
Panama	La Playita	24.19	27.90	32.18	23.74	0.054	0.005	0.006	0.101
Panama	Naos-STRI	25.36	25.96	32.04	31.91	0.050	0.068	0.015	0.006
<i>Within region</i>									
Alaska		12.07	14.10	21.43	22.29	0.022	0.100	0.062	0.059
California		19.09	17.22	31.25	18.03	0.082	0.167	0.049	0.305
Mexico		29.68	25.28	35.75	34.67	0.028	0.021	0.016	0.017
Panama		24.32	27.21	32.23	25.30	0.055	0.046	0.011	0.215
<i>Among regions</i>									
All regions		21.37	20.25	30.22	24.86	0.311	0.289	0.180	0.290

CHAPTER 4

PHYSICAL DISTURBANCE ALTERS THE FUNCTIONAL DIVERSITY AND STRUCTURE OF MATURE LOW LATITUDE MARINE COMMUNITIES

4.1 Abstract

Disturbance, either from natural or anthropogenic sources, is hypothesized to decrease the trait diversity of communities by restricting their trait profile to strategies that maximize survival. Whether this pattern holds true across latitudes and regardless of ongoing assembly mechanisms has not been previously explored. The inherent trait diversity of the system can also influence trait responses as a greater similarity of traits may serve as a buffer to resist disturbance. I examined the impact of a pulsed disturbance on sessile marine communities that assembled for either three or twelve months across 12 sites of four regions along the Pacific coast of North and Central America. Sessile communities were periodically disturbed by scraping off biomass until either 60% or 20% of the substrate was visible. Undisturbed controls were used for comparison but also to assess the trait diversity of the region. With disturbance, the functional diversity of lower latitude communities (Mexico and Panama) decreased, but only during late assembly and despite capturing changes in the inherent functional diversity of each region with time. A shift in trait strategies was only evident for late assembly in Mexico, and strategies related to regenerative and fast colonization abilities prevailed on disturbed communities. Pulsed physical disturbance had a greater impact on the functional structure and diversity of mature low latitude sessile marine communities, and ongoing assembly as well as trait diversity of each region determined the extent of the impact.

Therefore, lower latitude communities may be at greater risk of trait homogenization by shifting their strategies to resist disturbance.

4.2 Introduction

Human induced disturbances can change the structure of communities, including their composition, taxonomic and functional diversity (Biswas and Mallik 2010, Elo et al. 2016), and could disrupt ecosystem functions (MacDougall et al. 2013). A mechanistic understanding of disturbance impacts is informed by characterizing changes in trait diversity (Biswas and Mallik 2010, Castro et al. 2018) and trait strategies (Herben et al. 2018). The impact of a disturbance partly depends on the inherent trait diversity of the system (McLean et al. 2019) and whether assembly dynamics are disrupted (Elo et al. 2016). At a global scale, the functional diversity of communities generally follows a latitudinal gradient with increased diversity towards tropical regions (Lamanna et al., 2014; Swenson et al., 2012). This pattern, independent of taxonomic diversity (Stevens et al. 2003), is hypothesized to arise from the influence of different assembly mechanisms (Swenson et al., 2012). Therefore, detecting disturbance impacts on communities assembled under natural conditions across a latitudinal gradient can deepen our understanding of the consequences of physical disturbance across large geographic scales.

Disturbance, including the removal of biomass, can generate a re-organization of communities and act as a selective force on trait structure (Jentsch and White 2019). Generally, under intense disturbance the trait profile of a community is reduced to stress tolerant traits (Li and Shipley 2018), and the functional diversity of the assemblage tends

to decrease (Castro et al. 2018, Beiroz et al. 2018). This pattern has been shown in terrestrial and aquatic communities alike under wide-scale anthropogenic disturbances (e.g., pollution, land cover and river flow changes) or experimental manipulations (i.e., biomass removal) that simulate a strong physical disturbance (Castro et al. 2018, Li and Shipley 2018). Whether a reduction in trait diversity occurs uniformly across large-scale biogeographic gradients is still unknown. Moreover, disturbance can generate shifts in trait abundances before traits are completely removed from a community, and abundance weighted functional measures can detect disturbance effects prior to trait losses (Mouillot et al. 2013). Determining to what extent communities are susceptible to trait variability and/or trait loss as they respond to physical disturbances during assembly and across different latitudes can inform when and where communities are most likely vulnerable.

Disturbance sensitivity may be contingent on the diversity of traits in the system, with greater trait similarity acting as a buffer for stability (Díaz and Cabido 2001). For example, communities with similar and abundant traits are better equipped to resist disturbance (McLean et al. 2019), while communities with high trait diversity and perhaps rare trait combinations may be more susceptible and unable to fully recover after disturbances (McWilliam et al. 2020). Assembly dynamics determine the functional diversity of communities, but assembly and consequently functional diversity are known to vary with time (Spasojevic et al. 2014) and latitude (Swenson & Enquist, 2007). In sessile communities, biotic filters can increase functional diversity later in assembly (López and Freestone, *in prep*). Therefore, for a comprehensive examination of

disturbance, I need to consider the inherent functional diversity of the system to determine disturbance sensitivity and impact across time and latitude.

A shift in trait strategies can further reveal mechanisms through which disturbances impact communities. Shifts in mean traits in a community represent optimal strategies under current conditions (Muscarella and Uriarte 2016) and show how single traits may change under natural (López and Freestone, *in review*) or anthropogenic disturbances (Benítez et al. 2018). At local scales, disturbance can disrupt competitive dynamics by providing resources such as space (Schamp and Aarssen 2009), and reset communities to earlier assembly stages (Menge and Sutherland 1987). Therefore, species with good colonizing abilities can exploit available resources (Cadotte 2007), and shifts in trait strategies that facilitate rapid colonization may be evident in disturbed communities (Jentsch and White 2019). Shifts in trait strategies would further inform how the trait profile of communities is selected or reduced to specific strategies that reflect survival and resistance to disturbances.

Using standardized and periodic biomass removals from sessile marine invertebrate communities that developed for three or twelve-months across a latitudinal gradient, I tested the hypotheses that disturbance would decrease functional diversity of communities from regions and assembly stages that have an inherent high trait diversity. Specifically, communities from low latitude at any assembly stage as well as mature communities from any region would experience a decrease in functional diversity, and shifts in trait strategies related to stress tolerance and/or colonizing abilities would be evident in disturbed communities. I also expect disturbance to change trait abundances

instead of resulting in complete trait losses. Sessile invertebrates are an ideal model system as they make functional and phylogenetic rich communities that grow quickly and are readily found on nearshore habitats across all continents (Freestone et al. 2011, Bracewell et al. 2018). Few studies have assessed disturbance impacts on traits from multi-taxa systems (Fournier et al. 2015). This study, then, is the first to determine trait mediated disturbance impacts on highly diverse communities while considering inherent differences and changes in trait diversity across time and latitude.

4.3 Materials and methods

4.3.1 Study system

Sessile marine invertebrate communities are present in nearshore habitats across continental ranges and readily grow in natural as well as artificial structures which facilitate their comparison across large geographic scales (Freestone et al. 2011, Bracewell et al. 2017). These multi-taxa communities are composed of ascidians, bryozoans, bivalves, cirripeds, hydroids, sponges, and tube-forming polychaetes and are a tractable system to examine disturbance as they are fast growers (Bracewell et al. 2017) and can recover within weeks (Bonfim and Freestone, *in prep*). Physical disturbance and removal of individuals can also disrupt biotic interactions (Menge and Sutherland 1987), which act as important assembly filters on sessile marine invertebrate communities (López and Freestone, *in prep*). The influence of biotic filters, however, as well as recovery dynamics of sessile communities vary with latitude (Bonfim and Freestone, *in prep*, Freestone et al. *in review*), making them an ideal model system to determine disturbance impacts across latitude. From an evolutionary context, the recovery potential

and/or resistance from physical disturbance would be evident from a trait-based approach, and trait trade-offs can reveal strategies that increase susceptibility or lead to recovery (Jentsch and White 2019). I therefore assessed trait responses of sessile marine invertebrates to disturbance using standardized field biomass removal experiments across a latitudinal gradient.

4.3.2 Biomass removals – disturbance experiment

I performed standardized biomass removals to compare sessile marine invertebrate communities that experienced periodic disturbances during assembly against non-disturbed controls. Experiments were conducted across three sites per region, in four regions along the Pacific Coast of North and Central America, for 12 sites in total. I compared communities from southeast Alaska, USA (Ketchikan; 55° N, 131° W), California, USA (San Francisco; 37° N, 122° W), Baja California, Mexico (La Paz; 24°N, 110° W), and Panama (Panama City; 8° N, 79° W). I used polyvinyl chloride (PVC) settlement panels as habitat as this artificial substrate allows recruitment and growth of invertebrates while controlling for substrate type and development time (Newcomer et al. 2019). At each site, I positioned settlement panels (14 x 14 cm) one meter below the water surface with an abraded side facing the seafloor to facilitate settlement and development. I deployed experiments on floating docks at recreational boat marinas to facilitate access to communities and conduct biomass removals.

To assess physical disturbance, the following three treatments were assigned at random: (1) 60% surface scrape, (2) 20% surface scrape, and (3) 0% surface scrape (non-disturbed control). To scrape off biomass, I briefly removed experimental communities

from the water and used a putty knife to remove individuals until the surface of the panel was visible. On panels assigned a removal treatment, I did a total of three parallel scrapes or one scrape positioned randomly on the surface of the panel to reach the 60% or 20% surface opening, respectively. Invertebrate communities assembled for three (i.e., early assembly) or twelve (i.e., later assembly) months, and two or five rounds of removals were performed on developing communities (Table 4.1). After three months, biotic interactions already impact assembly and after a twelve month assembly period these mature communities are primarily influenced by competitive dynamics (López and Freestone, *in prep*). In Panama, I re-deployed experimental panels for the 12-month growth from one site at a later time, due to losses to wave action and storms (Table 4.1).

Table 4.1 Summary of assembly period and timing of biomass removals of experimental panels from each region. Experiments were conducted at three sites in each of the four regions. One site in Panama (Naos) was redeployed for the 12-month assembly experiment due to storm-related losses.

Region	Assembly timeframe	Biomass removals	N
<i>3-month assembly</i>			
Alaska	June – September 2015	After month 1 and 2	45
California	May – August 2016		45
Mexico	June – September 2017		45
Panama	December 2015 – March 2016		45
<i>12-month assembly</i>			
Alaska	June 2015 – July 2016	After month 1, 2, 6, 10, and 11	45
California	May 2016 – June 2017		45
Mexico	June 2016 – August 2017		45
Panama	December 2015-December 2016		30
Panama (Naos)	March 2016-April 2017		15

Approximately one month after the last biomass removal, I retrieved five panels of each treatment at each site for a total of 360 experimental communities. Upon retrieval, I identified all individuals present to the lowest taxonomic level using a stereoscope and assigned a species or a morphospecies identifier. In addition, I also identified invertebrates on a 50-point grid to get an estimate of percent cover by taxa. Field identifications were confirmed from fixed samples whenever possible with the help of taxonomic experts.

4.3.3 Functional characterization and indices

A pulse disturbance, such as periodic biomass removals, can disrupt local assembly dynamics (Chang and HilleRisLambers 2016, Jentsch and White 2019). While disturbance increases resource availability likely modifying competitive and recolonization dynamics in sessile communities, morphological and life history traits of potential colonizers can influence reestablishment (Sousa 1984). I therefore defined the functional space with traits that respond to biotic filters such as morphological and reproductive traits. In addition, I also included traits that relate to resource acquisition and colonization abilities to determine responses from physical disturbance (Table 1.1).

I developed a functional matrix for 178 taxa of which 151 were identified to genus or species and the remaining 27 to class or family. Trait data were collected from observations, laboratory measurements, or literature, and trait data were continuous, categorical, or binary (Table 1.1). When taxa specific traits were unavailable, I used the closest taxonomic level for which data were available (Weigel et al. 2016). A detailed description of field measurements and a list of literature sources are available in Chapter

2. This functional matrix along with the percent cover or presence-absence matrix were used to calculate an abundance weighted and presence-absence functional similarity index Rao quadratic entropy (RaoQ), respectively (Botta-Dukát 2005). This index was ideal to test my hypotheses that physical disturbance would decrease functional diversity at low latitudes and later assembly stages at any region because: (1) it captures the effect of disturbance at local scales, (2) it can detect the sensitivity of communities to trait variability or loss of trait combinations (Mouillot et al. 2013), and (3) it detects changes in assembly processes (López and Freestone, *in prep*).

Community weighted means (CWMs) represent the functional structure and community wide trait strategies under current conditions (Muscarella et al. 2016). I used CWMs to capture shifting trait strategies from physical disturbance. CWMs represent an abundance weighted mean trait value for continuous traits or a percent trait affinity for categorical or binary traits (Gutiérrez-Cánovas et al. 2019). For each region, I standardized all CWMs to range between 0 and 100 by calculating the percent value of the maximum CWM and/or multiplying by 100. The resulting matrices comprise community \times CWM of 34 corresponding traits and were used for subsequent analyses.

4.3.4 Data analyses

I tested the hypotheses that disturbance would decrease functional diversity (i.e., RaoQ) at low latitude communities and for late assembly for any region, and I tested for changes in abundance weighted and presence-absence indices. To do so, I examined the effect of disturbance treatments on RaoQ as follows. I used two identical linear mixed models (LMM) with region, assembly time, treatment, and their interaction as fixed

factors and corresponding random factors of site nested within region and its interaction with treatment and assembly time. I also used planned contrast to determine treatment effects for each region and assembly time focusing on the strongest disturbance (i.e., 0% vs. 60% removal treatment). Additionally, I explored changes in inherent functional diversity (i.e., undisturbed communities) for each region through time and differences among regions for each assembly time using planned contrasts.

I also tested whether the observed functional diversity was more or less similar than a random distribution. I randomized the abundance matrix to compare the observed functional diversity against 999 randomly assembled communities. I used constrained randomizations keeping constant the species abundance per site (Götzenberger et al. 2012). I performed randomizations using the species pool from individual sites as I expect local dynamics such as species interactions to influence disturbance patterns. I assessed patterns of trait convergence or divergence with standardize effect size (SES) scores calculated as follows:

$$SES = \frac{RaoQ_{observed} - RaoQ_{mean(random)}}{RaoQ_{sd(random)}},$$
 and used Wilcoxon signed-rank tests to measure

SES departure from zero (i.e., non-random). Randomization of presence-absence matrices was also used and described in Supporting information Figure 4.4 along the results.

I used a multivariate generalized linear model (*manyglm*) to detect shifts in trait strategies (i.e., CWMs) in response to disturbance across the gradient. The model included region, assembly time, treatment, and their interaction as predictors, and accounting for correlation between CWMs did not impact the results. I used a visual

assessment to validate normality and homoscedasticity assumptions of model residuals. I then tested predictor significance with Likelihood Ratio Tests (LRT) and used pairwise comparisons of the region * assembly time * treatment interaction to inform when and where disturbance shifted trait strategies. To determine which traits shifted between treatments, I fitted a separate *manyglm* for the regions and assembly stages with significant treatment interactions. Model results include univariate tests with step down resampling to adjust *p*-values for each CWM. All analyses were performed in R with the packages FD (Laliberté et al. 2014), lme4 (Bates et al. 2015), emmeans (Lenth 2019), picante (Kembel et al. 2010a), and mvabund (Wang et al. 2012).

4.4 Results

4.4.1 Disturbance and functional diversity

Disturbance decreased functional diversity, but only during late assembly and at low latitudes. In Mexico and Panama, I found lower functional diversity in later stages of assembly (i.e., 12-month communities) that experienced five disturbance events throughout development, but results were only evident when the abundance of traits were considered (Figs 4.1 and Supporting Information Fig 4.5). Undisturbed communities had higher functional diversity (Mexico: 0.124 ± 0.012 ; Panama: 0.067 ± 0.012) than communities that experienced physical disturbance (i.e., 60%) (Mexico: 0.062 ± 0.012 , $t = -7.555$, $P < 0.0001$; Panama: 0.046 ± 0.011 , $t = -2.478$, $P = 0.019$). Likewise, I found a shift to trait convergence under high disturbance at lower latitudes and during late assembly, primarily (Fig 4.2), and again these shifts were only evident when trait abundance was considered (Supporting Information Fig 4.6). In Mexico, SES values

were positive for undisturbed communities, indicating trait divergence, while disturbed communities had negative SES values, indicating trait convergence. In Panama, however, SES values for undisturbed communities were not different from zero, but disturbed communities also had negative SES values (Fig 4.2).

Figure 4.1 Effects of disturbance on functional diversity (abundance weighted RaoQ) and expressed as estimated marginal means from a linear mixed model (LMM). LMM interaction of interest: region*assembly time*treatment $F_{6,32} = 3.375$, $P = 0.011$. Asterisks indicate significant treatment contrasts comparing 0% and 60% removal treatments for each region and time ($\alpha=0.05$)

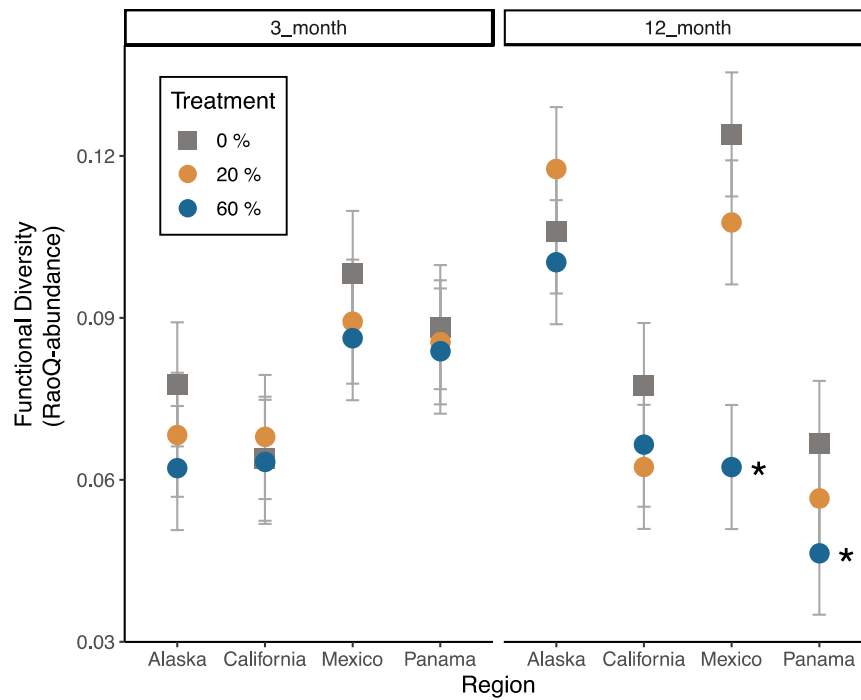
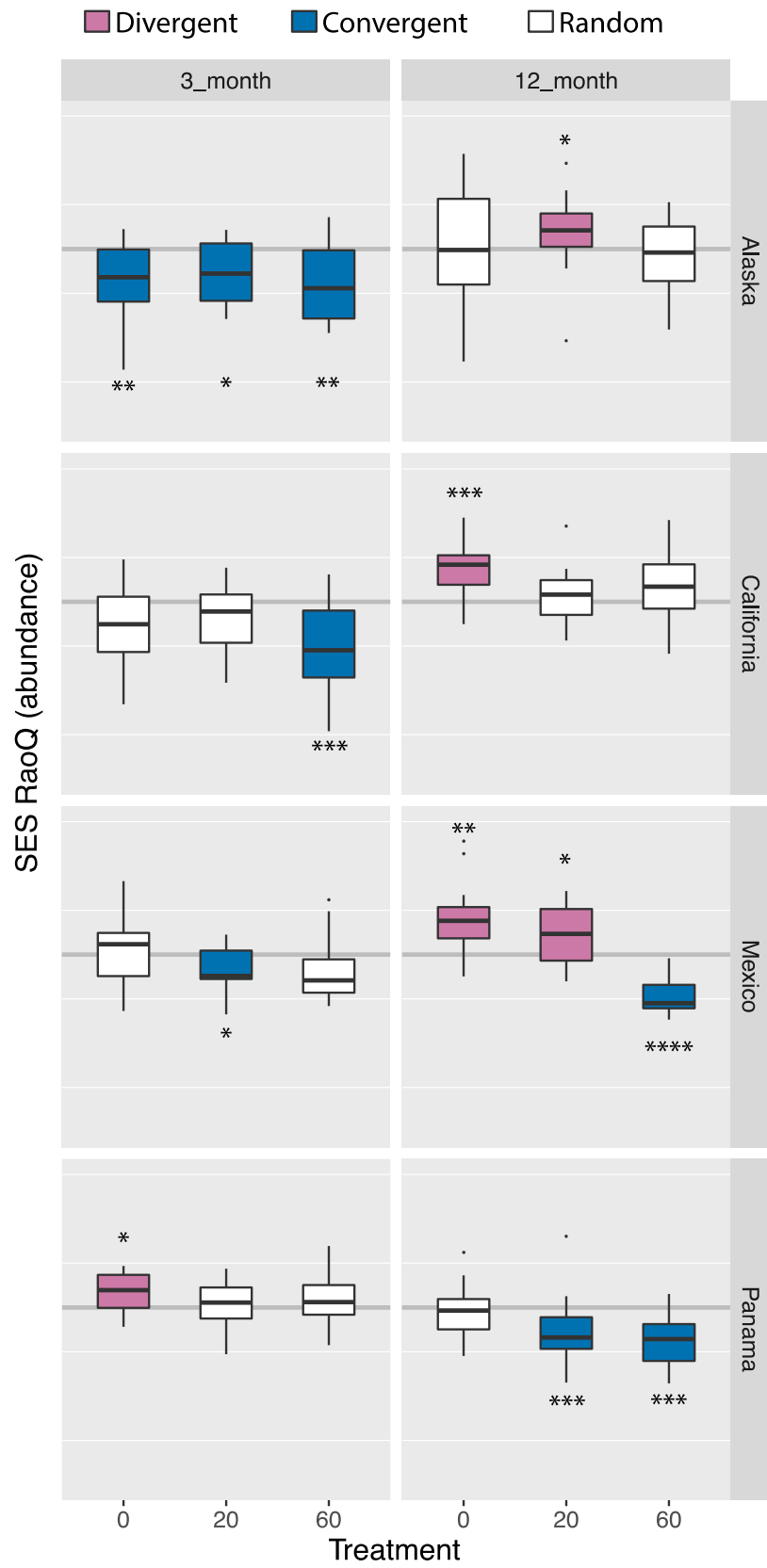


Figure 4.2 Distributions of standard effect size (SES) of RaoQ (abundance weighted) pooled by treatment for each region and assembly time and shown with box-plots. Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles, and dots represent outliers. Non-random trait distributions correspond to solid colored box-plots, random distributions are white box-plots. SES significantly greater or smaller than zero are based on Wilcoxon signed-rank tests. **** $P < 0.0001$; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.



4.4.2 Undisturbed communities functional diversity

The functional diversity of undisturbed communities, or the diversity of the system, shifted during development in most regions. I saw a shift to increased diversity with later assembly in Alaska and Mexico. In Panama, however, a shift to lower functional diversity occurred between early and late assembly (Fig 4.3). Differences in diversity between higher and lower latitude were only evident during late assembly, and a latitudinal gradient in functional diversity was not observed. I found higher functional diversity in Mexico (0.124 ± 0.012) versus California (0.0775 ± 0.012 , $t = 2.858$, $P = 0.013$) and Alaska (0.106 ± 0.012) versus Panama (0.067 ± 0.012 , $t = -2.407$, $P = 0.030$) during late assembly, and no difference between regions were observed during early assembly ($P > 0.05$).

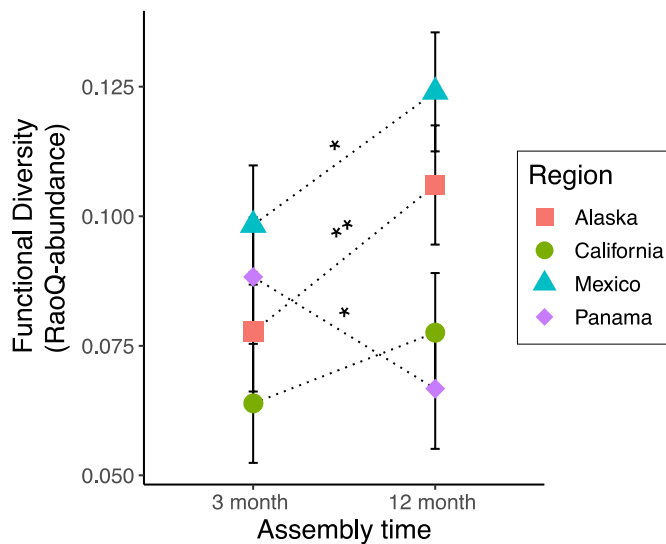


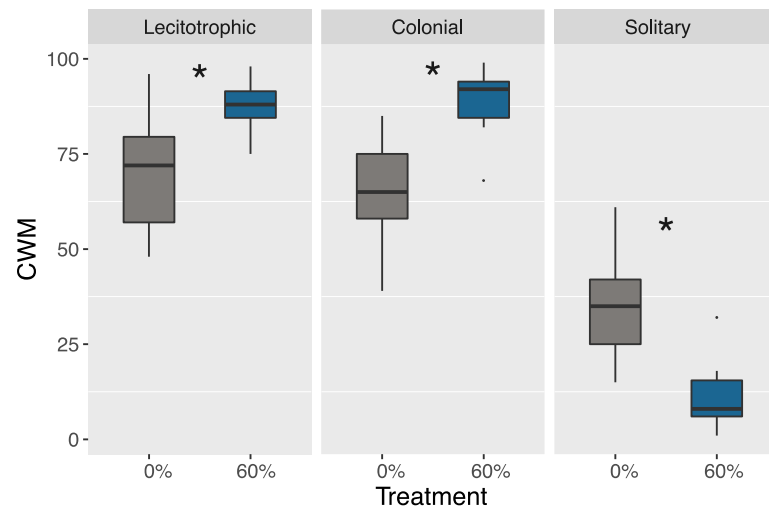
Figure 4.3 Effect of assembly time on the functional diversity (abundance weighted RaoQ) of undisturbed communities (i.e., 0% treatment) and expressed as estimated marginal means from a LMM. Planned contrasts ** $P < 0.01$; * $P < 0.05$.

4.4.3 Disturbance and functional structure

Disturbance also influenced CWMs during late assembly, and changes in functional structure were observed between undisturbed and disturbed communities (i.e., 60 %) in Mexico (LRT = 263, adjusted- P = 0.005) and Alaska (LRT = 245, adjusted- P = 0.005). Specifically, I found an increase in the abundance of individuals with a non-feeding larval strategy (i.e., lecithotrophic) coupled with a trade-off of individuals with colonial versus solitary body forms on disturbed communities in Mexico (Fig 4.4). In Alaska, however, I did not find individual traits that shifted with disturbance.

Figure 4.4 Shifts in

CWMs between undisturbed (i.e., 0% treatment) and disturbed (60% treatment) communities during late assembly (12-



month) in Mexico. Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles, and dots represent outliers. Results from univariate *manyglm* tests (*adjusted P < 0.05).

4.5 Discussion

Disturbance shaped the functional diversity and structure of communities from lower latitudes but during late assembly, only. I observed a decrease in functional diversity in

regions with high and low inherent functional diversity. Observed changes were only evident with trait variability (i.e., abundance-weighted) but not trait loss. I observed a greater impact of disturbance on subtropical communities where the inherent diversity of the region increased with time. In addition, functional structure of these subtropical communities shifted to disturbance resistant and fast colonization strategies. Despite having low inherent diversity, our manipulative disturbance also had an impact on the functional diversity of communities from the tropics, suggesting multiple mechanisms influenced their structure. These results support the hypothesis that disturbance can limit the trait profile of communities and decrease their functional diversity, but assembly stage, and factors that covary with latitude, such as inherent diversity of the system and the influence of other disturbances, contributed to the extent of the impact.

Disturbance influenced the functional diversity of communities as expected, but both latitude and assembly stage determined when and where decreased functional diversity was observed. Disturbance only impacted communities from lower latitude and later assembly, which could result from the greater and faster temporal turnover of species and traits that occur at low latitudes (Korhonen et al. 2010, Soininen 2010), and the sorting of individuals with traits adapted to disturbance may have occurred over time (Fraterrigo and Rusak 2008). In a parallel study, greater temporal turnover in community composition as well as faster recovery were observed at lower than higher latitudes (Bonfim and Freestone, *in prep*). In addition, the functional architecture of communities faced with disturbance is often gradually adjusted through time (Leigh et al. 2019). Therefore, the cumulative effect of periodic pulsed disturbance may only be evident at

later stages of assembly, and differences in temporal dynamics such as species turnover across latitude may further influence when and where trait changes occur.

The inherent functional diversity at lower latitudes influenced the extent of trait responses. Theory predicts with greater functional similarity there is a greater probability that communities maintain their properties when faced with a disturbance (Díaz and Cabido 2001). On the contrary, with higher trait diversity the probability of all existing traits being resistant to disturbance may be low (McWilliam et al. 2020) and a decrease in functional diversity generally occurs under disturbance (Beiroz et al. 2018). In subtropical Mexico, I observed an increase in functional diversity between early and late assembly, and a decrease in functional diversity with disturbance only occurred when the inherent functional diversity had increased. Moreover, with disturbance in these later assembled subtropical communities, I found shifts to trait strategies that confer rapid colonization and regenerative abilities, which align with theoretical expectations from pulsed disturbances (Herben et al. 2018, Jentsch and White 2019). The extent of trait responses to disturbance with changes in both functional diversity and structure were only evident when the system had higher trait diversity.

Decreased functional diversity with disturbance also occurred in Panama during later assembly despite observing a decrease in the inherent trait diversity of the region through time. Stronger predation is characteristic of the tropics when compared to higher latitudes (Freestone et al. 2011, 2020), and the decrease in trait diversity observed over time could result from the ongoing disturbance imposed by predators (López and Freestone, *in prep*). A further decrease in functional diversity found on disturbed

communities may result from a joint effect of predation and the imposed physical disturbance. Combined effects of biotic filters with disturbance are hypothesized to influence trait responses of communities (Mouillot et al. 2013), and limited empirical support show shifts in trait strategies (e.g., Tomas et al. 2015). These results provide evidence that a pulsed physical disturbance can further decrease the functional diversity of a system already under pressure from a natural disturbance. Trait shifts, however, were not evident as both predation and physical disturbance may select for a trait profile that withstand or quickly replaces removals of individuals.

The functional response of marine communities to a pulsed physical disturbance was not homogeneous across latitude. Communities from lower latitudes may be at greater risk of trait homogenization in response to repeated disturbance, despite being capable of quick recovery (Bonfim and Freestone, *in prep*). These results also highlight how trait responses are not an immediate outcome but perhaps accumulate through time with periodic disturbances. Time-delayed extinctions and loss of taxonomic diversity are also documented on disturbed habitats (Krauss et al. 2010), and could result from a slow reduction of trait profiles able to survive the repeated pressures from disturbances. Other studies that reveal trait responses from disturbance across large geographic scales and through time are scarce, but should become of greater importance as the frequency of natural and anthropogenic disturbances will only increase as a consequence of climate change and globalization (Nyström et al. 2000, Matuoka et al. 2020).

4.6 Supporting information

Figure 4.5 Effects of disturbance on functional diversity (RaoQ-presence) and expressed as estimated marginal means from a LMM. LMM interaction of interest $P > 0.05$.

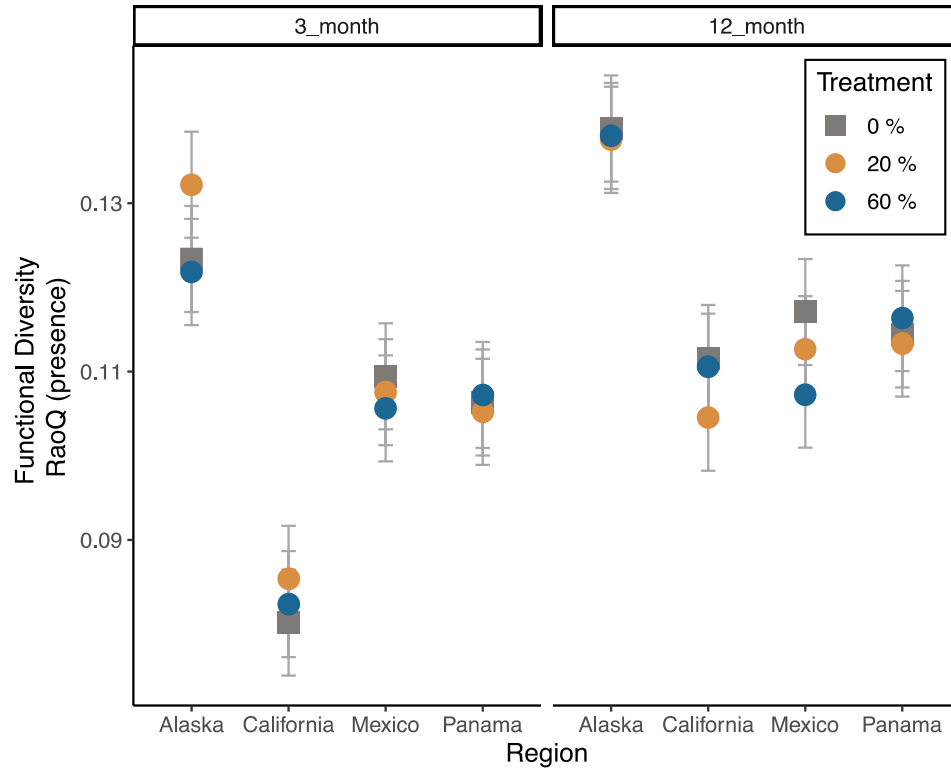
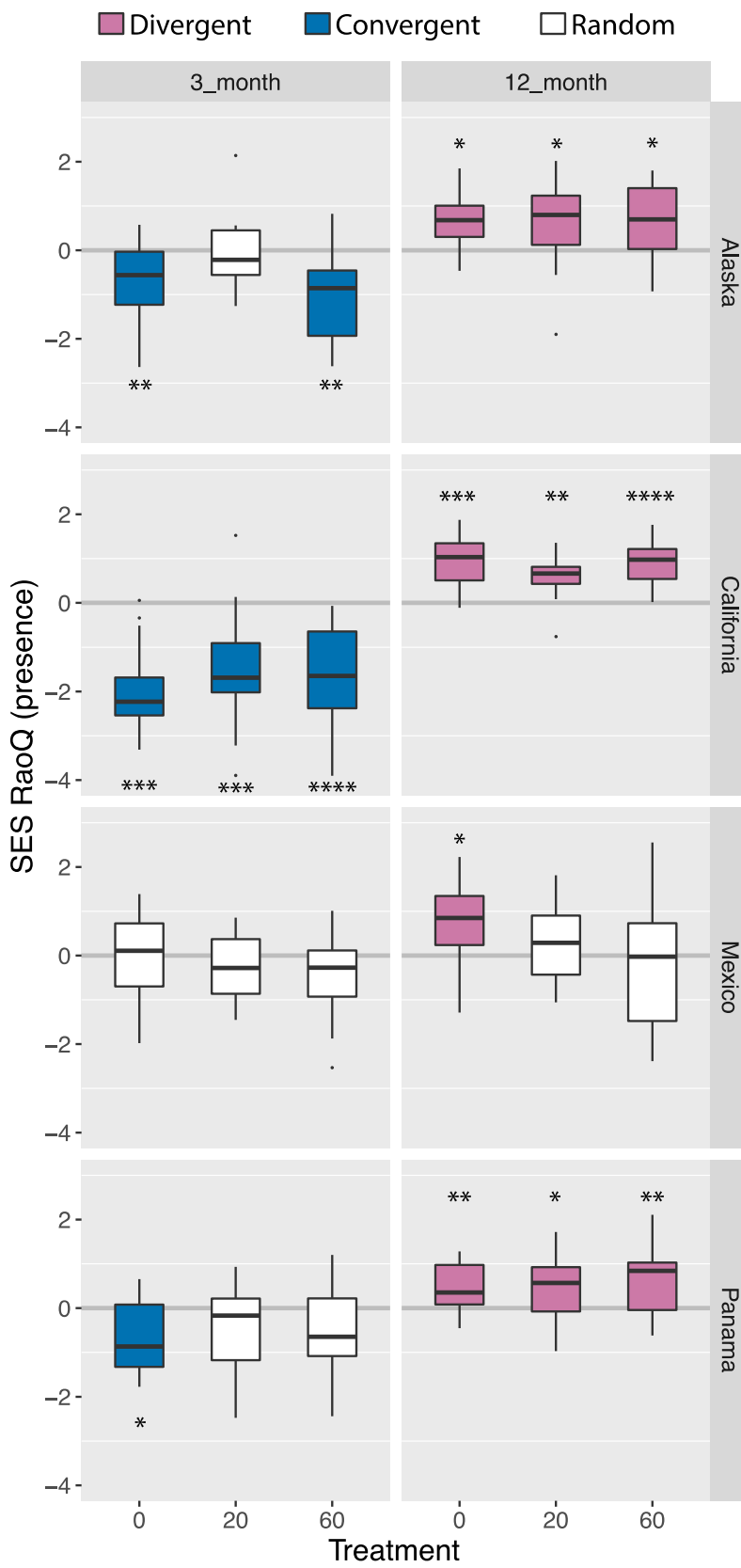


Figure 4.6 Randomizations to calculate SES values were performed by constraining richness per community and species frequency per site from the community matrices. Distributions of standard effect size (SES) of RaoQ (non-abundance weighted) pooled by treatment for each region and assembly time and shown with box-plots. Lines within boxes are medians, box ends are quartiles, whiskers extend to values no larger than 1.5 times quartiles, and dots represent outliers. Non-random trait distributions correspond to solid colored box-plots, random distributions are white box-plots. SES significantly greater or smaller than zero are based on Wilcoxon signed-rank tests. **** $P < 0.0001$; *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$



CHAPTER 5

CONCLUSIONS

In the present study, I show trait-based assembly can be influenced by different mechanisms across time and latitude in marine communities. Further, I provide evidence demonstrating that biotic interactions play an important role in the assembly of communities at local scales, while physical disturbance can disrupt ongoing mechanisms of assembly. Within a single region, primary assembly filters shifted with time. In the tropics, for example, both predation and competition influenced assembly at early and late assembly stages, respectively, while disturbance influenced trait patterns during late assembly only. In the subtropics, predation had an intermediate effect on trait patterns during early assembly, but disturbance had a strong influence on trait responses later in assembly. Competition also influenced later stages of assembly at higher latitudes, Alaska and California, but disturbance did not disrupt trait patterns at any assembly stage in these high latitude regions. I therefore demonstrate that assembly processes are highly dynamic and quickly change within a short time frame at all latitudes.

In my first chapter, I uncover trait mechanisms that lead to differential impacts of predation across latitude while considering the evolutionary history of interacting species. Despite growing evidence that predation can disproportionately impact prey communities at lower latitudes, experimental studies that explore impacts of predators on the functional architecture of prey across latitude are rare. Further, the evolutionary context of predator-prey interactions is often overlooked even in smaller-scale studies. Under global change, species invasions and novel interactions will continue to arise, thus it is

important to expand our understanding of these novel dynamics. This study is the first to determine trait responses of multiphyletic prey communities with distinct evolutionary histories across a large geographic range, spanning the subarctic to the tropics. With multiple lines of evidence, I show introduced prey are more susceptible to strong predation in the tropics, and evolutionary histories between predators and prey are key to detecting prey trait responses.

Understanding assembly is one of the fundamental goals in ecology. In my second chapter, I demonstrate how trait based-assembly helps to detect mechanisms that lead to changes in assembly across time and latitude. At high latitudes, colonizing strategies were important during early assembly while competitive strategies influenced later assembly. At lower latitudes, competitive dynamics were also important during later assembly, but predation shaped the trait profile of communities to those that maximize survival during early assembly. A lot of evidence support the hypothesis that predation is stronger at lower latitudes (Freestone et al. *in review*), but uncovering specific mechanisms prey communities use to respond and survive strong predation are rare. Moreover, competitive strength is also predicted to vary across latitude, but I demonstrate that competition maybe strong and influence later assembly at all latitudes. In this chapter, I demonstrate trait-based approaches are valuable to detect patterns and mechanisms of assembly and how these change with time across a large geographic scale.

Lastly, trait-based approaches were instrumental to determine when and where pulsed physical disturbances impact marine communities, but also to reveal mechanisms by

which communities respond. While many studies support the hypothesis that disturbance decreases functional diversity (Castro et al. 2018, Beiroz et al. 2018, McLean et al. 2019), this study shows that factors such as latitude, assembly time, and the trait diversity of each region can influence disturbance impacts on trait responses. Higher latitudes were able to resist trait changes from repeated physical disturbance, while lower latitudes lost trait diversity over time. Faster recovery and greater compositional turnover was observed at lower latitudes (Bonfim and Freestone, *in prep*), but the trait profile of disturbed communities was reduced and shifted to regenerative abilities and rapid colonization after many rounds of physical disturbance. Therefore, disturbance does not immediately impact the trait composition of low latitude communities but rather changes may accumulate through time with repeated disturbance.

Trait-based ecology serves as a unifying principle to better understand coexistence and assembly (Violle et al. 2007, Escudero and Valladares 2016). Both natural and anthropogenic sources of disturbance as well as biotic filters influenced trait-based assembly in nearshore marine communities, and interaction histories also shaped trait responses. In my dissertation, I was able to provide novel understanding of biotic interactions and disturbance impacts on marine communities from across 47 degrees latitude by showing trait mechanisms that respond to ongoing stressors.

BIBLIOGRAPHY

- Aburto-Oropeza, O., I. Dominguez-Guerrero, J. Cota-Nieto, and T. Plomozo-Lugo. 2009. Recruitment and ontogenetic habitat shifts of the yellow snapper (*Lutjanus argentiventris*) in the Gulf of California. *Marine Biology* 156:2461–2472.
- Adler, P. B., D. G. Milchunas, W. K. Lauenroth, O. E. Sala, and I. C. Burke. 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41:653–663.
- Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. Maron, K. A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M. G. Turner, and E. Werner. 2007. Filling Key Gaps in Population and Community Ecology. *Frontiers in Ecology and the Environment* 5:145–152.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32–46.
- Anderson, M. J., C. E. Diebel, W. M. Blom, and T. J. Landers. 2005. Consistency and variation in kelp holdfast assemblages: Spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology* 320:35–56.
- Anderson, M. J., R. N. Gorley, and K. R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E. Plymouth, UK.
- Barnes, D. K. A. 2002. Polarization of competition increases with latitude. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269:2061–2069.
- Barton, K. 2019. MuMIn: Multi-Model Inference.

- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67.
- Beiroz, W., E. Sayer, E. M. Slade, L. Audino, R. F. Braga, J. Louzada, and J. Barlow. 2018. Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-modified tropical forest landscape. *Ecological Indicators* 95:518–526.
- de Bello, F., J. Lepš, and M.-T. Sebastià. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* 29:801–810.
- de Bello, F., J. N. Price, T. Münkemüller, J. Liira, M. Zobel, W. Thuiller, P. Gerhold, L. Götzenberger, S. Lavergne, J. Lepš, K. Zobel, and M. Pärtel. 2012. Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93:2263–2273.
- de Bello, F., P. Šmilauer, J. A. F. Diniz-Filho, C. P. Carmona, Z. Lososová, T. Herben, and L. Götzenberger. 2017. Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. *Methods in Ecology and Evolution* 8:1200–1211.
- Benítez, A., G. Aragón, Y. González, and M. Prieto. 2018. Functional traits of epiphytic lichens in response to forest disturbance and as predictors of total richness and diversity. *Ecological Indicators* 86:18–26.
- Biswas, S. R., and A. U. Mallik. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. *Ecology* 91:28–35.

- Boersma, K. S., L. E. Dee, S. J. Miller, M. T. Bogan, D. A. Lytle, and A. I. Gitelman. 2016. Linking multidimensional functional diversity to quantitative methods: A graphical hypothesis-evaluation framework. *Ecology* 97:583–593.
- Botta-Dukát, Z. 2005. Rao’s quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* 16:533–540.
- Bracewell, S. A., G. F. Clark, and E. L. Johnston. 2018. Habitat complexity effects on diversity and abundance differ with latitude: an experimental study over 20 degrees. *Ecology* 99:1964–1974.
- Bracewell, S. A., E. L. Johnston, and G. F. Clark. 2017. Latitudinal variation in the competition-colonisation trade-off reveals rate-mediated mechanisms of coexistence. *Ecology Letters* 20:947–957.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Buckeridge, J. S., and J. M. Reeves. 2009. Some insights into how barnacles survive as sessile organisms. *Integrative Zoology* 4:395–401.
- Butterfield, B. J., and K. N. Suding. 2013. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology* 101:9–17.

- Buzzard, V., C. M. Hulshof, T. Birt, C. Violle, and B. J. Enquist. 2016. Re-growing a tropical dry forest: functional plant trait composition and community assembly during succession. *Functional Ecology* 30:1006–1013.
- Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: assessing community assembly with trait and evolutionary distances. *Ecology Letters* 16:1234–1244.
- Cadotte, M. W. 2007. Competition–colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88:823–829.
- Cadotte, M. W., D. V. Mai, S. Jantz, M. D. Collins, M. Keele, and J. A. Drake. 2006. On Testing the Competition-Colonization Trade-Off in a Multispecies Assemblage. *The American Naturalist* 168:704–709.
- Carlton, J. T. 1996. Biological Invasions and Cryptogenic Species. *Ecology* 77:1653–1655.
- Carlton, J. T., and J. B. Geller. 1993. Ecological roulette : the global transport of nonindigenous marine organisms. *Science* 261:78–82.
- Carmona, C. P., F. M. Azcárate, F. de Bello, H. S. Ollero, J. Lepš, and B. Peco. 2012. Taxonomical and functional diversity turnover in Mediterranean grasslands: Interactions between grazing, habitat type and rainfall. *Journal of Applied Ecology* 49:1084–1093.

- Carmona, C. P., N. W. H. Mason, F. M. Azcárate, and B. Peco. 2015. Inter-annual fluctuations in rainfall shift the functional structure of Mediterranean grasslands across gradients of productivity and disturbance. *Journal of Vegetation Science* 26:538–551.
- Castro, D. M. P. de, S. Dolédec, and M. Callisto. 2018. Land cover disturbance homogenizes aquatic insect functional structure in neotropical savanna streams. *Ecological Indicators* 84:573–582.
- Ceulemans, R., U. Gaedke, T. Klauschies, and C. Guill. 2019. The effects of functional diversity on biomass production, variability, and resilience of ecosystem functions in a tritrophic system. *Scientific Reports* 9:7541.
- Chang, C.-Y., and D. J. Marshall. 2016. Spatial pattern of distribution of marine invertebrates within a subtidal community: do communities vary more among patches or plots? *Ecology and Evolution* 6:8330–8337.
- Chang, C., and J. HilleRisLambers. 2016. Integrating succession and community assembly perspectives. *Frontiers in Ecology and the Environment* 14:2294.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5:302–315.
- Clarke, K. R., and R. N. Gorley. 2015. *PRIMER v7: User Manual/Tutorial* PRIMER -E. Plymouth, UK.
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721–733.

- Conti, L., S. Block, M. Parepa, T. Münkemüller, W. Thuiller, A. T. R. Acosta, M. van Kleunen, S. Dullinger, F. Essl, I. Dullinger, D. Moser, G. Klöner, O. Bossdorf, and M. Carboni. 2018. Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. *Journal of Ecology* 106:1607–1620.
- Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *The Journal of Animal Ecology* 61:1–12.
- Crombie, A. C. 1947. Interspecific Competition. *The Journal of Animal Ecology* 16:44.
- D’Andrea, R., G. Barabás, and A. Ostling. 2013. Revising the Tolerance-Fecundity Trade-Off; or, On the Consequences of Discontinuous Resource Use for Limiting Similarity, Species Diversity, and Trait Dispersion. *The American Naturalist* 181:E91–E101.
- deRivera, C. E., G. M. Ruiz, A. H. Hines, and P. Jivoff. 2005. Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. *Ecology* 86:3364–3376.
- Díaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D. G. Milchunas, C. Skarpe, G. Rusch, M. Sternberg, I. Noy-Meir, J. Landsberg, W. Zhang, H. Clark, and B. D. Campbell. 2007. Plant trait responses to grazing - A global synthesis. *Global Change Biology* 13:313–341.
- Díaz, S., and M. Cabido. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16:646–655.

- Dyrynda, P. E. J. 1986. Defensive Strategies of Modular Organisms. *Philosophical Transactions of the Royal Society B: Biological Sciences* 313:227–243.
- Elo, M., S. Kareksela, T. Haapalehto, H. Vuori, K. Aapala, and J. S. Kotiaho. 2016. The mechanistic basis of changes in community assembly in relation to anthropogenic disturbance and productivity. *Ecosphere* 7.
- Enquist, B. J., J. Norberg, S. P. Bonser, C. Violle, C. T. Webb, A. Henderson, L. L. Sloat, and V. M. Savage. 2015. Scaling from traits to ecosystems. Pages 249–318 *Advances in Ecological Research*. First edition. Elsevier Ltd.
- Escudero, A., and F. Valladares. 2016. Trait-based plant ecology: moving towards a unifying species coexistence theory. *Oecologia* 180:919–922.
- Fleming, P. A., D. Muller, and P. W. Bateman. 2007. Leave it all behind: a taxonomic perspective of autotomy in invertebrates. *Biological Reviews* 82:481–510.
- Fofonoff, P. W., G. M. Ruiz, B. Steves, C. Simkanin, and J. T. Carlton. 2018. National Exotic Marine and Estuarine Species Information System.
<http://invasions.si.edu/nemesis/>.
- Fournier, B., F. Gillet, R.-C. Le Bayon, E. A. D. Mitchell, and M. Moretti. 2015. Functional responses of multitaxa communities to disturbance and stress gradients in a restored floodplain. *Journal of Applied Ecology* 52:1364–1373.
- Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. Sage, Thousand Oaks, CA.

- Franklin, J., J. M. Serra-Diaz, A. D. Syphard, and H. M. Regan. 2016. Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences* 113:3725–3734.
- Fraterrigo, J. M., and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters* 11:756–770.
- Freestone, A. L., E. W. Carroll, K. J. Papacostas, G. M. Ruiz, M. E. Torchin, and B. J. Sewall. 2020. Predation shapes invertebrate diversity in tropical but not temperate seagrass communities. *Journal of Animal Ecology* 89:323–333.
- Freestone, A. L., and B. D. Inouye. 2015. Nonrandom community assembly and high temporal turnover promote regional coexistence in tropics but not temperate zone. *Ecology* 96:264–273.
- Freestone, A. L., and R. W. Osman. 2011. Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity. *Ecology* 92:208–217.
- Freestone, A. L., R. W. Osman, G. M. Ruiz, and M. E. Torchin. 2011. Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology* 92:983–993.
- Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tschardtke, W. Weisser, and R. Bommarco. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences* 282:20142620–20142620.

- Gestoso, I., P. Ramalhosa, and J. Canning-Clode. 2018. Biotic effects during the settlement process of non-indigenous species in marine benthic communities. *Aquatic Invasions* 13:247–259.
- Giam, X., and J. D. Olden. 2016. Environment and predation govern fish community assembly in temperate streams. *Global Ecology and Biogeography* 25:1194–1205.
- Gianuca, A. T., S. A. J. Declerck, M. W. Cadotte, C. Souffreau, T. De Bie, and L. De Meester. 2017. Integrating trait and phylogenetic distances to assess scale-dependent community assembly processes. *Ecography* 40:742–752.
- Götzenberger, L., F. de Bello, K. A. Bråthen, J. Davison, A. Dubuis, A. Guisan, J. Lepš, R. Lindborg, M. Moora, M. Pärtel, L. Pellissier, J. Pottier, P. Vittoz, K. Zobel, and M. Zobel. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews* 87:111–127.
- Grime, J. P. 2006. Trait convergence and trait divergence in herbaceous plant communities : mechanisms and consequences. *Journal of Vegetation Science* 17:255–260.
- Grosholz, E. D. 2002. Ecological and evolutionary consequences. *Trends in Ecology & Evolution* 17:22–27.
- Gross, N., L. Börger, R. P. Duncan, and P. E. Hulme. 2013. Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands? *Functional Ecology* 27:1262–1272.
- Gutiérrez-Cánovas, C., D. Sánchez-Fernández, M. Cañedo-Argüelles, A. Millán, J. Velasco, R. Acosta, P. Fortuño, N. Otero, A. Soler, and N. Bonada. 2019. Do all

- roads lead to Rome? Exploring community trajectories in response to anthropogenic salinization and dilution of rivers. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374:20180009.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community Structure, Population Control, and Competition. *The American Naturalist* 94:421–425.
- Hargreaves, A. L., E. Suárez, K. Mehltreter, I. Myers-Smith, S. E. Vanderplank, H. L. Slinn, Y. L. Vargas-Rodriguez, S. Haeussler, S. David, J. Muñoz, R. C. Almazán-Núñez, D. Loughnan, J. W. Benning, D. A. Moeller, J. F. Brodie, H. J. D. Thomas, and P. A. Morales. 2019. Seed predation increases from the Arctic to the Equator and from high to low elevations. *Science Advances* 5:1–11.
- Henriques-Silva, R., A. Kubisch, and P. R. Peres-Neto. 2019. Latitudinal-diversity gradients can be shaped by biotic processes: new insights from an eco-evolutionary model. *Ecography* 42:259–271.
- Herben, T., J. Klimešová, and M. Chytrý. 2018. Effects of disturbance frequency and severity on plant traits: An assessment across a temperate flora. *Functional Ecology* 32:799–808.
- Hiebert, L. S., E. A. Vieira, G. M. Dias, S. Tiozzo, and F. D. Brown. 2019. Colonial ascidians strongly preyed upon, yet dominate the substrate in a subtropical fouling community. *Proc. R. Soc. B* 286:512699.
- Hillebrand, H., and C. Kunze. 2020. Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters* 23:575–585.

- Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biological Reviews* 58:21–89.
- Jentsch, A., and P. White. 2019. A theory of pulse dynamics and disturbance in ecology. *Ecology* 100:e02734.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010a. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010b. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Kicklighter, C., and M. Hay. 2006. Integrating prey defensive traits : contrasts of marine worms from temperate and tropical habitats. *Ecological monographs* 76:195–215.
- Kohli, B. A., R. C. Terry, and R. J. Rowe. 2018. A trait-based framework for discerning drivers of species co-occurrence across heterogeneous landscapes. *Ecography* 41:1921–1933.
- Korhonen, J. J., J. Soininen, and H. Hillebrand. 2010. A quantitative analysis of temporal turnover in aquatic species assemblages across ecosystems. *Ecology* 91:508–517.
- Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29:592–599.
- Krauss, J., R. Bommarco, M. Guardiola, R. K. Heikkinen, A. Helm, M. Kuussaari, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, J. Pöyry, K. M. Raatikainen, A. Sang, C.

- Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecology Letters* 13:597–605.
- Laliberté, E., P. Legendre, and B. Shipley. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology.
- Laliberté, E., D. A. Norton, and D. Scott. 2013. Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. *Journal of Vegetation Science* 24:834–842.
- Laliberté, E., and J. M. Tylianakis. 2012. Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. *Ecology* 93:145–155.
- Lamanna, C., B. Blonder, C. Violle, N. J. B. Kraft, B. Sandel, I. Šímová, J. C. Donoghue, J.-C. Svenning, B. J. McGill, B. Boyle, V. Buzzard, S. Dolins, P. M. Jørgensen, A. Marcuse-Kubitza, N. Morueta-Holme, R. K. Peet, W. H. Piel, J. Regetz, M. Schildhauer, N. Spencer, B. Thiers, S. K. Wisser, and B. J. Enquist. 2014. Functional trait space and the latitudinal diversity gradient. *Pnas* 111:13745–50.
- Lavender, J. T., K. A. Dafforn, M. J. Bishop, and E. L. Johnston. 2017. An empirical examination of consumer effects across twenty degrees of latitude. *Ecology* 98:2391–2400.
- Leigh, C., T. W. H. Aspin, T. J. Matthews, R. J. Rolls, and M. E. Ledger. 2019. Drought alters the functional stability of stream invertebrate communities through time. *Journal of Biogeography* 46:1988–2000.

- Lenihan, H. S., and J. S. Oliver. 1995. Anthropogenic and natural disturbance to marine benthic communities in Antarctica. *Ecological Applications* 5:311–326.
- Lenth, R. 2019. emmeans: Estimated Marginal Means, aka Least-Squares Means.
- Lenzner, B., D. Leclère, O. Franklin, H. Seebens, N. Roura-Pascual, M. Obersteiner, S. Dullinger, and F. Essl. 2019. A Framework for Global Twenty-First Century Scenarios and Models of Biological Invasions. *BioScience* 69:697–710.
- Li, D., J. D. Olden, J. L. Lockwood, S. Record, M. L. McKinney, and B. Baiser. 2020. Changes in taxonomic and phylogenetic diversity in the Anthropocene. *Proceedings of the Royal Society B: Biological Sciences* 287:20200777.
- Li, Y., and B. Shipley. 2018. Community divergence and convergence along experimental gradients of stress and disturbance. *Ecology* 99:775–781.
- Liebergesell, M., B. Reu, U. Stahl, M. Freiberg, E. Welk, J. Kattge, J. H. C. Cornelissen, J. Peñuelas, and C. Wirth. 2016. Functional resilience against climate-driven extinctions – comparing the functional diversity of European and North American tree floras. *PLOS ONE* 11:e0148607.
- Lindquist, N., M. E. Hay, and W. Fenical. 1992. Defense of ascidians and their conspicuous larvae: adult vs. larval chemical defenses. *Ecological Monographs* 62:547–568.
- Lippert, H., and K. Iken. 2003. Palatability and nutritional quality of marine invertebrates in a sub-Arctic fjord. *Journal of the Marine Biological Association of the United Kingdom* 83:1215–1219.

- Logerwell, E. A., and M. D. Ohman. 1999. Egg-Brooding, Body Size and Predation Risk in Planktonic Marine Copepods. *Oecologia* 121:426–431.
- Lopanič, N. B. 2014. Chemical defensive symbioses in the marine environment. *Functional Ecology* 28:328–340.
- MacDougall, A. S., K. S. McCann, G. Gellner, and R. Turkington. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. *Nature* 494:86–89.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology & Evolution* 6:183–186.
- Maire, E., G. Grenouillet, S. Brosse, and S. Villéger. 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Global Ecology and Biogeography* 24:728–740.
- Martorell, C., and R. P. Freckleton. 2014. Testing the roles of competition, facilitation and stochasticity on community structure in a species-rich assemblage. *Journal of Ecology* 102:74–85.
- Matuoka, M. A., M. Benchimol, J. M. de Almeida-Rocha, and J. C. Morante-Filho. 2020. Effects of anthropogenic disturbances on bird functional diversity: A global meta-analysis. *Ecological Indicators* 116:106471.
- Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13:1085–1093.
- McGill, B. J. 2010. Matters of Scale. *Science* 328:575–576.

- McLean, M., A. Auber, N. A. J. Graham, P. Houk, S. Villéger, C. Violle, W. Thuiller, S. K. Wilson, and D. Mouillot. 2019. Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. *Global Change Biology* 25:3424–3437.
- McWilliam, M., M. S. Pratchett, M. O. Hoogenboom, and T. P. Hughes. 2020. Deficits in functional trait diversity following recovery on coral reefs. *Proceedings of the Royal Society B: Biological Sciences* 287:20192628.
- Menge, B. A., and J. P. Sutherland. 1987. Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment. *The American Naturalist* 130:730–757.
- Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132:87–106.
- Mouchet, M. A., S. Villéger, N. W. H. Mason, and D. Mouillot. 2010. Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24:867–876.
- Mouillot, D., N. A. J. Graham, S. Villéger, N. W. H. Mason, and D. R. Bellwood. 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28:167–177.
- Mukherjee, S., M. R. Heithaus, J. C. Trexler, J. Ray-Mukherjee, and J. Vaudo. 2014. Perceived risk of predation affects reproductive life-history traits in *Gambusia holbrooki*, but not in *Heterandria formosa*. *PLoS ONE* 9:e88832.

- Muscarella, R., and M. Uriarte. 2016. Do community-weighted mean functional traits reflect optimal strategies? *Proceedings of the Royal Society B: Biological Sciences* 283:20152434.
- Muscarella, R., M. Uriarte, T. M. Aide, D. L. Erickson, J. Forero-Montaña, W. J. Kress, N. G. Swenson, and J. K. Zimmerman. 2016. Functional convergence and phylogenetic divergence during secondary succession of subtropical wet forests in Puerto Rico. *Journal of Vegetation Science* 27:283–294.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Newcomer, K., B. M. Tracy, A. L. Chang, and G. M. Ruiz. 2019. Evaluating performance of photographs for marine citizen science applications. *Frontiers in Marine Science* 6:1–11.
- Nogueira, C., A. Nunes, M. N. Bugalho, C. Branquinho, R. L. McCulley, and M. C. Caldeira. 2018. Nutrient addition and drought interact to change the structure and decrease the functional diversity of a mediterranean grassland. *Frontiers in Ecology and Evolution* 6.
- Nyström, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology & Evolution* 15:413–417.
- Obertegger, U., and G. Flaim. 2015. Community assembly of rotifers based on morphological traits. *Hydrobiologia* 753:31–45.

- Palmer, A. R., J. Szymanska, and L. Thomas. 1982. Prolonged withdrawal: A possible predator evasion behavior in *Balanus glandula* (Crustacea: Cirripedia). *Marine Biology* 67:51–55.
- Palmer, M. A., J. D. Allan, and C. A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends in Ecology & Evolution* 11:322–326.
- Pearson, D. E., Y. K. Ortega, Ö. Eren, and J. L. Hierro. 2018. Community Assembly Theory as a Framework for Biological Invasions. *Trends in Ecology & Evolution* 33:313–325.
- Peralta, A. M. L., A. M. Sánchez, A. L. Luzuriaga, F. Bello, and A. Escudero. 2019. Evidence of functional species sorting by rainfall and biotic interactions: A community monolith experimental approach. *Journal of Ecology* 107:2772–2788.
- Priori, C., F. Erra, M. Angiolillo, and G. Santangelo. 2015. Effects of gastropod predation on the reproductive output of an overexploited deep octocoral. *Coral Reefs* 34:59–63.
- R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, Austria.
- Reed, D. C., J. C. Nelson, S. L. Harrer, and R. J. Miller. 2016. Estimating biomass of benthic kelp forest invertebrates from body size and percent cover data. *Marine Biology* 163:1–11.
- Reynolds, P. L., J. J. Stachowicz, K. Hovel, C. Boström, K. Boyer, M. Cusson, J. S. Eklöf, F. G. Engel, A. H. Engelen, B. K. Eriksson, F. J. Fodrie, J. N. Griffin, C. M.

- Hereu, M. Hori, T. C. Hanley, M. Ivanov, P. Jorgensen, C. Kruschel, K.-S. Lee, K. McGlathery, P.-O. Moksnes, M. Nakaoka, M. I. O'Connor, N. E. O'Connor, R. J. Orth, F. Rossi, J. Ruesink, E. E. Sotka, J. Thormar, F. Tomas, R. K. F. Unsworth, M. A. Whalen, and J. E. Duffy. 2018. Latitude, temperature, and habitat complexity predict predation pressure in eelgrass beds across the Northern Hemisphere. *Ecology* 99:29–35.
- Riisgård, H., and P. Larsen. 2010. Particle capture mechanisms in suspension-feeding invertebrates. *Marine Ecology Progress Series* 418:255–293.
- Ritson-Williams, R., and V. J. Paul. 2007. Marine benthic invertebrates use multimodal cues for defense against reef fish. *Marine Ecology Progress Series* 340:29–39.
- Rodman, K. C., T. T. Veblen, R. A. Andrus, N. J. Enright, J. B. Fontaine, A. D. Gonzalez, M. D. Redmond, and A. P. Wion. 2020. A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. *Journal of Ecology*:1365-2745.13480.
- Roslin, T., N. R. Andrew, A. Asmus, I. C. Barrio, Y. Basset, and E. Al. 2017. Higher predation risk for insect prey at low latitudes and elevations. *Science* 356:742–744.
- Ruiz, G. M., P. W. Fofonoff, J. T. Carlton, M. J. Wonham, and A. H. Hines. 2000. Invasion of Coastal Marine Communities in North America: Apparent Patterns, Processes, and Biases. *Annual Review of Ecology and Systematics* 31:481–531.

- Ruiz, G. M., A. L. Freestone, P. W. Fofonoff, and C. Simkanin. 2009. Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. Pages 321–333 *Marine Hard Bottom Communities: Patterns, Scales, Dynamics, Functions, and Shifts*.
- Sams, M., F. Warren-Myers, and M. Keough. 2015. Increased larval planktonic duration and post-recruitment competition influence survival and growth of the bryozoan *Watersipora subtorquata*. *Marine Ecology Progress Series* 531:179–191.
- Sasaki, T., S. Okubo, T. Okayasu, U. Jamsran, T. Ohkuro, and K. Takeuchi. 2009. Two-phase functional redundancy in plant communities along a grazing gradient in Mongolian rangelands. *Ecology* 90:2598–2608.
- Schamp, B. S., and L. W. Aarssen. 2009. The assembly of forest communities according to maximum species height along resource and disturbance gradients. *Oikos* 118:564–572.
- Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics* 40:245–269.
- Sebens, K. P. 1982. Competition for Space: Growth Rate, Reproductive Output, and Escape in Size. *The American Naturalist* 120:189–197.
- Seifan, M., T. Seifan, K. Schiffers, F. Jeltsch, and K. Tielbörger. 2013. Beyond the Competition-Colonization Trade-Off: Linking Multiple Trait Response to Disturbance Characteristics. *The American Naturalist* 181:151–160.

- Shea, K. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17:170–176.
- Soininen, J. 2010. Species Turnover along Abiotic and Biotic Gradients: Patterns in Space Equal Patterns in Time? *BioScience* 60:433–439.
- Sousa, W. P. 1984. The Role of Disturbance in Natural Communities. *Annual Review of Ecology and Systematics* 15:353–391.
- Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology* 100:652–661.
- Spasojevic, M. J., E. A. Yablon, B. Oberle, and J. A. Myers. 2014. Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere* 5:art129.
- Stark, J. S., S. L. Kim, and J. S. Oliver. 2014. Anthropogenic Disturbance and Biodiversity of Marine Benthic Communities in Antarctica: A Regional Comparison. *PLoS ONE* 9:e98802.
- Stevens, R. D., S. B. Cox, R. E. Strauss, and M. R. Willig. 2003. Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters* 6:1099–1108.
- Stocker, L. J., and A. J. Underwood. 1991. The relationship between the presence of neighbours and rates of sexual and asexual reproduction in a colonial invertebrate. *Journal of Experimental Marine Biology and Ecology* 149:191–205.

- Stoecker, D. 1980. Chemical defenses of ascidians against predators. *Ecology* 61:1327–1334.
- Stokes, C. J., and S. R. Archer. 2010. Niche differentiation and neutral theory: an integrated perspective on shrub assemblages in a parkland savanna. *Ecology* 91:1152–1162.
- Svensson, J. R., and D. J. Marshall. 2015. Limiting resources in sessile systems: Food enhances diversity and growth of suspension feeders despite available space. *Ecology* 96:819–827.
- Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94:451–459.
- Swenson, N. G., B. J. Enquist, J. Pither, A. J. Kerkhoff, B. Boyle, M. D. Weiser, J. J. Elser, W. F. Fagan, J. Forero-Montaña, N. Fyllas, N. J. B. Kraft, J. K. Lake, A. T. Moles, S. Patiño, O. L. Phillips, C. A. Price, P. B. Reich, C. A. Quesada, J. C. Stegen, R. Valencia, I. J. Wright, S. J. Wright, S. Andelman, P. M. Jørgensen, T. E. Lacher Jr, A. Monteagudo, M. P. Núñez-Vargas, R. Vasquez-Martínez, and K. M. Nolting. 2012. The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* 21:798–808.
- Tarjuelo, I., S. López-Legentil, M. Codina, and X. Turon. 2002. Defence mechanisms of adults and larvae of colonial ascidians: Patterns of palatability and toxicity. *Marine Ecology Progress Series* 235:103–115.

- Thompson, M., D. Marshall, and K. Monro. 2015. Non-contact competition in a sessile marine invertebrate: causes and consequences. *Marine Ecology Progress Series* 522:115–125.
- Thresher, R. 2009. Environmental and compositional correlates of growth rate in deep-water bamboo corals (Gorgonacea; Isididae). *Marine Ecology Progress Series* 397:187–196.
- Tomas, F., B. Martínez-Crego, G. Hernán, and R. Santos. 2015. Responses of seagrass to anthropogenic and natural disturbances do not equally translate to its consumers. *Global Change Biology* 21:4021–4030.
- Vance, R. R. 1973. On Reproductive Strategies in Marine Benthic Invertebrates. *The American Naturalist* 107:339–352.
- Vázquez, R. I., J. Rodríguez, L. A. Abitia, and F. Galván. 2008. Food habits of the yellow snapper *Lutjanus argentiventris* (Peters, 1869) (Percoidei: Lutjanidae) in La Paz Bay, Mexico. *Revista de biología marina y oceanografía* 43:295–302.
- Verhoeven, K. J., A. Biere, J. A. Harvey, and W. H. van der Putten. 2009. Plant invaders and their novel natural enemies : who is naive? *Ecology letters* 12:107–117.
- Verling, E., G. M. Ruiz, L. D. Smith, B. Galil, A. W. Miller, and K. R. Murphy. 2005. Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 272:1249–1257.

- Vesk, P. A., M. R. Leishman, and M. Westoby. 2004. Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology* 41:22–31.
- Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Wang, Y., U. Naumann, S. T. Wright, and D. I. Warton. 2012. mvabund - an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution* 3:471–474.
- Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. LeRoy Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* 13:267–283.
- Weigel, B., T. Blenckner, and E. Bonsdorff. 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos* 125:1421–1433.
- Wicksten, M. K. 1989. Why are there bright colors in sessile marine invertebrates? *Bulletin of Marine Science* 45:519–530.
- Widbom, B. 1984. Determination of average individual dry weights and ash-free dry weights in different sieve fractions of marine meiofauna. *Marine Biology* 84:101–108.

- Wilson, S. K., S. C. Burgess, A. J. Cheal, M. Emslie, R. Fisher, I. Miller, N. V. C. Polunin, and H. P. A. Sweatman. 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* 77:220–228.
- Wong, L., T. N. Grainger, D. Start, and B. Gilbert. 2017. An invasive herbivore structures plant competitive dynamics. *Biology Letters* 13:20170374.
- Zhang, H., H. Y. H. Chen, J. Lian, R. John, L. Ronghua, H. Liu, W. Ye, F. Berninger, and Q. Ye. 2018. Using functional trait diversity patterns to disentangle the scale-dependent ecological processes in a subtropical forest. *Functional Ecology* 32:1379–1389.

APPENDIX

List of sources of traits gathered from literature.

TRAIT	REFERENCE
Asexual reproduction	AquaNIS. Editorial Board, 2015. Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. www.corpi.ku.lt/databases/aquanis . Version 2.36+
Asexual reproduction	Carson, H. S., & Hentschel, B. T. (2006). Estimating the dispersal potential of polychaete species in the Southern California Bight: Implications for designing marine reserves. <i>Marine Ecology Progress Series</i> , 316, 105–113. https://doi.org/10.3354/meps316105
Asexual reproduction	Dixon, D. R. (1981). Reproductive biology of the serpulid <i>Ficopomatus (Mercierella) enigmaticus</i> in the Thames Estuary, S.E. England. <i>Journal of the Marine Biological Association of the United Kingdom</i> , 61(03), 805. https://doi.org/10.1017/S0025315400048220
Asexual reproduction	Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). National Exotic Marine and Estuarine Species Information System.
Asexual reproduction	Gili, J.-M., & Hughes, R. G. (1995). The ecology of marine benthic hydroids. <i>Oceanography and Marine Biology: An Annual Review</i> , 33, 351–426.
Asexual reproduction	Lee II, H. and Reusser, D. A., 2012. Atlas of Nonindigenous Marine and Estuarine Species in the North Pacific. Office of Research and Development, National Health and Environmental Effects Research Laboratory, EPA/600/R/12/631.
Asexual reproduction	Nishi, E. (1993). Notes on Reproductive Biology of Some Serpulid Polychaetes at Sesoko Island, Okinawa, with Brief Accounts of Setal Morphology of Three Species of <i>Salmacina</i> and <i>Filograna implexa</i> . <i>Marine Fouling</i> , 10(1), 11–16. https://doi.org/10.4282/sosj1979.10.11
Asexual reproduction	Prentiss, N. K., Tyler, M. S., & Dean, D. (2017). A morphological and histological investigation of the regeneration in <i>Myxicola infundibulum</i> (Montagu, 1808) (Sabellida, Annelida). <i>Journal of the Marine Biological Association of the United Kingdom</i> , 97(5), 1155–1165. https://doi.org/10.1017/S0025315417000248
Asexual reproduction	Obenat, S. M., & Pezzani, S. E. (2006). Life Cycle and Population Structure of the Polychaete <i>Ficopomatus enigmaticus</i> (Serpulidae) in Mar Chiquita Coastal Lagoon, Argentina.
Asexual reproduction	Rouse, G., & Pleijel, F. (2001). <i>Polychaetes</i> . Oxford University Press.
Asexual reproduction	Ten Hove, H. A., & Kupriyanova, E. K. (2009). Taxonomy of serpulidae (annelida, polychaeta): The state of affairs. In <i>Zootaxa</i> .
Asexual reproduction	Tovar-Hernández, M. A., Yáñez-Rivera, B., & Bortolini-Rosales, J. L. (2011). Reproduction of the invasive fan worm

	Branchiomma bairdi (Polychaeta: Sabellidae). <i>Marine Biology Research</i> , 7(7), 710–718. https://doi.org/10.1080/17451000.2010.547201
Asexual reproduction	Tovar-Hernández, M. A., & Dean, H. (2014). A new gregarious sabellid worm from the Gulf of California reproducing by spontaneous fission (Polychaeta, Sabellidae). <i>Journal of the Marine Biological Association of the United Kingdom</i> , 94(5), 935–946. https://doi.org/10.1017/S0025315414000186
Egg size	Abdelsalam, K. (2017). Fouling bryozoan fauna from Hurghada, Red Sea, Egypt. I. Erect species. <i>International Journal of Environmental Science and Engineering</i> , Vol. 7, 59–70.
Egg size	Adiyodi, K. G., & Adiyodi, R. G. (1983). Reproductive biology of invertebrates. In <i>Spermatogenesis and Sperm Function</i> (Vol. 2).
Egg size	Allen, M. J. (1957). The breeding of polychaetous annelids near Parguera, Puerto Rico. <i>The Biological Bulletin</i> , 113(1), 49–57. https://doi.org/10.2307/1538801
Egg size	Barnes, H., & Barnes, M. (1956). The general biology of Balanus glandula Darwin. <i>Pacific Sciences</i> , 10(1930), 415–421.
Egg size	Barnes, H., & Barnes, M. (1977). Studies on the reproduction of cirripedes. I. Introduction: Copulation, release of oocytes, and formation of the egg lamellae. <i>Journal of Experimental Marine Biology and Ecology</i> , 27(3), 195–218. https://doi.org/10.1016/0022-0981(77)90124-1
Egg size	Berrill, N. J. (1932). Ascidians of the Bermudas. <i>The Biological Bulletin</i> , 62(1), 77–88. https://doi.org/10.2307/1537145
Egg size	Bingham, B. L. (1997). Light Cycles and Gametogenesis in Three Temperate Ascidian Species. <i>Invertebrate Biology</i> , 116(1), 61. https://doi.org/10.2307/3226925
Egg size	Boero, F., Bucci, C., Colucci, A. M. R., Gravili, C., & Stabili, L. (2007). Obelia (Cnidaria, Hydrozoa, Campanulariidae): A microphagous, filter-feeding medusa. <i>Marine Ecology</i> , 28(SUPPL. 1), 178–183. https://doi.org/10.1111/j.1439-0485.2007.00164.x
Egg size	Carver, C. E., Mallet, A. L., & Vercaemer, B. (2006). <i>Biological synopsis of the colonial tunicates (Botryllus schlosseri and Botrylloides violaceus)</i> . Retrieved from http://www.dfo-mpo.gc.ca/Library/325201.pdf
Egg size	Dionisio, M., Rodrigues, A., & Costa, A. (2007). Reproductive biology of Megabalanus azoricus (Pilsbry), the Azorean Barnacle. <i>Invertebrate Reproduction & Development</i> , 50(3), 155–162. https://doi.org/10.1080/07924259.2007.9652240
Egg size	Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). National Exotic Marine and Estuarine Species Information System.
Egg size	Fukumoto, M. (1993). Morphological aspects of fertilization in Phallusia (Ascidia) nigra (Ascidacea, Tunicata). <i>Roux's Archives of</i>

	<i>Developmental Biology</i> , 202(6), 321–328. https://doi.org/10.1007/BF00188731
Egg size	Gambi, M., Patti, F., Micaletto, G., & Giangrande, A. (2001). Diversity of reproductive features in some Antarctic polynoid and sabellid polychaetes, with a description of <i>Demonax polarsterni</i> sp. n. (Polychaeta, Sabellidae). <i>Polar Biology</i> , 24(12), 883–891. https://doi.org/10.1007/s003000100287
Egg size	Gotelli, N. J. (1987). Spatial and temporal patterns of reproduction, larval settlement, and recruitment of the compound ascidian <i>Aplidium stellatum</i> . <i>Marine Biology</i> , 94(1), 45–51. https://doi.org/10.1007/BF00392899
Egg size	Harmer, S. F. (1898). On the development of <i>Tubulipora</i> , and some British and northern species of this genus. <i>The Quarterly Journal of Microscopical Science</i> , 41, 73–157.
Egg size	Haven, N. D. (1971). Temporal patterns of sexual and asexual reproduction in the colonial ascidian <i>metandrocarpa taylori</i> huntsman. <i>The Biological Bulletin</i> , 140(3), 400–415. https://doi.org/10.2307/1540277
Egg size	Herz, L. E. (1933). The morphology of the later stages of <i>Balanus crenatus</i> Bruguiere. <i>The Biological Bulletin</i> , 64(3), 432–442. https://doi.org/10.2307/1537209
Egg size	Hikosaka, A., Satoh, N., & Makabe, K. W. (1993). Regulated spatial expression of fusion gene constructs with the 5' upstream region of <i>Halocynthia roretzi</i> muscle actin gene in <i>Ciona savignyi</i> embryos. <i>Roux's Archives of Developmental Biology</i> , 203(1–2), 104–112. https://doi.org/10.1007/BF00539896
Egg size	Jeffery, W. R. (2006). Ascidian neural crest-like cells: phylogenetic distribution, relationship to larval complexity, and pigment cell fate. <i>Journal of Experimental Zoology Part B: Molecular and Developmental Evolution</i> , 306B(5), 470–480. https://doi.org/10.1002/jez.b.21109
Egg size	Kupriyanova, E. K., Nishi, E., Ten Hove, H. A., & Rzhavsky, A. V. (2001). Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. <i>Oceanography and Marine Biology: An Annual Review</i> , 39, 1–101.
Egg size	Lauzier, R. B., & Parker, G. (1999). <i>A Review of the Biology and Fisheries of the Pink Scallop and Spiny Scallop</i> . Ottawa.
Egg size	Loosanoff, V. L., & Davis, H. C. (1963). Rearing of Bivalve Mollusks. <i>Advances in Marine Biology</i> , 1, 1–136. https://doi.org/10.1016/S0065-2881(08)60257-6
Egg size	Manni, L., Zaniolo, G., & Burighel, P. (1993). Egg Envelope Cytodifferentiation in the Colonial Ascidian <i>Botryllus schlosseri</i> (Tunicata). <i>Acta Zoologica</i> , 74(2), 103–113. https://doi.org/10.1111/j.1463-6395.1993.tb01226.x

Egg size	Marine Life Information Network. (2006). BIOTIC - Biological traits information catalogue. Retrieved January 1, 2019, from www.marlin.ac.uk/biotic
Egg size	Ostrovsky, A. (2013). <i>Evolution of Sexual Reproduction in Marine Invertebrates</i> . https://doi.org/10.1007/978-94-007-7146-8
Egg size	Ostrovsky, A. N., Grischenko, A. V., Taylor, P. D., Bock, P., & Mawatari, S. F. (2006). Comparative anatomical study of internal brooding in three anascan bryozoans (Cheilostomata) and its taxonomic and evolutionary implications. <i>Journal of Morphology</i> , 267(6), 739–749. https://doi.org/10.1002/jmor.10438
Egg size	Ostrovsky, A. N., Vávra, N., & Porter, J. S. (2008). Sexual reproduction in gymnolaemate Bryozoa: history and perspectives of the research. <i>Annals of Bryozoology 2: Aspects of the History of Research on Bryozoans</i> , (January), 117–210. Retrieved from http://zoology.bio.spbu.ru/Articles/2008/Ostrovsky_etal_2008_An_Bryo.pdf
Egg size	Pasqua, M. Del, Lezzi, M., Licciano, M., & Giangrande, A. (2017). Larval development and post-larval growth of <i>Branchiommabairdi</i> (Annelida: Sabellidae) from a Mediterranean population. <i>Invertebrate Biology</i> . https://doi.org/10.1111/ivb.12171
Egg size	Pernet, B., & Jaekle, W. B. (2004). Size and Organic Content of Eggs of Marine Annelids, and the Underestimation of Egg Energy Content by Dichromate Oxidation. <i>The Biological Bulletin</i> , 207(1), 67–71. https://doi.org/10.2307/1543629
Egg size	Prodon, F., Chenevert, J., & Sardet, C. (2006). Establishment of animal–vegetal polarity during maturation in ascidian oocytes. <i>Developmental Biology</i> , 290(2), 297–311. https://doi.org/10.1016/j.ydbio.2005.11.025
Egg size	Raijman Nagar, L., & Shenkar, N. (2016). From Tropical to Sub-Tropical: Prolonged Reproductive Activity of the Invasive Ascidian <i>Microcosmus exasperatus</i> in the Eastern Mediterranean. <i>Frontiers in Ecology and Evolution</i> , 4(August), 1–11. https://doi.org/10.3389/fevo.2016.00102
Egg size	Reverberi, G. (1971). <i>Experimental Embryology of Marine and Fresh-Water Invertebrates</i> . Amsterdam: North-Holland Pub. Co.
Egg size	Ritter, W. E. (1905). <i>The pelagic Tunicata of the San Diego region, excepting the Larvacea</i> (p. p.[51]-112). p. p.[51]-112. Retrieved from file://catalog.hathitrust.org/Record/100446798
Egg size	Ryland, J. (1974). Behaviour, settlement and metamorphosis of bryozoan larvae: A review. In <i>Thalassia Jugosl</i> (Vol. 10).
Egg size	Ryland, J. S. (1977). Physiology and Ecology of Marine Bryozoans. In <i>Advances in Marine Biology</i> (Vol. 14, pp. 285–443). https://doi.org/10.1016/S0065-2881(08)60449-6

Egg size	Sahade, R., Tatián, M., & Esnal, G. (2004). Reproductive ecology of the ascidian <i>Cnemidocarpa verrucosa</i> at Potter Cove, South Shetland Islands, Antarctica. <i>Marine Ecology Progress Series</i> , 272(May), 131–140. https://doi.org/10.3354/meps272131
Egg size	Saito, Y., & Nagasawa, N. (2003). Studies on Japanese Botryllid Ascidiates. III. A New Species of the Genus Botryllus with a Vivid Colony Color from the Vicinity of Shimoda. <i>Zoological Science</i> , 20(6), 765–771. https://doi.org/10.2108/zsj.20.765
Egg size	Stenyakina, A., Walters, L. J., Hoffman, E. A., & Calestani, C. (2009). Food availability and sex reversal in <i>Mytella charruana</i> , an introduced bivalve in the southeastern United States. <i>Molecular Reproduction and Development</i> , 77, 222–230. https://doi.org/10.1002/mrd.21132
Egg size	Strathmann, M. F. (1987). <i>Reproduction and development of marine invertebrates of the northern Pacific coast: Data and methods for the study of eggs, embryos, and larvae</i> . (U. of W. Press, Ed.). Seattle: University of Washington Press.
Egg size	Sugimoto, K., & Nakauchi, M. (1974). Budding, Sexual Reproduction, And Degeneration In The Colonial Ascidian, <i>Symplegma Reptans</i> . <i>The Biological Bulletin</i> , 147(1), 213–226. https://doi.org/10.2307/1540579
Egg size	Terlizzi, A., Conte, E., & Giangrande, A. (2000). Settlement patterns of two Spirobridae (Annelida, Polychaeta) species in the harbour of Ischia (Gulf of Naples, Mediterranean Sea). <i>Italian Journal of Zoology</i> , 67(3), 303–306. https://doi.org/10.1080/11250000009356328
Egg size	Tovar-Hernández, M. A., & Dean, H. (2014). A new gregarious sabellid worm from the Gulf of California reproducing by spontaneous fission (Polychaeta, Sabellidae). <i>Journal of the Marine Biological Association of the United Kingdom</i> , 94(5), 935–946. https://doi.org/10.1017/S0025315414000186
Egg size	Tovar-Hernández, M. A., Méndez, N., & Villalobos-Guerrero, T. F. (2009). Fouling polychaete worms from the Southern Gulf of California: Sabellidae and Serpulidae. <i>Systematics and Biodiversity</i> , 7(3), 319–336. https://doi.org/10.1017/S147200009990041
Egg size	Wong, N. A., McClary, D., & Sewell, M. A. (2011). The reproductive ecology of the invasive ascidian, <i>Styela clava</i> , in Auckland Harbour, New Zealand. <i>Marine Biology</i> , 158(12), 2775–2785. https://doi.org/10.1007/s00227-011-1776-6
Eggs per adult	Tarjuelo, I., & Turon, X. (2004). Resource Allocation in Ascidiates : Reproductive Investment vs . Other Life-History Traits. <i>Invertebrate Biology</i> , 123(2), 168–180
Eggs per adult	Carver, C., Chisholm, A., & Mallet, A. (2003). Strategies to mitigate the impact of <i>Ciona intestinalis</i> (L.) biofouling on shellfish production. In <i>Journal of Shellfish Research</i> (Vol. 22).

Eggs per adult	Chadwick-Furman, N. E., & Weissman, I. L. (1995). Life Histories and Senescence of <i>Botryllus schlosseri</i> (Chordata, Ascidiacea) in Monterey Bay. <i>The Biological Bulletin</i> , 189(1), 36–41. doi: 10.2307/1542199
Eggs per adult	Costlow, J. D., & Bookhout, C. G. (1957). Body growth versus shell growth in <i>Balanus improvisus</i> . <i>The Biological Bulletin</i> , 113(2), 224–232. doi: 10.2307/1539080
Eggs per adult	Dionisio, M., Rodrigues, A., & Costa, A. (2007). Reproductive biology of <i>Megabalanus azoricus</i> (Pilsbry), the Azorean Barnacle. <i>Invertebrate Reproduction & Development</i> , 50(3), 155–162. doi: 10.1080/07924259.2007.9652240
Eggs per adult	Dyrynda, P. E. J., & King, P. E. (1982). Sexual reproduction in <i>Epistomia bursaria</i> (Bryozoa: Cheilostomata), an endozooidal brooder without polypide recycling. <i>Journal of Zoology</i> , 198(3), 337–352. doi: 10.1111/j.1469-7998.1982.tb02080.x
Eggs per adult	Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). National Exotic Marine and Estuarine Species Information System.
Eggs per adult	Gosling, E., & Gosling, E. M. (1992). <i>The Mussel Mytilus: Ecology, Physiology, Genetics, and Culture</i> . Retrieved from https://books.google.com/books?id=0VEYAQAIAAJ
Eggs per adult	Gotelli, N. J. (1987). Spatial and temporal patterns of reproduction, larval settlement, and recruitment of the compound ascidian <i>Aplidium stellatum</i> . <i>Marine Biology</i> , 94(1), 45–51. doi: 10.1007/BF00392899
Eggs per adult	Harris, V. A. (1990). <i>Sessile Animals of the Sea Shore</i> . London: Chapman and Hall.
Eggs per adult	Haven, N. D. (1971). Temporal patterns of sexual and asexual reproduction in the colonial ascidian <i>metandrocarpa taylori</i> huntsman. <i>The Biological Bulletin</i> , 140(3), 400–415. doi: 10.2307/1540277
Eggs per adult	Hirose, E., Adachi, R., & Kuze, K. (2006). Sexual reproduction of the Prochloron-bearing ascidians, <i>Trididemnum cyclops</i> and <i>Lissoclinum bistratum</i> , in subtropical waters: seasonality and vertical transmission of photosymbionts. <i>Journal of the Marine Biological Association of the United Kingdom</i> , 86(1), 175–179. doi: 10.1017/S0025315406013002
Eggs per adult	Karande, A. A., & Udhayakumar, M. (1992). Consequences of crowding on life-histories of cheilostome bryozoans in Bombay waters. In <i>Indian Journal of Marine Sciences</i> (Vol. 21).
Eggs per adult	Kupriyanova, E. K., Nishi, E., Ten Hove, H. A., & Rzhavsky, A. V. (2001). Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. <i>Oceanography and Marine Biology: An Annual Review</i> , 39, 1–101.

Eggs per adult	Litulo, C. (2007). Distribution, abundance and reproduction of the Indo-Pacific acorn barnacle <i>Balanus amphitrite</i> (Crustacea: Cirripedia). <i>Journal of the Marine Biological Association of the United Kingdom</i> , 87(3), 723–727. doi: 10.1017/S0025315407052757
Eggs per adult	MarLIN. (2006). BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Retrieved from %3Cwww.marlin.ac.uk/biotic%3E
Eggs per adult	Monniot, F., & Monniot, C. (2001). Ascidians from the tropical western Pacific. <i>Zoosystema</i> , 23(2), 201–383. Retrieved from www.mnhn.fr/publication/
Eggs per adult	Mukai, H., Koyama, H., & Watanabe, H. (1983). Studies on the reproduction of three species of perophora (ascidiacea). <i>The Biological Bulletin</i> , 164(2), 251–266. doi: 10.2307/1541143
Eggs per adult	Nielsen, C. (1981). On morphology and reproduction of ‘Hippodiplosia’ insculpta and Fenestulina malusii (Bryozoa, Cheilostomata). <i>Ophelia</i> , 20(1), 91–125. doi: 10.1080/00785236.1981.10426564
Eggs per adult	Ostrovsky, A. (2013). <i>Evolution of Sexual Reproduction in Marine Invertebrates</i> . doi: 10.1007/978-94-007-7146-8
Eggs per adult	Ostrovsky, A. N. (1998). Comparative Studies of Ovicell Anatomy and Reproductive Patterns in Cribrilina annulata and Celleporella hyalina (Bryozoa: Cheilostomatida). <i>Acta Zoologica</i> , 79(4), 287–318. doi: 10.1111/j.1463-6395.1998.tb01280.x
Eggs per adult	Ostrovsky, A. N., Vávra, N., & Porter, J. S. (2008). Sexual reproduction in gymnolaemate Bryozoa: history and perspectives of the research. <i>Annals of Bryozoology 2: Aspects of the History of Research on Bryozoans</i> , (January), 117–210. Retrieved from http://zoology.bio.spbu.ru/Articles/2008/Ostrovsky_etal_2008_An_Bryo.pdf
Eggs per adult	Pritchard, C., Shanks, A., Rimler, R., Oates, M., & Rumrill, S. (2015). The Olympia Oyster <i>Ostrea lurida</i> : Recent Advances in Natural History, Ecology, and Restoration . <i>Journal of Shellfish Research</i> , 34(2), 259–271. doi: 10.2983/035.034.0207
Eggs per adult	Ritter, W. E., & Forsyth, R. A. (1917). <i>Ascidians of the littoral zone of southern California</i> . [S.l.: University of California.
Eggs per adult	Rocha, Rosana M, & Costa, L. V. G. (2005). Ascidians (Urochordata: Ascidiacea) from Arraial do Cabo, Rio de Janeiro, Brazil. <i>Iheringia. Série Zoologia</i> , 95(1), 57–64. doi: 10.1590/S0073-47212005000100009
Eggs per adult	Rocha, Rosana Moreira da, & Faria, S. B. De. (2005). Ascidians at Currais islands, Paraná, Brazil: taxonomy and distribution. <i>Biota Neotropica</i> , 5(2), 167–186. doi: 10.1590/S1676-06032005000300013

Eggs per adult	Rouse, G., & Fitzhugh, K. (1994). Broadcasting fables: Is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. <i>Zoologica Scripta</i> , 23(4), 271–312. doi: 10.1111/j.1463-6409.1994.tb00390.x
Eggs per adult	Ryland, J. S. (1970). <i>Bryozoans</i> . London: Hutchinson.
Eggs per adult	Saito, Y., Mukai, H., & Watanabe, H. (1981). Studies of Japanese compound styelid ascidians. Two new species of botryllus from the vicinity of Shimoda. <i>Publications of the Seto Marine Biological Laboratory</i> , 26, 347–355.
Eggs per adult	Strathmann, M. F. (1987). <i>Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast</i> . Retrieved from http://www.jstor.org/stable/j.ctvcwnh8b
Eggs per adult	Sugimoto, K., & Nakauchi, M. (1974). Budding, Sexual Reproduction, and Degeneration in the Colonial Ascidian, <i>Symplegma Reptans</i> . <i>The Biological Bulletin</i> , 147(1), 213–226. doi: 10.2307/1540579
Eggs per adult	Svane, I., & Lundälv, T. (1981). Reproductive patterns and population dynamics of <i>Ascidia mentula</i> O.F. Müller on the Swedish west coast. <i>Journal of Experimental Marine Biology and Ecology</i> , 50(2–3), 163–182. doi: 10.1016/0022-0981(81)90048-4
Eggs per adult	Terlizzi, A., Conte, E., & Giangrande, A. (2000). Settlement patterns of two spirorbidae (annelida, polychaeta) species in the harbour of Ischia (Gulf of Naples, Mediterranean Sea). <i>Italian Journal of Zoology</i> , 67(3), 303–306. doi: 10.1080/11250000009356328
Eggs per adult	Tovar-Hernández, M. A., Yáñez-Rivera, B., & Bortolini-Rosales, J. L. (2011). Reproduction of the invasive fan worm <i>Branchiomma bairdi</i> (Polychaeta: Sabellidae). <i>Marine Biology Research</i> , 7(7), 710–718. doi: 10.1080/17451000.2010.547201
Eggs per adult	Vieira, L. M., Jones, M. E. S., & Winston, J. E. (2013). <i>Cradoscrupocellaria</i> , a new bryozoan genus for <i>Scrupocellaria bertholletii</i> (Audouin) and related species (Cheilostomata, Candidae): taxonomy, biodiversity and distribution. <i>Zootaxa</i> , 3707(1), 1. doi: 10.11646/zootaxa.3707.1.1
Eggs per adult	Woollacott, R. M., & Zimmer, R. L. (1977). <i>Biology of Bryozoans</i> . doi: 10.1016/C2013-0-07654-2
Fertilization type	Cadman, P. S., & Ryland, J. S. (1996). Redescription of <i>Alcyonidium mytili</i> Dalyell, 1848 (Bryozoa: Ctenostomatida). <i>Zoological Journal of the Linnean Society</i> , 116(4), 437–450.
Fertilization type	Lutz, R.A. & Kennish, M.J., 1992. Ecology and morphology of larval and early larval postlarval mussels. In <i>The mussel Mytilus: ecology, physiology, genetics and culture</i> , (ed. E.M. Gosling), pp. 53-85. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25]
Fertilization type	Nielsen, C. 1985. Ovicell formation in <i>Tegella</i> and four cellularioids (Bryozoa, Cheilostomata). In: Nielsen, C. & Larwood, G.P.

	(editors), Bryozoa: Ordovician to Recent: 213-220. Olsen & Olsen, Fredensborg.
Fertilization type	Yamaguchi, M. (1975). Growth and reproductive cycles of the marine fouling ascidians <i>Ciona intestinalis</i> , <i>Styela plicata</i> , <i>Botrylloides violaceus</i> , and <i>Leptoclinum mitsukurii</i> at Aburatsubo-Moroiso Inlet (central Japan). <i>Marine Biology</i> , 29(3), 253–259. https://doi.org/10.1007/BF00391851
Fertilization type	Ayling, A. L. (1980). P Patterns of sexuality, asexual reproduction and recruitment in some subtidal marine Demospongiae. <i>The Biological Bulletin</i> , 158(3), 271–282. doi: 10.2307/1540854
Fertilization type	AquaNIS. Editorial Board, 2015. Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. www.corpi.ku.lt/databases/aquanis . Version 2.36+
Fertilization type	Brousseau, D. J. (1984). Reproductive cycle of <i>Anomia simplex</i> (Pelecypoda: Anomiidae) from Cape Cod, Massachusetts. <i>The Veliger</i> , 26(4), 299–304.
Fertilization type	Coe, W. R. (1934). Alternation of Sexuality in Oysters. <i>The American Naturalist</i> , 68(716), 236–251. Retrieved from http://www.jstor.org/stable/2456831
Fertilization type	Dupont, L., Viard, F., Dowell, M. J., Wood, C., & Bishop I, J. D. D. (2009). Fine- and regional-scale genetic structure of the exotic ascidian <i>Styela clava</i> (Tunicata) in southwest England, 50 years after its introduction. <i>Molecular Ecology</i> , 18(3), 442–453. https://doi.org/10.1111/j.1365-294X.2008.04045.x
Fertilization type	Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). National Exotic Marine and Estuarine Species Information System.
Fertilization type	Gordon, D. P. (1993). Bryozoan frontal shields: studies on umbonulomorphs and impacts on classification. <i>Zoologica Scripta</i> , 22(2), 203–221. https://doi.org/10.1111/j.1463-6409.1993.tb00352.x
Fertilization type	Harris, V. A. (1990). <i>Sessile Animals of the Sea Shore</i> . London: Chapman and Hall.
Fertilization type	Kupriyanova, E. K., Nishi, E., Ten Hove, H. A., & Rzhavsky, A. V. (2001). Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. <i>Oceanography and Marine Biology: An Annual Review</i> , 39, 1–101.
Fertilization type	Lambert, C. C., Lambert, I. M., & Lambert, G. (1995). Brooding strategies in solitary ascidians: <i>Corella</i> species from north and south temperate waters. <i>Canadian Journal of Zoology</i> , 73(9), 1666–1671. https://doi.org/10.1139/z95-198
Fertilization type	Lee II, H. and Reusser, D. A., 2012. Atlas of Nonindigenous Marine and Estuarine Species in the North Pacific. Office of Research and Development, National Health and Environmental Effects Research Laboratory, EPA/600/R/12/631.

Fertilization type	López-Gappa, J., & Liuzzi, M. G. (2016). High density of the alien bryozoan <i>Fenestrulina delicia</i> in the fouling assemblage of a South American harbour (Argentina). <i>Marine Biodiversity</i> , 46(2), 509–513. https://doi.org/10.1007/s12526-015-0380-2
Fertilization type	Marine Life Information Network. (2006). BIOTIC - Biological traits information catalogue. Retrieved January 1, 2019, from www.marlin.ac.uk/biotic
Fertilization type	Micael, J., Gillon, A., Jardim, N., Rodrigues, P., & Costa, A. C. (2018). Sexual reproduction in the invasive bryozoan <i>Amathia verticillata</i> (Ctenostomatida: Vesiculariidae). <i>Journal of Coastal Conservation</i> , 22(2), 305–314. https://doi.org/10.1007/s11852-017-0577-6
Fertilization type	Ostrovsky, A. (2013). <i>Evolution of Sexual Reproduction in Marine Invertebrates</i> . https://doi.org/10.1007/978-94-007-7146-8
Fertilization type	Ostrovsky, A. N., Nielsen, C., Vávra, N., & Yagunova, E. B. (2009). Diversity of brood chambers in calloporid bryozoans (Gymnolaemata, Cheilostomata): comparative anatomy and evolutionary trends. <i>Zoomorphology</i> , 128(1), 13–35. https://doi.org/10.1007/s00435-008-0070-8
Fertilization type	Prentiss, N. K., Tyler, M. S., & Dean, D. (2017). A morphological and histological investigation of the regeneration in <i>Myxicola infundibulum</i> (Montagu, 1808) (Sabellida, Annelida). <i>Journal of the Marine Biological Association of the United Kingdom</i> , 97(5), 1155–1165. https://doi.org/10.1017/S0025315417000248
Fertilization type	Reverberi, G. (1971). <i>Experimental Embryology of Marine and Fresh-Water Invertebrates</i> . Amsterdam: North-Holland Pub. Co.
Fertilization type	Rouse, G., & Fitzhugh, K. (1994). Broadcasting fables: Is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. <i>Zoologica Scripta</i> , 23(4), 271–312. https://doi.org/10.1111/j.1463-6409.1994.tb00390.x
Fertilization type	Rouse, G., & Pleijel, F. (2001). <i>Polychaetes</i> . Oxford University Press.
Fertilization type	Ryland, J. S., & Porter, J. S. (2013). <i>Species of Alcyonidium (Ctenostomatida) from the Pacific Coast of North America: A Preliminary Account</i> . https://doi.org/10.1007/978-3-642-16411-8_19
Fertilization type	Strathmann, M. F. (1987). <i>Reproduction and development of marine invertebrates of the northern Pacific coast: Data and methods for the study of eggs, embryos, and larvae</i> . (U. of W. Press, Ed.). Seattle: University of Washington Press.
Fertilization type	Terlizzi, A., Conte, E., & Giangrande, A. (2000). Settlement patterns of two spirorbidae (annelida, polychaeta) species in the harbour of Ischia (Gulf of Naples, Mediterranean Sea). <i>Italian Journal of Zoology</i> , 67(3), 303–306. https://doi.org/10.1080/11250000009356328
Fertilization type	Tovar-Hernández, M. A., Yáñez-Rivera, B., & Bortolini-Rosales, J. L. (2011). Reproduction of the invasive fan worm

	Branchiomma bairdi (Polychaeta: Sabellidae). <i>Marine Biology Research</i> , 7(7), 710–718. https://doi.org/10.1080/17451000.2010.547201
Fertilization type	Whyte, J. N. C., Bourne, N., Ginther, N. G., & Hodgson, C. A. (1992). Compositional changes in the larva to juvenile development of the scallop <i>Crassadoma gigantea</i> (Gray). <i>Journal of Experimental Marine Biology and Ecology</i> , 163(1), 13–29. https://doi.org/10.1016/0022-0981(92)90144-Y
Fertilization type	Woollacott, R. M., & Zimmer, R. L. (1977). <i>Biology of Bryozoans</i> . https://doi.org/10.1016/C2013-0-07654-2
Fertilization type	Yagunova, E. B., & Ostrovsky, A. N. (2010). The influence of substrate type on sexual reproduction of the bryozoan <i>Cribrilina annulata</i> (Gymnolaemata, Cheilostomata): A case study from Arctic seas. <i>Marine Biology Research</i> , 6(3), 263–270. https://doi.org/10.1080/17451000903147443
Larval development	Zimmer, R. L., & Woollacott, R. M. (1993). Anatomy of the larva of <i>Amathia vidovici</i> (Bryozoa: Ctenostomata) and phylogenetic significance of the vesiculariform larva. <i>Journal of Morphology</i> , 215(1), 1–29. doi: 10.1002/jmor.1052150102
Larval development	AquaNIS. Editorial Board, 2015. Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. www.corpi.ku.lt/databases/aquanis . Version 2.36+
Larval development	Baker, P. (1995). Review Of Ecology And Fishery Of The Olympia Oyster, <i>Ostrea Lurida</i> With Annotated Bibliography. <i>Journal of Shellfish Research</i> , 14(2), 501–518.
Larval development	Bayne, B. L. (1965). Growth and the delay of metamorphosis of the larvae of <i>Mytilus edulis</i> (L.). <i>Ophelia</i> , 2(1), 1–47. doi: 10.1080/00785326.1965.10409596
Larval development	Bertrand, G. A. (1971). The ecology of the nest building bivalve <i>musculus-lateralis</i> commensal with the ascidian <i>molgula-occidentalis</i> . <i>The Veliger</i> , 14, 23–29. Retrieved from https://www.biodiversitylibrary.org/part/93609
Larval development	Carson, H. S., & Hentschel, B. T. (2006). Estimating the dispersal potential of polychaete species in the Southern California Bight: Implications for designing marine reserves. <i>Marine Ecology Progress Series</i> , 316, 105–113. doi: 10.3354/meps316105
Larval development	Cohen, A. N. (2011). The Exotics Guide: Non-native Marine Species of the North American Pacific Coast. Retrieved from http://www.exoticguide.org/
Larval development	COSEWIC. (2011). <i>COSEWIC assessment and status report on the Olympia Oyster <i>Ostrea lurida</i> in Canada</i> . Retrieved from (www.sararegistry.gc.ca/status/status_e.cfm)
Larval development	Davidson, B., Smith Wallace, S. E., Howsmon, R. A., & Swalla, B. J. (2003). A morphological and genetic characterization of

	metamorphosis in the ascidian <i>Boltenia villosa</i> . <i>Development Genes and Evolution</i> , 213(12), 601–611. doi: 10.1007/s00427-003-0363-3
Larval development	Department of Fisheries and Oceans, & Fisheries and Oceans Canada. (2011). <i>Updated framework for the pink and spiny scallop (Chlamys rubida and C. hastata) dive fishery in British Columbia</i> . Retrieved from http://www.dfo-mpo.gc.ca/Library/343819.pdf
Larval development	Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). National Exotic Marine and Estuarine Species Information System. Retrieved January 2, 2019, from http://invasions.si.edu/nemesis/
Larval development	Gambi, M., Patti, F., Micaletto, G., & Giangrande, A. (2001). Diversity of reproductive features in some Antarctic polynoid and sabellid polychaetes, with a description of <i>Demonax polarsterni</i> sp. n. (Polychaeta, Sabellidae). <i>Polar Biology</i> , 24(12), 883–891. doi: 10.1007/s003000100287
Larval development	Gibson, R. N., Barnes, M., & Atkinson, R. J. A. (2001). <i>Oceanography and Marine Biology, An Annual Review</i> . CRC Press.
Larval development	Kupriyanova, E. K., Nishi, E., Ten Hove, H. A., & Rzhavsky, A. V. (2001). Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. <i>Oceanography and Marine Biology: An Annual Review</i> , 39, 1–101.
Larval development	López-Gappa, J., & Liuzzi, M. G. (2016). High density of the alien bryozoan <i>Fenestrulina delicia</i> in the fouling assemblage of a South American harbour (Argentina). <i>Marine Biodiversity</i> , 46(2), 509–513. doi: 10.1007/s12526-015-0380-2
Larval development	Marine Life Information Network. (2006). BIOTIC - Biological traits information catalogue. Retrieved January 1, 2019, from www.marlin.ac.uk/biotic
Larval development	Marsden, J. R. (1987). Coral preference behaviour by planktotrophic larvae of <i>Spirobranchus giganteus corniculatus</i> (Serpulidae: Polychaeta). <i>Coral Reefs</i> , 6(2), 71–74. doi: 10.1007/BF00301376
Larval development	Mastrototaro, F., & Dappiano, M. (2008). New record of the non-indigenous species <i>Microcosmus squamiger</i> (Ascidiacea: Stolidobranchia) in the harbour of Salerno (Tyrrhenian Sea, Italy). <i>Marine Biodiversity Records</i> , 1, e12. doi: 10.1017/S1755267205001247
Larval development	Ostrovsky, A. (2013). <i>Evolution of Sexual Reproduction in Marine Invertebrates</i> . doi: 10.1007/978-94-007-7146-8
Larval development	Parker, T., & Tunnicliffe, V. (1994). Dispersal Strategies of the Biota on an Oceanic Seamount: Implications for Ecology and Biogeography. <i>The Biological Bulletin</i> , 187(3), 336–345. doi: 10.2307/1542290
Larval development	Rouse, G., & Fitzhugh, K. (1994). Broadcasting fables: Is external fertilization really primitive? Sex, size, and larvae in sabellid

	polychaetes. <i>Zoologica Scripta</i> , 23(4), 271–312. doi: 10.1111/j.1463-6409.1994.tb00390.x
Larval development	Ryland, J. S. (1970). <i>Bryozoans</i> . London: Hutchinson.
Larval development	Shanks, A. L., Grantham, B. A., & Carr, M. H. (2003). Propagule Dispersal Distance and the Size and Spacing of Marine Reserves. <i>Ecological Applications</i> , 13(SP1), S159–S169.
Larval development	Strathmann, M. F. (1987). <i>Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast</i> . Retrieved from http://www.jstor.org/stable/j.ctvcwnh8b
Larval development	Tovar-Hernández, M. A., Yáñez-Rivera, B., & Bortolini-Rosales, J. L. (2011). Reproduction of the invasive fan worm <i>Branchiomma bairdi</i> (Polychaeta: Sabellidae). <i>Marine Biology Research</i> , 7(7), 710–718. doi: 10.1080/17451000.2010.547201
Larval development	Woollacott, R. M., & Zimmer, R. L. (1977). <i>Biology of Bryozoans</i> . doi: 10.1016/C2013-0-07654-2
Larval life	Gili, J.-M., & Hughes, R. G. (1995). The ecology of marine benthic hydroids. <i>Oceanography and Marine Biology: An Annual Review</i> , 33, 351–426
Larval life	Scoresby, S., & Graham, E. (2013). <i>Ecology of Australian temperate reefs : the unique South</i> . Collingwood: CSIRO Publishing
Larval life	Karande, A. A., & Udhayakumar, M. (1992). Consequences of crowding on life-histories of cheilostome bryozoans in Bombay waters. In <i>Indian Journal of Marine Sciences</i> (Vol. 21)
Larval life	Allen, R. M., & Marshall, D. J. (2010). The larval legacy: cascading effects of recruit phenotype on post-recruitment interactions. <i>Oikos</i> , 119(12), 1977–1983. doi: 10.1111/j.1600-0706.2010.18682.x
Larval life	Bernstein, B. B., & Jung, N. (1979). Selective Pressures and Coevolution in a Kelp Canopy Community in Southern California. <i>Ecological Monographs</i> , 49(3), 335–355. doi: 10.2307/1942488
Larval life	Berrill, N. J. (1947). The development and growth of <i>Ciona</i> . <i>J. Mar. Biol. Assoc. U. K.</i> , 26, 616–625.
Larval life	Carson, H. S., & Hentschel, B. T. (2006). Estimating the dispersal potential of polychaete species in the Southern California Bight: Implications for designing marine reserves. <i>Marine Ecology Progress Series</i> , 316, 105–113. doi: 10.3354/meps316105
Larval life	Carver, C. E., Mallet, A. L., Vercaemer, B., & Oceanography, B. I. of. (2006). <i>Biological synopsis of the colonial tunicates (Botryllus schlosseri and Botrylloides violaceus)</i> . Retrieved from http://www.dfo-mpo.gc.ca/Library/325201.pdf
Larval life	Child, C. M. (1927). Developmental modification and elimination of the larval stage in the ascidian, <i>Corella willmeriana</i> . <i>Journal of Morphology</i> , 44(3), 467–514. doi: 10.1002/jmor.1050440305

Larval life	Clarke, C. L., & Therriault, T. W. (2007). <i>Biological Synopsis of the Invasive Tunicate Styela clava (Herdman 1881)</i> . Nanaimo.
Larval life	Cook, P. L. (1977). Early colony development in Aetea (Bryozoa). <i>Integrative and Comparative Biology</i> , 17(1), 55–61. doi: 10.1093/icb/17.1.55
Larval life	Davis, A. R., & Butler, A. J. (1989). Direct observations of larval dispersal in the colonial ascidian Podoclavella moluccensis Sluiter: evidence for closed populations. <i>Journal of Experimental Marine Biology and Ecology</i> , 127(2), 189–203. doi: 10.1016/0022-0981(89)90184-6
Larval life	DFO. 2011. Updated framework for the pink and spiny scallop (Chlamys rubida and C. hastata) dive fishery in British Columbia. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2010/078
Larval life	Dias, G. M., & Marshall, D. J. (2010). Does the relationship between offspring size and performance change across the life-history? <i>Oikos</i> , 119(1), 154–162. doi: 10.1111/j.1600-0706.2009.17725.x
Larval life	Dick, M. H., Grischenko, A. V., & Mawatari, S. F. (2005). Intertidal Bryozoa (Cheilostomata) of Ketchikan, Alaska. <i>Journal of Natural History</i> , 39(43), 3687–3784. doi: 10.1080/00222930500415195
Larval life	Dybern, B. I. (1965). The Life Cycle of Ciona intestinalis (L.) f. typica in Relation to the Environmental Temperature. <i>Oikos</i> , 16(1/2), 109. doi: 10.2307/3564870
Larval life	Dyrynda, P. E. J., Fairall, V. R., Occhipinti Ambrogi, A., & D'Hondt, J. L. (2000). The distribution, origins and taxonomy of tricellaria inopinata d'hondt and occhipinti ambrogi, 1985, an invasive bryozoan new to the Atlantic. <i>Journal of Natural History</i> , 34(10), 1993–2006. doi: 10.1080/00222930050144828
Larval life	Edwards, K. F., & Stachowicz, J. J. (2010). Multivariate trade-offs, succession, and phenological differentiation in a guild of colonial invertebrates. <i>Ecology</i> , 91(11), 3146–3152.
Larval life	El-Komi, M. M., & Kajihara, T. (1991). Breeding and moulting of barnacles under rearing conditions. <i>Marine Biology</i> , 108(1), 83–89. doi: 10.1007/BF01313474
Larval life	Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). National Exotic Marine and Estuarine Species Information System.
Larval life	Gosling, E., & Gosling, E. M. (1992). <i>The Mussel Mytilus: Ecology, Physiology, Genetics, and Culture</i> . Retrieved from https://books.google.com/books?id=0VEYAQAIAAJ
Larval life	Hart, S. P., & Keough, M. J. (2009). Does size predict demographic fate? Modular demography and constraints on growth determine response to decreases in size. <i>Ecology</i> , 90(6), 1670–1678. doi: 10.1890/08-1745.1
Larval life	Hayward, P. J., & Ryland, J. S. (1999). Cheilostomatous bryozoa Part 2. In R. S. K. Barnes & J. H. Crothers (Eds.), <i>Synopses of</i>

	<i>the British Fauna</i> (2nd ed.). The Linnean Society of London and the Estuarine and Coastal Sciences Association.
Larval life	Jablonski, D., & Lutz, R. A. (1983). Larval ecology of marine benthic invertebrates: paleobiological implications. <i>Biological Reviews</i> , 58(1), 21–89. doi: 10.1111/j.1469-185X.1983.tb00380.x
Larval life	Kupriyanova, E. K., Nishi, E., Ten Hove, H. A., & Rzhavsky, A. V. (2001). Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. <i>Oceanography and Marine Biology: An Annual Review</i> , 39, 1–101.
Larval life	Larwood, G. (Ed.). (1973). <i>Living and Fossil Bryozoa: Recent Advances in Research, Proceedings of the International Bryozoology Association Conference</i> . Academic Press.
Larval life	Loosanoff, V. L., & Davis, H. C. (1963). Rearing of Bivalve Mollusks. <i>Advances in Marine Biology</i> , 1, 1–136. doi: 10.1016/S0065-2881(08)60257-6
Larval life	Lynch, W. F. (1947). The behavior and metamorphosis of the larva of <i>Bugula neritina</i> (Linnaeus): experimental modification of the length of the free-swimming period and the responses of the larvae to light and gravity. <i>The Biological Bulletin</i> , 92(2), 115–150. doi: 10.2307/1538162
Larval life	Marine Life Information Network. (2006). BIOTIC - Biological traits information catalogue. Retrieved January 1, 2019, from www.marlin.ac.uk/biotic
Larval life	Marsden, J. R. (1987). Coral preference behaviour by planktotrophic larvae of <i>Spirobranchus giganteus corniculatus</i> (Serpulidae: Polychaeta). <i>Coral Reefs</i> , 6(2), 71–74. doi: 10.1007/BF00301376
Larval life	McCann, L. D., Hitchcock, N. G., Winston, J. E., & Ruiz, G. M. (2007). Non-native bryozoans in coastal embayments of the southern United States: New records for the western Atlantic. <i>Bulletin of Marine Science</i> , 80(2), 319–342.
Larval life	McHenry, M. J., & Strother, J. A. (2003). The kinematics of phototaxis in larvae of the ascidian <i>Aplidium constellatum</i> . <i>Marine Biology</i> , 142(1), 173–184. doi: 10.1007/s00227-002-0929-z
Larval life	Millar, R. H. (1971). The Biology of Ascidians. In <i>Adv. marine Biology</i> (Vol. 9, pp. 1–100). doi: 10.1016/S0065-2881(08)60341-7
Larval life	Monro, K., & Marshall, D. J. (2013). Evolutionary constraints and the maintenance of individual specialization throughout succession. <i>Evolution</i> , 67(12), 3636–3644. doi: 10.1111/evo.12220
Larval life	Nielsen, C. (1981). On morphology and reproduction of ‘Hippodiplosia’ <i>insculpta</i> and <i>Fenestrulina malusii</i> (Bryozoa, Cheilostomata). <i>Ophelia</i> , 20(1), 91–125. doi: 10.1080/00785236.1981.10426564

Larval life	Obenat, S. M., & Pezzani, S. E. (2006). Life Cycle and Population Structure of the Polychaete <i>Ficopomatus enigmaticus</i> (Serpulidae) in Mar Chiquita Coastal Lagoon, Argentina. <i>Estuaries</i> , 17(1), 263. doi: 10.2307/1352574
Larval life	Olson, R. R. (1985). The Consequences of Short-Distance Larval Dispersal in a Sessile Marine Invertebrate. <i>Ecology</i> , 66(1), 30–39. doi: 10.2307/1941304
Larval life	Parker, T., & Tunnicliffe, V. (1994). Dispersal Strategies of the Biota on an Oceanic Seamount: Implications for Ecology and Biogeography. <i>The Biological Bulletin</i> , 187(3), 336–345. doi: 10.2307/1542290
Larval life	Pasqua, M. Del, Lezzi, M., Licciano, M., & Giangrande, A. (2017). Larval development and post-larval growth of <i>Branchiomma bairdi</i> (Annelida: Sabellidae) from a Mediterranean population. <i>Invertebrate Biology</i> , 136(2), 207–216. doi: 10.1111/ivb.12171
Larval life	Pritchard, C., Shanks, A., Rimler, R., Oates, M., & Rumrill, S. (2015). The Olympia Oyster <i>Ostrea lurida</i> : Recent Advances in Natural History, Ecology, and Restoration . <i>Journal of Shellfish Research</i> , 34(2), 259–271. doi: 10.2983/035.034.0207
Larval life	Qiu, J., & Qian, P. (1997). Combined effects of salinity, temperature and food on early development of the polychaete <i>Hydroides elegans</i> . <i>Marine Ecology Progress Series</i> , 152, 79–88. doi: 10.3354/meps152079
Larval life	Reverberi, G. (1971). <i>Experimental Embryology of Marine and Fresh-Water Invertebrates</i> . Amsterdam: North-Holland Pub. Co.
Larval life	Rouse, G., & Pleijel, F. (2001). <i>Polychaetes</i> . Oxford University Press.
Larval life	Ryland, J. (1974). Behaviour, settlement and metamorphosis of bryozoan larvae: A review. In <i>Thalassia Jugosl</i> (Vol. 10).
Larval life	Ryland, J. S. (1960). Experiments on the Influence of Light on the Behaviour of Polyzoan Larvae. <i>Journal of Experimental Biology</i> , 37(4), 783–800. Retrieved from http://jeb.biologists.org/content/37/4/783.abstract
Larval life	Saito, Y., Mukai, H., & Watanabe, H. (1981). Studies of japanese compound styelid ascidians. Two new species of botryllus from the vicinity of shimoda. <i>Publications of the Seto Marine Biological Laboratory</i> , 26, 347–355.
Larval life	Sebastian, V. O. (1953). The development of <i>Herdmania pallida</i> (Heller). <i>Proceedings of the Indian Academy of Sciences - Section B</i> , 37(5), 174–187. doi: 10.1007/BF03050349
Larval life	Shanks, A. L. (2009). Pelagic Larval Duration and Dispersal Distance Revisited. <i>The Biological Bulletin</i> , 216(3), 373–385. doi: 10.1086/BBLv216n3p373

Larval life	Strathmann, M. F. (1987). <i>Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast</i> . Retrieved from http://www.jstor.org/stable/j.ctvcwnh8b
Larval life	Strathmann, R. R., Kendall, L. R., & Marsh, A. G. (2006). Embryonic and larval development of a cold adapted Antarctic ascidian. <i>Polar Biology</i> , 29(6), 495–501. doi: 10.1007/s00300-005-0080-7
Larval life	Sugimoto, K., & Nakauchi, M. (1974). Budding, sexual reproduction, and degeneration in the colonial ascidian, <i>Symplegma reptans</i> . <i>The Biological Bulletin</i> , 147(1), 213–226. doi: 10.2307/1540579
Larval life	Svane, I., & Lundälv, T. (1981). Reproductive patterns and population dynamics of <i>Ascidia mentula</i> O.F. Müller on the Swedish west coast. <i>Journal of Experimental Marine Biology and Ecology</i> , 50(2–3), 163–182. doi: 10.1016/0022-0981(81)90048-4
Larval life	Terlizzi, A., Conte, E., & Giangrande, A. (2000). Settlement patterns of two spirorbidae (annelida, polychaeta) species in the harbour of Ischia (Gulf of Naples, Mediterranean Sea). <i>Italian Journal of Zoology</i> , 67(3), 303–306. doi: 10.1080/11250000009356328
Larval life	Thiyagarajan, V., Harder, T., Qiu, J.-W., & Qian, P.-Y. (2003). Energy content at metamorphosis and growth rate of the early juvenile barnacle <i>Balanus amphitrite</i> . <i>Marine Biology</i> , 143(3), 543–554. doi: 10.1007/s00227-003-1077-9
Larval life	Van Name, W. G. (1945). The North and South American ascidians. <i>Bulletin of the American Museum of Natural History</i> , 84, 1–476.
Larval life	Wendt, D. E. (1998). Effect of Larval Swimming Duration on Growth and Reproduction of <i>Bugula neritina</i> (Bryozoa) Under Field Conditions. <i>The Biological Bulletin</i> , 195(2), 126–135. doi: 10.2307/1542820
Larval life	Werner, W. (1967). The distribution and ecology of the barnacle <i>Balanus trigonus</i> . <i>Bulletin of Marine Science</i> , 17(1), 64–84.
Larval life	Winston, J. E. (1982). Marine bryozoans (Ectoprocta) of the Indian River area (Florida). ; v. 173, article 2. <i>Bulletin of the AMNH</i> , 173(2), 99–176.
Larval life	Young, C. M. (1989). Selection of predator-free settlement sites by larval ascidians. <i>Ophelia</i> , 30(2), 131–140. doi: 10.1080/00785326.1989.10430840
Sexual reproduction	Ayling, A. L. (1980). P Patterns of sexuality, asexual reproduction and recruitment in some subtidal marine Demospongiae. <i>The Biological Bulletin</i> , 158(3), 271–282. doi: 10.2307/1540854
Sexual reproduction	AquaNIS. Editorial Board, 2015. Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. www.corpi.ku.lt/databases/aquanis . Version 2.36+

Sexual reproduction	Berger, M. S. (2009). Reproduction of the intertidal barnacle <i>Balanus glandula</i> along an estuarine gradient. <i>Marine Ecology</i> , 30(3), 346–353. doi: 10.1111/j.1439-0485.2009.00280.x
Sexual reproduction	Brousseau, D. J. (1984). Reproductive cycle of <i>Anomia simplex</i> (Pelecypoda: Anomiidae) from Cape Cod, Massachusetts. <i>The Veliger</i> , 26(4), 299–304.
Sexual reproduction	Capa, M., & Murray, A. (2015). Integrative taxonomy of <i>Parasabella</i> and <i>Sabellomma</i> (Sabellidae: Annelida) from Australia: description of new species, indication of cryptic diversity, and translocation of some species out of their natural distribution range. <i>Zoological Journal of the Linnean Society</i> , 175(4), 764–811. doi: 10.1111/zoj.12308
Sexual reproduction	Coe, W. R. (1934). Alternation of Sexuality in Oysters. <i>The American Naturalist</i> , 68(716), 236–251. Retrieved from http://www.jstor.org/stable/2456831
Sexual reproduction	Desai, D. V., Anil, A. C., & Venkat, K. (2006). Reproduction in <i>Balanus amphitrite</i> Darwin (Cirripedia: Thoracica): influence of temperature and food concentration. <i>Marine Biology</i> , 149(6), 1431–1441. doi: 10.1007/s00227-006-0315-3
Sexual reproduction	DFO. 2011. Updated framework for the pink and spiny scallop (<i>Chlamys rubida</i> and <i>C. hastata</i>) dive fishery in British Columbia. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2010/078
Sexual reproduction	Fofonoff, P. W., Ruiz, G. M., Steves, B., Simkanin, C., & Carlton, J. T. (2018). National Exotic Marine and Estuarine Species Information System.
Sexual reproduction	Gambi, M., Patti, F., Micaletto, G., & Giangrande, A. (2001). Diversity of reproductive features in some Antarctic polynoid and sabellid polychaetes, with a description of <i>Demonax polarsterni</i> sp. n. (Polychaeta, Sabellidae). <i>Polar Biology</i> , 24(12), 883–891. doi: 10.1007/s003000100287
Sexual reproduction	Holm, E. R. (1990). Attachment behavior in the barnacle <i>Balanus amphitrite</i> Darwin (Darwin): genetic and environmental effects. <i>Journal of Experimental Marine Biology and Ecology</i> , 135(2), 85–98. doi: 10.1016/0022-0981(90)90008-Z
Sexual reproduction	Kupriyanova, E. K., Nishi, E., Ten Hove, H. A., & Rzhavsky, A. V. (2001). Life-history patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. <i>Oceanography and Marine Biology: An Annual Review</i> , 39, 1–101.
Sexual reproduction	Lauzier, R. B., & Parker, G. (1999). <i>A Review of the Biology and Fisheries of the Pink Scallop and Spiny Scallop</i> . Ottawa.
Sexual reproduction	Leonard, V. K. (1969). Seasonal gonadal changes in two bivalve mollusks in Tomales Bay, California. <i>The Veliger</i> , 11(4), 382–390.

Sexual reproduction	Marine Life Information Network. (2006). BIOTIC - Biological traits information catalogue. Retrieved January 1, 2019, from www.marlin.ac.uk/biotic
Sexual reproduction	Nishi, E., Nishihira, M., Nishi, E., & Nishihira, M. (1994). Colony formation via sexual and asexual reproduction in <i>Salamasina dysteri</i> (Huxley) (Polychaeta, Serpulidae). <i>Zoological Science</i> , <i>11</i> , 589-595. Retrieved from https://www.biodiversitylibrary.org/part/71291
Sexual reproduction	Ostrovsky, A. (2013). <i>Evolution of Sexual Reproduction in Marine Invertebrates</i> . doi: 10.1007/978-94-007-7146-8
Sexual reproduction	Reverberi, G. (1971). <i>Experimental Embryology of Marine and Fresh-Water Invertebrates</i> . Amsterdam: North-Holland Pub. Co.
Sexual reproduction	Rouse, G., & Fitzhugh, K. (1994). Broadcasting fables: Is external fertilization really primitive? Sex, size, and larvae in sabellid polychaetes. <i>Zoologica Scripta</i> , <i>23</i> (4), 271–312. doi: 10.1111/j.1463-6409.1994.tb00390.x
Sexual reproduction	Rouse, G., & Pleijel, F. (2001). <i>Polychaetes</i> . Oxford University Press.
Sexual reproduction	Ryland, J. S. (1970). <i>Bryozoans</i> . London: Hutchinson.
Sexual reproduction	Stenyakina, A., Walters, L. J., Hoffman, E. A., & Calestani, C. (2009). Food availability and sex reversal in <i>Mytella charruana</i> , an introduced bivalve in the southeastern United States. <i>Molecular Reproduction and Development</i> , n/a-n/a. doi: 10.1002/mrd.21132
Sexual reproduction	Strathmann, M. F. (1987). <i>Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast</i> . Retrieved from http://www.jstor.org/stable/j.ctvcwnh8b
Sexual reproduction	Tovar-Hernández, M. A., Yáñez-Rivera, B., & Bortolini-Rosales, J. L. (2011). Reproduction of the invasive fan worm <i>Branchiomma bairdi</i> (Polychaeta: Sabellidae). <i>Marine Biology Research</i> , <i>7</i> (7), 710–718. doi: 10.1080/17451000.2010.547201