Applications of Dispersal Diversity on Food Web Stability Through a Synthesis of Current Literature and Observational Study

Danielle M.B. Mac Rae

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By: Danielle Mac Rae

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______________________________	**Examiner/Chair**
Dr. Emma Despland	
______________________________	**External Examiner**
Dr. Andrew Gonzalez	
______________________________	**Examiner**
Dr. Jean-Philippe Lessard	
______________________________	**Supervisor**
Dr. Eric Pedersen	
______________________________	**Co-Supervisor**
Dr. Jennifer Sunday	

Approved by ____

Dr. R. Weladji – Graduate Program Director

______________________________ 2022______________________________

Dean of Faculty- Pascale Sicotte

GENERAL ABSTRACT

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Danielle M.B. Mac Rae

Dispersal is a key mechanism that allows for spatially separated populations to interact across space and time. Rates of dispersal have been identified as a key factor shaping the stability of ecological communities. Dispersal diversity is the component of diversity that encompasses species dispersal abilities, driven by variation in dispersal-linked traits and condition-dependent movement behaviours. Frameworks that incorporate spatial dynamics often have not considered this source of diversity, opting for simpler methods of accounting for dispersal, but recent theoretical research has pushed for explicit inclusion of dispersal diversity within spatially structured (meta)communities. In my first chapter I reviewed literature that supports the stabilizing role of dispersal diversity and compiled intrinsic and extrinsic sources of variation that could be used to monitor stability in a trophic food web. In chapter two I tested whether local dispersal diversity predicted local community stability in the marine fish metacommunity of the Newfoundland and Labrador shelves, using dispersal trait measurements to quantify dispersal diversity and determine its impact on community stability over time. The results from chapter two support the stabilizing role of dispersal diversity, and that dispersal diversity can be measured applying the same methods as for functional diversity. This research highlights the importance of dispersal diversity for community stability, how dispersal diversity can be measured, and provides direction for future spatial studies on what traits to consider when accounting for dispersal diversity. Incorporating dispersal diversity into spatial models could provide better information to decision makers for managing spatially connected regions.

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Contribution of Authors

Chapter 1

Study concept and design: Mac Rae, Pedersen

Literature review: Mac Rae

Interpretation: Mac Rae

Drafting of manuscript: Mac Rae

Critical revision: Mac Rae, Sunday, Pedersen

Chapter 2

Study concept and design: Mac Rae, Sunday, Pedersen

Acquisition of data: Mac Rae, Di Girolamo

Analysis and interpretation: Mac Rae, Lucet, Sunday, Pedersen

Drafting of manuscript: Mac Rae

Critical revision: Mac Rae, Sunday, Pedersen

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General Introduction

It is well understood that through facilitating spatial interactions dispersal is a key mechanism for community stability (Crowley 1981; Bohonak & Jenkins 2003; Berkley *et al.* 2010; Figueiredo & Connolly 2012; Pedersen *et al.* 2016), however there has been less research on how community stability is established through the variation in dispersal behaviours (Bonte & Dahirel 2017; Bani *et al.* 2019; Sperry *et al.* 2019). Dispersal diversity is an aspect of functional diversity which encompasses the spectrum of intrinsic and extrinsic factors that lead to a species dispersal potential. There is still much to learn about how to account for and incorporate dispersal diversity in spatial models. My thesis attempts to define and summarize dispersal diversity and its role in stabilizing trophic interactions (Chapter 1), and then apply this theory to an empirical study system using dispersal linked traits to explore the relationship between dispersal diversity and community stability (Chapter 2).

In Chapter 1 I defined dispersal diversity and reviewed literature on how dispersal diversity can drive stability mechanisms in spatially structured food webs. I outlined intrinsic (individual traits) and extrinsic (habitat) sources of dispersal diversity which have been used to monitor community stability in theoretical and empirical research. This chapter highlights the multifaceted nature of dispersal diversity and its relationship with community stability and summarizes how creating variation between trophic levels of interacting species leads to community persistence through time.

In Chapter 2 I applied the theory of dispersal diversity to an empirical study system, the Newfoundland and Labrador (NF) shelves. I collected measurements of dispersal linked traits and used them to calculate dispersal dispersity. To determine the impact of dispersal diversity on the community, I looked at the relationship between the change in community stability and dispersal diversity. I found that there is a positive linear relationship between stability and dispersal diversity. I also saw that dispersal diversity did not correlate with taxonomic diversity, meaning that we are capturing another aspect of diversity by including dispersal in our research.

Chapter 1 looked only at the role of dispersal diversity in stabilizing trophic systems, but there has also been research on how dispersal diversity drives stability in competitive systems (Allesina & Tang 2012; Figueiredo & Connolly 2012; Aiken & Navarrete 2014). For competitive interactions we can still focus on how variation in dispersal supports asynchrony and the intrinsic and extrinsic factors that create dispersal diversity. In this way, dispersal diversity could be measured for whole food webs to explore more broadly its relationship with stability through multiple types of interactions. In Chapter 2 I found that many of the traits which are important for dispersal in Atlantic marine fish have not been well documented. Moving forward on this topic more investment should go into studies which will fill in missing data, for example through laboratory studies to determine species pelagic larval durations.

Overall, my thesis contributes to the growing knowledge of spatial ecology and emphasizes the importance of including dispersal variation in spatial research. My first chapter could be used as a guide for readers to understand the foundations and sources of dispersal variation, and my second chapter is an example of how dispersal traits can be measured and used to calculate dispersal diversity for empirical research. More research is still needed to refine the understanding of how to use and monitor dispersal diversity in natural communities, a good place to start would be including dispersal variation between trophic levels and competing species when simulating data, and widely measuring traits to get a full representation of functionality in species.

Chapter 1: Dispersal Mediated Community Stability in the Predator-Prey Model

Danielle M.B. Mac Rae, Jennifer M. Sunday, and Eric J. Pedersen

Abstract

Community stability is driven by patterns of species interactions which in turn depends on trait diversity. Dispersal is a widely recognized mechanism for the establishment and maintenance of species interactions across different spatial scales, which varies according to dispersal linked traits (dispersal diversity). Ecological research involving spatial dynamics i.e., metacommunities and trophic food webs, often have not included dispersal diversity when addressing spatiotemporal stability. To properly incorporate dispersal diversity in stability studies, we must first identify sources of variation in dispersal. Here we reviewed literature on how spatially structured food webs can be stabilized by the variation in dispersal responses. We compiled information on intrinsic (individual traits) and extrinsic (environmental condition, spatial heterogeneity) sources of dispersal variation, and reviewed theoretical studies on different mechanisms for how dispersal variation can influence food web stability based on theoretical models. We highlight the multifaceted nature of dispersal diversity and demonstrate how variation in dispersal behaviors between trophic levels contributes to community stability through asynchronous responses to the environment, differential rate of response to disturbance, and differential strength of species interactions.

Behind the Scenes of Stable Communities

The tendency of a food web to be stable over time (Holling 1973; Ives & Carpenter 2007) is important for the functioning of ecosystems and their provisioning to people. **Community stability** (see Glossary), broadly defined here as the tendency of species abundances to fluctuate around an average state (Ives & Carpenter 2007), can be influenced by the number of species present in a location as well as the patterns of interactions among them (May 1972, 1974; Allesina & Tang 2012; Gellner & McCann 2016; Gravel *et al.* 2016; Nilsson & McCann 2016). Although early models of ecological communities predicted that increased species richness tends to reduce community stability (May 1974), subsequent theoretical studies have shown that variation in species interactions across space (Allesina & Tang 2012; Gravel *et al.* 2016), as well as increased trait diversity, both within (Bolnick *et al.* 2011) and across trophic levels (Zhang *et al.* 2013), can stabilize diverse communities. Theoretical and empirical studies that have asked how trait diversity influences stability of food webs have primarily focused on the effects of trait diversity on consumption, growth, or reproduction (e.g., mandible strength, body size, rates of attack) (Zhang *et al.* 2013; Nilsson & McCann 2016; de Bello *et al.* 2021). However, organisms' movement in space away from their natal locations (dispersal), a key factor allowing interactions between spatially disconnected populations (Bohonak & Jenkins 2003; Pedersen *et al.* 2016), should also be considered. Both community-wide mean dispersal rates between patches and variation in dispersal rates among interacting species can play a critical role in stabilizing communities by distributing traits that drive patterns of food web interactions (Thompson & Gonzalez 2016; Pedersen and Guichard 2016; Pedersen *et al.* 2016). In this paper, we synthesize and review the rapidly growing theoretical literature on different mechanisms by which variation in dispersal response (both within and among species) can stabilize spatially structured food webs and examine the empirical evidence for ecologically relevant variation in dispersal ability in existing food webs.

To understand how variation in dispersal behavior can impact community stability, first we must clarify how dispersal itself is expected to have stabilizing outcomes. In an isolated habitat patch, population fluctuation is subject to environmental fluctuation, if habitat quality decreases and dispersal in not an option this population will perish. Under the same scenario for a trophic food web, predator and prey populations will fluctuate with the environment but also tend to follow abundance oscillations, as prey population increases predator abundance will also increase, causing a subsequent decrease in prey abundance from increased predation (Moran 1953, Huffaker 1958, Hastings 2001). In isolation this increased trophic interaction eventually causes the loss of both species. If dispersal occurs between connected habitat patches trophic interactions are less likely to drive the populations to extinction, as prey will have more opportunities to escape predation and increase in abundance (Pulliam 1988). This mechanism is supported through spatial averaging of population growth across spatially separated habitat, which results in higher mean biomass production (Ives *et al.* 2004, Gonzalez *et al.* 2009). Spatial averaging is a key part of the spatial insurance hypothesis, which suggests that in the presence of dispersal, stability can be established above the negative impacts of environmental change, and that this mechanism is most efficient at intermediate dispersal rates (Loreau *et al.* 2003).

Huffaker (1958) established the foundation for the importance of variation in dispersal processes for stabilizing trophic food webs through his study of multi-patch predator-prey systems using mites. While attempting to understand how these populations could persist in nature, he found that experimentally inducing a dispersal difference between the predator and prey populations would allow for both populations to persist through **asynchronous** abundance oscillations (Huffaker 1958). Between food patches, physical barriers (made of petroleum jelly) impeded predator dispersal and wooden posts facilitated prey dispersal. Wooden posts could only be exploited by prey who could climb and then drop off the posts to be carried by silken strands through the air currents. Dispersal variation between trophic levels facilitated food web stability, by allowing prey to colonize new predator-free patches before local populations could be eliminated by predation. Since Huffaker's experiment, theoretical and experimental studies on dispersal mediated stability have grown in complexity to push the limits of our understanding of this mechanism.

Dispersal and Spatial Synchrony

To understand the spatial effects of dispersal, we first must review how dispersal plays a role in **synchronization**. Synchronization occurs when a metacommunity experiences correlated fluctuations in abundance (Loreau & de Mazancourt 2008). It is understood that patch synchrony increases the chance of extinction, decreasing stability, when all populations experience extreme oscillations (Hastings 2001). Community synchrony can be caused by both correlated environmental fluctuations, known as the Moran effect (Moran 1953), or could be affected by dispersal between populations (Fontaine & Gonzalez 2005; Abbott 2011). Goldwyn and Hastings (2008) looked at community synchrony mathematically using a two-patch predator-prey model with varying levels of dispersal for both populations. They found that at low dispersal rates the metacommunity could avoid synchronization over many generations, highlighting that the rate at which dispersal occurs may be important to consider when determining spatial synchrony. Goldwyn and Hastings (2009) studied synchrony with a predator-prey model, this time accounting for spatial heterogeneity. They found that weak dispersal plus spatial heterogeneity further decreases the chance of synchronization (Goldwyn & Hastings 2009; Leng *et al.* 2010). Under this scenario dispersal is limited and spatially variable, decreasing the number of individuals from each species that can move patches successfully and decreasing the rate of predation.

Contrasting previous research, Fox et. al (2011) empirically demonstrated the synchronizing impact of short distance dispersal for a whole metapopulation. They performed experiments on a two species trophic community where they manipulated the occurrence of short-distance dispersal and environmental heterogeneity to determine which factor contributed to synchrony. Prey synchrony was increased both by short-distance dispersal, uniformly across the metapopulation, and by the Moran effect, which decayed with distance. This research highlights that even at low levels of dispersal spatially separated patches can easily be synchronized. Furthermore, in metapopulations that are already synchronized due to environmental synchronization or enrichment from high resource availability, dispersal fails to counter extinction risk (Laan & Fox 2020).

Dispersal has both synchronizing and stabilizing properties which occur simultaneously (Abbott 2011). The degree of environmental fluctuation and rate of dispersal can indicate whether the system is headed towards synchrony or asynchrony (Hayes & Anderson 2018). Although we must recognize the multifaceted nature that dispersal has for spatial dynamics, here we will focus on the mechanisms by which dispersal variation supports stability.

Stability Mechanisms and a Role for Dispersal Variation

Variation in traits among individuals have been found to increase food web stability by three major mechanisms (Ives & Carpenter 2007; Loreau & de Mazancourt 2013; Hammond *et al.* 2020),. First, asynchronous responses to environmental fluctuation allows species with similar niches to persist and compensate for similar functions by separating populations spatially or temporally (Loreau & de Mazancourt 2008). Asynchrony between spatially connected communities can be facilitated through **asymmetric dispersal**, a form of dispersal variation where species have unequal dispersal responses to the same environmental cues (Salomon *et al.* 2010; Aiken & Navarrete 2014). Second, different rates of responses to environmental perturbations can stabilize food webs by decorrelating abundance fluctuations among species across time. To the extent that dispersal influences such response rates (e.g. passive versus active dispersal), variation in dispersal can stabilize the temporal change in food webs as the species rate of response would not be simultaneous. The third stabilizing mechanism comes from variation in the strength of species interactions across species in a food web, and between locations in a landscape (Gellner & McCann 2016; Nilsson & McCann 2016). Dispersal affects both how species interact within a food web and with the landscape, e.g. dictating species' ability to forage, draw resources, find mates, and escape predation, and the variation in dispersal ability between species will affect the strength of these interactions (Crowley 1981; Urban *et al.* 2013). Huffaker's (1958) experiment with mites as explained above is an example of how through dispersal variation prey could use their landscape to find spatial refuges, decreasing predation interactions which stabilized this system (Huffaker 1958). Each mechanism for stability can be supported through the variation in dispersal ability, but the sources of dispersal variation and how these influences spatial patterns must be considered to understand the stability of communities over time.

There are three components that influence patterns of dispersal across landscapes: 1) the dispersal rate (i.e., the probability of a given individual to move from one site to a different site in a given period of time), 2) dispersal distance (i.e., how far individuals travel when dispersing), and 3) landscape connectivity (i.e., the ease or resistance of movement between habitat patches based on the landscape). Each of these three dispersal components are subject to variation within and among species (Ronce & Clobert 2012; Stevens *et al.* 2013; Bonte & Dahirel 2017; Jacob *et al.* 2019), and across ecological conditions (e.g., the dispersal rate of a species out of a site might vary as a function of population density or organism condition). We refer to variation among any of these three components within communities as **dispersal diversity**. Dispersal diversity has been shown to be stabilizing for both competitive (Berkley *et al.* 2010; Figueiredo & Connolly 2012; Aiken & Navarrete 2014; Pedersen & Guichard 2016) and predator-prey communities (Huffaker 1958; Pedersen *et al.* 2016; Gross *et al.* 2020). Berkeley et al. (2010), Figueiredo and Connolly (2012), and Aiken and Navarrete (2014) all found that differing dispersal patterns between competitors can establish coexistence due to a spatial storage effect (Warner & Chesson 1985). Similarly, Pedersen and Guichard (2016) found that intraspecific aggregation of propagules during dispersal (a specific dispersal pattern that many individual dispersing larvae follow) supports coexistence, as it increases the chance of conspecific interaction after dispersal which reduces negative interactions from strong interspecific competitors. Pedersen et al. (2016) and Gross et al. (2020) manipulated the rates of dispersal in model food webs and found that variation of dispersal rates among trophic levels leads to higher community stability. Rather than a hierarchical increase in dispersal, they found that a combination of both weak, strong, and intermediate levels of dispersal led to higher stability systems.

Dispersal diversity originates from the interaction of individual traits (intrinsic factors) with characteristics of the local environment (extrinsic factors) (Matthysen 2012; Starrfelt & Kokko 2012). Over the next two sections we review different sources of dispersal diversity, and how they can lead to more stable food webs. Section one will address the species-specific (intrinsic factors) sources of dispersal variation, including phenotype-dependent and condition-dependent dispersal.

Section two addresses variation that arises from the interaction between dispersal and spatial heterogeneity (extrinsic factors).

1. Intrinsic Sources of Dispersal Diversity

Individuals of the same population, or between populations of the same species, can exhibit dispersal variation dependent on natural variation that exists within morphological, physiological, and behavioral characteristics. This is known as ***phenotype-dependent dispersal*** (Clobert *et al.* 2009; Baguette *et al.* 2012). This concept has also been referred to as condition-dependent dispersal (Nanninga and Berumen 2014), however the latter terminology begets confusion as 'condition-dependent dispersal' has been simultaneously used to describe both the internal state of an organism and the external conditions that they experience (Bowler & Benton 2005; Bonte *et al.* 2012; Nanninga & Berumen 2014). For consistency, we will refer to all dispersal diversity originating from traits as phenotype-dependent dispersal.

We use the term **C*ondition-dependent dispersal*** (Clobert *et al.* 2009) to describe dispersal diversity originating from the external conditions that influence species dispersal behaviour e.g., density dependence, competition, foraging opportunities, and habitat quality. Another term seen frequently in dispersal literature is '**adaptive dispersal**' when specifically focused on the tendency to disperse from lower-fitness habitats to higher-fitness habitats (Duckworth 2008; Abrams & Ruokolainen 2011; Ruokolainen *et al.* 2011; Cressman & Křivan 2013; Wang & Zou 2016). Adaptive dispersal requires spatial information processing, defined as the cognitive ability of an organism to perceive, and make decision-based movements throughout their environment (Guzman et al. 2019). Adaptive dispersal behavior is a sub-set of condition-dependent dispersal according to the previously stated definition and will be included in the review of condition-dependent dispersal. Here we will review research that supports the stability benefits of phenotype-dependent and condition-dependent dispersal.

Phenotype-dependent dispersal diversity

Phenotype-dependent dispersal describes how different individuals within a population have variable probability of dispersal (Clobert *et al.* 2009; Cote *et al.* 2010), emerging from differences in dispersal-linked traits (Nanninga & Berumen 2014). Individual-level dispersal differences can have important implications for large scale community stability (Catalano *et al.* 2020; Sullivan *et al.* 2021). A dispersal kernel is one method to describe this variation, accounting for the probable distribution of dispersal distances away from a source location (Nathan *et al.* 2012; Pinsky *et al.* 2017). Guzman and Srivastava (2020) applied species-specific dispersal kernels in a community dynamic model with predator-prey interactions and found that variable dispersal within-species allowed for differential space use between the predator and prey, leading to persistence of predator-prey populations. This form of dispersal diversity can increase stability because alternative dispersal strategies, such as varying dispersal rates, within a species can ensure prey population survival by allowing different responses to perturbation (i.e. a portfolio effect; Schindler *et al.* 2010). In brief, this effect occurs because in a population with a diversity of traits, at least some individuals might have traits that allow them to adjust their dispersal response to improve fitness when environmental conditions change (Clobert *et al.* 2012b; Cote & Clobert 2012).

The importance of phenotype-dependent dispersal has also been demonstrated for competition-colonization trade-offs, allowing species that are weak competitors to coexist with strong competitors if weaker competitors are able to disperse across longer distances or can reach empty patches more readily (Calcagno *et al.* 2006).

Condition-dependent dispersal diversity

Condition-dependent dispersal arises from the interaction between phenotype-dependent dispersal and local conditions. Dispersal is '**random**' when the fraction of individuals dispersing, their dispersal distances, and which patches they move to, do not vary with location conditions. Condition-dependent dispersal occurs when dispersal propensities depend on local conditions such as density of conspecifics, competitors, predators, habitat quality, or resource availability (Fronhofer *et al.* 2015).

Filotas et al. (2008) simulated density-dependent dispersal for a multi-patch predator-prey model, specifically including resource availability and inter/intraspecific competition scenarios, which they termed 'community-driven' dispersal. Individual fitness ranged from low to high under different scenarios which determined the level of dispersal that occurred in their condition-dependent model. When compared to a model using density-independent dispersal, the density-dependent model allowed for a more complex metacommunity when the fitness, and therefore the dispersal, of individuals varied around intermediate values. As such, this mechanism may be an important stabilizing factor in natural food webs (Bowler & Benton 2005).

In predator-prey dynamics it has been shown that adaptive movement supports stability (asynchrony) more so than random movement (Abrams & Ruokolainen 2011; Cressman & Křivan 2013; Wang & Zou 2016). Fryxell and Lundberg (1993) studied the role of adaptive dispersal in predator-prey models, showing how adaptive local predator dispersal can maximize community stability by decreasing the temporal variability of predator population densities (Fryxell & Lundberg 1993). Predators exhibit adaptive dispersal if they consistently move to the patch with the highest abundance of prey resources. This tends to reduce predation pressure (interaction strength) on low-prey-abundance patches, desynchronizing predator-prey oscillations and reducing the chance of prey extirpation in these patches. This contrasts with purely random dispersal assumed in many metacommunity models, where large-scale dispersal patterns are unaffected by the combination of behavioral decisions and local conditions (Guzman *et al.* 2019; Thompson *et al.* 2020). In the case of metacommunities with three or more patches, random movement can also allow for asynchrony between patches. When considering spatial heterogeneity, random movement can increase stability at very high or very low heterogeneity, whereas adaptive movement stabilizes populations at moderate heterogeneity (Ruokolainen *et al.* 2011).

The effect of long-term predation can also drive coexistence between competing populations of prey, as predators can shift their use of prey resources subsequently controlling the prey density, driving down mean interaction strengths within the community (Karakoç *et al.* 2020). This supports dispersal as a stabilizing mechanism through achieving a combination of weak and strong species interactions at different spatial scales for predator-prey relationships (Mchich *et al.* 2007; Xiao *et al.* 2010; Flaxman *et al.* 2011; Massol *et al.* 2011).

An empirical study from Baines et al. (2014) looked at condition-dependent emigration rates of prey species as a function of competition and predation. This study showed that the effect of predation on dispersal was dependent on prey population density; to balance the cost of dispersal, competition, and predation risk, prey were more likely to emigrate at intermediate population density. Predation pressure and population density generated variability in prey dispersal as individuals responded to the cost associated with being consumed versus competing for resources.

This highlights the importance of including species-interactions into dispersal models, as differential strengths of interactions across spatial scales will impact dispersal outcomes (Pillai *et al.* 2012). The process of condition-dependent dispersal helps desynchronize predator-prey oscillations at larger spatial scales, reducing the interaction strength of predation. A similar study performed by Brown et al. (2020) focused on predator condition-dependent dispersal in a system with two species of lady beetle predators, an aphid prey, and the yucca plant as a resource or habitat patch. The experiment was performed in a patchy heterogeneous landscape, and they found a strong stabilizing effect due to a sub-optimal foraging behavior by predators caused by over-dispersing (Brown *et al.* 2021). Predator dispersal rates depended not only on prey density, but also on interactions between the two predator species. Lady beetles choose foraging patches where there were already predators of either species present but would also disperse more often out of patches to avoid competition. Seen in many of these examples, intrinsic dispersal characteristics rely heavily on spatial heterogeneity to achieve the full outcome of dispersal variation within trophic food webs.

2. Extrinsic Sources of Dispersal Diversity

Species at different trophic levels of a food web may interact at different spatial scales (Guzman *et al.* 2019), exposing them to different levels of spatial heterogeneity. When looking at the predator-prey interaction, environmental heterogeneity and other external drivers play an important role in establishing stability by creating variation in the timing or distance of dispersal (Holt 1984; Della Rossa *et al.* 2013; Blasius *et al.* 2020). Certain landscape features may impede dispersal of some species, facilitate movement of others, and provide areas of spatial refugia to temporarily escape predation (Clobert *et al.* 2009). Some predators may be slower dispersing than their prey; the interaction of spatial heterogeneity on species specific dispersal traits is what enabled prey survival in Huffaker's 1958 experiment. The ability of prey to disperse more quickly than their predators in this environment decreased the strength of the two species' interaction, i.e., reduced the per-capita rate of predation. Diffuse species interactions, supported by spatial heterogeneity acting on variation in dispersal, tend to be stabilizing (Wilson 1992; Gellner & McCann 2016). As Huffaker (1958) showed, a strong stabilizing effect in a heterogeneous environment emerges as prey are able to persist through the **rescue-effect** mechanism and slow-dispersing predators are less likely to experience local extinction caused by prey overconsumption (Crowley 1981; Gross *et al.* 2020).

When a natural environment is interrupted, through homogenization or connectivity loss, this can have a destabilizing effect on the residing community. A recent case study from Koranyi et al. (2021) assessed the predation rate of multiple predators on a single prey across an urbanized gradient. The study showed that predators with lower dispersal capability (found in natural areas) had higher consumption rates, which kept prey at a low population density (Korányi et al. 2021). Predators with long distance dispersal capability were found at higher abundances in urban areas, which correlated with increased prey population density, indicating that these species were less efficient predators. Prey populations were able to grow due to low predation, as the more efficient predators were dispersal limited. This research highlights the effects of environmental heterogeneity on the strength of species interactions through environmental filtering of dispersal diversity. Land-use changes that reduce the connectivity of habitat for low-dispersal predators can lead to unchecked prey populations in disturbed habitats, destabilizing community interactions. This has implications in natural pest control, as from the Koranyi et al. (2021) example, aphids in uncontrolled urban populations were over-consuming their resources.

Temporal fluctuations in spatial heterogeneity can impact dispersal variability. This is best understood through examples of stochastic dispersal, where connectivity patterns between patches in a landscape vary randomly over time due to e.g., variation in wind or ocean currents (Siegel *et al.* 2008). Siegel et al. (2008) describes how in a coastal marine system sedentary adult fish will spawn pelagic larvae which are aggregated into groups by ocean currents during dispersal, leading to intraspecific aggregation in larval settling locations. This stochastic aggregation process leads to spatiotemporal variability in dispersal patterns that affect larval connectivity and recruitment, which in turn can reduce interspecific competition and predation interaction strength relative to intraspecific competition strength (Berkley *et al.* 2010; Pedersen & Guichard 2016). These transient differences in connectivity among species can result in long-term changes in species dynamics. Dispersal variation combined with spatial heterogeneity and natural spatiotemporal fluctuations works to promote asynchrony in food webs, establishing weak species interactions that together support and maintain community stability.

Concluding Remarks

Dispersal connects interacting populations across space and the variation in these connections have an important influence on species interactions. The study of dispersal, spatial dynamics, is vital to understanding how complex systems are formed in nature (Leibold *et al.* 2004), as local communities are linked via dispersal, hence each species' dispersal ability can facilitate or reduce species interactions across different spatial scales. Dispersal variation can arise from innate factors such as morphology and spatial information processing, or extrinsic factors from time of dispersal and landscape heterogeneity. Between trophic levels this is a well-understood phenomenon (Pedersen et al. 2016), yet dispersal rates are generally assumed to be identical among species of the same trophic level in metacommunity models (Loreau et al. 2003; Thompson et al.

2020). Typically only one life stage of a species is assessed as their dispersal stage - for example larvae in marine systems (Edwards *et al.* 2007), and by neglecting the potential dispersal at other stages, stability from dispersal diversity may be overlooked. As species are lost from a system, without accurate knowledge of that species' interactions within the community it may be hard to determine how this would affect stability. It may have been that their dispersal facilitated an interaction between populations contributing to persistence, and if this connection is not accounted for, its loss could lead to larger repercussions in food web stability than realized.

It is important to note that a community should be able to withstand a certain level of loss before repercussions are reflected in ecosystem services, known as **ecological resilience** (Gunderson 2000). To understand which dispersal interactions have the most weight or importance for food web stability, communities must be studied thoroughly. However, for modeling purposes including all possible variations would require endless data collection and processing power. Realistic and attainable dispersal variation of focal species should be used when studying community, metacommunity and ecosystem level processes that focus on stability and spatiotemporal interactions. The degree of complexity to be included will be specific to the question being asked. Additionally, a framework for studying variation in dispersal ability needs to be laid out, so that specific strategy can be employed consistently across spatial research. Progress on this topic will not be made if theoretical research continues to use simple dispersal methods (random, spontaneous, density-independent, ubiquitous) in their models.

This review focused only on the predator-prey interaction of a trophic community; however most natural communities will be composed of a range of types of interactions. The stability mechanism of dispersal is also prevalent in coexistence models (Berkley *et al.* 2010; Figueiredo & Connolly

2012; Aiken & Navarrete 2014), and is even recognized at ecosystem level processes (Allesina & Tang 2012; Gravel *et al.* 2016; Thompson & Gonzalez 2016). When assessing the stability of a natural community both competitive and predation interactions should be considered at the species-specific level. Other approaches to stability have looked at **functional diversity** of the community, where an overlap in species functions contributes to maintenance of ecosystem services (Ricotta *et al.* 2016; Malaterre *et al.* 2019). This approach uses individual species traits to determine how they interact with their biotic and abiotic surroundings.

We propose that dispersal diversity can be measured using the same methods used for functional diversity, by measuring on the intraspecific traits which lead to an organism's ability to disperse, phenotype-dependent dispersal (i.e. wing, body size, propagule pressure) (Petchey & Gaston 2006; Suding *et al.* 2008). One example of ongoing research into dispersal trait diversity is the study of dispersal syndromes, which are described by patterns of covariation in morphological, behavioral, and life history traits that lead to dispersal (Ronce & Clobert 2012). These recent efforts to include more information on natural dispersal variation under new scopes is advancing the field of community stability. Traits which facilitate dispersal will be specific to the species or taxa of interest and ideally will be measurable and comparable to other species in the same system, one way this can be made possible is by calculating an index of trait diversity such as functional diversity. Measuring traits to determine dispersal ability has been used in functional diversity research as a proxy for biodiversity change, on birds (Sol *et al.* 2020), and for observing global and local connectivity patterns (Bradbury *et al.* 2008). Dispersal traits have even been used to monitor metapopulation stability through mathematical models (Bani *et al.* 2019). We hypothesis that variation in dispersal traits could be used as a reasonable proxy to calculate dispersal diversity relationship with community stability which we will explore in chapter two of this thesis.

When environmental conditions change some species' distributions can shift and redistribute in space if they can adequately disperse, while others may experience local extinctions (Lenoir *et al.* 2008, 2020; Pecl *et al.* 2017). Such population changes in space over time can disrupt interspecific interactions that might be important for stability and therefore ecosystem services (Urban *et al.* 2013; Pecl *et al.* 2017; Thompson & Gonzalez 2017; Thompson *et al.* 2017). Community models used to project how communities will change under environmental stress generally assume that all species disperse at the same rate (Leibold *et al.* 2022). Better quantification of variation in dispersal traits in natural ecosystems is needed to determine the extent to which dispersal diversity contributes to ecosystem stability, and will help managers identify how environmental pressures or other perturbations might affect dispersal diversity. Incorporating the stabilizing effects of dispersal diversity into community models will also help assess long-term effects on community stability due to landscape changes such as roads, farms, or water transit. Although dispersal and predator-prey interactions are only some of the pieces required for the community stability puzzle, understanding this relationship is an essential building block for research to come.

Glossary

Adaptive dispersal: Dispersal behavior is considered adaptive when fitness-affecting environmental conditions influence the choice of individual organisms to disperse (Bernstein *et al.* 1991).

Asymmetric dispersal: Dispersal patterns are not equal between patches of dispersing individuals, under the same environmental conditions (Salomon *et al.* 2010).

Asynchronous: Uncorrelated, or opposite, fluctuation in species responses to the environment across spatially connected patches (Loreau & de Mazancourt 2008).

Community stability: The temporal variation around an average value, could be for population abundances, community composition, or other ecosystem properties. Community stability can be monitored through spatial and temporal fluctuations in ecosystem services, population abundances, and community composition (Ives & Carpenter 2007).

Condition-dependent dispersal: Dispersal diversity originating from the external conditions that influence species dispersal outcomes e.g., density dependence, competition, foraging opportunities, and habitat quality (Clobert *et al.* 2009).

Dispersal: The movement of an individual away from their natal site (Clobert *et al.* 2012a).

Dispersal diversity: Encompasses all possible variation in dispersal related traits, which are traits that in someway support the individual's propensity to disperse.

Phenotype-dependent dispersal: Dispersal variation dependent on natural variation that exists within morphological, physiological and behavioral characteristics (Clobert *et al.* 2009).

Random dispersal: Dispersal which is independent of location conditions and decision-making (Abrams & Ruokolainen 2011).

Rescue effect: The prevention of local extinction due to immigration from another location (Pulliam 1988).

Ecological resilience: When referring to resilience, we use Holling's concept of ecological resilience, which recognizes that a system can have multiple stable-states; a community that is ecologically resilient to some perturbation can withstand a large degree of that perturbation without switching state (Holling 1973).

Synchronous: Correlated fluctuations in species response to the environment over space and time (Loreau & de Mazancourt 2008).

References

Abbott, K.C. (2011). A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. *Ecology Letters*, 14, 1158–1169.

Abrams, P.A. & Ruokolainen, L. (2011). How does adaptive consumer movement affect population dynamics in consumer–resource metacommunities with homogeneous patches? *Journal of Theoretical Biology*, 277, 99–110.

Aiken, C.M. & Navarrete, S.A. (2014). Coexistence of competitors in marine metacommunities: environmental variability, edge effects, and the dispersal niche. *Ecology*, 95, 2289–2302.

Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.

de Bello, F., Lavorel, S., Hallett, L.M., Valencia, E., Garnier, E., Roscher, C., *et al.* (2021). Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends in Ecology & Evolution*, 36, 822–836.

Berkley, H.A., Kendall, B.E., Mitarai, S. & Siegel, D.A. (2010). Turbulent dispersal promotes species coexistence. *Ecology Letters*, 13, 360–371.

Bernstein, C., Kacelnik, A. & Krebs, J.R. (1991). Individual Decisions and the Distribution of Predators in a Patchy Environment. II. The Influence of Travel Costs and Structure of the Environment. *Journal of Animal Ecology*, 60, 205–225.

Blasius, B., Rudolf, L., Weithoff, G., Gaedke, U. & Fussmann, G.F. (2020). Long-term cyclic persistence in an experimental predator–prey system. *Nature*, 577, 226–230.

Bohonak, A.J. & Jenkins, D.G. (2003). Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters*, 6, 783–796.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183–192.

Bonte, D. & Dahirel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos*, 126, 472–479.

Bonte, D., Dyck, H.V., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., *et al.* (2012). Costs of dispersal. *Biological Reviews*, 87, 290–312.

Bowler, D.E. & Benton, T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, 80, 205–225.

Brown, D., Bruder, A. & Kummel, M. (2021). Endogenous spatial heterogeneity in a multi-patch predator-prey system: insights from a field-parameterized model. *Theor Ecol*, 14, 107–122.

Calcagno, V., Mouquet, N., Jarne, P. & David, P. (2006). Coexistence in a metacommunity: The competition-colonization trade-off is not dead. *Ecology Letters*, 9, 897–907.

Catalano, K.A., Dedrick, A.G., Stuart, M.R., Puritz, J.B., Montes, H.R. & Pinsky, M.L. (2020). Quantifying dispersal variability among nearshore marine populations. *Molecular Ecology*, 30.

Clobert, J., Baguette, M., Benton, T.G. & Bullock, J.M. (2012a). *Dispersal Ecology and Evolution*. First Edition. Oxford University Press.

Clobert, J., Galliard, J.-F.L., Cote, J., Meylan, S. & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12, 197–209.

Clobert, J., Massot, M. & Galliard, J.-F.L. (2012b). Multi-determinism in natal dispersal: the common lizard as a model system. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 29–40.

Cote, J. & Clobert, J. (2012). Dispersal syndromes in the common lizard: personality traits, information use, and context-dependent dispersal decisions. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 152–160.

Cote, J., Clobert, J., Brodin, T., Fogarty, S. & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4065–4076.

Cressman, R. & Křivan, V. (2013). Two-patch population models with adaptive dispersal: the effects of varying dispersal speeds. *J. Math. Biol.*, 67, 329–358.

Crowley, P.H. (1981). Dispersal and the Stability of Predator-Prey Interactions. *The American Naturalist*, 118, 673–701.

Della Rossa, F., Fasani, S. & Rinaldi, S. (2013). Conditions for patchiness in plankton models. *Theoretical Population Biology*, 83, 95–100.

Duckworth, R.A. (2008). Adaptive Dispersal Strategies and the Dynamics of a Range Expansion. *The American Naturalist*, 172, S4–S17.

Edwards, K.P., Hare, J.A., Werner, F.E. & Seim, H. (2007). Using 2-dimensional dispersal kernels to identify the dominant influences on larval dispersal on continental shelves. *Mar. Ecol.-Prog. Ser.*, 352, 77–87.

Figueiredo, J. & Connolly, S.R. (2012). Dispersal-mediated coexistence under recruitment limitation and displacement competition. *Ecological Modelling*, 243, 133–142.

Flaxman, S.M., Lou, Y. & Meyer, F.G. (2011). Evolutionary ecology of movement by predators and prey. *Theor Ecol*, 4, 255–267.

Fontaine, C. & Gonzalez, A. (2005). Population Synchrony Induced by Resource Fluctuations and Dispersal in an Aquatic Microcosm. *Ecology*, 86, 1463–1471.

Fox, J.W., Vasseur, D.A., Hausch, S. & Roberts, J. (2011). Phase locking, the Moran effect and distance decay of synchrony: experimental tests in a model system. *Ecology Letters*, 14, 163–168.

Fronhofer, E.A., Klecka, J., Melián, C.J. & Altermatt, F. (2015). Condition-dependent movement and dispersal in experimental metacommunities. *Ecology Letters*, 18, 954–963.

Fryxell, J.M. & Lundberg, P. (1993). Optimal patch use and metapopulation dynamics. *Evol Ecol*, 7, 379–393.

Gellner, G. & McCann, K.S. (2016). Consistent role of weak and strong interactions in high- and low-diversity trophic food webs. *Nat Commun*, 7, 11180.

Goldwyn, E.E. & Hastings, A. (2008). When can dispersal synchronize populations? *Theoretical Population Biology*, 73, 395–402.

Goldwyn, E.E. & Hastings, A. (2009). Small Heterogeneity Has Large Effects on Synchronization of Ecological Oscillators. *Bull. Math. Biol.*, 71, 130–144.

Gonzalez, A., Mouquet, N. & Loreau, M. (2009). Biodiversity as spatial insurance: the effects of habitat fragmentation and dispersal on ecosystem functioning. In: *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective* (eds. Naeem, S., Bunker, D.E., Hector, A., Loreau, M. & Perrings, C.). Oxford University Press, p. 0.

Gravel, D., Massol, F. & Leibold, M.A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, 7, 12457.

Gross, T., Allhoff, K.T., Blasius, B., Brose, U., Drossel, B., Fahimipour, A.K., *et al.* (2020). Modern models of trophic meta-communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375, 20190455.

Gunderson, L.H. (2000). Ecological Resilience—In Theory and Application. *Annual Review of Ecology and Systematics*, 31, 425–439.

Guzman, L.M., Germain, R.M., Forbes, C., Straus, S., O'Connor, M.I., Gravel, D., *et al.* (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecology Letters*, 22, 19–33.

Guzman, L.M. & Srivastava, D.S. (2020). Genomic variation among populations provides insight into the causes of metacommunity survival. *Ecology*, 101, e03182.

Hammond, M., Loreau, M., Mazancourt, C. de & Kolasa, J. (2020). Disentangling local, metapopulation, and cross-community sources of stabilization and asynchrony in metacommunities. *Ecosphere*, 11, e03078.

Hastings, A. (2001). Transient dynamics and persistence of ecological systems. *Ecology Letters*, 4, 215–220.

Hayes, S.M. & Anderson, K.E. (2018). Beyond connectivity: how the structure of dispersal influences metacommunity dynamics. *Theor Ecol*, 11, 151–159.

Holling, C.S. (1973). Resilience and Stability of Ecological Systems. *Annu. Rev. Ecol. Syst.*, 4, 1–23.

Holt, R.D. (1984). Spatial Heterogeneity, Indirect Interactions, and the Coexistence of Prey Species. *The American Naturalist*, 124, 377–406.

Huffaker, C. (1958). Experimental studies on predation: Dispersion factors and predator-prey oscillations. *Hilgardia*, 27, 343–383.

Ives, A.R., Woody, S.T., Nordheim, E.V., Nelson, C. & Andrews, J.H. (2004). The Synergistic Effects of Stochasticity and Dispersal on Population Densities. *The American Naturalist*, 163, 375–387.

Ives, A.R. & Carpenter, S.R. (2007). Stability and Diversity of Ecosystems. *Science*, 317, 58–62.

Jacob, S., Chaine, A.S., Huet, M., Clobert, J. & Legrand, D. (2019). Variability in Dispersal Syndromes Is a Key Driver of Metapopulation Dynamics in Experimental Microcosms. The American Naturalist, 194, 613–626.

Karakoç, C., Clark, A.T. & Chatzinotas, A. (2020). Diversity and coexistence are influenced by time-dependent species interactions in a predator–prey system. *Ecology Letters*, 23, 983–993.

Korányi, D., Szigeti, V., Mezőfi, L., Kondorosy, E. & Markó, V. (2021). Urbanization alters the abundance and composition of predator communities and leads to aphid outbreaks on urban trees. *Urban Ecosyst*, 24, 571–586.

Laan, E. & Fox, J.W. (2020). An experimental test of the effects of dispersal and the paradox of enrichment on metapopulation persistence. *Oikos*, 129, 49–58.

Leibold, M.A., Holyoak, M. & Mouquet, N. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613.

Leibold, M.A., Rudolph, F.J., Blanchet, F.G., De Meester, L., Gravel, D., Hartig, F., *et al.* (2022). The internal structure of metacommunities. *Oikos*, 2022.

Leng, X., Musters, C.J.M. & Snoo, G.R.D. (2010). Spatial variation in ditch bank plant species composition at the regional level: the role of environment and dispersal. *Journal of Vegetation Science*, 21, 868–875.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., *et al.* (2020). Species better track climate warming in the oceans than on land. *Nat Ecol Evol*, 4, 1044–1059.

Lenoir, J., Gégout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008). A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. *Science*, 320, 1768–1771.

Loreau, M. & de Mazancourt, C. (2008). Species Synchrony and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments. *The American Naturalist*, 172, E48–E66.

Loreau, M. & de Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology Letters*, 16, 106–115.

Malaterre, C., Dussault, A.C., Rousseau-Mermans, S., Barker, G., Beisner, B.E., Bouchard, F., *et al.* (2019). Functional Diversity: An Epistemic Roadmap. *BioScience*, 69, 800–811.

Massol, F., Gravel, D., Mouquet, N., Cadotte, M.W., Fukami, T. & Leibold, M.A. (2011). Linking community and ecosystem dynamics through spatial ecology. *Ecology Letters*, 14, 313–323.

Matthysen, E. (2012). Multicausality of dispersal: a review. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 3–18.

May, R.M. (1972). Will a Large Complex System be Stable? *Nature*, 238, 413–414.

May, R.M. (1974). *Stability and Complexity in Model Ecosystems*. Princeton University Press.

Mchich, R., Auger, P. & Poggiale, J.-C. (2007). Effect of predator density dependent dispersal of prey on stability of a predator–prey system. *Mathematical Biosciences*, Arino Special Issue, 206, 343–356.

Moran, P. a. P. (1953). The statistical analysis of the Canadian Lynx cycle. *Aust. J. Zool.*, 1, 291–298.

Nanninga, G.B. & Berumen, M.L. (2014). The role of individual variation in marine larval dispersal. *Front. Mar. Sci.*, 1.

Nathan, R., Klein, E., Robledo-Arnuncio, J.J. & Revilla, E. (2012). Dispersal kernels: review. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 187–210.

Nilsson, K.A. & McCann, K.S. (2016). Interaction strength revisited—clarifying the role of energy flux for food web stability. *Theor Ecol*, 9, 59–71.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., *et al.* (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, eaai9214.

Pedersen, E.J. & Guichard, F. (2016). At what scales does aggregated dispersal lead to coexistence? *Oikos*, 125, 1677–1687.

Pedersen, E.J., Marleau, J.N., Granados, M., Moeller, H.V. & Guichard, F. (2016). Nonhierarchical Dispersal Promotes Stability and Resilience in a Tritrophic Metacommunity. *The American Naturalist*, 187, E116–E128.

Pedersen, E.J., Thompson, P.L., Ball, R.A., Fortin, M.-J., Gouhier, T.C., Link, H., *et al.* (2017). Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. *Royal Society Open Science*, 4, 170215.

Petchey, O.L. & Gaston, K.J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters*, 9, 741–758.

Pillai, P., Gonzalez, A. & Loreau, M. (2012). Evolution of Dispersal in a Predator-Prey Metacommunity. *The American Naturalist*, 179, 204–216.

Pinsky, M.L., Saenz-Agudelo, P., Salles, O.C., Almany, G.R., Bode, M., Berumen, M.L., *et al.* (2017). Marine Dispersal Scales Are Congruent over Evolutionary and Ecological Time. *Current Biology*, 27, 149–154.

Pulliam, H.R. (1988). Sources, Sinks, and Population Regulation. *The American Naturalist*, 132, 652–661.

Ricotta, C., Bello, F. de, Moretti, M., Caccianiga, M., Cerabolini, B.E.L. & Pavoine, S. (2016). Measuring the functional redundancy of biological communities: a quantitative guide. *Methods in Ecology and Evolution*, 7, 1386–1395.

Ronce, O. & Clobert, J. (2012). Dispersal syndromes. In: *Dispersal Ecology and Evolution*. Oxford University Press, p. chapter 10.

Ruokolainen, L., Abrams, P.A., McCann, K.S. & Shuter, B.J. (2011). The roles of spatial heterogeneity and adaptive movement in stabilizing (or destabilizing) simple metacommunities. *Journal of Theoretical Biology*, 291, 76–87.

Salomon, Y., Connolly, S.R. & Bode, L. (2010). Effects of asymmetric dispersal on the coexistence of competing species. *Ecology Letters*, 13, 432–441.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., *et al.* (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, 465, 609–612.

Siegel, D.A., Mitarai, S., Costello, C.J., Gaines, S.D., Kendall, B.E., Warner, R.R., *et al.* (2008). The stochastic nature of larval connectivity among nearshore marine populations. *PNAS*, 105, 8974–8979.

Starrfelt, J. & Kokko, H. (2012). The theory of dispersal under multiple influences. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 19–28.

Stevens, V.M., Trochet, A., Blanchet, S., Moulherat, S., Clobert, J. & Baguette, M. (2013). Dispersal syndromes and the use of life-histories to predict dispersal. *Evol Appl*, 6, 630–642.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., *et al.* (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, 14, 1125–1140.

Sullivan, L.L., Michalska-Smith, M.J., Sperry, K.P., Moeller, D.A. & Shaw, A.K. (2021). Consequences of ignoring dispersal variation in network models for landscape connectivity. *Conservation Biology*, 35, 944–954.

Thompson, P.L. & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97, 2867–2879.

Thompson, P.L. & Gonzalez, A. (2017). Dispersal governs the reorganization of ecological networks under environmental change. *Nature Ecology & Evolution*, 1, 1–8.

Thompson, P.L., Guzman, L.M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., *et al.* (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecology Letters*, 23, 1314–1329.

Thompson, P.L., Rayfield, B. & Gonzalez, A. (2017). Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*, 40, 98–108.

Townsend, D.L. & Gouhier, T.C. (2019). Spatial and interspecific differences in recruitment decouple synchrony and stability in trophic metacommunities. *Theor Ecol*, 12, 319–327.

Urban, M.C., Zarnetske, P.L. & Skelly, D.K. (2013). Moving forward: dispersal and species interactions determine biotic responses to climate change: Dispersal and species interactions. *Ann. N.Y. Acad. Sci.*, n/a-n/a.

Wang, X. & Zou, X. (2016). On a two-patch predator-prey model with adaptive habitancy of predators. *Discrete & Continuous Dynamical Systems - B*, 21, 677.

Warner, R.R. & Chesson, P.L. (1985). Coexistence Mediated by Recruitment Fluctuations: A Field Guide to the Storage Effect. *The American Naturalist*, 125, 769–787.

Wilson, D.S. (1992). Complex Interactions in Metacommunities, with Implications for Biodiversity and Higher Levels of Selection. *Ecology*, 73, 1984–2000.

Xiao, Z., Gao, X., Steele, M.A. & Zhang, Z. (2010). Frequency-dependent selection by tree squirrels: adaptive escape of nondormant white oaks. *Behavioral Ecology*, 21, 169–175.

Zhang, L., Thygesen, U.H., Knudsen, K. & Andersen, K.H. (2013). Trait diversity promotes stability of community dynamics. *Theor Ecol*, 6, 57–69.

Chapter 2: Stability Increased with Dispersal Diversity in the Newfoundland and Labrador Shelves

Danielle MB. Mac Rae, Valentin Lucet, Jennifer M. Sunday, and Eric J. Pedersen

Abstract

To understand and predict how regional diversity changes under directed environmental pressure, there needs to be more focus on monitoring broad-scale spatially connected communities (metacommunities). While the importance of dispersal behaviours in shaping community dynamics has long been recognized, much less is known about how variation among species in dispersal rates may affect community stability and complexity. Theoretical and experimental metacommunity studies have shown that functional diversity in dispersal types (i.e. dispersal diversity), can act to desynchronize population fluctuations, and may be as important for stabilizing community dynamics at landscape scales. Here we test the hypothesis that communities with greater dispersal diversity have greater stability in biomass over time. We quantified functional variation in dispersal-linked traits of groundfish species across space and time of the Newfoundland and Labrador (NL) shelves from 1995 to 2017. Local communities with higher dispersal diversity, measured using functional evenness, tended to be more stable over five-year intervals. This relationship held even after controlling for local taxonomic diversity as measured by effective species number. Our findings provide support for the hypothesis that dispersal diversity increases stability, suggesting this variable is a useful measure of metacommunity function and monitoring under environmental pressure.

Introduction

The importance of dispersal is widely understood as essential to the maintenance of metacommunity and community dynamics, because intermediate rates of dispersal can stabilize interspecific competition and predator-prey systems by desynchronizing population dynamics across space (Leibold *et al.* 2004, 2017; Convertino *et al.* 2009; Berkley *et al.* 2010; Chisholm *et al.* 2011; Figueiredo & Connolly 2012; Aiken & Navarrete 2014; Pedersen & Guichard 2016; Hayes & Anderson 2018; Pedersen *et al.* 2020; Thompson *et al.* 2020; Jiang *et al.* 2021). Dispersal, defined by the movement of an organism away from its natal site (Matthysen 2012; Bonte & Dahirel 2017), can also affect community response to environmental change (Travis *et al.* 2013; Thompson & Gonzalez 2016, 2017).

Metacommunity research has generally assumed dispersal to be equal across species (Pedersen *et al.* 2016; Guzman *et al.* 2019). Dispersal in marine systems is often treated as a specific event or occurrence at one point in a species' life cycle, typically during the larval stage (Suthers & Frank 1991; Bowler & Benton 2005; Kinlan *et al.* 2005; Lester & Ruttenberg 2005; Shanks 2009; Berkley *et al.* 2010), but adult dispersal also has a role in lifetime dispersal efforts (Sunday *et al.* 2015). Further, metacommunity models typically assume either that dispersal rates are identical among species, or that rates increase with trophic level (Pedersen *et al.* 2016; Guzman *et al.* 2019; Thompson *et al.* 2020). However, this generalizes movement behaviors and ignores species-specific adaptations in dispersal that may play an important role in supporting community stability. Variation in dispersal behaviour (hereafter referred to as dispersal diversity) can lead to stability through the cumulative effect of offset oscillations between predators and their prey and/or spatially asynchronous dispersal patterns between competitors (see Chapter 1) (Huffaker 1958; Pedersen & Guichard 2016; Thompson & Gonzalez 2016).

A well-known example of the effect of dispersal diversity on community stability comes from Huffaker's (1958) predator-prey experiments using mites. His experiment consisted of predator and prey mites interacting across a landscape of patches (partially exposed oranges arranged on a tray) separated by petroleum jelly dispersal barriers. He showed that predator and prey populations were only able to coexist across the landscape when he manipulated the experimental landscape so that each species dispersed at different rates between habitat patches. By introducing a small wooden post at each dispersal barrier, prey mites were able to float across to new habitat patches (oranges) using an adaptation not present in predators. This allowed prey to escape predation and repopulate new habitat patches. This experiment provides empirical evidence that variation in dispersal rates among species can facilitate coexistence and stability within a trophic metacommunity.

If dispersal diversity does increase community stability, we might be able to use proximal functional traits that affect dispersal behaviour as an indicator of stability (or resilience) and fold this into biodiversity monitoring. Previously explored proximal traits for dispersal behaviour include morphological and behavioral traits that affect a species' ability to disperse (Clobert *et al.* 2009; Cote & Clobert 2012; Ronce & Clobert 2012; Stevens *et al.* 2013; Jacob *et al.* 2019), throughout different life stages (Luiz *et al.* 2012, 2013). For example, a fish species with a pelagic larval stage (larval morphological trait) is expected to disperse farther than one fish with a demersal (i.e., bottom-associated) larval stage. However, dispersal traits can vary in their strength of association to dispersal and are different in terrestrial and marine environments. As such, the accumulation of traits and their contribution to dispersal could be used together allowing us to estimate dispersal diversity among groups of species.

Substantial interspecific variation in dispersal ability has been shown in plant (Sperry *et al.* 2019), macroinvertebrate (Jiang *et al.* 2021), bird (Sol *et al.* 2020), and aquatic communities (Rodríguez 2002; Bradbury *et al.* 2008; Radinger & Wolter 2014) both within and between trophic levels, yet accounting for dispersal diversity to monitor and predict stability in marine metacommunities has gone mostly underexplored (Kinlan & Gaines 2003; Heino *et al.* 2015). A study from Bani et al. (2019) used mathematical models and simulated dispersal traits to predict marine metapopulation growth and stability, finding that variation in pelagic larval duration would impact population stability outcomes. However, no studies to our knowledge have used empirically measured dispersal trait data to determine stability outcomes for a temperate marine metacommunity.

Although dispersal diversity can theoretically increase stability of communities, little work has gone into testing this relationship (Thompson & Gonzalez 2016, 2017). Here we use a time series of marine groundfish assemblages from the Newfoundland and Labrador (NL) shelf bioregion in Atlantic Canada to test the hypothesis that dispersal diversity increases community stability in a region undergoing change. This region has undergone extensive changes in community assemblage since the 1950's due to high fishing pressure, and has been consistently monitored since (Myers *et al.* 1997; Chadwick *et al.* 2007; Hutchings 2011; Pedersen *et al.* 2017, 2020; Bernier *et al.* 2018). The early 1990's groundfish collapse led to a region-wide regime shift, fish stocks decreased and invertebrate biomass increased, which to this day has not fully recovered to pre-collapse state making this a prime study site for monitoring stability (Pedersen *et al.* 2020).

We identify the effect of dispersal diversity against the effect of taxonomic species diversity by comparing effects of each on community stability and asking how dispersal diversity correlates with taxonomic diversity. We defined dispersal diversity as the accumulation of dispersal profiles in a community revealed through morphological or behavioral traits linked to dispersal potential, following the same techniques used for functional diversity (de Bello *et al.* 2021). Community stability was defined as the inverse of temporal fluctuation in biomass across the region. Under the hypothesis that dispersal diversity increases stability, we expected to see a decrease in the temporal fluctuation in biomass in communities with greater dispersal diversity, over and above any relationship between species diversity and stability. If identifiable, the dispersal-stability relationship can be monitored and used to predict future fluctuations in biomass for this region.

Methods

Study Area

The region of interest in this study is the NL shelves bioregion, located on the Canadian Atlantic coast (Figure 1). The abundance and composition of the groundfish community in this region has changed substantially several times in the past three decades (DFO 2009; Pedersen *et al.* 2017). This region is considered a distinct ecological zone, based on oceanographic and bathymetric characteristic similarities and marine community structure. Divisions within this region have been described by the Northwest Atlantic Fisheries Organization (NAFO) which are used for community monitoring (Bernier *et al.* 2018) and within these divisions smaller stratum boundaries, used to structure community sampling (Chadwick *et al.* 2007), have been designated by Fisheries and Oceans Canada (DFO) based on bathymetry and spatial location. The benthic community is sampled annually in the spring (NAFO divisions 3LNOP since 1971) or fall (NAFO Divisions 2J and 3K since 1977) by DFO via a random depth-stratified multi-species bottom trawl survey

(Chadwick *et al.* 2007). In our study we did not use data from NAFO divisions 2GH as these areas have not been monitored consistently in our data set. Surveys used Campelen shrimp trawls with a standardized tow length of 15 minutes at 3.0 knots, organisms were identified to species level when possible and weighed in kilograms. The number of sites sampled within a stratum are allocated as a function of stratum surface area and chosen randomly prior to the trawl survey (Chadwick *et al.* 2007). In this project we used species-specific biomass from the Newfoundland and Labrador shelves trawl surveys collected during surveys from 1995 to 2017.

We estimated trawl-specific biomass density of each species in the trawled area by dividing the biomass in the trawl by the area swept by the gear (i.e., the wingspread of the trawl net times the length of the trawl net, measured in km^2). We then aggregated data to the stratum level for each year by calculating the average species-specific biomass density from all trawls in a stratum for a given year. This gave us a total of 275 distinct strata in which we can quantify annual dispersal diversity and stability across the 23-year time series (Chadwick *et al.* 2007; Pedersen *et al.* 2020).

Dispersal Traits

We identified dispersal traits for marine fish species that had high coverage in our data searches and were deemed sufficiently related to dispersal behaviour. Studies of dispersal in marine organisms have largely focused on dispersal of the larval stage of fishes and invertebrates (Johannesson 1988; Bradbury & Snelgrove 2001; Grüss *et al.* 2011; Almany *et al.* 2013; Gary *et al.* 2020). Pelagic larval duration (PLD), vertical migration, and larval length are often cited as important traits determining larval dispersal (Johannesson 1988; Suthers & Frank 1991; Graham & Sebens 1996; Grantham *et al.* 2003; Fiksen *et al.* 2007; Bradbury *et al.* 2008; Shanks 2009). However, dispersal traits from other stages in the life cycle are likely important for overall dispersal potential within a species or population (Berkley *et al.* 2010; Grüss *et al.* 2011; Luiz *et al.* 2013; Aiken & Navarrete 2014; Radinger & Wolter 2014; Sunday *et al.* 2015; Martins *et al.* 2017). Traits that have an association with movement and lifetime dispersal potential were supported with literature-based evidence before collecting data (refer to Table 1 for complete list of traits and supporting evidence).

After identifying a long list of possible dispersal traits for the taxa of interest we then identified the subset of species for which the specific traits had been measured in the scientific literature. Many fish and invertebrate species found in the NL shelf survey were not consistently identified to species-level in the trawl data or were missing detailed dispersal trait data; we excluded these species from our analysis. We extracted fish community data from Rfishbase (Froese & Pauly 2022) for any species located in the Northwest Atlantic that was referenced on the DFO trawl data to narrow down the community to well monitored and identifiable species, assuring that biomass data was available for the whole community. The final species list included 98 fish species. Dispersal traits that were missing a large amount of data, specifically larval length, pelagic larval duration, and average movement distance, were searched for through directed literature searches. Efforts often resulted in only a few extra measurements gathered as larval traits are not well studied in North Atlantic marine species. We only included traits with at least 60% of completed data in analyses of functional diversity, resulting in 10 dispersal traits (Table S1). The final dispersal traits were morphological and behavioral leading to mixed numerical and categorical data.

Measuring Dispersal Diversity

All statistical analyses were performed in R statistical software version 4.1.2 (R Core Team 2022). Trait data was transformed into a distance matrix (species x trait) using Gower's dissimilarity coefficient, calculated using the *gowdis* function from the *FD* package. We chose this coefficient because it can handle our mixed data types and tolerates missing data by giving it a weight of 0 and returns an index value to represent trait differences between species. (Laliberté & Legendre 2010; Laliberté *et al.* 2014). We approached dispersal diversity in two ways. First, we clustered species based on their dispersal traits into dispersal groups, and second, we looked at the evenness of trait distributions within and between local communities based on species abundances. We used the dispersal group method to determine if there are general trends in dispersal profiles within marine communities and to see how these trends are reflected in the biomass (functional over redundancy (Mouillot *et al.* 2014)). Dispersal trait evenness was our measure of dispersal diversity for comparing how well-distributed traits are in the regional species pool and how diversity affects community stability.

1. Dispersal Groups

We used the Gower's distance matrix to perform hierarchical clustering, ran using the *hclust* function in the *stats* package, with the unweighted pair group method and algorithmic mean (UPGMA) with no traits weighted (Podani & Schmera 2006; Legendre & Legendre 2012). We chose this clustering method because it is robust and recommended as a standard technique, along with Gower's coefficient, when calculating functional diversity indices (Podani and Schmera 2006). We predicted how many clusters should be used to group the data using the silhouette width, calculated by the *silhouette* function in the *cluster* package (Rousseeuw 1987), a measure of the degree of dissimilarity between objects in a cluster compared to this measure computed for the next cluster (Borcard *et al.* 2018). To visualize the distance between species separated by their trait values we ran a PCoA ordination where vectors represent traits and points represent species. We ran the ordination using the *cmdscale* function from the *stats* package (Gower 1966).

2. Dispersal Trait Evenness

We calculated dispersal diversity with a distance-based framework which used species trait values and abundances to compute multidimensional functional diversity, using the *dbFD* function in the *FD* package (Laliberté *et al.* 2014). Functional diversity is a trait-based approach which measures the contribution of each species in a community to the ecosystem function (Malaterre *et al.* 2019). Although there are many measures for calculating functional diversity, due to time constraints we focused on functional evenness (FEve) to quantify dispersal diversity, defined as evenness of trait distribution in trait space weighted by the occurrence of the trait (species biomass density) (Villéger *et al.* 2008). This index has a range of zero to one, with zero corresponding to a completely uneven community where a single species or trait dominates, and one corresponding to a community where all trait values present are equally represented in the community. We chose FEve because it was simple to interpret, a higher index value reflects increased dispersal diversity, and has been demonstrated to be independent of species richness, the other diversity measure looked at for this project.

Taxonomic Diversity

We quantified taxonomic diversity in each stratum in each year by calculating the effective species number (based on the exponential of Shannon diversity, i.e. the Hill number when q=1; Chao & Ricotta 2019) The Shannon index considers the richness and the relative proportion of species abundance of each community, taking the exponential of the Shannon index returns the community's estimated effective species number. Effective species numbers are less sensitive to the presence or absence of very rare species relative to species richness, allowing us to compare across the regional species pool (Chao *et al.* 2014).

Correlation between Dispersal Diversity and Effective Species Number

To visualize patterns in the spatiotemporal relationship between taxonomic diversity and the dispersal groups we looked at the change of each. We calculated effective species number for dispersal groups to make the two measures comparable. We also wanted to know if there was a correlation between effective species number and dispersal diversity. We scaled the values of both diversity measures to make interpretation easier. Using a correlation test we determined if there was a linear relationship between taxonomic species diversity (as measured by effective species number) and functional dispersal diversity (as measured by FEve) to identify if local dispersal diversity was predictable from local taxonomic diversity. We were also interested to see how dispersal diversity compared to taxonomic diversity in the region, as species diversity is most often used to monitor biodiversity leading to management decisions.

Community Stability

We defined community stability as the inverse of the temporal fluctuation in total community biomass (kg/km2) at a given location (1), where minimal change in biomass (low fluctuation) indicates a more stable community (Ives & Carpenter 2007). We calculated stability for each stratum by summing the biomass densities of all species present in the stratum in each year, and then taking the standard deviation of the community biomass over time in each stratum within a fixed period. We took the inverse of the standard deviation and then log-transformed these values.

$$Stability = Log(SD\left(\frac{kg}{km^2}\right)^{-1}) \qquad (1)$$

Community Stability and Diversity

We split our 23-year time series into four 5-year bins and a final bin with the remaining 3 years. This was meant to balance the relevant change in biomass that could occur through time while maximizing the number of data points we could use for analysis.

To test if community stability increases as a function of dispersal diversity or taxonomic diversity (2), we ran a multiple regression with both measures using a generalized additive model (GAM) in the package *mgcv* (Wood 2011), with the models as follows:

$$Stability \sim scaled(FEve) + scaled(effective\ species\ number) + s(time\ bin) + s(stratum) \quad (2)$$

We calculated the mean values for dispersal diversity (FEve) and taxonomic diversity (effective species number) over the same time intervals as community stability for a total of five time points per stratum. We then z-score transformed both variables to that they could be interpreted on the same scale. We accounted for temporal autocorrelation using a random effect smoother, s(time bin), with six basis functions. We accounted for residual spatial autocorrelation using a spatial smooth term, s(stratum), with 200 basis functions, built using a Markov random field smoother, with an Intrinsic Conditional Autoregressive penalty (ICAR;(Rue & Held 2005)) that smooths estimated standard deviations for neighbouring strata toward one another. We used a gaussian distribution to fit the data and our method for estimating smoothing parameters was REML.

Results

Dispersal groups

We determined the optimum number of dispersal groups from our clustering algorithm to be 37 groups, however there was little change in silhouette width from 25 to 50 grouping indicating that the separation between 25 clusters to 50 clusters was not significantly different. For this reason, we chose to proceed with 25 dispersal groups as the lowest number of clusters in this range (Figure S1). Even with 25 dispersal groups, there were four groups that consisted of only a single species (singletons) and only 13 dispersal groups containing 3 or more species (Table S2 provides the breakdown of traits characterizing each dispersal group). The PCoA shows general trends of the species clusters overlaid with trait vectors (Figure 2). The first two PCoA axes explained 65% of the variation between species. Traits that were most involved in predicting clusters included larval strategy, adult body shape and adult position in the water column (Figure 2).

Correlation between Dispersal Diversity and Taxonomic Diversity

Dispersal diversity showed no significant correlation with taxonomic diversity (Pearson correlation coefficient = 0.0037, with 95% confidence interval [-0.048 ,0.055], p-value = 0.89, based on 1436 samples) (Figure S2). Looking at the spatiotemporal patterns of taxonomic diversity and dispersal groups, we could see that areas of high and low diversity of the two measures fluctuated similarly over time across strata (Figure S3).

Diversity and Community Stability

Community stability, as previously defined, had a strong positive relationship to dispersal diversity as measured by FEve, where stability is 11% higher for every 1 SD increase in FEve (Estimated slope = 0.11 with 95% confidence interval [0.043 ,0.18], R-sq.(adj) = 0.56, p-value = 0.0012) (Figure 3). This corresponds to biomass stability being higher in strata with high dispersal diversity. Stability across strata also showed a strong positive relationship with species diversity, where stability is 50% higher for every 1 SD increase in effective species number (Estimate coefficient 0.50 with 95% confidence interval [0.43 ,0.57], R-sq.(adj) = 0.56, p-value = 2e-16) (Figure 3).

Discussion

We demonstrated notable spatial and temporal variation in dispersal diversity occurred across the Newfoundland and Labrador shelf. This variability significantly predicted local stability in biomass, with higher-diversity strata showing lower variation on average biomass across 5-year intervals. We showed that dispersal diversity is not just an indicator of taxonomic diversity, as we did not find a strong correlation between taxonomic diversity (as measured by effective species number) and dispersal diversity (as measured by trait evenness) across space. Finally, we found that grouping species into dispersal profiles based on dispersal traits was not a useful method for identifying dispersal diversity in this system.

We hypothesized that areas with higher dispersal diversity would have increased local stability. Indeed, we found a decrease in biomass fluctuation when the local community had higher dispersal diversity across the region (Figure 3), consistent with this hypothesis. We also saw a strong relationship between stability and taxonomic diversity across the region. This result was not surprising as it is likely that there are many facets of diversity playing a role in maintaining community stability. The weak correlation between dispersal diversity and taxonomic diversity indicates that dispersal diversity is capturing another aspect of diversity in this region that may be overlooked when just using species diversity to monitor the region (Figure S2). For example, some communities (ex. Stratum 957) had low species diversity but a well-balanced representation of the dispersal traits leading to higher dispersal diversity than other communities (ex. Stratum 732) with high species diversity but where certain dispersal traits dominate.

Variation in dispersal was not accurately captured by dispersal clusters, except perhaps at the broadest level. We expected to see more distinct clusters because of the potential for general dispersal syndromes that have been identified for other study systems (Clobert *et al.* 2009; Cote & Clobert 2012; Stevens *et al.* 2013). If dispersal traits can be grouped in a predictable pattern this could help identify redundancy or rarity in dispersal response. Identifying dispersal syndromes could also potentially be used to assume dispersal traits of less well studied species. We saw a pattern of shared traits between adult position in the water column and larval strategy at the broadest level of our dispersal clustering, most strongly associated with the larval strategies; demersal, direct, or pelagic. This indicates that the position of adults in the water column (i.e., demersal or pelagic) could be used to identify the larval strategy of their offspring. Position in the water column is also a trait that can be used to determine the trophic position of the species. Similarly, many of the traits identified for dispersal could be used to predict other functions, as dispersal is only one aspect of functional diversity. Dispersal diversity proved to be difficult to measure for the majority of our marine fish species, which lack broad and detailed traits measurements.

Conclusions about spatial variation in dispersal diversity, and the potential existence or not of distinct trait clusters, depended heavily on the few dispersal-linked traits for which we could find good data coverage. Specifically under-represented in the data included adult dispersal distances, larval length, pelagic larval duration (PLD), and rafting (extent to which propagules tend to clump or aggregate in dispersal). Although identified as important dispersal traits, they are difficult to measure because of the turbulent nature of marine habitat and small size of larvae. Due to the lack of data for these traits, it is unlikely that the assumed dispersal groups in this project would provide insight into the dispersal ability of those species which are understudied. The dispersal groups here were not well defined but looking at how species are distributed along trait vectors in the PCoA does indicate room to explore this concept further with more dispersal trait measurements.

Our results are a starting point for testing the relationship between dispersal diversity and community stability, but further exploration is warranted. For example, we have only looked at one dimension of stability with one aspect of functional diversity, upon further investigation of stability and diversity measurements other relationships could arise. We did not compare different methods for calculating the distance matrix, dispersal diversity, or community stability, for which there are numerous other options for these analyses, however we did choose our methods based on their flexibility to accommodate our mixed data. The addition of community composition monitoring (measuring the change in abundance for each species within a community) could provide insight into the stability benefits of dispersal diversity in a region where there have been large-scale shifts in community assemblages, like the Newfoundland and Labrador shelves (Pedersen *et al.* 2020). Additionally, when looking at the change in stability between time periods of our results, there was not a clear trend for stability to remain consistent through time within strata, but instead varied across time. The non-linear variation overtime in stability was not explored in our project and warrants further exploration. Consequently, it is unlikely that we could use the results of our diversity stability relationships to predict future stability outcomes in this system.

External stressors of marine ecosystems, such as overfishing and rising ocean temperature, can result in biodiversity decline or the redistribution within community structure (Walther et al. 2002; Parmesan & Yohe 2003; Perdomo et al. 2012; Pedersen et al. 2020). Species redistribution can negatively impact community stability, the maintenance of which is essential for providing ecosystem services to society. Variation in dispersal rates, or intermediate dispersal, has been identified as a critical component for maintaining stability and increasing multifunctionality within interacting communities, a consistent finding across dispersal stability literature (Allesina & Tang 2012; Clobert *et al.* 2012; Gravel *et al.* 2016; Thompson & Gonzalez 2016). Taking this a step further, dispersal diversity is one aspect of multifunctionality which can increase local and regional stability by desynchronizing population oscillations (see Chapter 1).

Under directed environmental change, such as rising ocean temperatures (Bernier *et al.* 2018), species with higher capacity for rapid and long-distance dispersal are thought to shift their ranges more quickly with climate change at the leading range edge (Nye *et al.* 2009; Kortsch *et al.* 2015; Sunday *et al.* 2015). This phenomenon has been empirically shown in hundreds of studies (see review by Lenoir *et al.* 2020) where poleward range shifts were observed temporally as ocean temperatures increased. Climate change range shifts might therefore select for species with high dispersal abilities, potentially reducing overall dispersal diversity. This in turn will reduce dispersal diversity which our results show could lead to reduced community stability.

Including dispersal diversity in monitoring programs could provide valuable information on changes in stability. Moving forward, we suggest that metacommunity studies interested in monitoring stability should consider dispersal diversity when trying to capture and determine changes in diversity. Some study systems have more readily available information on dispersal traits of species (i.e. grasses Sperry *et al.* 2019; birds Sol *et al.* 2020; freshwater macroinvertebrates Jiang *et al.* 2021), generally due to the ease of measuring traits of interest either in field or laboratory studies. In the case of temperate marine fish, larval length and pelagic larval duration measurements could be taken using laboratory or hatchery studies. This could increase the robustness of dispersal diversity measurements in this system and its influence on community stability. With better representation of dispersal traits for species in the NF shelves, we could continue to investigate how dispersal diversity impacts other aspects of community stability, such as change in community composition, in this study system which has undergone extensive change over the past few decades. Importantly, continuing to study dispersal diversity could help researchers develop strategies to predict spatiotemporal changes in ecosystem function and services.

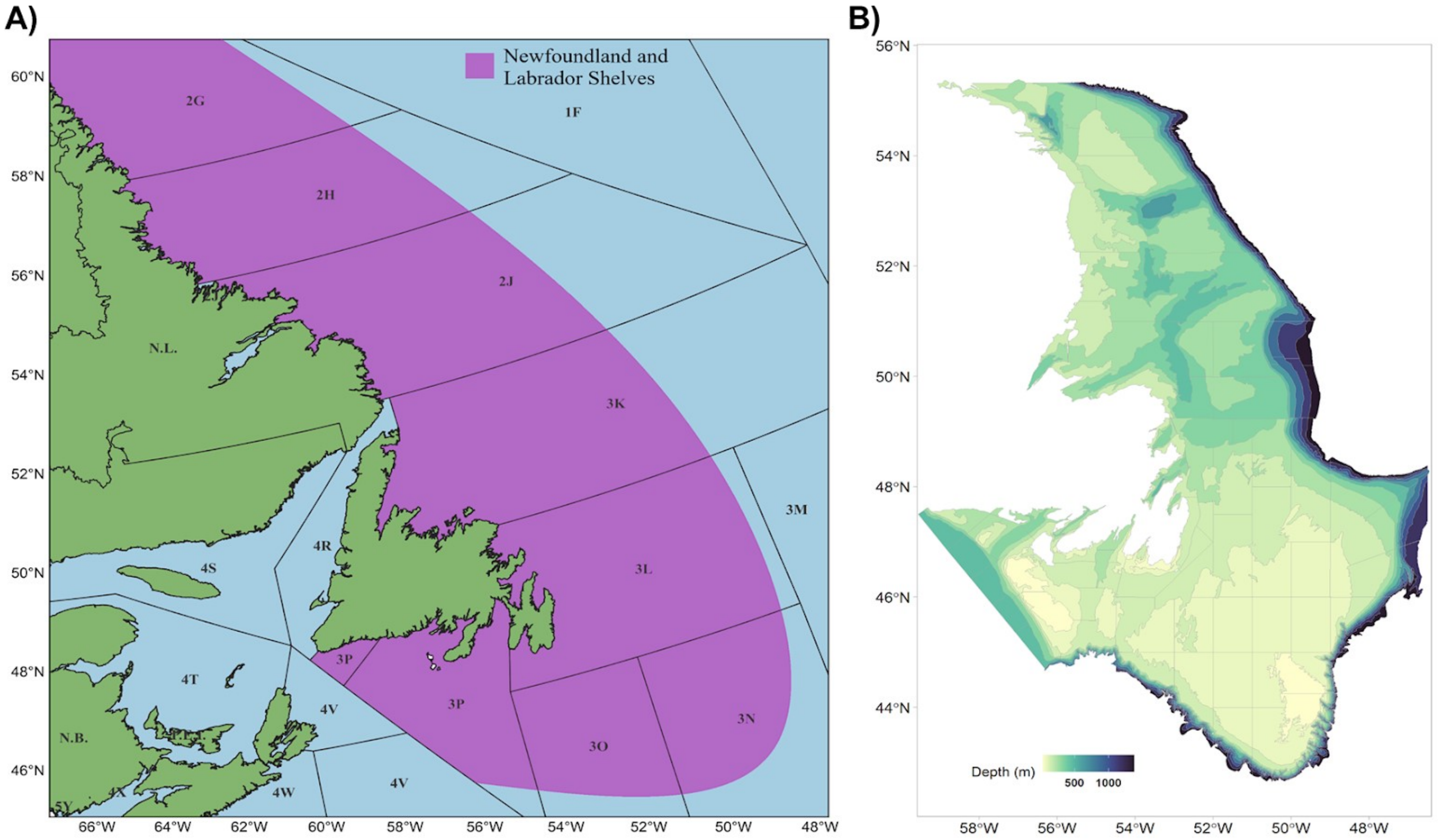


Figure 1: A) map of the Northwest Atlantic Ocean, black lines separating NAFO divisions. The Newfoundland and Labrador shelves are shaded in purple. B) bathymetry map for the Newfoundland and Labrador Shelves showing the strata used in the analysis (this excludes NAFO divisions 2G and 2H). Each stratum is outlined in grey and color represents the average area depth (darker colors are deeper waters).

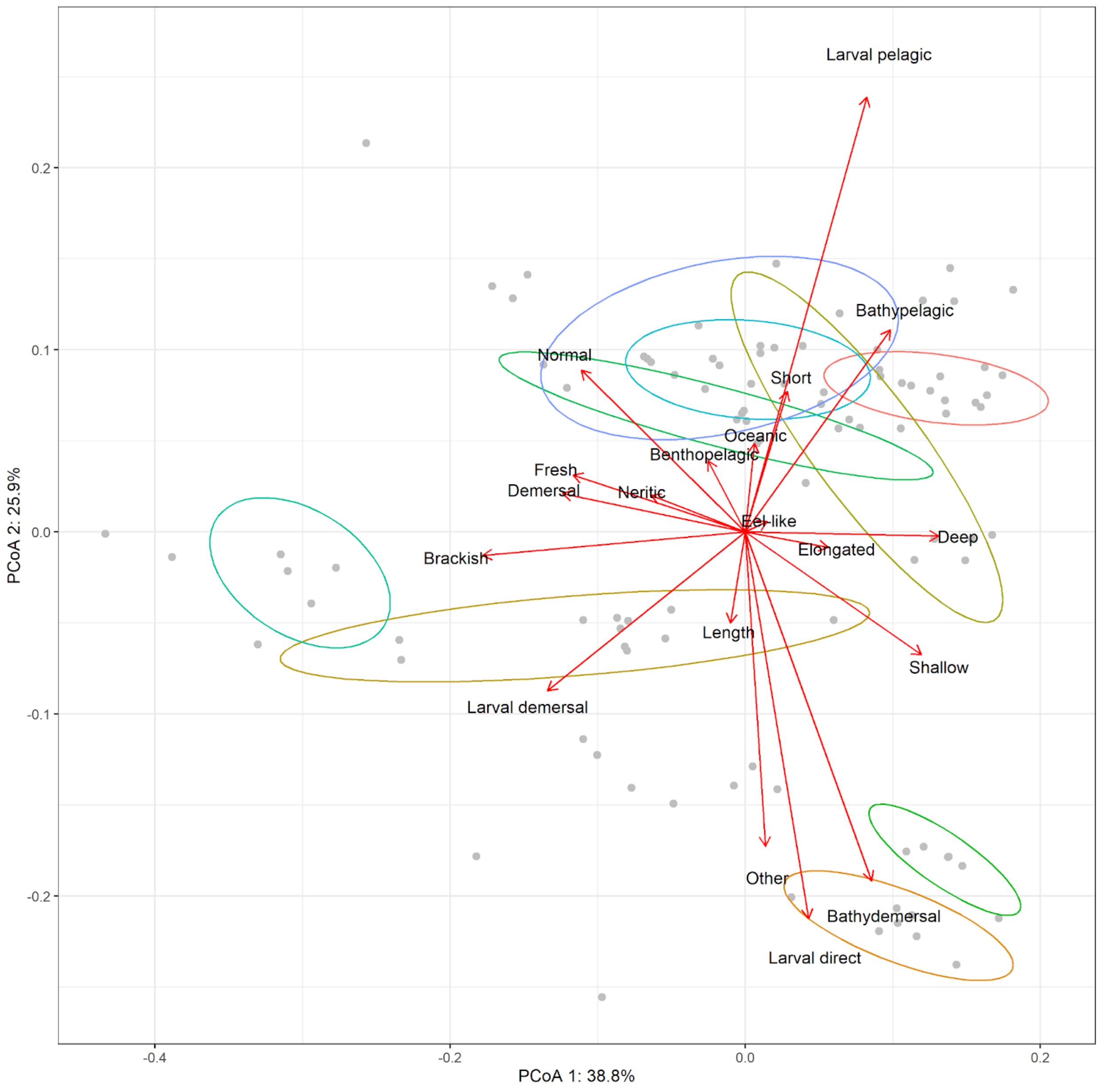


Figure 2: PCoA of the gower's distance matrix, where each grey point is a species and vectors (red arrows) represent dispersal traits. The longer the vector the stronger the relationship between that dispersal trait and the species distribution in trait space. Ellipses encircle 9 of the 25 dispersal groups which had enough data points to create an ellipse.

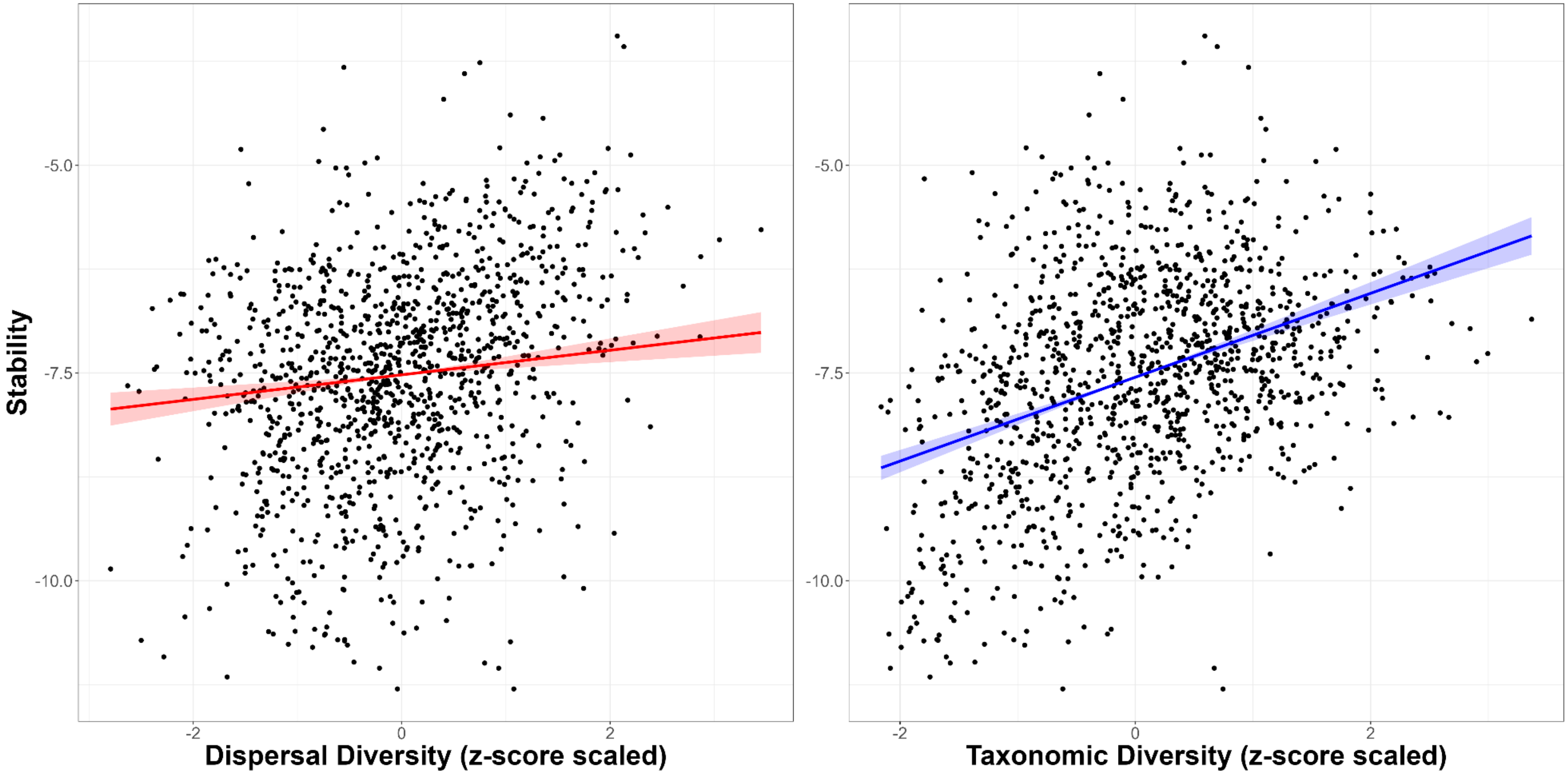


Figure 3: Performed in separate regressions, the **left panel** shows the effect of dispersal diversity, measured by trait evenness, on community stability (red regression line with 95% confidence intervals) and **right panel** shows the effect of taxonomic diversity, measured by effective species number, on community stability (blue regression line with 95% confidence intervals) across the strata of the Newfoundland and Labrador Shelves from 1995-2017. Each point is a stratum, stability is measured as the log, inverse-standard

deviation in biomass change over 5-year intervals and the average value of the respective diversity metrics are measured for the same time period.

Table 1: Marine fish dispersal-linked traits, including the definition and justification for being considered toward dispersal ability.

Trait	Description	Justification
Latitudinal range	Maximum and minimum latitude of a species range.	The latitudinal range of a species is correlated with their biotic and abiotic tolerances. A broader range indicates more versatility (Hengeveld 1990) and may indicate better strategies for long distance dispersal.
Depth range	Maximum and minimum depth a species inhabits, as well as their common depth range.	Position in the water column can contribute to how much individuals are affected by ocean currents and indicate population connectivity by mode of dispersal (Hilário *et al.* 2015).
Mobility type	The ability of the adult phase of the species to disperse actively (swimming) or is anchored in place (sessile).	Adult mobility has a direct effect of range expansion (Sunday *et al.* 2015) and therefore has a direct effect on a species dispersal capability. Dispersal in the adult phase can increase dispersal potential (Martins *et al.* 2017).
Body length	The average body length of adult individuals.	Larger adult body sizes have been positively correlated with farther dispersal (Radinger & Wolter 2014).
Body shape	Lateral body shape and cross section of species at the adult stage.	Body shape can indicate species level swimming ability (Videler & Wardle 1991; Wardle *et al.* 1995) which is important for dispersal at the adult stage.

Spawning time	Time of the year when mature individuals reproduce and release spawn.	Stochastic spawning could lead to competition avoidance for propagules (Berkley *et al.* 2010; Aiken & Navarrete 2014) and larval dispersal via ocean currents can differ throughout the year based on ocean and wind patterns (Edwards *et al.* 2007).
Fecundity	The average relative or absolute number of offspring a female will produce during a single reproductive event.	More offspring into the environment can lead to a greater chance of survival and increase dispersal potential (Warner & Chesson 1985).
Larval strategy	Larvae can have a high dispersal potential either as lecithotrophic or planktotrophic, or a form of direct development that has a low dispersal potential.	The type of larvae produced can greatly impact dispersal potential, direct development (brooded or crawlers) will have a lower dispersal potential then pelagic or free-swimming larvae (Grantham *et al.* 2003). However, species with brooded larvae have been seen to be more effective colonizers (Johannesson 1988)..
Pelagic	Pelagic vs. demersal spawning/hatching species.	Demersal hatching species tend to have lower dispersal potential than pelagic hatching species (Suthers & Frank 1991). Planktonic larvae tend to disperse farther and more uniformly carried by ocean currents (Almany *et al.* 2013).
Pelagic larval duration (PLD)	The length of time larvae will remain in the pelagic zone before settling. Usually determined on the size of their yolk sac.	The length of time a larva can stay in the pelagic before settling will reflect the dispersal potential (Graham & Sebens 1996; Bradbury *et al.* 2008). Trends show that short PLD and long PLD happen to disperse less far than intermediate PLD (Shanks 2009).
Dispersal distance	The distance traveled away from the natal site by the dispersal stage of a species life cycle.	Dispersal distances can vary widely in a population. Dispersal kernels are the shape that a population creates from dispersing, constructed from propagules, to determine the most probable distance they will disperse from a given location (Edwards *et al.* 2007; Pinsky *et al.* 2017). The minimum, maximum and average distances can all provide important information on how populations are connected via dispersal.

Larval length	Average length of larvae upon hatching.	Smaller larvae upon hatching tend to travel farther, they typically have larger yolk sacs allowing them to survive in the water column for longer (Suthers & Frank 1991) and are more easily carried away by ocean currents.
Rafting	Clumping or aggregation of larvae or adults that disperse as a unit, usually by ocean currents.	Aggregations of larvae tend to have better dispersal potential as they settle together which is better for establishment (Pedersen & Guichard 2016).
Vertical Movement	Movement of individuals up and down the water column, perhaps daily.	Vertical migration of larvae for feeding can subject them to variable current force leading to stochastic dispersal (Suthers & Frank 1991). Diel vertical migration is also important for survival and growth, as light and predation is variable at different depths (Fiksen *et al.* 2007).

References

Aiken, C.M. & Navarrete, S.A. (2014). Coexistence of competitors in marine metacommunities: environmental variability, edge effects, and the dispersal niche. *Ecology*, 95, 2289–2302.

Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.

Almany, G.R., Hamilton, R.J., Bode, M., Matawai, M., Potuku, T., Saenz-Agudelo, P., *et al.* (2013). Dispersal of Grouper Larvae Drives Local Resource Sharing in a Coral Reef Fishery. *Current Biology*, 23, 626–630.

de Bello, F., Lavorel, S., Hallett, L.M., Valencia, E., Garnier, E., Roscher, C., *et al.* (2021). Functional trait effects on ecosystem stability: assembling the jigsaw puzzle. *Trends in Ecology & Evolution*, 36, 822–836.

Berkley, H.A., Kendall, B.E., Mitarai, S. & Siegel, D.A. (2010). Turbulent dispersal promotes species coexistence. *Ecology Letters*, 13, 360–371.

Bernier, R.Y., Jamieson, R.E. & Moore, A.M. (2018). State of the Atlantic Ocean Synthesis Report. *Canadian Technical Report of Fisheries and Aquatic Sciences 3167*.

Bonte, D. & Dahirel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos*, 126, 472–479.

Borcard, D., Gillet, F. & Legendre, P. (2018). Cluster Analysis. In: *Numerical Ecology with R*, Use R! (eds. Borcard, D., Gillet, F. & Legendre, P.). Springer International Publishing, Cham, pp. 59–150.

Bowler, D.E. & Benton, T.G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, 80, 205–225.

Bradbury, I.R., Laurel, B., Snelgrove, P.V.R., Bentzen, P. & Campana, S.E. (2008). Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1803–1809.

Bradbury, I.R. & Snelgrove, P.V.R. (2001). Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. *Can. J. Fish. Aquat. Sci.*, 58, 811–823.

Chadwick, E., Brodie, W., Colbourne, E., Clark, D., Gascon, D. & Hurlbut, T. (2007). History of Annual Multi-Species Trawl Surveys on the Atlantic Coast of Canada. *AZMP Bull.*, 6.

Chao, A., Chiu, C.-H. & Jost, L. (2014). Unifying Species Diversity, Phylogenetic Diversity, Functional Diversity, and Related Similarity and Differentiation Measures Through Hill Numbers. *Annu. Rev. Ecol. Evol. Syst.*, 45, 297–324.

Chao, A. & Ricotta, C. (2019). Quantifying evenness and linking it to diversity, beta diversity, and similarity. *Ecology*, 100, e02852.

Chisholm, C., Lindo, Z. & Gonzalez, A. (2011). Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. *Ecography*, 34, 415–424.

Clobert, J., Galliard, J.-F.L., Cote, J., Meylan, S. & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, 12, 197–209.

Clobert, J., Massot, M. & Galliard, J.-F.L. (2012). Multi-determinism in natal dispersal: the common lizard as a model system. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 29–40.

Convertino, M., Muneepeerakul, R., Azaele, S., Bertuzzo, E., Rinaldo, A. & Rodríguez-Iturbe, I. (2009). On neutral metacommunity patterns of river basins at different scales of aggregation. *Water Resources Research*, 45.

Cote, J. & Clobert, J. (2012). Dispersal syndromes in the common lizard: personality traits, information use, and context-dependent dispersal decisions. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 152–160.

DFO. (2009). Development of a Framework and Principles for the Biogeographic Classification of Canadian Marine Areas. *Can. Sci. Advis. Sec. Sci. Advis. Rep.*, 2009/056, 17.

Edwards, K.P., Hare, J.A., Werner, F.E. & Seim, H. (2007). Using 2-dimensional dispersal kernels to identify the dominant influences on larval dispersal on continental shelves. *Mar. Ecol.-Prog. Ser.*, 352, 77–87.

Figueiredo, J. & Connolly, S.R. (2012). Dispersal-mediated coexistence under recruitment limitation and displacement competition. *Ecological Modelling*, 243, 133–142.

Fiksen, Ø., Jørgensen, C., Kristiansen, T., Vikebø, F. & Huse, G. (2007). Linking behavioural ecology and oceanography: larval behaviour determines growth, mortality and dispersal. *Marine Ecology Progress Series*, 347, 195–205.

Froese, R. & Pauly, D. (2022). *FishBase. World Wide Web electronic publication.* Available at: www.fishbase.org. Last accessed .

Gary, S.F., Fox, A.D., Biastoch, A., Roberts, J.M. & Cunningham, S.A. (2020). Larval behaviour, dispersal and population connectivity in the deep sea. *Scientific Reports*, 10, 10675.

Gower, J.C. (1966). Some Distance Properties of Latent Root and Vector Methods Used in Multivariate Analysis. *Biometrika*, 53, 325–338.

Graham, K.R. & Sebens, K.P. (1996). The Distribution of Marine Invertebrate Larvae Near Vertical Surfaces in the Rocky Subtidal Zone. *Ecology*, 77, 933–949.

Grantham, B.A., Eckert, G.L. & Shanks, A.L. (2003). Dispersal Potential of Marine Invertebrates in Diverse Habitats. *Ecological Applications*, 13, S108–S116.

Gravel, D., Massol, F. & Leibold, M.A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, 7, 12457.

Grüss, A., Kaplan, D.M. & Hart, D.R. (2011). Relative Impacts of Adult Movement, Larval Dispersal and Harvester Movement on the Effectiveness of Reserve Networks. *PLOS ONE*, 6, e19960.

Guzman, L.M., Germain, R.M., Forbes, C., Straus, S., O'Connor, M.I., Gravel, D., *et al.* (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecology Letters*, 22, 19–33.

Hayes, S.M. & Anderson, K.E. (2018). Beyond connectivity: how the structure of dispersal influences metacommunity dynamics. *Theor Ecol*, 11, 151–159.

Heino, J., Melo, A.S., Siqueira, T., Soininen, J., Valanko, S. & Bini, L.M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology*, 60, 845–869.

Hengeveld, R. (1990). *Dynamic Biogeography*. Cambridge University Press.

Hilário, A., Metaxas, A., Gaudron, S.M., Howell, K.L., Mercier, A., Mestre, N.C., *et al.* (2015). Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. *Front. Mar. Sci.*, 2.

Huffaker, C. (1958). Experimental studies on predation: Dispersion factors and predator-prey oscillations. *Hilgardia*, 27, 343–383.

Hutchings, J.A. (2011). Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. *Canadian Journal of Fisheries and Aquatic Sciences*.

Ives, A.R. & Carpenter, S.R. (2007). Stability and Diversity of Ecosystems. *Science*, 317, 58–62.

Jacob, S., Chaine, A.S., Huet, M., Clobert, J. & Legrand, D. (2019). Variability in Dispersal Syndromes Is a Key Driver of Metapopulation Dynamics in Experimental Microcosms. *The American Naturalist*, 194, 613–626.

Jiang, X., Xu, X., Tao, M., Li, Z., Zhang, S. & Li, H. (2021). The effects of dispersal ability on metacommunity structure of macroinvertebrates in subtropical Chinese high-mountain streams: seasonal shifts in relative contribution of local environment and spatial processes. *Environ Sci Pollut Res*, 28, 38573–38583.

Johannesson, K. (1988). The Paradox of Rockall: Why Is a Brooding Gastropod *(littorina Saxatilis)* More Widespread Than One Having a Planktonic Larval Dispersal Stage *(l. Littorea)*? *Mar. Biol.*, 99, 507–513.

Kinlan, B.P. & Gaines, S.D. (2003). Propagule Dispersal in Marine and Terrestrial Environments: A Community Perspective. *Ecology*, 84, 2007–2020.

Kinlan, B.P., Gaines, S.D. & Lester, S.E. (2005). Propagule dispersal and the scales of marine community process. *Diversity and Distributions*, 11, 139–148.

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V. & Aschan, M. (2015). Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151546.

Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.

Laliberté, E., Legendre, P. & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. *R package version*, 1, 0–12.

Legendre, P. & Legendre, L. (2012). *Numerical Ecology*. Elsevier.

Leibold, M.A., Chase, J.M. & Ernest, S.K.M. (2017). Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. *Ecology*, 98, 909–919.

Leibold, M.A., Holyoak, M. & Mouquet, N. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7, 601–613.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., *et al.* (2020). Species better track climate warming in the oceans than on land. *Nat Ecol Evol*, 4, 1044–1059.

Lester, S.E. & Ruttenberg, B.I. (2005). The Relationship between Pelagic Larval Duration and Range Size in Tropical Reef Fishes: A Synthetic Analysis. *Proceedings: Biological Sciences*, 272, 585–591.

Luiz, O.J., Allen, A.P., Robertson, D.R., Floeter, S.R., Kulbicki, M., Vigliola, L., *et al.* (2013). Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 16498–16502.

Luiz, O.J., Madin, J.S., Robertson, D.R., Rocha, L.A., Wirtz, P. & Floeter, S.R. (2012). Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes. *Proceedings: Biological Sciences*, 279, 1033–1040.

Malaterre, C., Dussault, A.C., Rousseau-Mermans, S., Barker, G., Beisner, B.E., Bouchard, F., *et al.* (2019). Functional Diversity: An Epistemic Roadmap. *BioScience*, 69, 800–811.

Martins, G., Matias, M., Moniz, I., Rius, C., Sanderson, J., Neto, A.I., *et al.* (2017). Post-settlement dispersal ability determines structure of marine benthic metacommunities. *Marine Ecology Progress Series*, 569.

Matthysen, E. (2012). Multicausality of dispersal: a review. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 3–18.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J.E., Bender, M., *et al.* (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13757–13762.

Myers, R.A., Hutchings, J.A. & Barrowman, N.J. (1997). Why Do Fish Stocks Collapse? The Example of Cod in Atlantic Canada. *Ecological Applications*, 7, 91–106.

Nye, J.A., Link, J.S., Hare, J.A. & Overholtz, W.J. (2009). Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series*, 393, 111–129.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

Pedersen, E.J. & Guichard, F. (2016). At what scales does aggregated dispersal lead to coexistence? *Oikos*, 125, 1677–1687.

Pedersen, E.J., Koen-Alonso, M. & Tunney, T.D. (2020). Detecting regime shifts in communities using estimated rates of change. *ICES J Mar Sci*, 77, 1546–1555.

Pedersen, E.J., Marleau, J.N., Granados, M., Moeller, H.V. & Guichard, F. (2016). Nonhierarchical Dispersal Promotes Stability and Resilience in a Tritrophic Metacommunity. *The American Naturalist*, 187, E116–E128.

Pedersen, E.J., Thompson, P.L., Ball, R.A., Fortin, M.-J., Gouhier, T.C., Link, H., *et al.* (2017). Signatures of the collapse and incipient recovery of an overexploited marine ecosystem. *Royal Society Open Science*, 4, 170215.

Perdomo, G., Sunnucks, P. & Thompson, R.M. (2012). The role of temperature and dispersal in moss-microarthropod community assembly after a catastrophic event. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 3042–3049.

Pinsky, M.L., Saenz-Agudelo, P., Salles, O.C., Almany, G.R., Bode, M., Berumen, M.L., *et al.* (2017). Marine Dispersal Scales Are Congruent over Evolutionary and Ecological Time. *Current Biology*, 27, 149–154.

Podani, J. & Schmera, D. (2006). On dendrogram-based measures of functional diversity. *Oikos*, 115, 179–185.

R Core Team. (2022). R: A language and environment for statistical computing.

Radinger, J. & Wolter, C. (2014). Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries*, 15, 456–473.

Rodríguez, M.A. (2002). Restricted Movement in Stream Fish: The Paradigm Is Incomplete, Not Lost. *Ecology*, 83, 1–13.

Ronce, O. & Clobert, J. (2012). Dispersal syndromes. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 119–138.

Rousseeuw, P.J. (1987). Silhouettes: A graphical aid to the interpretation and validation of cluster analysis. *Journal of Computational and Applied Mathematics*, 20, 53–65.

Rue, H. & Held, L. (2005). *Gaussian Markov Random Fields: Theory and Applications*. Chapman and Hall/CRC, New York.

Shanks, A.L. (2009). Pelagic Larval Duration and Dispersal Distance Revisited. *The Biological Bulletin*, 216, 373–385.

Sol, D., Trisos, C., Múrria, C., Jeliazkov, A., González-Lagos, C., Pigot, A.L., *et al.* (2020). The worldwide impact of urbanisation on avian functional diversity. *Ecology Letters*, 23, 962–972.

Sperry, K.P., Hilfer, H., Lane, I., Petersen, J., Dixon, P.M. & Sullivan, L.L. (2019). Species diversity and dispersal traits alter biodiversity spillover in reconstructed grasslands. *Journal of Applied Ecology*, 56, 2216–2224.

Stevens, V.M., Trochet, A., Blanchet, S., Moulherat, S., Clobert, J. & Baguette, M. (2013). Dispersal syndromes and the use of life-histories to predict dispersal. *Evol Appl*, 6, 630–642.

Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., *et al.* (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18, 944–953.

Suthers, I.M. & Frank, K.T. (1991). Comparative persistence of marine fish larvae from pelagic versus demersal eggs off southwestern Nova Scotia, Canada. *Mar. Biol.*, 108, 175–184.

Thompson, P.L. & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97, 2867–2879.

Thompson, P.L. & Gonzalez, A. (2017). Dispersal governs the reorganization of ecological networks under environmental change. *Nature Ecology & Evolution*, 1, 1–8.

Thompson, P.L., Guzman, L.M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel, B., *et al.* (2020). A process-based metacommunity framework linking local and regional scale community ecology. *Ecology Letters*, 23, 1314–1329.

Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., *et al.* (2013). Dispersal and species' responses to climate change. *Oikos*, 122, 1532–1540.

Videler, J.J. & Wardle, C.S. (1991). Fish swimming stride by stride: speed limits and endurance. *Rev Fish Biol Fisheries*, 1, 23–40.

Villéger, S., Mason, N.W.H. & Mouillot, D. (2008). New Multidimensional Functional Diversity Indices for a Multifaceted Framework in Functional Ecology. *Ecology*, 89, 2290–2301.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., *et al.* (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395.

Wardle, C., Videler, J. & Altringham, J. (1995). Tuning in to fish swimming waves: body form, swimming mode and muscle function. *Journal of Experimental Biology*, 198, 1629–1636.

Warner, R.R. & Chesson, P.L. (1985). Coexistence Mediated by Recruitment Fluctuations: A Field Guide to the Storage Effect. *The American Naturalist*, 125, 769–787.

Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73, 3–36.

General Conclusion

It is well understood that through facilitating spatial interactions dispersal is a key mechanism for community stability (Crowley 1981; Bohonak & Jenkins 2003; Berkley *et al.* 2010; Figueiredo & Connolly 2012; Pedersen *et al.* 2016), however there has been less research on how community stability is established through the variation in dispersal behaviours (Bonte & Dahirel 2017; Bani *et al.* 2019; Sperry *et al.* 2019). Dispersal diversity is an aspect of functional diversity which encompasses the spectrum of intrinsic and extrinsic factors that lead to a species dispersal potential. There is still much to learn about how to account for and incorporate dispersal diversity in spatial models. My thesis attempts to define and summarize dispersal diversity and its role in stabilizing trophic interactions (Chapter 1), and then apply this theory to an empirical study system using dispersal linked traits to explore the relationship between dispersal diversity and community stability (Chapter 2).

In Chapter 1 I defined dispersal diversity and reviewed literature on how dispersal diversity can drive stability mechanisms in spatially structured food webs. I outlined intrinsic (individual traits) and extrinsic (habitat) sources of dispersal diversity which have been used to monitor community stability in theoretical and empirical research. This chapter highlights the multifaceted nature of dispersal diversity and its relationship with community stability and summarizes how creating variation between trophic levels of interacting species leads to community persistence through time.

In Chapter 2 I applied the theory of dispersal diversity to an empirical study system, the Newfoundland and Labrador Shelves. I collected measurements of dispersal linked traits and used them to calculate dispersal dispersity. To determine the impact of dispersal diversity on the community, I looked at the relationship between the change in community stability and dispersal diversity. I found that there is a positive linear relationship between stability and dispersal diversity. I also saw that dispersal diversity did not correlate with taxonomic diversity, meaning that we are capturing another aspect of diversity by including dispersal in our research.

Chapter 1 looked only at the role of dispersal diversity in stabilizing trophic systems, but there has also been research on how dispersal diversity drives stability in competitive systems (Allesina & Tang 2012; Figueiredo & Connolly 2012; Aiken & Navarrete 2014). For competitive interactions we can still focus on how variation in dispersal supports asynchrony and the intrinsic and extrinsic factors that create dispersal diversity. In this way, dispersal diversity could be measured for whole food webs to explore more broadly its relationship with stability through multiple types of interactions. In Chapter 2 I found that many of the traits which are important for dispersal in Atlantic marine fish have not been well documented. Moving forward on this topic more investment should go into studies which will fill in missing data, for example through laboratory studies to determine species pelagic larval durations.

Overall, my thesis contributes to the growing knowledge of spatial ecology and emphasizes the importance of including dispersal variation in spatial research. My first chapter could be used as a guide for readers to understand the foundations and sources of dispersal variation, and my second chapter is an example of how dispersal traits can be measured and used to calculate dispersal diversity for empirical research. More research is still needed to refine the understanding of how to use and monitor dispersal diversity in natural communities, a good place to start would be including dispersal variation between trophic levels and competing species when simulating data, and widely measuring traits to get a full representation of functionality in species.

References

Aiken, C.M. & Navarrete, S.A. (2014). Coexistence of competitors in marine metacommunities: environmental variability, edge effects, and the dispersal niche. *Ecology*, 95, 2289–2302.

Allesina, S. & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483, 205–208.

Bani, R., Fortin, M.-J., Daigle, R.M. & Guichard, F. (2019). Dispersal traits interact with dynamic connectivity to affect metapopulation growth and stability. *Theor Ecol*, 12, 111–127.

Berkley, H.A., Kendall, B.E., Mitarai, S. & Siegel, D.A. (2010). Turbulent dispersal promotes species coexistence. *Ecology Letters*, 13, 360–371.

Bohonak, A.J. & Jenkins, D.G. (2003). Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters*, 6, 783–796.

Bonte, D. & Dahirel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos*, 126, 472–479.

Clobert, J., Massot, M. & Galliard, J.-F.L. (2012). Multi-determinism in natal dispersal: the common lizard as a model system. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 29–40.

Crowley, P.H. (1981). Dispersal and the Stability of Predator-Prey Interactions. *The American Naturalist*, 118, 673–701.

Figueiredo, J. & Connolly, S.R. (2012). Dispersal-mediated coexistence under recruitment limitation and displacement competition. *Ecological Modelling*, 243, 133–142.

Gravel, D., Massol, F. & Leibold, M.A. (2016). Stability and complexity in model meta-ecosystems. *Nature Communications*, 7, 12457.

Guzman, L.M., Germain, R.M., Forbes, C., Straus, S., O'Connor, M.I., Gravel, D., *et al.* (2019). Towards a multi-trophic extension of metacommunity ecology. *Ecology Letters*, 22, 19–33.

Huffaker, C. (1958). Experimental studies on predation: Dispersion factors and predator-prey oscillations. *Hilgardia*, 27, 343–383.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009). The velocity of climate change. *Nature*, 462, 1052–1055.

Matthysen, E. (2012). Multicausality of dispersal: a review. In: *Dispersal Ecology and Evolution*. Oxford University Press, pp. 3–18.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.

Pedersen, E.J. & Guichard, F. (2016). At what scales does aggregated dispersal lead to coexistence? *Oikos*, 125, 1677–1687.

Pedersen, E.J., Koen-Alonso, M. & Tunney, T.D. (2020). Detecting regime shifts in communities using estimated rates of change. *ICES J Mar Sci*, 77, 1546–1555.

Pedersen, E.J., Marleau, J.N., Granados, M., Moeller, H.V. & Guichard, F. (2016). Nonhierarchical Dispersal Promotes Stability and Resilience in a Tritrophic Metacommunity. *The American Naturalist*, 187, E116–E128.

Perdomo, G., Sunnucks, P. & Thompson, R.M. (2012). The role of temperature and dispersal in moss-microarthropod community assembly after a catastrophic event. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 3042–3049.

Sperry, K.P., Hilfer, H., Lane, I., Petersen, J., Dixon, P.M. & Sullivan, L.L. (2019). Species diversity and dispersal traits alter biodiversity spillover in reconstructed grasslands. *Journal of Applied Ecology*, 56, 2216–2224.

Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., *et al.* (2015). Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters*, 18, 944–953.

Thompson, P.L. & Gonzalez, A. (2016). Ecosystem multifunctionality in metacommunities. *Ecology*, 97, 2867–2879.

Thompson, P.L. & Gonzalez, A. (2017). Dispersal governs the reorganization of ecological networks under environmental change. *Nature Ecology & Evolution*, 1, 1–8.

Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., *et al.* (2013). Dispersal and species' responses to climate change. *Oikos*, 122, 1532–1540.

Urban, M.C., Zarnetske, P.L. & Skelly, D.K. (2013). Moving forward: dispersal and species interactions determine biotic responses to climate change: Dispersal and species interactions. *Ann. N.Y. Acad. Sci.*, n/a-n/a.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., *et al.* (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395.

Appendix A: Supplementary Material

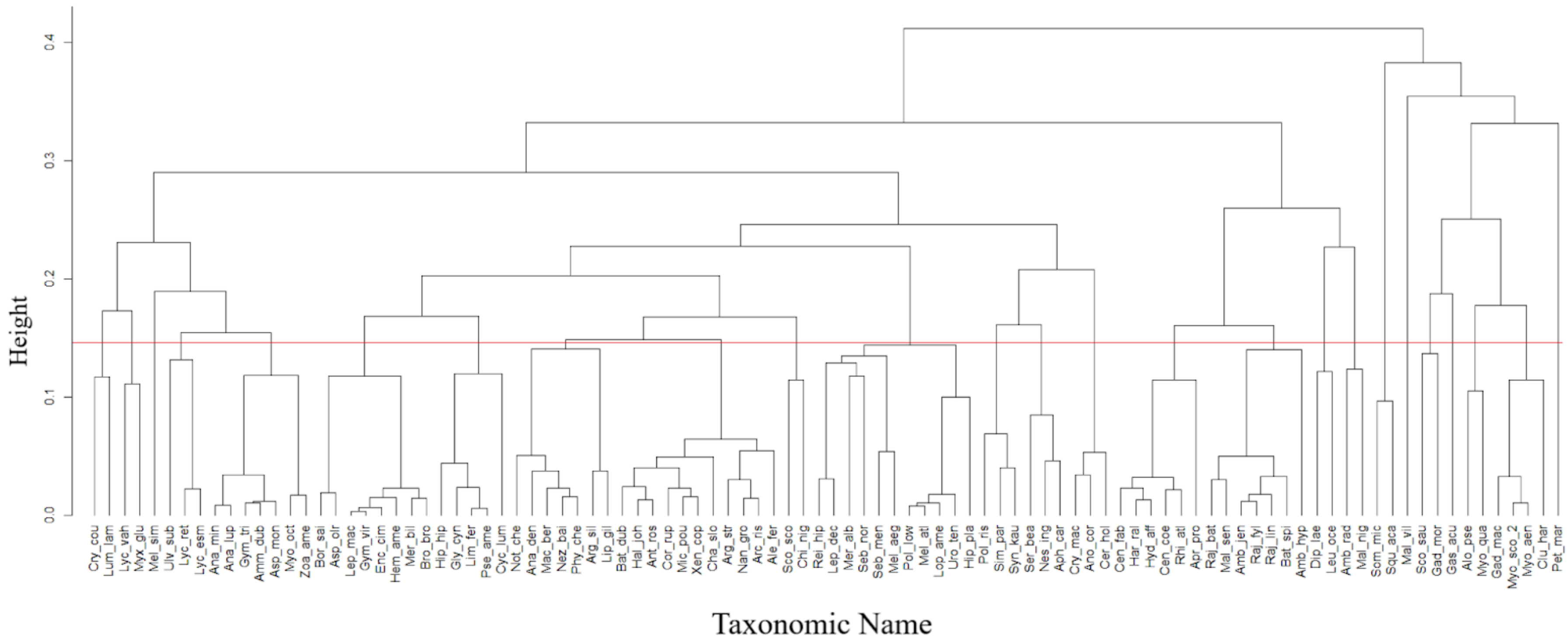


Figure S1: Hierarchical clustering of the marine fish community by dispersal trait values, using the unweighted pair group method and algorithmic mean (UPGMA). The y-axis is the height indicating the distance between clusters, and the red line cuts the dendrogram into the 25 identified clusters.

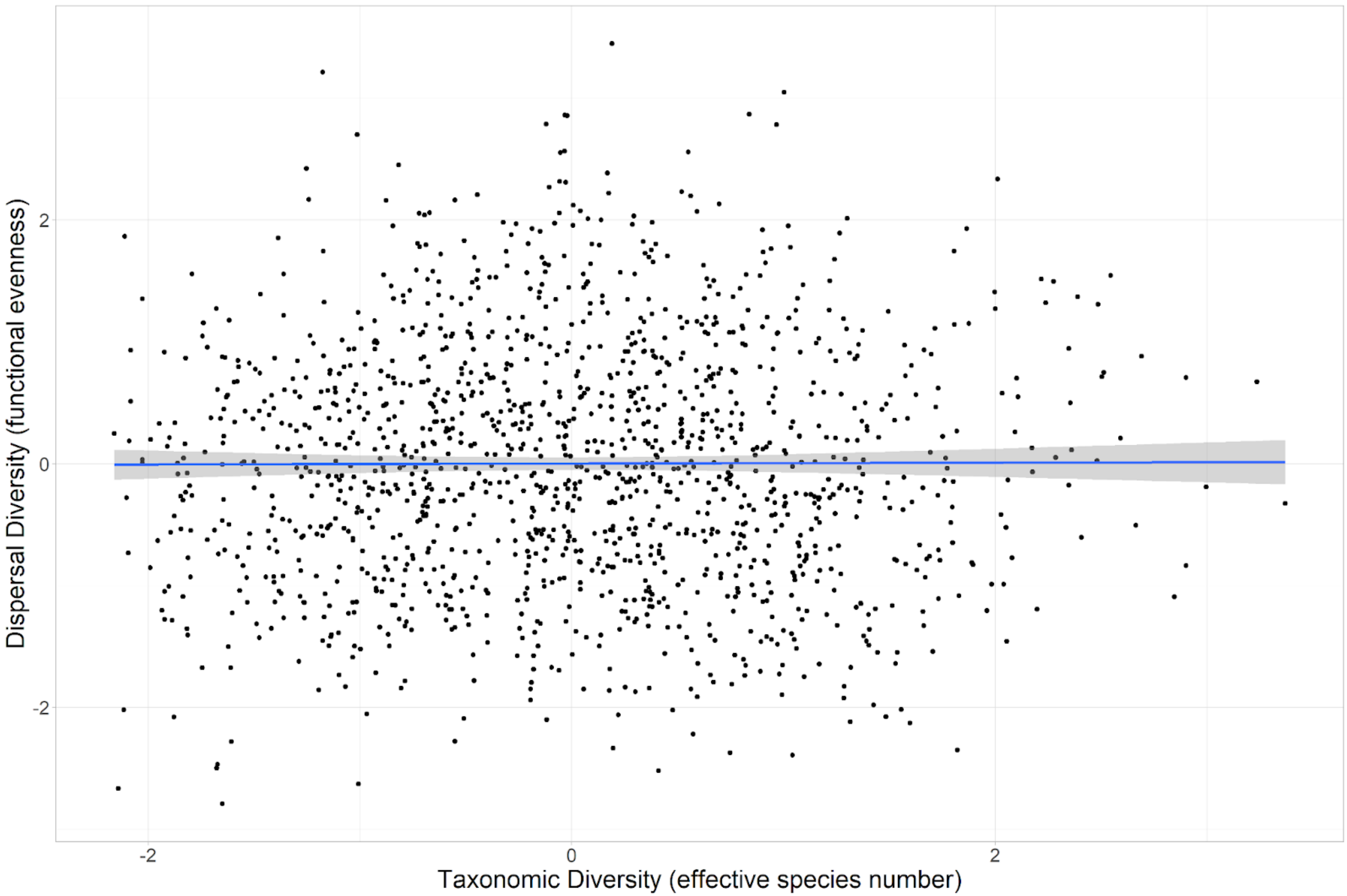
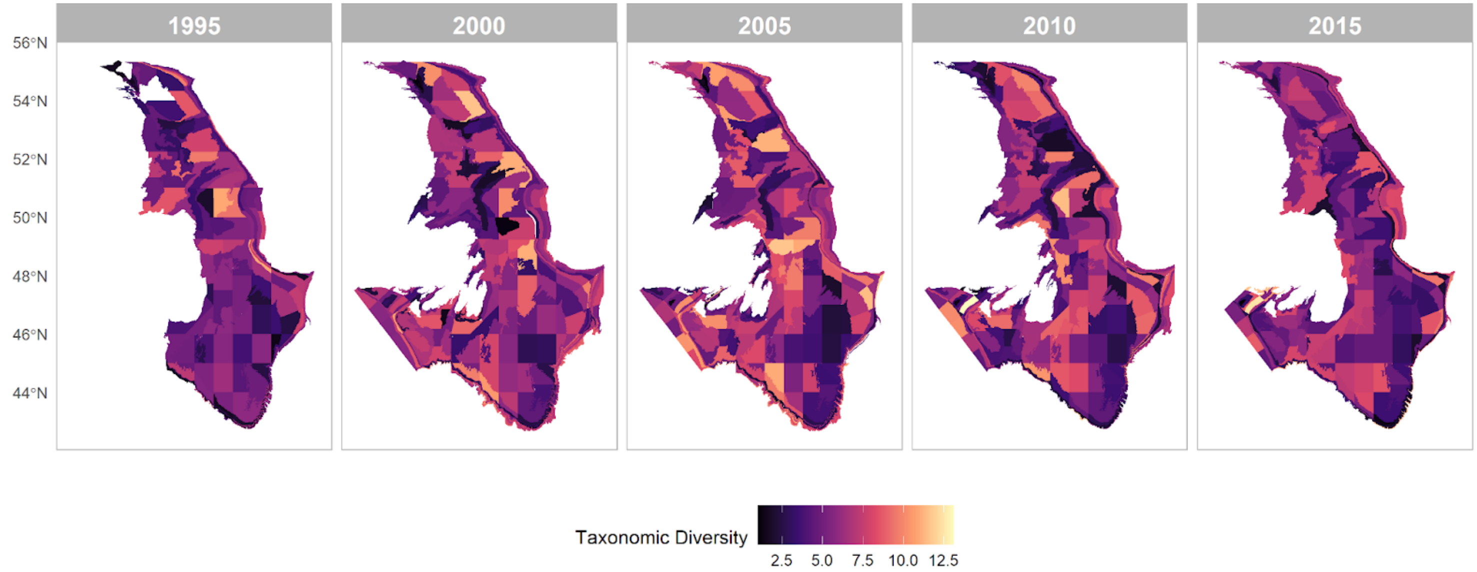


Figure S2. Correlation between effective species diversity and dispersal diversity, averaged over five year intervals from 1995-2017, shown in blue with the 95% confidence intervals represented in grey.


1995
2000
2005
2010
2015
56°N
54°N
52°N
50°N
48°N
46°N
44°N
Taxonomic Diversity
2.5
5.0
7.5
10.0
12.5

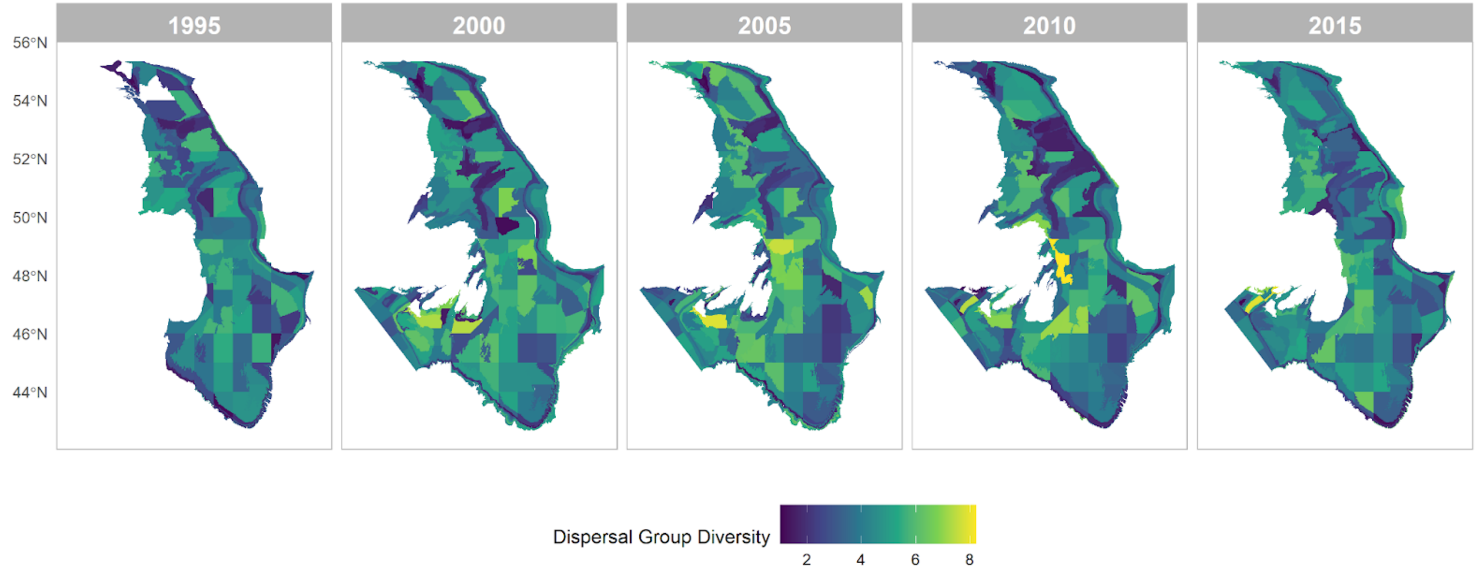

1995
2000
2005
2010
2015
56°N
54°N
52°N
50°N
48°N
46°N
44°N
Dispersal Group Diversity
2
4
6
8

Figure S3. Top panel shows taxonomic diversity (lighter color represents areas of higher diversity), measured by effective species number, per stratum every five years from 1995 until 2015. Bottom panel shows dispersal groups (lighter color represents areas of higher diversity), measured by effective species number for each group, per stratum every five years from 1995 until 2015.

Table S1: Data distribution for measured fish dispersal traits.

Trait	Trait Class	n missing	Complete rate (%)	Level count	Top levels	Numeric mean	Numeric SD
Anadromous/Catadromous	Factor	53	45.9	3	oceanodromous: 35, non: 6, anadromous: 4	NA	NA
BodyShape*	Factor	0	100	5	elongated: 48, fusiform:20, eel-like:11, other:11	NA	NA
Demersal/Pelagic*	Factor	0	100	6	demersal: 34, bathyd: 23, bathyp: 20, bentho: 15	NA	NA
FecundityType	Factor	62	36.7	3	absolute: 26, litter: 6, relative: 4	NA	NA
LarvalStrategy*	Factor	0	100	3	pelagic: 58, demersal: 23, direct: 17	NA	NA
LarvalVertical	Factor	71	27.8	2	no: 25, yes: 2	NA	NA
Mobility*	Factor	0	100	1	active: 98	NA	NA
Rafting	Factor	71	27.8	2	no: 25, yes: 2	NA	NA

Schooling	Factor	59	39.8	9	both: 18, shoal: 7, school: 6, bot: 2	NA	NA
SpawningSeason	Factor	58	40.8	5	spr: 11, sum: 11, win: 10, fal: 6	NA	NA
WeightFemale	Factor	94	4.1	4	?41: 1, 250: 1, 450: 1, 500: 1	NA	NA
AvePLD	Numeric	91	7.1	NA	NA	9.8e+01	5.3e+01
AverageDispersal	Numeric	93	5.1	NA	NA	6.4e+01	6.8e+01
Brack*	Numeric	0	100	NA	NA	1.9e-01	4.0-01
CommonLength	Numeric	63	35.7	NA	NA	4.9e+01	3.4e+01
CommonLengthF	Numeric	92	6.1	NA	NA	7.1e+01	3.2e+01
DepthRangeDeep*	Numeric	0	100	NA	NA	1.6e+03	1.3e+03
DepthRangeShallow*	Numeric	0	100	NA	NA	1.1e+02	1.8e+02
FecundityMax	Numeric	67	31.6	NA	NA	9.7e+05	3.0e+06
FecundityMean	Numeric	89	9.1	NA	NA	1.1e+05	3.1e+05
FecundityMin	Numeric	66	32.7	NA	NA	1.8e+05	4.4e+05
Fresh*	Numeric	0	100	NA	NA	5.1e-02	2.2e-01

LarvalLength	Numeric	60	38.8	NA	NA		2.7e+01	7.3e+01
Length*	Numeric	0	100	NA	NA		8.2e+01	7.1e+01
LongevityWild	Numeric	60	38.8	NA	NA		3.4e+01	6.2e+01
MaxDispersal	Numeric	95	3.1	NA	NA		1.0e+02	7.2e+01
MaxPLD	Numeric	90	8.1	NA	NA		2.1e+02	2.0e+02
MinDispersal	Numeric	96	2.0	NA	NA		5.2e+01	5.9e+01
MinPLD	Numeric	90	8.1	NA	NA		2.9e+01	1.4e+01
Saltwater*	Numeric	0	100	NA	NA		1.0e+00	0
Weight	Numeric	62	36.7	NA	NA		4.3e+04	1.4e+05

*Traits with at least 60 percent of trait measurements available, used for analysis of functional diversity (n = 10).

Table S2: Breakdown of traits characterizing the 25 dispersal clusters identified by hierarchical clustering using the unweighted pair group method and algorithmic mean (UPGMA).

Species Name	Species Code	BodyShape	Fresh	Brack	Saltwater	Demers Pelag	Depth Range Shallow	Depth Range Deep	Length	Mobility	Larval Strategy	Cluster ID
Alepisaurus ferox	Ale_fer	elongated	0	0	1	bathypelagic	0	1830	215	Active	pelagic	1
Antimora rostrata	Ant_ros	elongated	0	0	1	bathypelagic	350	3000	75	Active	pelagic	1
Arctozenus risso	Arc_ris	elongated	0	0	1	bathypelagic	0	2200	30	Active	pelagic	1
Argentina striata	Arg_str	elongated	0	0	1	bathypelagic	100	600	24	Active	pelagic	1
Bathypterois dubius	Bat_dub	elongated	0	0	1	bathypelagic	500	3237	13	Active	pelagic	1
Chauliodus sloani	Cha_slo	elongated	0	0	1	bathypelagic	200	4700	35	Active	pelagic	1
Coryphaenoides rupestris	Cor_rup	elongated	0	0	1	bathypelagic	180	2600	110	Active	pelagic	1
Halargyreus johnsonii	Hal_joh	elongated	0	0	1	bathypelagic	450	3000	56	Active	pelagic	1
Micromesistius poutassou	Mic_pou	elongated	0	0	1	bathypelagic	150	3000	55.5	Active	pelagic	1
Nansenia groenlandica	Nan_gro	elongated	0	0	1	bathypelagic	0	1400	24.5	Active	pelagic	1
Xenodermichthys copei	Xen_cop	elongated	0	0	1	bathypelagic	100	2650	31	Active	pelagic	1
Alosa pseudoharengus	Alo_pse	fusiform / normal	1	1	1	pelagic-neritic	5	145	40	Active	demersal	2
Myoxocephalus quadricornis	Myo_qua	fusiform / normal	1	1	1	demersal	0	100	60	Active	demersal	2
Amblyraja hyperborea	Amb_hyp	other	0	0	1	bathydemersal	92	2925	112	Active	demersal	3
Amblyraja jenseni	Amb_jen	other	0	0	1	bathydemersal	165	2550	74.25	Active	direct	3
Bathyraja spinicauda	Bat_spi	other	0	0	1	bathydemersal	140	1463	170	Active	direct	3
Malacoraja senta	Mal_sen	other	0	0	1	bathydemersal	450	1570	70	Active	direct	3
Rajella bathyphila	Raj_bat	other	0	0	1	bathydemersal	600	2300	90	Active	direct	3
Rajella fyllae	Raj_fyl	other	0	0	1	bathydemersal	170	2050	60	Active	direct	3
Rajella lintea	Raj_lin	other	0	0	1	bathydemersal	150	2117	123	Active	direct	3
Amblyraja radiata	Amb_rad	other	0	1	1	demersal	5	1540	105	Active	direct	4
Malacosteus niger	Mal_nig	other	0	1	1	bathydemersal	46	914	61	Active	direct	4
Ammodytes dubius	Amm_dub	elongated	0	0	1	demersal	0	108	25	Active	demersal	5
Anarhichas lupus	Ana_lup	elongated	0	0	1	demersal	1	600	150	Active	demersal	5

Anarhichas minor	Ana_min	elongated	0	0	1	demersal	25	600	180	Active	demersal	5
Aspidophoroides monopterygius	Asp_mon	elongated	0	0	1	demersal	0	695	22	Active	demersal	5
Gymnocanthus tricuspis	Gym_tri	elongated	0	0	1	demersal	0	320	56	Active	demersal	5
Myoxocephalus octodecemspinosus	Myo_oct	elongated	0	1	1	demersal	1	190	46	Active	demersal	5
Zoarces americanus	Zoa_ame	elongated	0	1	1	demersal	0	388	110	Active	demersal	5
Anarhichas denticulatus	Ana_den	elongated	0	0	1	benthopelagic	60	1700	180	Active	pelagic	6
Argentina silus	Arg_sil	elongated	0	0	1	bathydemersal	140	1440	70	Active	pelagic	6
Lipogenys gillii	Lip_gil	elongated	0	0	1	bathydemersal	400	2000	50	Active	pelagic	6
Macrourus berglax	Mac_ber	elongated	0	0	1	benthopelagic	100	1000	110	Active	pelagic	6
Nezumia bairdii	Nez_bai	elongated	0	0	1	benthopelagic	16	1000	40	Active	pelagic	6
Notacanthus chemnitzii	Not_che	elongated	0	0	1	benthopelagic	125	3285	120	Active	pelagic	6
Phycis chesteri	Phy_che	elongated	0	0	1	benthopelagic	90	1500	42	Active	pelagic	6
Anoplogaster cornuta	Ano_cor	short and / or deep	0	0	1	bathypelagic	2	4992	18	Active	pelagic	7
Ceratias holboelli	Cer_hol	short and / or deep	0	0	1	bathypelagic	400	4400	16	Active	pelagic	7
Cryptacanthodes maculatus	Cry_mac	short and / or deep	0	0	1	bathypelagic	0	3085	7.3	Active	pelagic	7
Aphanopus carbo	Aph_car	eel-like	0	0	1	bathypelagic	200	2300	151	Active	pelagic	8
Nessorhamphus ingolfianus	Nes_ing	eel-like	0	0	1	bathypelagic	0	1800	59.8	Active	pelagic	8
Serrivomer beanii	Ser_bea	eel-like	0	0	1	bathypelagic	0	6000	78	Active	pelagic	8
Apristurus profundorum	Apr_pro	elongated	0	0	1	bathydemersal	1100	1750	54.2	Active	direct	9
Centroscymnus coelolepis	Cen_coe	elongated	0	0	1	bathydemersal	180	2250	107	Active	direct	9
Centroscyllium fabricii	Cen_fab	elongated	0	0	1	bathydemersal	128	3700	120	Active	direct	9
Harriotta raleighana	Har_ral	elongated	0	0	1	bathydemersal	200	3100	120	Active	direct	9
Hydrolagus affinis	Hyd_aff	elongated	0	0	1	bathydemersal	300	3000	130	Active	direct	9
Rhinochimaera atlantica	Rhi_atl	elongated	0	0	1	bathydemersal	200	1500	140	Active	direct	9
Aspidophoroides olrikii	Asp_olr	elongated	0	1	1	demersal	0	632	8.6	Active	pelagic	10
Boreogadus saida	Bor_sai	elongated	0	1	1	demersal	0	1383	40	Active	pelagic	10
Brosme brosme	Bro_bro	elongated	0	0	1	demersal	18	1000	120	Active	pelagic	10
Enchelyopus cimbrius	Enc_cim	elongated	0	0	1	demersal	20	650	41	Active	pelagic	10
Gymnelus viridis	Gym_vir	elongated	0	0	1	demersal	0	556	30	Active	pelagic	10

Hemitripterus americanus	Hem_ame	elongated	0	0	1	demersal	2	180	64	Active	pelagic	10
Leptoclinus maculatus	Lep_mac	elongated	0	0	1	demersal	2	607	20	Active	pelagic	10
Merluccius bilinearis	Mer_bil	elongated	0	0	1	demersal	55	914	76	Active	pelagic	10
Chiasmodon niger	Chi_nig	elongated	0	0	1	pelagic-oceanic	700	2745	25	Active	pelagic	11
Scomber scombrus	Sco_sco	elongated	0	0	1	pelagic-oceanic	0	30	50	Active	pelagic	11
Clupea harengus	Clu_har	fusiform / normal	0	1	1	benthopelagic	0	364	45	Active	demersal	12
Gadus macrocephalus	Gad_mac	fusiform / normal	0	1	1	demersal	10	1280	119	Active	demersal	12
Myoxocephalus aenaeus	Myo_aen	fusiform / normal	0	1	1	demersal	1	357	18	Active	demersal	12
Myoxocephalus scorpius	Myo_sco_2	fusiform / normal	0	1	1	demersal	0	451	60	Active	demersal	12
Cryptopsaras couesii	Cry_cou	eel-like	0	0	1	demersal	1	110	97	Active	pelagic	13
Lumpenus lampretaeformis	Lum_lam	eel-like	0	0	1	demersal	30	373	50	Active	demersal	13
Cyclopterus lumpus	Cyc_lum	short and / or deep	0	0	1	benthopelagic	0	868	61	Active	pelagic	14
Glyptocephalus cynoglossus	Gly_cyn	short and / or deep	0	0	1	demersal	18	1570	60	Active	pelagic	14
Hippoglossus hippoglossus	Hip_hip	short and / or deep	0	0	1	demersal	10	3000	82.6	Active	pelagic	14
Limanda ferruginea	Lim_fer	short and / or deep	0	0	1	demersal	27	364	64	Active	pelagic	14
Pseudopleuronectes americanus	Pse_ame	short and / or deep	0	0	1	demersal	5	143	64	Active	pelagic	14
Dipturus laevis	Dip_lae	other	0	0	1	demersal	0	750	163	Active	demersal	15
Leucoraja ocellata	Leu_oce	other	0	0	1	demersal	0	120	110	Active	direct	15
Gadus morhua	Gad_mor	fusiform / normal	0	1	1	benthopelagic	0	600	200	Active	pelagic	16
Scomberesox saurus	Sco_sau	fusiform / normal	0	1	1	pelagic-neritic	0	1000	60	Active	pelagic	16
Gasterosteus aculeatus	Gas_acu	fusiform / normal	1	1	1	benthopelagic	0	100	11	Active	pelagic	17
Hippoglossoides platessoides	Hip_pla	fusiform / normal	0	0	1	demersal	50	2000	470	Active	pelagic	18
Leptagonus decagonus	Lep_dec	fusiform / normal	0	0	1	benthopelagic	127	1880	44	Active	pelagic	18
Lophius americanus	Lop_ame	fusiform / normal	0	0	1	demersal	0	800	120	Active	pelagic	18

Melanogrammus aeglefinus	Mel_aeg	fusiform / normal	0	0	1	bathypelagic	0	800	2.9	Active	pelagic	18
Melanostigma atlanticum	Mel_atl	fusiform / normal	0	0	1	demersal	10	450	112	Active	pelagic	18
Merluccius albidus	Mer_alb	fusiform / normal	0	0	1	bathydemersal	80	1170	40.6	Active	pelagic	18
Polymixia lowei	Pol_low	fusiform / normal	0	0	1	demersal	37	364	130	Active	pelagic	18
Reinhardtius hippoglossoides	Rei_hip	fusiform / normal	0	0	1	benthopelagic	1	2200	110	Active	pelagic	18
Sebastes mentella	Seb_men	fusiform / normal	0	0	1	bathypelagic	300	1441	77.5	Active	pelagic	18
Sebastes norvegicus	Seb_nor	fusiform / normal	0	0	1	pelagic-oceanic	100	1000	100	Active	pelagic	18
Urophycis tenuis	Uro_ten	fusiform / normal	0	0	1	demersal	100	1000	133	Active	pelagic	18
Lycodes esmarkii	Lyc_esm	elongated	0	0	1	bathydemersal	143	1090	75	Active	demersal	19
Lycodes reticulatus	Lyc_ret	elongated	0	0	1	bathydemersal	18	930	36	Active	demersal	19
Ulvaria subbifurcata	Ulv_sub	elongated	0	0	1	benthopelagic	0	55	18	Active	demersal	19
Lycodes vahlii	Lyc_vah	eel-like	0	0	1	bathydemersal	39	1200	52	Active	demersal	20
Myxine glutinosa	Myx_glu	eel-like	0	0	1	benthopelagic	20	1200	95	Active	demersal	20
Mallotus villosus	Mal_vil	elongated	1	1	1	pelagic-oceanic	0	725	20	Active	pelagic	21
Melamphaes simus	Mel_sim	elongated	0	0	1	bathypelagic	400	1853	15	Active	demersal	22
Petromyzon marinus	Pet_mar	eel-like	1	1	1	demersal	1	4099	120	Active	demersal	23
Polyacanthonotus rissoanus	Pol_ris	eel-like	0	0	1	bathydemersal	500	2800	9.5	Active	pelagic	24
Simenchelys parasitica	Sim_par	eel-like	0	0	1	bathydemersal	100	3000	61	Active	pelagic	24
Synaphobranchus kaupii	Syn_kau	eel-like	0	0	1	bathydemersal	120	4800	100	Active	pelagic	24
Somniosus microcephalus	Som_mic	elongated	0	1	1	benthopelagic	0	2992	427	Active	direct	25
Squalus acanthias	Squ_aca	elongated	0	1	1	benthopelagic	0	1460	95	Active	direct	25