AN ABSTRACT OF THE DISSERTATION OF

Shannon M. Hennessey for the degree of Doctor of Philosophy in Integrative Biology presented on June 18, 2020.

Title: The Influence of Prey Predictability on the Foraging Behavior and Movement of Intertidal Predators

Abstract approved: ____

Mark Novak

Fluctuations and spatial heterogeneity of habitat and resources is thought to underlie niche variation in animal populations, with intraspecific differences serving to produce or maintain population-, community-, or ecosystem-level patterns. Individual diet variation, defined as individual variation in food resource use within a population that is consistent over time, is gaining recognition as an important factor influencing larger-scale processes. Spatial and temporal predictability of prey resources, individual movement behaviors, and diet choice may all serve to maintain individual diet specialization. However, the relationships between these factors in establishing and maintaining individual-level variation at ecological scales remains poorly understood. This dissertation provides insight into the dependence of individual diet specialization on the predictability, productivity, and spatial structure of prey by integrating feedbacks between individual behaviors, populations, and communities at local and regional scales.

Foraging theory seeks to understand the relationships between the energetic demands of a predator, prey selection, patchiness of prey, and individual movement. To maximize energetic intake, a foraging predator must balance energy expended by foraging movements with energy gained via prey consumption, with foraging success greatly impacted by the scale of patchiness of prey. In Chapter 2, I correlated scale-dependent prey patchiness and predator feeding rates to predict predator movement in a heterogeneous prey environment. I then compared these predictions to observed movement of a predatory intertidal whelk *Nucella ostrina* over a 3-month period. I found that combining prey patchiness and predator feeding rates sufficiently explains predator movement rates, highlighting a tradeoff between prey heterogeneity and individual energetic demands in determining predator foraging behavior.

Foraging behavior can maintain variation in individual diet, with differential habitat use and prey selection correlated with different foraging strategies. Optimal search strategies for a foraging predator depend on the abundance and predictability of prey, therefore differences in individual diet breadth are thought to produce different foraging patterns. In Chapter 3, I connected the broad-scale movement patterns found in Chapter 2 with variation in individual foraging behavior by quantifying variation in individual foraging patterns and correlating these patterns to habitat use and diet breadth. I found evidence for variation in individual behaviors, habitat use, and diet diversity. However, there was an overwhelming influence of tidal cycles on movement patterns, rather than associations with prey choice or habitat occupancy. This is likely due to the high degree of prey productivity at my focal study site, making random search patterns and small foraging movements sufficiently efficient for finding prey.

While prey heterogeneity and individual behaviors within a population can maintain variation in individual diet at local scales, the processes that establish individual diet variation requires further study. The lack of environmental predictability has been posited to promote inter-individual differences on both ecological and evolutionary timescales, as tradeoffs between being a prey specialist versus a generalist result in one being favored over the other in certain environmental predictability regimes. In Chapter 4, I used manipulative laboratory experiments to investigate the role of site-specific environmental unpredictability on the relative contributions of learning and heritable diet plasticity in shaping the foraging efficiency of whelk hatchlings. My results indicated the importance of learning in individual foraging and prey handling efficiency. Additionally, there is suggestive evidence that prey predictability at the population source location decreases foraging times as well. However, site attributes or behavioral modification may play a larger role than prey predictability in determining individual foraging abilities I detected.

The Influence of Prey Predictability on the Foraging Behavior and Movement of Intertidal Predators

by

Shannon M. Hennessey

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APPROVED:

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Shannon M. Hennessey, Author

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Mark Novak assisted with the study design and writing of Chapters 2, 3, and 4. The Novak Lab also provided the unpublished feeding rate and invertebrate community composition datasets used in Chapter 2.

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DEDICATION

In loving memory of my grandparents,

William and Kathleen Hennessey – for always encouraging

curiosity and instilling the joy of simply

observing the natural world.

The Influence of Prey Predictability on the Foraging Behavior and Movement of Intertidal Predators

Chapter 1 – General Introduction

Variation is ubiquitous in biological systems, and has long been recognized as important in maintaining differences in niche utilization within animal populations. Environmental unpredictability and scale-dependent patchiness of communities underlie observed ecological patterns at landscape scales, with variation in habitat and prey resources impacting prey selection and foraging success (Pyke 1984). Variation among individuals within a population has recently come to the forefront of ecological inquiry, and these intraspecific differences are thought to produce ecological patterns across scales of biological organization (Futuyma & Moreno 1988). Individual-based approaches, therefore, aim to gain a more mechanistic view of how inter-individual differences create or maintain patterns observed at population, community and ecosystem levels (Careau & Garland 2012; Dall *et al.* 2012; Sih *et al.* 2012; Toscano *et al.* 2016).

The importance of individual variation is well established among evolutionary biologists, as natural selection operates on heritable differences between individuals. Similarly, the influences of individual variation on important ecological processes, such as species interactions (Schreiber *et al.* 2011; Gibert & Brassil 2014; Hart *et al.* 2016) and food web structure (Araújo *et al.* 2008; Gibert & DeLong 2017), has undergone much recent study. Indeed, individual variation can have greater ecological impacts than differences among species (Rall *et al.* 2011; Rudolf & Rasmussen 2013; Des Roches *et* *al.* 2018; Raffard *et al.* 2019). As evolution can occur over ecological time scales (i.e., eco-evolutionary dynamics: Pelletier *et al.* 2009; Post & Palkovacs 2009; Schreiber *et al.* 2011), linking ecological and evolutionary processes by understanding the extent and impacts of variation among individuals can help provide a more comprehensive and mechanistic view of how individual differences produce or maintain population-, community-, or ecosystem-level patterns (Bolnick *et al.* 2011; Schreiber *et al.* 2011; Careau & Garland 2012).

Behavioral traits often co-vary among individuals, with this variation persisting over time and across ecological contexts (Gosling 2001; Sih *et al.* 2004). Animal behavior is a key component in maintaining differences between individuals and is thought to underlie individual-level specialization of habitat use, foraging behavior, and prey selection. In particular, recent literature has highlighted the connection between animal personality syndromes and movement ecology, with attention focusing on the correlation of foraging behaviors and niche specialization (Sih *et al.* 2004, 2012; Réale *et al.* 2010; Dall *et al.* 2012; Quinn *et al.* 2012; Spiegel *et al.* 2017). Differences in predator foraging movement, for example, can have cascading ecological impacts by altering individual interactions with their environment.

One way that such individual differences in foraging behavior have been studied is in the context of prey choice and diet specialization. Individual diet specialization, defined as individual differences in food resource use within a population that is consistent over time (Bolnick *et al.* 2003), is increasingly recognized as important to population- and community-level processes. In populations exhibiting individual diet specialization, individuals function as specialists, utilizing a subset of the resources used by the population as a whole (Van Valen 1965; Bolnick *et al.* 2003). It has been proposed that cryptic variation in traits correlated to resource use or behavior underlies these individual differences in diet specialization (Bolnick *et al.* 2003; Araújo *et al.* 2008), but this has rarely been formally assessed.

Foraging theory has been used to explain the degree of diet specialization within a population (Emlen 1966; Stephens & Krebs 1986), with optimal search strategies for a foraging predator being dependent on the abundance and predictability of prey. Ultimately, predator individuals are thought to maximize fitness by consuming prey that will maximize energetic intake given costs and risks, and therefore make foraging decisions that directly impact fitness (Emlen 1966; Pyke 1984). A predator's specialization on a certain prey type should allow the predator to enhance its predation success, whether through innate or learned efficiency in finding certain prey in a patchy environment, or by increased proficiency in consuming a particular prey type.

Prey acquisition is therefore integral to maximizing fitness. However, environmental variation can have large influences on the behavior of predators foraging within patchy landscapes, as the abundance and spatial distribution of resources rarely stays constant. The predictability of resource availability is thought to impact the foraging success of predators within that environment, with the flexibility of individual foraging behaviors underlying the foraging success of a predator when switching from a preferred prey species to another prey when the preferred prey becomes rare (Curio 1976). Specializing on a certain prey could be costly if that prey is not consistently or predictably available (Futuyma & Moreno 1988; Van Tienderen 1991). Theory posits that under predictable environmental conditions, individual specialists outcompete generalists because specialists have greater foraging efficiency on preferred prey. By contrast, in unpredictable environments, generalism is favored because generalist individuals can be quicker to adapt to alternative resources (Futuyma & Moreno 1988). The combined tradeoffs between specializing and generalizing in different environments suggests that feedbacks exist between resource predictability, an individual's degree of diet specialization, and the subsequent effects of that variation on community structure.

This dissertation investigates the mechanisms that establish and maintain individual diet variation in a predatory intertidal whelk, *Nucella ostrina*, integrating across spatial scales, environmental predictability regimes, and levels of biological organization. Specifically, I (1) linked scale-dependent prey patchiness and individual feeding rates to predict predator foraging movement in a patchy prey landscape, (2) evaluated the roles of prey microhabitat occupancy and individual diet selection in shaping individual-level foraging behaviors, and (3) assessed the relative contributions of learning and heritability in determining individual diet specialization across a gradient of prey predictability.

Foraging theory predicts that prey patchiness can have strong influences on the movement of consumers across the prey landscape (Smith 1974; O'Neill *et al.* 1988; Russell *et al.* 1992). Within a heterogeneous environment, predator individuals are responding to the prey landscape and making behavioral decisions based on their abilities to detect prey. A predator's decision to stay within a patch or search for a new patch depends, in part, on the scale at which the patches occur, as well as the predator's movement relative to the scale of prey patchiness (Morse & Fritz 1982). Hence there is a balance between energetic intake via prey consumption and energy expended by foraging movement to maximize fitness. In Chapter 2, I quantified the scale-dependent patchiness of a rocky intertidal invertebrate community to characterize prey patchiness from the perspective of individual whelk predators foraging in a patchy prey environment. Coupled with individual feeding rates, I then predicted population movement rates and compared them to observed rates of movement. My results suggest that population movement rates are well-explained by the combined influences of prey patchiness and feeding rates, demonstrating the importance of prey spatial structure and individual energetic demands in shaping predator foraging behaviors.

To understand mechanisms underlying inter-individual patterns of prey use, we need to better identify the factors influencing individual prey choice and differences in foraging behaviors. Individual foraging behaviors are dependent on individual perceptions of prey distributions and prey selection (Wiens 1976; Kurvers *et al.* 2010; van Overveld & Matthysen 2010, 2013; Sih *et al.* 2012; Patrick & Weimerskirch 2014; Spiegel *et al.* 2017; Schirmer *et al.* 2019), with optimal search strategies depending on the abundance and predictability of prey. In Chapter 3, I characterized differences in individual foraging behaviors by tracking whelk individuals in the rocky intertidal over a 3-month period. I then linked variation in predator movement patterns to use of prey habitat and individual diet selection to better understand how individual foraging decisions are made in a heterogeneous prey environment, and by individuals with different diets. My results suggest that variation in individual foraging behaviors cannot be generalized to inter-individual differences in microhabitat community composition or individual diet specialization, especially within a highly productive prey environment. Instead, foraging activity and predation events were largely influenced by tidal cycles rather than diet specialization.

While individual diet specialization is maintained by individual variation in resource use or foraging behavior (Araújo *et al.* 2011), the underlying factors that establish individual diet specialization are less clear. Learned and heritable differences in prey detection or handling have been proposed as mechanisms establishing individual diet specialization (eg. Dunkin & Hughes 1984; Bolnick *et al.* 2002; Newsome *et al.* 2019). However, the predictability of prey resources may also play a large role in the relative strength of these mechanisms in shaping individual foraging behaviors. In Chapter 4, I investigated how prey preferences are established in populations across a range of prey predictability regimes. Specifically, by examining the influences of prior prey exposure on individual foraging and handling times in manipulative laboratory experiments using individuals sourced from sites experiencing different predictability regimes, I quantified the relative contributions of learning and heritable diet plasticity in shaping individual specialization for whelk hatchlings. I found that regardless of the resource predictability of an individual’s source location, prior foraging experience on mussels decreased their subsequent foraging time compared to whelks naïve to mussels. Counterintuitively, whelk consumption time of mussels was longer with prior exposure to mussels. As I saw only weak evidence for patterns with prey predictability, these results suggest that site attributes or behavioral modification may play a larger role in determining individual foraging abilities I detected. The combined influences of learned and heritable foraging efficiency seen here suggest that feedbacks exist between resource predictability, an individual’s degree of diet specialization, and subsequent effects of that variation on community composition.

Chapter 2 – Feeding rates and prey predictability predict predator movement in a rocky intertidal community

Shannon M. Hennessey and Mark Novak

2.1 Abstract

The perceived patchiness of prey depends on a predator’s rate of movement. To optimize net energy gain, predators should move through the environment at speeds that reduce perceived prey patchiness, minimizing energy expenditure while maximizing the homogeneity of prey encounter rates. Here, we test this expectation in an intertidal predatory whelk, *Nucella ostrina*, by quantifying the scale-dependent patchiness of the invertebrate community and individual feeding rates on focal prey taxa to predict optimal whelk movement rates. We then compare predicted movement to the observed movement of individually marked whelks relocated daily over a 3-month period. We found that movement rates are well-explained by the combined influences of prey patchiness and predator feeding rates. Our study demonstrates the importance of prey spatial structure and individual energetic demands for individual foraging behaviors, linking the behavior of individuals to the broader community patterns they affect.

2.2 Introduction

Predator-prey interactions have long been the subject of ecological inquiry (Stephens & Krebs 1986), as predators can be key in shaping the structure of biological communities (Paine 1966, 1974; Menge 1976; Robles 1987; Wootton 2002). Within a patchy prey environment, predator individuals are responding to the prey landscape and making behavioral decisions based on their abilities to detect prey in a patchy environment. A predator’s decision to stay within a patch or search for a new patch depends, in part, on the scale at which the patches occur, and the predator’s movement relative to the scale of prey patchiness (Morse & Fritz 1982). Thus, the scale-dependent degree of prey patchiness can have strong influences on the movement of consumers across the prey landscape (Smith 1974; O'Neill *et al.* 1988; Russell *et al.* 1992).

Prey patchiness is inherent to ecological systems, and is dependent on multiple biological and physical factors acting across spatial scales influencing the prey landscape (Crisp & Meadows 1962; Paine & Levin 1981; Shanks & Wright 1986). Physical disturbances, as well as the colonization and settlement of taxa, generally influence communities at larger spatial scales, while the effects of interspecific interactions and predation can be more prominent at small spatial scales (Berlow 1997; Wootton 2002). However, the scales at which these mechanisms underlying community heterogeneity operate are often different than the scales at which patterns in community structure are observed by those studying it (Levin 1992). Scale and pattern are inextricably linked (Hutchinson 1953), so by better understanding the relationship between the scale at which patterns are described and the relevant scales of processes influencing said pattern we can gain a more mechanistic view of drivers shaping interactions within biological communities.

Despite continued efforts to better understand the relationship between prey patchiness and predator foraging movements (eg. Calcagno *et al.* 2014), the processes that determine the scale at which prey landscape heterogeneity most impacts predator foraging behavior have not been well identified. Within a patchy environment, each predator individual must balance time spent foraging in a patch with time spent moving between patches, maximizing the encounter rate of preferred prey while minimizing energy expenditure (eg. Weihs 1975; Ware 1978; Norberg 1981; Pyke 1981; Gendron & Staddon 1983). The rate of predator movement is also dependent on variation in between-patch quality, with the average movement rates predicted to decrease with reduced patch heterogeneity (Calcagno *et al.* 2014). As such, predator perceptions of the prey environment are subject to their rate of movement throughout that landscape, with changes in predator movement increasing or decreasing prey encounter and the perceived patchiness of prey while foraging (Wiens 1969, 1976).

While predator individuals may be able to compensate for the effects of patchiness in the prey environment by altering foraging movements, variation in patchiness through time can also influence forager behavior (Wiens 1969, 1976; Levin 1992). In temporally variable environments, behavioral flexibility becomes increasingly important for organisms interacting with their prey (Hazlett 1988). As experienced environmental heterogeneity is solely determined by the individual's perspective, variation in an individual's prey choice may modify the individual's perceived patchiness of the prey environment it experiences at any given time, and the subsequent foraging behaviors that accompany it. Therefore, the patchiness of the prey environment can have strong influences on the foraging behaviors of predator individuals, as well as the aggregate responses of the predator population and their resulting impact on the prey environment.

Here, we quantify patchiness in invertebrate community composition in a rocky intertidal system across spatial scales to infer the scales of optimal prey homogeneity from the perspective of an individual whelk predator, *Nucella ostrina*. By considering this optimal scale in conjunction with observed whelk feeding rates, we then test our hypothesis that *N. ostrina* moves at rates that maximize the homogeneity of prey encounter, while minimizing energy expenditure. We then compare our predicted movement rates to those measured by tracking the movement of individual whelks for three months. We find that tradeoffs in seasonality of the optimal scale of prey patchiness and individual predator feeding rates result in predicted predator movement rates consistent with the range of observed individual movement. These results suggest that the tradeoffs between patchiness in the prey environment and individual energetic demands play a key role in shaping individual predator foraging behaviors as they move through a patchy prey landscape.

2.3 Methods

2.3.1 Predicting movement rates

Predator movement rates should reflect a balance between scale-dependent patchiness in prey and individual energetic demands. We characterized the scale-dependent variation of prey patchiness through space and through time to predict the optimal velocity with which whelks should move to maximize prey calorie intake at minimal cost and how this tradeoff should change movement rates over time. We first identified two main components: (1) the "*scale of optimal prey homogeneity*", defined as the scale at which, from an individual predator's perspective, the prey's abundance is homogeneous enough to minimize variation in prey encounter rates, and (2) per-capita feeding rates, defined as the number of prey eaten per predator per day. We then related these components to individual predator movement via the following equation:

Expected movement rate (m/day) =

*Scale of optimal prey homogeneity (m/prey item) **

Per-capita feeding rate (prey items/day) (2.1)

2.3.1.1 Study system

Our study site consisted of three flat rocky shore benches near Yachats, Oregon, USA (44.323 N, 124.107 W) (e.g., see the idealized "bench" in Figure 2.1). The study site is part of the Cape Perpetua region, characterized by intermittent upwelling, retentive currents, and a wide continental shelf. This region exhibits high nutrient availability and primary production, high sessile invertebrate recruitment, and fast growth of sessile and mobile invertebrates, making it a highly productive site with rapid turnover. These features of the site thus facilitate studies of variation in community composition (Menge *et al.* 2015) and predator-prey interactions (Navarrete 1996).

2.3.1.2 Prey patchiness

Each bench was divided into two sub-benches, within which 1.5x1.5m experimental patches ("patch" in Figure 2.1; n = 18) were scraped to bare rock within the mid-zone among mussel (*Mytilus californianus*) beds in July 2013 and marked at the corners with lag screws. Within each patch, permanent quadrats (25x35cm) ("quadrat" in Figure 2.1; n = 9) were marked with lag screws. To characterize patchiness in the invertebrate community, patches were surveyed monthly with each of the quadrats within each patch being photographed to quantify invertebrate community change. Invertebrate taxa were counted in three randomly selected quadrat photographs within each patch using ImageJ (Abràmoff *et al.* 2004) and converted to densities per square meter. The same three quadrats in each patch were counted at each of the 36 months of the sampling duration (the photos of all three quadrats of one patch for one month were lost).

To assess variation in invertebrate community composition across a range of spatial scales, invertebrate count data from each quadrat were parsed or aggregated at discrete spatial scales. To quantify densities at the smallest spatial scale, invertebrates were counted in four "sub-quadrats" ($0.0025m^2$ each, n=216 fixed sub-quadrats per time point; Figure 2.1) of the central 10x10cm square of each quadrat. To estimate invertebrate densities at larger-than-quadrat spatial scales, quadrat-level invertebrate densities were grouped by larger spatial extents and averaged across quadrats. To produce patch-level densities, quadrats were averaged within each patch at each sampling date ($2.25m^2$, n=18 per time point). Patch densities were further averaged across groups of 4-5 proximate patches to produce sub-bench invertebrate densities ($100m^2$, n=4 per time point), and groups of 8-10 proximate patches across the site for bench densities ($400m^2$, n=2 per time point; Figure 2.1).

To quantify variation in invertebrate community homogeneity over time, we assessed how invertebrate community β-diversity at each spatial scale changed through time, and how β-diversity varied across spatial scales at each time point. Invertebrate densities were first characterized using nonmetric multidimensional scaling (NMDS, Bray-Curtis distance; Kruskal 1964) at each of the five spatial scales (bench, sub-bench, patch, quadrat, sub-quadrat) using all 36 months of data combined (see Appendix A.1; Figure A.1; Tables A1-6). The best ordination for each spatial scale was selected based on the final minimum stress. We then calculated the mean dispersion of sample units (Anderson *et al.* 2006) at each time point for a given spatial scale using the *'betadisp'* function from the *vegan* package (Oksanen *et al.* 2019) in R (R Core Team 2017; see Appendix A.2). These analyses were repeated for three distinct taxonomic subsets of the community – (1) all species, (2) small mussels (primarily *Mytilus trossulus*) and acorn barnacles (*Balanus glandula*), hereafter referred to as 'focal prey', representing *Nucella*'s dominant and preferred prey (Novak *et al.* 2017), and (3) all invertebrates excluding the focal prey, hereafter 'non-prey'. The distinction among these groups allowed us to disentangle the influence of variation in focal vs. non-focal prey on predator movement.

With β-diversity quantified across time, spatial scales, and by community subsets, we then estimated the scale of optimal prey homogeneity. This optimal scale over which whelks should move in a given period of time represents the maximum distance for which, for a small additional increase in movement rate, a predator perceives a negligibly small additional decrease in prey patchiness. To assess this, we first fit a 4th order polynomial to the mean β-diversity across each of the five spatial scales in a given sampling month to provide a continuous approximation of the change in community patchiness across scale. We then calculated the scale at which the 2nd derivative of each polynomial was equal to zero to locate the inflection point in the relationship between prey patchiness and spatial scale. We used this point as the predator's optimal scale of movement (see Figure A.3 for graphical representation of this process). Generalized additive models were then fit to the spatial scale optima across monthly time points to examine seasonal trends in the scale of optimal prey homogeneity for each community subset. The models were fit using restricted maximum likelihood (REML) and a cyclic cubic regression spline smoothed response.

2.3.1.3 Whelk feeding rates

To quantify whelk feeding rates on focal prey taxa, monthly feeding surveys were performed in the same experimental patches as our invertebrate community characterization. Within each of the 18 patches, we located all whelk individuals and recorded their feeding status. If the individual was feeding (i.e. actively drilling its prey), the identity and size of the prey was recorded. Following Novak (2013), these snapshot feeding surveys were then used to calculate patch-level per capita feeding rates for a given prey type based on the fraction of whelks feeding at a given time.

The expected handling time of a given feeding event observed in the field was estimated using temperature-dependent handling time regression coefficients from Novak (2013). Estimates were dependent on prey size and identity, as well as the mean monthly field temperature for the given feeding survey. Per capita attack rates c_{ij} were calculated using Novak & Wootton's (2008) observational method, which estimates attack rates as

$$c_{ij} = F_{ij} * A_{xj} \,/\, (F_{xj} - A_{xj}) * h_{ij} * N_i \,. \tag{2.2}$$

F_{ij} is the proportion of observed feeding predator j individuals feeding on focal prey i, A_{xj} is the proportion of all observed predator individuals (regardless of feeding status) feeding on prey species x, h_{ij} is the mean handling time of each predator–prey pair, and N_i is the mean density of the focal prey. Feeding rates (f_{ij}), in grams of prey consumed per predator per day, were calculated by

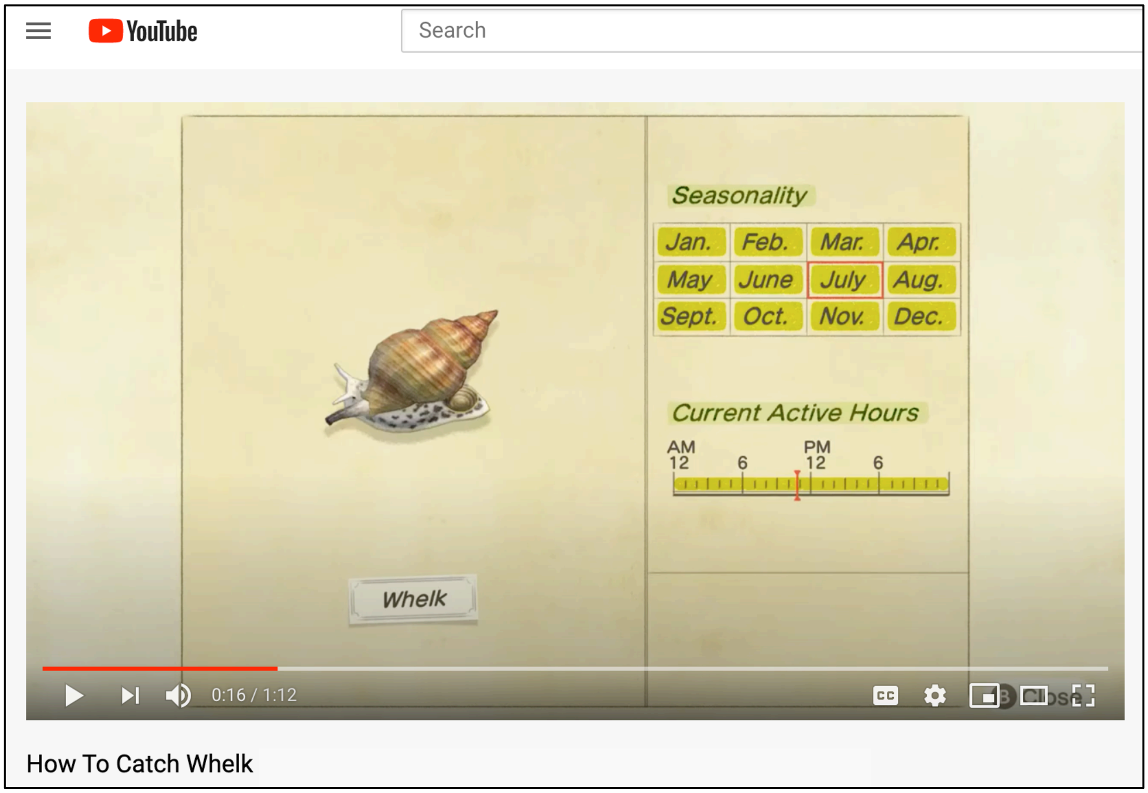
$$f_{ij} = w_{ij} * c_{ij} * N_i \,/\, 1 + \Sigma\, c_{kj}\, h_{kj}\, N_k\,, \tag{2.3}$$

with w_{ij} as the mean wet weight of the prey i individuals consumed by predator j (Novak & Wootton 2008; Novak 2013). Allometric relationships from Novak (2013) were used to estimate prey weight from observed prey sizes.

To determine whelk feeding rates across multiple focal prey taxa, we then converted estimated prey-specific feeding rates to calories. We calculated total daily calories consumed and then divided these estimates by the average number of calories per prey item (see Appendix B). To provide a continuous estimate of feeding rate throughout the year, we fit a generalized additive model to the feeding rates across a yearly cycle. The model was fit using REML and a cyclic cubic regression spline smoothed response to the 'calendar day' covariate, with each sampling date weighted by the number of feeding observations.

2.3.1.4 Predicted movement rates

The scale of optimal prey homogeneity through time was multiplied by the estimated per



Seasonality

Jan.	Feb.	Mar.	Apr.
May	June	July	Aug.
Sept.	Oct.	Nov.	Dec.

How To Catch Whelk

Plate 2.1 Local experts on Whelk behavior must be consulted to ensure maximum success when attempting to catch Whelk. For example, I took into account Seasonality and Current Active Hours to make sure Whelk could be found to study movement rates (see also Chapter 3).

capita feeding rates to predict individual displacement over the course of a year (Equation 2.1). To estimate confidence and prediction intervals on predicted individual movement, we multiplied simulated posterior distributions of the optimal scale and feeding rate model parameters.

2.3.2 Observed whelk movement

To estimate rates of whelk movement, thus allowing us to test the predictions made about optimal individual velocities, 100 marked *Nucella ostrina* individuals were monitored daily from June – August 2017 along the same mid-zone intertidal bench as the experimental patches. Individuals were uniquely marked, and their location relative to two fixed lag screws at the extremes of the spatial area was recorded daily, tides permitting (see Chapter 3, section 3.3.2 for more details on movement data collection).

We then fit a shape-constrained additive model (Pya & Wood 2014; *SCAM* package in R) to the log-transformed cumulative displacement of each individual. For each individual model, we used the *'predict'* function at daily intervals from the first to last day that individual was observed, and calculated the slope between each predicted value to estimate individual daily movement rates on the log scale. Whelks with fewer than 10 observations over the course of the sampling period were excluded from the analysis. To provide an estimate of population movement rates throughout the summer, a generalized additive model was then fit to the pooled summer movement rates by smoothed 'calendar day' and the random effect of individual identity, using REML and assuming a log-normal distribution. 'Calendar day' is defined as the numeric day of year, and allows us to make daily predictions based on our fitted models. A 95% prediction interval was calculated by simulating from the posterior distribution of the model parameter. This range of observed population-level whelk summer movement rates was then compared to the predicted movement rates based on the scale of prey patchiness and individual feeding rates.

2.4 Results

We found variation in the scale of optimal prey homogeneity both across the year and by community subset (Figure 2.2), with consistent seasonal fluctuations in the invertebrate community driven primarily by the patchiness of mussels and barnacles. The full community model included the smoothed response to the ‘calendar day’ covariate ($p = 0.077$), with the model explaining 13.2% of the deviance in the data. The scale of optimal prey homogeneity peaked in late April at 0.65 m/prey ± 0.06 (standard error), indicating higher patchiness at this time, and had a minimum of 0.46 ± 0.08 m/prey in late October (Figure 2.2a). By contrast, the non-prey optimal scale showed a wide range of variation, ranging from close to 0 m/prey to over 1.5 m/prey. The best-fit model included the intercept only (0.72 ± 0.06 m/prey, ‘calendar day’ $p = 0.755$), reflecting no relationship between optimal scale and calendar day (Figure 2.2c). There were clear seasonal patterns in focal prey patchiness, however, with the best-fit model consisting of the smoothed term ‘calendar day’ ($p = 0.025$) and explaining 20% of the deviance in the data. There was a predicted late April peak in the focal prey optimal scale of 0.66 ± 0.06 m/prey and a minimum of 0.44 ± 0.06 m/prey in October (Figure 2.2b).

Of over 6500 feeding observations, whelks were observed consuming mussels 57% of the time, and on barnacles 33% of the time. Whelk caloric feeding rates on mussels and barnacles also exhibited predictable seasonality, with the best-fit model including the smoothed covariate ‘calendar day’ ($p = 0.002$) and explaining 33.8% of the deviance in the data. The lowest per-capita feeding rates of 0.46 ± 0.11 prey/day occurred in mid-May, with a peak of 0.84 ± 0.17 prey/day in early September (Figure 2.3).

The expected estimated rate of an individual whelk predator moving through the prey landscape was generally constant throughout the year, at approximately 0.30 (± 0.02) m/day. This consistency in predicted movement reflects the counteracting influences of prey patchiness and feeding rates, with peak prey patchiness and lowest feeding rates occurring in late spring (Figure 2.4a). There was, however, a large increase in predicted movement beginning in early June, peaking at 0.43 ± 0.015 m/day in the middle of August (Figure 2.4b). This was associated with an increase in peak estimated feeding rates in June that was not countered by a corresponding decrease in scale of optimal heterogeneity at that time.

Observed movement rates exhibited relatively consistent fluctuations on time scales that were shorter than predicted movement, with a mean between 0.11-0.15 m/day throughout the summer (Figure 2.4b). The best-fit model included a smoothed response to ‘calendar day’ ($p < 0.001$) and a random effect of individual identity ($p < 0.001$), and explained 35.9% deviance. The upper limit of the prediction interval ranged from 0.33 - 0.62 m/day over time, with the lower bound ranging from 0.008 - 0.015 m/day (Figure 2.4b).

Combining the optimal scale of prey heterogeneity and daily per-capita calorie consumption over a year's cycle were consistent with individual whelk movement rates well within the bounds of the observed movement interval, with the mean predicted movement falling within the upper bounds of the observed movement (Figure 2.4b). While during the summer the predicted movement was 0.41 ± 0.275 m/day and observed movement was approximately half that, the considerable overlap between the two prediction intervals indicates a match in our ability to predict population movement rates.

2.5 Discussion

Patchiness in the prey environment, predator movement through that environment, and predator foraging are intrinsically linked. Predators foraging in heterogeneous prey environments are subject to both the patchiness of their prey as well as their own energetic demands and environmental constraints, balancing the exploitation of preferred prey patches with time spent moving between these patches (eg. Weihs 1975; Ware 1978; Norberg 1981; Pyke 1981; Gendron & Staddon 1983). By identifying the scale of optimal prey homogeneity and whelk feeding rates, we set expectations for how a whelk individual should move through the prey landscape over the course of a yearly cycle.

The scale of optimal prey homogeneity modifies the tradeoff between time spent moving and time spent feeding, as increases in scale necessitate greater individual movement to experience the same level of homogeneity in the prey landscape. Our analyses revealed seasonal patterns in the underlying patchiness of the preferred prey landscape, which points to a combination of biotic and abiotic factors that may influence this characteristic scale of patchiness in mussels and barnacles. The optimal scale of prey homogeneity for preferred prey taxa was highest during the spring, indicating a larger spatial extent of patches within the prey landscape at this time (Figure 2.2b). Increased wave activity during the winter months can lead to the removal of large patches of mussel beds and other sessile invertebrates (Hunt & Scheibling 2001), increasing the scale of invertebrate patchiness. These newly-cleared swaths of bare rock provide substrate for the subsequent recruitment of mussels and barnacles that peak in the summer (Menge *et al.* 2009, 2011), and serves to decrease the overall scale of prey patch structure throughout the summer and into the fall.

Our analyses also identified seasonality in the magnitude of per-capita whelk feeding rates, but with an opposite temporal trend than the optimal scale of prey patchiness. Predator feeding rates increased through the spring, peaking in the late summer (Figure 2.3). This likely reflects the combined influences of increasing temperatures and higher reproductive output necessitating greater individual energetic demands at this time. Elevated ambient temperature during the summer, especially while whelks are exposed at low diurnal tides, can increase internal body temperatures in *Nucella ostrina*, an ectothermic predator, and thus increase metabolic demands (Dahlhoff *et al.* 2001; Helmuth *et al.* 2002). Additionally, whelk reproduction peaks in the summer in Oregon (Spight & Emlen 1976), requiring increased feeding to compensate for energetic outputs at this time.

Predicted whelk movement fell well within the observed range of individual movement, supporting the importance that prey patchiness and predator feeding rates play in governing foraging movement in a patchy prey environment. Predator movement was predicted to be generally stable, at approximately 0.3 ± 0.06 m/day, throughout most of the year. However, during the summer we saw an increase in movement, reflecting seasonality in the tradeoff between prey patchiness and energetic demands. The observed decreases in optimal scale of focal prey during the summer, likely driven by increased barnacle and mussel recruitment, reduced the overall spatial scale of patchiness of the prey community during this time of the year. Increased summer reproduction and daytime temperatures that whelks experience also contributed to increased metabolic demands, resulting in peak feeding rates during the summer. This increase in feeding rates requires greater time spent foraging, which may lead to increases in net movement as individuals move between patches of prey (Iwasa *et al.* 1981). Therefore, based on the combined influences of prey patchiness and predator feeding rates, our prediction that whelk predators increase their daily movement during the summer is consistent with a shift in behavior to meet energetic demands despite a more homogeneous prey landscape at that time.

While the predicted whelk movement fell within the range of observed movement, the expected increase in predator movement rates we predicted during the summer was not reflected in the observed whelk population's daily movement. Observed whelk movement rates were approximately half the expected movement rates throughout the year, on average, and exhibited fluctuations in their aggregate movement rates over the course of the summer, with considerable variation across individuals. The fitted model predictions exhibited regular fluctuations in the mean population movement, with these oscillations coinciding with cycles in daily tidal submersion time of our study site. The observed mean movement rates were slightly higher during periods of increased tidal submersion, especially during the daytime. The period, timing, and amplitude of tidal cycles have been shown to have strong influences on whelk foraging behavior, with decreases in daily foraging movements and feeding rates with increased emersion times, especially when low tide is during midday (Spight 1982; Hayford *et al.* 2015), as tidal cycles are important drivers of temperature and moisture retention in the exposed intertidal environment (Mislan *et al.* 2009). So, although we predicted increased whelk movement during the summers to accommodate higher energetic demands, local abiotic factors such as tidal cycles and subsequent changes desiccation stress may lead to shifts in behavior that are more influential in determining the magnitude of predator foraging movements in this environment than prey patchiness and feeding rates alone.

While the abiotic environment may explain some of the discrepancy between the trends in mean predicted and observed whelk movement, the estimation of population feeding rates may also impact expectations of increased population movement during the late summer and its mismatch in trend with the observed summer whelk movement. The large increase in feeding rates during the summer can be explained in part by elevated energetic demands due to both higher temperatures and metabolic rates (Helmuth *et al.* 2002), and increased reproductive activity during this time (Spight & Emlen 1976). However, this peak in feeding rates may also be slightly artificially amplified due to the conversion to calorie feeding rates across several prey taxa. An individual mussel has a greater caloric content than a barnacle, and by combining feeding rates on mussels and barnacles by daily calories consumed, the average number of ‘prey’ needed to fulfill an individual whelk’s daily caloric demand is inflated slightly. Based on the average caloric contents of these preferred prey taxa and the proportion of individuals feeding on a given prey type during a feeding survey, the average per capita feeding rate on a ‘prey item’ increased or decreased by 0.25 prey/day, on average, if all of the calories consumed were allocated to either barnacle or mussel individuals, respectively. This may have increased the amplitude in the feeding rate dynamics over the course of the year when whelks were feeding on larger mussels. This effect is especially pronounced for surveys with fewer observed whelks, such as those conducted in the later summer, which may have contributed to a slight inflation of the peak in predicted whelk movement rates starting in the summer and continuing into the early fall. Nonetheless, due to the weighting of these data by number of observations in the fitted GAM, this effect is likely small compared to the underlying trend in feeding rates.

While predator feeding, foraging movement, and the prey environment are interconnected, the ways in which these factors influence each other is less straightforward. Either (a) predator foraging movements are determined by both the patchiness of the prey landscape and their own energetic demands (eg. Weihs 1975; Ware 1978; Norberg 1981; Pyke 1981; Gendron & Staddon 1983), or (b) the scale of prey patchiness influences predator movement and thus constrains the foraging success and feeding rates of predators (Smith 1974). While the underlying patchiness of the prey community should depend on both prey dynamics and predation, we are unable to disentangle feedbacks that happen between the two, especially using observational methods. Here, we do see congruence between the processes influencing prey communities as well as the community patchiness itself, linking prey community patchiness with predator movement and feeding rates. The resulting combination of both prey patchiness and energetics that we present here emphasizes the importance of several concurrent biological factors that influence the movement of predators through the prey landscape. Such scale-dependent patterns of predator movement and community variation are important for understanding how predators respond to their environment, linking the behavior of individuals to the broader community patterns they affect.

Acknowledgements

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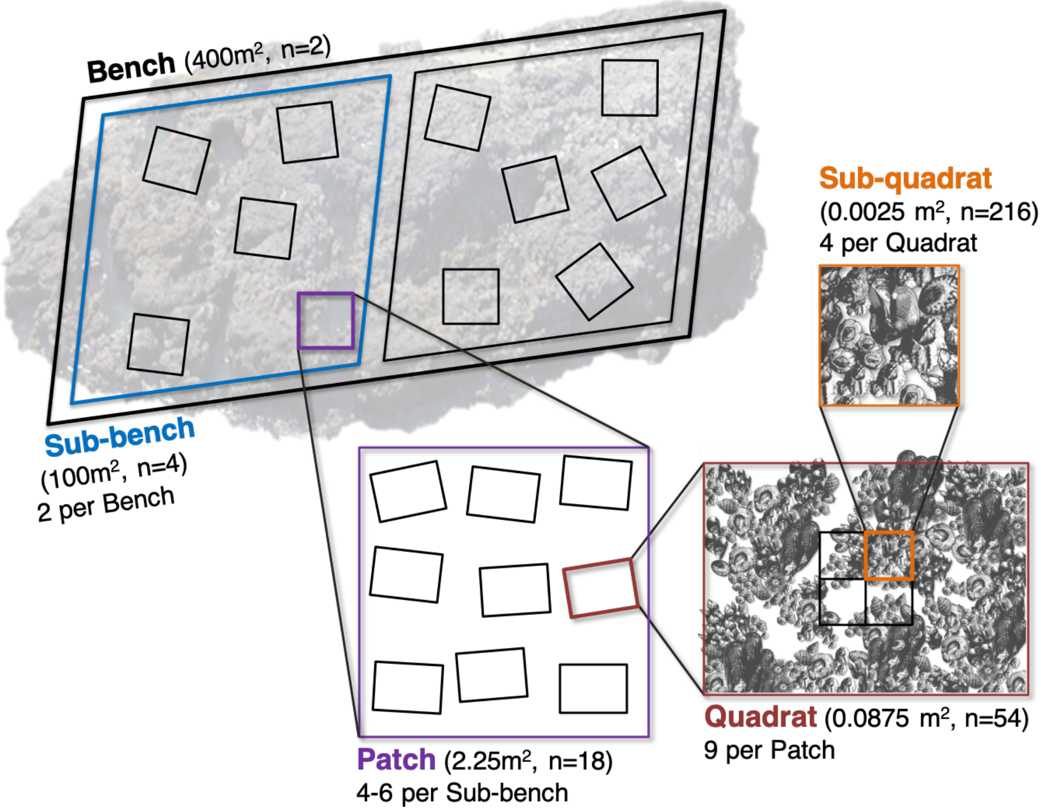


Figure 2.1 Spatial structure of invertebrate community data.

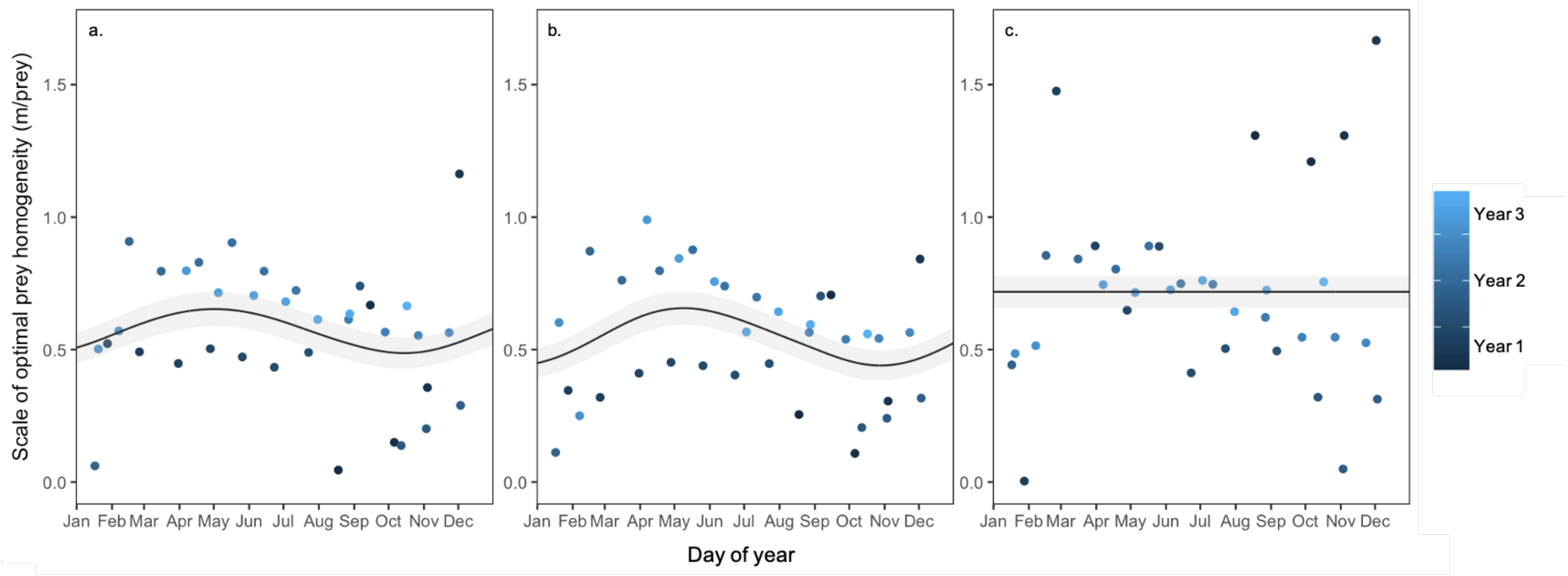


Figure 2.2 Scale of optimal prey homogeneity by day of year for (a) the full invertebrate community, (b) focal prey only, and (c) non-prey. Black lines indicate the predicted values from the best-fit GAM model, with grey shading indicating the standard error of those predicted values. Point colors represent the sample dates through time across multiple years.

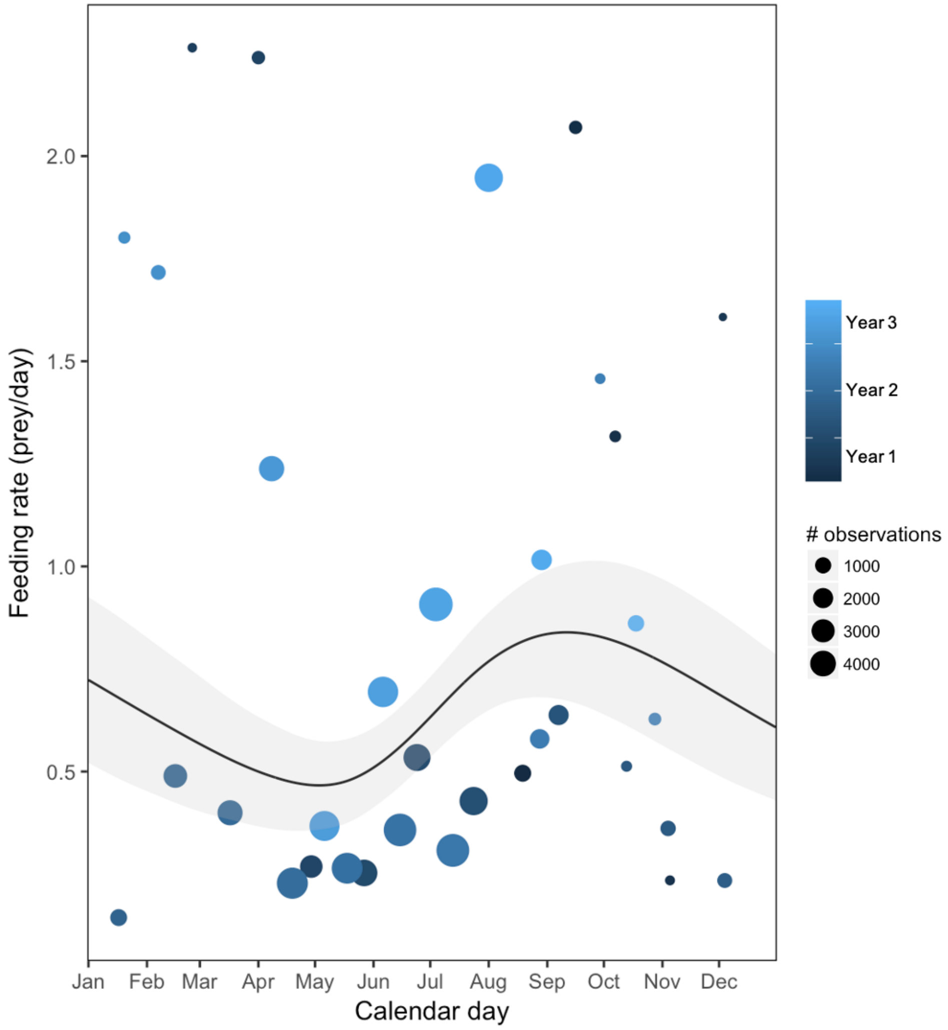


Figure 2.3 Whelk feeding rates by calendar day. The size of the point indicates the number of individuals feeding (# observations) at that sampling time, while the black line is the best fit feeding rates from the GAM with the grey shading indicating the standard error of the predicted values.

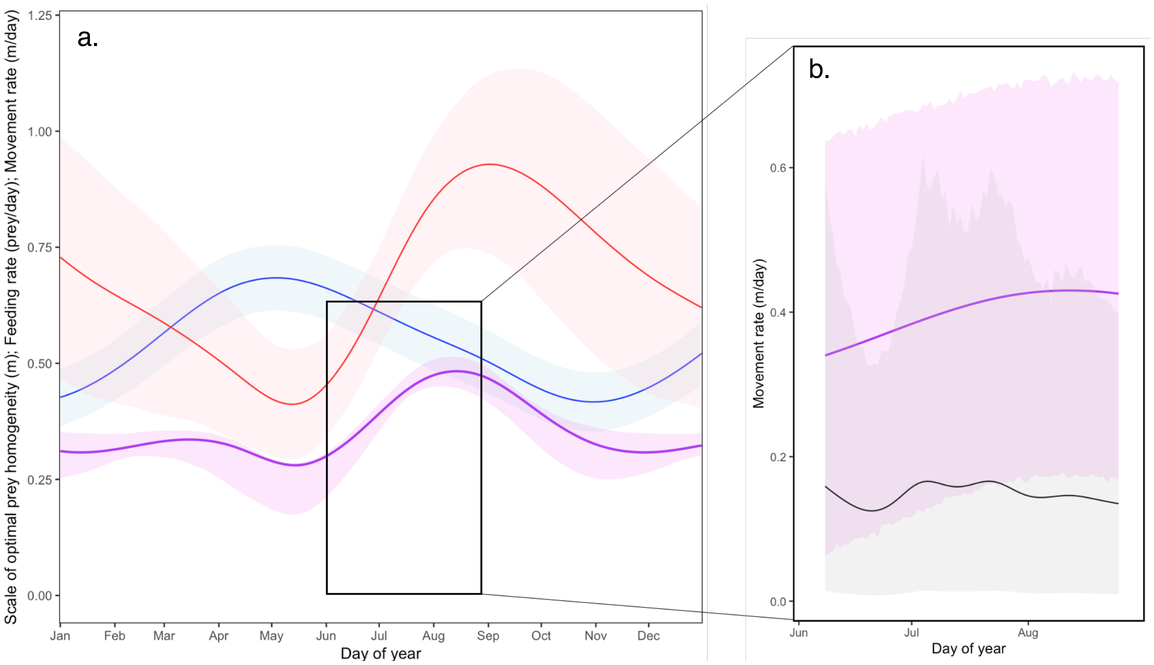


Figure 2.4 (a) Scale of optimal prey homogeneity (m/prey; blue line ± standard error), per-capita feeding rates (prey/day; red line ± standard error), and predicted individual movement rates (m/day; purple line ± standard error) throughout a calendar year, and (b) a comparison of predicted (purple line ± 95% prediction interval) and observed (black line ± 95% prediction interval) whelk movement rates (m/day).

Chapter 3 – Predator foraging behavior and diet variation in a patchy prey community

Shannon M. Hennessey and Mark Novak

3.1 Abstract

Individual variation in behavior is integral to maintaining differences among individuals, whether with respect to individual-level specialization of habitat use, foraging behavior, or prey selection. Differences in predator foraging movement can alter individual interactions with their environment, and variation across individuals can impact important ecological processes. Optimal search strategies for a foraging predator depend on the abundance and predictability of prey. Lévy flight characterizations, a class of random walk processes that describe many small steps with few longer steps, aim to identify the underlying processes that influence individual movement. Individual differences in foraging behavior by prey or habitat type have undergone much study. However, how individual predator movement behaviors depend on their degree of individual diet specialization is less well understood. Here, we track individuals of the rocky intertidal predatory whelk *Nucella ostrina* over a 3-month period to assess variation in individual predator movement patterns. We then correlate individual movement patterns with prey microhabitat occupancy and individual diet selection to better understand how individual foraging decisions are made in a heterogeneous prey environment, and by individuals with different diets. We find considerable variation in individual movement patterns, microhabitat occupancy composition, and diet, but no evidence for Lévy flight movement or relationships between foraging movement behaviors and diet specificity. We do find correlations between individual movement step length distributions and feeding activity, as well as large influences of tidal cycles on movement magnitude and feeding. We hypothesize that the lack of correlation between

individual diet specialization and foraging behaviors is due to the high degree of prey productivity at the study site, making random search patterns and small foraging movements sufficiently efficient to find prey.

3.2 Introduction

Variation is inherent in biological systems, and has long been a subject of study in explaining observed ecological patterns. Variation occurs across levels of biological organization. However, mounting evidence also indicates that recognizing individual-level differences in organisms is integral to better understanding population and community dynamics (Careau & Garland 2012; Dall *et al.* 2012; Sih *et al.* 2012; Toscano *et al.* 2016). Indeed, individual variation can have greater ecological impacts than variation among species (eg. Rall *et al.* 2011; Rudolf & Rasmussen 2013). Characterizing variation among individuals can therefore provide a more comprehensive and mechanistic view of how individual differences produce or maintain population-, community-, or ecosystem-level patterns.

Animal personality, defined as individual behavioral differences that are consistent over time and across ecological contexts (Gosling 2001; Sih *et al.* 2004), is increasingly recognized as a key component in maintaining differences between individuals, and is thought to underlie individual-level specialization of habitat use, foraging behavior, and prey selection. Consistent inter-individual differences in behavior can impact important ecological processes through variation in each individuals' interactions with their environment (Webster *et al.* 2009; Bolnick *et al.* 2011; Brodersen *et al.* 2012; Wolf & Weissing 2012; Pearish *et al.* 2013; Holtmann *et al.* 2017). Recent literature has highlighted the connection between animal personality syndromes and movement ecology, with particular attention to foraging behaviors and niche specialization (Sih *et al.* 2004, 2012; Réale *et al.* 2010; Dall *et al.* 2012; Quinn *et al.* 2012; Spiegel *et al.* 2017). Personality-dependent variation in predator foraging behavior (Kurvers *et al.* 2010; van Overveld & Matthysen 2010, 2013; Sih *et al.* 2012; Patrick & Weimerskirch 2014; Spiegel *et al.* 2017; Schirmer *et al.* 2019) has been used to infer behavioral processes, as well as the effects of interactions between individuals and their habitat (Kobler *et al.* 2011; Breed *et al.* 2013; Fagan *et al.* 2013; Pearish *et al.* 2013; Potts *et al.* 2013; Leclerc *et al.* 2016).

Predator foraging movement, in particular, has been studied in the context of movement behavior variation, with the aim of identifying underlying processes that influence individual movement. The Lévy flight foraging model (Viswanathan *et al.* 2008), is commonly hypothesized to describe foraging behavior, with the optimal search strategy assumed to be dependent on the abundance and predictability of prey. Lévy flights are a class of random walk processes, where step lengths are drawn from a probability distribution with a power-law tail (Viswanathan *et al.* 2008; Humphries *et al.* 2010; Breed *et al.* 2015). Animal movement is thereby described by many small steps and few longer steps, and to have a probability density function $P(l_j) < l_j^{-\mu}$, where l_j is the length of step j. The power-law exponent, μ, is defined to be between 1 and 3 for Lévy flight movement, with $\mu \geq 3$ indicating Brownian movement, and $\mu \leq 1$ for ballistic movement. Parameter value μ therefore describes the tail behavior, with smaller parameter values indicate a heavier-tailed distribution and a higher frequency of longer step lengths than distributions with large values. When prey are scarce and distributed unpredictably, the Lévy flight hypothesis predicts that predators should adopt a Lévy flight search strategy to efficiently find prey, but that when prey are abundant, Brownian movement is sufficiently efficient (Viswanathan *et al.* 1999; Bartumeus *et al.* 2002, 2005; Humphries *et al.* 2010).

While Lévy flight foraging may provide a hypothesis for how individuals foraging within a prey environment should differ in movement behaviors, individual differences in predator diet specificity can also influence individual behavior. Individual diet specialization is taxonomically ubiquitous (Bolnick *et al.* 2003; Poore & Hill 2006; Araújo *et al.* 2011), and can alter resource competition (Svanbäck & Bolnick 2007) and food webs (Araújo *et al.* 2011; Layman *et al.* 2015). The degree of individual variation within a population depends on competition and productivity of the environment (Van Valen 1965; Roughgarden 1972, 1979), with individuals generally expected to exhibit more generalized diets when food is scarce and more specialized diets when food is abundant (Macarthur & Pianka 1966; Schoener 1971). Variation in diet has been linked to differences in foraging movement and behavior (Estes *et al.* 2003; Laidre & Jameson 2006; Tinker *et al.* 2007, 2009; Woo *et al.* 2008; Toscano *et al.* 2016). For example, predators foraging in a sparse prey environment have been shown to exhibit Lévy flight foraging behaviors while displaying Brownian movement in environments with abundant prey (Humphries *et al.* 2010). How foraging behaviors should differ based on diet breadth within a single environment, rather than across habitat types, is less understood.

In caterpillars, generalist species had a lower foraging efficiency than their co-occurring specialized congeners, with shorter and more frequent feeding instances (Bernays *et al.* 2004). However, evaluating these differences in foraging behavior within a species requires more study. An individual's perception of the sparseness of abundance of prey is dependent on their diet specificity (Wiens 1976). Therefore for predators foraging within the same prey environment, but with differing degrees of diet specialization, it follows that individual specialists should exhibit Lévy flight foraging and generalists should exhibit Brownian movement, as the predictability of prey an individual experiences within the same prey environment depends on the breadth of the predator's diet.

Here, we characterize variation in individual predator movement patterns by tracking individuals of the rocky intertidal predatory whelk *Nucella ostrina* over a 3-month period. We then link variation in predator movement patterns, habitat use, and individual diet selection to better understand how individual foraging decisions are made by individuals with different degrees of specialization within the same prey environment. We hypothesized that individuals will vary in their foraging behaviors, and that there will be differences in invertebrate community habitat use that correspond to movement patterns. We also expected that movement behaviors will differ based on an individual's degree of diet specialization, with more specialized individuals exhibiting Lévy flight movement and more generalized individuals showing Brownian movement. By examining individual-level foraging responses to the prey community in the context of predator diet specialization, we inferred how individual diet breadth and prey selection influence subsequent interactions with the prey community and maintained individual differences in foraging behavior.

3.3 Methods

3.3.1 Study system

A study site was established over a large flat bench in the mid-zone of the rocky intertidal at Yachats, Oregon, USA (44.323 N, 124.107 W). The study site is situated in the Cape Perpetua region of the Oregon coast that has a wide continental shelf, retentive currents, and intermittent summer upwelling. These physical factors help maintain high nutrient availability and subsequent primary production, as well as high sessile invertebrate recruitment and fast invertebrate growth (Connolly & Roughgarden 1998; Menge *et al.* 2015). The high abundances of both predators and prey at this site provide an ideal environment to study predator-prey interactions (Navarrete 1996), as well as an environment that should facilitate individual specialization in the *Nucella ostrina* predator population (Futuyma & Moreno 1988).

3.3.2 Data collection

To correlate individual foraging behavior, habitat use, and variation in diet, 100 *Nucella ostrina* individuals were uniquely marked and monitored daily from June – August 2017. Each individual's locations were measured relative to two fixed lag screws at the extremes of the bench, and were recorded daily, tides permitting, for the duration of the three-month study period. Each time an individual was located, their feeding status (feeding or not feeding) was recorded. If actively consuming a prey, the species and size of that prey item was noted. To assess individual microhabitat occupancy, a photograph was taken of a 10x10cm quadrat placed over each located individual at each resighting date, with the whelk at the center. Invertebrate taxa were identified and counted from photographs using ImageJ (Abràmoff *et al.* 2004) and converted to densities per square meter for community analyses.

3.3.3 Individual movement

Whelk locations with respect to the two lag screws were translated into an (*x,y*) coordinate system using the following geometric formulas:

$$C_x = \frac{-a^2 + b^2 + c^2}{2c} \tag{3.1}$$

$$C_y = \frac{\pm\sqrt{(-a+b+c)\,(a-b+c)\,(a+b-c)\,(a+b+c)}}{2c} \tag{3.2}$$

where C_x is the *x* coordinate for point *C,* and C_y is the *y* coordinate. Length *c* is the distance between the fixed lag screws, *b* is the distance from the northern lag screw and the whelk individual, and *a* is the distance from the southern lag screw and the whelk individual. The coordinates for point *A* were set to (0,0) and the coordinates for point *B* to (*c,*0), allowing us to solve for C_y and C_x (the *x* and *y* coordinates for point *C*; Figure 3.1).

Using the converted coordinates for each whelk trajectory, daily step lengths (meters) and turning angles (degrees) were calculated for each pair of sequential daily observations. To make inferences on the directionality of individual movement trajectories, we compared individual distributions of turning angles to randomly-generated uniform distributions. Upon visual inspection, each individual distribution of turning angles was determined to be unbiased in the positive or negative direction, and therefore the absolute values of turning angles were used. We generated null distributions by taking 1000 random draws from a uniform distribution on the interval [0, 180], and then compared each individual's turning angle distributions to these using Kolmogorov–Smirnov tests. If the individual and uniform distributions of turning angles were not deemed clearly different (i.e. $p > 0.05$), an individual was considered to be moving along a random pathway.

To assess individual movement behaviors, we tested for Lévy flights following the procedure detailed by Edwards *et al.* (2007, 2012). Using maximum-likelihood optimization, we fit two candidate probability distributions to the individual distributions of step length: (1) an unbounded power law distribution, typically used to test Lévy flight movement, and (2) an unbounded exponential distribution describing the simplest alternative null model to a power law. For each individual, distributions were fit to step length data using the *poweRlaw* package in R (Gillespie 2015). The two probability density functions $f(x)$ for step lengths x were taken from Clauset *et al.* (2009). The first model, a Lévy flight unbounded power law, follows the form:

$$f(x) = Cx^{-\mu}, \quad x \geq a, \tag{3.3}$$

with parameter μ, minimum movement length a, and constant $C = (\mu - 1)\, a^{\mu-1}$. The second model, an unbounded exponential, follows the form:

$$f(x) = \lambda e^{-\lambda(x-a)}, \quad x \geq a, \tag{3.4}$$

with parameter λ. Unlike a Lévy flight power law parameter between 1 and 3 providing support for a characteristic movement pattern, the exponential parameter does not have a direct link to specific individual behaviors. However, it can be interpreted relative to other parameter values, with small values indicating higher relative frequencies of large steps and large λ values describing high frequencies of very small steps.

3.3.4 Community associations

To link individual movement patterns with prey community microhabitat occupancy through time, we first used nonmetric multidimensional scaling (NMDS; Kruskal 1964) to characterize community composition from the microhabitat photos that were taken around each whelk at each observation. We restricted all community analyses to 20 whelk individuals with the most resighting observations over the study period to allow for robust comparisons to be made between community associations and individual movement. Invertebrate densities of the top nine invertebrate species from each of the 10x10cm quadrat photos (n = 836 photos total) were ordinated using the *vegan* package (Oksanen *et al.* 2019) in R with Bray-Curtis distance. The best ordination was selected based on the final minimum stress.

To represent individual shifts in community occupancy over time, we then calculated step length distributions for each individual's movement through community space based on the NMDS ordination. By taking the Euclidean distance between sequential time points in ordination species space, we constructed distributions of turning angles and step lengths of community distance moved for each individual. With these community turning angle and step length distributions, we then tested for uniformity in turning angles and fit the same two candidate probability distributions to community step lengths as in the movement analyses.

3.3.5 Foraging behaviors

We examined responses of individual step lengths and feeding activity to tidal cycle. Tidal height data were obtained from the TWC0843 Newport, Oregon 'Yaquina Bay' station (44.633 N, 124.050 W) using the R package '*rtide*' (Thorley *et al.* 2020). Tide heights were extracted at 1-minute intervals. As daytime exposure during the summer is most stressful to intertidal organisms due to increased temperatures and desiccation stress (Wethey 1983; Helmuth 1998; Helmuth *et al.* 2002; Przeslawski *et al.* 2005), we quantified daytime exposure of the study site by calculating the number of minutes during daylight hours (06:00 – 20:00 hours for the summer months) that the tidal height was below 1m (mean lower low water). With the time the study site was exposed each day over the course of the summer quantified, we then fit a linear regression to log-transformed daily step lengths and daily submersion times to assess the influence of tidal cycles on daily movement. We also quantified the probability of feeding on a given day based on that day's submersion time using logistic regression.

3.3.6 Individual diet

Sixteen whelk individuals were observed feeding 4 or more times over the duration of the study period and were selected for further analysis of individual diet specialization and diet composition. To quantify variation in specialization between whelk individuals, we calculated individual diet diversity (D_{si}; s = Shannon index, and i = individual; Roughgarden 1979; Bolnick *et al.* 2002; Sargeant 2007) following the form:

$$D_{si} = -\Sigma_j \, p_{ij} \, ln(p_{ij}), \tag{3.5}$$

with p_{ij} representing the proportion of diet item j in the diet of individual i. A diet diversity of 0 indicates a high degree of specialization, while a higher diet diversity indicates a larger individual niche breadth and therefore a more generalized individual. In addition to diet breadth, we also characterized each of the 16 individuals by their dominant prey species to look at further associations of diet composition with microhabitat occupancy patterns.

3.3.7 Linking movement, community shifts, and diet specialization

To assess correlations between individual foraging movement patterns and individual prey choice or habitat use, we fit linear models to the individual movement step length (μ_m and λ_m) and community step length fitted parameters (μ_c and λ_c), as well as the calculated individual diet diversity for the focal 16 individuals. We first fit a full model, with movement fitted parameter, diet diversity, and an interaction term as predictors of community step length fitted parameters. We then fit successive models eliminating non-significant parameters until all remaining terms were well supported, using a cutoff of $p > 0.05$. To make broader population-level inferences on the relationship between distributions of movement step lengths and individual foraging activity, defined as the number of times an individual was seen actively feeding, we computed a Pearson's correlation coefficient for the relationship between movement fitted parameters and individual total feeding observations.

3.4 Results

3.4.1 Individual movement

Whelks with less than 15 sequential observations over the study period were excluded from further analysis (following Breed *et al.* 2015), leaving 62 of 100 individually marked whelks with sufficient information for consideration. The majority of individuals showed no evidence for directional bias in their movement trajectory turning angles (Figure 3.2; Table C.1). However, eight individuals (C7, C8, C10, C12, C34, C35, C36) had non-uniform distributions of turning angles, all with a bias towards large turns (>150 degrees; $p < 0.05$).

We saw no evidence for Lévy flight movement behavior across individuals. Individual step length distributions were all best described by an exponential distribution (Figure 3.2). Individuals exhibited a wide range of variation in exponential parameter (λ) values, ranging from 2.39 to 30.99, with a mean of 8.62 ± 0.73 standard error (Table

C.2). This characterizes a wide range of variation in individual step length distributions, with some individuals moving very little (high λ_m values) and others taking larger steps at a relatively high frequency (low λ_m values) The goodness of fit for the exponential parameters showed that the step length data were well explained by the fitted exponential distributions overall, ranging from 0.058 to 0.26, with a mean of 0.12 ± 0.005 (Table C.2). Seven individuals (in ascending order of λ_m values: D1, D36, C21, C15, D23, E1, D26) had step length distribution fitted parameter values that were higher than all other individuals (ie. non-overlapping 95% confidence intervals), indicating very little overall movement by these individuals (Figure 3.3a).

3.4.2 Invertebrate community associations

The non-metric multidimensional scaling (NMDS) ordinations to characterize the invertebrate community reached a 2-dimensional solution after 600 iterations with a final stress of 0.17 (Table 3.1). Five species had significant correlations with the ordination axes: mussels *Mytilus trossulus*, barnacles *Balanus glandula*, *Chthamalus dalli*, and *Semibalanus cariosus*, and gooseneck barnacles, *Pollicipes polymerus* (Figure 3.4; Table 3.2).

The 20 individuals with the most resightings were selected for further analysis of associations with the invertebrate community and had between 27 and 51 observations over the duration of the study period. No focal individual showed evidence for non-random turning angles through community space, but three whelks (E2, D5, D6) showed suggestive evidence ($p < 0.1$) for non-random angles (Figure 3.5; Table C.3). However, there was variation across individual community step length distribution fitted parameter values. All individual community step length distributions were best fit by an exponential model (Figure 3.5). Exponential parameters for movement through community space (λ_c) had a considerably smaller range than movement step length distributions, with a range of 2.25 to 5.43 and a mean of 3.45 ± 0.20 (standard error). The parameter goodness of fits ranged from 0.053 to 0.148, with a mean of 0.09 ± 0.20 (Table C.4). Four individuals (E2, D6, D23, C43**)** had parameter values that were higher than the other individuals (non-overlapping 95% confidence intervals), indicating very little movement in community space by these individuals (Figure 3.3b).

3.4.3 Foraging behaviors

Individual feeding activity, measured by number of total feeding observations, correlated with individual movement step length parameter. Whelks with a higher parameter value, and thus a greater frequency of small steps and lower movement activity, had fewer observed feeding instances than whelks with lower exponential parameters, with a Pearson's correlation of -0.14 ($p = 0.26$; Figure 3.6).

Tidal submersion time influenced population-level foraging movement and feeding activity. Increased submersion time increased daily step length across individuals, with a 1cm increase in daily step length, on average, for each additional minute of daily tidal submersion ($p = 0.007$; 1, 1069 df; Figure 3.7). The probability of an individual feeding was also dependent on the duration of tidal submersion, with a 0.7% decrease in probability of feeding with increased submersion ($p < 0.001$; 4925 df).

3.4.4 Individual diet

Sixteen whelks had sufficient feeding observations to characterize individual diet breadths and thus their degree of individual specialization. The two dominant prey consumed were small mussels (*Mytilus trossulus*), which were consumed by all 16 whelks except for a single barnacle-only specialist, and acorn barnacles (*Balanus glandula*), which were consumed by all but 3 of the focal whelks. Two individuals specialized on just one prey type, while the others ranged from 2 – 4 diet items of 5 prey species (Table 3.3).

3.4.5 Linking movement, community shifts, and diet specialization

Individual shift in community space was dependent on the exponential parameter of movement step length distributions. The best-fit model did not include an effect of individual diet diversity ($p = 0.98$). Individual community step length parameters (λ_c) were positively correlated with movement parameters (λ_m), and explained 21% of the variation in the data ($p = 0.02$; $R^2 = 0.21$; Table 3.4; Figure 3.8).

3.5 Discussion

Variation in predator foraging behavior is thought to help maintain individual-level specialization of both habitat use and prey selection (Kurvers *et al.* 2010; van Overveld & Matthysen 2010, 2013; Kobler *et al.* 2011; Sih *et al.* 2012; Pearish *et al.* 2013; Patrick & Weimerskirch 2014; Leclerc *et al.* 2016; Spiegel *et al.* 2017). Characterizing individual foraging behaviors by patterns in movement, habitat use, and diet breadth allowed us to quantify variation across individuals and make inferences as to how these factors underlie inter-individual differences in foraging. We found that while there was considerable variation in individual patterns of movement, invertebrate community use, and diet, we did not see evidence for characteristic Lévy flight movement behavior. There was also little to no population-wide relationship between microhabitat community occupancy and individual diet breadth or prey identity, with only suggestive patterns in a few individuals. However, our results evidenced a detectable impact of tidal cycles on individual movement and foraging activity. This suggests that the abiotic environment plays a more dominant role in governing foraging behaviors through time than behavioral differences across individuals.

Individual movement patterns varied by turning angle distributions and step lengths. The majority of whelk individuals exhibited randomly distributed turning over the course of the study period, with the exception of eight individuals that made a higher frequency of sharp turns (C7, C8, C10, C12, C34, C35, C36; Figure 3.2; Table C.1). This suggests that most whelks within this population are undergoing random foraging movements through the prey environment. The few individuals that have a higher frequency of sharp turns may be exhibiting foraging movement reminiscent of patch foraging (i.e. turning sharply within a small area; Guo *et al.* 2009; Teimouri *et al.* 2018). However, there was no clear association between these individuals and other movement patterns, with each of them exhibiting step length parameters spanning the range of population-wide parameters. Three of the individuals with non-random turning (C7, C12, C36) had sufficient feeding observations for diet analysis, but there was no clear relationship between these individuals' diet diversity or composition, with each individual consuming multiple prey taxa at different relative frequencies. Theory suggests that generalized individuals should move more randomly within the prey environment (Bernays *et al.* 2004; Humphries *et al.* 2010), however we find no evidence here that individuals with sharp turning angles are foraging within a patch.

The step length distributions of all individuals were best-fit by exponential distributions, indicating no evidence for Lévy flight movement. This limits the inferences we can make with regards to characteristic movement patterns of each individual. Unlike a Lévy flight power law parameter between 1 and 3 providing support for a characteristic movement pattern, fitted exponential parameters have not been linked to specific individual behaviors and the lack of clear bounds on the exponential parameter limits interpretations to relative comparisons. In this regard, it is important to note that the prevalence of Lévy flight step length distributions may be overestimated in natural systems due to the mixing of multiple movement behaviors through time or across individuals at the population level, despite their common use in characterizing movement behaviors (see Breed *et al.* 2015). Therefore, the exponential fit of our individual step length distributions is appropriate in capturing the underlying movement behaviors. Additionally, the fitted exponential distribution parameter, λ, can be related to relative movement patterns across individuals, with large values of λ indicating high frequencies of very small step lengths and small values describing step length distributions with a heavier tail of longer steps. Some whelk individuals, such as the seven with considerably higher λ values than the rest (D1, D36, C21, C15, D23, E1, D26), exhibited extremely frequent small steps and very infrequent large steps, and therefore could be characterized by localized movement akin to Brownian movement. Individuals with small parameter values, on the other hand, can be described by movement closer to ballistic relative to the other individuals. We also saw a relationship between individual step length distribution parameters and feeding activity. Individuals with lower step length distribution parameters, and thus a higher frequency of larger movement lengths, were correlated with more feeding observations (Figure 3.6).

There was a similar lack of clarity in individual shifts in invertebrate community composition as to variation in individual foraging movement. None of the 20 most frequently observed individuals had turning angle distributions that differed from uniform expectations, and there was variation in exponential distribution parameters fitted to community step length distributions. Additionally, there was a positive relationship between individual movement fitted parameters and community step length parameters (Figure 3.8). This indicates that individuals that moved very little also shifted very little in community space, which is to be expected, but also that individuals that displayed larger step lengths also shifted in their community composition more. The latter points to a lack of overall selectivity of microhabitat invertebrate community composition by individuals at the population level, regardless of overall movement activity level.

Two whelks (E2, D6) did display interesting correlations between movement and microhabitat occupancy. These two individuals showed suggestive evidence for sharp turns and exhibited very little movement through community space (the two highestranked community λ_c values), in addition to having sufficient feeding observations for diet analysis. Both of these individuals had movement exponential parameters (λ_m) near the population mean, and therefore undertook larger daily steps with a moderate frequency, but despite this, did not make comparable shifts in community composition. Coupled with their higher frequencies of large turning angles, this suggests that these two individuals display a higher degree of invertebrate community selectivity, foraging within patches of similar composition despite larger movements across the landscape. These two whelks were also moderately generalized in their prey selection, consuming only small mussels (*Mytilus trossulus*) and small barnacles *(Balanus glandula* and *Chthamalus dalli*). Whelk E2 showed association with two microhabitat types over time, one dominated by gooseneck barnacles, and the other with high relative contributions of *M. trossulus* and *B. glandula*. D6 occupied microhabitats with higher contributions of *C. dalli*, as well as those with abundant gooseneck barnacles (Figure 3.5). This suggests that these two whelks had some fidelity to habitats with their preferred prey.

Other than the above two focal individuals, however, there was little inference that could be made about the role of individual diet in foraging movement patterns and individual microhabitat occupancy, especially in relation to the degree of individual specialization. We did find evidence for individual specialists and generalists within the population, but there doesn't appear to be corresponding consistency in other behaviors. Individuals also did not show correlation between primary prey and the abundance of that prey within the microhabitats they occupied. This may be due, in part, to the overall site-level productivity of prey. The study site is particularly productive, with high abundances and hence predictability of primary prey (Connolly & Roughgarden 1998; Menge *et al.* 2015). Because prey are abundant, individuals foraging within this environment would have very little difficulty finding a preferred prey item, regardless of the individual's degree of diet specialization. Therefore, a random search pattern and small foraging movements may be sufficiently efficient to find prey (Humphries *et al.* 2010), leading to other biotic or abiotic factors exerting stronger control over foraging behaviors.

Tidal cycles were important in shaping population-level foraging movement and feeding activity levels. During periods of increased daytime tidal submersion, individuals were more likely to have longer daily step lengths, with a predicted 1cm increase in average step length with an additional minute of submersion (Figure 3.7). Counterintuitively, the probability of an individual feeding decreased slightly with increased daytime submersion. This contrasts with previous work that has shown that whelk foraging activity peaks during times when daytime tides are highest and therefore submersion time is maximized (Vaughn *et al.* 2014; Hayford *et al.* 2015). This suggests that individuals that travel longer distances have higher feeding rates, but may also be feeding and undertaking larger foraging movements during different parts of the monthly tidal cycle, as the probability of feeding increases with more daily exposure and individuals take larger steps with increased submersion.

3.6 Conclusions

Our analyses show a wide range of variation across individuals, in patterns of foraging movement, microhabitat community composition, and diet composition and breadth. We found a relationship between individual feeding activity and step length distribution, with more active individuals feeding more, as well as increased population-level daily movement with greater daytime tidal submersion. However, there were no consistent patterns in foraging modes or prey community selectivity across individuals with individual diet specialization. Our hypothesis that individuals with increased diet specialization would exhibit Lévy flight foraging behavior, while generalized individuals would display Brownian foraging patterns (Humphries *et al.* 2010; Sims *et al.* 2012) was not supported. Instead, we saw no evidence for Lévy flight foraging for any individual, and no correlation between foraging patterns and diet. We speculate that in environments similar to the intertidal where tidal cycles can impose substantial abiotic stress, and productivity is high, may therefore outweigh the constraints on finding sufficient prey for any given individual, regardless of prey preferences.

Acknowledgements

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. 1840998. We are immensely grateful for Sage Dale’s assistance in locating whelks and taking microhabitat community photos.

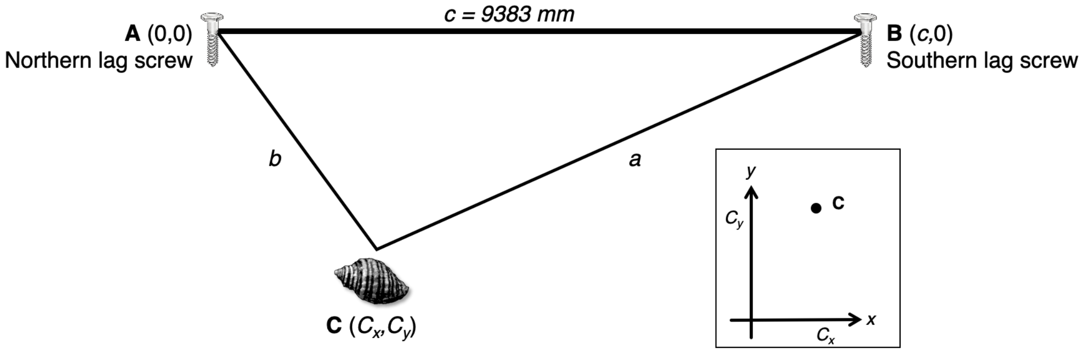


Figure 3.1 Diagram of the conversion of whelk locations relative to lag screws to an (x,y) coordinate system.

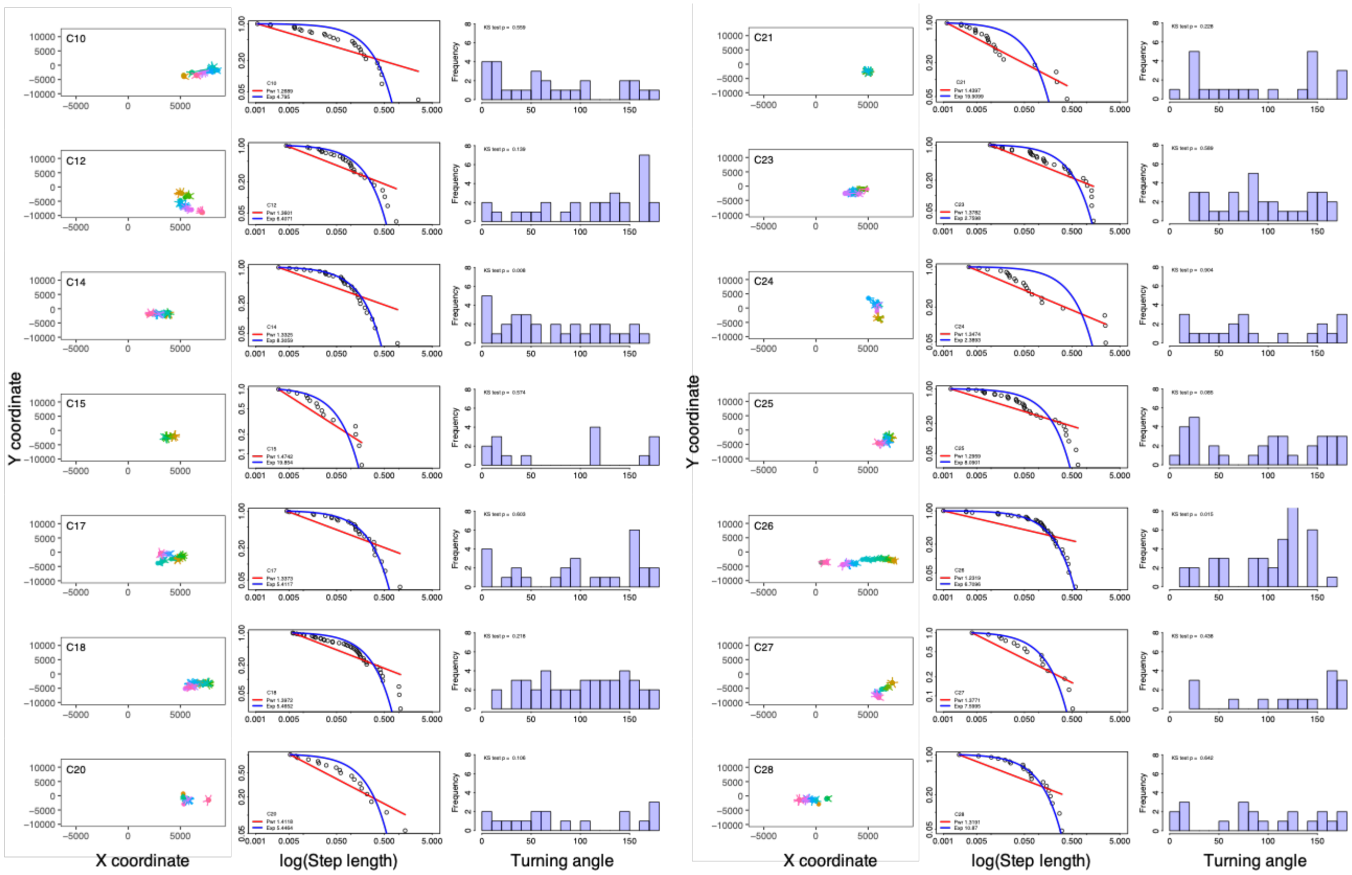
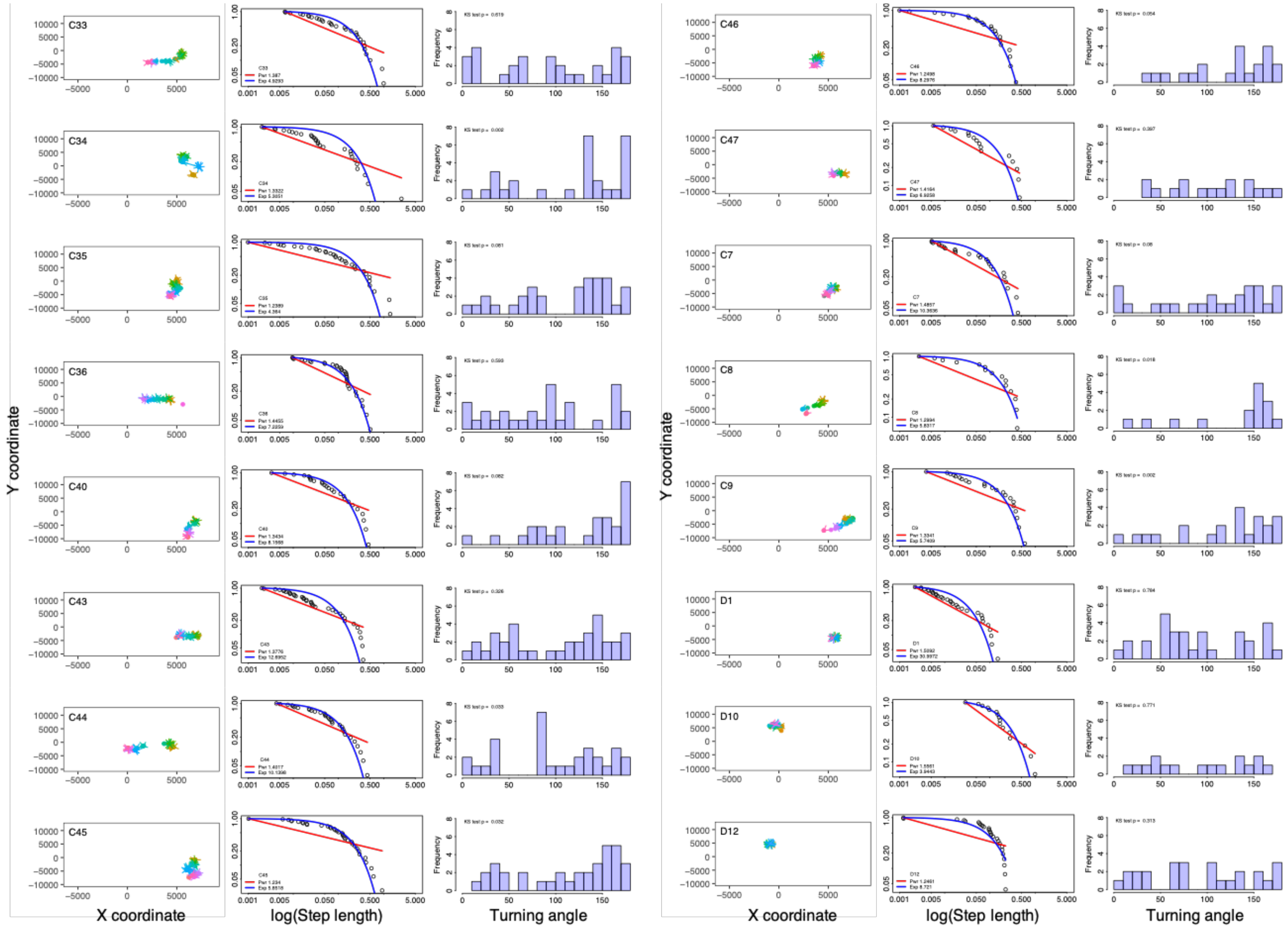


Figure 3.2 Individual movement trajectories, step length distributions with power law (μ_m; red line) and exponential distribution fits (λ_m; blue line) on a log:log scale, and movement turning angle frequency distributions.



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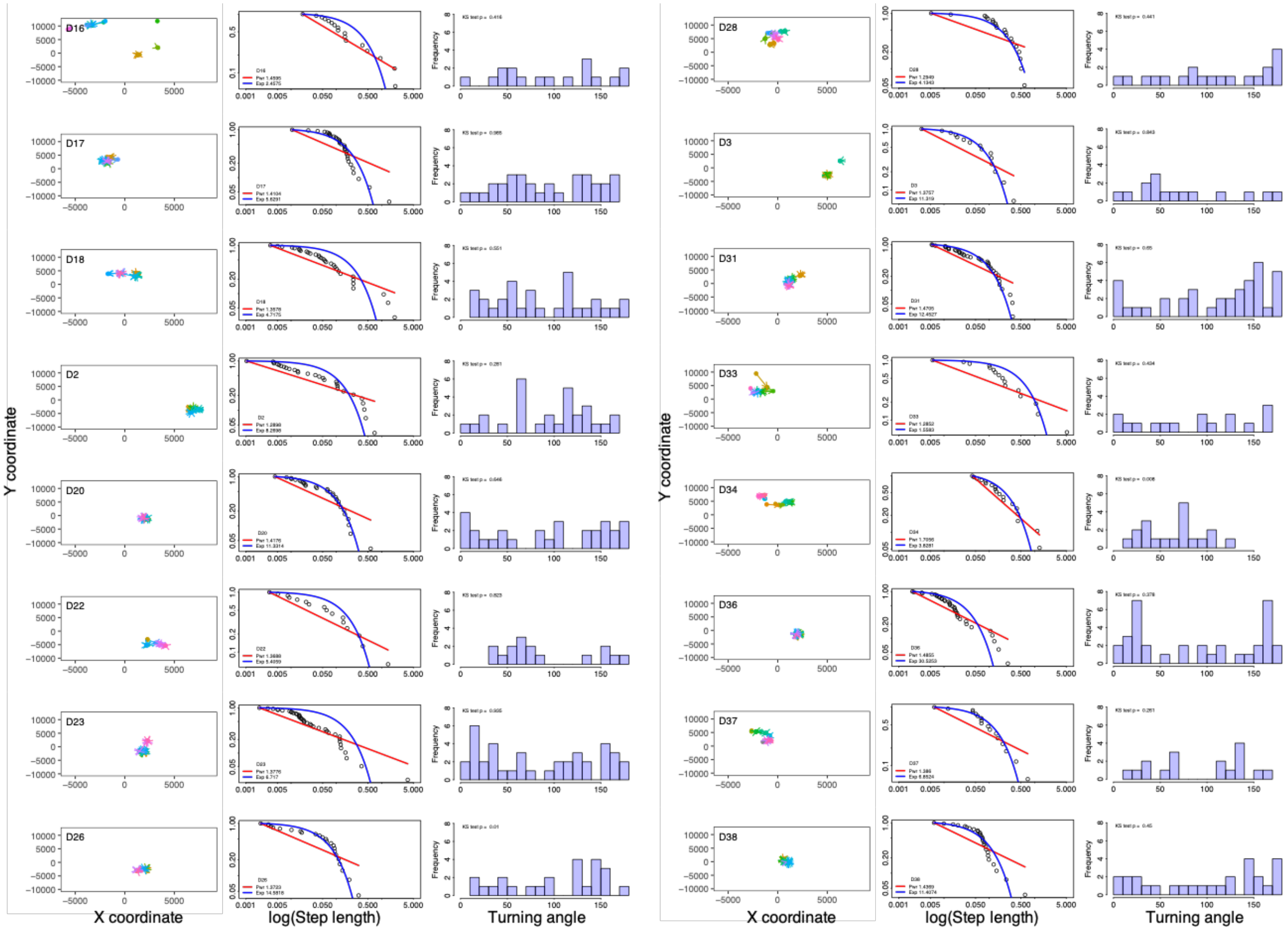

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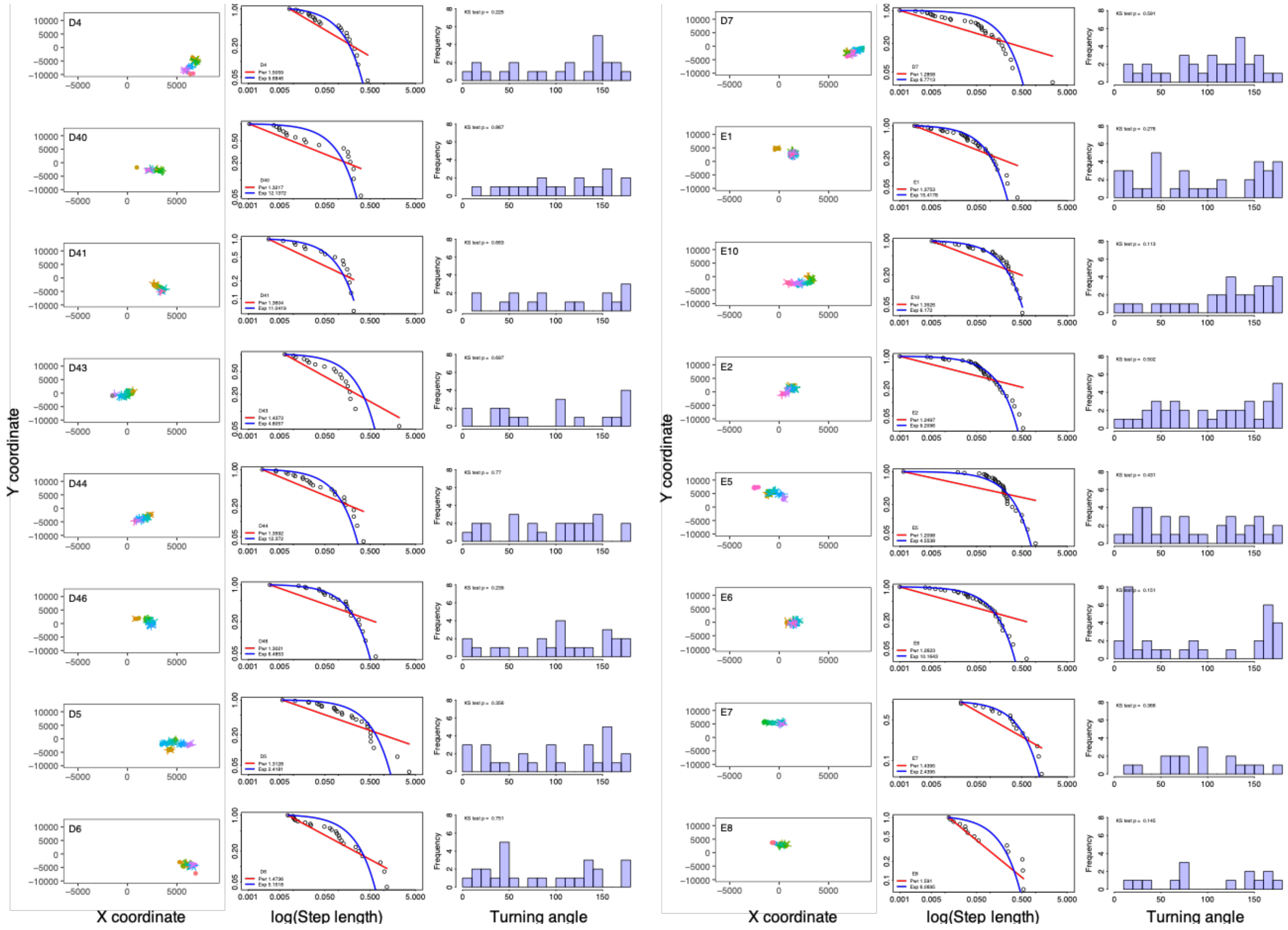

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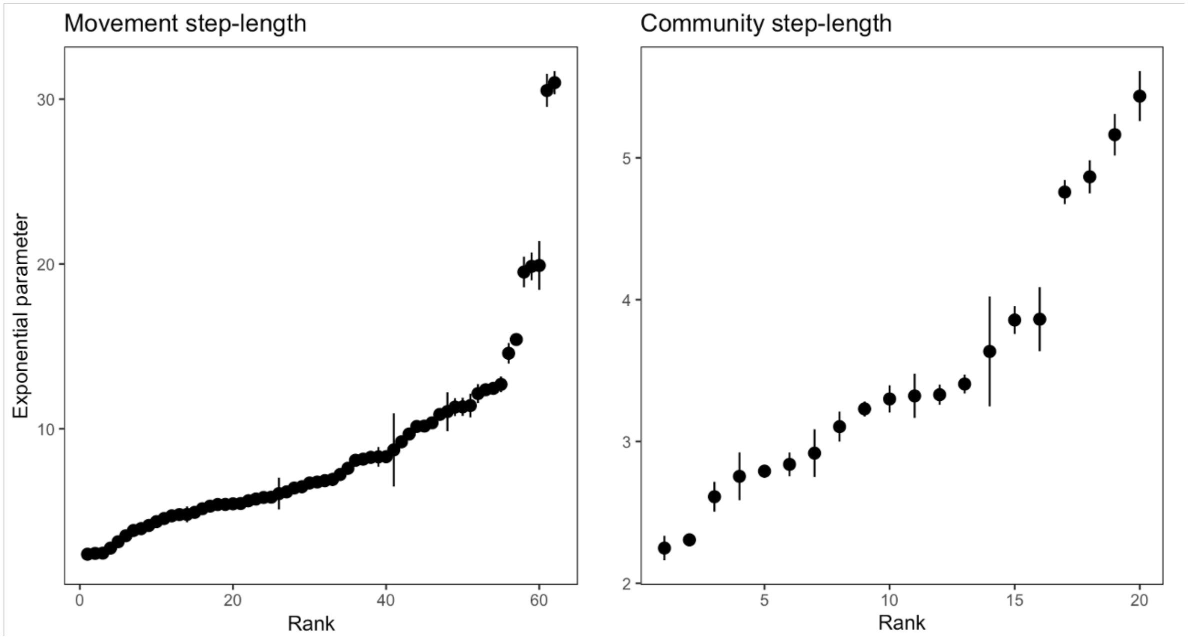

Figure 3.3 Rank distributions for the fitted exponential distribution parameters (λ) for (a) individual movement step length distributions (λ_m), and (b) individual shifts in community (λ_c).

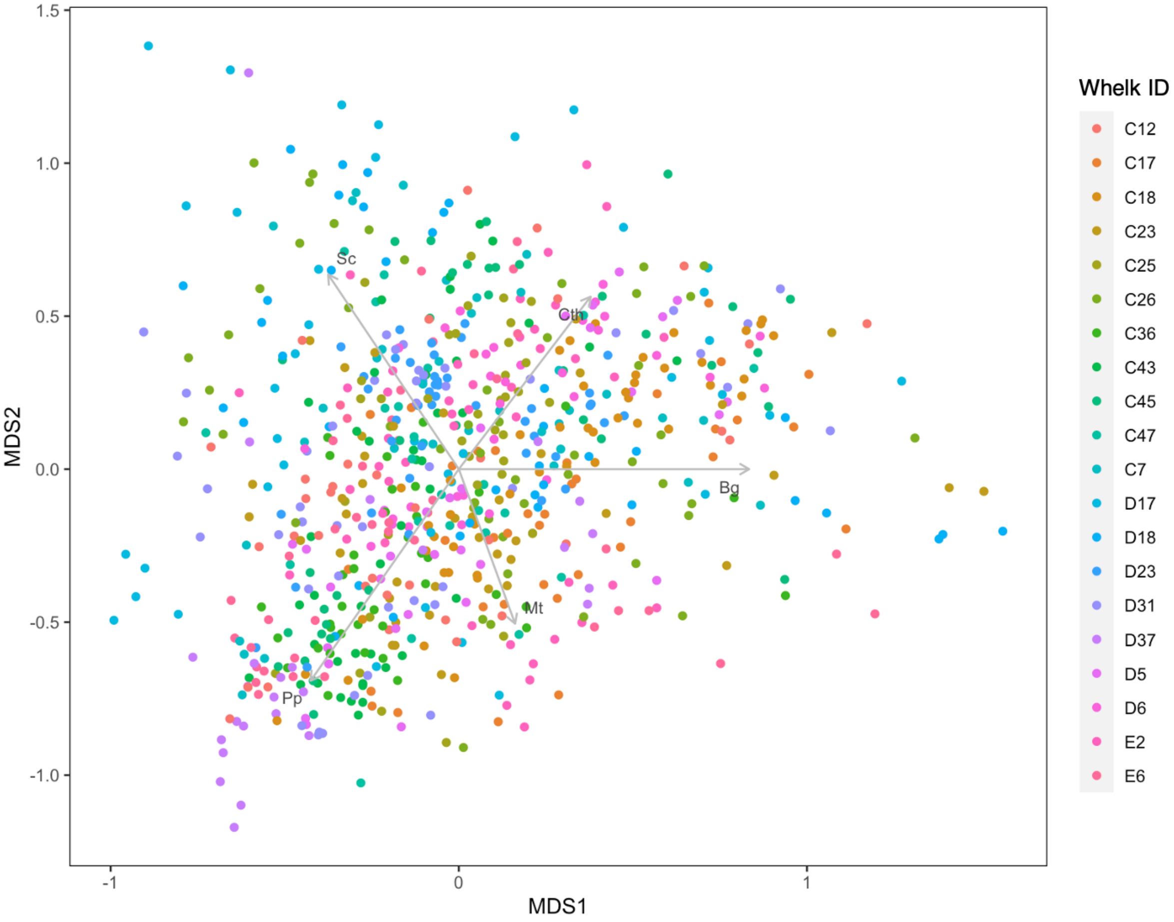

Figure 3.4 Non-metric multidimensional scaling ordination of invertebrate community composition. Colors indicate communities occupied by individual whelks in species space. Vectors indicate significant invertebrate species correlations with the ordination axes (R^2>0.2), with Bg, Cth, and Sc denoting the barnacles *Balanus glandula*, *Chthamalus dalli*, and *Semibalanus cariosus*, respectively, Mt for the mussel *Mytilus trossulus*, and Pp for gooseneck barnacles *Pollicipes polymerus*.

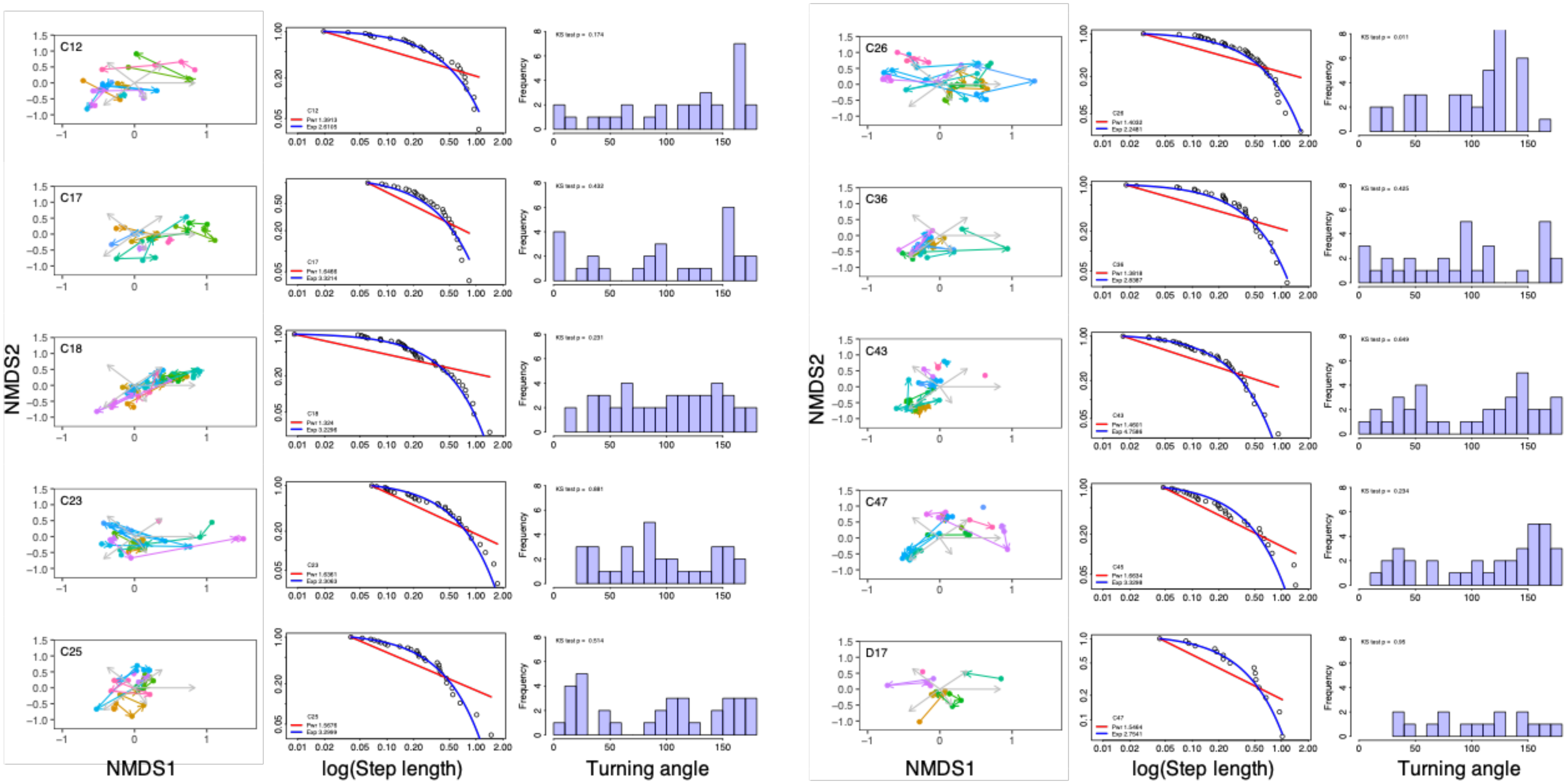

Figure 3.5 Individual trajectories in community space with individual species correlations with the ordination axes, community step length distributions with power law (μ_c; red line) and exponential distribution fits (λ_c; blue line) on a log:log scale, and community turning angle frequency distributions.

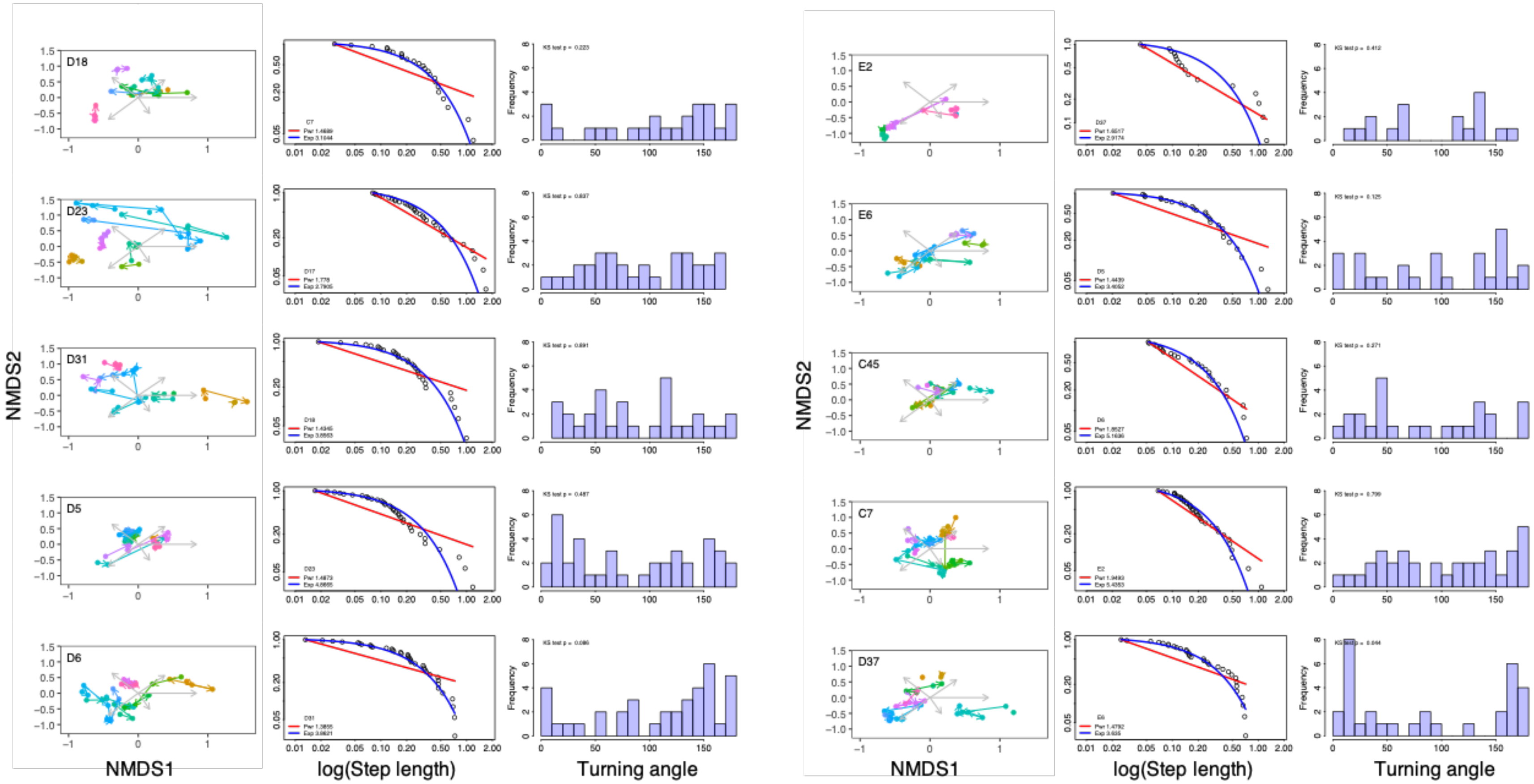

Figure 3.5 (Continued)

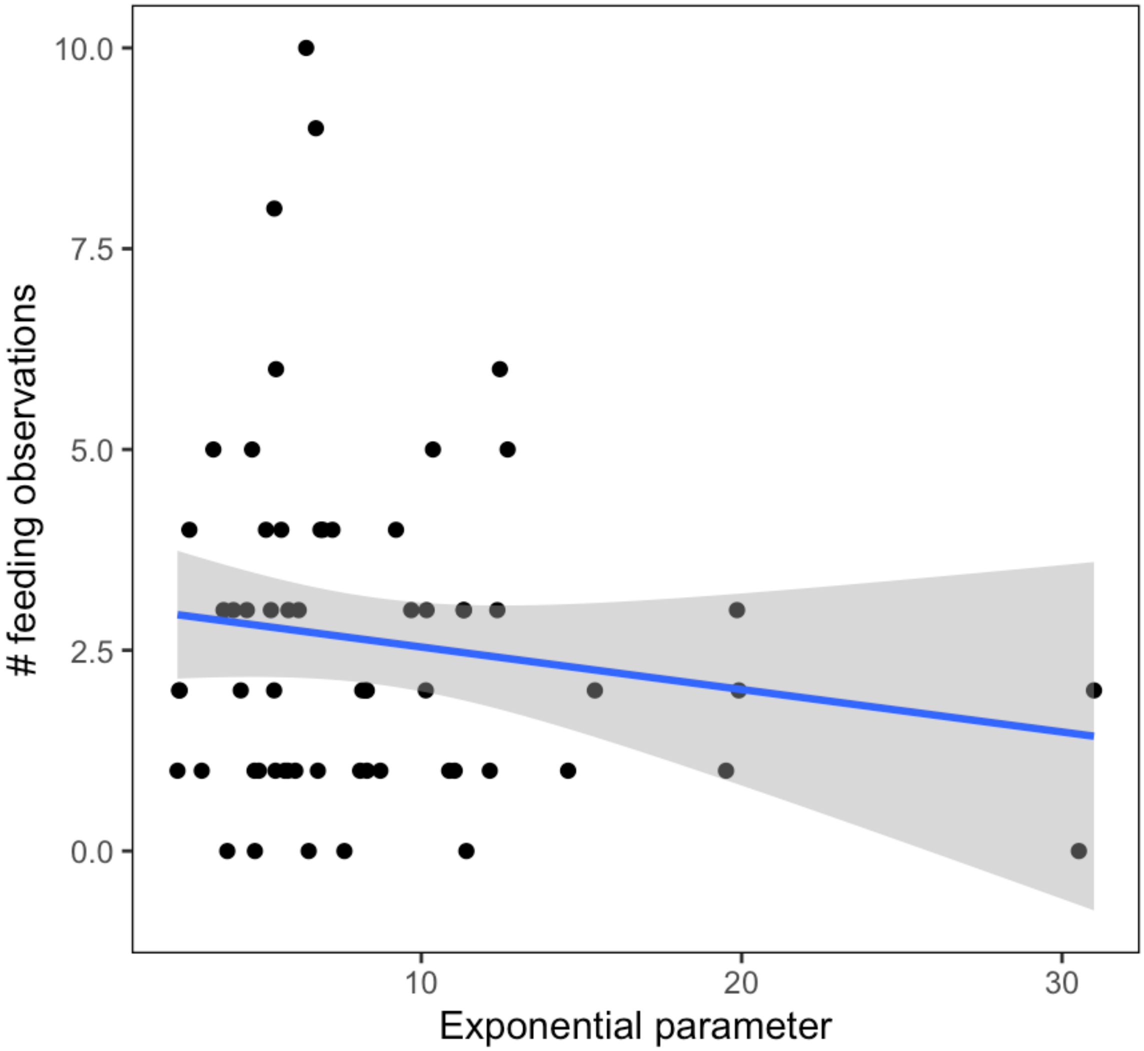

Figure 3.6 Relationship between individual movement step length distribution parameters (λ_m) and number of feeding observations, with a linear regression.

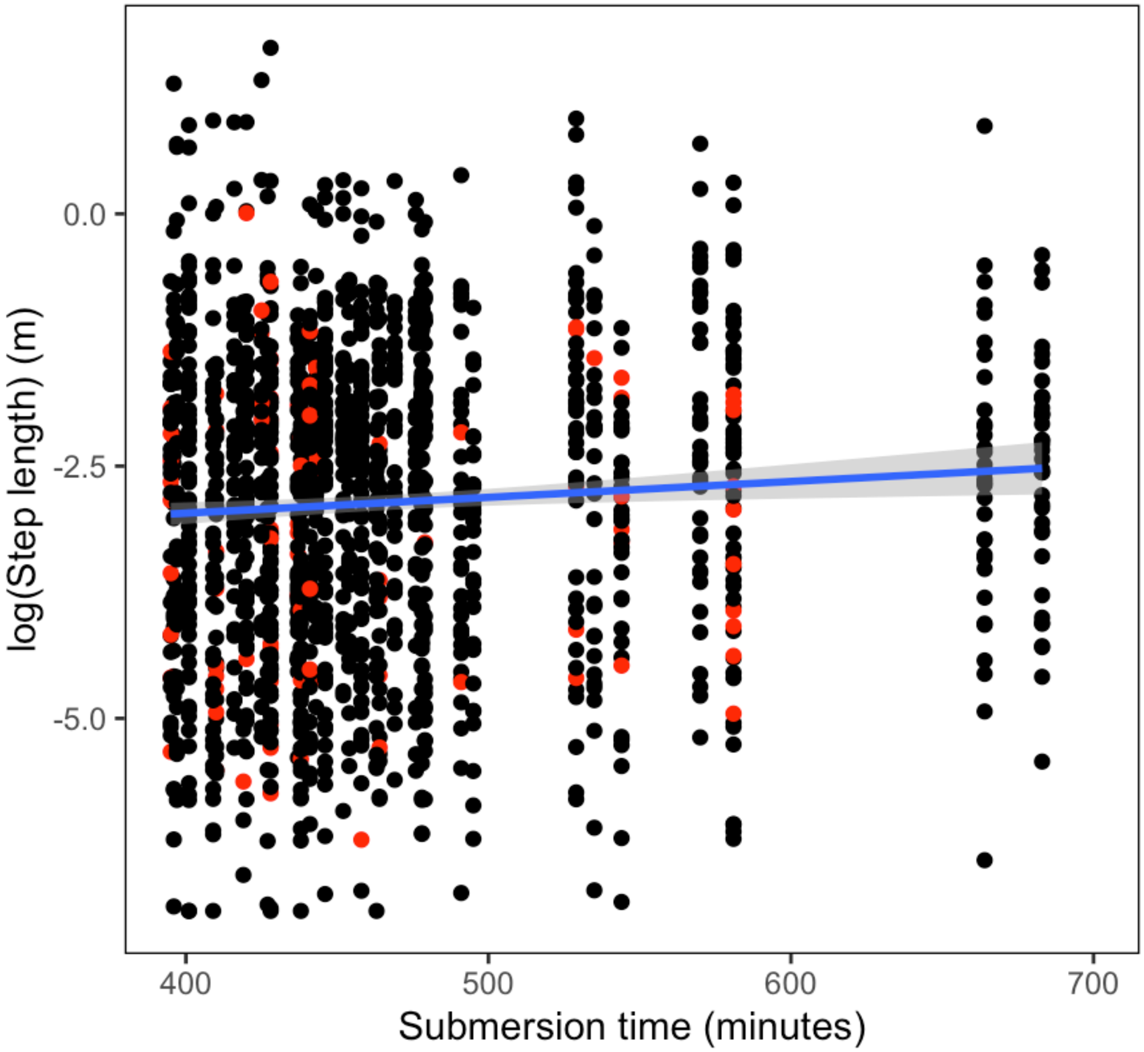

Figure 3.7 Pooled population daily step lengths (m) on the log scale with respect to daily tidal submersion times (minutes). Red points indicate a feeding observation, and the blue line shows a linear regression and standard error.

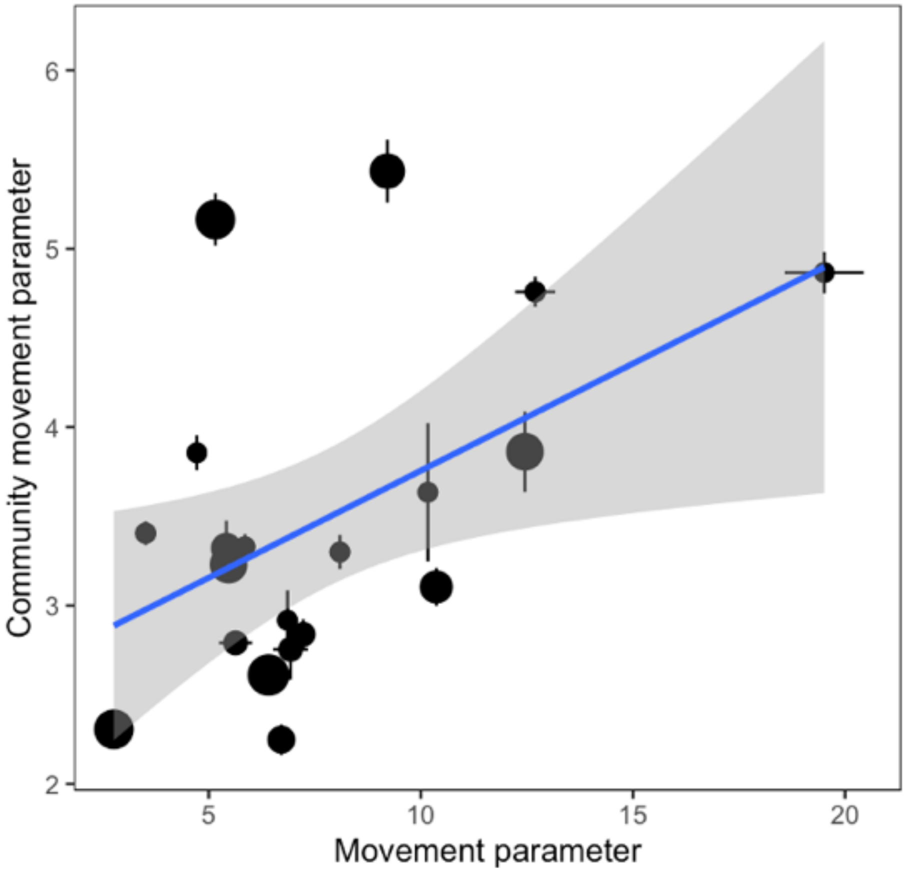

Figure 3.8 Relationship between individual movement distribution fitted parameter values (λ_m) and community movement parameters (λ_c), with a linear regression. Point size represents diet diversity values for a given individual, with SE bars for both the movement and community movement parameter values.

Table 3.1 Non-metric multi-dimensional scaling summary statistics for the invertebrate community ordination. Values below include the number of dimensions, final stress, number of iterations, whether a convergent solution was reached, the ordination correlation with Axis 1 and Axis 2, the total variance explained, and the orthogonality of the solution.

Dimensions	**Final stress**	**Iterations**	**Convergent solution**	**Axis 1 R^2**	**Axis 2 R^2**	**Total variance explained**	**Orthogonality (R^2)**
2	0.167	600	Yes	0.65	0.18	0.83	0.82

Table 3.2 Invertebrate species Pearson and Kendall Correlations with ordination axes for the full invertebrate community from whelk microhabitat photos. Bolded numbers indicate R^2 values greater than 0.20 and thus significant species correlations with the ordination axes.

Invertebrate species	abbr.	Axis 1	Axis 2	R^2	Pr(>r)
Anthopleura elegantissima	Ae	-0.05	0.99	0.00	0.54
Balanus glandula	**Bg**	**1.00**	**0.00**	**0.70**	**<0.001**
Chthamalus dalli	**Cth**	**0.56**	**0.83**	**0.46**	**<0.001**
Limpets	Lim	0.03	-0.99	0.00	0.29
Littorine snails	Ls	0.75	-0.66	0.12	<0.001
Mytilus californianus	Mc	-0.60	0.80	0.05	<0.001
Mytilus trossulus	**Mt**	**0.30**	**0.95**	**0.28**	**<0.001**
Pollicipes polymerus	**Pp**	**-0.52**	**-0.85**	**0.66**	**<0.001**
Semibalanus cariosus	**Sc**	**-0.51**	**0.86**	**0.55**	**<0.001**

Table 3.3 Number of feeding observations, proportion of prey taxa in individual diets, and diet diversity (D_{si}) of the 16 individuals with 4 or more feeding observations.

Whelk ID	**# feeding observations**	***Mytilus trossulus***	***Mytilus californianus***	***Balanus glandula***	***Chthamalus dalli***	***Nucella ostrina***	**Dsi**
D18	5	0	0	1.00	0	0	0
D37	4	1.00	0	0	0	0	0
C43	5	0.80	0.20	0	0	0	0.50
D5	5	0.80	0	0.20	0	0	0.50
C36	4	0.75	0.25	0	0	0	0.56
C47	4	0.75	0	0.25	0	0	0.56
D17	4	0.75	0	0.25	0	0	0.56
C26	9	0.33	0	0.67	0	0	0.64
C17	8	0.38	0	0.63	0	0	0.66
C7	5	0.40	0	0.60	0	0	0.67
E2	4	0.50	0	0.50	0	0	0.69
C18	6	0.50	0.17	0.33	0	0	1.01
D31	6	0.50	0.17	0.33	0	0	1.01
C23	4	0.50	0.25	0.25	0	0	1.04
D6	4	0.25	0	0.50	0.25	0	1.04
C12	11	0.27	0	0.55	0.09	0.09	1.12

Table 3.4 Model summary for linear models testing the relationship between individual niche width (D_{si}), individual movement distribution fitted parameters (λ_m), and community movement parameters (λ_c). The best fit model (in bold) was selected by sequential removal of non-significant terms.

Model	Term	Estimate	SE	t-value	p-value
Intercept + λ_m + D_{si} + λ_m:D_{si}	(Intercept)	2.51	1.77	1.42	0.18
	λ_m	0.13	0.27	0.48	0.64
	D_{si}	0.001	2.23	0.001	0.99
	λ_m:D_{si}	0.002	0.34	0.006	0.99
Intercept + λ_m + D_{si}	(Intercept)	2.50	0.80	3.11	0.008
	λ_m	0.13	0.09	1.50	0.16
	D_{si}	0.013	0.74	0.02	0.98
Intercept + λ_m	**(Intercept)**	**2.56**	**0.42**	**6.07**	**<0.0001**
	λ_m	**0.12**	**0.05**	**2.45**	**0.025**

Chapter 4 – Effects of prey predictability on foraging and handling times of predatory whelk hatchlings

Shannon M. Hennessey and Mark Novak

4.1 Abstract

Individual diet variation in predator populations is increasingly recognized as important to population- and community-level processes, yet the processes generating and maintaining variation at ecological scales remain poorly understood. Individual specialization is expected to increase in predictable resource environments because greater individual-level foraging efficiency can increase fitness and decrease intraspecific competition. In contrast, the lack of predictability in resources should promote generalist diets as these can confer fitness advantages in times of resource scarcity. These predictions are subject to assumptions regarding a generalist's diet plasticity via learning and heritability and remain largely untested. Here, we use manipulative laboratory experiments to quantify the relative contributions of learning and heritable diet plasticity in shaping individual specialization in the hatchlings of six populations of *Nucella ostrina* from sites across a gradient of prey predictability. We find that, regardless of the resource predictability of an individual's source location, prior foraging experience on mussels decreases their subsequent foraging time, defined as time from initiating foraging movement to beginning to feed on a mussel prey, compared to whelks naïve to mussels. We also find suggestive evidence that prey predictability at the population source location decreases foraging times on mussels, regardless of prior experience with mussels. Counterintuitively, however, the time taken by whelks to handle prey is longer with prior exposure to mussels, suggesting that other factors such as site attributes, other than prey predictability, or behavioral modification may play a role in determining individual foraging abilities we detect. The combined influences of learned and heritable

foraging efficiency we see here suggest that feedbacks exist between resource predictability, an individual's degree of diet specialization, and subsequent effects of that variation on community composition.

4.2 Introduction

Interactions between consumers and their resources are fundamental to understanding how species interactions shape natural systems. Prey choice is central to determining a predator's influence on their prey, and can have further impacts on species interactions and the structure of the surrounding community (Pianka 1981; Sih *et al*. 1985; Wilbur & Fauth 1990; Wootton 1992; Mittelbach & Osenberg 1994; Sih & Christensen 2001). Ultimately, predator individuals seek to maximize fitness by consuming prey that will maximize energetic intake given costs and risks, and therefore make foraging decisions that directly impact fitness (Emlen 1966; Pyke 1984). When foraging, a predator's specialization on a certain prey type should allow the predator to enhance its predation success, whether through innate or learned efficiency in finding certain prey in a patchy environment or proficiency in consuming a particular prey type.

Within the same prey landscape, not all predators in the same population exhibit comparable diet specificity. This phenomenon, termed 'individual diet specialization', has undergone much study over recent years, showing that variation in diet across individuals within a population is widespread, occurring in a wide range of ecosystems and organisms (Bolnick *et al.* 2003). Individual diet specialization has also been cited as an important factor to consider when making population-level inferences about predator impacts on prey communities, as including individual variation can alter predictions as to how populations might respond to environmental changes (Saloniemi 1993; Bolnick *et al.* 2003; Okuyama 2008; Vindenes *et al.* 2008; Araújo *et al.* 2011; Des Roches *et al.* 2018).

Environmental variation itself can have large influences on the behavior of predators foraging within patchy landscapes. Species responses to environmental unpredictability has undergone much study, linking variation in individual habitat and prey resource use to the evolution of ecological specialization. The predictability of resource availability is thought to impact the foraging success of predators within that environment, as the flexibility of individual foraging behaviors can underlie the foraging success of a predator when switching from a preferred prey species to another prey when the preferred prey becomes rare (Curio 1976). Theory predicts that under predictable environmental conditions, individual specialists can often outcompete generalists due to increased foraging efficiency on preferred prey. Specialization can also decrease competition between individuals within a population, with conspecifics feeding on different prey resources. However, in unpredictable environments, generalism is favored because generalist individuals can be quicker to adapt to alternative resources. Specializing on a certain prey could be costly if that prey is not consistently or predictably available (Futuyma & Moreno 1988; Van Tienderen 1991).

Despite the ubiquity of individual diet specialization in natural systems, there is a wide range of mechanisms maintaining individual specialization within consumer populations. In general, mechanisms include those entailing learned efficiency in foraging behaviors that are advantageous in finding and consuming certain prey (e.g.

Hughes 1979; Rovero *et al*. 1999; Woo *et al*. 2008; Tinker *et al*. 2009; Newsome *et al*. 2019), or heritable morphological differences in ecotypes that confer an advantage when foraging in specific habitat types or on certain prey (eg. Svanbäck & Persson 2004; Svanbäck & Bolnick 2005, 2007). Many cases of individual diet specialization are thought to be in response to a spatially or temporally unpredictable landscape, balancing tradeoffs between being a specialist or generalist while making foraging decisions (Iguchi *et al*. 2004; Courbin *et al*. 2018). For example, in sea otters, individual diet specialization was more prominent in spatially-heterogeneous habitats, lessening intraspecific competition and reflecting differences in prey diversity, relative abundance, and the skills required to efficiently consume prey (Newsome *et al*. 2019).

Here, we investigate how prey preferences are established and maintained in populations of an intertidal predatory whelk, *Nucella ostrina*, across a range of prey predictability regimes. We hypothesized that increased prey predictability would favor the establishment of individual specialists within populations, as multiple consistently available prey taxa would allow for individuals to learn and maintain efficiency in foraging for and consuming a given prey. This would also serve to lessen intraspecific competition within the population. By raising and conditioning whelk hatchlings on specific diets, we assessed the influences of prior prey exposure and site-specific prey predictability on whelk foraging and handling times. Comparing foraging and handling times across different regimes of prey predictability allowed us to assess the influence of both heritability and learning on individual diet preferences and its potential role in establishing individual diet specialization in this important intertidal predator.

4.3 Study System

4.3.1 Whelks

Nucella ostrina is a common whelk predator in the rocky intertidal zone that feeds primarily on small mussels (*Mytilus spp.*) and barnacles (*Balanus glandula*) (Novak *et al.* 2017). Handling times on these prey taxa are long, often exceeding 24 hours (Novak *et al.* 2017). Individual diet specialization has been well-documented for *N. ostrina* (West 1986), and several mechanisms underpinning this variation in individual prey preference have been proposed (but see Coblentz 2019). For example, whelks maintained in the lab on a single prey type have been shown to primarily choose those prey in subsequent multi-prey settings, suggesting ingestive conditioning or retentive learning (Hughes 1979, 1988; Dunkin & Hughes 1984; West 1986; Vadas *et al*. 1994; Matthews-Cascon 2001). Heritable differences in prey preferences have also been shown, with whelks from different populations raised on common prey displaying differences in prey preferences as well as drilling ability with differences in their site's prey community (Wieters & Navarrete 1998; Sanford & Worth 2009). This suggests genetically controlled behavioral traits and implies a limit to an individual's ability to learn prey handling skills (Rovero *et al*. 1999). If learning is a large component of individual prey choice, it follows that this preference could be established early in life. If there are heritable differences in foraging plasticity or drilling ability, there should be differences across individuals from different prey predictability backgrounds regardless of prior individual experience.

Whelks are an ideal system to examine this as not only do they inhabit a highly dynamic ecosystem with high variation in prey recruitment and settlement across wide spatial scales, but they also have crawl-away larvae that feed on sessile prey (Moran & Emlet 2001), leading to local adaptation of individual foraging habits (Sanford *et al.* 2003). Whelk hatchlings have been shown to preferentially feed on small mussels and barnacles (Crothers 1985), and provide a system with which we can closely examine the relationship between prey predictability and the generative factor determining the degree of individual specialization.

4.3.2 Sites and predictability gradient

To assess the influence of prey predictability on individual specialization with *Nucella ostrina* populations, we collected egg capsule clusters from six populations along the Oregon coast. The coastal waters off the US west coast are characterized by the intermittent upwelling of nutrient-rich waters in the summer, leading to areas of high nutrient availability and invertebrate recruitment (Huyer 1983; Menge *et al.* 2004, 2015; Menge & Menge 2013). Variation in coastal shelf width leads to different regimes of primary and invertebrate productivity, providing a gradient of prey predictability regimes along the Oregon coast, with differences in consistency and magnitude of annual mussel and barnacle recruitment at three main capes (Connolly & Roughgarden 1998; Broitman *et al.* 2008; Menge *et al.* 2015). We selected two sites from each of the three capes as follows, from South to North: (1) in the southern Oregon region, with a rocky intertidal ecosystem characterized by relatively low productivity, a prey community that largely consists of acorn barnacles (*Balanus glandula*) and patchy beds of California mussels (*Mytilus californianus*), and usually very low and unpredictable recruitment of small mussels, we sampled at Cape Blanco State Park (42.84 N, 124.56 W) and Cape Arago State Park (43.31 N, 124.40 W); (2) in the Cape Perpetua region, characterized by high primary productivity, and a consistent, diverse prey community, including abundant acorn barnacles and mussels, we sampled at Strawberry Hill (44.25 N, 124.11 W) and Yachats Beach (44.32 N, 124.11 W); and (3) in the Cape Foulweather region, characterized by intermediate productivity and patchy barnacle and mussel cover with intermediate predictability in mussel recruitment, Manipulation Bay (44.83 N, 124.06 W) and Fogarty Creek (44.85 N, 124.05 W) (Menge *et al*. 2015; Figure 4.1). As each site is separated by several kilometers of coastline, the whelk populations can be treated as genetically distinct due to limited larval dispersal and population connectivity (Marko 1998; Sanford *et al*. 2003).

4.4 Methods

At each of the six sites, we collected 15 distinct clusters of ripe *Nucella ostrina* egg capsules between May 16-19 2018, taking care to keep the clusters separated to maintain family identity. After transporting the egg clusters to a lab at Oregon State University, in Corvallis, Oregon, USA, they were housed under common garden conditions in eight flow-through tanks. Seawater was maintained at ambient coastal temperatures (10.8-11.0°C) with a 12:12 hour light:dark cycle. Each cluster of egg capsules was housed individually in small mesh pouches. Pouches from each site were randomized across the eight tanks.

Newly-settled mussels (*Mytilus spp*.) and barnacles (*Balanus glandula*) were collected as needed from Yachats Beach (44.32 N, 124.11 W). Mussels were collected on strips of medium density foam rubber (0.5 cm thick) attached to the rock with stainless steel mesh. Barnacles were scraped from the rock in patches where settlers had cemented to older conspecifics, allowing us to sacrifice the bottom layer of barnacles while the small recruits remained intact. All prey individuals provided were less than 3mm in total length to ensure that whelk hatchlings could successfully drill the prey items (Gosselin & Chia 1996).

After hatchling emergence in a given cluster, three randomly-selected hatchlings from that cluster were collectively placed into each of three prey conditioning treatments for 8 weeks. The available prey in these treatments consisted of either: (1) barnacles only, (2) mussels only, and (3) an equal number of barnacles and mussels. Each conditioning treatment had 10 prey individuals. Prey densities were checked every 2-3 days, and any consumed prey were replaced to maintain prey densities throughout the duration of the training period. Whelks reach adult sizes at around nine months (Sanford *et al*. 2003). The 8-week initial feeding and growth period therefore allowed for sufficient conditioning of whelks on the initial prey type. Although it has been shown that exposure to barnacle chemical cues in the water medium can increase *Nucella* preference for barnacles (Vadas *et al*. 1994), barnacles are rarely if ever absent from natural systems and their odors in the water are not sufficient to provide information on the abundance and distribution of nearby prey (Gosselin & Chia 1996). Therefore, we did not consider the presence of barnacles in the flow through tank system a possible confounding factor across our prey conditioning treatments.

After the initial conditioning period, a randomly selected individual from each of the three conditioning treatments was removed from its respective prey treatment for a mussel consumption trial. Each individual was starved for two weeks prior to the start of this trial to ensure a baseline level of hunger across individuals. Consumption trials were conducted in individual experimental arenas with one whelk and a single 3mm mussel prey. Each consumption trial arena was conducted in a fully submerged 1oz clear plastic container (43mm diameter) within a tank. Each container had three 25mm-diameter holes drilled in the side and one hole in the bottom, covered with 500-micron mesh, to enable adequate water exchange. The mussel was settled in the experimental arena 24 hours prior to the start of the addition of the whelk to ensure adequate time for it to settle and limit mussel evasion of the whelk.

Whelk behavior was monitored continuously via overhead cameras throughout the duration of the trial, and foraging times and handling times were scored from the video. Foraging times were defined as the time, in hours, from the start of continuous whelk movement (either from the start of the consumption trial, or after being stationary for at least 2 hours if there were periods of resting) to the individual reaching the mussel, and were used to assess the effects of prior mussel exposure on prey recognition. Handling times were defined as the time in hours it took for the whelk to fully consume the mussel from its initial encounter to a characteristic ‘waggle’ when finished feeding.

Due to variation in hatching success and survivorship across clusters and treatments, the sample sizes for sites and capes were as follows (equal for each of the three conditioning treatments): (1) Cape Blanco had 9 families and Cape Arago had 4, making a total of 13 replicate individuals for the Cape Blanco region, (2) Strawberry Hill and Yachats Beach had 9 and 6 families, respectively, for a total of 15 replicate individuals from Cape Perpetua, and (3) Manipulation Bay and Fogarty Creek had 9 and 6 families, respectively, with a total of 15 replicate individuals from Cape Foulweather. Only trials with a complete set of the three conditioning treatments for a given family were used for subsequent analyses.

We hypothesized that whelks raised on different diets would exhibit different feeding behaviors. As learning has been shown as an important component in a whelk's ability to efficiently find and consume a certain prey item (Dunkin & Hughes 1984; West 1986; Vadas *et al*. 1994; Sanford & Worth 2009), we expected that whelks would learn efficiency in drilling their initial prey over time. Therefore, we predicted that whelks raised on mussels only (treatment 1) would exhibit decreased foraging and handling times compared to those naïve to mussels (treatment 2), with those exposed to barnacles and mussels (treatment 3) showing an intermediate response. We also predicted that prey predictability regime, determined by whelk site of origin, would influence average foraging and handling times, as increased predictability should favor individual specialists with heritable efficiency in handling prey (Underwood *et al*. 2004). To that end, whelk hatchlings from sites with predictable prey should exhibit faster foraging and handling times, regardless of prior mussel exposure from the conditioning treatment.

We used linear mixed effects models to assess the impacts of site-specific prey regimes and prey identity from first feeding, as determined by conditioning treatment, on whelk foraging and handling times. An important covariate that emerged over the course of the experiment was whelk size, and we therefore also included size as a covariate. These models allowed us to account for variation in response (slope and/or intercept) across whelk families, as well as the nested statistical dependency of cluster and site within prey predictability (as defined by cape). To determine which random effect structure was best for a given response variable, we first constructed three full models. All models had fixed effects including training prey treatment, cape, whelk size, and all pairwise interaction terms. The 3 models differed by having either no random effect (i.e. generalized least squares regression), a random slope based on cluster identity, or a random slope and intercept for each cluster. Relative model performance was assessed using the corrected Akaike information criterion (AICc; Burnham & Anderson 2002). With the random effect structure determined by the best performing model, we then fit successive models eliminating fixed effects with low statistical clarity (sensu Dushoff *et al*. 2019) until all remaining terms were well supported following Zuur *et al*. (2009).

4.5 Results

Whelk size emerged as an important covariate over the course of the experiment, therefore we also included size as a covariate in our foraging and handling time models. Whelks used in the mussel consumption trials were on average 3.67 ± 0.55mm in size. Whelk size after the conditioning period was negatively correlated with conditioning treatment (Pearson’s correlation coefficient = -0.964), indicating that whelks were generally largest from the barnacle-only treatment and smallest when fed only mussels. Whelk size did not influence foraging times, and therefore was omitted from the final model ($p = 0.62$). However, larger whelks consumed the experimental mussel faster, with an approximately 1mm increase in whelk size estimated to decrease handling times by 14.77 ± 3.49 hours ($p < 0.001$).

4.5.1 Foraging times

Whelk foraging times on the mussels in the consumption trials depended on prior mussel exposure, determined by the composition of their prey conditioning diet. The structure of best- performing model as judged by AICc did not include a random effect (Table 4.1). Through the sequential elimination of fixed effects that did not provide adequate statistical clarity, the best model included only the categorical covariate of treatment ($p = 0.051$), with shorter whelk foraging times correlated with prior mussel exposure (Table 4.2). The mean time for a whelk conditioned on barnacles only to reach the experimental mussel prey was 2.49 ± 0.21 (standard error) hours, while whelks conditioned on a combination of mussels and barnacles took an average of 2.0 ± 0.30 hours to begin feeding (combination vs. barnacle treatment $p = 0.102$). Whelks conditioned on only mussels were the quickest to begin feeding, with a mean of 1.77 ± 0.30 hours to reach the experimental mussel (mussel vs. barnacle treatment $p = 0.017$) (Figure 4.2).

While the best-fit model did not include the fixed effect of cape, the second best-fit model did include the effect of cape, but with less statistical clarity than our threshold for inclusion in the final model ($p = 0.082$; Table 4.2). This relationship between cape and foraging times revealed suggestive evidence regarding the effect of cape-dependent prey predictability on whelk foraging times. With the inclusion of cape as a predictor, whelks from Cape Foulweather, the prey regime with intermediate predictability, were estimated to find their mussel prey 0.67 (± 0.30) hours faster, on average, than those from the other two capes ($p = 0.027$; Figure 4.2).

4.5.2 Handling times

The relationship between handling times, conditioning treatment, cape of origin, and whelk size in the mussel consumption trial was best described by a linear mixed effects model with a random intercept based on cluster identity nested within site of origin (Table 4.3), indicating a heritable component to handling time. This model indicated that whelk handling times were dependent both on prior mussel exposure in the conditioning treatment ($p < 0.001$) and whelk size ($p < 0.001$; Table 4.4). Whelks conditioned on the barnacle-only diet took the shortest time to consume the experimental mussel, with an average of 47.80 ± 1.97 (standard error) hours (2 days). Being raised on the combination or mussel-only diet significantly increased the average handling time by 10.61 ± 4.56 ($p = 0.02$) and 9.76 ± 5.50 ($p = 0.08$) hours, respectively (Figure 4.3).

4.6 Discussion

Prey predictability is thought to impact the degree of specialization that individuals within a predator population exhibit (Kassen 2002; Abrams 2006; Poisot *et al.* 2011, 2012), with the strength of an individual's prey preference linked to their ability to effectively find and consume their preferred prey. Raising *Nucella ostrina* hatchling kin groups from populations with site-specific regimes of prey predictability on different diets from first feeding allowed us to assess the influences of learning and heritable plasticity on individual ability to efficiently forage for and consume mussel prey. We found that whelk foraging behavior was largely constrained by prior mussel exposure, regardless of region of origin, with increased experience with mussels leading to shorter foraging times (Figure 4.2). Whelk handling times also showed an effect of prey conditioning treatment, with individuals from the barnacle-only treatment having the shortest handling times overall (Figure 4.3). These results largely met our expectations, as learning has been attributed to increased efficiency in consuming prey as well as preference for certain prey with prolonged exposure (Dunkin & Hughes 1984; Vadas *et al*. 1994; Gosselin & Chia 1996). However, considerable between-site variation in hatchling response also points to potential heritable traits, such as behavioral plasticity, that may also underlie individual foraging responses to unpredictable prey resources.

Whelk foraging times during the mussel consumption trials were dependent on prior mussel exposure from the prey conditioning treatments. The inclusion of mussels in the conditioning diet decreased average foraging times on the experimental mussel from 2.5 hours to approximately 1.75, showing a clear effect of learning in finding a preferred prey item. This significant decrease in prey encounter time ought to play a considerable role in successful foraging in a spatially and temporally heterogeneous prey landscape, allowing for individuals to respond to prey resource availability (Hughes 1986). The effect of increased encounter rates on subsequent prey preference has been demonstrated for congeners of *Nucella ostrina*, with individuals raised on mussels or barnacles showing increased preference for that prey item (Matthews-Cascon 2001). Additionally, differential prey encounter rates by individuals within a population, coupled with learning, may serve to establish or maintain individual specialization on certain prey, which suggests an important influence of prey abundances as well as predictability of these resources.

While we did not see statistically clear evidence of heritable foraging behaviors, when we included cape as a predictor of foraging times in the linear model there was a suggestive influence of cape-specific prey predictability regimes on individual foraging times. Notably, the cape with the intermediate predictability (Cape Foulweather) was predicted to have the shortest foraging times, with an over 30% decrease in mean foraging time compared to the other capes. This effect of prey predictability does not support the expectation that regions with more predictable prey having increased efficiency in foraging on preferred prey, as we would expect a greater proportion of individual specialists under these prey regimes (Courbin *et al.* 2018). Alternatively, the potential for heritable differences in foraging plasticity could provide an advantage in areas with unpredictable prey resources, allowing for individuals to successfully forage on intermittent resources as they become available. This may reflect population-level adaptations to resource fluctuations (Hazlett 1988) rather than degree of individual specialization within the population.

Although individual handling times also showed a relationship with prior mussel exposure as dictated by prey conditioning treatments, we found that whelks naïve to mussels were able to consume mussels more quickly than those raised on mussels. Additionally, there was no effect of prey predictability regime on individual handling times in the mussel consumption trials. These results are counter to our predictions that exposure to mussels would increase an individual's ability to consume that prey more quickly via learning (Matthews-Cascon 2001; Sanford *et al.* 2003), and that increased prey predictability ought to lead to increased efficiency in drilling. However, we also saw a strong correlation between whelk size and training diet, with whelks raised on barnacles growing considerably larger than those with no barnacles, on average. Hence, any effect of treatment on individual handling time may have been partially confounded with this factor, as these factors could not be statistically disentangled.

The fact that prior exposure to mussels does not appear to increase a hatchling's ability to efficiently consume mussels, coupled with the rapid growth of hatchlings trained on barnacles, may have interesting implications for individuals in environments with sporadic mussel recruitment. In these environments, barnacles would likely serve as a primary prey source (Dunkin & Hughes 1984). Whelk hatchlings can successfully consume barnacles much larger than themselves, providing an energetically rich source of prey that may allow for faster growth (Palmer 1990; Gosselin & Chia 1996). Additionally, along the Oregon coast, barnacle recruits typically settle earlier in the summer than mussels, coinciding with the peak hatching of whelks (Broitman *et al.* 2008; Menge *et al.* 2009, 2011). This temporal match of hatching at prey recruitment may have important implications for the early prey encounter and growth of whelk hatchlings, and could underlie population-level differences in individual preferences with differential prey recruitment.

Our results demonstrate the importance of learning, via exposure to specific prey from first hatching, on the foraging success of *Nucella ostrina* hatchlings. Increased experience with mussel prey led to faster foraging times, allowing these hatchlings to more efficiently find their preferred prey. We also found suggestive evidence that site-level attributes may decrease foraging times, notably at sites with intermediate prey predictability. Hatchlings were also larger when fed non-preferred barnacle prey, and were subsequently able to consume mussels more quickly. In unpredictable foraging environments, efficiency in finding and consuming specific prey, whether through learning or heritable behaviors, is central to the foraging success of individual predators. Further, variation in prey choice can have implications at both the individual and population levels, as frequency of prey encounters is dependent on the availability and abundance of preferred prey and can impact individual fitness, while individual interactions with conspecifics can increase intraspecific competition if resources are scarce (Svanbäck & Bolnick 2005). The combined influences of learned and heritable foraging efficiency we see here suggest that feedbacks exist between resource predictability, an individual's degree of diet variation, and subsequent effects of that variation on community composition.

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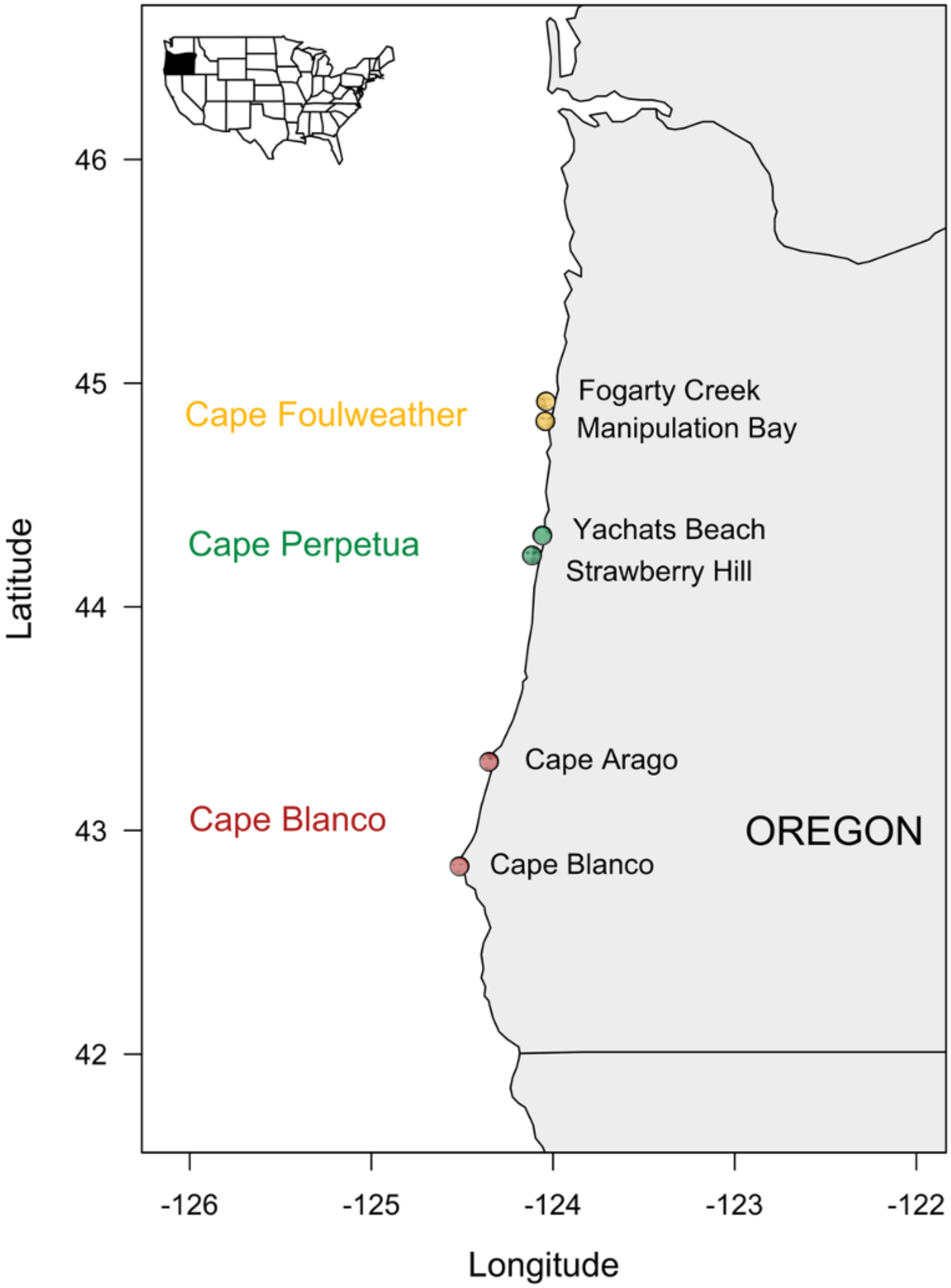

Figure 4.1 Map of the Oregon coast and field sites. Colors indicate level of prey productivity and predictability of annual mussel and barnacle recruitment, with green as high, yellow as medium, and red as low prey productivity and predictability.

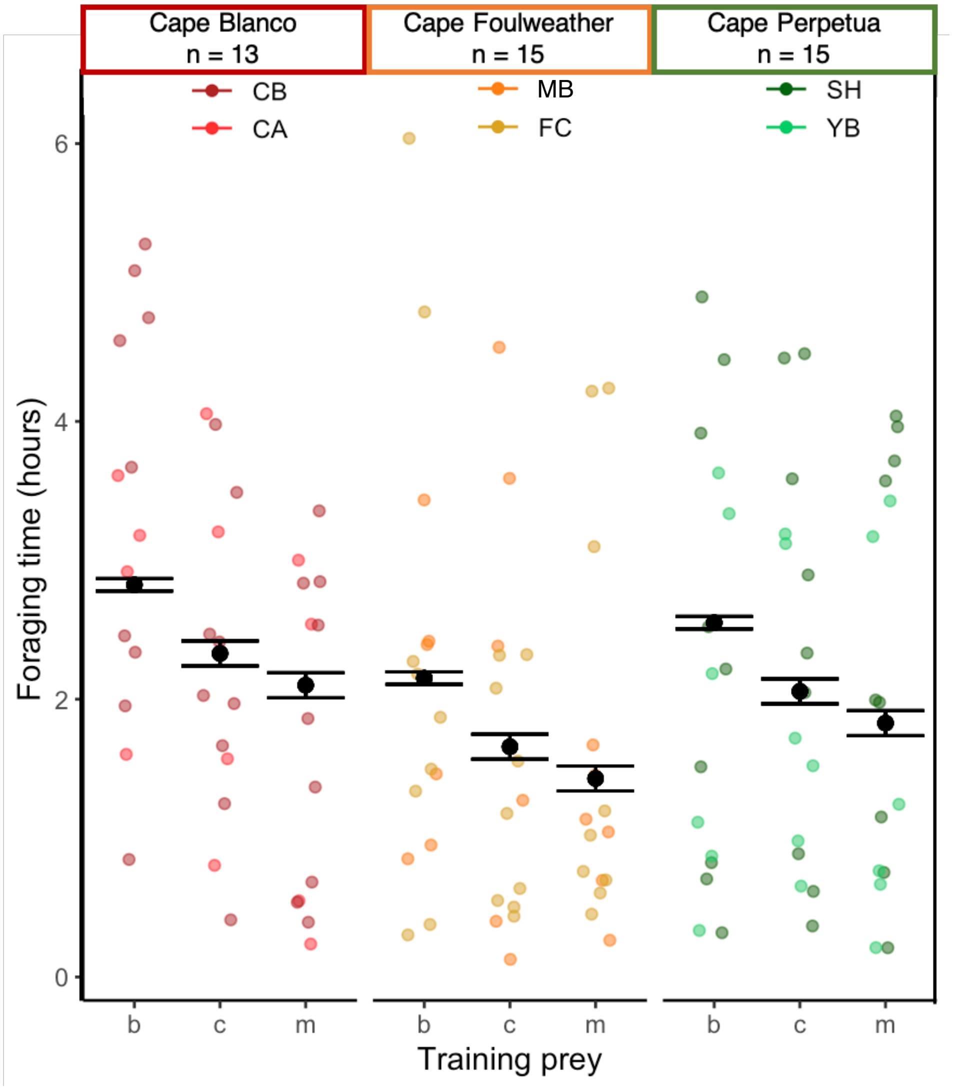

Figure 4.2 Foraging times (hours) by cape and prey conditioning treatment (b = barnacles only, c = combination of mussels and barnacles, m = mussels only). Colors indicate cape and site of origin, while the black dot is the model predicted mean for a given treatment, with the standard error.

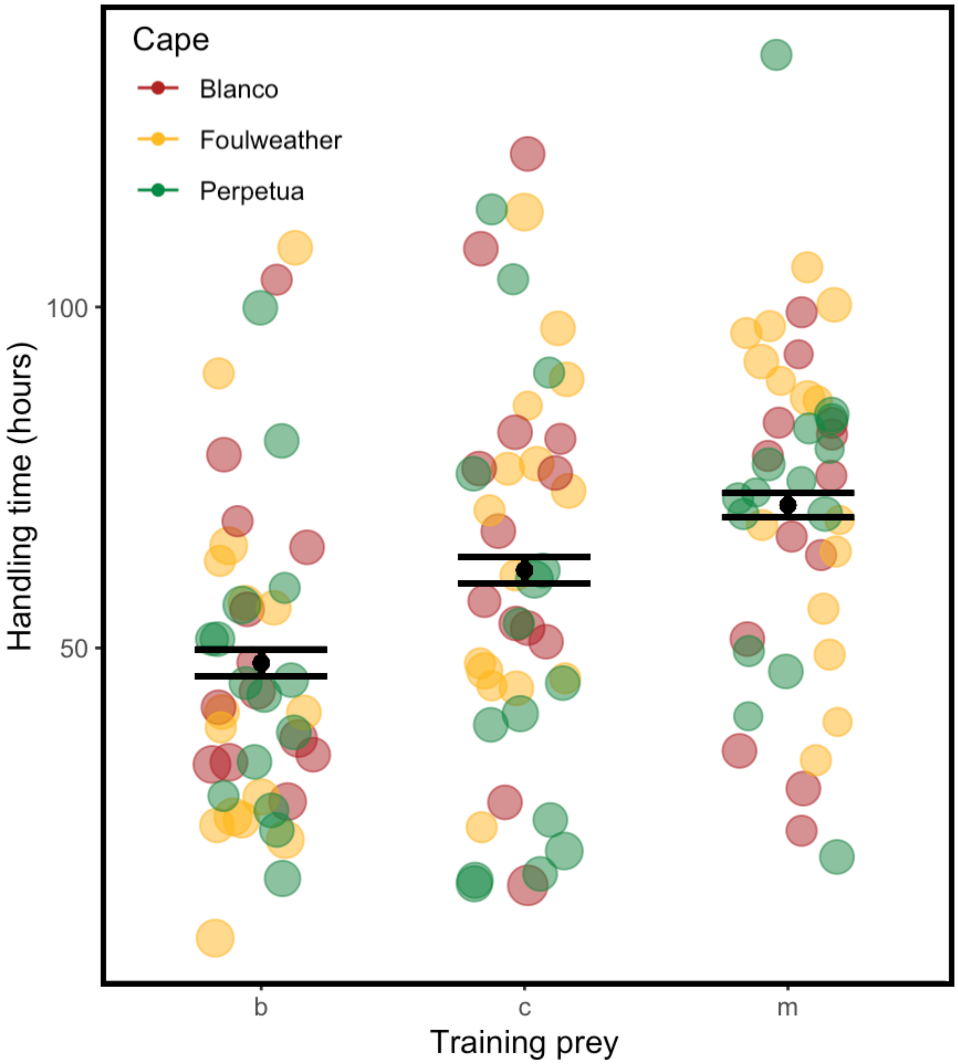

Figure 4.3 Handling times (hours) by prey conditioning treatment (b = barnacles only, c = combination of mussels and barnacles, m = mussels only). Point colors indicate cape of origin, and points are scaled by individual whelk size. The black dot is the model predicted mean for a given treatment, with the standard error.

Table 4.1 Model structure, AICc values, and ΔAICc values for linear models testing the fixed effects of prey conditioning treatment, cape of origin, and the interaction of treatment and cape on whelk hatchling foraging times on their mussel prey. The three models include one with no random effect, one with a random intercept of cluster nested within site of origin, and the third with a random slope and intercept of treatment given cluster nested within site of origin. The random effect structure of the full model (in bold) was selected by the lowest ΔAICc.

Model: foraging times – random effect structure	**AICc**	**ΔAICc**	**df**
Intercept + Treatment + Cape + Treatment:Cape	**461**	**0**	**10**
Intercept + Treatment + Cape + Treatment:Cape, random intercept = ~ 1|Site/Cluster	465	4	12
Intercept + Treatment + Cape + Treatment:Cape, random intercept and slope = ~ 1 + Treatment|Site/Cluster	481	20	22

Table 4.2 Model summary for linear models testing the fixed effects of prey conditioning treatment, cape of origin, and the interaction of treatment and cape on whelk hatchling foraging times. The best fit model (in bold) was selected by sequential removal of non-significant terms.

Model: foraging times	**Term**	**df**	**F-value**	**p-value**
Intercept + Treatment + Cape + Treatment:Cape	(Intercept)	1	298.08	<0.0001
	Cape	2	2.56	0.082
	Treatment	2	3.11	0.048
	Cape:Treatment	4	0.96	0.432
Intercept + Treatment + Cape	(Intercept)	1	298.46	<0.0001
	Cape	2	2.56	0.082
	Treatment	2	3.11	0.048
Intercept + Treatment	**(Intercept)**	**1**	**291.25**	**<0.0001**
	Treatment	**2**	**3.04**	**0.051**

Table 4.3 Model structure, AICc values, and ΔAICc values for linear models testing the fixed effects of prey conditioning treatment, cape of origin, hatchling size, and all 2- and 3-way interaction terms on whelk hatchling handling times of their mussel prey. The three models include one with no random effect, one with a random intercept of cluster nested within site of origin, and the third with a random slope and intercept of treatment given cluster nested within site of origin. The random effect structure of the full model (in bold) was selected by the lowest ΔAICc.

Model: handling times – random effect structure	**AICc**	**ΔAICc**	**df**
Intercept + Treatment + Cape + Size + Treatment:Cape + Treatment:Size + Cape:Size + Treatment:Cape:Size	1144	5	13
Intercept + Treatment + Cape + Size + Treatment:Cape + Treatment:Size + Cape:Size + Treatment:Cape:Size, random intercept = ~ 1|Site/Cluster	**1139**	**0**	**15**
Intercept + Treatment + Cape + Size + Treatment:Cape + Treatment:Size + Cape:Size + Treatment:Cape:Size, random intercept and slope = ~ 1 + Treatment|Site/Cluster	1153	14	25

Table 4.4 Model summary for linear mixed models testing the fixed effects of prey conditioning treatment, cape of origin, hatchling size, and all 2- and 3-way interaction terms on whelk hatchling handling times of their mussel prey. A random intercept of cluster nested within site of origin was also included. The best fit model (in bold) was selected by sequential removal of non-significant terms.

Model: handling times	Term	Num df	Denom df	F-value	p-value
Intercept + Cape + Treatment + Size + Cape:Treatment + Treatment:Size + Cape:Size, random intercept = ~ 1|Site/Cluster	(Intercept)	1	75	455.95	<0.0001
	Cape	2	3	0.51	0.644
	Treatment	2	75	13.27	<0.0001
	Size	1	75	18.04	<0.0001
	Cape:Treatment	4	75	0.91	0.462
	Treatment:Size	2	75	0.52	0.597
	Cape:Size	2	75	3.82	0.026
Intercept + Cape + Treatment + Size + Cape:Treatment + Cape:Size, random intercept = ~ 1|Site/Cluster	(Intercept)	1	77	535.47	<0.0001
	Cape	2	3	0.60	0.603
	Treatment	2	77	13.17	<0.0001
	Size	1	77	17.64	<0.0001
	Cape:Treatment	4	77	0.90	0.467
	Cape:Size	2	77	3.74	0.028
Intercept + Cape + Treatment + Size + Cape:Size, random intercept = ~ 1|Site/Cluster	(Intercept)	1	81	501.06	<0.0001
	Cape	2	3	0.56	0.620
	Treatment	2	81	13.10	<0.0001
	Size	1	81	17.65	<0.0001
	Cape:Size	2	81	1.82	0.169
Intercept + Cape + Treatment + Size, random intercept = ~ 1|Site/Cluster	(Intercept)	1	83	479.50	<0.0001
	Treatment	2	83	13.14	<0.0001
	Cape	2	3	0.54	0.632
	Size	1	83	17.78	<0.0001
Intercept + Treatment + Size, random intercept = ~ 1|Cape/Site/Cluster	**(Intercept)**	**1**	**83**	**472.71**	**<0.0001**
	Treatment	**2**	**83**	**13.36**	**<0.0001**
	Size	**1**	**83**	**18.08**	**<0.0001**

Chapter 5 – General Conclusions

Individual-level trait variation is a fundamental part of natural systems. Variation in niche width in animal populations is thought to depend on environmental fluctuations and spatial heterogeneity of habitat and resources, and these differences produce or maintain observed population-, community-, or ecosystem-level patterns. Differences in diet among individuals, termed individual diet specialization, is widespread (Bolnick *et al.* 2003; Araújo *et al.* 2008), and may have important consequences for populations and communities (Bolnick *et al.* 2011; Schreiber *et al.* 2011; Hart *et al.* 2016). In this dissertation, I have explored mechanisms in the establishment and maintenance of individual diet specialization, integrating the predictability and scale-dependent nature of prey resources with variation in individual foraging behaviors and prey selection.

Predator foraging behaviors do not occur in isolation. Instead, a predator's behavior is dependent on the composition, spatial structure, and temporal consistency of the prey community, as well as individual energetic demands (Pianka 1981; Sih *et al*. 1985; Wilbur & Fauth 1990; Wootton 1992; Mittelbach & Osenberg 1994; Sih & Christensen 2001). Establishing how scale-dependent prey patchiness and feeding rates influence predator foraging movements can therefore lend insight into the importance of these factors in shaping population and community processes. In Chapter 2, I showed that combining scale-dependent prey patchiness and individual energetic demands can predict population-level foraging activity of *Nucella ostrina* foraging in a patchy prey environment. However, there are inherent feedbacks between predator foraging behaviors, the spatial patchiness of prey, and predator feeding rates, which poses a problem in disentangling relationships between the components of the system, especially using observational methods. The nature of my data render us unable to assess causality, as either (1) predator foraging movements are dictated by their own energetic demands and the patch structure of prey (eg. Weihs 1975; Ware 1978; Norberg 1981; Pyke 1981; Gendron & Staddon 1983), (2) the scale of prey patchiness influences predator movement and thus constrains the foraging success and feeding rates of predators (Smith 1974), or (3) a combination of both. Despite these challenges, my results emphasize the importance in understanding how predators respond to their environment, linking the behavior of individuals to the broader community patterns they affect.

While population-level foraging movements are correlated with the scale-dependent patchiness of the prey community and feeding rates, providing useful insight into how broader-scale patterns influence dynamics at the population scale, incorporating individual-level variation has also been shown to have marked impacts on inferences when scaled from the individual- to population- level (Bolnick *et al.* 2003). Thus, examining variation in individual foraging behaviors can provide a deeper understanding of individual-scale processes and how the factors influencing individual behavioral patterns generate observed ecological patterns. In Chapter 3, I characterized individual patterns in foraging behavior, correlating behavioral differences among individuals with patterns of microhabitat occupancy and diet diversity. I found a wide range of variation in foraging movement, microhabitat community composition, and diet diversity across individuals, but no evidence for Lévy flight foraging for any individual. There were also no consistent pattern in foraging modes or prey community selectivity across individuals with differing degrees of diet specialization. However, tidal cycles had considerable impact on individual movement and foraging activity, suggesting that the abiotic environment may play a more dominant role in governing foraging behaviors through time than behavioral differences across individuals in this system. The substantial abiotic stress associated with tidal cycles in this dynamic environment, coupled with the high degree of site-level prey productivity, may outweigh the constraints on finding sufficient prey for any given individual, regardless of prey preferences. The lack of consistent inter-individual patterns in foraging behavior, habitat use, and diet shown here, combined with the inferences made in Chapter 2, emphasizes the utility of examining ecological patterns across scales of biological organization, and highlights the importance of environment in shaping foraging behaviors, whether at the individual- or population-level.

Environmental predictability is a key factor hypothesized to influence individual niche width variation (Futuyma & Moreno 1988), underlying inter-individual differences on both ecological and evolutionary timescales. Individual diet specialization is expected to increase in predictable resource environments because greater individual-level foraging efficiency can increase fitness and decrease intraspecific competition. In contrast, the lack of predictability in resources should promote generalist diets as these can confer fitness advantages in times of resource scarcity. These predictions are subject to assumptions regarding a generalist's diet plasticity via learning and heritability. Therefore, my aim in Chapter 4 was to assess the relative contributions of learning and heritable diet plasticity in shaping individual specialization across a gradient of prey predictability using manipulative laboratory experiments. My results demonstrate the importance of learning, via exposure to specific prey from first hatching, on the foraging success of *Nucella ostrina* hatchlings. Increased experience with mussel prey led to faster foraging times, allowing these hatchlings to more efficiently find their preferred prey. I also found suggestive evidence that site-level attributes may decrease foraging times, notably at sites with intermediate prey predictability. The combined influences of learned and heritable foraging efficiency suggest that feedbacks exist between resource predictability, an individual's degree of diet variation, and subsequent effects of that variation on community composition.

Chapters 2 and 3 both showed the importance of the abiotic environment in shaping foraging movement, and by studying individual foraging variation within a highly productive prey environment, I showed that site-level prey productivity may outweigh the constraints of finding sufficient prey for any given individual, regardless of prey preferences. In Chapter 4, my focus was on the role of prey productivity and predictability regimes on individual foraging efficiency, changing the scale of inference. Individuals from sites with intermediate prey predictability had the fastest foraging times, regardless of prior prey exposure, which suggests heritability of traits associated with prey detection within the whelk populations at these sites. However, I predicted that whelks from the most predictable sites would show evidence for heritability, which I did not see. There was also a lack of evidence for consistent correlations of individual foraging behavior with habitat use or diet diversity at a highly productive site (Chapter 3). This suggests that while prey predictability can play a large role in shaping individual foraging behaviors on both ecological and evolutionary scales, it may not scale linearly.

Instead, there may be some optimum in the productivity and predictability of prey that promotes individual specialization across populations. In environments with high prey abundances, the fitness costs associated with heritable foraging traits may be greater than those associated with a slight decrease in foraging efficiency, especially when Brownian foraging movement may be sufficient to find preferred prey. In this case, learning may play a more dominant role in determining prey preferences within a highly productive environment. In environments with low predictability, then, individual generalists would be favored due to the unpredictable nature of their resources.

Overall, my dissertation integrates inferences about the influence of spatial and temporal prey predictability, variation in individual foraging behaviors, and individual diet specialization across spatial scales, eco-evolutionary scales, and scales of biological organization. I showed that at the population level, scale-dependent patchiness in the prey environment and individual feeding rates can predict predator movement. Within this same system, individual-level variation in foraging behaviors is widespread, but does not correlate with microhabitat occupancy or diet diversity. Instead, foraging behaviors are instead largely influenced by tidal cycles. I also found evidence for learning and heritability in foraging traits, but with variable effects depending on prey predictability regimes. The combination of these results suggests that multiple, complex interactions between prey predictability, individual behaviors, and diet choice shape individual foraging patterns, and emphasizes the importance of integrating across scale in studying the maintenance of individual diet specialization.

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APPENDICES

Appendix A – Chapter 2 Prey Heterogeneity

A.1 Invertebrate community characterization results

Each of the 15 non-metric multidimensional scaling (NMDS) ordinations of intertidal invertebrates, for each of the 5 spatial scales and 3 community subsets, reached a 2-dimensional solution after 600 iterations with final stresses ranging from 0.056 to 0.205 (Table A.1). All ordinations at the bench and sub-bench scale, regardless of which taxonomic subset was used, converged on a stable 2D solution. While the other ordinations did not reach a convergent solution, based on final stresses and total variance explained by the two axes, the ordinations at smaller spatial scales were determined to be sufficient characterizations of the invertebrate taxa represented. Variance explained along both Axis 1 and Axis 2 for each ordination ranged from 0.73-0.95, with the total variance explained increasing with larger spatial scales. Ordination axis orthogonalities were between 0.72-1.00, and were typically highest for ordinations using only non-prey taxa (Table A.1).

Pearson's correlations with each invertebrate taxon, sample year, and relative submersion time of each patch were calculated to provide the magnitude and direction of taxon correlation with the ordination axes. For each ordination, species correlations with the two ordination axes support well-established understandings of successional sequence of taxa in rocky intertidal systems, with early colonizing species such as the acorn barnacle (*Balanus glandula*) and small mussels (*Mytilus trossulus*) negatively correlated with Axis 1 and vector direction corresponding to spatial units from early sampling dates for all ordinations (Figure A.1, Tables A.2-6). Mobile taxa, such as limpet and littorine snail grazers, as well as predatory stars (*Pisaster ochraceus* and *Leptasterias sp.*) and whelks (*Nucella ostrina* and *N. canaliculata*), were generally positively correlated with both axes, but with greater strength of correlation along Axis 2, corresponding to spatial units with sample dates after initial colonization of acorn barnacles and small mussels (Figure A.1, Tables A.2-6). Late successional taxa, such as large barnacles (*Semibalanus cariosus*), gooseneck barnacles (*Pollicipes polymerus*), California mussels (*Mytilus californianus*), and anemones (*Anthopleura elegantissima*) were consistently and strongly correlated with Axis 1 and spatial units at time points much later in the successional sequence (Figure A.1, Tables A.2-6). These taxon-specific patterns were generally consistent across spatial scales as well as community subsets (when present), which highlights the robust successional patterns in intertidal invertebrate densities.

A.2 Community patchiness results

Patchiness in community composition varied by spatial scale, with mean β-diversity decreasing across scale, reflecting increased patchiness in invertebrate composition at smaller spatial scales (Table A.1). However, community patchiness varied considerably through time across both spatial scales and invertebrate community subsets. For the full invertebrate community, mean β-diversity generally increased for the first two and a half years after the initial clearing of the experimental patches, with two peaks in β-diversity during autumns (August-October) following the first year of succession. This increasing trend is especially apparent for the smallest three spatial scales: sub-quadrat, quadrat, and patch. The sub-bench and bench scales exhibited markedly lower patchiness than the smaller scales, and although there was a slight increase in patchiness through time, it was much less apparent at these scales for the full community. However, there was a decrease in mean β-diversity across all spatial scales for the last six months of the sampling period, indicating some convergence in community composition as succession approached three years of progression (Figure A.2a).

Patterns of β-diversity for just the focal prey were much more consistent through time and across spatial scale, with initially low patchiness at all scales and a general increase in patchiness through time. The three smallest spatial scales exhibited similar peaks in patchiness in the autumns as the full community, but the patchiness remained high and variable in the last year of the sampling period. While the larger two spatial scales also increased through time, albeit at consistently lower values, they also exhibited increased variation in the latter year of the sampling period (Figure A.2b).

The non-prey community exhibited a reciprocal pattern in patchiness than the focal prey through time, while maintaining the same pattern across spatial scales. Mean β-diversity in the non-prey, regardless of scale, started high and decreased throughout the sampling period. Consistent with the other two community subsets, patchiness in the smallest three spatial scales non-prey tended to exhibit similar patterns in β-diversity to each other, while the largest two scales showed similar dynamics to each other (Figure A.2c).

Across all three community subsets, the full community patterns in β-diversity are reflected in the patterns for different time windows of the focal prey and non-prey communities. Focal prey β-diversity for the initial 2/3 of the sampling period exhibits peaks in patchiness similar in timing and magnitude to that of the full community at the corresponding time points, across spatial scales (Figure A.2a,b). Conversely, patterns in non-prey patchiness for the latter 1/3 of the sampling period reflect the patterns in β-diversity for the corresponding portion of the full community (Figure A.2a,c). This points to differential contributions of early-successional (focal prey) and late-successional (non-prey) taxa in influencing the β-diversity patterns in the full invertebrate community.

A.3 Relative patch submersion time

To examine the influence of differences in patch submersion time on invertebrate community structure, two ONSET HOBO Pendant® Temperature/Light 64K Data Loggers (UA-002-64) were placed at each experimental patch, mounted on 0.5m tall 3/8” rebar tripod stand that were bolted to the rock just outside the patch at approximately the midpoint of the patch tidal height. One logger was mounted just off the substrate on the rebar stand, while the other was mounted at 0.5m, with a foam sleeve between each logger and the rebar to mitigate the influence of heat conduction along the stand.

We used the temperature difference between the logger just off the substrate and the logger mounted 0.5m above the substrate to detect when the patch was submerged or exposed to the air. Temperature was logged every 30 seconds for 48 hours, capturing four complete tidal cycles at each patch. For each patch, submersion time was calculated relative to each of the other patches with the patch highest in tidal height set to zero. The relative submersion time of all other patches was calculated as the difference, in minutes, between when that patch was submerged by the incoming tide and when the highest patch was submerged by that same tide. Relative submersion times were averaged across the four captured tidal cycles to account for potential variation in environmental factors.

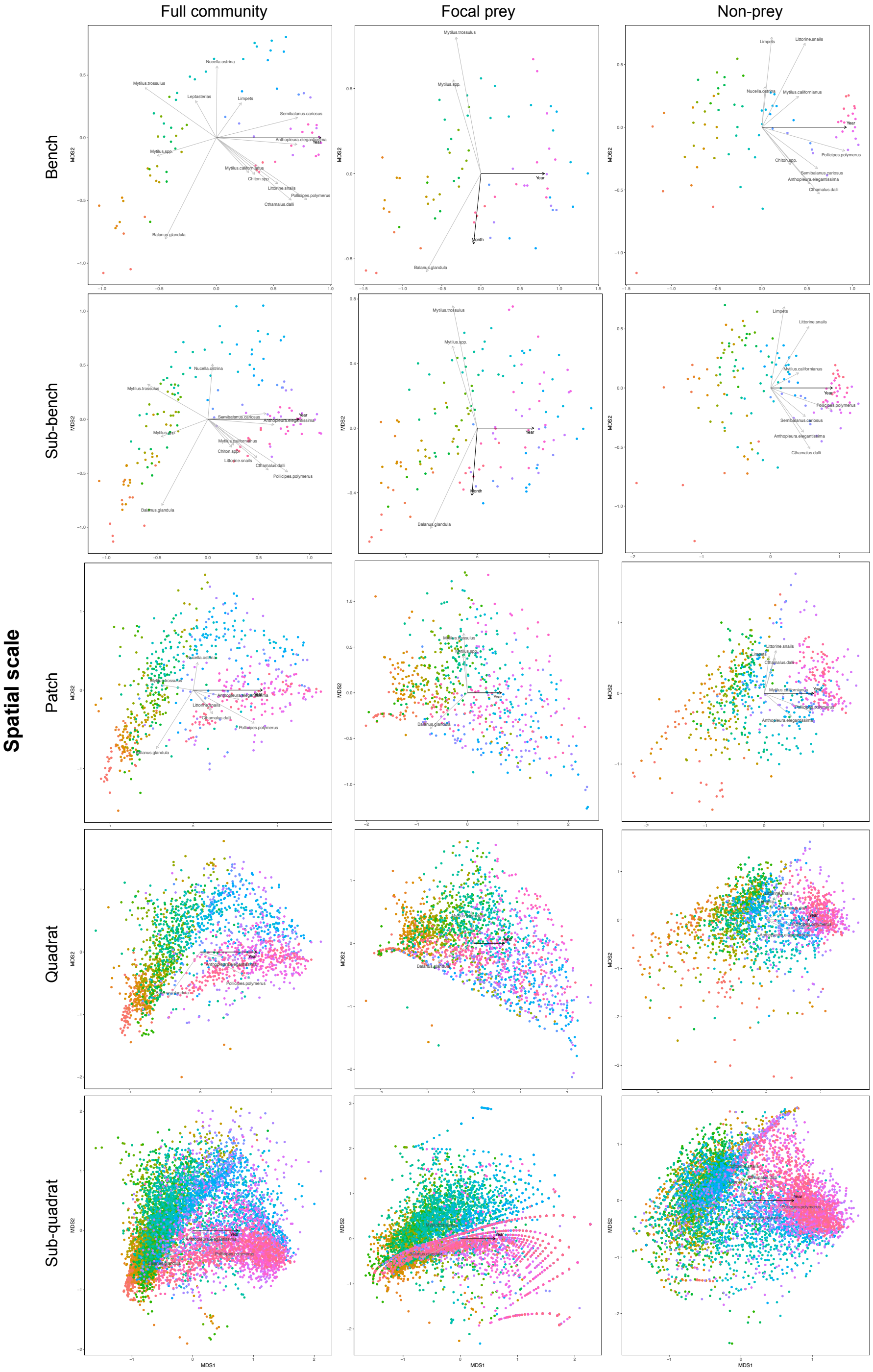

Figure A.1 Nonmetric multidimensional scaling (NMS) plots of sample units (experimental patches at each sampling data) in species space. Points are coded by sample date. Gray lines are species correlations with the ordination axes, and black lines are correlations of environmental variables with the ordination axes. All ordinations were rotated so that sample year was correlated to the x-axis of the ordination.

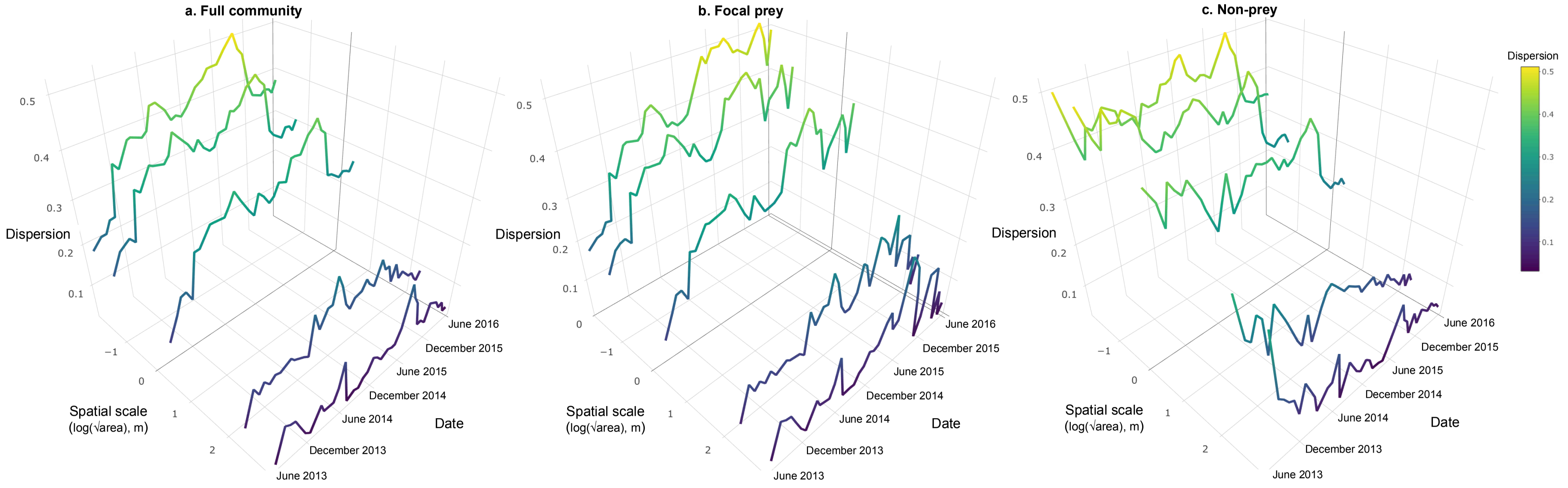

Figure A.2 Mean monthly β-diversity across spatial scales for (a) the full invertebrate community, (b) focal prey only, and (c) non-prey.

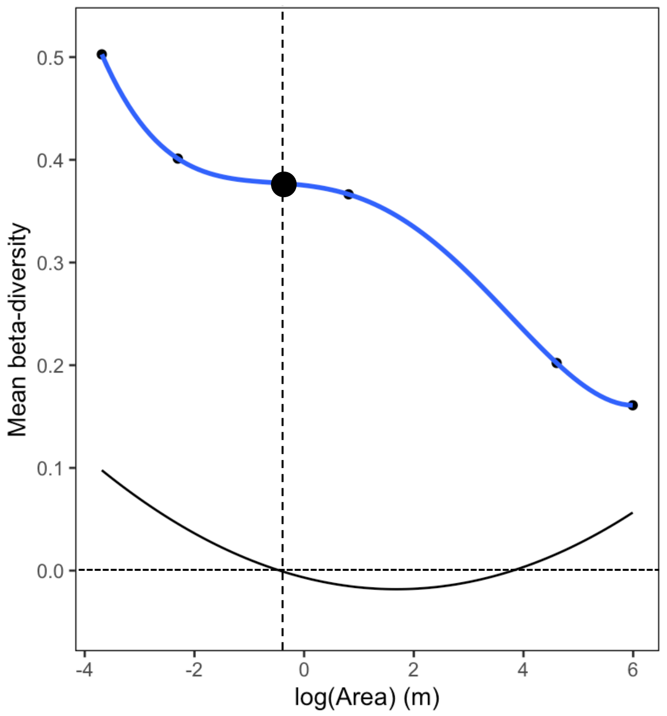

Figure A.3 Graphical example of the optimal scale of prey homogeneity calculation for a given sampling date. The blue line shows an example of a 4th order polynomial fitted to the log-transformed mean β-diversity across each of the five spatial scales at one sampling date, while the black line represents the 2nd derivative of the polynomial. The large black point is where the polynomial's 2nd derivative is equal to zero, giving the location of inflection point in the relationship between prey patchiness and spatial scale. This point (on the natural scale) is the optimal scale of movement for this sample date.

Table A.1 Non-metric multi-dimensional scaling summary statistics for each ordination from a given invertebrate community subset (full community, focal prey only, and non-prey) at each spatial scale (bench, sub-bench, patch, quadrat, and sub-quadrat). Values below include the number of dimensions, final stress, number of iterations, whether a convergent solution was reached, the ordination correlation with Axis 1 and Axis 2, the total variance explained, the orthogonality of the solution, and the mean and standard error of the monthly β-diversity for the given ordination.

Spatial scale	**Spatial units (N)**	**Dimensions**	**Final stress**	**Iterations**	**Convergent solution**	**Axis 1 R^2**	**Axis 2 R^2**	**Total variance explained**	**Orthogonality (R^2)**	**Monthly β-diversity (mean ± SE)**
Full community										
Bench	72	2	0.071	600	Yes	0.75	0.20	0.95	0.72	0.077 ± 0.006
Sub-Bench	144	2	0.090	600	Yes	0.71	0.23	0.94	0.77	0.146 ± 0.007
Patch	647	2	0.145	600	No	0.56	0.29	0.84	0.83	0.294 ± 0.011
Quadrat	1917	2	0.158	600	No	0.51	0.30	0.81	0.86	0.335 ± 0.012
Sub-quadrat	7667	2	0.187	600	No	0.47	0.29	0.77	0.98	0.383 ± 0.014
Focal prey										
Bench	72	2	0.056	600	Yes	0.87	0.06	0.94	0.91	0.088 ± 0.010
Sub-Bench	144	2	0.063	600	Yes	0.86	0.07	0.93	0.85	0.157 ± 0.009
Patch	647	2	0.089	600	No	0.76	0.09	0.85	0.92	0.307 ± 0.013
Quadrat	1917	2	0.182	600	No	0.70	0.12	0.83	0.85	0.350 ± 0.013
Sub-quadrat	7474	2	0.151	600	No	0.59	0.19	0.79	0.99	0.400 ± 0.016
Non-prey										
Bench	72	2	0.069	600	Yes	0.87	0.07	0.94	0.98	0.096 ± 0.009
Sub-Bench	144	2	0.100	600	Yes	0.79	0.11	0.90	1.00	0.176 ± 0.010
Patch	646	2	0.156	600	No	0.63	0.17	0.80	0.91	0.339 ± 0.010
Quadrat	1915	2	0.099	600	No	0.55	0.18	0.74	0.97	0.389 ± 0.011
Sub-quadrat	6902	2	0.205	600	No	0.48	0.25	0.73	1.00	0.425 ± 0.008

Table A.2 Pearson and Kendall Correlations with ordination axes for environmental variables and invertebrate species for the full community, prey taxa only, and the non-prey community at the bench spatial scale. Bolded numbers indicate R^2 values greater than 0.10.

Bench scale		**Full community**				**Prey only**				**Non-prey community**			
		Axis 1	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**
Environmental Variables													
Year		**1.00**	**0.00**	**0.84**	**<0.001**	**1.00**	**0.00**	**0.66**	**<0.001**	**1.00**	**0.00**	**0.87**	**<0.001**
Month		-0.16	-0.99	0.09	0.04	**-0.22**	**-0.97**	**0.18**	**<0.001**	-0.30	0.96	0.05	0.20
Relative submersion		0.06	1.00	0.00	0.84	0.60	0.80	0.01	0.71	0.01	-1.00	0.05	0.17
Invertebrate species;	**abbr.**												
Anthopleura elegantissima	**Ae**	**1.00**	**-0.07**	**0.50**	**<0.001**	--	--	--	--	**0.76**	**-0.65**	**0.48**	**<0.001**
Balanus glandula	**Bg**	**-0.48**	**-0.87**	**0.85**	**<0.001**	**-0.77**	**-0.64**	**0.82**	**<0.001**	--	--	--	--
Chiton spp.	**Chi**	**0.76**	**-0.65**	**0.20**	**<0.001**	--	--	--	--	**0.73**	**-0.69**	**0.19**	**<0.001**
Chthamalus dalli	**Cth**	**0.80**	**-0.60**	**0.68**	**<0.001**	--	--	--	--	**0.77**	**-0.64**	**0.69**	**<0.001**
Leptasterias sp.	**Lep**	**-0.52**	**0.85**	**0.12**	**0.01**	--	--	--	--	-0.83	-0.56	0.01	0.71
Limpets	**Lim**	**0.62**	**0.79**	**0.13**	**0.01**	--	--	--	--	**0.15**	**0.99**	**0.53**	**<0.001**
Littorine snails	**Ls**	**0.83**	**-0.56**	**0.42**	**<0.001**	--	--	--	--	**0.58**	**0.81**	**0.68**	**<0.001**
Mytilus californianus	**Mc**	**0.72**	**-0.70**	**0.16**	**<0.001**	--	--	--	--	**0.85**	**0.52**	**0.22**	**<0.001**
Mytilus spp.	**Myt**	**-0.96**	**-0.27**	**0.29**	**<0.001**	**-0.54**	**0.84**	**0.43**	**<0.001**	--	--	--	--
Mytilus trossulus	**Mt**	**-0.84**	**0.54**	**0.55**	**<0.001**	**-0.37**	**0.93**	**0.74**	**<0.001**	--	--	--	--
Nucella canaliculata	**Nc**	-0.65	0.76	0.08	0.04	--	--	--	--	**-0.27**	**0.96**	**0.14**	**0.01**
Nucella ostrina	**No**	**0.01**	**1.00**	**0.33**	**<0.001**	--	--	--	--	**0.11**	**0.99**	**0.11**	**0.02**
Pisaster ochraceus	Pis	0.83	0.56	0.05	0.14	--	--	--	--	0.92	-0.40	0.05	0.17
Pollicipes polymerus	**Pp**	**0.85**	**-0.53**	**0.87**	**<0.001**	--	--	--	--	**0.98**	**-0.20**	**0.87**	**<0.001**
Semibalanus cariosus	**Sc**	**0.98**	**0.22**	**0.53**	**<0.001**	--	--	--	--	**0.88**	**-0.47**	**0.49**	**<0.001**

Table A.3 Pearson and Kendall Correlations with ordination axes for environmental variables and invertebrate species for the full community, prey taxa only, and the non-prey community at the sub-bench spatial scale. Bolded numbers indicate R^2 values greater than 0.10.

Sub-bench scale		**Full community**				**Prey only**				**Non-prey community**			
		Axis 1	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**
Environmental Variables													
Year		**1.00**	**0.00**	**0.81**	**<0.001**	**1.00**	**0.00**	**0.62**	**<0.001**	**1.00**	**0.00**	**0.81**	**<0.001**
Month		**-0.21**	**-0.98**	**0.10**	**<0.001**	**-0.17**	**-0.98**	**0.18**	**<0.001**	-0.34	0.94	0.03	0.16
Relative submersion		-0.17	0.99	0.01	0.51	0.96	-0.29	0.01	0.47	-0.13	-0.99	0.08	<0.001
Invertebrate species;	**abbr.**												
Anthopleura elegantissima	**Ae**	**1.00**	**-0.08**	**0.43**	**<0.001**	--	--	--	--	**0.79**	**-0.62**	**0.37**	**<0.001**
Balanus glandula	**Bg**	**-0.49**	**-0.87**	**0.84**	**<0.001**	**-0.72**	**-0.69**	**0.81**	**<0.001**	--	--	--	--
Chiton spp.	**Chi**	**0.67**	**-0.74**	**0.12**	**<0.001**	--	--	--	--	0.55	-0.83	0.08	0.01
Chthamalus dalli	**Cth**	**0.78**	**-0.62**	**0.57**	**<0.001**	--	--	--	--	**0.74**	**-0.67**	**0.59**	**<0.001**
Leptasterias sp.	**Lep**	-0.43	0.90	0.08	<0.001	--	--	--	--	-0.87	-0.50	0.01	0.60
Limpets	**Lim**	**0.96**	**0.29**	**0.10**	**<0.001**	--	--	--	--	**0.28**	**0.96**	**0.51**	**<0.001**
Littorine snails	**Ls**	**0.81**	**-0.59**	**0.36**	**<0.001**	--	--	--	--	**0.73**	**0.68**	**0.58**	**<0.001**
Mytilus californianus	**Mc**	**0.73**	**-0.68**	**0.12**	**<0.001**	--	--	--	--	**0.95**	**0.30**	**0.18**	**<0.001**
Mytilus spp.	**Myt**	**-0.94**	**-0.33**	**0.24**	**<0.001**	**-0.56**	**0.83**	**0.38**	**<0.001**	--	--	--	--
Mytilus trossulus	**Mt**	**-0.88**	**0.48**	**0.46**	**<0.001**	**-0.41**	**0.91**	**0.69**	**<0.001**	--	--	--	--
Nucella canaliculata	Nc	-0.54	0.84	0.08	<0.001	--	--	--	--	-0.20	0.98	0.08	0.01
Nucella ostrina	**No**	**0.09**	**1.00**	**0.26**	**<0.001**	--	--	--	--	0.22	0.98	0.08	<0.001
Pisaster ochraceus	Pis	0.95	0.30	0.02	0.17	--	--	--	--	0.98	-0.20	0.02	0.16
Pollicipes polymerus	**Pp**	**0.85**	**-0.53**	**0.85**	**<0.001**	--	--	--	--	**0.98**	**-0.20**	**0.82**	**<0.001**
Semibalanus cariosus	**Sc**	**1.00**	**0.09**	**0.33**	**<0.001**	--	--	--	--	**0.90**	**-0.43**	**0.31**	**<0.001**

Table A.4 Pearson and Kendall Correlations with ordination axes for environmental variables and invertebrate species for the full community, prey taxa only, and the non-prey community at the patch spatial scale. Bolded numbers indicate R^2 values greater than 0.10.

Patch scale		**Full community**				**Prey only**				**Non-prey community**			
		Axis 1	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**
Environmental Variables													
Year		**1.00**	**0.00**	**0.68**	**<0.001**	**1.00**	**0.00**	**0.46**	**<0.001**	**1.00**	**0.00**	**0.70**	**<0.001**
Month		-0.32	-0.95	0.07	<0.001	-0.56	-0.83	0.08	<0.001	-0.60	0.80	0.03	<0.001
Relative submersion		-0.86	0.50	0.02	<0.001	-0.30	-0.95	0.04	<0.001	-0.46	0.89	0.07	<0.001
Invertebrate species;	**abbr.**												
Anthopleura elegantissima	**Ae**	**0.98**	**-0.21**	**0.31**	**<0.001**	--	--	--	--	**0.82**	**-0.58**	**0.32**	**<0.001**
Balanus glandula	**Bg**	**-0.51**	**-0.86**	**0.75**	**<0.001**	**-0.88**	**-0.47**	**0.70**	**<0.001**	--	--	--	--
Chiton spp.	**Chi**	0.70	-0.72	0.03	<0.001	--	--	--	--	0.97	-0.25	0.05	<0.001
Chthamalus dalli	**Cth**	**0.61**	**-0.79**	**0.14**	**<0.001**	--	--	--	--	**0.34**	**0.94**	**0.28**	**<0.001**
Leptasterias sp.	**Lep**	-0.10	0.99	0.01	0.14	--	--	--	--	0.38	-0.93	0.00	0.23
Limpets	**Lim**	0.92	-0.39	0.02	<0.001	--	--	--	--	**0.15**	**0.99**	**0.28**	**<0.001**
Littorine snails	**Ls**	**0.65**	**-0.76**	**0.11**	**<0.001**	--	--	--	--	**0.31**	**0.95**	**0.41**	**<0.001**
Mytilus californianus	**Mc**	0.77	-0.63	0.07	<0.001	--	--	--	--	**1.00**	**-0.04**	**0.11**	**<0.001**
Mytilus spp.	**Myt**	-0.70	-0.72	0.07	<0.001	**-0.21**	**0.98**	**0.17**	**<0.001**	--	--	--	--
Mytilus trossulus	**Mt**	-0.98	0.18	0.14	<0.001	**-0.11**	**0.99**	**0.43**	**<0.001**	--	--	--	--
Nucella canaliculata	**Nc**	-0.64	0.77	0.01	0.03	--	--	--	--	-0.52	0.85	0.01	0.05
Nucella ostrina	**No**	**0.14**	**0.99**	**0.13**	**<0.001**	--	--	--	--	0.91	0.41	0.01	0.03
Pisaster ochraceus	Pis	0.93	-0.36	0.01	0.01	--	--	--	--	0.78	-0.62	0.02	<0.001
Pollicipes polymerus	**Pp**	**0.87**	**-0.50**	**0.71**	**<0.001**	--	--	--	--	**0.95**	**-0.31**	**0.68**	**<0.001**
Semibalanus cariosus	**Sc**	0.99	0.11	0.07	<0.001	--	--	--	--	1.00	-0.08	0.07	<0.001

Table A.5 Pearson and Kendall Correlations with ordination axes for environmental variables and invertebrate species for the full community, prey taxa only, and the non-prey community at the quadrat spatial scale. Bolded numbers indicate R2 values greater than 0.10.

Quadrat scale		**Full community**				**Prey only**				**Non-prey community**			
		Axis 1	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**
Environmental Variables													
Year		**1.00**	**0.00**	**0.63**	**<0.001**	**1.00**	**0.00**	**0.43**	**<0.001**	**1.00**	**-0.01**	**0.63**	**<0.001**
Month		-0.36	-0.93	0.06	<0.001	-0.66	-0.75	0.07	<0.001	-0.68	0.74	0.02	<0.001
Relative submersion		-0.79	0.61	0.03	<0.001	-0.42	-0.91	0.03	<0.001	-0.62	0.78	0.04	<0.001
Invertebrate species;	**abbr.**												
Anthopleura elegantissima	**Ae**	**0.97**	**-0.25**	**0.26**	**<0.001**	--	--	--	--	**0.89**	**-0.45**	**0.23**	**<0.001**
Balanus glandula	**Bg**	**-0.53**	**-0.85**	**0.71**	**<0.001**	**-0.94**	**-0.35**	**0.67**	**<0.001**	--	--	--	--
Chiton spp.	**Chi**	0.74	-0.67	0.01	<0.001	--	--	--	--	0.75	-0.66	0.02	<0.001
Chthamalus dalli	**Cth**	0.58	-0.81	0.06	<0.001	--	--	--	--	**0.88**	**0.48**	**0.12**	**<0.001**
Leptasterias sp.	**Lep**	-0.18	0.98	0.00	0.17	--	--	--	--	0.32	-0.95	0.00	0.03
Limpets	**Lim**	0.67	-0.75	0.02	<0.001	--	--	--	--	**0.32**	**0.95**	**0.24**	**<0.001**
Littorine snails	**Ls**	0.56	-0.83	0.09	<0.001	--	--	--	--	**0.39**	**0.92**	**0.40**	**<0.001**
Mytilus californianus	**Mc**	0.77	-0.63	0.07	<0.001	--	--	--	--	**1.00**	**0.07**	**0.10**	**<0.001**
Mytilus spp.	**Myt**	-0.50	-0.86	0.05	<0.001	-0.35	0.94	0.08	<0.001	--	--	--	--
Mytilus trossulus	**Mt**	**-1.00**	**0.08**	**0.10**	**<0.001**	**-0.09**	**1.00**	**0.26**	**<0.001**	--	--	--	--
Nucella canaliculata	**Nc**	-0.59	0.81	0.01	<0.001	--	--	--	--	-0.56	0.83	0.00	0.07
Nucella ostrina	**No**	0.36	0.93	0.07	<0.001	--	--	--	--	0.86	0.51	0.01	<0.001
Pisaster ochraceus	Pis	0.97	-0.23	0.00	0.03	--	--	--	--	0.95	-0.30	0.00	0.02
Pollicipes polymerus	**Pp**	**0.86**	**-0.52**	**0.67**	**<0.001**	--	--	--	--	**0.97**	**-0.23**	**0.58**	**<0.001**
Semibalanus cariosus	**Sc**	1.00	0.04	0.03	<0.001	--	--	--	--	0.99	0.14	0.03	<0.001

Table A.6 Pearson and Kendall Correlations with ordination axes for environmental variables and invertebrate species for the full community, prey taxa only, and the non-prey community at the sub-quadrat spatial scale. Bolded numbers indicate R^2 values greater than 0.10.

Sub-quadrat scale		**Full community**				**Prey only**				**Non-prey community**			
		Axis 1	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**	**Axis 1**	**Axis 2**	**R^2**	**Pr(>r)**
Environmental Variables													
Year		**1.00**	**0.00**	**0.56**	**<0.001**	**1.00**	**0.00**	**0.37**	**<0.001**	**1.00**	**0.00**	**0.55**	**<0.001**
Month		-0.49	-0.87	0.05	<0.001	-0.51	-0.86	0.05	<0.001	-0.59	0.81	0.01	<0.001
Relative submersion		-0.73	0.69	0.03	<0.001	-0.93	0.38	0.00	<0.001	-0.61	0.79	0.06	<0.001
Invertebrate species;	**abbr.**												
Anthopleura elegantissima	**Ae**	**0.98**	**-0.21**	**0.15**	**<0.001**	--	--	--	--	**0.82**	**-0.57**	**0.15**	**<0.001**
Balanus glandula	**Bg**	**-0.66**	**-0.75**	**0.67**	**<0.001**	**-0.85**	**-0.53**	**0.63**	**<0.001**	--	--	--	--
Chiton spp.	**Chi**	0.76	-0.65	0.00	0.39	--	--	--	--	0.98	-0.17	0.00	0.22
Chthamalus dalli	**Cth**	0.40	-0.91	0.02	<0.001	--	--	--	--	**0.38**	**0.93**	**0.28**	**<0.001**
Leptasterias sp.	**Lep**	-0.20	0.98	0.00	0.30	--	--	--	--	0.17	-0.99	0.00	0.44
Limpets	**Lim**	-0.35	-0.94	0.00	0.02	--	--	--	--	**0.04**	**1.00**	**0.17**	**<0.001**
Littorine snails	**Ls**	0.09	-1.00	0.06	<0.001	--	--	--	--	**0.21**	**0.98**	**0.29**	**<0.001**
Mytilus californianus	**Mc**	0.75	-0.66	0.06	<0.001	--	--	--	--	0.99	-0.12	0.07	<0.001
Mytilus spp.	**Myt**	-0.43	-0.90	0.06	<0.001	-0.59	-0.80	0.06	<0.001	--	--	--	--
Mytilus trossulus	**Mt**	**-0.79**	**0.62**	**0.10**	**<0.001**	**-0.52**	**0.85**	**0.22**	**<0.001**	--	--	--	--
Nucella canaliculata	**Nc**	-0.41	0.91	0.01	<0.001	--	--	--	--	-0.62	-0.78	0.00	<0.001
Nucella ostrina	**No**	0.55	0.84	0.02	<0.001	--	--	--	--	0.71	-0.70	0.00	0.03
Pisaster ochraceus	Pis	0.92	-0.39	0.00	<0.001	--	--	--	--	0.80	-0.60	0.00	0.00
Pollicipes polymerus	**Pp**	**0.81**	**-0.59**	**0.62**	**<0.001**	--	--	--	--	**0.97**	**-0.24**	**0.62**	**<0.001**
Semibalanus cariosus	**Sc**	0.99	-0.17	0.01	<0.001	--	--	--	--	0.95	0.33	0.01	<0.001

Appendix B – Chapter 2 Feeding Rates

B.1 Feeding rates for multiple prey taxa

To generalize whelk feeding rates across focal prey taxa, prey items consumed based on our feeding observations were first converted to calories to allow a calculation of daily calories consumed by a whelk predator as follows:

$$calories_{(mussel+barnacle)}/day = calories_{mussel}/day + calories_{barnacle}/day$$

$$= (prey_{mussel}/day\ /\ prey_{mussel}/calorie_{mussel}) + (prey_{barnacle}/day\ /\ prey_{barnacle}/calorie_{barnacle})$$

$$= (F_{mussel}\ /\ prey_{mussel}/calorie_{mussel}) + (F_{arnacle}\ /\ prey_{\ barnacle}/calorie_{\ barnacle})$$

Using this metric of combined calories per day, as well as the average number of prey items consumed per calorie, we then estimated the daily per capita feeding rate on a general prey item as:

$$F_{(mussel+barnacle)} = calories_{(mussel+barnacle)}/day * prey_{(mussel+barnacle)}/calorie_{(mussel+barnacle)}\ /\ n\ prey\ types$$

To fulfill the above calculation, we then took the inverse of calories per each prey consumed and averaged those values across patches at each sampling date to provide taxon-specific estimates of number of prey consumed per calorie throughout the year. To then obtain prey per calorie combined across both prey taxa, we averaged total prey consumed per calorie, regardless of identity, across patches at each sampling date. Together, these values allowed us to calculate combined prey per capita feeding rates for the whelk population at each sampling date.

A GAM was then fit to the generalized feeding rates by calendar day to provide a continuous estimate of feeding rate throughout the year. Each sampling date was weighted by the number of feeding observations, and the covariate 'calendar day' was smoothed using a cyclic cubic regression spline to match the beginning and end of year predicted value, and a gamma set to 0.6 to decrease the level of penalization for the smoothing parameter.

B.2 Prey allometry and calorie calculation

To calculate calories per prey item, 195 *Mytilus trossulus* mussels and 78 *Balanus glandula* barnacles were haphazardly collected in July of 2013 and 2015 at the study site, near Yachats, OR. Mussel length was determined by the longest length, and barnacle width was measured as the widest aperture width. Tissue was scraped from each specimen and placed in a drying oven 24 hours at 60 °C, after which the tissue dry mass was measured.

The log of the aperture width or maximum length for barnacles and mussels, respectively, were regressed against the log of the oven-dried tissue weight (g) to provide allometric relationships of dried tissue weight for the focal prey taxa. Mean calories per dry gram of mussel or barnacle tissue (Bruce Menge unpublished data, 1967-1977) were then multiplied by the predicted dry tissue weight for each prey item consumed to provide calorie values for each prey item.

The fitted allometric relationship for barnacles explained approximately 68% of the variance in the data, with an intercept of -9.13 and a slope of 2.79 ($p < 0.001$, $R^2 = 0.68$; Figure B.1a). The allometric model for mussels included a strong relationship between mussel tissue dry weight and shell length ($p < 0.001$, $R^2 = 0.97$), with an intercept of -11.866 and a slope of 2.85 (Figure B.1b).

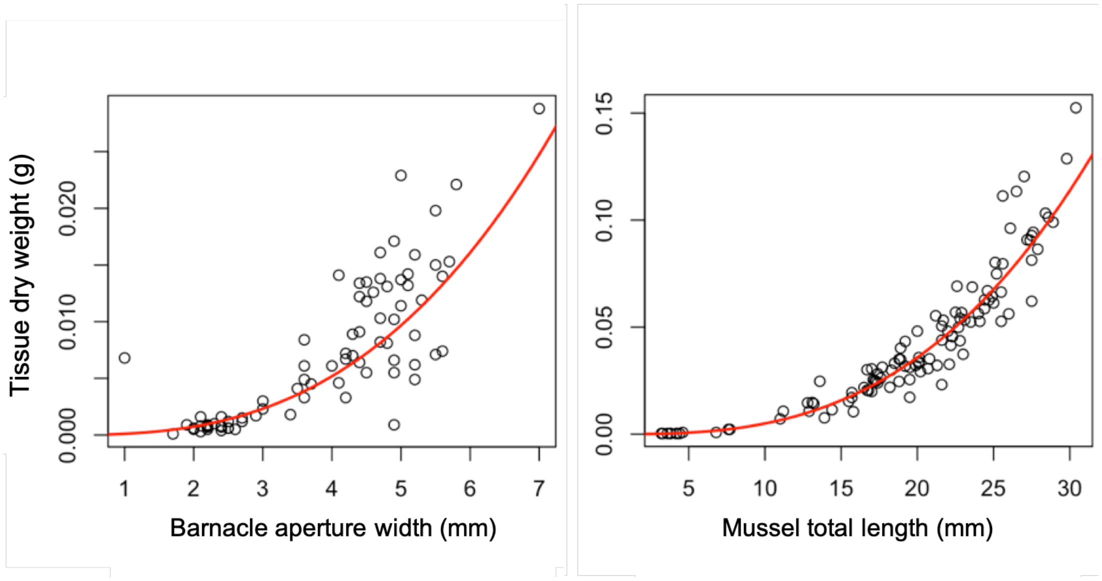

Figure B.1 Allometric relationships for (a) barnacles (*Balanus glandula)* and (b) mussels (*Mytilus trossulus*).

Appendix C – Chapter 3 Supplementary Material

Table C.1 Test statistic and p-values for Kolmogorov–Smirnov tests comparing individual movement turning angle distributions and a randomly generated uniform distribution. Bolded entries indicate individuals with non-random turning angle distributions.

Whelk ID	D-statistic	p-value
C7	**0.440**	**0.005**
C8	**0.619**	**0.001**
C9	0.247	0.336
C10	**0.364**	**0.025**
C12	**0.459**	**0.001**
C14	0.228	0.275
C15	0.267	0.528
C17	0.289	0.114
C18	0.167	0.473
C20	0.196	0.734
C21	0.248	0.382
C23	0.219	0.318
C24	0.251	0.349
C25	0.146	0.743
C26	0.224	0.192
C27	0.284	0.332
C28	0.135	0.951
C33	0.252	0.197
C34	**0.431**	**0.005**
C35	**0.451**	**<0.0001**
C36	**0.318**	**0.047**
C40	0.310	0.086
C43	0.162	0.611
C44	0.306	0.060
C45	0.242	0.167
C46	0.357	0.065
C47	0.359	0.134
D1	0.185	0.512
D2	0.192	0.536
D3	0.289	0.416
D4	0.223	0.437
D5	0.293	0.125
D6	0.159	0.801
D7	0.269	0.120
D10	0.197	0.741
D12	0.242	0.313
D16	0.174	0.858
D17	0.175	0.571
D18	0.178	0.566
D20	0.230	0.294
D22	0.354	0.157
D23	0.213	0.239
D26	0.212	0.487
D28	0.266	0.302
D31	0.361	0.007
D33	0.146	0.975
D34	0.409	0.035
D36	0.148	0.743
D37	0.267	0.368
D38	0.220	0.405
D40	0.289	0.257
D41	0.100	0.999
D43	0.141	0.958
D44	0.152	0.827
D46	0.229	0.431
E1	0.157	0.674
E2	0.280	0.071
E5	0.193	0.425
E6	0.265	0.126
E7	0.128	0.987
E8	0.279	0.465
E10	0.301	0.068

Table C.2 Exponential parameters (λ_m), bootstrapped 95% confidence interval, minimum movement length (*a*), and goodness of fit for individual step length distribution fitted exponential models.

Whelk ID	Number of observations	Exponential parameter (λ_m)	95% CI	Minimum movement length (*a*)	Goodness of fit
C7	25	10.36	0.33	0.005	0.11
C8	15	5.83	0.33	0.003	0.12
C9	22	5.74	0.21	0.004	0.09
C10	28	4.80	0.18	0.001	0.20
C12	29	6.41	0.15	0.004	0.12
C14	31	8.31	0.30	0.003	0.08
C15	15	19.85	0.84	0.003	0.17
C17	27	5.41	0.11	0.005	0.08
C18	43	5.47	0.30	0.006	0.13
C20	18	5.45	0.24	0.005	0.13
C21	22	19.91	1.49	0.001	0.20
C23	32	2.76	0.05	0.009	0.14
C24	21	2.39	0.37	0.003	0.21
C25	34	8.09	0.23	0.001	0.14
C26	39	6.71	0.11	0.001	0.07
C27	16	7.60	0.20	0.004	0.13
C28	21	10.87	0.29	0.002	0.10
C33	30	4.93	0.13	0.007	0.09
C34	28	5.31	0.28	0.002	0.22
C35	33	4.36	0.08	0.001	0.10
C36	31	7.23	0.21	0.010	0.13
C40	26	8.16	0.23	0.003	0.10
C43	36	12.70	0.47	0.002	0.12
C44	31	10.14	0.16	0.004	0.07
C45	35	5.85	0.10	0.001	0.06
C46	22	8.30	0.59	0.001	0.08
C47	16	6.93	0.41	0.006	0.18
D1	31	31.00	0.71	0.002	0.11
D2	29	8.27	0.28	0.001	0.14
D3	15	11.32	0.55	0.003	0.10
D4	23	9.68	0.34	0.008	0.08
D5	26	3.51	0.13	0.006	0.12
D6	25	5.15	0.12	0.008	0.17
D7	33	6.77	0.29	0.001	0.22
D10	16	3.94	0.21	0.029	0.14
D12	26	8.72	2.23	0.001	0.14
D16	17	2.46	0.11	0.018	0.17
D17	32	5.63	0.39	0.011	0.15
D18	31	4.72	0.20	0.004	0.11

Table C.2 (Continued)

Whelk ID	Number of observations	Exponential parameter (λ_m)	95% CI	Minimum movement length (a)	Goodness of fit
D20	29	11.33	0.55	0.004	0.08
D22	16	5.41	0.23	0.003	0.17
D23	38	19.51	0.93	0.002	0.14
D26	24	14.58	0.62	0.002	0.09
D28	20	4.13	0.18	0.005	0.09
D31	38	12.45	0.30	0.005	0.10
D33	15	3.15	0.14	0.006	0.17
D34	19	3.83	0.11	0.042	0.16
D36	35	30.53	1.00	0.002	0.12
D37	17	6.85	0.25	0.006	0.08
D38	27	11.41	0.72	0.006	0.15
D40	19	12.14	0.58	0.001	0.11
D41	16	11.04	1.18	0.003	0.10
D43	18	4.81	0.48	0.006	0.26
D44	24	12.37	0.18	0.002	0.12
D46	23	6.49	0.18	0.003	0.09
E1	35	15.42	0.27	0.002	0.06
E2	37	9.21	0.16	0.001	0.08
E5	34	4.55	0.20	0.001	0.12
E6	33	10.16	0.18	0.001	0.07
E7	17	2.44	0.08	0.022	0.10
E8	15	6.07	0.97	0.012	0.13
E10	30	6.17	0.33	0.005	0.09

Table C.3 Test statistic and p-values for Kolmogorov–Smirnov tests comparing - turning angle distributions of individuals in community space and a randomly generated uniform distribution. Bolded values indicate individuals with suggestive significant non-random turning angle distributions.

Whelk ID	D-statistic	p-value
C7	0.21	0.808
C12	0.13	0.992
C17	0.19	0.853
C18	0.16	0.723
C23	0.20	0.710
C25	0.30	0.241
C26	0.19	0.635
C36	0.25	0.449
C43	0.17	0.791
C45	0.19	0.853
C47	0.18	0.997
D5	**0.38**	**0.095**
D6	**0.40**	**0.081**
D17	0.19	0.733
D18	0.12	0.996
D23	0.11	0.997
D31	0.19	0.615
D37	0.33	0.536
E2	**0.32**	**0.079**
E6	0.23	0.501

Table C.4 Exponential parameters (λ_c), bootstrapped 95% confidence interval, minimum movement length (*a*), and goodness of fit for exponential models fitted to individual step length distributions through community space.

Whelk ID	Exponential parameter (λ_c)	95% CI	Minimum movement length (*a*)	Goodness of fit
C7	3.10	0.03	0.06	0.11
C12	2.61	0.02	0.10	0.11
C17	3.32	0.06	0.08	0.16
C18	3.23	0.01	0.08	0.05
C23	2.31	0.07	0.05	0.04
C25	3.30	0.04	0.07	0.10
C26	2.25	0.03	0.09	0.09
C36	2.84	0.02	0.11	0.08
C43	4.76	0.02	0.05	0.09
C45	3.33	0.05	0.11	0.07
C47	2.75	0.04	0.15	0.17
D17	2.79	0.08	0.11	0.05
D18	3.86	0.02	0.10	0.10
D23	4.87	0.02	0.10	0.12
D31	3.86	0.01	0.09	0.23
D37	2.92	0.04	0.13	0.17
D5	3.41	0.02	0.06	0.07
D6	5.16	0.05	0.08	0.15
E2	5.44	0.07	0.09	0.18
E6	3.63	0.03	0.10	0.39