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Connecting Seasonal Patterns of Predation Risk with Prey Traits, Predator Communities, and
Prey Abundance

By

CLAIRE ELIZABETH MURPHY
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

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ABSTRACT

Predation risk varies through space and time due to changing refuge quality, predator communities, and prey traits. This variation may be an important determinant of species coexistence and local diversity. Despite this, predation risk is hard to estimate empirically, and often logistics restrict sampling to a limited number of sites, prey species, and time points. In my dissertation, I used amphipods and isopods associated with temperate seagrass in Northern California to explore the causes and consequences of seasonal variation in predation risk for a community of morphologically distinct prey across sites with a range of environmental conditions. I tethered live individuals of the four most abundant and widespread prey species at six field sites every two to six weeks over 2.5 years and used cameras and field surveys to understand the relationships between predation risk and associated prey and predator communities.

In my first chapter, I focused on the role of prey species traits played in influencing predation risk patterns, and how seasonal patterns of predation risk related to seasonal patterns of abundance. I found that all species shared a peak in predation risk in the fall but differed in both the magnitude of that peak and when they reached maximum abundance relative to it. The most morphologically defended species experienced consistently lower predation risk and peaked in abundance after maximum predation risk, potentially exploiting reduced competition following declines of less-defended prey. In contrast, the least morphologically defended species reached peak abundance earlier in the season, potentially as a mechanism to minimize the impacts of high predation intensity. These findings were only apparent when I used functional data techniques to examine entire seasonal trajectories of predation risk and abundance, rather than just univariate summarized metrics. My results suggest that complex insights into species interactions emerge

when entire seasonal trajectories are analyzed and that temporal predator avoidance strategies may promote coexistence among prey species.

In my second chapter, I found that sites with greater seagrass cover had less annual variation in community-level predation risk and more variation in predation risk among the four species at any given time point. On the other hand, at sites with low levels of seagrass habitat, each prey species in the community had similar levels of predation risk throughout the year and predation as a community-level process was much more seasonal and variable. This suggests that the habitat provided by seagrass allowed the prey to better utilize their unique antipredator traits, resulting in temporal complementarity that stabilized overall trophic transfer.

Finally, in my third chapter, I examined how seasonal and spatial changes in the predator communities related to these patterns of predation risk. I found that overall predator community composition predicted broad seasonal changes in predation risk, but after controlling for season there was little spatial variation in predator communities, and this variation did not clearly predict predation risk. However, when I focused on variation in a single key predator group – surfperch – I did find relationships with predation risk both seasonally and between sites. I hypothesize that this variation in surfperch may be driven in part by behavioral avoidance of a top predator, diving birds. Thus, while broad community metrics did not clearly predict variation in predation risk, when considering behavioral interactions and variation in a key predator group, patterns between predators and the risk they exert on prey emerged.

Together, these findings show how habitat structure and prey traits interact with seasonal predator dynamics to shape both individual risk and community stability. More broadly, they demonstrate that high resolution temporal data and analyses focused on understanding the whole temporal shape of ecological processes, rather than just the magnitude and variance, can yield

new insights into the mechanisms linking species traits, habitat stability, and predator-prey interactions.

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CHAPTER 1: Trait-dependent temporal strategies decouple seasonal predation risk from prey abundance in seagrass epifauna

Claire E. Murphy, John J. Stachowicz

Abstract

Variation in the strength of predation is an important driver of prey population dynamics and community structure. Despite this, how temporal variation in predation risk relates to subsequent variation in prey abundance is not clear. Prey traits and environmental conditions can shift the threshold at which predation impacts prey abundance, and evolution in response to strong predation risk may favor traits that lead to an increase, rather than decrease, in prey abundance with increasing predation risk. Disentangling these relationships requires frequently collected data and analysis of entire temporal trajectories. We used small crustaceans associated with temperate seagrass beds and functional data analysis to test how seasonal predation risk relates to prey abundance. We collected data on three species with distinct antipredator traits at five sites across 16 time points throughout a year, generating seasonal curves describing each species' unique pattern of predation risk and abundance. We found that morphologically defended species experienced consistently lower predation risk and peaked in abundance after maximum predation risk, potentially exploiting reduced competition following declines of less-defended prey. The least morphologically defended species reached peak abundance earlier in the season. The species experiencing the highest predation risk showed the most variable abundance timing across sites. Our results demonstrate that complex insights into species interactions emerge when entire seasonal trajectories are analyzed and suggest that temporal predator avoidance strategies promote coexistence among prey species.

Introduction

Variation in predation is important in structuring natural communities. Despite this, the strength of predation is often treated as a constant in ecological research. Ecologists can measure the strength of predation by estimating “predation risk” (i.e., the relative chance a prey may be consumed at a certain place and time). Practical constraints often restrict sampling to a limited number of time periods, sites, or prey species, however predation risk has been shown to follow regular and predictable temporal patterns (1), change across environmental gradients (2), and vary with different antipredator strategies of the prey (3). Understanding these patterns can give insights into the drivers of different aspects of prey communities, such as population dynamics or long-term selection pressures. Thus, measuring predation risk continuously rather than a series of key events or average condition may improve our understanding of the effects of predation on the abundance and diversity of a prey community (4, 5).

In order to interpret continuous patterns of predation risk and abundance, we first need clear expectations for what different relationships mean biologically. However, this is not intuitively obvious, even when datasets with high temporal resolution exist. For example, there may be lags between increased predation risk and a subsequent decrease in prey abundance, or a threshold at which predation risk becomes meaningfully high enough to influence abundance, both of which are difficult to determine and can shift among species and seasons (6, 7). Furthermore, the direction of this relationship can vary. Mobile predators alter their foraging through space and time to track prey populations, especially during times of increased metabolic demand (e.g., thermally stressful time periods (8), during reproductive seasons (9), through migrations (10)) or in areas with patchy prey availability overall (11). This would result in a predation risk increasing only after increases in prey abundance. Alternatively, if prey abundance

is primarily controlled by the consumptive effects of predation, then increased predation risk would be correlated with subsequently lower prey abundance. Over time, all of these can occur within the same assemblage. For example, high prey density may initially attract predators, leading to a positive correlation, followed by predators depleting prey, resulting in a negative correlation. This leads to major limitations in the interpretation of predator-prey abundance correlations.

In addition to these varied responses by predators, prey also differ greatly in how they respond to increased risk (12), further complicating the expectations of these relationships. For example, prey may increase their local abundance through aggregation, to mitigate their individual risk of predation, resulting in a positive relationship between predation risk and abundance (13). On the other hand, they may instead respond to predator cues by dispersing to less risky habitats, resulting in a negative relationship. Given that both of these can happen within the same system, one-time measurements or average predation risk will be unlikely to be consistently related to prey abundance (5). Furthermore, prey defenses (morphological, behavioral, or life history-based) likely interact with seasonal variation in predation to create species-specific responses to risk. For example, within a community of functionally similar prey that experiences high predation risk on the whole, partitioning enemy free time, either throughout the day or across seasons, may provide an avenue towards lowered competition and niche differentiation and allow for coexistence (14, 15).

Yet despite broad appreciation for seasonal variation in factors underlying variation in predation (e.g., predator life histories, prey vulnerability, habitat structure) studies rarely measure or analyze predation continuously. Indeed, two recent meta-analyses demonstrated that the current literature finds little connection between measured patterns of predation risk and

resulting field patterns of prey (16, 17). Both found that there was a dearth of studies that measured both predation risk and unaltered field abundance patterns in an attempt to connect them (17), and those that did were often relatively short term experiments (16). Even when high-resolution data exist, analyses often focus on discrete events such as the timing of peak risk or single snapshots of abundance, missing both chronic effects of sustained predation and acute impacts from repeated pulses of elevated risk.

We used the small crustacean epifaunal grazers associated with eelgrass (*Zostera marina*) to address these questions about how annual patterns of predation risk relate to annual patterns of abundance for different species across a range of environments. Considerable research focuses on the impacts of predation on these species. Field experiments with cages designed to exclude predators have found increased abundance, biomass and diversity of epifaunal invertebrates (18–20) and observational studies have linked spatial changes in predator communities to changes in prey communities (21). Thus, while it is clear that predation is a strong force influencing these communities, how these prey respond seasonally and at shorter time scales is not obvious.

We used tethering assays to measure predation on live prey and of abundance of prey at 2–4-week intervals throughout a year (16 times total) at five sites for three different species with distinct predator avoidance mechanisms. We used these data to assess how seasonal patterns of predation risk related to patterns of abundance. Rather than summarizing our periodic data into a few key metrics, such as the maximum and minimum values or time of reaching a threshold as is often done in ecological studies, we used functional data analysis to understand how specific temporal trajectories of predation and abundance vary from the average trajectory in the community and relate to each other (Figure 1). Functional data analysis (FDA) seeks to understand patterns of variation using functions describing entire curves, rather than univariate

metrics summarizing the distribution of data (22, 23). It is a common approach in many fields that use continuous data measured over time to interpret patterns, such as chemistry (24), human biomechanics (25), neuroscience (26), and physical oceanography (27). However, it has received minimal attention from ecologists (but see: 28, 29), especially when describing temporal patterns of species interactions, despite the increasing recognition and collection of long-term datasets of timeseries data suited to these techniques. Furthermore, underlying assumptions about how the data might vary or different curves may relate to each other do not need to be incorporated into the analysis – instead the patterns observed in the data can drive hypotheses. For complex processes, like species interactions such as predator-prey interactions, where it is unclear how these patterns should relate to each other due to the lack of previous long-term studies across diverse systems, this may be a good first step to create hypotheses. We used FDA to assess how temporal patterns of predation and abundance relate to each other, and how unique prey traits explain these connections.

Results

Descriptive patterns of predation risk and abundance

We deployed and retrieved 5840 tethers across five sites and 16 time points over the course of one year. Species differed in their average predation risk across the year (Figure 2A). The amphithoid amphipod *Ampithoe lacertosa* had the highest average predation risk across the year at all five sites, while the isopod *Pentidotea resecata* had the lowest risk at all but one site. Across all sites and time points, 62.7% of the tethered amphithoids (SE = 0.04%), 44.1% of the tethered caprellid amphipods *Caprella californica* (SE = 0.05%), and 33.0% of the tethered isopods (SE = 0.05%) were consumed within 24 hours. Hereafter we will refer to the prey species as amphithoids, isopods, and caprellids.

Prey species also differed consistently in their local abundances. Caprellids were the most abundant species across the year at all sites, and at four of the five sites amphithoids were the least abundant (Appendix 1: Figure S1). We found an average of 108 caprellids (SE = 13.6, range = 0 – 517), 13.7 isopods (SE = 2.7, range = 0 – 113), and 5.1 amphithoids (SE = 0.8, range = 0 – 34) per 15-minute survey. We scaled these values to their proportion of the maximum abundance for each species-site combination so that we could more easily compare their temporal patterns, as each species had such different densities (Figure 2B).

Temporal patterns of predation risk and abundance

We used functional principal components analyses (FPCAs) to examine how the temporal patterns of predation risk and abundance varied among species and sites. The inputs for these analyses are functions describing curves, with each curve representing the annual temporal pattern for either predation risk or abundance for one species at one site (i.e., a single box in Figure 2). By plotting the resulting loadings from each FPC axis against their corresponding dates, we visualized the dominant temporal patterns in the data. The FPC scores corresponding to each axis indicate how much each species-site combination's deviation from the average temporal trajectory can be explained by that FPC axis' particular temporal pattern. When considering variation across all three FPC axes for each analysis, species differed significantly in their temporal patterns of predation risk (PERMANOVA: $F_{2,12} = 7.84$, $R^2 = 0.57$, $p = 0.0024$) but not abundance (PERMANOVA: $F_{2,12} = 1.96$, $R^2 = 0.25$, $p = 0.115$). For both datasets, we used the first FPC axis, which describes the most variation in each time series, as a continuous measure to understand the dominant drivers of variation in the shape of the data and where each species fell along this axis. This approach does not require significant clustering among species

to be informative, as the axis scores themselves describe meaningful variation in the shape of the temporal data regardless of whether species separate significantly.

When averaged across all species-site combinations, predation risk had a unimodal trend, rising throughout the spring and summer from a minimum risk of 20.2% in April to a maximum risk of 71.1% in October before falling again throughout the winter and early spring (Figure 3A). The first FPC axis of the predation FPCA explained most of the variation (72.0%) in each species-site combination's divergence from this average (Figure 3B; Appendix 1: Figure S2), thus, we focused our analysis and interpretation on only this first axis. Species-site combinations with high scores on this axis had a higher-than-average and more sustained peak in predation around October, while low scores meant a lower-than-average peak in predation and flatter overall predation risk profile across the year.

The average scaled abundance per 15-minute survey also showed a unimodal pattern throughout the year, with a peak in October that was 2.3 times higher than the minimum in April (Figure 3C). The first PC axis of the abundance FPCA explained 52.6% of the variation from the average pattern of scaled abundance through time (Figure 3D; Appendix 1: Figure S3). High positive scores on this axis correspond to lower-than-average abundance from April to October, and then higher-than-average abundance from October to March. The absence of significant species differences in abundance timing was largely driven by variable abundance timing in amphipods across sites. When compared to each other separately, caprellids and isopods showed more consistent and distinct timing strategies (PERMANOVA: $R^2 = 0.30$, $p = 0.055$).

Relationships between seasonal predation risk and abundance

We used each species range of scores on the first axis of both FPCAs to understand how they differ in their seasonal trajectories (Figure 4). The caprellids clustered around 0 on the predation risk FPC1, showing a moderate peak in predation in October. They clustered on the negative side of the abundance FPC1, meaning they had an earlier than average peak in abundance (i.e., peaking in abundance before their peak in predation in October). The isopods had a lower-than-average predation risk peak (negative scores on predation risk FPC1) and a later than average abundance peak, after the average peak in predation (positive scores on abundance FPC1). Finally, the amphipods had a higher-than-average peak in predation (positive scores on predation risk FPC1) and variable abundance timings (a large range of scores on abundance FPC1).

Discussion

Each prey species had unique temporal patterns of predation risk and abundance. While all species experienced a peak in predation risk in October, they varied in the magnitude of peak predation risk that they experienced, and whether their peak abundance occurred prior to or after peak predation. This variation resulted in differences within predation-abundance seasonal space (Figure 4), which align with prior knowledge about each species' predator avoidance traits and natural history. We suggest that our results represent different strategies these functionally similar grazers use to persist and co-occur under strong predation risk. More broadly, these results suggest that temporal strategies to avoid predation may be an underappreciated mechanism promoting coexistence of functionally similar prey. Detecting these patterns, however, required treating predation risk and abundance as continuous seasonal trajectories

rather than discrete events. We suggest that this approach may be useful to understand the temporal structure of species interactions across a wide range of systems.

The species with the strongest morphological defenses (the isopod *Pentidotea resecata*) experienced a lower predation risk peak in the fall than the other two species (Figure 2A, Figure 4). Indeed, in our predation assays isopods were consistently consumed at the lowest rates, and previous work has found that their relatively large body size and ability to camouflage in the eelgrass results in them mostly being eaten incidentally (30–32). This ability to withstand periods of high overall predation with less risk than the rest of the community may explain their higher-than-average scaled abundance following peak predation risk (Figure 2B, Figure 4). This timing may allow the isopods to exploit a time of lowered competition for resources after other species' populations decreased due to high predation.

The species with limited morphological defenses but rapid reproduction (the caprellid *Caprella californica*) peaked in abundance in the spring and summer (Figure 2B, Figure 4) before the period of the highest predation risk (Figure 2A, Figure 4). In our abundance surveys caprellids were always at the highest average densities. This matches previous work in eelgrass beds which found that while caprellids have minimal morphological defenses and are often at very high densities, they make up a relatively small portion of most predators diets except for a brief seasonal peak corresponding to surfperch migrations (33, 34). Following this predation peak, caprellid numbers dramatically decreased (34). While one interpretation of this pattern can be that predation by fish are controlling caprellid population sizes following this peak, we believe this also may reveal a strategy caprellids have evolved in response to predictable high periods of predation. Perhaps they tradeoff investing in strong morphological defenses by instead

putting energy into greater reproduction before peak predation to withstand the strong top-down forces.

Finally, the species with the most behavioral defenses (the amphipod *Ampithoe lacertosa*) had variable abundance timing across sites (Figure 2B, Figure 4) despite consistently higher-than-average peaks in predation risk (Figure 2A, Figure 4). They are the least morphologically defended of these prey species, and instead use the creation of temporary silk tubes to avoid predation (35). However, due to the temporary nature of these tubes, and the patchiness of the substrates they use to build them, they are more mobile than most members of the community as well (36). While amphipods will construct tubes on eelgrass, they prefer and actively seek out the macroalgae *Ulva* sp., which is patchily distributed both in space and time (37). Thus, perhaps there is a lack of a strong pattern in their seasonal abundance because to withstand the consistently high levels of predation they experience, they mitigate their risk by moving to different spatial refuges, rather than temporal ones.

We believe that the patterns we observed are most consistent with trait-based temporal strategies. While we cannot explicitly rule out alternative hypotheses for the abundance patterns we observed, as we did not test all possible drivers, our FDA approach can help us to evaluate which alternative drivers best fit the data. For example, a common driver of increased reproduction rates is increased metabolisms under a seasonal rise in temperature (38), and a common driver of species distributions is high stressful temperatures (39). In our system, temperatures peak around mid-summer, during which our sites span a temperature gradient, ranging from 16°C to 22°C (40, 41). In the late fall and winter, temperatures stabilize to the same values at all sites. We do not see variation in the timing of increases in abundance across sites that would align with expectations from temperature-driven patterns. If high temperatures were

limiting abundance, we would expect to see the hottest sites clustering on the positive side of PC1, indicating increased abundance during the cooler and less stressful part of the year, and yet we see the opposite. If high temperatures were increasing the abundances of certain species through increased metabolisms, we would expect to see them clustered on the negative side of PC1, indicating increased abundance during the hottest part of the year. Indeed, we see that the caprellids cluster here, but even if this is a signal of increased reproduction from temperature, this aligns with our argument that they are increasing their population quickly to minimize the individual impacts of predation. Similarly, if alternative prey availability was driving patterns of predation risk, we would expect that most of the variation in our predation risk data would be explain by shifts in timing. However, most of the variation was explained by the magnitude of the peak in predation, not the timing, a distinction that would have been impossible to make without treating these patterns as complete seasonal trajectories. While there can be many potential explanations for observational patterns, our results are consistent with the hypothesis that different temporal abundance strategies are favored to tolerate predation in the context of each species' natural history.

Had we not used entire seasonal trajectories to examine these relationships we would have missed important patterns. We calculated the time lag between each species' peak in predation risk and abundance – the univariate equivalent of our analysis (see Appendix 1). Qualitatively this gives the same general result as the FPCAs: caprellids peak in abundance before predation risk, isopods and amphipods peak after, with the isopods showing a greater lag (Appendix 1: Figure S4). However, these results were not quantitatively significant and discarded a significant amount of information contained in complex seasonal curves. In contrast, the FDA approach revealed differences among species by retaining information about when, how

much, and how consistently predation and abundance varied throughout the year (Figure 4).

Treating temporal patterns as complete functions rather than summary statistics can help reveal important insights into the structure of ecological processes and communities. For longer time series, this approach could improve our understanding of how climate variation has differentially shifted the timings of prey abundance and predation risk patterns, helping to explain the variable response of predator-prey interactions to changing temperatures (42).

There has been a shift from focusing mostly on spatial mechanisms of predator avoidance (i.e., partitioning enemy-free space; 35) to the recognition that partitioning “enemy-free time” may be equally important to the persistence of prey (1). However, while spatial techniques have continued to become more sophisticated, allowing for a more complex understanding of how species move to avoid predation, temporal analyses are often still done at short time scales at a coarse resolution or with summary statistics (4, 44). For example, there is a large body of literature focused on the impacts of predators on the activity patterns of prey across diel (14, 45–47) and lunar cycles (48). However, there is less research on seasonal patterns of temporal niche partitioning as a way to avoid predation and this research often focuses on competitive release driven by increased predation on a less defended competition during particular times of the year (49). High resolution temporal data related to predation risk and abundance, combined with natural history based knowledge of prey traits has led to similar explanations of the seasonal rotation of abundances of small desert rodents - another system of small mobile, prey with overlapping resource use (50). Thus, our finding of temporal niche partitioning in relation to predator avoidance as a coexistence mechanism may be more common than is what is currently reported in the literature. By allowing patterns from continuous data to emerge without first constraining our analysis with hypotheses around how predation risk and abundance might relate

seasonally, we found surprising results demonstrating more complex patterns than might be expected and that would likely be overlooked using the most common analytical approaches in use.

We have shown that functionally similar prey species may use both spatial and temporal strategies to partition refuge and withstand high levels of predation risk. Importantly, our results highlight the complex insights that can be gained when entire seasonal trajectories are analyzed, rather than univariate summaries. Understanding how diverse communities of prey persist under high predation requires looking at not just when species are abundant or when predation peaks, but how these temporal patterns relate to each other and to species traits. As continuous and long-term datasets become more available for a wide range of systems, we believe that FDA can be a valuable addition to the ecologist's toolkit, allowing for better understanding of species interactions and phenology through time in a changing climate (4, 51, 52).

Methods

Study system

We conducted all experiments and surveys at five eelgrass (*Zostera marina*) beds in Bodega Harbor or Tomales Bay, California, USA. Prior work has shown both spatial and seasonal variation in these beds (42, Murphy and Stachowicz, in press), which host a diversity of invertebrates and fishes (21, 37, 41, 53). In this study, we focused on three abundant epifaunal crustaceans that occur across all sites in both estuaries and throughout the northeast Pacific— the caprellid amphipod *Caprella californica*, the ampithoid amphipod *Ampithoe lacertosa*, and the isopod *Pentidotea resecata*. These three species differ in predation avoidance strategies from slower reproducing heavily defended species to faster growing poorly defended species (31).

Predation assays

Detailed methods and justifications for how we measured predation risk, including the evaluation of potential artifacts of tethering, can be found in (54). Briefly, we tethered live individuals of each prey species to string attached to clear acrylic rods. We maintained consistent transects at each of the five sites, and every 2-6 weeks for one year (a total of 16 times from April 2022 to March 2023), at low tide we placed 20 tethered individuals of each prey species along the transect. Each tether was 0.5 meters apart from each other and we alternated prey species. We returned to each transect 24 hours later and retrieved the tethers. The proportion of tethers with missing prey items from each species was recorded as the relative level predation risk that species was experiencing at that site at that time.

Field abundance surveys

We estimated local prey abundance to assess relationships between seasonal patterns of predation risk and the local abundance for each of our prey species. Concurrent with the predation assays, we conducted 15-minute field surveys within an area extending about 2.5 meters on each side of the transect at each site to measure prey abundance. The lead author (CEM) searched the seagrass and any drift algae, and carefully scraped and combed through the macrophytes, identifying and counting any of the four focal species. All our focal prey species are relatively conspicuous and easy to identify in the field due to unique morphological traits relative to the local species pool. Each survey was completed within one hour of low tide. Similar timed surveys are commonly used to estimate abundance in other systems with patchily distributed or highly mobile animals and offers many advantages over destructive surveys where the species of interest are sufficiently distinct as is the case here. Further details are in Appendix 1.

Functional data analysis

To compare the entire annual trajectories of predation risk and prey abundance, we had to first convert our time series data into smooth, continuous functions. To do this, we fit a separate generalized additive model (GAM) for each species by site combination, for both the predation risk and abundance data. For the abundance data, we first scaled the values to be proportions relative to the maximum abundance observed for each species-site combination. This allowed us to better compare the temporal abundance trajectories of species with very different densities, as we were most interested in the timing of increases and decreases rather than in the absolute magnitude.

For all GAMs we used a cubic regression spline smoother with a fixed basis dimension ($k = 7$ for predation, $k = 7$ for abundance), ensuring consistent smoothness across all species-site combinations rather than allowing the smoothing to vary based on each curve's data. For the predation data we used a quasibinomial error distribution, while for the scaled abundance data we used a Gaussian error distribution. A few predicted values were slightly below 0 so we truncated our model results at 0, as abundance cannot be negative. We fit all models using the 'gam' function in the 'mgcv' R package (55). Model diagnostics for all GAMs showed that the chosen basis dimensions were adequate to accurately describe the temporal variation in the data. Because smoothing parameter choices can influence GAM fits, we explored a range of fitting approaches including penalized smooths across a range of smoothing parameters (0.1 to 500) and fixed basis dimensions ranging from 5 to 14 to ensure that our model fitting choices were not influencing our results. We found qualitatively similar final patterns regardless of the selected values.

Next, we conducted functional principal components analyses (FPCAs) to identify the dominant temporal patterns in the data using ‘fda’ package in R (56). We used GAMs to smooth our data as our predation data was best modeled with a quasibinomial error distribution and this is not easily integrated directly in the ‘fda’ package. Thus, we had to convert our GAMs to function objects before proceeding with our analysis. To do this we used a B-spline basis (14 basis functions, order 4) with a near-zero penalty parameter ($\lambda = 1e-10$), preserving the smoothness already captured by the GAMs. We visually checked these new functions for alignment with our original GAMs.

For each dataset (predation risk and abundance) we separately applied the ‘pca.fd’ function to the functional objects from all species-site combinations. This approach outputs principal components which represent the dominant temporal patterns in the data. We retained three principal components from each analysis. The resulting scores for each species-site combination indicate how strongly that curve follows each PC’s temporal pattern. Positive scores indicate the curve follows that pattern more than average, while negative scores indicate the inverse (see Figure 1 for a schematic of our approach).

We used PERMANOVAs (‘adonis2’ function in the ‘vegan’ R package; 45, 46) to test whether prey species differed in their temporal patterns. We conducted separate PERMANOVAs for predation risk and abundance using scores from the first two PC axes for each species-site combination with prey species as the grouping factor. Prior to each PERMANOVA, we tested for homogeneity of multivariate dispersions among species using ‘betadisper’ in the ‘vegan’ R package (58) to ensure that significant results reflected differences in centroid locations rather than dispersion (59). To visualize the ecological meaning of the relationship between temporal patterns of predation risk and abundance, we plotted the first axis of the predation FPCA against

the first axis of the abundance FPCA, as they explained the most variation in each respective dataset.

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Figures

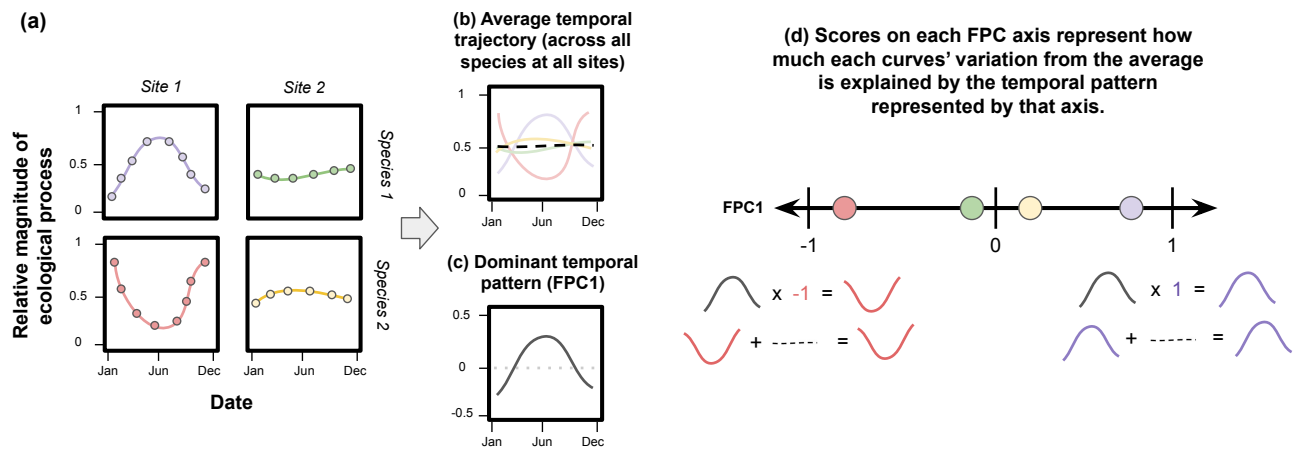


Figure 1. A conceptual diagram demonstrating how to conduct and interpret functional principal components analysis (FPCA). Panel (a) shows dummy data representing repeated temporal measurements of an ecological process for two species (rows) at two sites (columns). Values have been scaled relative to the maximum observed for each species-site combination, allowing the shapes of temporal trajectories to be compared independently of differences in magnitude. Points are observed data and lines are smoothed curves fitted to represent the underlying temporal pattern. Panel (b) shows the mean of all four curves, representing the average temporal trajectory of the process across all species and sites. Panel (c) shows the loadings from the first FPC axis plotted over time. This curve depicts the single temporal pattern that explains the most variation among species-site combinations in their deviations from the average trajectory. Panel (d) shows the FPC1 score for each species-site combination, which indicates how strongly and in what direction that combination's trajectory deviates from the average in the pattern described by FPC1. For example, the red point represents species 2 at site 1, which has a score of approximately -1 on FPC1. This means that multiplying the FPC1 loading curve by -1 and

adding it to the average curve best captures that species-site combination's deviation from the average in the dimension of variation described by FPC1, as illustrated in panel (d).

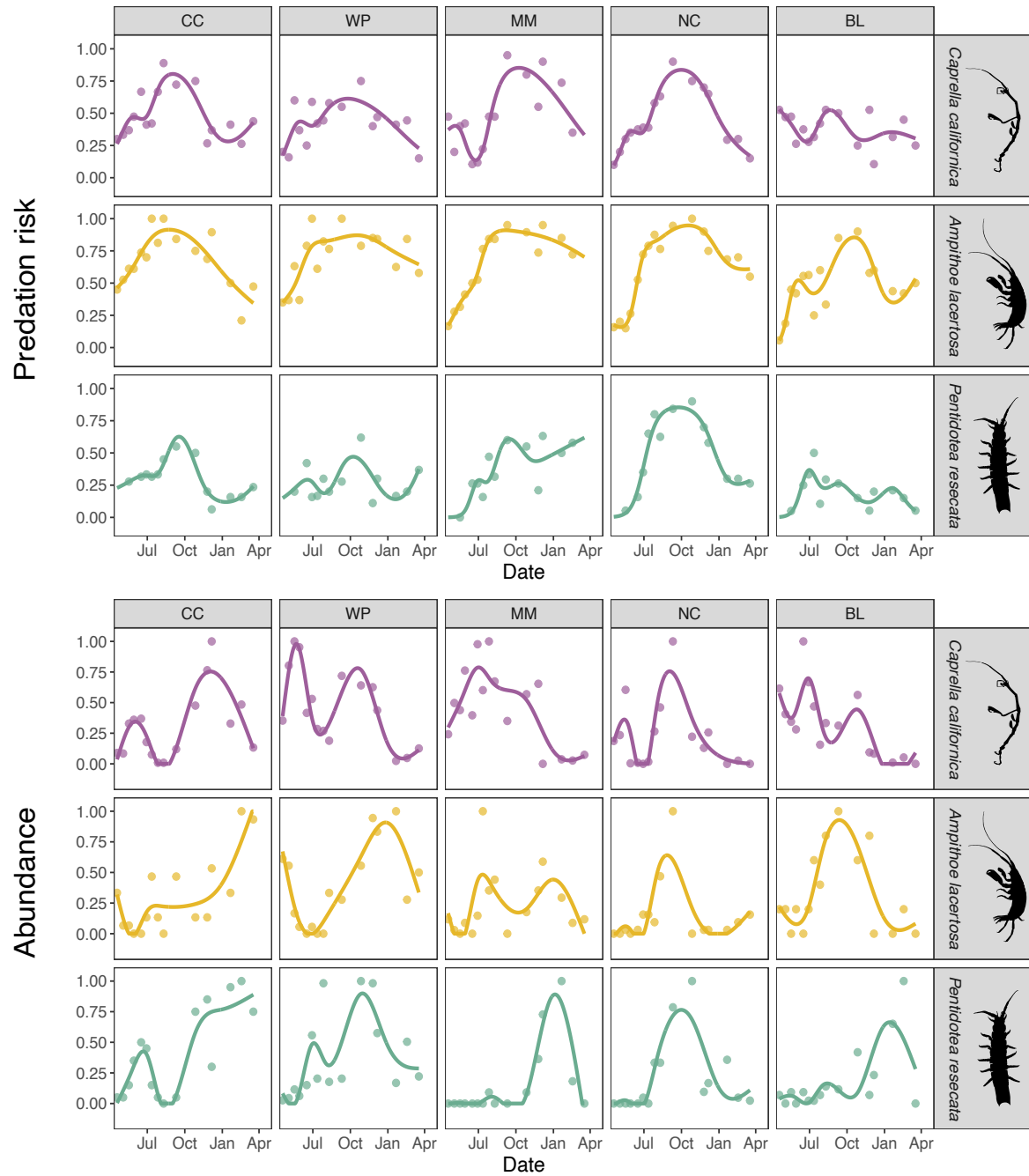


Figure 2. Plots showing the predation risk (a) and abundance (b) for each species-site combination across the year. Each column represents a site, and each row represents a species. Points show the observed values at each time point and the curves show the predicted values from the fitted GAMs.

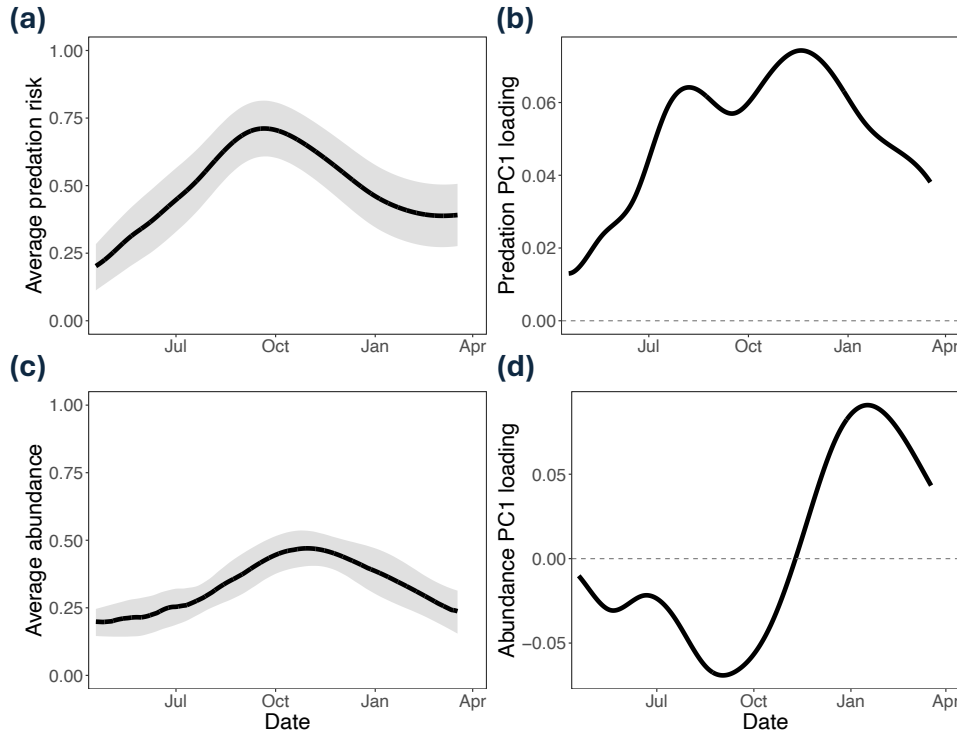


Figure 3. The plots in the left column show the average predation risk (a) and scaled abundance (c) for all species and sites across the year. Values are averaged model results from the GAMs and the shaded area represents the standard error. Plots in the right column show the loadings from the first PC axis from the predation risk (b) and abundance (d) functional PCAs plotted over time. Every species-site combination's score on those respective axes demonstrates how much variation from the average temporal pattern is explained by the pattern that emerges from the PC1 loadings. For example, a high positive score on predation risk PC1 would mean that that particular species-site combination has a larger and more sustained peak in predation around October than average, while a large negative score would indicate a smaller peak in predation than average.

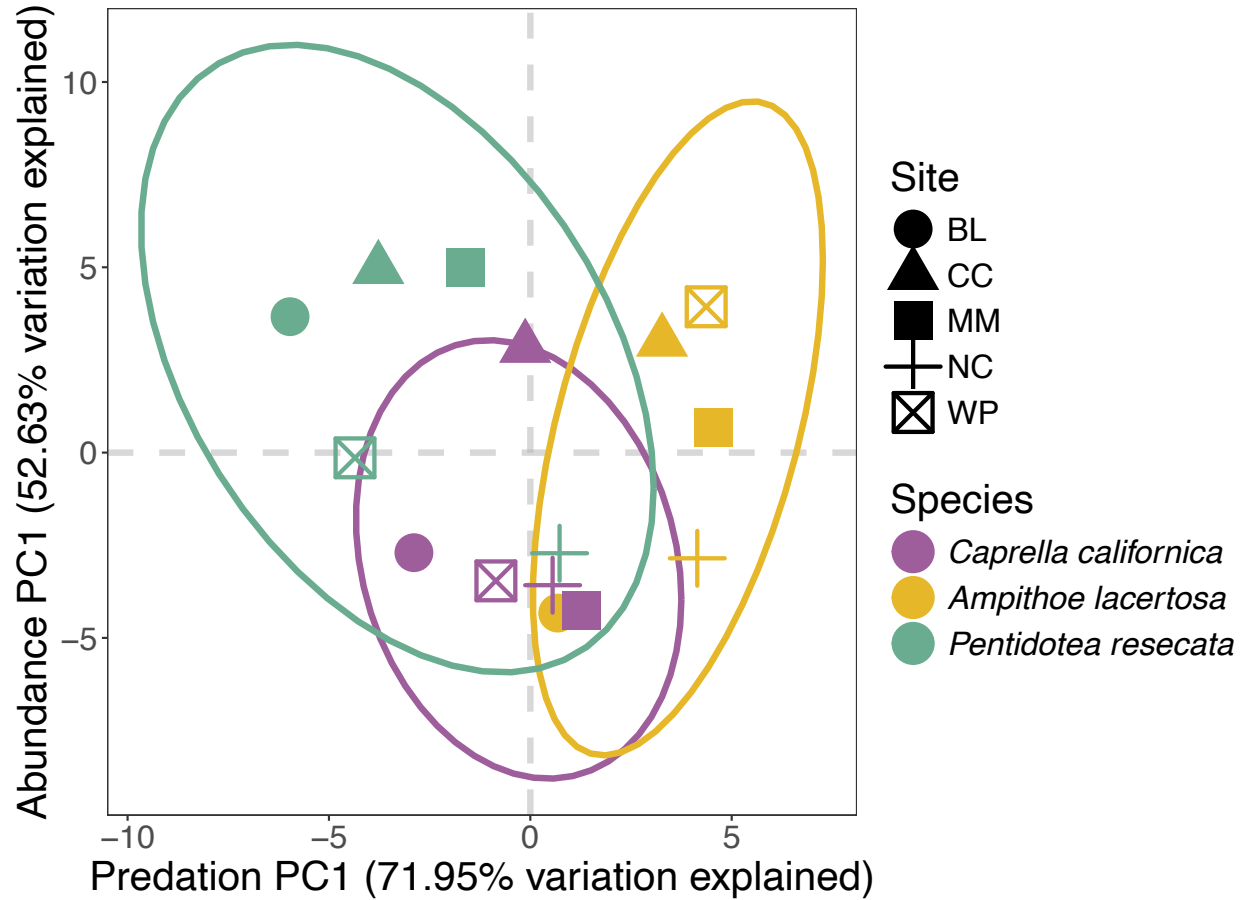


Figure 4. We plotted the first axis of each FPCA against each other to better understand how the prey species differed in their temporal strategies. Each shape represents a different site, and each color represents a species. Interpretations of what each point's score on both axes mean can be derived from Figure 2. Briefly, caprellids show an average peak in predation in October, but an earlier than average peak in abundance. Isopods have a lower-than-average predation risk peak and a later than average abundance peak. Ampithoids have a higher-than-average peak in predation and variable abundance timings. The ellipses show the 90% confidence interval for each species using a t-distribution.

CHAPTER 2: Seasonal differences in predation risk among seagrass epifauna species stabilize community-level predation over time

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Abstract

Predation risk varies through space and time due to changing refuge quality, predator communities, and prey traits. Despite this, ecological research is often focused on measuring average predation risk at the community level. While this can give important information about overall trophic transfer and ecological efficiency, it ignores differences in predation risk among prey species within a community, which may be important determinants of species coexistence and local diversity. We used crustaceans associated with temperate seagrass in Northern California to explore the relationship between seasonal variation in among-species and community-level predation risk for a community of morphologically distinct prey. We measured predation risk of the four most abundant and widespread prey species at six field sites every two to six weeks for one year. At the community level, sites differed significantly in their annual variation in predation risk, and these differences were correlated with the amount of variation in the among-species predation risk. When there was greater within-year variation in predation risk

among the four prey species, predation risk at the community level was more stable across the year. On the other hand, when each prey species in the community had similar levels of predation risk throughout the year, predation as a community-level process was much more seasonal and variable. Variation in predation risk also changed across a gradient of seagrass cover, a proxy for refuge quality. Sites with greater seagrass cover had less annual variation in community-level predation risk and more variation in predation risk among the four species at any given time point. In contrast, at sites with less eelgrass, all species were consumed at the same rate throughout the year, suggesting previously demonstrated differences in antipredator strategies among species are less relevant in the absence of habitat-forming species. We suggest that larger species-specific differences in predation risk throughout a year result in a more stable level of predation risk for the whole community. This may be driven by the increased refuge provided by seagrass habitat mediating different prey species' relative levels of susceptibility to predation.

Introduction

The strength of predation, and thus the risk that a prey community experiences, is dependent on three main factors: predator communities (composition and abundance), the refuge available in the environment (type and amount), and prey traits. The same prey community can experience different levels of risk across geographic gradients as refuge availability and predator communities shift, such as through changing habitat structure (e.g., Schneider 2001, Warfe and Barmuta 2004), predator composition and behavior (e.g., Brown-Saracino et al. 2007), or even hunting regulations (e.g., Selden et al. 2017). On top of this, within a prey community different species often have unique traits or behavioral responses to these changing environmental

conditions, and a context that favors the antipredator responses of one species may make another more vulnerable (Ives and Dobson 1987). Furthermore, habitat or predator community contexts are not static – seasonal shifts can change which antipredator responses are most effective and as a result, which prey species experience the most risk (Gratton and Denno 2003, Mappes et al. 2014).

Despite this potential for large variation in risk, understanding the aggregate “community-level predation risk” (i.e., the average risk each member of the prey community experiences, regardless of species identity; the solid lines on Figure 1), can give important information about trophic transfer and ecological efficiency. Across a year, community-level predation risk may fluctuate in seasonal environments as predator communities or refuge availability change (Figure 1A). In contrast, more stable environments have more consistent predator communities and refuge availability and so prey communities might experience constant levels of predation risk (Figure 1B & 1C). However, consistency in community-level predation risk throughout a year could arise from two very different mechanisms (Figure 1B & 1C). In one scenario, there are equally consistent, hierarchical predation patterns for each individual species in the community (Figure 1B). Alternatively, low seasonal variation in community-level predation can also be the result of compensatory dynamics in which the risk hierarchy among species varies considerably across the year, but the averaged total risk is relatively constant (Figure 1C).

This variation in species-specific predation risk across a prey community could play an important role in prey co-occurrence patterns and how they change across seasons or regions. At a site with a constant hierarchy in predation risk among species, the most vulnerable prey might be unable to persist, having to rely on high levels of dispersal or reproduction to counteract

predation (Amezcu and Holyoak 2000). Alternatively, if prey experience complementary and seasonally variable amounts of risk, it may be that no one species is able to remain dominant due to regular periods of high predation, promoting prey diversity and stability (Rakowski et al. 2021). Despite these differences, both scenarios would display stable community-level predation risk across the year. Furthermore, because species differ in predator-avoidance strategies, a generic prey item may misrepresent not only predation risk to individual species and but also the total community-level risk, if used as a proxy (Mihalitsis et al. 2021). Thus, while aggregate risk is a useful measure of total trophic transfer at a site, understanding predation's effects on the whole community requires separate assessments of risk for each prey species. These species-specific predation risk data are also critical to connect patterns of variation in predation risk to prey population and community dynamics. Despite this, high-frequency data measuring the relative predation risk among dominant species are rarely available.

Temperate seagrass meadows systems, such as those dominated by eelgrass (*Zostera marina*), support invertebrates with a diversity of antipredator adaptations that may be effective against different predators (Lürig et al. 2016). These eelgrass beds are known to vary spatially and seasonally in invertebrate community composition (Ha and Williams 2018, Gross et al. 2022), abundance and diversity of predators (Douglass et al. 2010, Ruesink et al. 2019), and habitat structure (Hovel et al. 2002, Duffy et al. 2022) and provide a tractable system in which to understand the drivers of temporal variation in predation risk in the field. Considerable research has considered how habitat amount and structure, the main form of refuge, affects the abundance and predation risk of these epifaunal invertebrates (Boström et al. 2006, Yarnall et al. 2022). Generally, increased habitat, either measured through increased total seagrass biomass (Virnstein et al. 1984), total shoot surface area (Sirota and Hovel 2006), or percent cover (Reed and Hovel

2006), is positively associated with increased diversity and abundance of epifauna. A common explanation invoked for this is that more complex habitats result in lower predation (Sredl and Collins 1992, Hovel et al. 2021, Gigliotti et al. 2021). However, reduced community-level predation does not necessarily lead to higher prey diversity (Finke and Denno 2005, Ryberg et al. 2012), and a better understanding of how predation risk varies among species in changing habitat contexts through space and time is needed to link predation and local community composition. Additionally, the interpretation of geographic comparisons in predation risk using standard prey items (Reynolds et al. 2018, Whalen et al. 2020) requires a better understanding of the consistency of among-species variation in predation.

Here we measure predation in the field on four species of peracarid crustacean at six sites at ~3-week intervals over the course of an entire year. We evaluate the relationships between within-year variation in predation risk and habitat amount by addressing two questions: 1) what is the relationship between seasonal variation in species-specific and community-level predation risk? and 2) how does this relationship change across a gradient of habitat amount?

Methods

Study sites and focal species

We conducted all experiments and surveys in the seagrass beds in Bodega Harbor and Tomales Bay, California. Both estuaries support extensive beds of *Zostera marina* (eelgrass), a widespread temperate foundation species, exhibit strong seasonal and spatial environmental changes, and host a diversity of invertebrates and fishes (Olyarnik and Stachowicz 2012, Best and Stachowicz 2014, DuBois et al. 2022, Gross and Stachowicz 2024). Full names and locations

of each of our six sites are found in Appendix 2: Figure S1. All this work was based out of the University of California, Davis Bodega Marine Laboratory.

We focused on four abundant, widespread, and functionally distinct species of epifauna – the caprellid amphipod *Caprella californica*, the ampithoid amphipods *Ampithoe lacertosa* and *Ampithoe valida*, and the isopod *Pentidotea resecata* – which represent the wide range of predation avoidance traits found in epifaunal communities (Best and Stachowicz 2012). The caprellid amphipod, *C. californica*, occurs at high densities (Ha and Williams 2018) and reproduces quickly with large and frequent broods (Keith 1971). They are thin and inconspicuous, allowing them to blend in with the seagrass, and individually they have low caloric value (Caine 1991). They are relatively easy for predators to capture and seem to counteract the impacts of predation through rapid reproduction and large populations (Caine 1989, Hosono 2014). In contrast, the isopod *P. resecata* grows to be one of the largest members of the grazer community (Lürig et al. 2016). They camouflage in the eelgrass by matching the blades in shape and color (Lee and Gilchrist 1972). This unique morphology may allow them to evade predation, especially when there is a high density of eelgrass blades to hide among (Best and Stachowicz 2012). Finally, the ampithoids *A. valida* and *A. lacertosa* have specialized silk glands which allow them to create temporary protective tubes within the eelgrass or macroalgae, decreasing their risk of predation (Nelson 1979). Beyond this they are neither morphologically defended nor particularly cryptic on eelgrass. All these species are generalist herbivores that consume both live and dead eelgrass, epiphytes, and macroalgae to varying degrees (Best and Stachowicz 2012).

Predation assays

To measure predation risk, we tethered live individuals of each of the species by gluing them (using Loctite Ultra Gel Control cyanoacrylate super glue) to a 10 cm long monofilament line attached to the top of a 35 cm long clear acrylic rod, which we then embedded in the sediment, leaving about 15 cm above ground. We did this at 6 sites every 2-6 weeks (a total of 16 times from April 2022 to March 2023). At low tide at each site, we placed 20 individuals of each species along a set transect, with each tether 0.5 m apart from the next, alternating between the focal species. At the three Tomales Bay sites we included all four focal species (resulting in 40 m transects) but excluded *A. valida* in Bodega Harbor (resulting in 30 m transects) since it does not regularly occur there and may be non-native (Harper et al. 2022). We collected individuals to tether from all six sites, depending on where each species was most common and easy to collect at each time point, and occasionally supplemented this with laboratory cultures as needed. In a few instances, weather or low availability prevented the inclusion of particular sites or species at a time point.

We retrieved the tethers at low tide approximately twenty-four hours later. For each tether that was recovered, we recorded whether the prey item was missing, which we assumed meant it had been consumed. Underwater videos showed fish eating tethered individuals, demonstrating that predation was a reason for their removal (Appendix 2: Figure S2A; Video S1). Sometimes tethered individuals were crushed or ripped in half, presumably by a predator consuming them (Appendix 2: Figures S2B & S2C). In addition, in laboratory pilot experiments, no individuals of any of the four species came unglued from tethers, even after 5 days, suggesting that individuals missing from tethers in the field most likely not the result of glue failure. We discuss additional evidence in the Results that suggests that temperature or water

motion were unlikely to cause the patterns we observe due to a lack of correlation between frequencies of missing prey and any environmental driver.

We calculated predation risk for each species at each site by time point combination as the proportion of tethers with missing prey items. While tethering experiments do not give absolute measures of predation risk, we can use data collected from them to understand the relative risk different species might experience, and how this risk might change through space and time (Peterson and Black 1994, Aronson and Heck 1995, Baker and Waltham 2020, Rhoades et al. 2024). Within one deployment, we inferred that the tethered species that were consumed the most at a site also had the highest risk of being consumed in the field at that point in time. Across deployments, if a particular species was missing from more tethers at one point in time relative to another, we concluded there was a greater risk of predation at that time. We acknowledge that tethering can differentially impact species and inflate the predation risks of prey with more behavioral predator avoidance strategies. Yet we observed tethered tube builders (*Ampithoe* spp.) constructing tubes in a similar manner to free untethered ones (Appendix 2: Figure S2D & S2E), and we regularly observed tethered *P. resecata* individuals clinging to blades of eelgrass to camouflage (Appendix 2: Figure S2F & S2G). Furthermore, there were points in the year where each species had very low levels of predation risk (e.g., an average proportion of 0.148 of all tethers at a site consumed at one deployment), and these did not always coincide among species (see Results). Together, this suggests that tethering did not completely eliminate prey defenses and that our data reflect relative risk of predation among species and times for the taxa and sites we used.

Habitat surveys

Preliminary examination of predation risk data indicated that habitat amount (the percent cover and shoot density of eelgrass) one month after concluding the tethering experiments (March 2023) was associated with differences in predation risk among sites, prompting us to include measures of habitat in our analysis. However, due to the frequency and intensity of the sampling required to measure predation risk during the year of tethering, and the limited duration of low tides, we could not also feasibly measure habitat concurrently. We returned to each site every four to six weeks ($n = 11$) over the next year from April 2023 to March 2024. Along the same transects that we had deployed the tethers, we estimated the percent cover and shoot density of the seagrass in five 0.25 m² quadrats, evenly spaced along the length of the transect. We also noted the percent cover of any additional macroalgae or sessile invertebrates present within the quadrat. To measure percent cover, we estimated the amount of ground covered by each substrate in the quadrat, both visually and by touch. Total measures of percent cover could exceed 100% within a given quadrat if different substrates were layered on top of each other. When multiple observers were involved, measurements were standardized before collecting data to ensure consistency in the percent cover estimates. We measured both percent cover and shoot density of the seagrass as they provide slightly different but complimentary information about the bed. Shoot density gives a measure of how complex the habitat is, while percent cover better represents the total amount of habitat. For example, the same number of shoots may yield different percent cover estimates if they are seedlings in the spring versus large adult shoots in the late summer.

We believe that these data are representative of the rank-order differences in habitat among sites during the year we conducted the tethering for several reasons. Our initial habitat

survey occurred just one month after our last predation survey, and the rank order of the sites in terms of percent cover and shoot density measurements from this time point are strongly correlated with the rank order of sites based on our yearlong averages (shoot density: $\rho = 0.968$, $df = 4$, $p = 0.002$; percent cover: $\rho = 0.904$, $df = 4$, $p = 0.013$). Slight differences in the timing of seasonal growth and senescence of the eelgrass among sites does result in changes in the rank order of sites with respect to eelgrass cover, especially throughout the winter. To account for this, we only use these data to assess the influence of mean eelgrass cover differences among sites, rather than fine scale differences in the precise timing of peak habitat, which we do expect could vary among years. Finally, for months where we do have multiple years of habitat cover data from the same sites (from April – July 2023 and 2024), there was a strong correlation in the rank orders of sites calculated using both the shoot densities and percent cover of seagrass between the two years (percent cover: all ρ values between 0.812 and 0.943; all p -values between 0.005 and 0.049; shoot density: all ρ values between 0.886 and 0.943; all p -values between 0.005 and 0.019). Thus, we feel comfortable concluding that the relative amount of habitat present at each of our sites was consistent during the years of our study.

In our analysis, we assessed Pearson correlations between different metrics of predation risk (see below) with the average shoot density, and the average percent cover of seagrass, bare ground, and macroalgae. We focused on spatial differences in habitat amount across the whole year, rather than seasonal variation within the year as, with respect to habitat, the sites differed to a greater degree among than within sites across the year (Appendix 2: Figure S1). Since there were large differences in the average amount of habitat between the sites, it was impossible to disentangle whether differences in the annual variation of habitat amount were driven by real differences in the level of seasonality at a site, or just by these differences in the means (which

were positively correlated with variance). Habitat metrics were not confounded with site temperature, as neither the rank order of average shoot density nor average seagrass percent cover correlated with summer temperature at each site (shoot density: $\rho = -0.143$, $df = 4$, $p = 0.803$; percent cover: $\rho = -0.086$, $df = 4$, $p = 0.919$; temperature data from Schiebelhut et al. 2023).

Predation and habitat analysis

We calculated seasonal variation in among-species differences in predation risk and overall aggregate community-level predation risk across a year and then assessed the relationships between these two metrics with each other and eelgrass cover.

First, to assess whether the species all followed similar temporal patterns of predation risk (as in Figures 1A & 1B), or if the species differed in their patterns (as in Figure 1C) we compared the distributional shapes of the annual predation patterns. To do this we used a method originally designed to compare the shapes and distributions of flowering schedules of individual plants (Austen et al. 2014). This gave us a metric of how variable the seasonal predation risk was among the species in the prey community at each site.

We created a distance matrix of Kolmogorov-Smirnov (KS) test statistics. KS tests evaluate the likelihood that one distribution was sampled from another reference probability distribution. We then ran pairwise KS tests to compare the distributions of predation risk through time between each species at each site (i.e. within each box in Figure 2A we analyzed how different the overall shape of each colored curve was from the others). Lower KS test statistic values indicated that the distribution of predation risk through time was more similar for two unique species x site combinations. Values can range from 0 to 1, with a value of 0 indicating that two distributions are identical. KS test statistics, and thus our measures of among-species

variation in predation risk, are sensitive to both differences in the magnitude as well as the timing of peaks between different distributions. To visualize these multivariate differences, we ran a principal coordinates analysis (PCoA) on the KS distance matrix. These KS distances do not imply a specific temporal structure or allow for conclusions about synchrony. For example, a shift in the peak of the distribution by 1 month will produce an identical KS distance regardless of whether the peaks occur in March and April or August and September. Nevertheless, they do allow clear conclusions about the extent to which the timing and magnitude of predation peaks are similar for each pair of distributions compared. We ensured that our KS distances fulfilled the triangle inequality and we only interpreted our results based on the positive eigenvalues.

We also tested whether there were differences in the dispersion of KS distances in multivariate space, either by site or species groups, to get a measure of how variable or consistent different groups were in their distributions of predation risk across the year. We used the *betadisper* function in the *vegan* package (Oksanen et al. 2017) to calculate the centroid of each species or site grouping in multivariate space, based on their pairwise KS distances, and then to calculate how far the seasonal pattern of predation risk for each unique species and site combination was from those centroids (i.e., dispersion). A lower level of dispersion at a site would indicate that the predation patterns of each species may resemble Figure 1A or 1B, while larger differences would suggest the patterns are more like Figure 1C. We used the level of dispersion between species-specific predation patterns as our measure of “among-species variation in predation risk” for each site.

Next, we wanted to understand how predation risk varied across the year at the aggregate community level regardless of species-specific risk. To calculate this community-level predation risk for each site, we calculated the proportion of all tethered animals consumed at each time

point, regardless of which species they were. Then, to quantify how seasonally variable predation was at the community level for each site (“community-level variation in predation risk”), we took the standard deviation of this average community predation risk across all the time points within a site. This gave us one value per site.

To assess the relationship between the annual variation in species- and community- level predation risk within a site, we calculated Pearson r correlation coefficients. This allowed us to understand how variation in among-species predation risk underlies different patterns of variation in community-level predation risk. To understand how habitat might relate to variation in prey susceptibility at each site, we calculated Pearson r correlation coefficients between mean eelgrass shoot density and percent cover of eelgrass, bare ground, and macroalgae and the community- and species- level variation in predation risk. Finally, to assess the role each individual species played in driving patterns of variation in predation risk at the community level (both aggregated and between the species), we calculated the standard deviation of the annual predation risk for each species at each site (i.e., the standard deviation of each colored line in Figure 2A) and correlated these values with the average percent cover of seagrass. This allowed us to see how the degree of seasonality of predation risk that prey items experienced changed across sites, and if this variation was related to habitat.

Results

Predation assays

Across all sites ($n = 6$) and time points ($n = 16$), we deployed and retrieved 5840 tethers over the course of one year. Variability in predation risk differed both among species and sites (Figure 2A). If prey items became unglued in the field as the result of some extreme environmental

condition not present in these laboratory tanks, like high temperatures or strong currents, we would expect to see consistently high removal of all the species at all the sites during times of the year with peak water temperature (July – August; DuBois et al. 2022) or frequent storm events (February – March; Bromirski et al. 2003). However, there was wide variation in the predation risk observed during these periods, including some of the lowest values we observed across the whole year (Figure 2A). All this, in addition to the relative consistency we observed in predation risk when conducting assays on the same species at the same site at frequent intervals (Figure 2A), gives us confidence in assuming prey items were removed by consumption from predators, rather than some external environmental factor.

Across all sites, variation in among-species and community-level predation risk were negatively associated ($r = -0.96$, $df = 4$, $p = 0.002$; Figure 3A): sites with more consistent aggregate community predation risk had larger differences in among-species susceptibility on average across the year (Figure 3A). At sites with the largest differences in the risk experienced by the different species (BL, WP), there was very little variation in the average predation risk of the whole community across the year (such as the scenarios depicted in Figure 1B or 1C). However, these sites also had the most variation in the distributions or “shape” of seasonal predation risk for each species (Figures 2B & 2C), indicating that the pattern is more like what is shown in Figure 1C than Figure 1B. On the other hand, at the site with the smallest differences among species at any point in time (NC), total community predation risk was highly variable across the year, reaching its lowest point in the spring and peaking in the fall (similar to the depiction in Figure 1A).

When we ran the PCoA on our KS-distance matrix, only 12% of the total variation was explained by negative eigenvalues. We scaled the variation explained by the first two PCoA axes

to be relative to the total variation explained by all the positive axes. Without this scaling, these first two axes explained 65% and 20% of the total variation explained, and after the scaling they represented 53% and 16% of the variation explained by all the positive axes.

Habitat metrics

Sites varied in their average amount of seagrass cover across the year, ranging from 2% (annual range: 0% to 10% cover, at site NC; Appendix 2: Figure S1A) to 50% (annual range: 13% to 89% cover, at site BL; Appendix 2: Figure S1A). The average amount of cover at a site was negatively correlated with the variation in community-level predation risk ($r = -0.963$, $df = 4$, $p = 0.002$; Figure 3B) and positively correlated with the variation in species-specific predation risk ($r = 0.975$, $df = 4$, $p < 0.001$). Sites also varied in average shoot density, ranging from 1.15 (annual range: 0 to 3.8 at NC) to 34.8 (annual range: 13 to 100 at BL) shoots per 0.25 m² (Appendix 2: Figure S1B). These values were also correlated with variation in predation risk both among species ($r = 0.921$, $df = 4$, $p = 0.009$) and at the community level ($r = -0.946$, $df = 4$, $p = 0.004$). Similarly, the average amount of bare ground, which can be used as a proxy for the total amount of structure-free space (with no eelgrass, algae, or large sessile invertebrates) ranged from 50.1% (at BL) to 94.0% (at NC) and increased with the community-level variation in predation risk ($r = 0.884$, $df = 4$, $p = 0.019$) but decreased as the among-species variation increased ($r = -0.902$, $df = 4$, $p = 0.014$). The mean percent cover of just macroalgae ranged from 0.067% (at BL) to 36.4% (at CC) and was not correlated with either metric of predation risk variability (among-species: $r = 0.051$, $df = 4$, $p = 0.924$; community-level: $r = 0.114$, $df = 4$, $p = 0.829$).

Considering each species separately across sites, annual variation in predation risk was correlated with habitat metrics for only two of the four species. The standard deviation of risk

decreased with increasing percent eelgrass cover and shoot density for the isopod *P. resecata* and the caprellid *C. californica* (percent cover: $r = -0.882$, $df = 4$, $p = 0.020$; shoot density: $r = -0.797$, $df = 4$, $p = 0.057$ and percent cover: $r = -0.877$, $df = 4$, $p = 0.022$; shoot density: $r = -0.917$, $df = 4$, $p = 0.010$, respectively; Figure 4). In other words, how predation risk changed with habitat amount varied among species. At the sites with least eelgrass, the annual predation risk of the isopods and caprellids becomes more temporally variable, resembling the predation risk patterns the amphithoids experience across all sites. This is also evident in the KS distance PCoA (Appendix 2: Figure S3), where the distributions of predation risks for the amphithoids overlap with the distributions of caprellids and isopods at the site with the least eelgrass, while the predation patterns for the isopods and caprellids are much more variable across sites, especially at those with highest eelgrass cover. In other words, all species converged on a similar seasonal pattern of predation risk at low habitat availability sites but were more differentiated at high habitat availability sites.

Discussion

We found that at sites where each prey species in the community had more distinct annual predation patterns, there were more stable levels of aggregate community predation risk across the year. We suggest a possible explanation for this pattern is that sites with high eelgrass cover facilitated the expression of species-specific predator avoidance strategies that depend on habitat. At sites with high habitat availability, each prey species differed in the timing of seasonal peaks and troughs in predation risk, creating complementarity which averaged to constant total (summed across all species) prey consumption through the year. At sites with low amounts of habitat, in contrast, all species had the same strongly seasonal pattern of predation

risk, with a maximum in early fall and a minimum in winter. We suggest that these patterns may be a result of habitat amount influencing both the effectiveness of different antipredator strategies and the composition of seasonal predator communities and hypothesize that this altering of seasonal predation patterns could promote prey community diversity and stability.

The four species we used exhibit a range of predator avoidance strategies, which we speculate may contribute to the differences in predation risk patterns we observed at sites with varying amounts of habitat. At all sites, regardless of habitat amount, the two prey species with the most behavioral antipredator strategy (the amphipods *A. lacertosa* and *A. valida*, which construct temporary silk tubes to hide in) were always consumed at the highest (Figure 2A) and most seasonally variable rates (Figure 4). In contrast, the species with the strongest morphological predator defenses (the isopod *P. resecata*, which has a large bulky body and camouflages well in seagrass; Lee and Gilchrist 1972), was consumed at relatively low, less seasonally variable rates at sites with high eelgrass cover (Figure 2A; Figure 4), resulting in higher among-species variation in predation risk at these sites. However, as the amount of habitat decreased, the strong defenses of this species seemed to be less effective, as it was eaten more frequently during the late summer, experiencing the same predation risk as the amphipods (Figure 4) and reducing the overall among-species variation in predation risk at low eelgrass cover sites (Figure 3). The remaining prey species, the caprellid *C. californica*, was intermediate in how predation varied among sites with different eelgrass cover. Morphologically, caprellids are thin and thus relatively inconspicuous to visual predators when still, but behaviorally, when feeding or dispersing their jerky movement and large claw-like gnathopods may make them more easily detected by visual predators like fish (Virmstein et al. 1984, Caine 1989). This mix of traits translated to a similar pattern to what was seen with *P. resecata*, where *C. californica* was

eaten at more seasonably variable rates as the amount of habitat decreased (Figure 4). However, *C. californica* consistently had a higher predation risk than *P. resecata* (Figure 2A), potentially due to weaker morphological defenses and their increased visibility.

When prey rely on distinct modes of predator avoidance, tethering may differentially interact with these strategies. For example, tethering could have reduced the effectiveness of behavioral avoidance strategies more than the morphological ones, potentially resulting in inflated estimates of predation risks. However, we do not believe this greatly influenced our results, as the hierarchy of predation risk among species is consistent with tether-free studies including both lab experiments and gut content analyses of prey selectivity (Nelson 1979, Stoner 1979, Best and Stachowicz 2012).

Seasonal changes in predation may also be influenced by an interaction between habitat and the abundance or behavior of predators. Though we did not measure the predator community abundance or composition here, eelgrass beds, like other complex, biogenic habitats, provide shelter for many small bodied fish in the summer months – both juveniles of more transient species and adults of localized resident ones (Lefcheck et al. 2019). This general increase in abundance of predator communities might explain the general shift in magnitude of predation risk between the winter and summer months. However, changing foraging behaviors across habitat contexts may explain the seemingly decreased effectiveness of predator avoidance strategies at the relatively barren sites. In addition to reduced effectiveness of defenses described above, generalist predators should become less selective in their prey choice as the costs of foraging increase (Prokopenko et al. 2023). Thus, mesopredators (such as the species that eat isopods and amphipods in our study) hunting in lower density habitats often become more generalist in their prey selection, regardless of available prey densities in the field (Holbrook and

Schmitt 1988, Verdolin 2006), perhaps because they are more vulnerable to their own predators and thus spend less time selecting among prey. At the sites with more habitat, predators may be less vulnerable themselves and spend more time foraging (Mukherjee et al. 2009, Dhellemmes et al. 2021), which can promote selective feeding throughout the year. Overall, the high habitat cover throughout the year means that the site always has the potential to support a predator community that is selective of the prey they consume. This may have led to the temporally complementary patterns we observed in the predation risk at the high habitat sites (e.g., BL in Figure 2A, similar to Figure 1C), where each species was consumed at high rates at different points in the year.

The differences we observed in the seasonality of predation risk within the prey community may also influence prey abundance and co-occurrence. Across many marine predator types, increased habitat structural complexity has been shown to lead to a shift from type II to type III functional responses (Dunn and Hovel 2020), potentially due to the increased complexity facilitating low density refuges and prey-switching, common drivers of type III functional responses (Murdoch 1969). In denser and more structurally complex habitats, it is more important for predators to develop a specific search image to find their prey (Siddon and Witman 2004), which may be easier to do than for some of our prey species than others. Large dissimilarities in the costs of either finding or capturing different prey species also incentivizes predators to prey-switch (Prokopenko et al. 2023). These phenomena may help explain why we observed more variable seasonal predation patterns among prey species at sites with more habitat. Furthermore, all these drivers have been shown in other systems to lead to more stable prey populations (Oaten and Murdoch 1975). An intriguing hypothesis worthy of future testing is that increased habitat cover could mediate the stability of the prey community by amplifying the

effects of different predator avoidance strategies and incentivizing prey-switching between higher density prey.

Overall, we found that sites with greater differences in their species-specific predation risk had more stable levels of community-level predation risk, seemingly driven by temporal complementarity. Furthermore, habitat cover was correlated with these differences. We suggest that increased habitat may mediate the importance of among-species differences in predator-avoidance strategies across the entire year, resulting in variable timings of peak predation risk for different prey species and thus more stable levels of predation as a community-level process. Different species are at an advantage across the year as they experience different periods of relief from predation, potentially mediating prey co-occurrence and acting as a mechanism for prey diversity maintenance. Our results suggest a series of hypotheses that, if tested, would improve our understanding of how interactions between refuge availability and prey traits, even without knowledge of the predator community, alter predation risk, leading to a better understanding of prey population dynamics across space and time.

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Figures

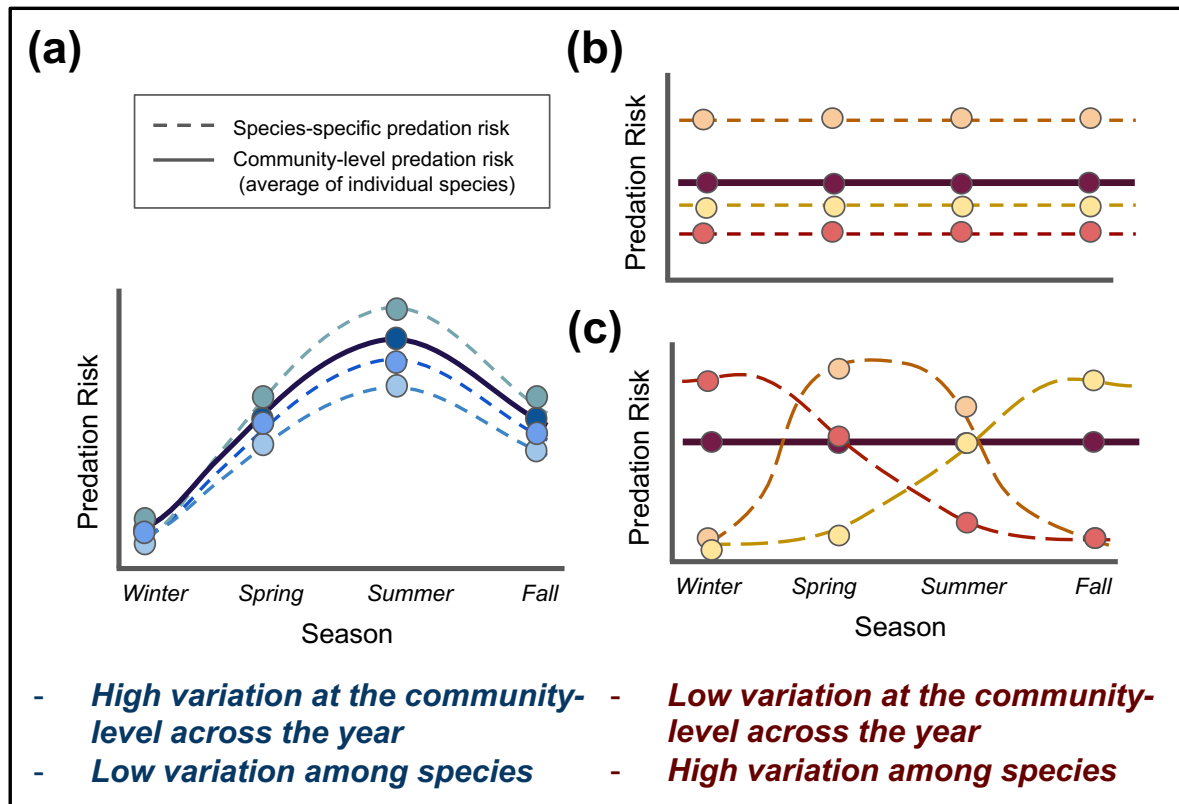


Figure 1. Hypothetical scenarios demonstrating the two extremes of variation in community-level predation risk across a year and the individual species-level patterns that can lead to them. Each different colored line represents a different species and the predation risk it experiences across a year. The solid lines represent the community-level predation risk, or the average risk all species experience at any given time point. Panel (a) represents a prey community that experiences high annual variation in community-level predation risk, while panels (b) and (c) represent two different scenarios that lead to stable community-level predation risk across a year.

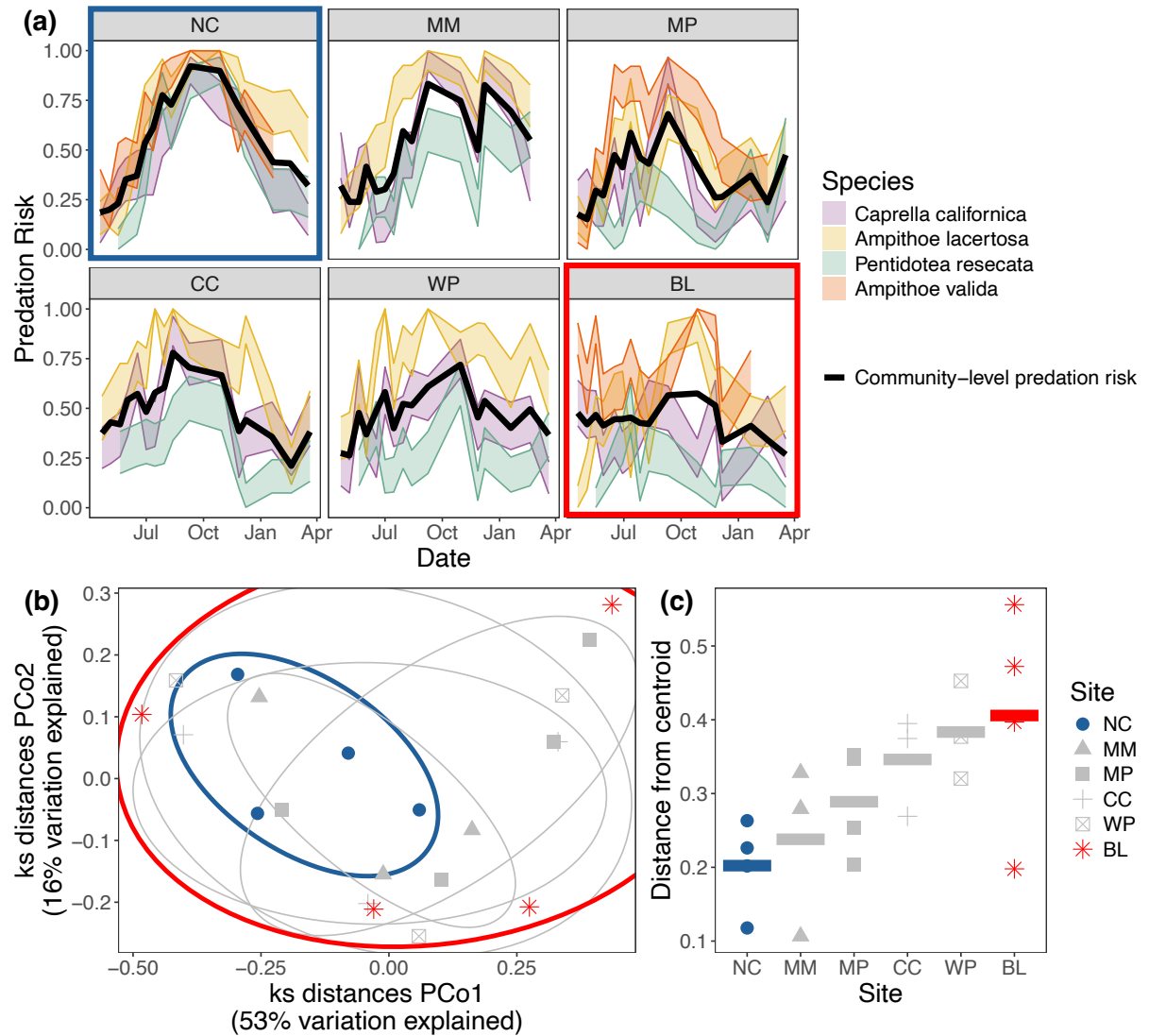


Figure 2. Panel (a) shows the seasonal patterns of predation risk for the four species community at each of the six sites. The width of the shaded lines represents the standard error around the average predation value (the average proportion of recovered tethers that had been eaten) at each time point. Each colored line represents a species, and the solid black line represents the community-level average predation risk. Sites are ordered from the site with least habitat to the site with the most. In panel (b), each species by site predation pattern is plotted in Kolmogorov-Smirnov (KS) multivariate space. Each point represents a distribution of predation risk across the

year (e.g., one of the colored lines in a) for each species at every site. The distance between two points correlates to how similar those two distributions are (e.g., the similarity of the shapes of two different colored lines in a). Sites varied in the level of similarity of the predation patterns for each species (c). In (c), sites are ordered on the x-axis from the lowest amount of seagrass cover to the highest amount of seagrass cover, and the y-axis represents how spread out the predation patterns of each species at that site are in KS space (represented in b). Sites with more seagrass have more variation in the distributions and shape of the seasonal predation risk for each species (as in Figure 1C). The sites with the most and least dispersion in KS space are colored red and blue respectively in all three panels. Sites are represented by abbreviations. Full site names are NC = Nick's Cove, MM = Mason's Marina, MP = Millerton Point, CC = Campbell Cove, WP = Westside Park, and BL = Blake's Landing.

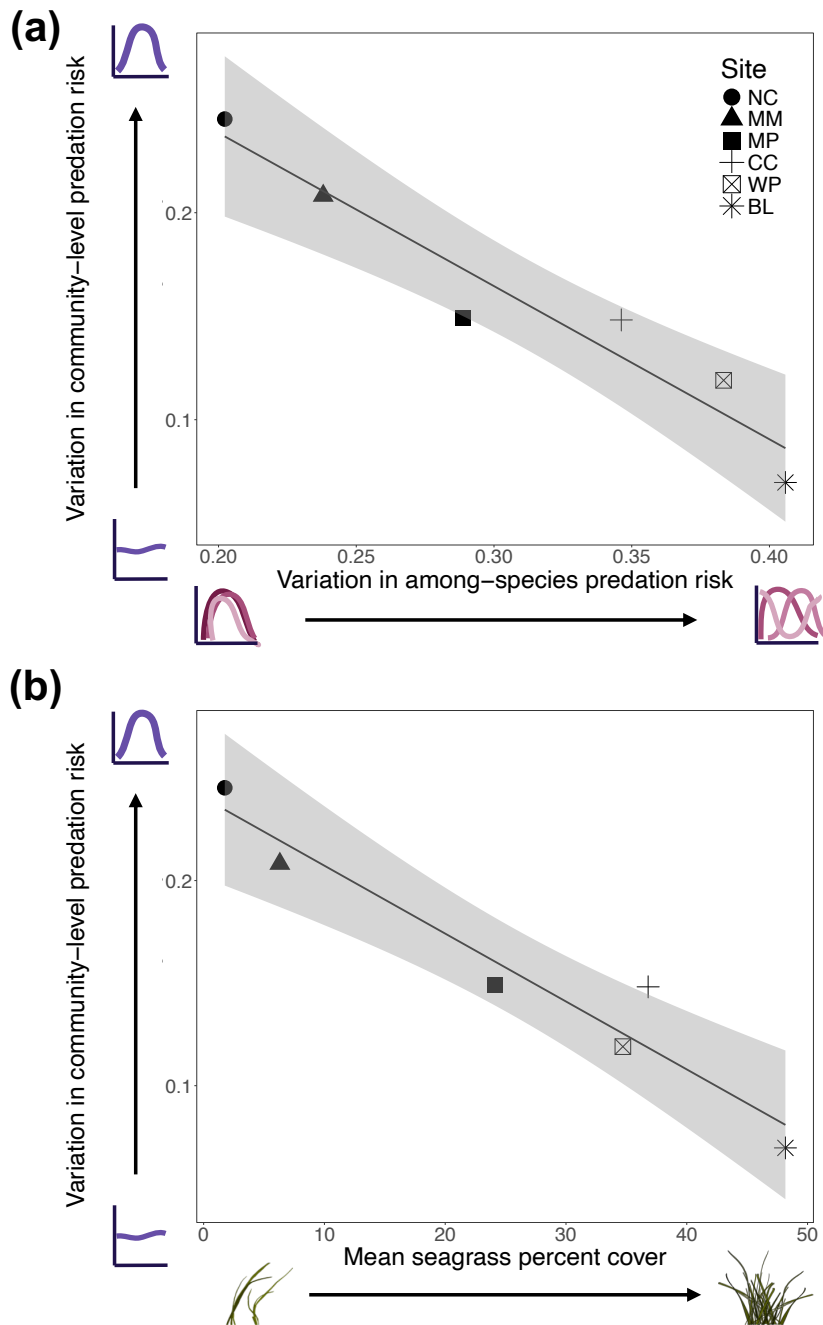


Figure 3. Increased stability in community-level predation risk is correlated with increased variation in among-species predation risk (a) and these are both correlated with increased seagrass cover (b), a potential driver of this pattern. Each differently shaped dot corresponds to a different site. Shaded areas represent the 95% confidence interval around each line. Seagrass illustrations are by Claire E. Murphy.

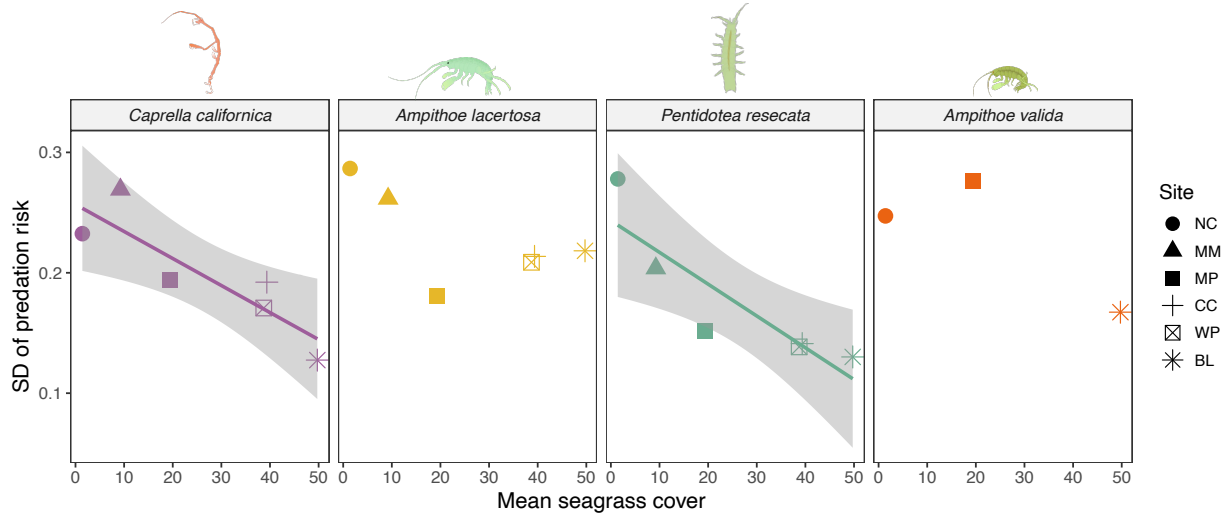


Figure 4. The standard deviation of the predation risk each species experiences at each site only decreases with increasing seagrass cover for the species with the most morphological defenses (*Pentidotea resecata* for both mean and standard deviation and *Caprella californica* for standard deviation). Trendlines with shaded areas representing the 95% confidence intervals are shown for the significant linear relationships. Crustacean illustrations are by Collin Gross.

CHAPTER 3: Seasonal and spatial variation in predator assemblages influences predation risk of eelgrass mesograzers communities

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Abstract

Predator community composition, as well as the predation risk they exert on prey communities, both vary seasonally and spatially. However, how they relate to each other across these different scales is not immediately clear. Eelgrass ecosystems have well-documented spatial and temporal variation in habitat structure, and this heterogeneity has been shown to influence both predator and prey communities, as well as interactions between the two. However, simultaneous variation both across seasons and sites can make it difficult to disentangle habitat-driven changes in predator communities from subsequent predator driven variation in predation risk. We used field video surveys and tethering experiments to ask whether overall community composition or specific predator groups are better correlated with direct measures of predation risk in the field across both seasonal and spatial gradients. We found that overall predator community composition predicted broad seasonal changes in predation risk, but after controlling for season there was little spatial variation in predator communities and this variation did not clearly predict predation risk. However, when we focused on variation in a single key predator group – surfperch – we did find relationships with predation risk both seasonally and between sites. We hypothesize that this variation in surfperch may be driven in part by behavioral avoidance of a top predator, diving birds. Thus, while broad community metrics did not clearly predict variation in predation risk, when considering behavioral interactions and variation in a key predator group, patterns between predators and the risk they exert on prey emerged.

Introduction

Predation risk and trophic structure are shaped by multiple aspects of predator communities (e.g., abundance: Forstmeier and Weiss 2004; species richness: Nilsson et al. 2008, Deacon et al. 2018; composition: Binz et al. 2014, Wesner et al. 2015). In seasonal and environmentally heterogeneous habitats, all these attributes vary across space and time. Locally harsh abiotic conditions may select for different predator species than nearby hospitable areas (Cheng & Grosholz, 2016), while seasonal resource limitation can reduce overall predator abundance (Beukema & Dekker, 2014). Furthermore, environmental variation not only influences aspects of predator and prey community structure (Menge & Sutherland, 1987), but also how these two groups interact. For example, the same predator may forage differently in different habitats, acting as ambush predators in complex habitats and pursuit predators in more open habitats (e.g., Říha et al. 2021). These behavioral shifts are often a response to a predator experiencing predation risk itself, resulting in a reallocation of energy from foraging to predator avoidance potentially decreasing the amount of predation risk they are exerting on their prey (Higginson et al., 2012). Thus, we would expect the predation risk experienced by prey to vary as environmental conditions change through space and time. Yet it is less clear whether that variation in predation risk is best predicted by metrics describing the whole predator assemblage, or by focusing on key predator groups whose behavior and abundance shift most meaningfully with environmental contexts (Ford & Goheen, 2015; Smith et al., 2020).

Temperate eelgrass (*Zostera marina*) beds are well-suited for examining this problem because they vary in habitat structure both seasonally and spatially (Clausen et al., 2014; Frederiksen et al., 2004), generating natural gradients across which predator communities, prey communities, and their interactions all shift simultaneously (Douglass et al., 2010; Jackson et al., 2006; Ruesink et al., 2019). Predator-prey interactions within eelgrass beds have been well-characterized (Hovel et al., 2021; Murphy & Stachowicz, 2026; Orth et al., 1984; Reynolds et al., 2018), providing a strong foundation for asking whether variation in predator communities predicts the actual predation risk experienced by prey. In this system small

epifaunal invertebrates act as the prey, sheltering within the structure of the seagrass, while mesopredatory fish and crabs are the predators. Each group uses the seagrass both to forage – the prey on epiphytes and the predators on invertebrates – and to attempt to mitigate their own predation risk through refuge provided by complex habitat structure.

Within seagrass meadows, habitat structure has been shown to alter every aspect of predator-prey interactions, yet relating different aspects of these interactions to the observed predation risk is not straightforward due to the simultaneous variation both across neighboring meadows and seasons. Lower levels of habitat structure filter predator communities, selecting for mesopredators that are not at risk of being consumed themselves (e.g., Horinouchi et al. 2009, Canion and Heck 2009). Some predators may alter their foraging strategy when in denser seagrass beds, shifting from active pursuit to ambush predation (James & Heck, 1994). Increased habitat structure also alters the composition of the prey community by increasing species richness and abundance, even when predators are excluded (e.g., Bell and Westoby 1986, Edgar 1990, Murphy et al. 2021). Yet despite this mechanistic understanding of how environmental variation influences each individual component of predator-prey interactions, predicting the actual predation risk experienced by prey remains difficult as all these effects operate simultaneously and vary across the spatial and seasonal gradients (Hovel et al., 2016, 2021).

Previous work in Tomales Bay and Bodega Harbor, California, USA has shown that in these estuaries predation varies both throughout the year, and spatially within a season (Murphy & Stachowicz, 2026). Prey items with stronger morphological defenses were eaten at higher rates during the annual peak of predation at sites with less seagrass cover. As seagrass cover increased, they were eaten at lower rates, seemingly due to increased effectiveness of their antipredator defenses when there was more habitat. Consistent with this, at these same sites habitat structure filtered summer predator communities into distinct trait distributions that were correlated with differences in prey community trait distributions (Gross & Stachowicz, 2024). These patterns suggest that predator community composition may be a useful predictor of predation risk. However, whether this is true across both spatial and temporal gradients

and what aspects of the predator community are the most predictive remains untested. We aimed to fill this gap and understand 1. how predator communities vary through space and time, and 2. whether overall community composition or key individual predators are correlated with direct measures of predation risk in the field.

Methods

Study system

All our sampling occurred in six eelgrass beds around Bodega Harbor and Tomales Bay, CA, which are home to a diverse community of animals (Best & Stachowicz, 2013; Gross & Stachowicz, 2024; Kelly & Condeso, 2017). The isopod *Pentidotea resecata*, amphithoid amphipod *Ampithoe lacertosa*, and caprellid amphipod *Caprella californica* are found at varying levels of abundance across both estuaries throughout the whole year (Murphy and Stachowicz, in prep.). Each has distinct morphologies and behavioral traits to avoid predation that collectively represent the dominant strategies within the broader epifaunal grazer community (Best et al. 2013). Previous work has found that these species also vary in their overall levels of predation risk across the year – with *A. lacertosa* experiencing the most risk, *P. resecata* experiencing the least, and *C. californica* in the middle (Murphy & Stachowicz, 2026). Thus, we used them to represent the prey community in this system. The predator community consisted of birds, crabs, and fish which forage among the structure provided by the eelgrass.

Field surveys

At seven times across the year (approximately every two months from August 2023 to July 2024) we took measures of predation risk, habitat metrics, and predator community composition along set transects at each of our six sites. Detailed methods and justifications for how we measured predation risk, including the evaluation of potential artifacts of tethering, can be found in Murphy and Stachowicz (2026). Briefly, we tethered live individuals of each prey species to string attached to clear acrylic rods. At each sampling timepoint, we placed 20 tethered individuals of each prey species along the transect at

low tide. Each tether was 0.5 meters apart from each other and we alternated prey species. We returned to each transect 24 hours later and retrieved the tethers. The proportion of tethers with missing prey items from each species was recorded as the relative level of predation risk that species experienced at that site and time. We calculated the “community-level predation risk” as the average predation risk all the prey species experienced at a particular site and time.

To quantify the habitat where these predation events were occurring, we counted all shoots in five 0.25 m² quadrats, evenly spaced along the length of the transect and estimated the percent of ground covered by seagrass in the quadrat, both visually and by touch as described in Murphy and Stachowicz (2026). Shoot density gives a measure of how complex the habitat is, while percent cover better represents the total amount of habitat. For example, the same number of shoots may yield different percent cover estimates if they are seedlings in the spring versus large adult shoots in the late summer.

To describe the predator communities that the tethers were exposed to, we placed unbaited GoPro Hero 9 and GoPro Hero 10 cameras along each transect at low tide. Each camera was set to start recording during the daytime high tide that overlapped with our tether deployment at each site. We chose to sample at these times both to allow us to easily see the organisms in the videos, but also because most of the predators in this community are visual and thus may require daylight and sufficient water depth to forage (Orth et al., 1984). Furthermore, previous work has found no diel differences in fish communities in other eelgrass systems (Gross et al., 2019). The cameras recorded video continuously until the battery died, usually for two to three hours. We aimed to place four cameras along each transect at each sampling time, but technical difficulties occasionally limited this to only three cameras at a site. We placed the cameras evenly along the transect (approximately 10 meters apart) and alternated the direction each one was facing. We set them to record on the widest view setting (SuperView) to maximize the area being sampled.

Video analysis

To get measures of how the predator community changed throughout the year at each site, we recorded data on each potential predator seen in the videos. When a fish, crab, or bird entered the frame, we first identified it to the lowest taxonomic level possible, using a variety of resources including local species pool lists from previous studies (e.g., Gross and Stachowicz 2024), California Department of Fish and Wildlife identification guides (e.g., Miller and Lea 1972), iNaturalist, and consultation with taxonomic experts. Often this allowed us to classify organisms to the species level, but for some groups, such as flatfish, we were only confident in our ability to classify to broad functional groups due to a lack of distinct morphological traits visible in the videos. After identifying each organism, we recorded the times in the video at which it entered and left the frame, if it was with conspecifics, and if so, how many. Each video was watched at least once by an observer, but for videos with taxonomic groups that were difficult to resolve (e.g., crabs or forage fish) or with poor visibility, multiple observers confirmed any measurements collected.

Technical difficulties and logistical problems resulted in uneven sampling across months and sites. At sites with lots of drifting macroalgae, occasionally cameras would be knocked over or totally covered, resulting in limited visibility of passing predators. Additionally, a hard drive containing many of the videos from March and May failed, resulting in limited data from those months. We accounted for this uneven sampling by running our analyses on rates of predator observations for each site at each deployment, scaling by video length and thus the chance of seeing a particular predator in the video. Hereafter we will refer to these measures of relative species observations as “encounter rates.”

Not only did the number of videos recorded vary through space and time, but the visibility in those videos did as well. We scored each video’s turbidity on a scale of zero to four, with zero being totally clear water where we could see up to 3 meters away from the GoPro and four representing the

most turbid videos, where visibility significantly declined after approximately 30 cm from the camera (Appendix 3: Figure S1). We checked for patterns of consistently high or low turbidity across specific sites and months using Kruskal-Wallis tests, followed by pairwise Wilcoxon tests with Bonferroni correction for significant results. We interpreted our predator community results with these patterns in mind.

Analysis of predator community composition

First, we were interested in how the predator communities that the tethered prey were exposed to varied by site and month, and if this variation related to differences in predation risk, both at the species and aggregate community levels. To look at general community patterns through both time and space, we ran non-metric multidimensional scaling (NMDS) ordination on the predator encounter rate data (counts of each species scaled by the length of video recorded for each site at each deployment), using the ‘metaMDS’ function in the *vegan* package in R (Oksanen et al., 2017). We Hellinger transformed the data first (took the square root of the relative abundance) due to the large number of 0s in our dataset and used Bray-Curtis dissimilarities. We used rates of predators, rather than an approach that attempts to minimize counting the same fish twice (such as MaxN; Schobernd et al. 2014) as we were interested in the community the tethers were exposed to, rather than just the community composition as a whole. That is, if the same predator happened to swim past the camera multiple times, we counted it each time because on each additional pass it was allowed another opportunity to potentially eat our tethered prey and increase our measured predation risk.

We ran permutational multivariate analysis of variation tests (PERMANOVAs; using ‘adonis2’ in *vegan*) with 999 permutations to test whether predator community composition differed significantly by site or month. We ran models with three different groupings: month only, site only, and both. We tested for homogeneity of multivariate dispersions using ‘betadisper’ to verify that significant PERMANOVA results reflected differences in centroid locations between groups, rather than simply differences in dispersion. We ran a SIMPER analysis (using ‘simper’ in *vegan*) to look at which predators were most

responsible for driving the differences in the winter and summer communities. We compared December, January, and March to the rest of the year.

We looked at if eelgrass habitat metrics (shoot density and percent cover) were associated with particular predator communities through space and time by using ‘envfit’ in *vegan*. This tests how much variation in each habitat variable was explained by position in NMDS space, where a high r^2 indicates that sites with similar communities also tend to have similar habitat conditions.

We ran two distance-based redundancy analyses (dbRDAs), first conditioned on site and then month, to understand how community composition varied seasonally, after controlling for broad spatial differences and spatially, after controlling for broad seasonal differences. While NMDS allowed us to see dominant patterns across the whole dataset, with dbRDA we could explore the proportion of total variation either explained by strictly spatial or strictly seasonal patterns in community composition, and the primary species driving these differences. Then to relate these constrained community patterns directly to predation risk, we regressed the predation risk experienced by each prey species, as well as the overall community level predation risk, against the first two axes of each dbRDA (CAP1 and CAP2). We performed these analyses with ‘capscale’ in *vegan*.

Analysis of specific functional groups

To understand how different groups of predators might be influencing the predation risks of certain prey, we grouped our species level data into seven broader, ecologically meaningful functional groups (surfperch, silversides, crabs, diving birds, benthic fish [gobies and sculpins], pipefish, and rockfish). We then calculated Pearson correlations between encounter rate of each functional group, the predation risk of each prey species and the aggregate community-level predation risk.

Because a few main groups (surfperch, silversides, and diving birds) drove separation of communities in our ordinations (see Results), we focused our subsequent analysis of how these predator groups may be driving the seasonal and spatial patterns we observed in both the predator community and

the predation risk data. We focused our analysis on the seasonal relationship between diving birds and surfperch, and the subsequent impact on predation risk for each prey species. In our community analyses, the winter months (December, January, and March) were characterized by the arrival of migratory waterfowl, and a corresponding decrease in surfperch encounter rate. To test if the diving birds were associated with lower surfperch encounter rates and potentially playing a role in this shift in the fish community, we fit a Bayesian negative binomial mixed model using ‘brm’ in *brms* (Bürkner, 2017) on data from just these winter months (220 videos across 46 cameras). We used the number of surfperch individuals counted per video as the response, bird binary presence/absence and month as fixed effects, log(video length in minutes) as an offset to account for variation in video file duration, and camera identity as a random intercept. We fit this model at the video, rather than camera level. When a camera recorded, it split the recording into approximately 12-minute videos, as an artifact of how the files were stored. We used these video chunks within each camera as random repeated subsamples of the same tidal session, to give us more statistical power to look at these instantaneous interactions, while still accounting for the non-independence of videos from the same camera with the random intercept. In the winter, surfperch were restricted to only a subset of our sites. To ensure that the sites with no surfperch, regardless of if there were birds diving or not, were not driving the results of our model, we ran the full model again but restricted our data to only the sites with surfperch present in the winter. We then compared our results to the unrestricted model. We also tested whether eelgrass cover influenced the bird-surfperch relationship by comparing models (using leave-one-out cross-validation) with eelgrass cover added either as an additive covariate or interactive term with bird presence.

Next, we looked at how surfperch abundance related to the predation risk of each prey species, to see what cascading effects may result from these inter-predator interactions. As predation risk was measured once per site per deployment, rather than separately for each camera or video, we modeled this relationship at the deployment level. The surfperch rate data was right skewed, with many zeroes. The negative binomial modeling structure when looking at the impact of bird presence inherently accounted

for this, but here we log transformed the encounter rate data to correct for this. We calculated the log of the average surfperch abundance per minute of video for each site at each time point and then centered these values within each deployment. This controlled for overall differences in the rate of surfperch observed between deployments and allowed us to isolate a within-deployment spatial signal. We used ‘brm’ to fit Bayesian binomial mixed models with the proportion of tethers eaten as the response. Previous work has shown that these prey species are all consumed consistently at different rates across sites (Murphy & Stachowicz, 2026), so we estimated a separate intercept and slope of the surfperch effect for each prey species. We included a random intercept for deployment.

Results

Variation in predation risks and habitat metrics

Overall, we deployed and retrieved 2254 tethers across seven deployments at our six sites. Prey species varied in their average predation risk across all sites (Appendix 3: Figure S2). *Ampithoe lacertosa* was eaten at the highest rate (70.4% of all prey were consumed), *Caprella californica* had a medium level of predation risk (48.2% of prey consumed), and *Pentidotea resecata* was eaten the least (32.6% of prey consumed). Sites varied minimally in their average community-level predation risk. At all sites about 50% of all tethered prey were consumed across the year (with a minimum of 48.4% at MM and maximum of 55.8% at CC).

Sites varied in their habitat, as reported in Murphy and Stachowicz (2026). NC had the lowest seagrass cover and shoot density across the year (averages of 2% and 1.15 shoots per m²) while BL had the highest (average of 50% cover and 34.8 shoots per m²). Sites with the lowest levels of cover also tended to appear more turbid in the predator videos. Turbidity differed significantly by site (chi sq = 40.8, df = 5, p < 0.001). MM and NC were consistently more turbid than CC and MP (all pairwise p < 0.005), while BL and WP were intermediate. Turbidity also differed by month (Kruskal-Wallis: chi sq = 15.6, df = 6, p = 0.016), however, after Bonferroni corrections, only one pairwise comparison was significant:

January had higher turbidity than December ($p = 0.027$). Thus, high turbidity across sites in January likely drove this overall trend.

Predator community composition

Overall, we analyzed 178.3 hours of videos. In these videos, we observed a total of 5257 individual predators across 41 species, including 30 species of fish, six species of crabs, and five species of birds. The sampling was roughly evenly distributed across sites, with total hours of footage ranging from 21 (at MP) to 30.7 (at BL). March and May had the lowest amount of footage, due to the hard drive failure (13.6 and 3.8 hours, respectively), but there were approximately 30 hours of video for each of the remaining months.

Predator community composition differed significantly across months and sites combined (PERMANOVA: $F(11, 25) = 2.65$, $R^2 = 0.54$, $p = 0.001$; Figure 1). Month alone explained 37% of variation ($F(6, 30) = 2.93$, $p = 0.001$) while site alone was not significant ($F(5, 31) = 1.32$, $R^2 = 0.18$, $p = 0.141$). Multivariate dispersion did not differ significantly by month or site (site $p = 0.57$; month $p = 0.928$), supporting our PERMANOVA results. The NMDS ordination had a moderately high stress value of 0.104, indicating the three-dimensional ordination may not have best represented all the variation in the data, but is still interpretable. Our SIMPER analysis revealed that five species accounted for 81% of the community differences between winter and summer. Winter was characterized by lower rates of shiner perch (*Cymatogaster aggregata*) and higher rates of jacksmelts (*Atherinopsis californiensis*), topsmelts (*Atherinops affinis*), buffleheads (*Bucephala albeola*), and common loons (*Gavia immer*). Bufflehead and common loon were effectively absent in non-winter months and contributed significantly to the contrast (both $p < 0.005$).

Eelgrass percent cover and shoot density were both significantly associated with NMDS position (envfit $r^2 = 0.382$, $p = 0.001$ and $r^2 = 0.180$, $p = 0.031$, respectively), indicating that sites with similar predator communities also tended to have similar habitat conditions. However, when habitat metrics were

added as a covariate in the PERMANOVA before site and month, they only explained an additional 4% of variance in community composition (model R^2 increased from 0.54 to 0.58). Seasonal patterns remained as the dominant driver of predator community composition.

The dbRDA results complemented the NMDS findings. After controlling for site, month explained 34.5% of total variation in community composition ($F(6, 25) = 2.98$, $p = 0.001$), with the first dbRDA axis (CAP1) representing 59.6% of that constrained variation (Figure 2A). Jacksmelt and topsmelt loaded positively on CAP1 (representing the winter community; Figure 2B), while shiner perch and striped surfperch loaded negatively (representing the summer community; Figure 2B), mirroring the SIMPER results. In contrast to the nonsignificant effect of site on the unconstrained data, after controlling for month, site did explain 16.5% of remaining variation ($F(5, 25) = 1.71$, $p = 0.002$), with CAP1 representing 55.5% of the constrained spatial variation (Figure 2C). Jacksmelt and green crab (*Carcinus maenas*) loaded most strongly on the positive end of the spatial axis, while surfperch species dominated the negative end (Figure 2D).

Association of predator community composition with predation risk

Broad seasonal changes in predation risk at the community level ($r = -0.537$, $p = 0.001$) and for the two more vulnerable prey species (*Ampithoe lacertosa* and *Caprella californica*; Murphy and Stachowicz 2026) tracked broad seasonal changes in the predator communities (*A. lacertosa*: $\beta = -0.101$, $p = 0.010$, $R^2 = 0.18$; *C. californica*: $\beta = -0.132$, $p < 0.001$, $R^2 = 0.35$). However, when we controlled for seasonal differences in community composition, there were no clear relationships between spatial patterns in community structure and predation risk for any species (*A. lacertosa*: $\beta = -0.049$, $p = 0.211$, $R^2 = 0.049$; *C. californica*: $\beta = -0.054$, $p = 0.134$, $R^2 = 0.071$; *P. resecata*: $\beta = 0.052$, $p = 0.130$, $R^2 = 0.081$). In contrast, when controlling for spatial differences in community composition, the seasonal signal remained a strong predictor of predation risk at the community level ($r = -0.537$, $p = 0.001$) and for the two more vulnerable prey species (*A. lacertosa*: $\beta = -0.101$, $p = 0.010$, $R^2 = 0.18$; *C. californica*: $\beta = -0.132$, $p < 0.001$, $R^2 = 0.35$).

Predator functional groups

Surfperch were the most frequently observed predator functional group (mean 14.8 individuals per hour, present in 65% of deployment x site combinations), followed by silversides, which include smelt (9.75 per hour, 70%) and crabs (2.00 per hour, 81%). More surfperch per hour were correlated with higher predation risk for *Ampithoe lacertosa* ($r = 0.375$, $df = 35$, $p = 0.022$), *Caprella californica* ($r = 0.351$, $df = 35$, $p = 0.033$), and the aggregate prey community ($r = 0.403$, $df = 35$, $p = 0.013$). More crabs observed per hour were correlated with increased community-level predation ($r = 0.369$, $df = 35$, $p = 0.025$), but no other functional groups showed any correlations with measures of predation risk.

Trophic cascade (birds, surfperch, and epifaunal predation risk)

Bird observations were relatively rare, even in winter videos during following the seasonal migration of ducks to the area. We observed birds in 42 of the 220 total winter videos, and 22 out of the 46 cameras had videos both with and without birds in them, with an average of 2 out of 6 videos with birds present per camera. We only observed surfperch in 1 of the 42 videos where birds were present, and 27 of the 28 videos with surfperch contained no birds. Our model results are likely being driven by this near total temporal separation of bird and surfperch observations within cameras.

When looking at just videos in the winter, bird presence was correlated with fewer surfperch of all species (median IRR: 0.22; 95% CrI: 0.038-0.913; posterior $P(\text{bird effect} < 0) = 0.98$; Figure 3). In videos in which diving birds were present, the rate of surfperch observed was 78% lower than videos from the same camera with no birds. This effect did not change when eelgrass cover was added as a covariate (posterior $P(\text{bird effect} < 0) = 0.975$, median IRR = 0.26, 95% CrI: 0.059–0.992). Furthermore, when we restricted our analysis to only sites with surfperch present in the winter (CC, BL and WP), we found nearly identical results (median IRR: 0.21; 95% CrI: 0.039-0.851; posterior $P(\text{bird effect} < 0) = 0.986$). The wide credible intervals on these predictions indicate that while it is clear that more birds are

associated with fewer surfperch in our data, the magnitude of this effect is uncertain, likely due to limited within-camera variation in bird presence across the winter deployments.

We also explored whether the amount of eelgrass cover at a site mediated this relationship. Model comparison showed some support for an interaction between eelgrass cover and bird presence in terms of their effect on surfperch (ΔELPD vs next best model = 4.1, $\text{SE} = 2.4$), suggesting that the negative effect of birds on surfperch observation rate may be stronger at higher cover sites (posterior $P(\text{interaction} < 0) = 0.983$, median coefficient = -1.70, 95% CrI: -3.68 to -0.11). When looking at surfperch rates across sites in the summer months, the site with the least seagrass (NC, 6.8% cover) had the highest surfperch observation rate (56.4 individuals per hour), while the site with the most seagrass (BL, 39.4% cover) had far fewer (13.4 per hour). However, in winter this pattern reversed - surfperch were essentially absent at low-cover sites (MM, MP, and NC all had 0 individuals per hour) and were only observed at the two highest-cover sites, CC (5.36 per hour) and BL (0.51 per hour). Thus, this finding that birds have a stronger effect on surfperch observation rate in the winter at higher habitat sites is likely being driven by a lack of surfperch at low habitat sites during this time of year due to changing seasonal habitat selection.

Surfperch encounter rate was a strong positive predictor of predation risk for two of the three prey species (Figure 3, Figure 4). The Bayesian model estimated a positive surfperch effect for both *A. lacertosa* (posterior $P(\text{surfperch effect} > 0) > 0.99$; median log-odds = 0.22; 95% CrI: 0.09–0.35) and *C. californica* (posterior $P(\text{surfperch effect} > 0) > 0.99$; median log-odds = 0.21; 95% CrI: 0.10–0.31), but not *P. resecata* (median log-odds = -0.05; 95% CrI: -0.16 to 0.06; Figure 4).

Discussion

Predator communities were more variable across seasons than sites (Figures 1 & 2), and broad seasonal shifts in communities correlated with declines in predation risk across the region. When controlling for these seasonal differences, sites were relatively homogeneous in their predator communities (Figures 1 & 2), despite differences in the available habitat and measured predation risk

across sites. However, variation in the most commonly observed predator group (surfperch) did relate to both seasonal and spatial variation in predation risk, suggesting that key predators may be more informative than overall community composition when predicting predation risk in this system. We propose that a behavioral trophic cascade may be the mechanism linking surfperch to both seasonal and spatial variation in predation risk.

Seasonal increases in predation risk occurred in the late summer, during which the predator communities across the region we sampled were dominated by surfperch. We identified ten surfperch species overall, most frequently observing shiner perch (*Cymatogaster aggregata*), and as a group they had both the greatest encounter rates and correlations with predation risk. Predation risk started to decrease in the fall, at which point the predator communities shifted and were instead defined by increases in smelt and diving birds. Across both seasons and sites within the same season, when diving birds were present in a video there were many fewer surfperch observed. Consequently, when there were fewer surfperch observed, the predation risk on the two most vulnerable prey species, *Ampithoe lacertosa* and *Caprella californica*, was lower. Many species of surfperch are year-round residents in coastal eelgrass beds, but older adults move into deeper waters seasonally during the fall and winter, potentially to mate or search for more abundant prey (C. Gross et al., 2019; Koval et al., 2025; Ruesink et al., 2019). Smaller, younger fish face high predation risk themselves, and so staying in structured habitat, such as an eelgrass bed, provides them protection against visual predators like larger fish (Ebeling & Laur, 1985). While this seasonal shift in surfperch habitat use is well documented, the proximate mechanism driving it remains unclear. We propose that migratory diving birds may play a role.

Many diving bird species commonly feed on surfperch throughout the year (Ainley et al., 1996; Barr, 1996; Good et al., 2022), and excluding wading birds like herons from eelgrass patches has been shown to trigger a trophic cascade through reduced fish predation on epifauna (Huang et al., 2015). However, some of the most common bird species that we observed do not feed readily on fish (e.g., bufflehead, common goldeneye, surf scoters; Eadie and Keast 1982, Gammonley and Heitmeyer 1990,

Anderson et al. 2008). Surfperch may leave areas where diving birds are present in response to perceived predation risk caused by splashing from dives, even if those birds rarely consume them directly. For juvenile surfperch, the structural complexity of eelgrass may provide sufficient refuge from larger fish predators (Ebeling & Laur, 1985). However, for the larger bodied adults, the relatively thin eelgrass blades may not hide the surfperch from predators scanning from above the surface of the water, making deeper water, out of the striking distance of a diving bird, a more effective refuge during the winter months.

The influence of habitat structure on the bird-surfperch relationship adds nuance to this hypothesis. We found that in the winter, birds had a larger effect on the abundance of surfperch at sites with more eelgrass cover. However, this appears to be driven by a broader seasonal shift in surfperch habitat selection, rather than by a direct effect of habitat cover on bird-surfperch interactions. In the summer, surfperch were present across all sites but were observed at higher rates at low cover sites. This is possibly due to the larger adults foraging through more of the region, while mitigating their own predation risk by traveling in schools through less protected unvegetated areas, inflating our encounter rates in these areas. In the winter, however, surfperch were only observed at the highest cover sites. This may be reflective of the large proportion of juvenile fish in the winter community, which rely more heavily on structural refuge from predators (Domke et al., 2026; Hughes et al., 2002). Turbidity may further influence surfperch winter habitat selection. The sites with the least eelgrass cover also had the highest turbidity in winter, likely due to reduced eelgrass across the whole region and increased storms resulting in higher sedimentation (Bromirski et al., 2003). Since surfperch are visual predators (Cummings & Partridge, 2001), low visibility at unvegetated sites may make foraging there less successful, regardless of bird presence, further restricting winter surfperch to the few high cover sites. With juveniles concentrated at the high cover sites in the winter, birds also moving to denser eelgrass beds to forage would impact a disproportionately high share of the surfperch population, producing the strong bird effect we observed both at those sites and throughout the entire region.

An alternative explanation for this negative association between birds and surfperch is competition for shared resources, rather than fear. In eelgrass, both surfperch and small diving ducks feed on small invertebrates (like amphipods and isopods; Vermeer 1982, Carr and Boyer 2014). Perhaps the seeming avoidance of surfperch to the ducks is due to spatial partitioning of prey resources. Birds arrive at a time of eelgrass senescence and decreased epifaunal prey abundance (Ha & Williams, 2018), so maybe in response to increased competition for limited resources, the surfperch move to deeper waters following prey availability. In an algal dominated rocky habitat, two surfperch species (*Embiotoca lateralis* and *Embiotoca jacksoni*) were shown to partition depth in the winter due to seasonal food scarcity, so this is a known response to competition in this group (Schmitt & Holbrook, 1986). Furthermore, it has been hypothesized that one of the same duck species we observed in our videos (goldeneyes) compete with lake fish for food resources, resulting in a lack of spatial overlap between birds and fish in those systems as well (Eadie & Keast, 1982; Eriksson, 1979). Thus, while we see a clear negative relationship between bird presence and surfperch abundance, understanding the mechanism driving this interaction requires further study.

Our choice of sampling methods may have influenced our results. We chose to use unbaited remote video cameras to monitor the predators in our system as they are relatively noninvasive compared to other methods (such as trawl or seine nets, diver surveys, or baited cameras; Murphy and Jenkins 2010) and thus we felt that they would give us the best idea of what predators had the opportunity to consume our tethered prey and increase our measured predation risk. While the strengths of this method include minimal disturbance of the predators and the ability to observe species and behaviors we may not have with other techniques (such as diving birds feeding in the eelgrass), it also may have biased which species we were best able to sample. In terms of species richness, video surveys have been shown to capture a large portion of the community compared to other methods (e.g., observed more mobile species swimming above the seagrass canopy than trawl nets: French et al. 2021; and oversampled benthic species relative to seine nets: Gross et al. 2018). However, our encounter rate data was likely higher for

more mobile species than sedentary ones as a more mobile species can swim by the camera multiple times within a single video. We measured abundance like this by choice, as each new pass by our cameras represented a new opportunity for the predator to decide to eat one of our tethered prey. However, we recognize that this sampling design may have minimized the potential importance of sit and wait predators in this system.

We found that while overall predator community composition was not a strong predictor of predation risk, the encounter rate of a single functionally important group (surfperch) was strongly correlated with both seasonal and spatial variation in predation risk. Shifts in surfperch encounter rates, potentially mediated by diving bird presence, appear to be the primary driver of the predation risk patterns we observed, while the remainder of the community varied in ways that were disconnected from our observed predation risk. Identifying this required sampling across both seasons and sites simultaneously. Had we sampled at a single timepoint or site, the role of habitat cover in mediating the relationship between surfperch and predation risk would have been overshadowed by broad seasonal community patterns. We suggest that predation risk may depend less on overall community composition and more on key predators whose behavior, and thus the risk they impose, shifts with environmental contexts in ways that whole community metrics may obscure.

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Figures

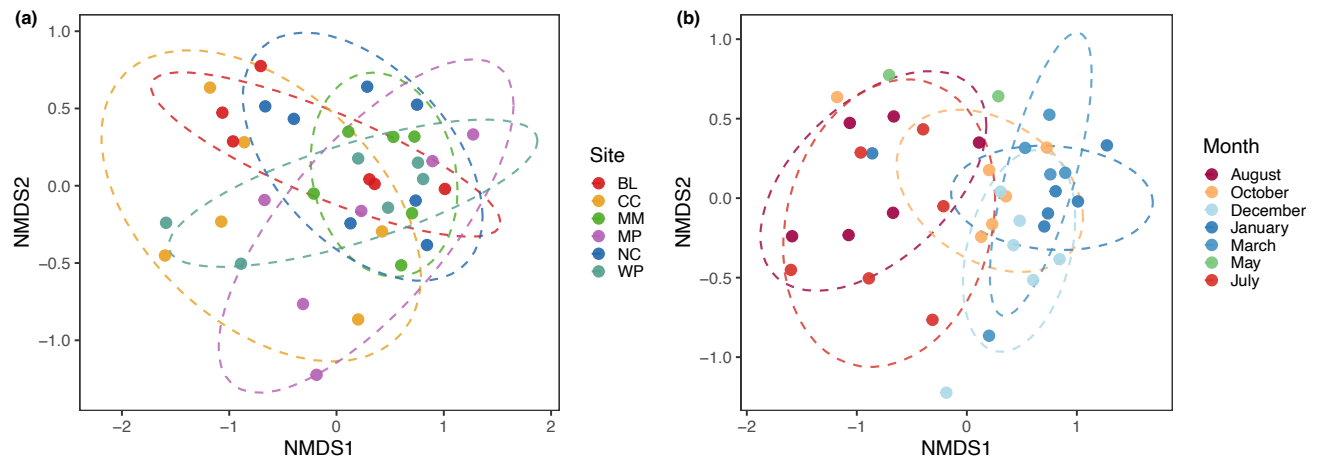


Figure 1. Non-metric multidimensional scaling shows that the predator communities did not clearly cluster by site (a) but did group by season (b). Each point represents the predator community observed at a specific site and time. The number of predators in each species was scaled by the total length of video recorded in that sampling. The data were Hellinger transformed and distances between communities were calculated as Bray-Curtis distances.

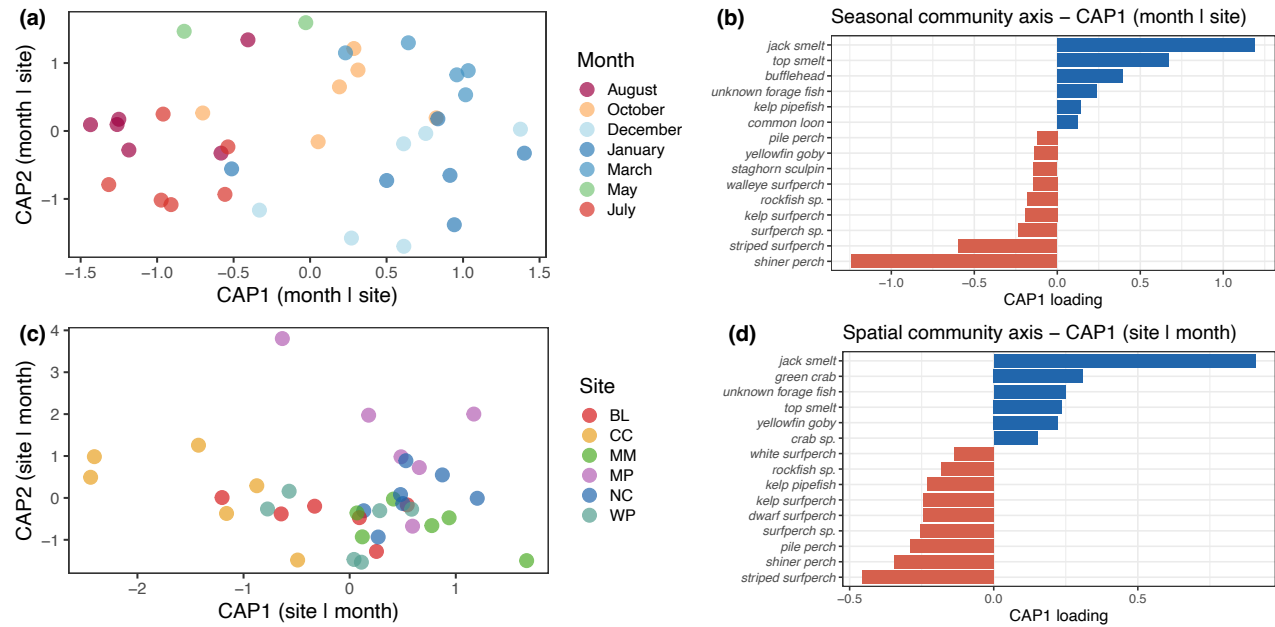


Figure 2. Distance-based redundancy analyses (dbRDAs) showing predator communities grouping by month, while controlling for spatial differences (a) and by site, and while controlling for seasonal differences (c), and the loadings on the first axes for each of these constrained analyses for the 15 most important predator species in driving this separation (b, d).

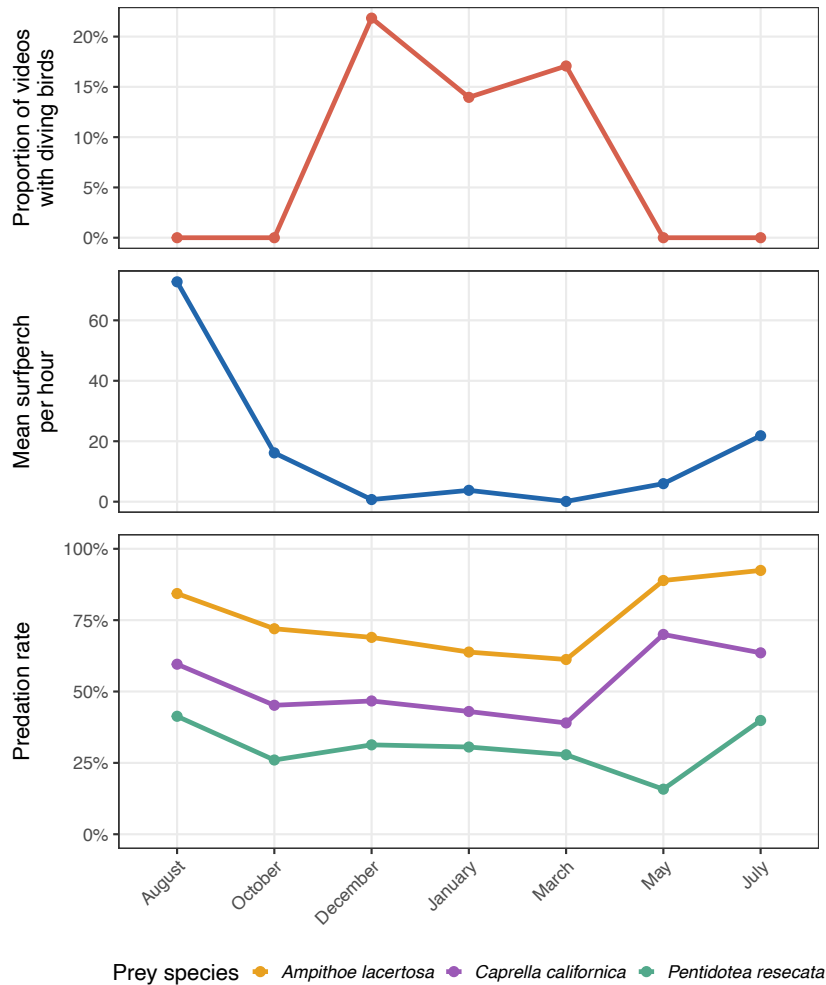


Figure 3. Timeseries data showing the proportion of videos with diving birds in them, the average surfperch per hour, and the predation risk on each of the 3 prey species, all averaged across all the sites. As the proportion of videos with diving birds starts to increase, the average number of surfperch observed per hour decreases, and the measured predation risk for *Ampithoe lacertosa* and *Caprella californica*, the two more vulnerable prey species, starts to decrease. When diving birds are absent from the videos again, the rate of observed surfperch and the predation risks all start to rise again. While surfperch rates start to decline slightly before the birds appear, this may be due to our videos missing rarer bird encounters as they first enter the region.

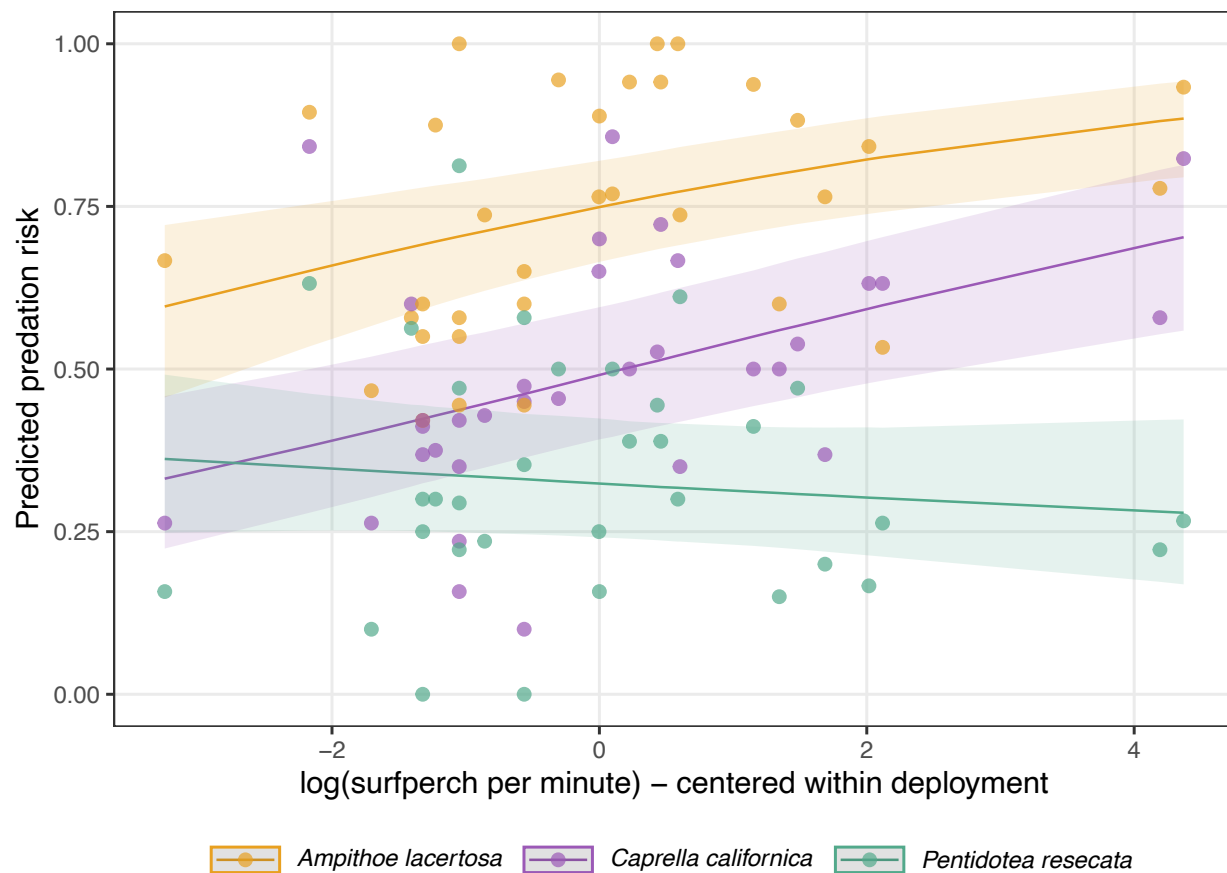


Figure 4. Model predictions of predation risk for each of the three prey species, predicted by the log of the rate of surfperch present, centered around each deployment. Our observed data are represented by the points. *Ampithoe lacertosa* and *Caprella californica* are predicted to have higher predation risks at sites with a higher surfperch encounter rate than the average for that deployment, while *Pentidotea resecata* predation risk shows no relationship with surfperch rate.

APPENDIX 1: Chapter 1 Supplementary Material

Additional abundance methods justification:

Similar timed surveys are commonly used to estimate abundance in other systems with patchily distributed or highly mobile animals (e.g., pollinators: Kadlec et al. 2012, Barkmann et al. 2023, birds: Buckland 2006, camera trapping methods: Gilbert et al. 2021). Furthermore, alternative methods used for epifaunal communities (e.g, grab bags: Virnstein and Howard 1987) involve destructive sampling of habitat, and given the frequency with which we wanted to collect data, this would have decreased habitat density and potentially altered our estimates of predation risk.

Additionally, sampling continuously along a transect increased the chance that both high- and low-density patches of prey items would be proportionally included in the final abundance measure, which may be less likely with smaller numbers of destructive samples that cover a smaller area more intensively. Timed surveys potentially result in a negative correlation between habitat density and area surveyed, which means that our abundance measurements are not strictly measurements of prey density but do represent a sense of relative population sizes between sites and dates. During surveys in high habitat density area, we likely undercounted the number of prey, however, we still counted more prey in high eelgrass density sites than in places with lower eelgrass density. Previously, we have shown that the rank order of these sites in terms of their habitat amounts is relatively stable across the calendar year (Murphy & Stachowicz, in press). Thus, even if more area was covered within low density sites, this bias should have been consistent within a site across the year, resulting in accurate temporal trends in relative abundance, which is what we ran our analyses on. Furthermore, our unscaled abundance data is

relatively consistent across weeks for each specific species at each site (Appendix 1: Figure S1), suggesting that we were able to consistently sample prey abundances across different surveys.

Univariate statistical analysis

We compared our FDA approach to a univariate alternative focused on the same question, to understand what additional information our FDA approach was allowing us to capture. To explore how the timing of predation risk and abundance differed by species, we calculated the time lag between each species-site combination's peak predation risk and peak abundance. We identified peaks as the day of maximum value from the fitted GAM predictions for each species-site combination and then calculated lags as the difference in days between the abundance peak and the predation peak. Negative values indicated that abundance peaked before predation risk while positive values indicated that abundance peaked after. We then tested whether lags differed among prey species using a one-way ANOVA with Tukey's HSD post-hoc test. Species did not differ statistically in how these univariate temporal patterns of abundance and predation risk were related (ANOVA: $F_{2,12} = 0.76$, $p = 0.49$; Appendix 1: Figure S4). However, the general patterns recovered in the FPCA analyses were reflected in this coarser approach, as caprellids peaked in abundance 18 days before peak predation risk (SE = 43.8 days), while amphipods and isopods peaked after, by 25.8 (SE = 50.5) and 67.2 (SE = 52.3) days respectively.

Video S1. A shiner perch (*Cymatogaster aggregate*) can be seen eating a tethered *Ampithoe valida* before swimming off at a site with a high amount of eelgrass cover (Blake's Landing).

Video was taken by Claire Murphy.

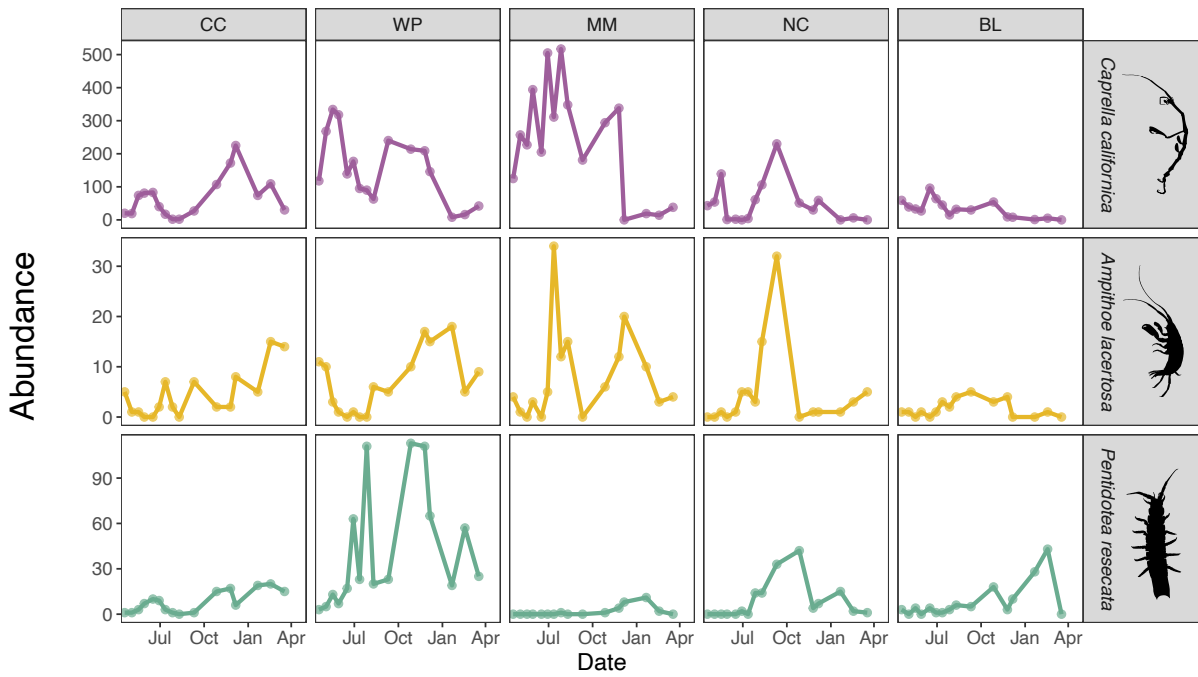


Figure S1. The unscaled abundance for each species at each site across the year. Each column represents a site, and each row represents a species. Note the different y-axis scales for each of the species.

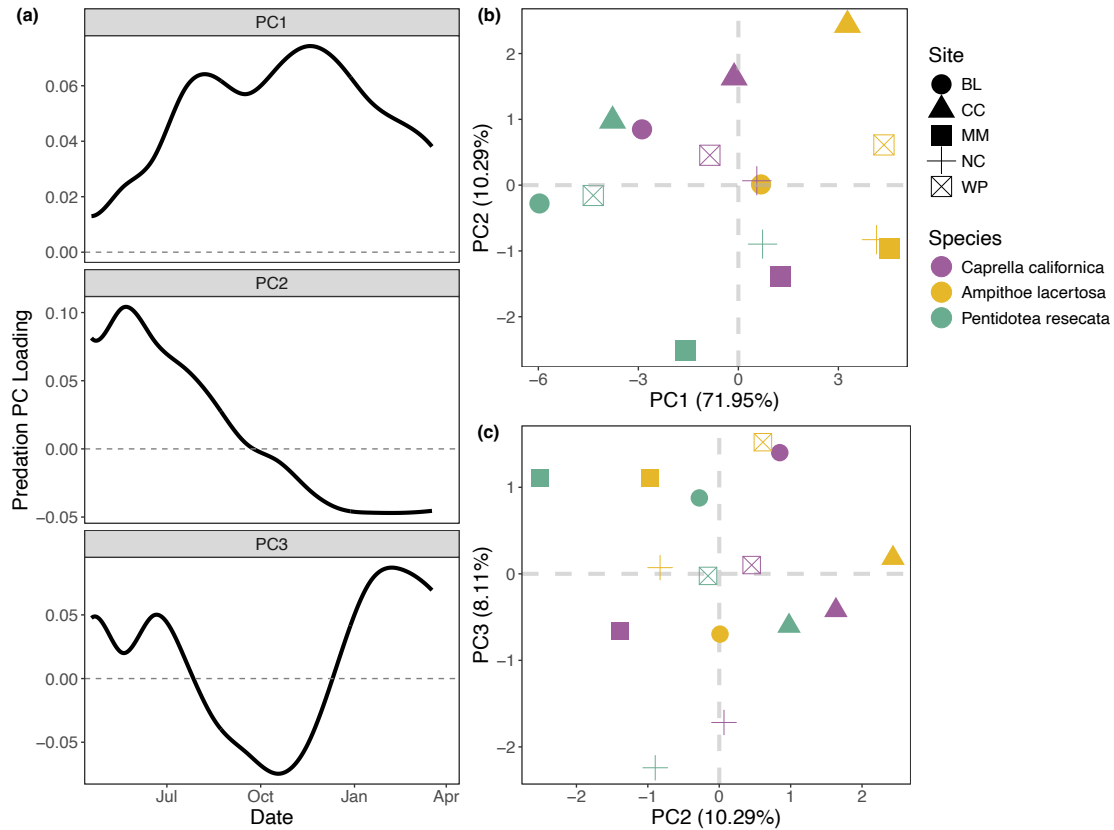


Figure S2. The left panel (a) shows the loadings for all 3 axes of the predation FPCA. Panel (b) shows the scores of PC1 plotted against the score of PC2, while panel (c) shows the scores of PC2 plotted vs the scores of PC3. PC1 explains the most variation in the predation risk data (71.95%) and describes variation in the magnitude of the peak of predation risk. PC2 explains 10.29% of the variation in the data and seems to describe variation in the timing of peak of predation risk. PC3 explains an additional 8.11% of the variation in the data.

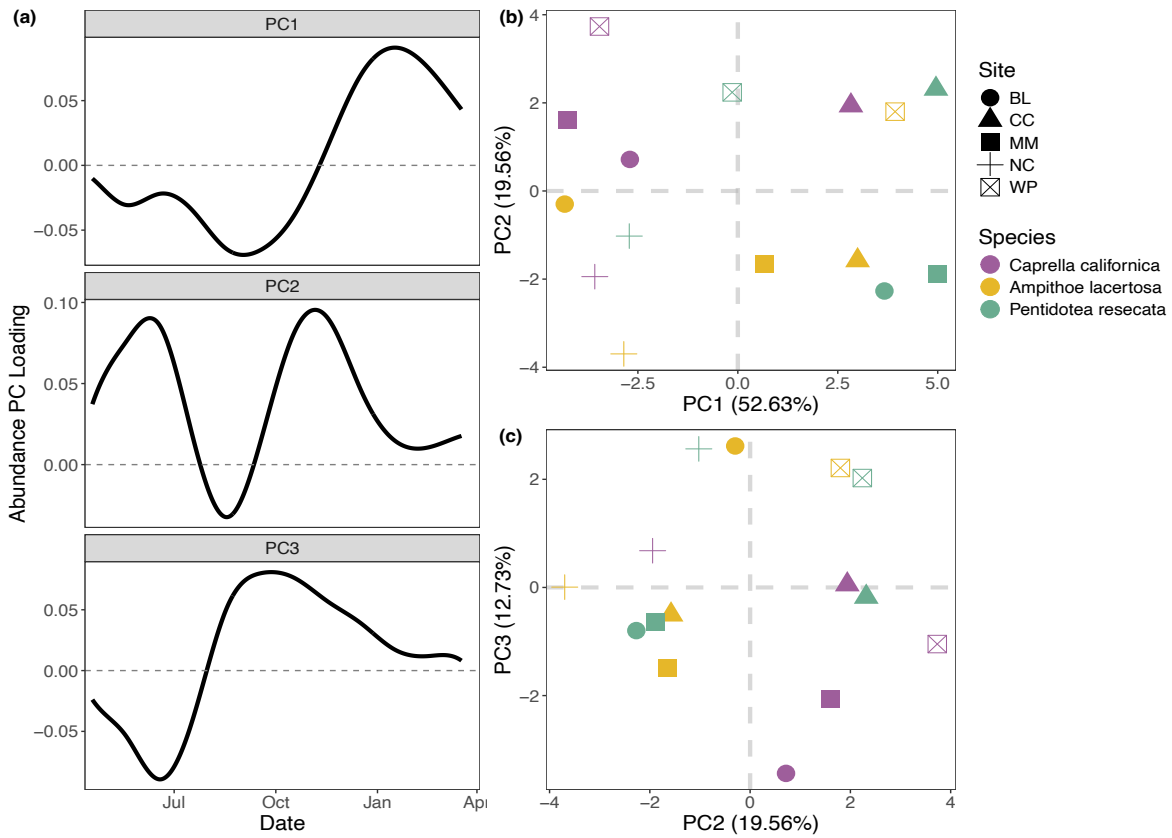


Figure S3. The left panel (a) shows the loadings for all 3 axes of the scaled abundance FPCA. Panel (b) shows the scores of PC1 plotted against the score of PC2, while panel (c) shows the scores of PC2 plotted vs the scores of PC3. PC1 explains the most variation in the scaled abundance data (52.63%) and describes the majority of the variation in the timing of the peak of abundance. PC2 and PC3 explain an additional 19.56% and 12.73% of the variation in the data, respectively. Both axes seem to relate to timing of abundance peaks as well.

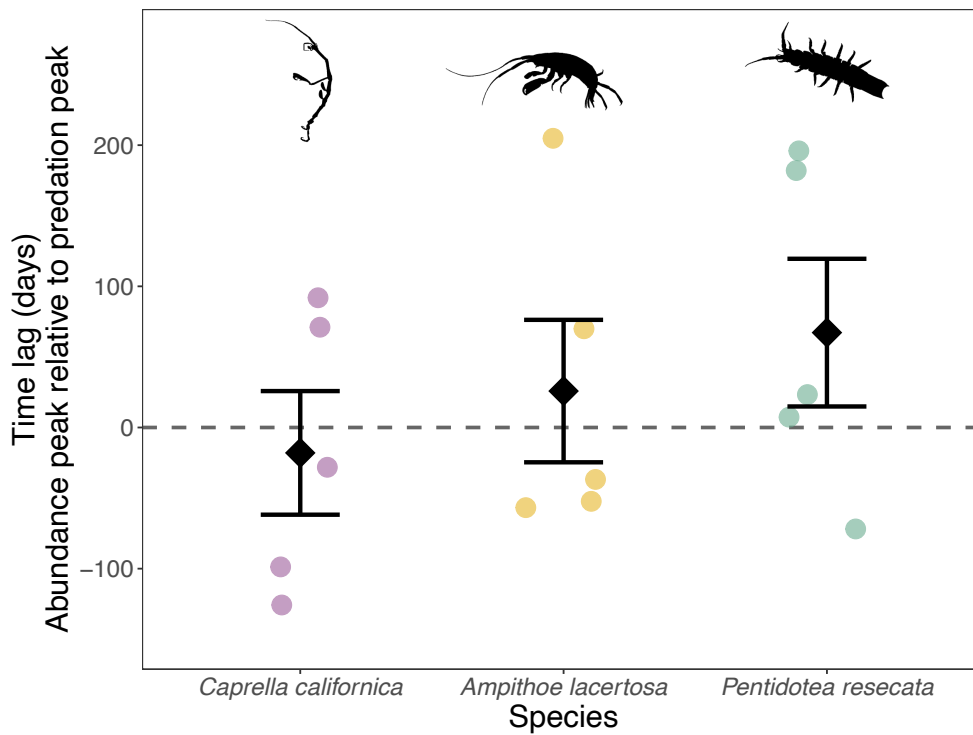


Figure S4. The univariate version of our analysis – comparing the difference in the timing of peak abundance and peak predation risk for each of our three prey species. Similar patterns are roughly observed as from our FDA analysis, but differences between the species are not significant and information about the variation in the magnitude of predation risk is lost.

APPENDIX 2: Chapter 2 Supplementary Material

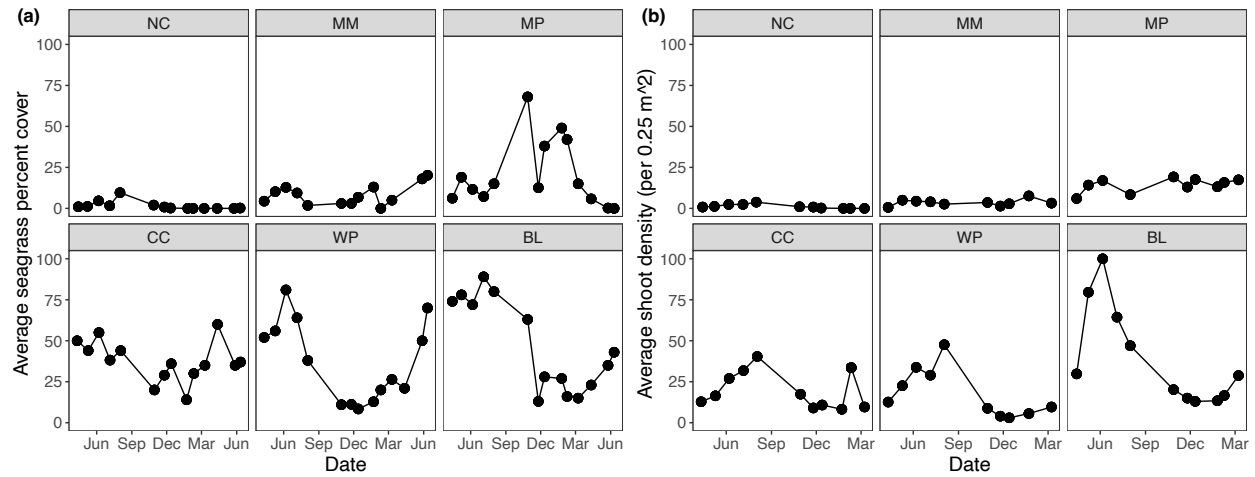


Figure S1. The average seagrass percent cover (a) and shoot density per 0.25 m² (b) across the year at each of the six sites, represented by the six boxes in each panel. Sites are represented by abbreviations.

Full site names are NC = Nick's Cove (38.203614, -122.926317), MM = Mason's Marina (38.333867, -123.059485), MP = Millerton Point (38.104536, -122.845707), CC = Campbell Cove (38.309971, -123.056176), WP = Westside Park (38.320690, -123.053746), and BL = Blake's Landing (38.178462, -122.909039).

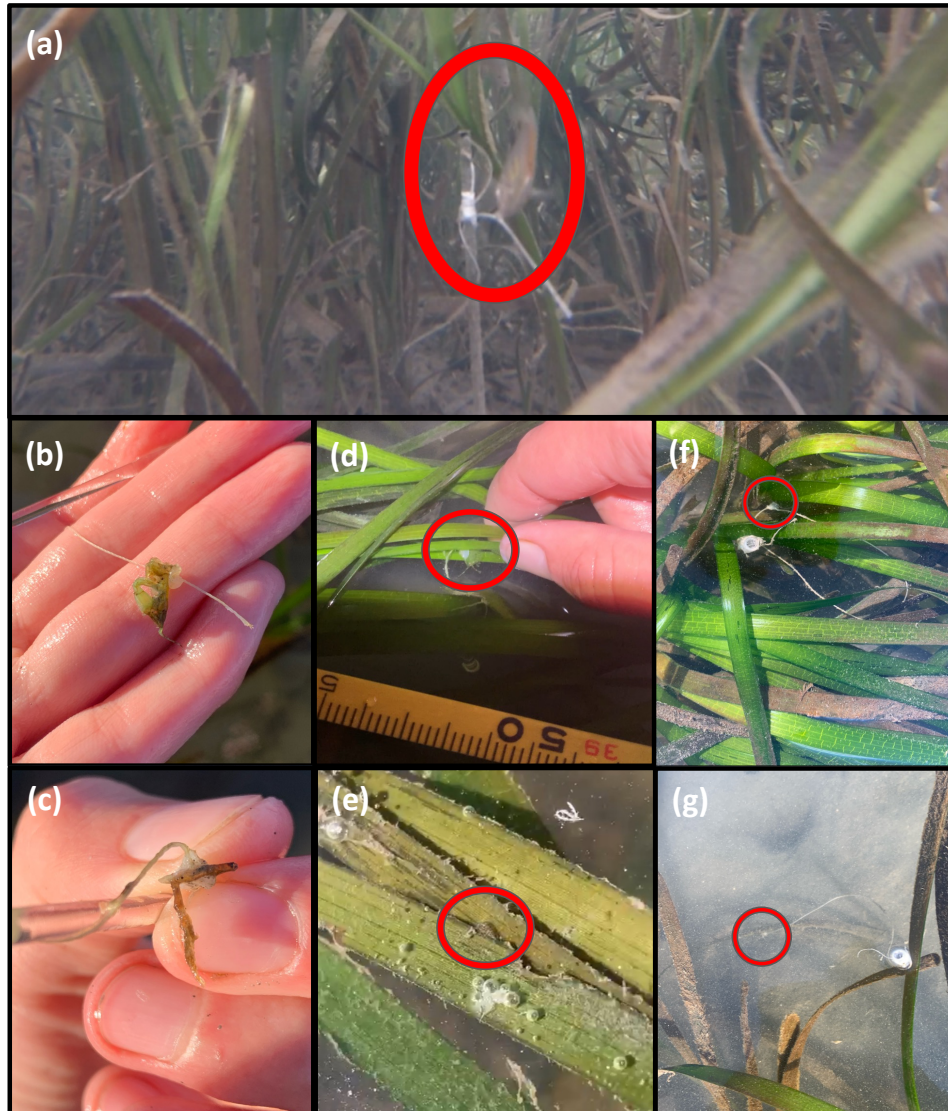


Figure S2. Various pictures from the field giving support to our conclusions that tethering assays measure the relative predation risks of our four species. These photos show shows a juvenile surf perch consuming a tethered *A. valida*, which is a still from Video S1 (a); partially consumed *A. lacertosa* and *C. californica* (b & c); a tethered amphipod using blades of eelgrass to create a protective tube (d) in the same manner as an untethered amphipod (e), both of which are circled in red; and tethered isopods (circled in red) finding eelgrass blades to cling to and hide on in both high and low habitat environments (f & g). Together these images show that tethered individuals can exhibit normal behaviors, and missing individuals at retrieval are likely removed due to predation. All photos by Claire E. Murphy.

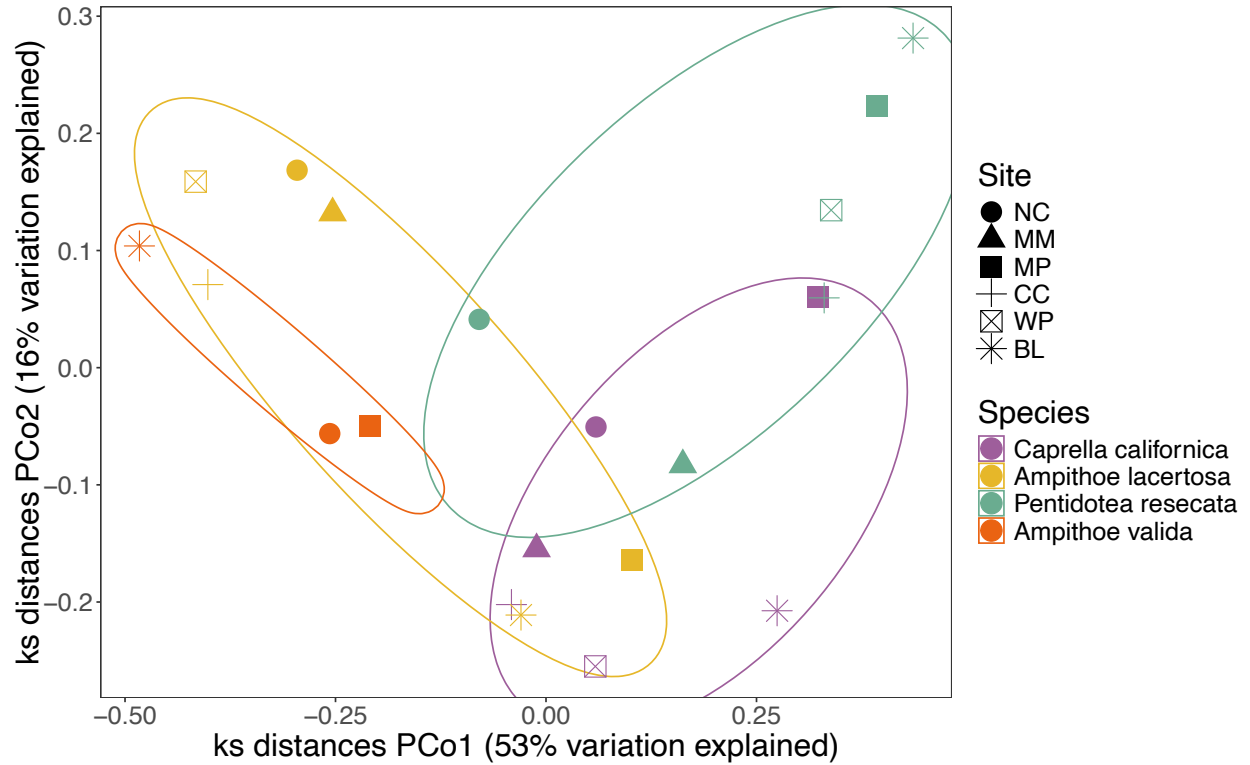


Figure S3. Each species by site predation pattern plotted in Kolmogorov-Smirnov (KS) multivariate space group more by species identity than by site. Each point represents a distribution of predation risk across the year (e.g., one of the colored lines in Fig. 2A) for each species (represented by colors) at every site (represented by shapes). The distance between two points correlates to how similar those two distributions are (e.g., the similarity of the shapes of two different colored lines in Fig. 2A).

APPENDIX 3: Chapter 3 Supplementary Material

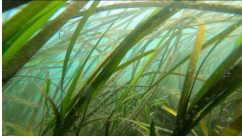
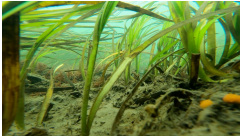
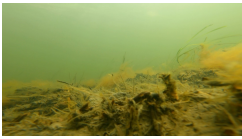
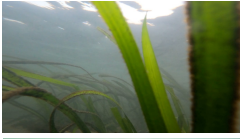
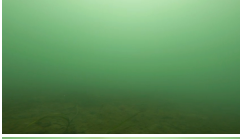
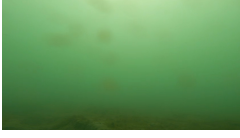
Relative turbidity level	Example videos			
0		CC in October		MP in December
		MP in August		CC in March
		BL in December		WP in December
		MM in December		BL in January
		BL in January		NC in December

Figure S1. Stills from videos depicting the clarity found at each qualitative level of relative turbidity. Field testing showed that level 0 resulted in a view of up to 3 m from the camera, while at level 4 the visibility was only approximately 30 cm. Each video's turbidity level was scored by two independent observers to standardize scores across videos. Full site names are CC = Campbell Cove (38.309971, -123.056176), WP = Westside Park (38.320690, -123.053746), MM = Mason's Marina (38.333867, -123.059485), NC = Nick's Cove (38.203614, -122.926317), BL = Blake's Landing (38.178462, -122.909039), and MP = Millerton Point (38.104536, -122.845707).

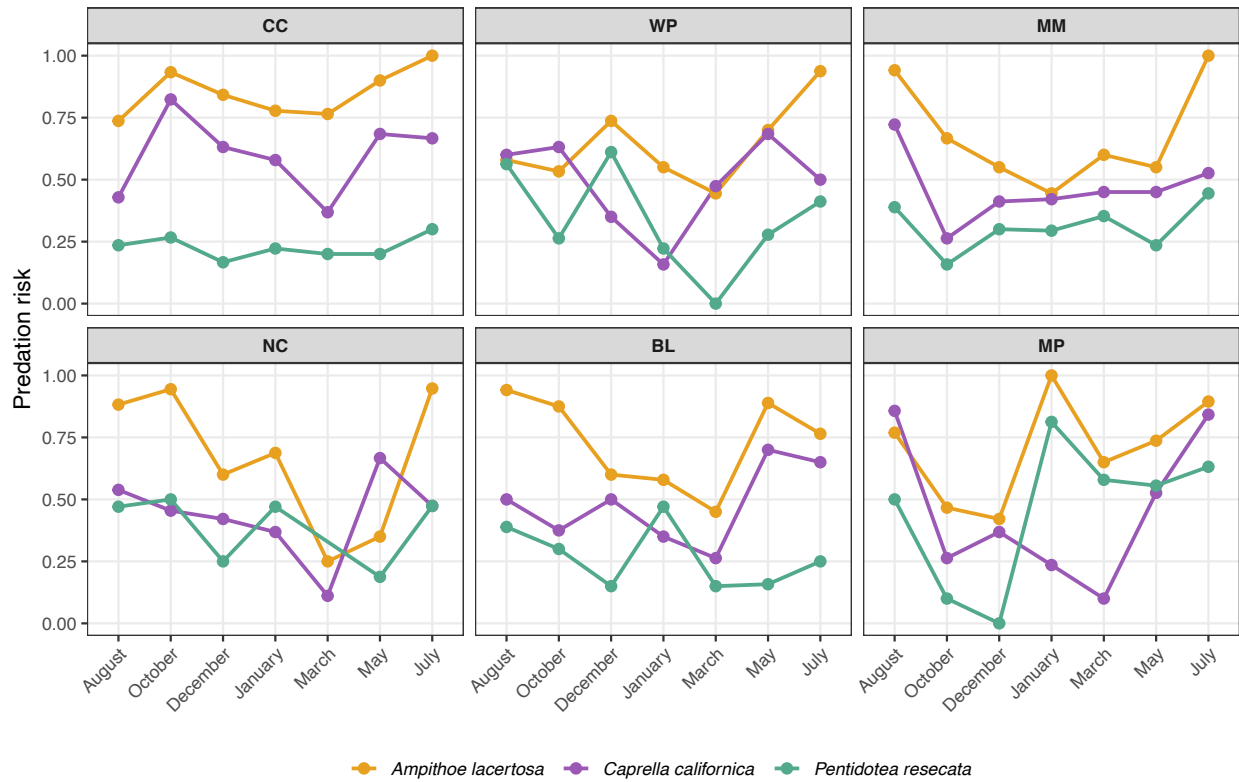


Figure S2. The predation risk each prey species experienced throughout the year, at each site. A value of 1 means all the tethers at that time point and site were eaten after 24 hours, while a value of 0 means none of them were.