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Scale and the guild functional response: Density-dependent predation varies with plot size

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ABSTRACT

The predator functional response is an important mechanism determining the persistence of prey species; however, little is known about the effects of spatial scale on the functional response. We used a manipulative field experiment to quantify the effects of plot size on the guild functional response on the clam *Mercenaria mercenaria*, replicating the experiment in the summer in Chesapeake Bay, Virginia, and in the spring and fall in Indian River Lagoon, Florida, to examine the effects of predator and alternative prey abundance. In Virginia, the predation rate increased with both patch size and predator density, and was described by a modified sigmoid Type III functional response model that incorporated the effects of patch size. In Florida in the spring, the predator functional response was a Type III and did not vary with plot size, but in the fall it was a linear Type I at small plot sizes, and a Type III at a larger plot size. We hypothesize that the difference is primarily driven by changes in predator abundance and species between sites. In showing that the functional response can vary with plot size and season, our results indicate that small-scale experiments do not always scale up spatially or temporally. We suggest that the predictive power of such experiments may be limited by the complexity of the food web.

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1. Introduction

The predator functional response (Hassell et al., 1977; Holling, 1959), how predation rates vary with prey density, is a key mechanism in determining the persistence of prey species (e.g., Seitz et al., 2001). The predator functional response can be modified by the presence and density of alternative prey (Colton, 1987), predator density (Tschanz et al., 2007) and identity (Chase et al., 2001), and habitat differences (Seitz et al., 2001). Although functional response models are well described, integrating the effect of scale on the functional response is difficult. Plot size (e.g., Chase et al., 2001; Santos et al., 2009; Wellenreuther and Connell, 2002; Whitlatch et al., 1997), plot spacing (e.g., Vahl et al., 2007; Hines et al., 2009), fractal dimension (Pitt and Ritchie, 2002), and study extent (e.g., Forrester and Steele, 2004) can all affect predation rates, but we are not aware of any study that has explicitly examined the effect of plot size on the functional response in the field.

The spatial arrangement of prey can affect predation rates by several means. Patches of prey can attract predators (i.e. the predator aggregative response), leading to higher predation rates (Wellenreuther and Connell, 2002), but a local increase in predator density can lead to an increase in antagonistic interactions and a decrease in predation rate (Clark et al., 1999). The relative importance of predator aggregation and antagonism can vary with spatial scale (Hines et al., 2009). Also, predator foraging strategies can favor either more or less patchily distributed prey, leading to different effects of patchiness with different predator species (Chase et al., 2001).

Small scale laboratory or field experiments, where highly controlled environments allow for detailed observations of behavior (e.g. Clark et al., 1999; Eggleston et al., 1992), can be used to define the predator functional and aggregative responses, and these responses can integrate up to population level effect in field experiments where predator behavior often cannot be directly observed (e.g. Seitz et al., 2001), however this is not always the case (Kuhlmann and Hines, 2005). In some cases where predator behavior can be observed or inferred, as in rays feeding on bivalves where their excavation pits provide a direct measure of predator behavior (Hines et al., 1997), field studies can directly confirm or refute predictions based on such models. Additionally, examining patterns at an appropriately small scale (Whitlatch et al., 1997), as well as at a larger scale (Thrush et al., 1997) can assist in extending these patterns into environments and at scales where inferences about behavior are much less certain.

In this study, we determined the effect of prey patch size on the predator-guild functional response (sensu Seitz et al., 2001), which is a combination of the predator functional response and the aggregative response. We used bivalve prey in soft sediment as an ideal system for isolating the effects of plot size. The prey were arranged in a relatively unstructured, 2-dimensional habitat, which removes many of the complicating factors of structure (e.g., Forrester and Steele, 2004), such as

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reefs, seagrass beds, or plants that may correlate with prey patches (e.g., Hovel and Lipcius, 2001). We replicated the experiment in space and time in areas that differed in prey and predator abundance and diversity to see if the results would scale up in space or time. Further, by contrasting the guild functional responses in a relatively simple food web, with that in a more complex one, we were able to examine how useful simple models of predator–prey interaction based on paired-species interactions in predicting field predation rates (e.g. Hines et al., 1997, 2009).

2. Materials and methods

This study was performed in two widely separated locations: Onancock Creek (37° 43.1′N, 75° 48.4′W), Chesapeake Bay, Virginia (hereafter Virginia); and Fort Pierce (27° 27.4′N, 80° 18.6′W), Indian River Lagoon, Florida (hereafter Florida). The clam *Mercenaria mercenaria*, our prey species, is endemic to both Chesapeake Bay and the Indian River Lagoon, where it is a fishery and aquaculture species. The two sites were selected to provide a contrast in the density and diversity of both benthic predators and alternative bivalve prey. In Virginia shallowly buried bivalves are preyed upon by blue crabs (*Callinectes sapidus*), Atlantic croaker (*Micropogonias undulatus*), and possibly spot (*Leiostomus xanthurs*), all of which are mobile predators that actively seek prey patches. Low alternative prey density and diversity leads to a relatively simple food web and thus minimizes complicated interaction among prey and predator species, enabling strong inferences about the underlining behavioral mechanisms (Hines et al., 1997). In Florida, much wider diversity of predators prey upon bivalves including highly mobile fish and crustaceans as Virginia, but also less mobile predators such as gastropods. These are combined with a much larger suite of alternative prey. Such high diversity is likely to result in a complex food web with many direct and indirect effects which likely reduces the strength of inferences that are able to be drawn. Experimental plots were established in shallow, sandy habitats along the shoreline at, or slightly deeper than, the mean low-water mark. The sediment in both areas was fine sand. The Virginia sediment was completely unstructured; sparse *Halodule beaudettei* and macroalgae were present in most areas in Florida. Experiments were performed in 2008 in the spring (April–May) and fall (September–October) in Florida and in the summer (July) in Virginia.

Juvenile *Mercenaria* were obtained from local hatcheries in both Virginia and Florida to ensure that they were adapted to local conditions. The shell lengths of about 30 haphazardly chosen clams were measured for each experiment. The average shell lengths ($\pm$SD) were similar among the experiments: Virginia— 6.95 ± 0.74 mm, Florida spring— 6.22 ± 0.48 mm, Florida fall— 6.6 ± 1.59 mm. For each experiment, plots were established at four prey densities: 52 m^{-2}, 100 m^{-2}, 252 m^{-2}, and 500 m^{-2}, and at three plot sizes: 0.25 m^2, 1 m^2, and 4 m^2, in a fully crossed replicated design. Plot sizes of 0.25 and 1 m^2 are used in other field based research on clams in soft sediments (e.g. Clark et al., 1999; Hines et al., 2009) and we included 4 m^2 to extend the results beyond scales typically used in such experiments. The 1 and 4 m^2 plots were divided into 0.25 m^2 subplots and the prey were counted out for each subplot to ensure a uniform distribution of prey. We established 3–5 (4 in all but 3 cases) replicate plots at each of the plot size and prey density treatments during each experiment. Each plot was randomly assigned a treatment in a randomized block design in Florida and a fully randomized design in Virginia. It took 4 days to establish all the plots for each experiment. The 1 m^2 and 4 m^2 plots were subdivided into 0.25 m^2 subplots and the clams were counted and planted in each subplot individually to ensure a uniform density distribution of clams across each patch. Plots were at least 2 m apart; the foraging range of the likely predators in this system ranges from a couple of meters for gastropods to 100s of meters or even larger for large crabs and piscine predators. Each plot was marked with polyvinyl chloride stakes and covered with netting made of plastic mesh (mesh size ~4 × 3 mm) overnight to allow the clams a chance to acclimate. The plots were exposed to predators for ~28 days in the Florida experiments, and ~5 h in the Virginia experiment. In Virginia the experiment was run over 4 sequential days. Each day we would expose the plots established the day before to predation and during the exposure period we would establish the plots for the next day before resampling the plots that had been exposed. The plots were only exposed to predation during the day. The target experimental duration was determined by trial experiments to achieve a target average of approximately 50–70% mortality across the treatments for each site. Eight control plots were established during each experiment in order to ensure effective resampling at a plot size of 0.25 m^2 and clam density of 252 m^{-2}. These were covered with mesh for the duration of the experiment. High non-predatory mortality at some control plots during the spring Florida experiment, probably caused by plots being covered with sediment, prompted us to resample half the control plots within a few days after they were established and the other half at the end of the fall experiment. This was unnecessary in the Virginia experiments because of the short duration.

After the experimental period, plots were resampled with a suction sampler to a depth of 5–10 cm (Eggleston et al., 1992) using a bag with a 2 mm mesh size. One randomly selected subplot from the 1 m^2 plots and three from the 4 m^2 plots were resampled. Samples were brought back to the lab and stored at −20 °C before processing. Each sample was sorted to remove all bivalves. Proportional predation (clams recovered/clams planted, normalized by time exposed) was calculated for each plot. Clams recovered dead but with shells intact were counted as recovered because they represented non-predatory mortality (Long and Seitz, 2008), but these mortalities were noted separately. Ambient clams were identified to species and counted. Predators captured on the plots were also identified and counted.

Predators were also sampled with otter trawls towed at a constant speed. The Virginia trawl had a 4.8 m wide mouth and the Florida trawl had a 2.4 m mouth. Because the trawls and boats differed, the catch per unit effort (CPUE) cannot be compared between sites. Five to six 2–5 min trawls were performed during or shortly after each of the experiments near enough to the experimental plots that the mobile predators captured could have easily moved to the plots. The sediment type was similar to the area of the plots, although in Florida the trawl occasionally sampled in some seagrass beds that were immediately (within a few meters) adjacent to the plots. However, predators in the seagrass beds would be able to move to and feed in the experimental area. All species caught in the trawl were identified and the CPUE (number min^{-1}) was calculated.

Percent recovery in control plots was compared among experiments using an analysis of variance (ANOVA). In this and all other general linear models we tested the assumptions of normality with an Anderson–Darling test and homogeneity of variance with Levine's test. In cases where the data failed to meet the assumptions, a non-parametric Kruskal–Wallis (K–W) test was used. Predation rates were analyzed with an analysis of covariance (ANCOVA), with plot size fully crossed with prey density as factors, date the plots were established as a blocking factor, and alternative prey density as a covariant. Where there was a significant difference multiple comparisons were done with Fisher's least-significant difference test. We used the ANCOVA results to develop a set of functional response models to fit the data. Where there was no effect of plot size, we pooled all plot sizes and used maximum likelihood to fit the data to continuous time Type I, $P = m$, II, $P = \frac{a}{1+aT_hN}$, and III, $P = \frac{bN}{1+cN+bT_hN}$ functional response models, assuming a normal distribution of errors. P is the proportional predation rate, m is the constant predation rate, N is the density of prey, a is the attack rate, T_h is the handling time, and b and c are parameters of the attack rate in a Type III functional response (Hassell et al., 1977; Holling, 1959). Where there was a