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Predator diversity stabilizes and strengthens trophic control of a keystone grazer

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Despite the global vulnerability of predators to extinction, and the critical functional role they play in many ecosystems, there have been few realistic tests of the consequences of predator species deletion (conversely, predator diversity) in natural ecosystems. We performed a four-month field experiment in a southeastern United States salt marsh to test the role of predatory crab diversity in regulating populations of a keystone grazer that can decimate marsh vegetation at high densities. Our results revealed that a combination of this system's two resident predator species, in comparison to individual species, both stabilize and strengthen predation rates on the potent grazer. Monthly monitoring of predation rates from intense, hot summer months into the cooler autumn indicate this diversity benefit arises from predators responding differentially to changing environmental conditions across seasons. This study provides some of the first experimental field support for the insurance hypothesis from marine ecosystems, suggests that predator temporal complementarity may be more common than currently perceived, and argues for conservation of predator diversity to ensure reliable and effective control of potentially habitat-destroying grazers.

Keywords: biodiversity; insurance hypothesis; temporal complementarity

1. INTRODUCTION

Ecological theory implies that extinction of predator species, and the resulting erosion of predator species diversity, may reduce the stability [1] and strength [2] of top-down control of potentially habitat-destroying primary consumers. The applicability of this theory to real-world scenarios remains unknown, however, because most empirical tests have not been conducted in the field under natural conditions (reviewed by Schmitz [3]). This lack of experimental realism may obscure important natural phenomena and lead to underestimation of the consequences of species extinction [4]. For example, experiments in laboratory mesocosms or short-term experiments in the field do not incorporate the seasonal environmental changes that characterize the world's temperate ecosystems, precluding temporal complementarity among species

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that may often arise owing to differential thermal tolerance or peak seasonal activities (e.g. [5]).

The insurance hypothesis [1,6] states that differential responses of species to changing environmental conditions can have important benefits for the functioning of ecosystems by buffering food webs against environmental changes [7] and reducing temporal variability (thus enhancing stability) of aggregate processes. Interspecific temporal complementarity may also lead to reduced levels of competition in diverse assemblages, increasing overall rates of ecological processes, including predation [2]. The greater stability and strength of top-down control potentially provided by diverse predator assemblages is likely to be especially important in temperate communities characterized by potent grazers that, when left unchecked by predators, can increase in numbers and transform plant-dominated ecosystems to barren flats [8].

In the highly productive salt marshes of the southeastern United States, multiple coexisting predators consume the keystone, plant-grazing snail, *Littoraria irrorata*, a species that can strongly suppress growth of the dominant primary producer, salt marsh cordgrass (*Spartina alterniflora*), and drive ecosystem die-off at high densities [8]. Two species of burrowing predatory crab probably play a key functional role in the expansive intermediate *Spartina* zone of these marshes by controlling snail densities [9]. While these predators have similar body sizes, foraging modes (sit-and-wait) and space use, we hypothesized that their predation rates would respond differentially to changes in thermal conditions across seasons, based on the fact that one is predominantly tropical in its distribution while the other is predominantly temperate (the mud crab *Panopeus herpistii* extends to approximately 42.5° N, while the mangrove crab *Eurytium limosum* only extends approximately 1.3° N of our study site to 32.5° N). Using a four-month, manipulative field experiment spanning hot summer conditions to cooler autumn conditions, we monitored species-specific predation rates through time to test for temporal complementarity and impacts of combining predator species (predator diversity) on both the temporal stability and mean rate of consumption of the potent grazer, *Littoraria*.

2. MATERIAL AND METHODS

We conducted this study within the intermediate *Spartina* zone at Dean Creek; Sapelo Island, Georgia, USA (31°23' N, 81°16' W). This marsh zone is immersed by flooding tides approximately 15 per cent of the time and is the spatially dominant zone in Georgia salt marshes, comprising from 50 to 80 per cent of the marsh surface.

To test the hypotheses that predator diversity can (i) stabilize and (ii) strengthen rates of predation on the keystone grazer, *Littoraria*, we manipulated predator diversity in a field experiment over four months, from summer (15th August) until late autumn (15th December) 2009, using 1 m⁻³ galvanized wire mesh field enclosures as experimental units [8]. We used a substitutive design, establishing single-species treatments of both predators (*Panopeus* and *Eurytium* monocultures) at four individuals per square metre (ind. m⁻²), and a diverse treatment with a combination of the two predator species at equal total density (two *Panopeus* and two *Eurytium* individuals per square metre); We observed that these densities are within the natural range at the study site (5.9 ± 2.9 (mean ± s.d.) ind. m⁻²). The substitutive design tests the effect of changing species richness while holding total density constant, but has been criticized for the limited mechanistic insight it permits ([2]; electronic supplementary material 1). We therefore also included half density (2 ind. m⁻²) single-species treatments in our field experiment and, following the additive design, used observed predation in appropriate half-density

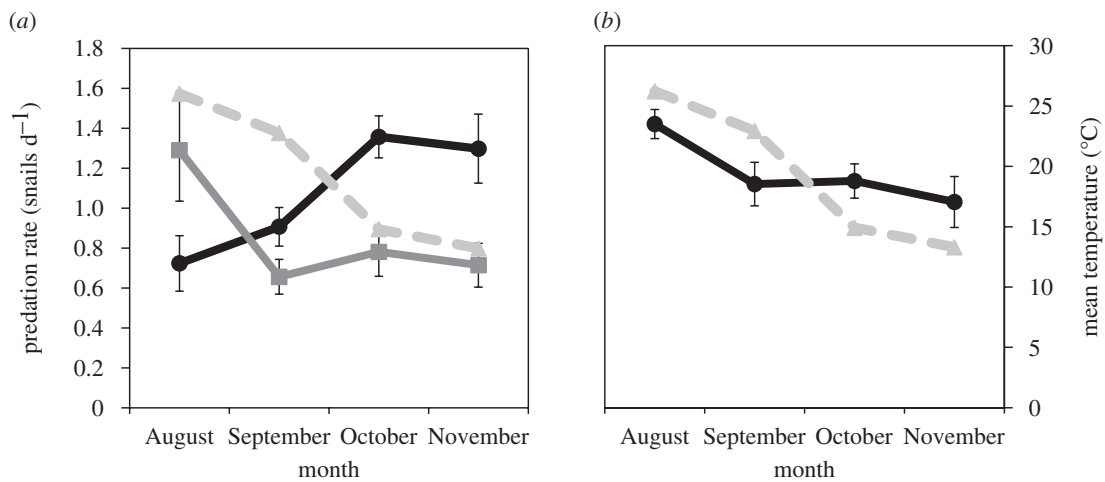


Figure 1. Mean predation rates over successive months as exhibited by (a) individual species and (b) both species combined at full-densities (see §2). Mean daily air temperature within each month is shown—water temperature is omitted for clarity (see §2 for correlation with air temperature). Months ran from the middle (15th) of the month shown to the middle (15th) of the following month. Error bars are ± 1 s.e. (a) Circles with black line, *Panopeus*; squares with grey line, *Eurytium*; triangles with dashed line, temperature. (b) Circles with black line, combination; triangles with dashed line, temperature.

treatments to calculate expected predation in all three full-density treatments using the multiplicative risk model ([10]; electronic supplementary material 1). Deviations from expected rates were then used as an estimate of the direction and strength of predator–predator interactions within respective full-density treatments.

Adult crabs (33–40 mm) of both species were collected by hand from burrows in local marshes, haphazardly assigned to treatment replicates, and transplanted into field enclosures. Each enclosure was stocked with an initial density of 300 adult (16.3 ± 1.05 (mean \pm s.d.) mm) *Littoraria*, a naturally occurring intermediate density [8]. Consumed snails were not replaced, thus predation naturally reduced adult snail densities during the experiment. All treatments were replicated seven times and randomly assigned to enclosures.

Rates of predation on *Littoraria* were measured monthly by counting shells that had been cracked open by predatory crabs (electronic supplementary material 2). The temporal variability (coefficient of variation (CV), the inverse of temporal stability) and mean daily rate of predation were calculated for each replicate. To examine species-specific responses to changing environmental conditions, and thus test a key tenet of the insurance hypothesis, we performed separate linear regression analyses between mean air and sea surface temperatures (from stations less than 5 km from the study site) and mean daily predation rate for replicates within separate treatments during each month of the experiment. Mean monthly air and water temperatures were closely related to each other ($r = 0.98$, $p = 0.024$).

To analyse the effect of predator diversity across full-density treatments on the temporal variability (stability) and mean rate of predation, we first calculated expected values of these response variables in the predator combination (the mean of the two component single-species treatments), before using two-tailed one-sample t -tests to establish whether observed values of response variables differed from respective expected values. Treatment effects were further elucidated using standard statistical comparisons (electronic supplementary material 3).

3. RESULTS

The two predators exhibited clear differences in temporal patterns of predation rates, which was consistent with interspecific differences in responses to changing environmental conditions across seasons (figure 1a). Predation rates of *Panopeus* were strongly and negatively correlated to mean daily air (figure 1a; $\beta = -0.48$, $r^2 = 0.39$, $p < 0.001$) and water ($\beta = -0.48$, $r^2 = 0.31$, $p = 0.001$) temperatures, while predation rates of *Eurytium* were positively,

although not significantly at $\alpha = 0.05$ level, related to the same variables (figure 1a; air: $\beta = 0.03$, $r^2 = 0.12$, $p = 0.070$; water: $\beta = 0.03$, $r^2 = 0.09$, $p = 0.102$). Predation rates in the species combination were weakly and positively related to air (figure 1b; $\beta = 0.02$, $r^2 = 0.17$, $p = 0.031$) and water ($\beta = 0.03$, $r^2 = 0.16$, $p = 0.036$) temperature. In line with the insurance hypothesis, independent temporal variation in species-specific predation rates acted to stabilize predation rates through time when species were combined, reducing CV relative to that expected by 47 per cent (figure 2a; $t_6 = -4.89$, $p = 0.003$).

In monoculture both predator species exhibited a similar mean rate of predation (figure 2b). When both species were combined (higher predator diversity) however, mean predation was enhanced by 37 per cent compared with expected (figure 2b; $t_6 = 4.44$, $p = 0.004$), and also exceeded both of the monocultures (figure 2b). Comparisons of observed and expected predation rates in full-density treatments gave an insight into mechanisms driving this effect. Predation within both single-species treatments was less than expected (*Panopeus*: figure 2c; $p = 0.001$; *Eurytium*: figure 2c; $p = 0.037$) indicating that competition was the predominant interaction between conspecifics in both species. When species were combined, however, there was no significant deviation from expected predation rates (figure 2c; $t_6 = 0.720$, $p = 0.499$), thus there was no detectable net effect of interspecific interactions (i.e. the two species have additive effects).

4. DISCUSSION

By performing a manipulative field experiment across changing seasons we found support for the insurance hypothesis, revealing that two predator species respond differently to changing environmental conditions, stabilizing and strengthening overall predation rate when combined.

Monitoring of temporal changes in predation rates of individual species suggests that complementarity

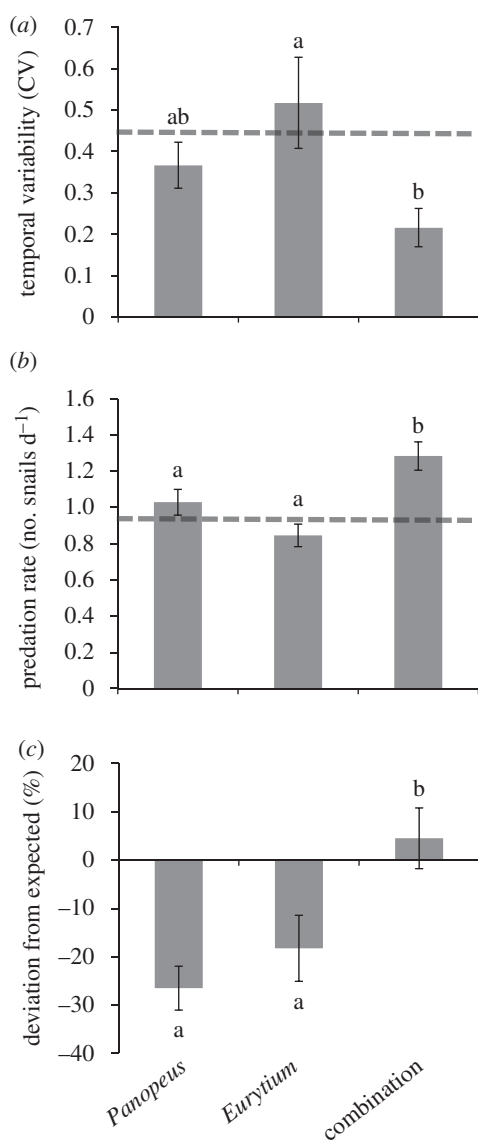


Figure 2. Effects of predator species composition on (a) temporal variation (CV) of predation, (b) the mean rate of predation on *Littoraria* and (c) predator–predator interactions as shown by the deviation from expected mean predation rate calculated from observed predation in half-density single-species treatments (see §2). Dashed horizontal lines indicate expected means based on the single-species treatments. Letters above bars were assigned based on post hoc tests. Error bars are ± 1 s.e.

resulted from species' differential responses to temperature (figure 1a); an explanation consistent with the differing northern distributional limits of these predators. The combination of predator species with contrasting responses to changing conditions ensured that, while neither species was able to maintain high predation rates throughout the changing seasons, one of the species was exerting relatively strong predation pressure during all four months of the experiment, i.e. *Eurytium* in hot summer conditions and *Panopeus* in cooler autumn conditions, acting to stabilize predation rates through time (figure 1a). Notably, moderately depleted snail densities late in the experiment may also have influenced observed predation rates. Importantly however, despite a lower average snail density in the autumn months (electronic supplementary material 4),

Panopeus maintained higher predation rates compared with *Eurytium* during this period (figure 1a), lending further support to the overwhelming role of species differences in driving observed temporal patterns.

Predator diversity not only stabilized predation, but also elevated its mean strength to a level that could not be matched by either species alone at equal density, implying that extinction of either of these predators would weaken top-down control of *Littoraria*. Enhancement of predation with predator diversity can result from a range of mechanisms [2], but several lines of evidence suggest that in the present study it resulted from weaker interspecific compared with intraspecific competition—the hallmark of species complementarity [11,12]. First, the strong density-dependent suppression of predation rate that occurred within single-species treatments was not apparent when species were combined (figure 2c). Second, while interspecific facilitation, through mechanisms such as conflicting escape behaviour of prey, could have counteracted a potentially negative effect of density in the predator combination, both predators have similar patterns of habitat use and foraging methods, making this an unlikely explanation (see [3]). The evidence thus strongly indicates that temporal complementarity exhibited by the two predators contributed to the observed elevation of mean predation strength by alleviating interspecific interference competition, although other forms of complementarity (dietary, spatial) cannot be completely ruled out.

Our results suggest that by incorporating contrasting responses to shifting seasonal conditions, predator diversity provides biological insurance, stabilizing aggregate predation rates in the face of environmental changes. Our experiment also adds to a growing body of evidence that predator diversity can enhance the overall strength of top-down control by alleviating predator–predator competition as a result of species complementarity. We propose that conserving predator diversity, especially where that includes diverse responses to environmental conditions, should be a priority to avoid destabilizing and weakening top-down control of potentially habitat-destroying grazers.

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