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Estimating the impact of consumers in ecological communities: Manual removals identify the complex role of individual consumers in the Gulf of Maine

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ABSTRACT

In intertidal communities, consumers (especially carnivorous gastropods) have historically been thought to exert strong top-down control on community composition by regulating competitively dominant mussels and barnacles. This paradigm was formulated based on wire mesh cage exclusion experiments, which have well-known artifacts such as altering hydrodynamics and excluding non-target, but potentially important, consumer species. Recent research highlights the potential importance of multiple consumers that are often subtle and transient, as well as the modifications of consumer pressure by spatial and temporal environmental variability and bottom-up processes. Manipulative experiments that target individual taxa will be essential to more clearly identify their roles in complex ecological communities.

The predatory gastropod *Nucella lapillus* has long been considered an important consumer controlling the structure and dynamics of intertidal communities in the Gulf of Maine. To test the role of *N. lapillus* in shaping community structure, we manually reduced its densities for 2.33 years. Species composition, stable stage community composition (based on a Markov model), and transition probabilities (as measures of ecological pathway strength) were compared between treatments (control vs. density reductions), and among seasons (spring, summer, fall, winter). In contrast to previous studies, exclusions had no effect on community composition or long-term Markov model predictions of stable stage community structure. Reducing *N. lapillus* abundance increased the persistence and reduced the mortality of the barnacle *Semibalanus balanoides* in the model, but did not affect blue mussels, *Mytilus edulis*, in a similar way. Reducing *N. lapillus* abundance had additional indirect effects of increasing *Ralfsia* spp. mortality and increasing hydroid persistence. Despite differences in transition probabilities among treatments, compensatory changes in direct and indirect pathways led to communities that converged over the long-term. Our results contrast previous estimates of the role of *N. lapillus* in intertidal communities and might reflect low mussel recruitment, predation by alternate consumers (e.g., *C. maenas*, *C. borealis*, *Tautogolabrus adspersus*, birds), or spatial and/or temporal environmental variation that influenced the role of *N. lapillus* in structuring these communities. The role of *N. lapillus* may be more limited, or variable, than often assumed in the Gulf of Maine, and the methods manipulating broad functional groups such as "consumers", though useful in developing basic conceptual models, blur the effects of individual species in community assembly and dynamics.

1. Introduction

Understanding the relative importance of specific species in controlling community structure and dynamics is essential for developing a comprehensive perspective on the forces that shape patterns of biodiversity and ecosystem function. Coupling targeted manipulative experiments with approaches that quantify complex webs of species interactions is a powerful method to investigate the direct and indirect effects of individual species (Wootton, 1994). If species effects are manipulated within a complete web of ecological interactions, rather than in an isolated subset of interactions, indirect effects within the web can more easily be estimated (Bender et al., 1984; Yodzis, 1988; Wootton, 1994; Menge, 1995; Polis and Strong, 1996; Palumbi et al., 2008; Stachowicz et al., 2008). Manipulations are only informative, however, so far as they exclusively target the species or process of interest. Inadvertent manipulations of non-target species or processes can

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alter pathways of species interaction and may lead to misinterpretation of causal mechanisms.

In rocky intertidal systems, consumer species can impose strong top-down forcing on community structure and dynamics (Connell, 1961; Paine, 1966; Menge, 1976; Lubchenco, 1980). The Gulf of Maine (GOM) rocky intertidal provides an excellent model system to test the effects of individual consumers, as it has a rich history of studies investigating top-down effects (e.g., Menge, 1976, 1978; Leonard et al., 1998; Bertness et al., 2004), and a well-documented natural history (e.g., Lubchenco and Menge, 1978; Lubchenco, 1980; Menge and Sutherland, 1987). Further, climate is changing faster in the GOM than most other coastal communities (Pershing et al., 2015), and better understanding how top-down forces operate in GOM communities would be useful in understanding and forecasting future changes. Experiments in the GOM intertidal have identified the carnivorous dog whelk, *Nucella lapillus*, as an important consumer (Menge, 1976, 1978; Lubchenco and Menge, 1978). On exposed shores, *N. lapillus* is thought to be the primary consumer of blue mussels (*Mytilus edulis*) and acorn barnacles (*Semibalanus balanoides*), the competitively dominant sessile species in the GOM (Menge, 1976, 1978; Lubchenco and Menge, 1978; Leonard, 2000; Bertness et al., 2004). Predation by *N. lapillus* presumably reduces competition and increases species richness and evenness (Menge, 1976). Consistent with this notion, experiments that used wire mesh cages to reduce consumer pressure found increased persistence of *M. edulis* and *S. balanoides* across a range of wave exposures (Menge, 1976, 1978; Bertness et al., 1999, 2004). Although the cages excluded predators other than *N. lapillus* (e.g. crabs, birds, fish), the increase in barnacles and mussels was attributed to *N. lapillus* predation. This inference was based on decreased barnacle and mussel abundance in *N. lapillus* enclosures (Menge, 1976), and high estimated feeding rates for *N. lapillus* relative to other potential consumer species on mid-intertidal exposed shores (Menge, 1978). More recent experiments in the Gulf of Maine, which used locations and caging methods similar to those of previous studies, observed quite different changes in communities that were not explained by variations in *N. lapillus* abundance (Menge, 1976 vs. Bryson et al., 2014). *Mytilus edulis* persisted in experimental plots in areas of high *N. lapillus* density, but not in areas of low *N. lapillus* density (Bryson et al., 2014). In contrast, *M. edulis* persistence varied more predictably with the abundance of other consumer species (i.e. *Carcinus maenas*), suggesting that the role of *N. lapillus* in Gulf of Maine rocky intertidal systems might have been overstated, or changed. The cage exclusion methods employed make isolating the role of any individual consumer species, such as *N. lapillus*, difficult.

The caging methods used in previous studies to reduce consumer pressure introduced artifacts because they altered environmental variables that may modulate ecological interactions (e.g., wave force, temperature, desiccation, algal whiplash, and flow), and they potentially restricted access of a variety of non-target species (Virnstein, 1978; Hall et al., 1990; Miller and Gaylord, 2007). In many cases, it is possible to control for treatment artifacts with careful and comprehensive experimental designs and controls (e.g., Johnson, 1992; Peterson and Black, 1994; Benedetti-Cecchi and Cinelli, 1997; Underwood, 1997; O'Connor and Crowe, 2005), but artifacts associated with flow (Miller and Gaylord, 2007), and exclusion of non-targeted mobile species (Edwards et al., 1982; Petraitis, 1990) often remain.

Manual removal of slow-moving predators has been effective for quantifying the role of consumers in intertidal communities (e.g. starfish: *Pisaster ochraceus*, Paine, 1966; gastropods, sea stars, limpets, and chitons, Menge and Lubchenco, 1981; chiton: *Katharina tunicata*, Palumbi, 1985; urchins: *Paracentrotus lividus*, Kitching and Ebling, 1961; *Strongylocentrotus droebachiensis*, Witman, 1987; limpets: *Patella candei*, Martins et al., 2010; whelks: *Morula marginalba*, Fairweather and Underwood, 1991) without the confounding influence of a cage. Removals may provide a better estimate of the role of *N. lapillus* in the GOM, and help explain disparate outcomes among individual experiments (Menge, 1976 vs Bryson et al., 2014; Petraitis and Dudgeon, 2001 vs. Bertness et al., 2004).

The role of *N. lapillus* within intertidal communities is likely to involve both direct and indirect pathways, which are more easily deciphered through a modeling framework. Utilizing models also provides a platform to investigate more complex ecological properties; such as the time it takes for a community to reach stable stage equilibrium. Multispecies Markov chain models (hereafter referred to as Markov models or MMCMs) are one such option, and are also a proven method of integrating experimental manipulations into a framework of complex interactions (e.g., Nelis and Wootton, 2009). Markov models use transition probabilities from one state (i.e., species) to the same or different state over a fixed period of time, and can detect and incorporate subtle changes in community dynamics to predict community composition in temperate intertidal (Wootton, 2001) and other (tropical coral reef, Tanner et al., 1994; temperate subtidal, Hill et al., 2002) marine ecosystems. Transition probabilities are summarized in an *n* x *n* dimensional table, where *n* is the number of potential states a point in the community may transition from (column labels) and to (row labels). Individual table elements (probabilities) are representative of specific ecological pathways - a term we use generally to encompass the interactions among species and other species-specific ecological processes (e.g. disturbance, mortality, recruitment, growth; mortality - transitions from a sessile species to bare rock; Tanner et al., 1994). Comparing the magnitude and distribution of table elements between treatments can provide important insights about the direct and indirect responses of communities to novel circumstances (i.e., experimental manipulation; Wootton, 2004; Nelis and Wootton, 2009).

To more accurately estimate the relative importance of *N. lapillus* on community structure and dynamics in the Gulf of Maine, we quantified transition probabilities in both control and density reduction plots where *N. lapillus* were manually removed. We compared community composition from plots, numerical predictions from Markov models (long-term stable stage community composition), and transition probabilities (measures of ecological pathway strength), between treatments (control vs. density reduction) and among seasons (spring, summer, fall, winter) to determine the direct and indirect effects of *N. lapillus*. Based on previous research in southern GOM intertidal (Menge, 1976; Lubchenco and Menge, 1978; Bertness et al., 2002, 2004), and the assumption that *N. lapillus* is the primary consumer of *M. edulis* and *S. balanoides* in the mid-intertidal (Menge, 1976, 1978), we predicted that *M. edulis* and *S. balanoides* mortality would decrease, leading to an overall increase in *M. edulis* and *S. balanoides* persistence when *N. lapillus* density was reduced. We also predicted that reducing *N. lapillus* density would alter the stable stage community composition by increasing the percent cover of *M. edulis* and *S. balanoides*.

2. Methods

2.1. Data collection and quantification of transition probabilities

Experiments were conducted in rocky intertidal communities occupying the mid-intertidal zone (1 m tide height above mean low water) at shores experiencing intermediate wave exposures (mean: 12.67 N ± 1.05 SE, Morello, 2015). Twelve permanent 25 cm × 25 cm plots were established at each of three replicate sites in Cape Ann, Massachusetts (UMass Field Station, FS, 42° 40′ 13.09″ N, 70° 40′ 24.39″ W; Seaside Cemetery, SC, 42° 41′ 04.45″ N, 70° 39′ 03.72″ W; Loblolly Point, LL, 42° 38′ 28.43″ N, 70° 35′ 31.79″ W). Six plots were randomly assigned as *N. lapillus* manual removal plots (hereafter referred to as the "density reduction" treatment, or "DRT" plots) and the other six as controls. Plots were randomly spaced along a 200 m transect, and separated by a minimum of 5 m to provide independence among individual plots and treatments. The tidal-height of each plot was measured using an Emery shore profiling method and local National Oceanographic and Atmospheric Administration tide