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ZT Long
Virginia Institute of Marine Science

JF Bruno

JE Duffy
Virginia Institute of Marine Science

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Zachary T. Long[1]*†, John F. Bruno[2] and J. Emmett Duffy[1]

[1]*Virginia Institute of Marine Sciences, The College of William and Mary, Gloucester Point, VA, 23062, USA; and* [2]*Department of Marine Sciences, The University of North Carolina, Chapel Hill, NC, 27599, USA*

Summary

1. Using a subtidal marine food web as a model system, we examined how food chain length (predators present or absent) and the prevalence of omnivory influenced temporal stability (and its components) of herbivores and plants. We held the density of top predators constant but manipulated their identity to generate a gradient in omnivory prevalence.

2. We measured temporal stability as the inverse of the coefficient of variation of abundance over time. Predators and omnivory could influence temporal stability through effects on abundance (the 'abundance' effect), summed variance across taxa (the 'portfolio effect') or summed covariances among taxa (the 'covariance effect').

3. We found that increasing food chain length by predator addition destabilized aggregate herbivore abundance through their cascading effects on abundances. Thus, predators destabilized herbivores through the overyielding effect. We also found that the stability of herbivore abundance and microalgae declined with increasing prevalence of omnivory among top predators. Aggregate macroalgae was not affected, but the stability of one algal taxon increased with the prevalence of omnivory.

4. Our results suggest that herbivores are more sensitive than plants to changes in food web structure because of predator additions by invasion or deletions such as might occur via harvesting and habitat loss.

Key-words: covariance effect, food chain length, food web, *Lagodon rhombiode,* omnivory, portfolio effect, stability, subtidal, trophic cascade

Introduction

The relationship between food web complexity and stability has long fascinated ecologists (May 1973; McCann 2000; de Ruiter, Wolters & Moore 2005). Much attention has focused on two properties of food web complexity, food chain length and omnivory (Pimm & Lawton 1977; Pimm 1984; Lawton & Warren 1988; Polis, Myers & Holt 1989; Lawler & Morin 1993; Morin & Lawler 1996; Polis & Strong 1996; Polis 1998). Early theoretical studies suggested that longer food chains tend to be less stable (generally defined as variability in population dynamics or return time to a locally stable composition following disturbance) than shorter chains (Pimm 1984; Pimm & Kitching 1987; Lawton & Warren 1988), and these predictions received partial support from the few experimental tests designed to explicitly evaluate this question (Lawler & Morin 1993). More recent work, however, suggests that longer food chains can exhibit more stable population dynamics; Sterner *et al.* (1997) modified the earlier models by including negative density dependence and found that including the negative density dependence could stabilize longer food chains, depending on where in the food chain the self-damping terms were included. Recently, Halpern *et al.* (2005) addressed these differing theoretical predictions with a meta-analysis designed to test how the presence of a predator influenced the stability of herbivores and primary producers. They found that, on average, predators decreased the stability of herbivores, but that this effect did not penetrate appreciably to affect the stability of primary producers (Halpern *et al.* 2005).

Similarly, theoretical studies have reached different conclusions as to whether omnivores, i.e., species that feed from more than one trophic level, tend to stabilize or destabilize food webs. A number of theoretical studies and limited empirical evidence suggest that omnivory can destabilize food webs (Lawler & Morin 1993; Holt & Polis 1997; Diehl & Feissel 2000; Tanabe & Namba 2005; Vandermeer 2006).

*Correspondence author. E-mail: longz@uncw.edu
†Present address: Department of Biology and Marine Biology, University of North Carolina Wilmington, 601 South College Road, Wilmington, NC 28403, USA.

Other theoretical work that incorporates variation in the strength of trophic links suggests that omnivory can stabilize webs when trophic interactions are weak (McCann & Hastings 1997; Borrvall, Ebenman & Jonsson 2000; Emmerson & Yearsley 2004), and again, there is some empirical evidence supporting a stabilizing effect of omnivores on populations or food chains (Lawler & Morin 1993; Fagan 1997; Holyoak & Sachdev 1998).

Marine food webs are currently experiencing structural changes as a result of invasions of exotic species (Byrnes, Reynolds & Stachowicz 2007) and harvesting of higher trophic levels (Pauly *et al.* 1998; Jackson *et al.* 2001; Duffy 2003). Additionally, even though omnivory tends to be more prevalent in marine systems compared to both freshwater and terrestrial systems (Menge 1995; Thompson *et al.* 2007), it still remains unclear whether and how the prevalence of omnivores can influence the stability and dynamics of marine food webs. Here, we use a subtidal marine system to experimentally determine the singular and interactive effects of decreasing food chain length and increasing omnivory on temporal stability of the lower trophic levels.

The temporal coefficient of variation (CV, Cottingham *et al.* 2001, Steiner 2005; Romanuk, Vogt & Kolasa 2009) or its inverse (CV^{-1}, Lehman and Tilman 2000, Tilman & Lehman 2001) is frequently used as a measure of temporal stability (Tilman & Lehman 2001; Steiner 2005; Romanuk, Vogt & Kolasa 2009). We use CV^{-1} here because increases in CV^{-1} indicate increases in temporal stability. Specifically, temporal stability (S_T) is quantified as

$$S_T = \frac{\mu_T}{\sigma_T}$$

where μ_T is the mean abundance over the course of observations, and σ_T is the temporal standard deviation of abundance. When considering aggregations of species (e.g., trophic levels), the temporal average abundance is the sum of the temporal average of each species, and the standard deviation can be decomposed into the summed variance of each species and summed covariances of pairs of species ($\sigma_T = \sqrt{\sum_{i=1}^{N} \text{var}(M_i) + \sum_{i=1}^{N}\sum_{j=1}^{i-1} \text{cov}(M_i, M_j)}$) within the aggregation. The development and most recent uses of this measure are to evaluate how 'horizontal' species diversity (diversity within a trophic level) influences stability in three ways (Tilman & Lehman 2001; Steiner 2005; Romanuk, Vogt & Kolasa 2009). First, diversity may increase stability by increasing μ_T (the 'overyielding effect' (e.g., Tilman, Reich & Knops 2006). Second, diversity could increase stability through the 'portfolio effect,' a decrease in the summed variances of species abundances because of the statistical averaging of the fluctuations of species' abundances (e.g., Steiner 2005; Tilman, Reich & Knops 2006). The portfolio effect occurs because, under some circumstances (Tilman, Lehman & Bristow 1998) such as when species fluctuations are partially out of phase with one another, the variability of the sum of many species is less than the variability in the sum of fewer species (Doak *et al.* 1998; Tilman 1999; Lhomme & Winkel 2002; Tilman, Reich & Knops 2006). Third, the 'covariance effect' suggests that covariance among competing species should decrease with increasing diversity because of competition among species, and stability should increase with decreasing covariance. In contrast to most previous studies using this approach, we investigated how changing food chain length (i.e., diversity across trophic levels) influences each component of temporal stability and did not consider 'horizontal' diversity (diversity within a trophic level). We use the terms developed in studies of 'horizontal' diversity and temporal stability to be consistent except that 'overyielding' does not apply outside the context of diversity studies so we use 'abundance'.

These three effects have not been investigated explicitly in a food web context. It seems plausible that predators could affect all three measures: they could influence the overyielding effect via trophic cascades, the portfolio effect by either increasing or decreasing temporal variance and the covariance effect by modifying competition among prey. Additionally, omnivory may also influence the three component effects on stability because omnivores, by feeding on adjacent trophic levels, could decrease the potential for trophic cascades and subsequent effects on temporal variance and covariances.

To determine how predators influence the temporal stability of lower trophic levels, we evaluated whether food chain length, i.e., presence of predators, influenced the temporal stability of lower trophic levels by testing for differences between S_T and its components in the presence and absence of predators. To investigate whether changes in the prevalence of omnivory influenced temporal stability, we tested for relationships between the per cent of omnivores in a food web and S_T and its components. Because aggregate stability of a trophic level may mask changes within the constituent populations in that trophic level (Tilman 1996), we also calculated the temporal stability of constituent groups within the lower trophic levels, consisting of two taxonomic groupings of herbivores and three macroalgal species.

Materials and methods

EXPERIMENTAL DESIGN

We conducted this experiment in the outdoor, flow-through seawater mesocosm system at the University of North Carolina at Chapel Hill's Institute of Marine Sciences in Morehead City, North Carolina, USA. Our food webs were constructed and maintained within mesocosms (30-L plastic aquaria) housed in tables under larger dump buckets. The dump buckets gradually filled with gravel-filtered seawater pumped from the adjacent Bogue Sound. The dump buckets emptied into the mesocosms at periodic intervals of less than once per minute, aerating the water, diluting exuded wastes and simulating the turbidity and wave action typical of hard-substrate shallow marine habitats (Duffy & Hay 2000; Bruno & O'Connor 2005). Treatments were randomly assigned to mesocosms, and mesocosms were randomly assigned to tables and position within tables. Mesocosms were randomly rearranged every 2–3 days to minimize any potential location artefact.

On 14 June 2005, we added 20 g (wet mass) each of three species of macroalgae, *Gracilaria tikvahiae* McLachlan (red), *Ulva lactuca* Linnaeus (green) and *Sargassum filipendula* C. Agardh (brown), to each mesocosm. Algal stipes were fastened to 25 by 25-cm plastic vexar screens secured to the bottoms of each mesocosm. Algae were collected from local sites and represent dominant species typically found in this area at this time of year (Hay 1986; O'Connor & Bruno 2007). Any organisms that were not dislodged from the algae owing to collection, transportation, sorting of species and weighing (which involved approximately 15 revolutions in a salad spinner) were not actively removed and therefore were added to the mesocosms at this time. On June 15, 17, 18 and 19, we actively added approximately 50 individual herbivores to each mesocosm. Here, we use two broad taxonomic classifications for herbivores: caprellid amphipods and non-caprellid amphipods (henceforth caprellids and amphipods, respectively; see O'Connor & Bruno (2007) for a detailed list of species found locally during this time period). Caprellids generally consume microalgae, whereas some non-caprellid amphipods also effectively consume macroalgae (Duffy 1990). We added a section of rope to the mesocosms to provide an additional habitat for the herbivores and microalgae and to provide a means to temporally subsample herbivore abundance. The rope habitat was constructed by folding one large piece (approximately 30 cm) of nylon rope in half, fastening at one end and then unravelling the resulting two ~15-cm-long free ends to expose individual strands (Edgar 1991).

On June 20 (henceforth 'day 1'), we added predators. These included four individual carnivores and/or omnivores added to each mesocosm. Our carnivores were juvenile croaker (*Micropogonias undulatus* Linnaeus, average mass of a subsample of individuals at the end of the experiment = 4·79 ± 0·56 g, N = 15) and juvenile mummichog (*Fundulus heteroclitus* Linnaeus, average mass = 3·89 ± 0·37 g, N = 15). Our omnivores were juvenile pinfish (*Lagodon rhombiode* Linnaeus, average mass = 3·53 ± 0·30 g, N = 15) and grass shrimp (*Palaemonetes* sp., average mass = 0·31 ± 0·03 g, N = 13). Feeding trials verified the diet of each predator (Bruno & O'Connor 2005 and personal observations). By manipulating the number of strict carnivores and omnivores, we created five different levels of omnivory. These levels were the following: no omnivores (four carnivores), 25% omnivores (three carnivores and one omnivore), 50% omnivores (two of each), 75% omnivores (three omnivores and one carnivore) and 100% omnivores (four omnivores). We also established one treatment without carnivores or omnivores to allow us to evaluate how a change in food chain length, i.e., the presence of predators, influenced abundances and stability of the two lower trophic levels. The species compositions of the carnivores or omnivores were determined randomly, thus compositions were allowed to differ within a level of omnivory. Each level of omnivory and the predator-free treatment were replicated ten times, producing a total of 60 mesocosms. During the experiment, missing or dead predators were replaced to maintain their initial density. We also wanted to examine how these food webs responded to perturbation and subjected half of the 10 replicates within each level of omnivory to a resource pulse (slow release N–P–K fertilizer) halfway through the experiment. The resource pulse did not significantly influence any variable presented here, and thus is ignored in all analyses.

The abundances of macroalgae and herbivores were sampled at 2- to 3-day intervals following predator addition for 16 days. We sampled macroalgae non-destructively by visually estimating the per cent cover of each species. To sample the herbivores non-destructively, we collected the rope section and beat it against a white tray. We then counted the number of amphipods, caprellid amphipods and isopods visible and returned them to the mesocosm. We destructively sampled the epiphytic microalgal community. We placed small, roughened plastic tiles (approximately 2·54 by 2·54 cm) in each mesocosm with the initial macroalgae inoculation. At each sampling date (except the first), a single tile was collected from each mesocosm. Tiles were cold-preserved until the end of the experiment when we extracted and measured chlorophyll a using standard techniques (Jespersen and Christoffersen 1987).

Planned contrasts were used to test whether the addition of predators influenced stability, average abundances, and standard deviation (for individual taxa) or summed variances and summed covariances (for trophic levels). Contrasts compared treatments with predators to the no predator treatment. Analyses were separately conducted for each of our two taxonomic groupings of herbivores (amphipods and caprellids), the total density of herbivores, each of the three macroalgal species (*Gracilaria*, *Ulva* and *Sargassum*), total algae (*Gracilaria* + *Ulva* + *Sargassum*) and microalgae (chlorophyll a). We log-transformed the data and retained the original sign to reduce heterogeneity of variances.

We tested whether the degree of omnivory in a food web influenced the stability of the above taxa with linear regression. We used connectance (the number of realized trophic links divided by the number of all possible links) to quantify the degree of omnivory. We regressed S_T and its components on connectance in a food web for each taxonomic grouping described previously.

Results

EFFECT OF PREDATORS ON STABILITY OF LOWER TROPHIC LEVELS

Predators increased the stability of total plant cover ($P = 0.05$, Fig. 1a). This occurred because of the decrease in cover ($P = 0.05$, Fig. 1b) and an increase in the summed covariances ($P = 0.01$, Fig. 1d) in the absence of predators. Predators did not affect the summed variances ($P = 0.22$, Fig. 1c). Despite a significant increase in cover in the presence of predators ($P = 0.02$), overall stability of *Sargassum* was not influenced by predation ($P = 0.09$). Predators did not influence stability or its components for the other two algal species (all $P > 0.14$) or microalgae (all $P > 0.19$).

Predators decreased the stability of herbivores ($P = 0.04$, Fig. 2a). There was a significant decrease in herbivore density in the presence of predators ($P < 0.01$, Fig. 2b). However, the decrease in summed variance ($P < 0.01$, Fig. 2c) and summed covariance ($P < 0.01$, Fig. 2d) in the presence of predators had a stabilizing effect, opposing the destabilization because of the decrease in density.

Predators decreased overall stability ($P < 0.01$, Fig. 3a), abundance ($P < 0.01$, Fig. 3b) and the temporal standard deviation of amphipods ($P < 0.01$, Fig. 3c). The decrease in abundance and temporal standard deviation would have opposing effects on stability. The decrease in amphipod stability occurred because the decrease in stability because of decreased density outweighed any stabilizing effect attributable to the decrease in standard deviation. The overall stability of caprellids was unaffected by predator presence ($P = 0.68$, Fig. 4a) because the destabilizing effect predators
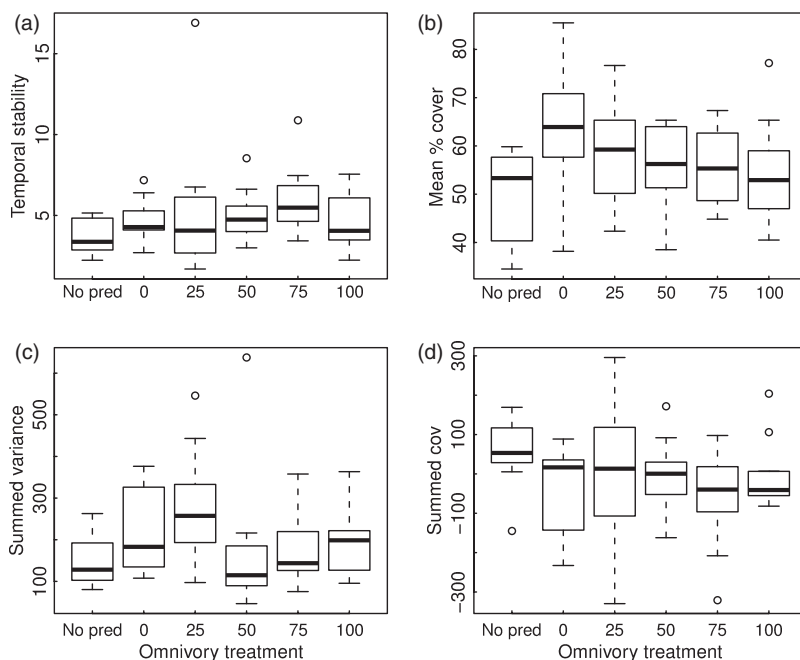
Fig. 1. Average temporal stability of algae (a) estimated by algal abundance (per cent cover averaged over time, b), summed temporal variance (c) and summed covariance (d) within predator treatments.
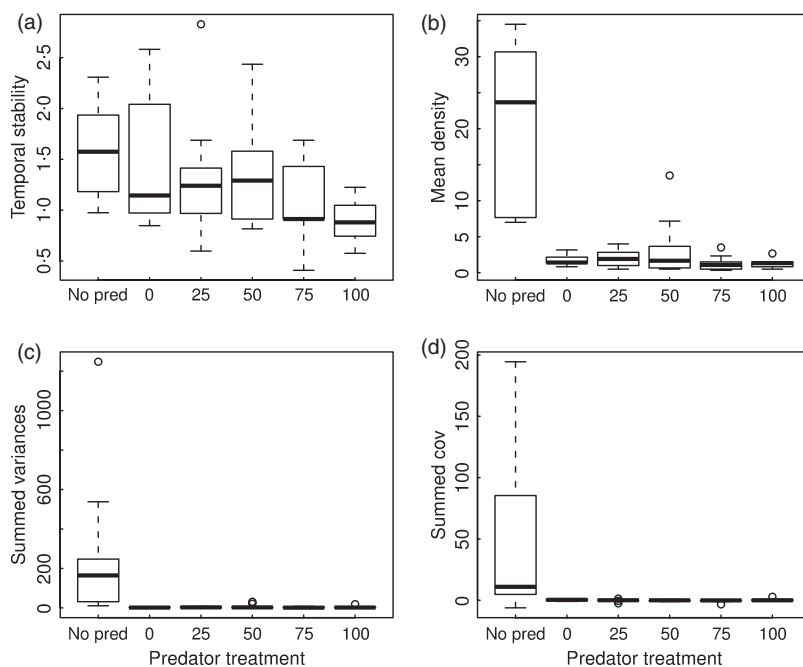

Fig. 2. Average temporal stability of herbivores (a) estimated by herbivore density (measured as the number of amphipods and caprellids found on the frayed 30-cm rope averaged over time, b), summed temporal variance (c) and summed covariance (d) within predator treatments.

had as a result of decreased density ($P = 0.01$, Fig. 4b) was countered by stabilization because of a decrease in the standard deviation with predators ($P < 0.01$, Fig. 4c).

Increasing connectance destabilized *Gracilaria* ($P = 0.04$, Fig. 5a). This occurred because *Gracilaria* cover decreased with connectance ($P = 0.03$, Fig. 5b). The temporal stan-

dard deviation was not affected by connectance ($P = 0.93$, Fig. 5c). The stabilities of the cover of the other individual macroalgal species and of total algae were not significantly influenced by connectance (all $P > 0.12$). Increasing connectance stabilized microalgae ($P = 0.05$, Fig. 6a) despite decreasing microalgal abundance ($P = 0.05$, Fig. 6b). The
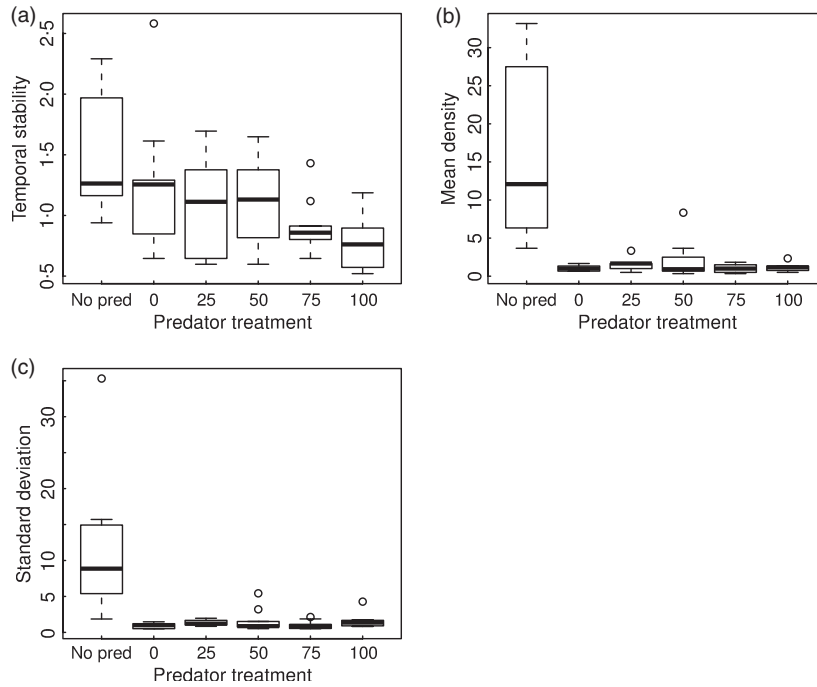
Fig. 3. Average temporal stability of amphipods (a) estimated by amphipod density (measured as the number of amphipods found on the frayed 30 cm rope averaged over time, b) and summed temporal variance (c).
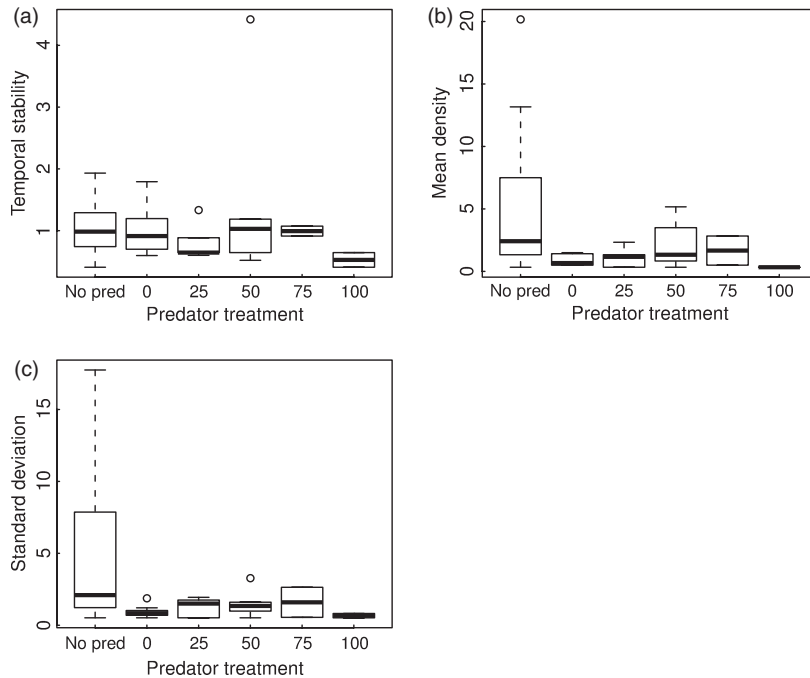

Fig. 4. Average temporal stability of caprellids (a) estimated by caprellid density (measured as the number of caprellids found on the frayed 30 cm rope averaged over time, b) and summed temporal variance (c).

stability of total herbivores ($P = 0.02$, Fig. 7a) and amphipods ($P = 0.02$, Fig. 8a) decreased with increasing connectance. None of the components of stability were related to connectance for amphipods or total herbivores (all $P > 0.13$, Figs 7b,c and 8b,c). Caprellids were not influenced by connectance ($P = 0.87$).

Discussion

We found that the composition and diet breadth of higher trophic levels determined temporal stability of lower trophic levels. Our results are partly in line with Halpern *et al.* (2005), who combined the results of 40 experiments and
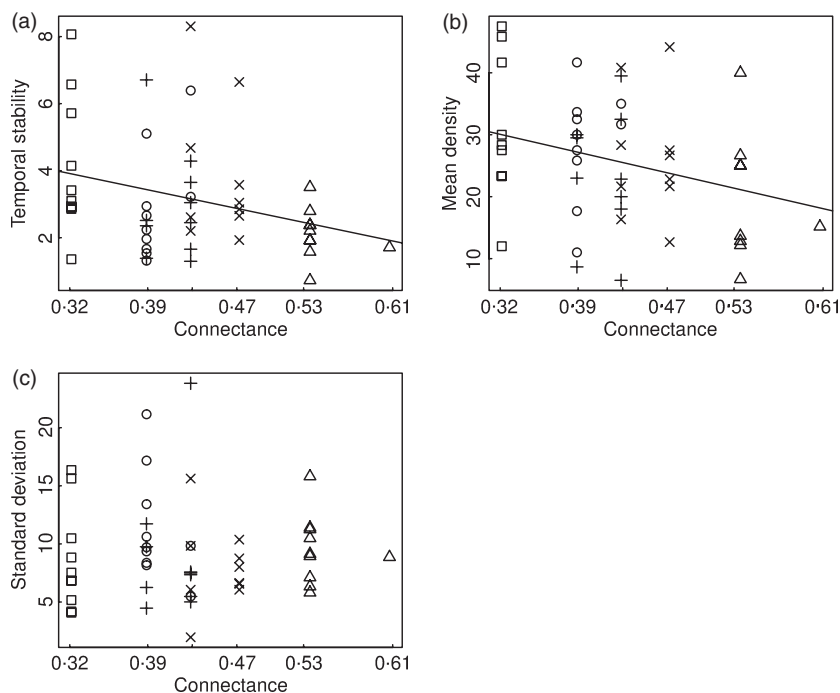
Fig. 5. The relationships between connectance and stability (and its components) of *Gracilaria*. The different symbols represent the different percentages of omnivores in the top trophic level. Squares indicate 0% omnivory, circles indicate 25%, plus signs indicate 50%, '×' indicates 75%, and triangles indicate 100%.
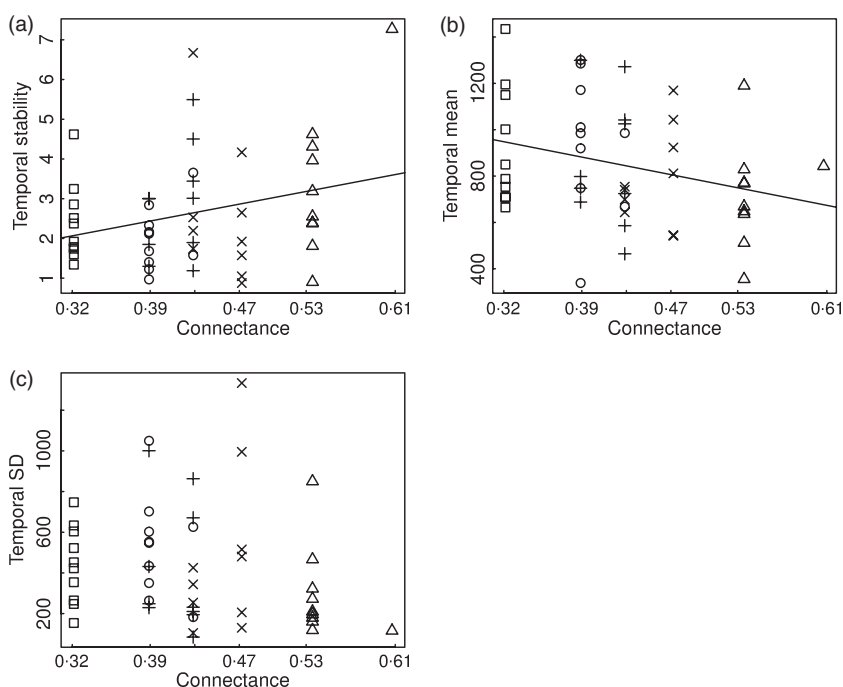

Fig. 6. The relationships between connectance and stability (and its components) of microalgae. The different symbols are as defined in Fig. 5.

found that predators destabilized herbivores but had little effect on plants. We also found that predators destabilized herbivores, but our results suggest that predators can stabilize plants. The stability of total plant cover was greater when predators were present. Stability was increased because of the 'abundance effect'. Predators increased the abundance of plants through an indirect effect (i.e., a trophic cascade sensu Hairston, Smith & Slobodkin 1960; Shurin *et al.* 2002; Borer *et al.* 2005; Bruno & O'Connor 2005). Predators also increased stability through the 'covariance effect'. This may
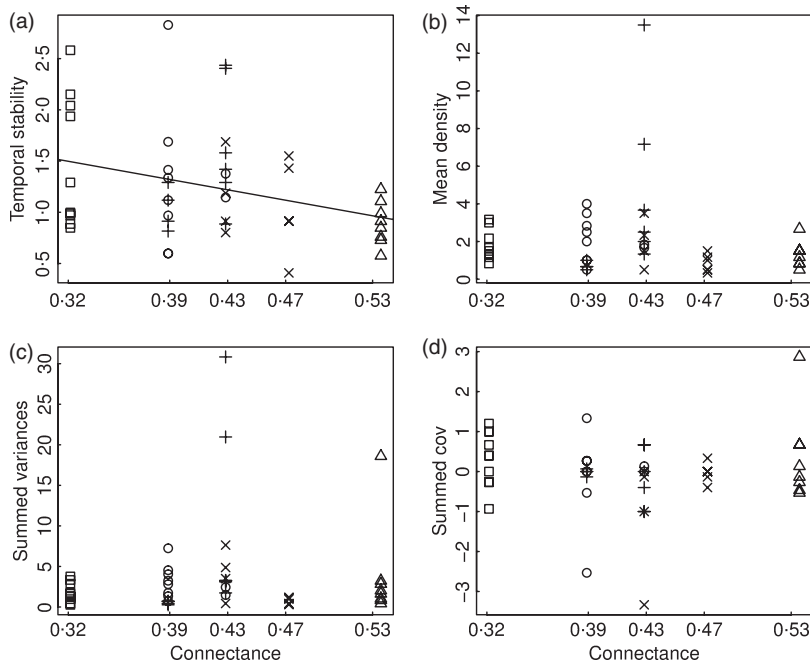
Fig. 7. The relationships between connectance and stability (and its components) of total herbivores. The different symbols are as defined in Fig. 5.
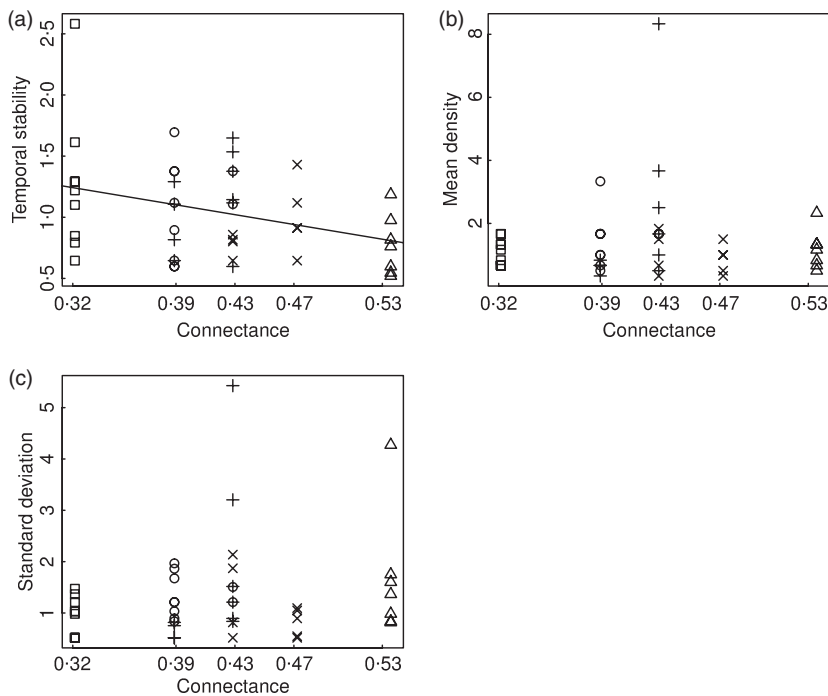

Fig. 8. The relationships between connectance and stability (and its components) of amphipods. The different symbols are as defined in Fig. 5.

have occurred because of stronger competitive interactions among the plants when predators were present to suppress herbivores.

In contrast to plants, predators always decreased prey abundance (both aggregate and individual taxa). However, this did not always lead to decreased stability because predators also always decreased temporal variability (a stabilizing

effect). Because of these opposing effects, predators decreased the stability of amphipods and total herbivores, but did not affect caprellid stability. Again, this result is partially consistent with Halpern *et al.* (2005) who found that predators destabilized herbivores, but the strength of a trophic cascade did not affect herbivore stability. Our results suggest this may occur because a cascade's destabilizing

effect on abundance can be countered by the stabilizing effect of reduced temporal variability of herbivores. Effects of predators on the stability of lower trophic levels may occur because of trophic cascades, but the strength of the trophic cascades may not necessarily influence stability because of opposing effects of predators on the components of stability.

Recent reviews suggest that omnivory dominates consumptive relationships in natural food webs. Arim & Marquet (2004) found between 58·4% and 87·6% of taxa were omnivorous. Thompson *et al.* (2007) analysed 58 food webs and found that while plants and herbivores fall in a distinct trophic level, the taxa found above herbivores in a food web 'are better characterized as a tangled web of omnivores'. They also found that the prevalence of omnivory varied among ecosystem types, with marine systems (such as the one investigated here) exhibiting the highest prevalence of omnivory, in line with earlier suggestions (Menge 1995; Thompson *et al.* 2007). Despite the increasing awareness of the presence of omnivorous relationships in food webs, how omnivory influences stability of lower trophic levels has received little attention. Here, we provide the first experimental evidence that the temporal stability of herbivore abundance declines with increasing omnivory, while the response of primary producers can vary. Specifically, we found that the stability of amphipods and total herbivores decreased as the prevalence of omnivory increased. The components of stability, however, were not influenced by the prevalence of omnivory. This suggests that the decrease in stability with omnivory occurred because of relationships between herbivore density and temporal variability within replicates. We also found that the stability of one of our algal species (*Gracilaria*) increased with omnivory as a result of the abundance effect, while the stability of microalgae decreased with omnivory, despite significant increases in microalgal abundance.

The negative relationship between omnivory and herbivore stability we observed contrasts previous empirical work that found stabilizing effects of omnivory. In protist food chains, Holyoak & Sachdev (1998) found that omnivores tended to be more stable than predators, and that the stability of prey was unaffected by omnivory. Fagan (1997) found more rapid recovery of arthropod food webs that had higher relative abundances of omnivores. Theory suggests that omnivory can stabilize or increase persistence when weaker omnivorous links dampen the dynamic behaviour of stronger consumptive interactions (McCann & Hastings 1997; Neutel, Heesterbeek & de Ruiter 2002; Emmerson & Yearsley 2004). The omnivores used by Holyoak & Sachdev (1998) either could not persist on diets that consisted of only basal resources (suggesting that the omnivorous link was weak) or were cannibals that self-dampen their abundance. The omnivores in the food webs investigated by Fagan (1997) were generalist wolf spiders that consumed arthropods from multiple trophic levels that presumably had weaker interactions with their multiple prey than the other predator, a damselbug that specializes on herbivores. In our study, however, one of the omnivores (pinfish) is a more effective consumer of amphipods than the other predator (Bruno & O'Connor 2005).

When omnivores are efficient or strong consumers, they can destabilize food webs and decrease the persistence of lower trophic levels (McCann & Hastings 1997; Emmerson & Yearsley 2004). This suggests that the negative relationship between herbivore stability and the prevalence of omnivory that we observed results from the increased probability of including a pinfish in the food web. A *t*-test comparing stability of herbivores and amphipods with and without pinfish suggests that replicates that had at least one pinfish were less stable (Welch two sample *t*-tests: $t = 4·10$, df = 28·76, $P < 0·01$ for total herbivores and $t = 2·95$, df = 35·99, $P < 0·01$ for amphipods).

We also note that another difference between our study and previous work is the absence of a numerical response in our top predators. Prey abundances could influence omnivore and predator population sizes in both Holyoak & Sachdev (1998) and Fagan (1997). While we show clear effects on lower trophic levels, our design does not allow us to determine stability of the top trophic levels. It is certainly possible that a greater prevalence of omnivores would increase stability in the top trophic level because of the ability to consume both plants and herbivores. Whether an increase in stability of the top trophic level would cascade to lower trophic levels is an open question.

The negative response of herbivore stability to predator presence we observed and the results of Halpern *et al.* (2005) indicate that the introduction or loss of predators will influence the stability of food webs largely through their effects on herbivores. It remains unclear how the exploitation of top predators in marine food webs (Pauly *et al.* 1998; Jackson *et al.* 2001; Duffy 2003) will affect herbivore stability. The loss of predators could destabilize herbivores if it increases the relative abundance of omnivores. Additionally, whether increasing omnivory destabilizes or stabilizes lower trophic levels will depend on the identity of the remaining species and the strengths of their trophic links. Understanding the potential effects of omnivores on the temporal stability of food webs will require an understanding of the preferences of the dominant consumers in the food web.

Acknowledgements

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