

LETTER

The biogeography of trophic cascades on US oyster reefs

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Abstract

Predators can indirectly benefit prey populations by suppressing mid-trophic level consumers, but often the strength and outcome of trophic cascades are uncertain. We manipulated oyster reef communities to test the generality of potential causal factors across a 1000-km region. Densities of oyster consumers were weakly influenced by predators at all sites. In contrast, consumer foraging behaviour in the presence of predators varied considerably, and these behavioural effects altered the trophic cascade across space. Variability in the behavioural cascade was linked to regional gradients in oyster recruitment to and sediment accumulation on reefs. Specifically, asynchronous gradients in these factors influenced whether the benefits of suppressed consumer foraging on oyster recruits exceeded costs of sediment accumulation resulting from decreased consumer activity. Thus, although predation on consumers remains consistent, predator influences on behaviour do not; rather, they interact with environmental gradients to cause biogeographic variability in the net strength of trophic cascades.

Keywords

Behaviour, consumptive effect, density-mediated indirect interaction, environmental gradient, foundation species, non-consumptive effect, predation, recruitment, trait-mediated indirect interaction.

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INTRODUCTION

Trophic cascades occur when top predators maintain populations of basal prey (e.g. plants) by controlling mid-trophic level consumers such as herbivores (Hairston *et al.* 1960; Paine 1966; Estes & Palmisano 1974; Carpenter *et al.* 1985). These predator effects can be far reaching, with implications for ecosystem processes such as primary production, nutrient cycling and decomposition (Schmitz 2008a; Schmitz *et al.* 2010). However, the degree to which predator effects cascade to lower trophic levels varies considerably among ecosystems (Strong 1992; Shurin *et al.* 2006; Hall *et al.* 2007; Pawar *et al.* 2012), and at times, to an even greater degree within ecosystems (Shurin *et al.* 2002).

In ecosystems with basal prey that are strongly controlled by mid-trophic consumers, variation in trophic cascades has been linked to several factors including predator diversity (Byrnes *et al.* 2006), energy input (Oksanen *et al.* 1981), habitat complexity and refuge availability (Grabowski 2004; Orrock *et al.* 2013) and consumer foraging behaviour (Schmitz 2008a). Although these factors differ in how they cause within-system variability, they all ultimately operate by influencing how mid-trophic consumers balance their need to eat with their need to avoid being eaten (Abrams 1984; Schmitz *et al.* 2004; Schmitz 2008b). Therefore, the variability of trophic cascades within ecosystems may fundamentally depend on how multiple factors influence

consumer behaviour, and in turn predator–consumer interactions.

Interactions between predators and mid-trophic consumers can vary due to both historical and contemporary environmental gradients (Power *et al.* 1996). For instance, and with regard to the latter, waterfall barriers in Peruvian tributaries partition guppy populations into guppies that coexist with pike cichlids or killifish (Reznick & Bryant 2007). Pike frequently eat large-bodied guppies and killifish eat guppies of immature size. As a result, guppies experience a gradient in predation pressure that alters their abundance, foraging behaviour and size distribution (Reznick & Bryant 2007). Even in systems with the same predator assemblage, changes in resource supply and/or environmental factors can determine not only if predator effects cascade to basal prey (c.f. the pike effect on prey of guppies) but also whether the indirect interactions from a given predator are positive or negative (Carpenter *et al.* 2010). Because resource and environmental conditions change spatially (Menge & Branch 2001; Stapp & Polis 2003), independent tests of the same trophic cascade throughout broad ecosystems may commonly produce conflicting results. Consequently, understanding why trophic cascades vary within ecosystems requires simultaneous monitoring and manipulation of tri-trophic dynamics along broad environmental gradients.

We used this geographic approach to investigate oyster reef communities across the Southeastern Atlantic Bight (hereafter

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SAB, Fig. 1a). Previous experiments in the north of the SAB demonstrated that predators (toadfish, *Opsanus tau*; blue crab, *Callinectes sapidus*) indirectly benefitted basal prey (juvenile oysters, *Crassostrea virginica*) primarily by altering the feeding behaviour – not the abundance – of consumers (mud crab, *Panopeus herbstii*; Grabowski 2004; Grabowski *et al.* 2008). However, on natural oyster reefs of the SAB, we observed that an increasing biomass of predators from north to south was associated with a weaker corresponding gradient in oyster biomass than expected, if predators indirectly benefit oysters as proposed by Grabowski *et al.* (2008) (Fig. 1b–d; see Appendix S1 for methods). Thus, we tested whether the trophic cascade in Grabowski *et al.* (2008) operates similarly throughout the SAB or whether the general application of this trophic cascade is inhibited by broad environmental gradients.

Based on prior research and tidal predictions along this coastline (http://tidesandcurrents.noaa.gov/tide_predictions.html), we suspected that tides and resource supplies on oyster reefs vary spatially in key ways. In particular, the geomorphology of the SAB creates spatial variation in the submergence of reefs by water. Tidal submergence could dictate the presence of pelagic predators and the dissemination of their waterborne cues (Smee & Weissburg 2006), or create differential exposure to physiologically stressful air temperatures, thereby altering predator–consumer interactions across space. The supply of oyster larvae (food for consumers) and phytoplankton (food for oysters) can also differ spatially because of coastal morphology (*sensu* Menge *et al.* 2003). High recruitment could reduce the population-level effect of mud crab foraging at some sites by numerically compensating for any consumed oysters (Gaines & Roughgarden 1985). Similarly, phytoplankton-rich sites may minimise population-level mortality of oysters in the face of strong consumer pressure by increasing the rate at which small oysters grow into a size refuge (Kimbro *et al.* 2009).

Our experiment involved simultaneous field manipulations of three trophic levels at six sites that encompassed 1000 km of the SAB (Fig. 1a,e). We quantified direct predator effects on consumer abundance (consumptive effects) as well as consumer foraging rates (non-consumptive effects). In addition to quantifying how these direct effects cascade to oyster reef production, we monitored several potentially influential environmental factors and we used a model-selection approach to identify which of these factors best explain why trophic cascades on oyster reefs shifted geographically. Finally, we tested whether these dynamics help explain the observed geographic trophic structure of oyster reefs (i.e. Fig. 1b–d).

MATERIAL AND METHODS

Trophic manipulation

In June 2011, we selected six sites that were at least 50 km apart to create interspersed, replicated sites within the north, central and south regions of the SAB. Constraints on available habitat inhibited true interspersed, especially with respect to the two southern sites. At each site, we established nine circular plots (2.5 m diameter) that were separated by 3 m of mudflat. Each plot was encircled with a mesh cage (12 × 12 mm openings), which was buried 0.5 m into the sed-

iment, and covered with a mesh top (19 × 19 mm, Fig. 1e). The cage was anchored in place by six 1.5 m rebar poles that were hammered to a depth of 1.0 m around the cage's perimeter. Within each cage, we created circular oyster reefs (1.5 m diameter) that comprised a base layer of dead oyster shell (1 bushel, volume = 35.2 L) and three bushels of living oyster clusters (cluster biomass = 200–400 g). This material was collected from nearby natural reefs and rinsed with fresh water to remove associated mobile invertebrates.

Each cage was randomly assigned among three trophic level treatments: (1) basal bivalve prey (oysters, clams and mussels); (2) basal prey and consumers (oyster drills and mud crabs); (3) basal prey, consumers and predators (toadfish and blue crab). All organisms were collected on site. Cages assigned to receive consumers were stocked with 35 adult mud crabs (carapace width > 20 mm) and 12 adult oyster drills (length > 25 mm). Predator reefs were stocked with one toadfish (length > 150 mm) and one male blue crab (carapace width > 100 mm), as well as with the 35 mud crabs and 12 oyster drills. Per unit area of reef, these predator and consumer densities reflect mean values observed on natural reefs (Grabowski & Kimbro 2005; Kimbro *et al.* 2009). Throughout the experiment, predators were replaced with new individuals to minimise the influence of any individual predator on our results. Because of the anticipated arrival of Hurricane Irene, we ended this experiment after 90 days.

Consumer foraging

We evaluated consumer foraging rates by quantifying juvenile oyster mortality in the presence and absence of consumers (c.f. Grabowski 2004). To ensure consistency across sites, we purchased a stock of juvenile oysters (mean size = 8 mm) from a single hatchery in Florida, USA. Using marine epoxy, we attached 12 juvenile oysters to ceramic tiles (10 × 10 cm), and then used aquarium-safe silicone to attach tiles on concrete pavers (12 × 12 cm). Three tiles were deployed equidistantly around the perimeter of each reef. Oyster mortality was monitored at 3, 7 and 14 days, but because prey depletion occurred by 14 days, we analysed the 7-day sampling point. Midway through the experiment, we conducted a second trial with new oysters and tiles. For each cage, the results of these two trials were averaged.

Consumer abundance

At the end of the experiment, we destructively searched each reef and quantified the abundance of mud crabs and oyster drills. In addition, we quantified the number of juvenile blue crabs that emigrated into our reefs because they represented a third mid-trophic consumer species. Hurricane Irene prevented us from quantifying consumers at the central 1 site, so that site was excluded from the analysis of consumer abundance.

Oyster reef biomass

We quantified the change in oyster cluster biomass over the course of the experiment as a proxy for oyster reef production. This metric integrates changes in the density of adult and juvenile oysters as a function of mortality, oyster growth and oyster recruitment (Meyer & Townsend 2000; Grabowski *et al.* 2005). During reef construction at each site, we measured the

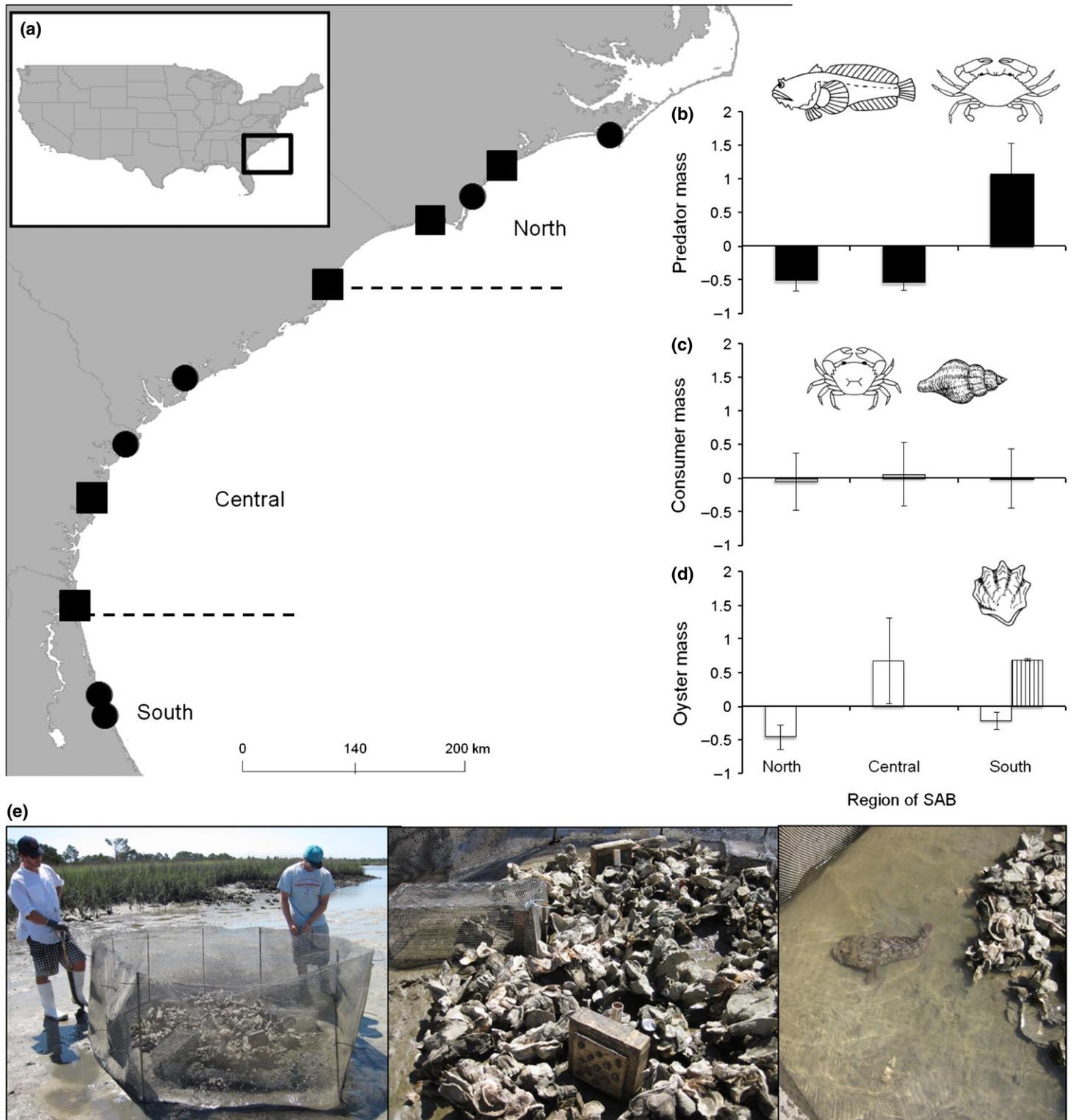


Figure 1 (a) Map of study locations throughout the Southeastern Atlantic Bight (SAB); circles denote monitoring and experimental sites, whereas squares denote monitoring only sites. Observed biomass of predators (b), consumers (c) and oysters (d) on oyster reefs of the SAB. In (b–d), data are partitioned into three different regions of the SAB (i.e. north, central and south). In (d), hatched bar illustrates expected oyster biomass given the observed biomass of predators and the results of Grabowski *et al.* (2008). To better illustrate the variation of biomass within and among trophic levels, the regional data were normalised according to the overall mean and standard deviation of a particular trophic level ($[\text{overall mean} - \text{regional mean}]/\text{overall standard deviation}$). (e) Images of experimental oyster reefs within field enclosures.

individual biomass of 54 oyster clusters (200–400 g) and marked each cluster with a numeric plastic tag. Each cluster was rinsed to remove sediments, and all fauna other than oysters were removed. Thus, oyster cluster biomass in this experiment equals all of the living and dead oysters attached to each other in the cluster. Six clusters were placed equidistantly around the circumference of each reef. At the end of the experiment, we retrieved each cluster, rinsed and removed all attached organisms other than oysters and quantified the change in oyster cluster biomass (except at the central 1 site, which was excluded from the analysis of oyster cluster biomass).

Environmental and resource availability gradients

We monitored two environmental variables over the course of the experiment: water submergence and aerial temperature. First, we deployed a pressure gauge (Onset HOBO, U20-001-04) in a waterproof phone case on the benthos that recorded pressure at 20-min intervals. At each site, an additional gauge was secured above the water at a known elevation to account for atmospheric pressure changes. Subtracting data of the latter from the former yielded site-specific measurements of water level, which we used to estimate reef submergence. Second, the same loggers also quantified the maximum aerial temperature during low tide. Both of these data types were binned into 2-week intervals that matched the spring-neap tidal cycle. These binned data were averaged and used as site-specific metrics of tidal submergence and desiccation stress respectively. At the end of the experiment, we noticed differences in sediment accumulation among reefs. Because sediment accumulation on reefs impacts oyster growth and mortality (Lenihan 1999), we measured the burial depth of eight oyster clusters per reef from standardised locations. Although we equated this measurement to the amount of sediment that accumulated on a reef surface, we recognise that this metric also includes local subsidence, which could be significant and variable.

To estimate the supply of food to oysters and consumers, we sampled site-specific concentrations of water-column chlorophyll *a* and densities of juvenile oysters in the reef respectively. Chlorophyll *a* was sampled monthly via triplicate water samples at each site (250 mL; depth of 0.5 m). After collection, samples were immediately placed in the dark, transported on ice to the laboratory, filtered on GFF filters (Whatmann) and stored frozen. At a later date, these samples were extracted and analysed according to standard methods. Prior to the experiment, we quantified the natural abundance of juvenile oysters in each reef by haphazardly selecting six adult clusters, removing all organisms other than oysters, and quantifying their biomass and the density of newly recruited oysters. The ratio of juvenile oysters to cluster biomass was then multiplied by the average amount of reef biomass at each site to estimate initial spatial variation in juvenile oyster abundance.

Sediment accumulation experiment

We conducted a second field experiment to test whether mud crabs influence sediment accumulation on the oyster reef surface. At a site with high sediment accumulation and low oys-

ter recruitment in NW Florida, we selected five oyster reefs that were spaced 50 m apart. Within each reef, we deployed four plastic habitat trays (0.23 × 0.35 × 0.20 m) that were lined with mesh screen (12 × 12 mm openings) and contained 3.8 kg of loose dead oyster shell, two clusters of living oysters and six adult oyster shells with five juvenile oysters affixed on each. These six oysters were immobilised by being fastened to trays with cable ties. The trays were then randomly assigned among four treatments: (1) cage enclosure (mesh sides and top over the tray) with five adult mud crabs (> 20 mm carapace width); (2) cage enclosure with no mud crabs; (3) cage control with mesh sides but no top; and (4) no cage control (i.e. the tray only). Cages were used to control mud crab density, and juvenile oysters were deployed to standardise food availability for mud crabs. After 4 weeks, we recovered the six oyster shells with juvenile oysters attached and six haphazardly selected shells from each tray. At the laboratory, we quantified sediment accumulation by rinsing each shell, filtering the contents on to pre-weighed filter paper, drying at 60 °C for 24 h and weighing the sediment.

Data analyses of trophic manipulation experiment

The first field experiment produced site-specific results for direct predator effects on consumer foraging and consumer abundance, as well as how these interactions cascaded to influence oyster cluster biomass (a proxy for oyster reef production). Because oyster mortality in our feeding assays remained low in the absence of consumers, and because previous experiments showed that our predators do not appreciably increase juvenile oyster mortality (Grabowski *et al.* 2008), we equated oyster mortality in treatments with consumers to the foraging rate of consumers. For all three data types, we examined the residual variances of each treatment to verify conformance with parametric assumptions. When assumptions were met, we used univariate ANOVA to test whether the response variable depended on trophic level treatment (fixed effect), site (fixed effect), or the treatment × site interaction. We then used Tukey's *post hoc* test only to compare means of basal prey treatments across sites. For the oyster biomass production results, we also evaluated whether means ± 95% CIs contained the value of zero (no production), were above the value of zero (positive production), or were below the value of zero (negative production).

Direct and indirect predator interactions

To understand how predators influenced our results, we estimated their direct consumptive (CE) and non-consumptive (NCE) effects on consumer abundance (*A*) and consumer foraging (*F*). Because our analysis of *F* demonstrated a significant interaction between site and treatment – while our analysis of *A* did not – we calculated site-specific NCEs, but only one CE for the entire SAB.

$$CE = 1 - ([A_{p,c,o} - A_o]/[A_{c,o} - A_o]) \quad (1)$$

$$NCE = 1 - ([F_{p,c,o} - F_o]/[F_{c,o} - F_o]) \quad (2)$$

In (1–2), subscripts denote whether an experimental reef contained predators (p), consumers (c) and/or oysters (o). For

(1), the numerator used consumer abundance on each replicate reef with predators ($A_{p,c,o}$), whereas the denominator used the average of $A_{c,o}$ across all sites. The denominator consisted of an average value because each replicate of $A_{p,c,o}$ was not paired with a unique replicate of $A_{c,o}$ (see Trussell *et al.* 2008). To account for autogenic changes in the control reefs (i.e. oysters only), we subtracted the average A_o across all sites from both the numerator and denominator (Kimbrow 2012). This approach yielded 15 estimates of CE because data from the Central 1 site were not collected. In contrast to our CE calculations, the values of $F_{c,o}$ and F_o were calculated by averaging the foraging rate of consumers across all replicates *within a site*, yielding three estimates of NCE for each site (total $n = 18$).

To evaluate the indirect effect (IE) of predators on oysters, we used the same site-specific approach as (2). However, this calculation (3) concerned data on the change in oyster biomass (B) during the experiment.

$$IE = 1 - ([B_{p,c,o} - B_o] / [B_{c,o} - B_o]) \quad (3)$$

For the NCEs and IEs, we conducted a one-way ANOVA with site as a fixed factor. We also used the mean and 95% CI of each site to evaluate whether the effects of predators were positive (i.e. CI > zero), negative (CI < zero), or equal to zero (CI contains zero).

Identifying causal factors of biogeographic variation in predator effects

Because the NCEs and IEs differed among sites, we used a model-selection approach to investigate which variable(s) best explain this within-system variation. As previously discussed, we suspected that several physical and resource supply factors could be influential (Appendices S2–S3). Therefore, each response variable was related to a simple null model (intercept of 1) as well as a series of nested linear-mixed effects models that ranged from simple to complex, with site being designated as a random effect. The most parsimonious model was then identified according to Akaike's Information Criterion corrected for small sample sizes (AIC_c). In this procedure, models were ranked according to their Akaike weight (w_i), which was calculated as the model likelihood normalised by the sum of all model likelihoods; values close to 1 indicate greater confidence in the best model. Mean values were then plotted according to the best model (Burnham & Anderson 1998). When the best model contained two factors, we used partial correlations to assess the relationship between each predictor and the strength of the predator effect after first accounting for the influence of the other predictor.

Observed and expected trophic structure on US oyster reefs

From Grabowski *et al.* (2008), we extracted the mean (\pm SD) indirect effect of predators on oysters. These data were used to generate a normal distribution, from which we randomly selected 10 000 interaction strengths. From our monitoring results on southern oyster reefs, we extracted the mean (\pm SD) biomass of predators, generated a normal distribution and randomly selected 10 000 values. These two vectors of

data were then multiplied, which yielded 10 000 replicates of expected oyster biomass based on Grabowski *et al.* (2008) and the north-south increase in observed predator biomass (Fig. 1b). We plotted the mean (\pm 95% CI) of these expected values and used non-overlapping confidence intervals to determine whether it differed from the observed oyster biomass (Fig. 1d).

After obtaining site-specific estimates of the trophic cascade on southern *experimental* reefs, we obtained the mean (\pm SD) of these interaction strengths ($n = 6$) and used the aforementioned simulation procedure to reevaluate our expectation of oyster biomass.

Data analysis of sediment accumulation experiment

Using the aforementioned model-selection process, we examined whether the accumulation of sediment on the reef surface was better explained by a single-factor model distinguishing among treatments or a null model that did not. In these two models, reef was designated as a random effect and the alternative model was considered a better fit if its ΔAIC_c score exceeded that of the null model by a value of 2.0 (Richards 2005). Because the model with the treatment factor was stronger, we partitioned the data set into two treatment categories: treatments that did not exclude mud crabs and the enclosure treatment that did. We then examined whether sediment accumulation was better explained by a single-factor model distinguishing among treatment categories or a null model that did not. Finer scale partitioning among treatment means was not supported by model selection. All data were analysed with R 3.0.2 (The R Foundation for statistical computing, Vienna, Austria; available at: <http://www.R-project.org>).

RESULTS

Trophic manipulation

Consumer abundance

Final consumer abundance on oyster reefs depended on site and treatment, but not their interaction (Table 1a). While pair-wise differences among sites were not significant, significant differences were detected among treatments (Fig. 2a): recovery of consumers was highest on consumer-bivalve reefs and lowest on bivalve-only reefs, with an intermediate number recovered from predator–consumer-bivalve reefs.

Consumer foraging

The number of oysters eaten by consumers differed among treatments and these differences changed with site (Table 1b; Fig. 2b). In the absence of predators and consumers, oyster mortality was low at all sites. In contrast, in the presence of consumers and/or predators, oyster mortality due to consumer foraging varied across our sites.

Oyster reef biomass

Change in oyster cluster biomass (a proxy for reef production) differed among the treatments and these differences changed with site (Table 1c; Fig. 3a). On bivalve-only reefs, cluster biomass increased in the north and central SAB (i.e. 95% CI

Table 1 Results of univariate ANOVA for (a) the final abundance of consumers, (b) the foraging rate of consumers and (c) the change in oyster biomass; Results of ANOVA for (d) the direct influence of multiple predators on consumer foraging behaviour and (e) the indirect influence of multiple predators on oyster biomass production

	d.f.	Sum of Squares	Mean Squares	F-ratio	P-value
(a) Consumer abundance					
Treatment	2	2816.18	1408.09	36.79	<0.001*
Site	4	813.64	203.41	5.32	<0.05*
Treatment × Site	8	221.82	27.73	0.72	0.67
	30	1148	38.27		
(b) Consumer foraging rate					
Treatment	2	3.87	1.93	241.95	<0.001*
Site	5	0.43	0.09	10.65	<0.001*
Treatment × Site	10	0.51	0.05	6.44	<0.001*
	36	0.29	0.008		
(c) Oyster reef biomass					
Treatment	2	15 091	7545	9.37	<0.001*
Site	4	210 577	52644	65.37	<0.001*
Treatment × Site	8	28 552	3569	4.43	0.001*
	25	20 134	805		
(d) Strength of direct predator effects on consumer foraging					
Site	5	39.59	7.92	22.69	<0.001*
	12	4.19	0.35		
(e) Strength of indirect predator effects on oyster biomass					
Site	4	100.77	25.19	5.49	<0.05*
	9	41.29	4.58		

*Denotes significant statistical result ($P < 0.05$).

above zero). In the southern SAB, cluster biomass did not change significantly over the course of the experiment (i.e. 95% CI contains zero). On reefs with consumers and/or predators, changes in oyster cluster biomass were spatially idiosyncratic.

Direct and indirect predator interactions

The regional CE on consumer abundance was negative (-0.43 ± 0.22). In contrast, the site-specific NCEs on consumer foraging varied spatially (Table 1d; Fig. 2c). Predators suppressed consumer foraging at all sites except for central 1, with the strongest and weakest suppression occurring in the north 1 and central 2 sites respectively. This spatial variation was strongly linked to the natural abundance of juvenile oysters within a reef (Appendix S2, Fig. 2c): as juvenile oyster abundance increased, the influence of predators on consumer foraging decreased ($R^2 = 0.82$; Fig. 2d).

The site-specific IEs on oyster cluster biomass also varied spatially: the positive IE in the north generally decreased towards the south (Table 1e; Fig. 3b). This variation was strongly explained by a single-factor model that included the accumulation of sediment on reefs (Appendix S3, Fig. 3c): with increasing sediment accumulation, the IE changed from positive to negative ($y = -0.8934x + 0.0976$, Adjusted- $R^2 = 0.98$; Fig. 4a). A second model including sediment accumulation and the natural abundance of juvenile oysters also received strong support (Appendix S3, Fig. 3c), with the IE shifting from positive to negative as resource supply increased ($y = -1.3594x - 2E-06$; Adjusted- $R^2 = 0.98$; Fig. 4b). Collectively, these two candidate models accounted for the majority of the total possible weight (0.73 of 1.0).

Observed and expected trophic structure on US oyster reefs

Based on Grabowski *et al.* (2008), we expected that the north-south increase in predator biomass would be accompanied by a stronger corresponding increase in oyster biomass (0.69 ± 0.013) than was observed (-0.26 ± 0.16 ; S1C). When we reevaluated this pattern with site-specific trophic cascades from our *experiment*, the directional outcome of expected oyster biomass matched that of the observed biomass (i.e. negative). However, this reevaluation did not improve the accuracy of expected oyster biomass when compared to observed biomass (-1.60 ± 0.05 vs. -0.26 ± 0.16).

Sediment accumulation experiment

In our second field experiment, sediment accumulation on the oyster reef surface was strongly explained by a model that distinguished among treatments ($w_i = 0.99$, Fig. 4c). In treatments that were isolated from mud crabs, we observed nearly twice the amount of sediment accumulation compared to treatments that were exposed to mud crabs ($w_i = 0.96$, $\Delta AICc > 2.0$).

DISCUSSION

This study demonstrates that the non-consumptive effect of predators on mid-trophic level consumers and the resultant indirect effects on oyster reefs vary throughout the south-eastern Atlantic Bight, even though the direct consumptive effects of predators do not. Multiple predator species in our *experiment* consistently ate a small fraction of consumers at all sites

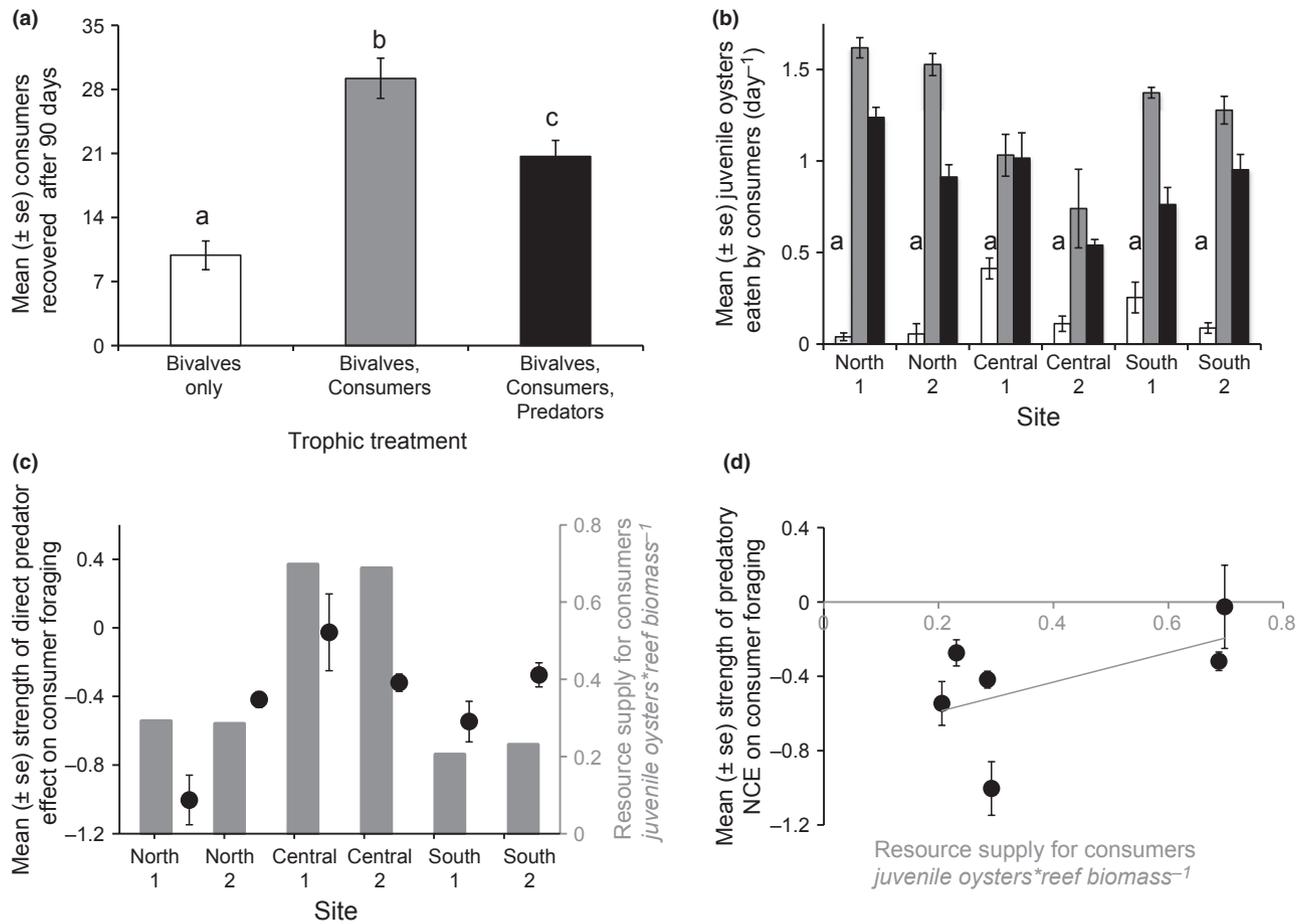


Figure 2 (a) Mean (\pm SE) density of consumers recovered on experimental oyster reefs after 90 days as a function of trophic treatment across all sites. (b) Mean (\pm 95% CI) foraging rate of consumers on juvenile oysters as a function of site and trophic level treatment. (c) At each site, the mean (\pm 95% CI) strength of direct predator effects on the foraging rate (closed circles) of consumers and the ambient supply of resources (grey bars) for consumers. (d) The relationship between the effect of predators on consumer foraging and the ambient supply of resources for consumers. For all panels, different letters indicate a significant mean comparison. In (a) and (b), open symbols refer to reefs with only bivalves, grey symbols refer to reefs with bivalves and consumers and closed symbols refer to reefs with bivalves, consumers and predators.

(Fig. 2a,c), but they inconsistently suppressed consumer foraging across sites (Fig. 2b,c). The cascading indirect effect on oyster reef production displayed even more spatial variation, with predators indirectly benefitting northern SAB oyster reefs and harming oyster reefs elsewhere (Fig. 3b). Because consumer abundances were consistent across sites at the end of the experiment, this spatial variation in trophic dynamics is most likely caused by an interaction between consumer behaviour and environmental gradients (Fig. 3c). Furthermore, the directional outcome of these spatially explicit results was congruent with observed patterns of oyster biomass on natural reefs throughout the south-eastern Atlantic Bight (Fig. 1b–e; S1).

Spatial variation in predation is common (Menge & Branch 2001; Freestone *et al.* 2011) and thus it is intriguing that the CEs of multiple predators were spatially uniform in our experiment. Admittedly, we did not allow for natural variation in the abundance and diversity of predators, one mechanism by which predation pressure may differ spatially in the SAB and elsewhere (Schemske *et al.* 2009; Freestone *et al.* 2011). In addition, had our experiment run longer and incor-

porated seasonality differences (i.e. colder winters in the north), or had we manipulated predator and consumer densities, we may have observed non-linear species interactions and more complex trophic dynamics. However, our sites encompassed substantial variation in multiple environmental gradients, including 10% variability in maximum aerial temperature, 40% variation in water submergence and 70% variation in resource availability to consumers. Thus, multiple predators combined to consistently affect consumer abundance despite considerable variation in environmental stress and resource availability, factors known to influence predation pressure (Gaines & Roughgarden 1985; Menge *et al.* 2003; Preisser *et al.* 2009). The refuge created by oyster reef structure may provide a solution to this apparent discrepancy: empirical (Grabowski 2004) and theoretical (Holt *et al.* 2010) work showed that refuges can minimise the strength of CEs and dampen unstable trophic dynamics by preventing consumer depletion. Because our experimental oyster reefs were constructed similarly across sites, the refuge value provided by these reefs may have consistently reduced the strength of CEs.

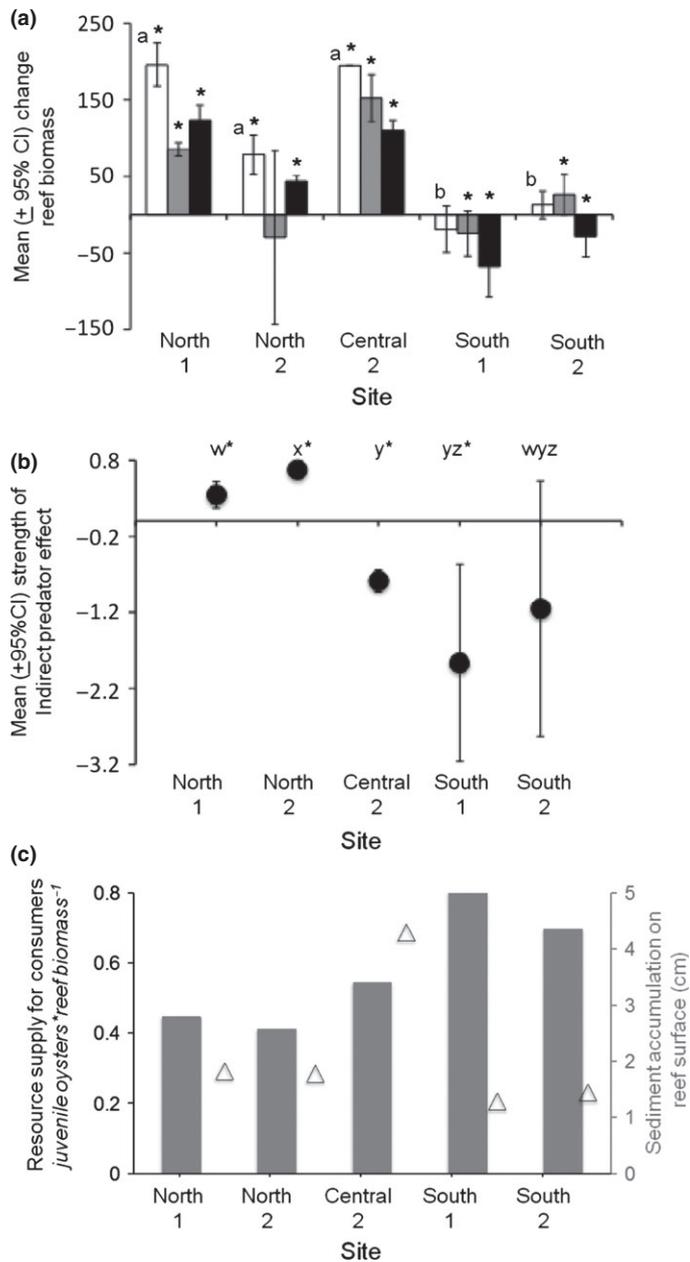


Figure 3 (a) Over 90 days, the mean (\pm 95% CI) of net oyster biomass production on experimental reefs. Open symbols refer to reefs with only bivalves, grey symbols refer to reefs with bivalves and consumers and closed symbols refer to reefs with bivalves, consumers and predators. An asterisk indicates a significant gain or loss in reef biomass. (b) Mean (\pm 95% CI) strength of indirect predator effect on oyster production over 90 days with an asterisk indicating either a significant indirect benefit (mean \pm 95% CI > 0) or an indirect cost (mean \pm 95% CI < 0). Different letters above means indicate a significant mean comparison. (c) Mean abundance of resources available to consumers (juvenile oysters per gram of experimental oyster reef, triangles) and mean accumulation of sediment on reef surface (grey bars).

Given that the CEs of predators were consistent, it is interesting to consider why the NCEs of predators were not (Fig. 2b,c). Predator effects on consumer foraging were inversely related to consumer resource availability (Fig. 2c,d). Although we did not directly manipulate this variable, the

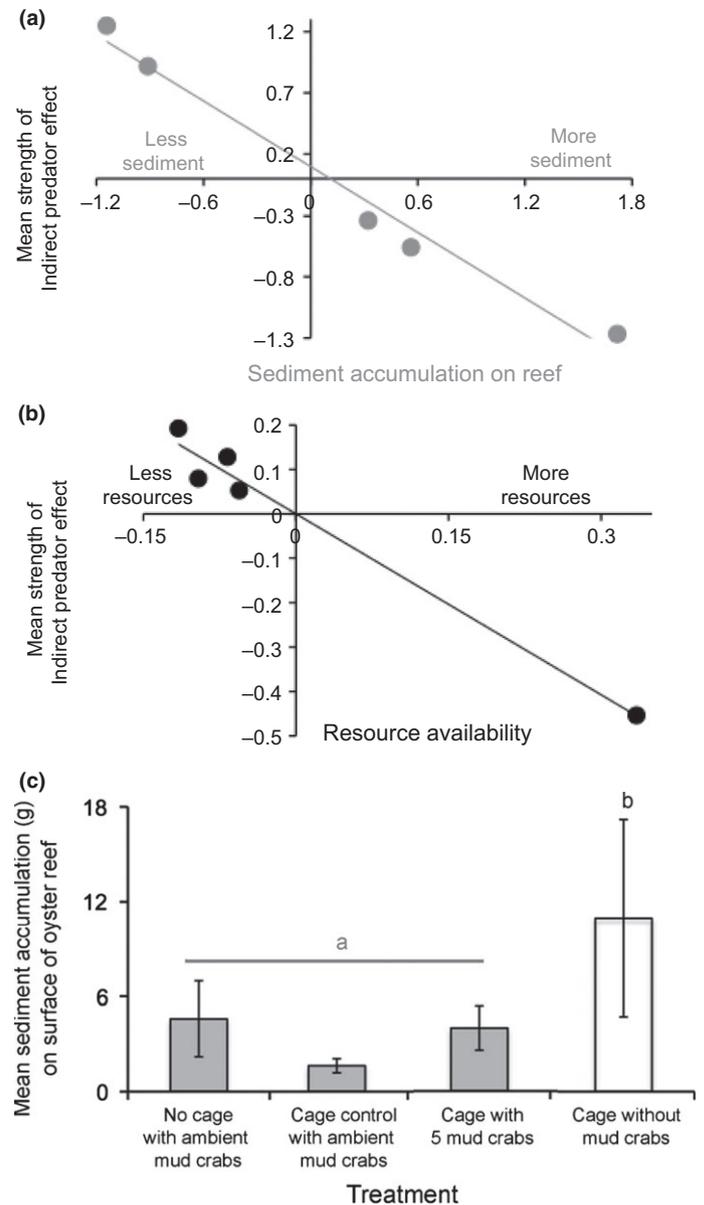


Figure 4 The partial correlation of the indirect predator effect on oyster production versus (a) the amount of sediment accumulation on the reef surface (grey line) and (b) the resource availability to consumers (black line). (c) From the second field experiment, the mean (\pm SE) of sediment accumulation across treatments that manipulated the presence of mud crabs. Open symbols refer to reefs with only bivalves and grey symbols refer to reefs with bivalves and mud crabs.

influence of resource availability is supported by previous work in this system (Grabowski 2004; Grabowski *et al.* 2008), and more broadly by studies on predator–consumer dynamics (Abrams 1991; Peacor 2002; Luttbeg *et al.* 2003). For instance, if the peak abundance of juvenile oysters that occurs on central reefs represents a spatially persistent elevation of resources, then the probability of consumer starvation should be lowest on central reefs. The consequences of reduced searching activity on energy income should thus be minimised on central reefs and maximised on northern and southern reefs (Abrams 1991). Therefore, the direct effect of predators

on consumer activity as well as consumer encounters with our focal resource may have been reduced on central reefs, where high resource availability minimises the need for consumers to search for food. Meanwhile, the higher probability of starvation in the northern and southern reefs may promote consumer foraging activity and encounters with our focal resource in the absence, but not presence of predators.

While NCEs on consumer foraging varied across our sites (coefficient of variation, $CV = -0.83$; Fig. 2c), variation in how these NCEs cascaded to oyster reef production doubled (i.e. over 60% greater; $CV = -2.17$; Fig. 3b). At first glance, this enhanced variability across trophic levels is surprising because predator effects typically attenuate with trophic transfer (Strong 1992; Shurin *et al.* 2002; Novak *et al.* 2011). However, this trophic attenuation of species interactions may be more relevant for the average interaction strength, and not its variance. In fact, it has long been suspected that direct effects are less variable than indirect effects in terms of direction (positive or negative) and strength, primarily because there are more opportunities for other factors to exert influence on indirect interactions (Wootton 2002). Our results suggest that this variability may be even more common for trophic cascades that are mediated by changes in consumer behaviour than consumer density.

Although the presence and strength of trophic cascades were variable throughout our study region, this variability was not random. Rather, it was explained by spatial gradients in resource supply and sediment accumulation (Fig. 3c). As we observed on our experimental reefs, enhanced resource supply can lead to decreased consumer movement (Abrams 1991). Furthermore, we showed that reduced consumer movement is associated with increased sediment accumulation on experimental reefs (Fig. 4c), particularly in areas where potential sediment loading is high such as in the southern SAB (Meade 1982). Thus, the net indirect predator effect on oyster reef production reflects a balance between the benefits of suppressed crab foraging on juvenile oysters and the costs of reduced foraging behaviour in terms of increasing sediment accumulation on living oysters.

Our biogeographic manipulation of a diverse tri-trophic oyster community demonstrated that the indirect effects of predators vary spatially, even though their direct effects on consumer abundance were relatively consistent. This suggests that even high-resolution knowledge about the consumptive effects of predators may be insufficient for predicting community and ecosystem dynamics across broad spatial scales, underscoring the need for integrating non-trophic interactions into food-web theory (Kefi *et al.* 2012). While this objective may initially seem futile given the uncertainty already associated with indirect interactions (Berlow 1999; Novak *et al.* 2011), we demonstrated that this uncertainty can reflect predictable influences of environmental and resource gradients on locally deterministic biotic interactions. Consequently, we suggest that the range in responses may be informative in and of itself, much as a recent research focus on variance in climate variables has been shown to produce better predictions and management options at smaller spatial scales (Ganguly *et al.* 2009; Ghosh & Katkar 2012). Accordingly, a focus on variance in species interactions may be nec-

essary for improving our understanding of within-system variation in trophic cascades such as that demonstrated by the trophic structure of oyster reef communities throughout the south-eastern US

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STATEMENT OF AUTHORSHIP

DLK, JEB, JHG, ARH and MFP jointly developed and conducted this study; DLK performed statistical analysis; DLK wrote the first draft while JEB, JHG, ARH and MFP edited and contributed to subsequent drafts.

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