

# Consumption pressure in coastal marine environments decreases with latitude and in artificial vs. natural habitats

Jonathan R. Rodemann<sup>1,2</sup>, Simon J. Brandl<sup>2,\*</sup>

<sup>1</sup>Marine Science Center, Northeastern University, Nahant, Massachusetts 01908, USA

<sup>2</sup>Tennenbaum Marine Observatories Network, Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USA

**ABSTRACT:** The biotic interactions hypothesis (BIH) is often cited as a driver for the latitudinal diversity gradient (LDG), yet few studies have quantified biotic interactions using standardized methods across a broad geographic range. Similarly, despite increasing interest in the ecological properties of man-made marine habitats, no large-scale comparisons of ecological processes in natural versus artificial habitats have been performed. Here, we used a simple, standardized consumption assay to test the BIH and its consistency in natural habitats and docks across 17° of latitude. We deployed 1205 ‘squidpops’ underneath and 10–15 m away from marine docks in 4 mid-latitude locations on the US east coast (Florida, North Carolina, Massachusetts, and Maine), and monitored the squidpops for consumption of the bait after 1 and 24 h. Consumption rates decreased significantly with latitude and were consistently higher away from docks as compared to underneath docks after 24 h. Our results indicate that, when controlling for prey and habitat type, there is a consistent latitudinal gradient in consumption pressure for a specific group of consumers, which supports the BIH as a potential driver of the LDG. Furthermore, the geographically consistent reduced rates of consumption under docks compared to nearby habitats indicate generality in reduced predation pressure in docks vs. natural habitats, which has previously been reported at local scales. Our results suggest that, despite high local-scale variability, docks and squidpops may provide a useful avenue for future large-scale ecological studies and aid the understanding of ecological processes in highly developed coastal marine ecosystems.

**KEY WORDS:** Latitudinal gradient · Predation · Top-down control · Fish · Ecosystem function · Biodiversity · Pier · Anthropogenic habitat

*Resale or republication not permitted without written consent of the publisher*

## INTRODUCTION

Although the latitudinal diversity gradient (LDG) is a well-established pattern in ecology, the main driving mechanisms have been extensively debated (Pianka 1966, Schemske 2002, Hillebrand 2004, Mittelbach et al. 2007). Three primary hypotheses currently exist to explain the LDG, distinguishing between evolutionary (Jablonski et al. 2006), ecological (Willig et al. 2003), and historical (Mittelbach et al. 2007) mechanisms. One prominent evolutionary theory is the biotic interactions hypothesis (BIH;

Schemske 2009). The BIH states that a global disparity of biotic interactions, with stronger interactions taking place closer to the equator, has resulted in increased rates of adaptation and speciation in the tropics, ultimately resulting in the LDG (reviewed by Schemske et al. 2009).

To date, evidence from a variety of systems supports the idea that biotic interactions are stronger in the tropics, including studies involving predation (Palmer 1979, Menge & Lubchenco 1981), herbivory (Coley & Barone 1996, Pennings & Silliman 2005, Becerra 2015), parasitism (Merino et al. 2008), and pollination

\*Corresponding author: brandls@si.edu

(Regal 1982). More recently, however, this evidence has been challenged. A wide range of literature contradicts the BIH and instead suggests that the BIH largely survives due to a citation bias (Moles & Ollerton 2016). In fact, several recent syntheses and empirical studies have shown that herbivory (Moles et al. 2011), predation (Harper & Peck 2016), and parasitism (Torchin et al. 2015) are not stronger in the tropics and may decrease at low latitudes. However, the vast majority of evidence against the BIH originates from herbivory studies (Moles et al. 2011, Moles & Ollerton 2016). In contrast, studies that investigate predation largely support the BIH (Jeanne 1979, Bertness et al. 1981, Heck & Wilson 1987, Peterson et al. 2001; but see Harper & Peck 2016). Nonetheless, there is a lack of biotic interaction studies along a broad geographical range (Schemske et al. 2009, Freestone et al. 2011), which impedes our ability to infer the mechanisms that structure local communities in a macroecological context.

Hairston et al. (1960) presented 3 means by which communities can be structured: bottom-up, top-down, and side-in. Bottom-up control, driven by primary production, has been well quantified on a global scale due to its perceived importance and the ease of data collection involving primary producers and herbivores (Field et al. 1998, Running et al. 2004, Elser et al. 2007). Side-in control (e.g. ecological perturbations) is also well studied, which is largely due to the increasing frequency and intensity of anthropogenic disturbances worldwide (see Richmond 1993). In contrast, despite the demonstrable effect of top-down control on lower trophic levels (Shears & Babcock 2002, Moore et al. 2003, Borer et al. 2006, Freestone et al. 2013), studies that investigate secondary consumption rates are rarely performed at regional or global scales (but see Freestone & Osman 2011, Freestone et al. 2011). Furthermore, a synthesis of trophic food web literature suggests that top-down control is stronger in aquatic systems than in terrestrial systems (Shurin et al. 2006). Consequently, there has been a recent push for large-scale, standardized studies to investigate the strength and impact of marine consumption rates in a comparative framework (Heck & Wilson 1987, Duffy et al. 2015, Meyer et al. 2015, Lefcheck et al. 2016). However, habitats often differ across latitudes and therefore impede standardization. While attempts to standardize marine predation studies have focused on using similar habitats across a latitudinal gradient, such as seagrass beds (Heck & Wilson 1987, Peterson et al. 2001) and rocky substrate (Menge & Lubchenco 1981), direct comparisons can be problematic due to regional dif-

ferences in foundation species. For example, Peterson et al. (2001) compared predation pressure in seagrass habitats in temperate (Maine; consisting of *Zostera marina*) and subtropical (Florida; consisting of *Thalassia testudinum*). Given the structural differences between the 2 species, the authors concluded that habitat-associated effects as well as latitude drive much of the observed variation. Thus, habitats that are consistent across latitudes may represent the most promising opportunity for large-scale studies of biotic interactions.

One habitat type that may satisfy the criterion of standardization and reproducibility across latitudes is the habitat emerging from the construction of anthropogenic structures in coastal environments, such as marine docks. As humans expand along shorelines, numerous artificial structures designed to bring ease-of-access and protection are built. As a consequence, these structures are now common along most coastlines on Earth (Bacchiocchi & Airoldi 2003, Bulleri & Chapman 2004), and different structures (e.g. docks, pontoons, jetties, breakwaters, etc.) can provide relatively homogeneous habitats, commonly situated in shallow, coastal environments. The accessibility and increasing prevalence of, for instance, docks in coastal areas have led to an ongoing investigation of ecological communities and processes associated with them. For example, invasive sessile epifauna species appear to thrive on artificial structures as compared to native species (Glasby et al. 2007, Dumont et al. 2011, Simkanin et al. 2012), with the uniformity and regularity of docks along coastlines creating a corridor for invasive species (Airoldi et al. 2015). Aside from intrinsic factors of dock pilings that may benefit invasive species (such as the material from which pilings are constructed or the strictly vertical orientation of dock pilings; Glasby 1999a, Connell 2001), another reason for the success of invasive species on dock pilings may be rooted in altered predation regimes and other ecological processes between artificial structures and their surrounding habitat (Simkanin et al. 2013, Rogers et al. 2016), for example mediated by the availability of light and primary production (Able et al. 1998, 2013, Grothues et al. 2016); thus, docks may represent a distinct habitat with specific ecological communities and processes (Glasby 1999b, Clynick et al. 2008, Pagliosa et al. 2012, Ferrario et al. 2016). However, evidence for altered ecological processes within dock-specific communities currently only exists for local scales, with no large-scale studies examining the consistency of specific alterations to ecosystem processes in artificial habitats such as marine docks.

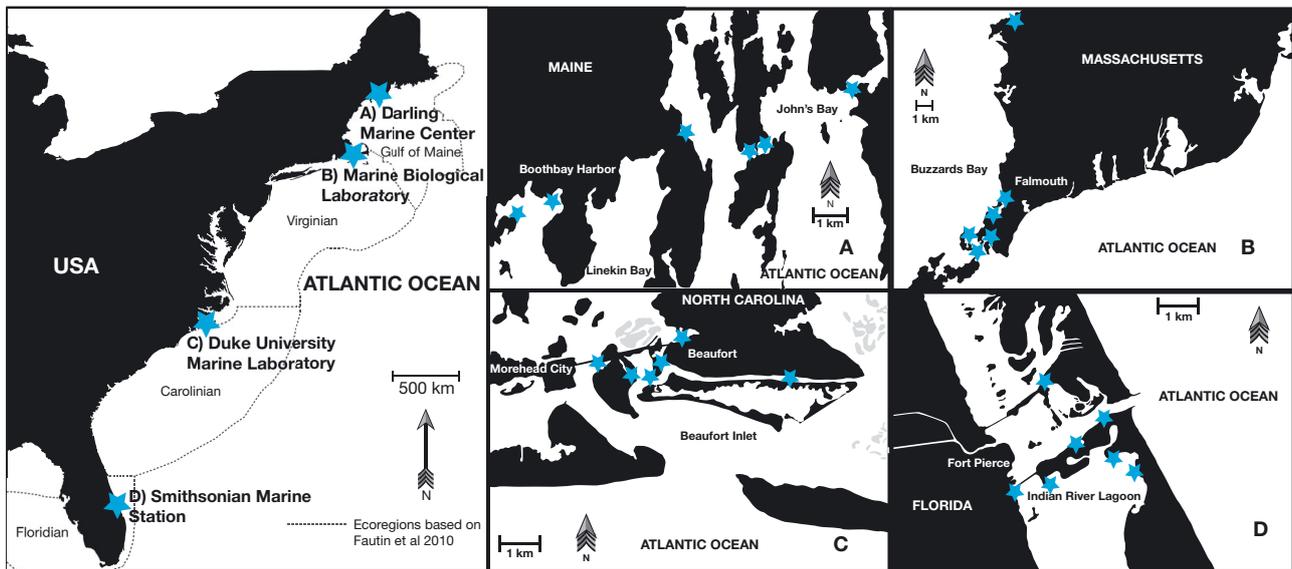


Fig. 1. Eastern US coast with sampling locations (stars) and ecoregions (dashed lines) outlined by Fautin et al. (2010). Sampling sites (stars) at each location: (A) Darling Marine Lab, Maine, (B) Marine Biological Laboratory, Massachusetts, (C) Duke University Marine Laboratory, North Carolina, and (D) Smithsonian Marine Station, Florida

Similar to problems arising from geographic variation in habitats, methodologies used to assess consumption often introduce unwanted geographic variation. Previous research has focused on tethering (Peterson et al. 2001), predator exclusion (Freestone et al. 2011), and shell repair (Bertness et al. 1981, Harper & Peck 2016). While these methods are useful, they are time consuming and, contingent on local prey, not standardized across studies. To address this issue, 'squidpops' have been proposed as a standardized, simple assay to assess consumption (Duffy et al. 2015; see 'Materials and methods' for more details). While squidpops have been shown to be an accurate proxy of relative consumption pressure by consumers capable and partial to feeding on small prey between habitats, depths, and seasons (Duffy et al. 2015), they have not yet been used to compare consumption pressure across a broad geographical scale.

Here, we used squidpops to investigate the biotic interactions hypothesis through a latitudinal comparison of consumption rates. Specifically, we sought to: (1) investigate consumption rates across a latitudinal gradient, (2) compare consumption rates between natural habitats and docks, (3) assess the local predator community, and (4) interpret these results in light of increasing marine urbanization and the need for standardized, large-scale experiments. We hypothesized that consumption will decrease with increasing latitude, supporting the biotic interactions hypothesis, and that consumption will be lower under docks because docks have been reported to

create adverse foraging conditions for piscine consumers (Duffy-Anderson & Able 1999), resulting in lower ambient predation pressure (Simkanin et al. 2013, Rogers et al. 2016).

## MATERIALS AND METHODS

### Study areas

Consumption was measured across 17° of latitude on the US east coast. In the summer months of June and July 2016, 4 locations were sampled: Maine (Darling Marine Center; 44°N, 70°W; 22–25 July), Massachusetts (Marine Biological Laboratory; 42°N, 71°W; 14–17 July), North Carolina (Duke University Marine Laboratory; 35°N, 77°W; 3–11 June), and Florida (Smithsonian Marine Station; 27°N, 80°W; 17–24 June; Fig. 1). Six (North Carolina, Massachusetts, Maine) to 7 (Florida) sites were chosen at each location. Each site contained a dock that was easily accessible and located in waters with fully marine salinity (on average >30 ppt). In addition, the dock had to be situated in an environment that also featured an area of open water 10–15 m from the dock. Both habitats (under docks or away from docks) were subtidal with depths between 0.45 and 3.2 m at low tide, with depth varying consistently among sites at each location.

At each site, the coarse characteristics of the benthos (seagrass, sand, mud) were recorded as well as

the time of the initial deployment. While type of benthos was not standardized between sites (because dock selection was performed independent of ambient habitat), habitat was always consistent within sites (i.e. underneath and away from the docks). Google Earth was then used to determine the exact latitude of each dock, the above-water surface area of each dock sampled, the average distance between sites at every location, and the distance each site exhibited to open ocean. Due to regional characteristics in human settlement patterns and the accessibility of shoreline, standardization of distances among sites was impossible. 'Open ocean' was defined as the dark blue bathymetric contour in Google Earth. A summary of the conditions and location of each dock is provided in Table 1.

### Data collection

To quantify consumption, we used squidpop assays, which represent a standardized, simple, and relatively rapid method of measuring consumption

(Duffy et al. 2015). Each squidpop was made from a 60 cm fiberglass garden stake with a circular piece of dried squid 1.3 cm in diameter attached to the top with a thin (6 or 8 pound test monofilament) fishing line and electrical tape (for more detail, see Duffy et al. 2015 and Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m574p167\\_supp.pdf](http://www.int-res.com/articles/suppl/m574p167_supp.pdf); also see the link in the Supplement for squidpop visualization). After assembly, the squidpops were bundled together in groups of 25 and transported to the site; 50 squidpops were deployed at every site, including under the dock (n = 25) and 10–15 m away from the dock in open water (n = 25). Deployment was accomplished on snorkel by driving the squidpops into the substrate in 2 rows while positioning them 0.5–1 m apart (Fig. S1). The time of deployment was recorded and split into 3 categories: morning (09:00–12:00 h), midday (12:00–15:00 h), and afternoon (15:00–18:00 h). Squidpops were monitored and scored after 1 h and then again after 24 h. If the bait was still present (partial or fully), a score of 0 was assigned. Otherwise, a score of 1 was given.

Table 1. Characteristics of the study docks. The date, time, and benthos are as recorded at the time of deployment. Depth (under and 10–15 m away from dock) was estimated at the time of deployment and then later standardized to depth at low tide using tide tables. Dock area and distance to open ocean were measured using Google Earth. SMS: Smithsonian Marine Station, ODD: Opposite Duke Dock, MBL: Marine Biological Laboratory

Location	Site	Coordinates	Date (mo/d/yr)	Time of day (h:min)	Depth under (m)	Depth away (m)	Benthos	Dock area (m <sup>2</sup> )	Distance to open ocean (km)
Florida	Blade's dock	27.47° N, 80.30° W	6/23/2016	12:30	1.57	1.57	Sand	107.71	1.46
Florida	Ft. Pierce Yacht Club	27.46° N, 80.32° W	6/22/2016	12:45	1.60	1.85	Sand	48.16	4.36
Florida	Little Jim's	27.48° N, 80.31° W	6/22/2016	12:15	1.60	1.10	Sand	104.97	3.56
Florida	Mariner's Bay	27.45° N, 80.29° W	6/24/2016	13:00	3.07	1.57	Mud	665.02	6.80
Florida	SMS dock	27.46° N, 80.31° W	6/17/2016	11:00	2.12	1.62	Sand	136.69	4.78
Florida	Sunburst	27.46° N, 80.30° W	6/17/2016	14:00	2.00	1.75	Mud	111.54	2.42
Florida	Thumb Point	27.46° N, 80.29° W	6/21/2016	09:30	1.35	1.35	Sand	333.36	6.54
North Carolina	Boat ramp	34.71° N, 76.63° W	6/7/2016	17:30	2.00	2.00	Mud	213.41	6.99
North Carolina	Condo complex	34.71° N, 76.68° W	6/9/2016	13:00	1.00	1.50	Sand	101.86	3.67
North Carolina	Dive shop	34.72° N, 76.67° W	6/9/2016	18:00	1.75	1.50	Mud	317.32	5.75
North Carolina	Duke dock	34.71° N, 76.67° W	6/3/2016	14:00	1.75	2.25	Mud	100.54	4.62
North Carolina	ODD	34.72° N, 76.67° W	6/11/2016	12:00	0.45	0.95	Sand	10.47	4.10
North Carolina	Snug Harbor	34.72° N, 76.68° W	6/7/2016	14:00	0.66	0.92	Mud	123.79	5.22
Massachusetts	Academy	41.54° N, 70.66° W	7/14/2016	12:30	1.74	1.99	Seagrass	84.16	3.73
Massachusetts	Eel Pond	41.53° N, 70.67° W	7/16/2016	11:00	1.45	1.45	Mud	168.22	4.81
Massachusetts	Fiddler's Cove	41.65° N, 70.64° W	7/17/2016	15:00	1.80	2.05	Mud	434.80	12.40
Massachusetts	MBL dock	41.52° N, 70.67° W	7/16/2016	10:30	1.99	2.24	Seagrass	140.75	4.46
Massachusetts	Quissett Harbour	41.54° N, 70.65° W	7/14/2016	14:00	3.20	1.70	Mud	191.56	4.10
Massachusetts	Woods Hole Yacht Club	41.53° N, 70.68° W	7/17/2016	17:00	2.04	2.04	Seagrass	179.51	4.51
Maine	Aquarium	43.84° N, 69.64° W	7/25/2016	10:00	1.75	1.75	Sand	141.07	9.27
Maine	Gamage shipyard	43.86° N, 69.56° W	7/23/2016	17:00	1.50	1.75	Mud	538.53	6.97
Maine	Ocean Point Marina	43.87° N, 69.58° W	7/24/2016	22:00	3.00	2.50	Mud	546.94	7.85
Maine	Pemaquid Fort	43.88° N, 69.52° W	7/24/2016	15:00	2.00	2.50	Sand	153.50	5.92
Maine	The Gut	43.86° N, 69.55° W	7/22/2016	15:00	1.75	2.00	Mud	113.41	7.35
Maine	Tugboat Inn	43.85° N, 69.63° W	7/23/2016	11:00	2.25	2.00	Mud	568.91	9.70

To quantify predator communities, 2 types of underwater video were employed. The first underwater video method was baited remote underwater video (BRUV), which was used in Florida and North Carolina. BRUVs have been used regularly in recent years due to their ease of deployment and accuracy relative to other survey methods (Willis et al. 2000, Lowry et al. 2012). For the BRUVs, a 70 cm segment of PVC was inserted into a cinderblock for stabilization. A bait arm made from a 1 m segment of PVC was glued to the top parallel to the base. Vexar marine-grade mesh was folded into a 20 cm × 15 cm pouch and attached to the bait arm with zip-ties to form a bait bag. In order to attach GoPro cameras, a 5 cm segment of PVC with a hole drilled near one edge was mounted on top of the bait arm over the stand. Once transported to the site, an equal mixture of frozen fish (menhaden *Brevoortia tyrannus*) and squid was placed in the bait bag. The BRUVs were deployed on snorkel both under the dock and in open water (approximately 2 m away from the squidpop array). The BRUVs were picked up after 1 h while monitoring the squidpops.

The success of the BRUVs was limited, and many videos did not capture any consumer species on video. For this reason, a second underwater video method was employed in Florida (at the final 2 sites, Little Jim's and Fort Pierce Yacht Club), Massachusetts, and Maine. GoPro cameras were taped to squidpop garden stakes, and once the squidpops were deployed, the GoPro apparatus was sunk into the substrate approximately 0.5 m from a squidpop, attempting to capture other squidpops in the background of the picture. Collection occurred while monitoring the squidpop assays after 1 h. This method was equally limited in its success at quantifying predator communities as the BRUVs, but had the advantage of not needing bait and being much more portable.

### Analysis

To quantify differences in consumption, we used the binary data from squidpops (0 = not eaten, 1 = eaten) to run 2 binomial generalized linear mixed models (GLMMs) for data collected after 1 h and after 24 h. For the first monitoring period (1 h), the effects of latitude (continuous), habitat (underneath the dock or away from the dock), and 3 abiotic factors (distance from open ocean [continuous], depth [continuous], and time of day [morning, midday, afternoon]) on consumption were analyzed. Benthos type

was not included in the 1 h analysis, as the exclusive occurrence of zero counts in habitats dominated by seagrasses induced complete separation, which precluded satisfactory model convergence. As the second monitoring included a full diurnal cycle, time of day of the deployment was omitted from the second GLMM (24 h), while all other predictor variables (including benthos type [seagrass, sand, mud]) were included. To account for the non-independent nature of each squidpop deployed at a given site, and the spatial correlation of sites with a given location, a random intercept was specified for site nested within location for both GLMMs. An interaction effect was specified between latitude and habitat to determine whether consumption rates varied consistently between natural and artificial habitats across latitude. Collinearity of all predictors was assessed using pairplots and Pearson correlation coefficients (Fig. S2 in the Supplement). The surface area of docks was not included as a predictor, as it was strongly collinear with the distance of sites to open ocean (i.e. larger marinas are commonly located in more sheltered areas, farther away from open ocean), which significantly impacted model convergence. Model fit for both full models (the 1 and 24 h models) was assessed using marginal and conditional  $R^2$ -values, and visually by superimposing mean values and 95% confidence intervals obtained from model predictions on the raw data. In a separate model including only dock surface area as a predictor for squidpop consumption, dock surface area was non-significant and explained limited variation in squidpop consumption ( $R^2 = 0.09$ ). All continuous predictors were scaled and centered prior to analyses to facilitate comparison of model parameter estimates.

Due to the methodological inconsistencies in the visual censuses of potential predator species and the limited success of both census techniques, no statistical treatment of the data was performed. However, in order to provide data on the presence/absence of different predator species across locations, underwater videos were analyzed for mobile fishes. The most common families and species at each location were identified. To visualize the difference in the community composition of mobile consumers among locations and habitats, multidimensional scaling (MDS) ordinations were performed using the Jaccard distance metric for presence-absence data. Sites with 0 occurrences of species ( $n = 11$ ) were excluded from this analysis. All statistical analyses were run using R version 3.3.1 (R Core Team 2016) and the packages *vegan*, *lme4*, and *merTools* (Bates et al. 2015, Knowles & Frederick 2016, Oksanen et al. 2016).

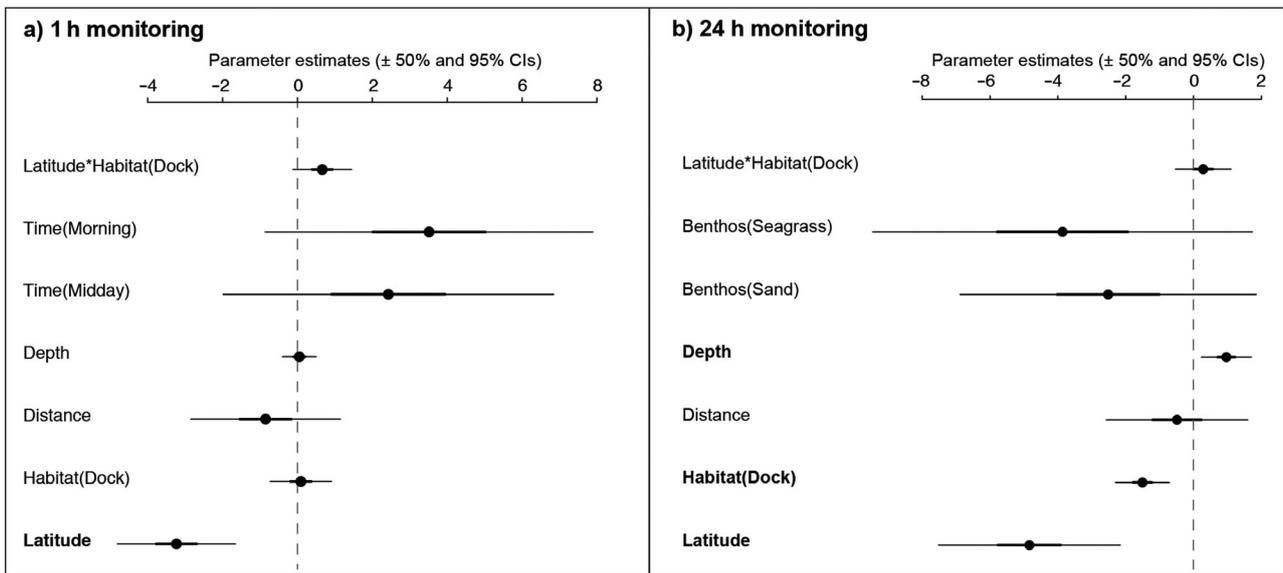


Fig. 2. Standardized parameter estimates ( $\pm 50\%$  and  $95\%$  CIs, thick and thin black lines, respectively) for binomial generalized linear mixed models (GLMMs) after (A) 1 h and (B) 24 h. All continuous predictors were scaled and centered (mean = 0, SD = 1) prior to the modeling procedure. Estimates for levels of categorical predictor variables relate to the reference level (Habitat: away from the dock; Time: after-noon; Benthos: mud), which are included in the 0 intercept. Significant ( $p < 0.05$ ) effects are highlighted in **bold**

**RESULTS**

Overall, 1205 squidpops were deployed, 231 of which were eaten after 1 h and 871 (including the 231 after 1 h) of which were eaten after 24 h. Consumption exhibited significant variation across latitude after both 1 h (standardized parameter estimate  $\beta = -3.234 \pm 0.805$  [SE],  $p < 0.0001$ ) and 24 h ( $\beta =$

$-4.840 \pm 1.369$ ,  $p = 0.000406$ ; Fig. 2). Specifically, approximately half of the bait was eaten after 1 h in Florida (52%), whereas less than 17% of the bait was consumed in North Carolina (16.9%), Massachusetts (0.7%), and Maine (0.4%). After 24 h, most of the squidpops were eaten in Florida (99%) and North Carolina (94%) while the proportion lost was considerably less in Massachusetts (50%) and Maine (40%)

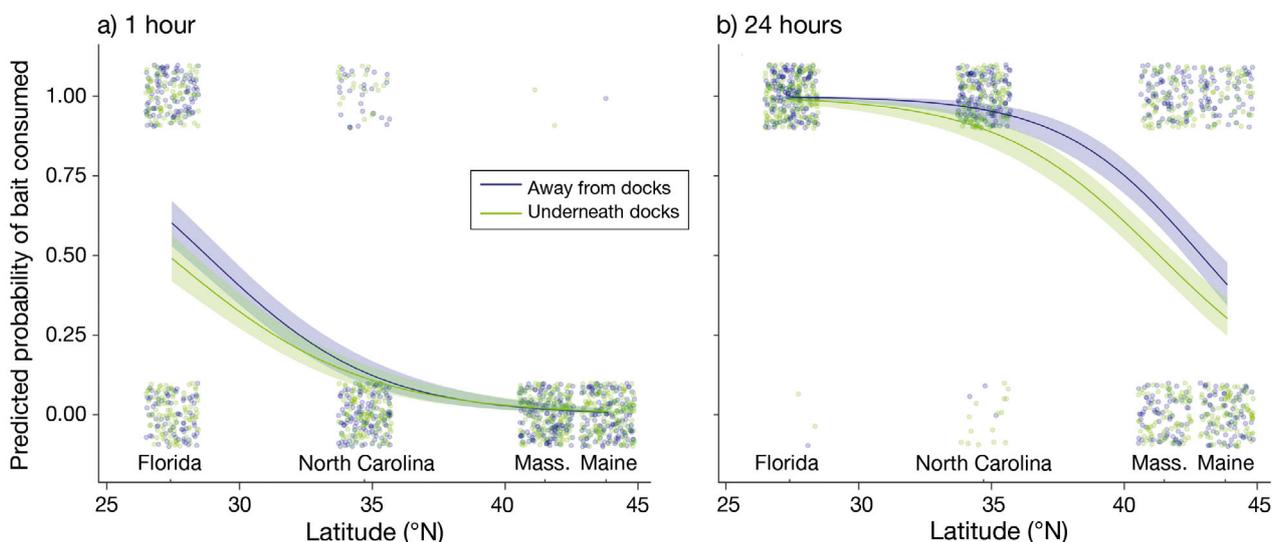


Fig. 3. Probability of bait consumption across latitudes and habitats after 1 and 24 h. The trendlines mark the predicted probability ( $\pm 95\%$  CI, shading) of bait being consumed both away (blue) and under the docks (green) obtained from the binomial generalized linear mixed models (GLMMs). Point clouds centered on 1 and 0 on the y-axis represent superimposed binary raw data (i.e. bait eaten = 1, bait not eaten = 0) with a random, constrained jitter applied to facilitate detection of patterns

(Fig. 3). The difference between consumption in natural and artificial habitats was less pronounced (Figs. 2 & 3. After 1 h, 18% of bait was lost under docks and 21% was lost away from the docks across latitudes, resulting in a non-significant effect of habitat (Dock:  $\beta = 0.091 \pm 0.418$ ,  $p = 0.828$ ). However, in Florida, the amount consumed away from the dock was considerably higher (57%) than under the dock (47%). After 24 h, overall consumption was significantly higher in natural (away from the dock; 77% eaten) compared to artificial (under the dock; 68% eaten) habitats (Dock:  $\beta = -1.508 \pm 0.408$ ,  $p = 0.000203$ ). In contrast to the 1 h measurement, Florida was the only location where bait loss was undistinguishable between habitats after 24 h (100% eaten away from the dock and 99% eaten under the dock). There was no significant interaction between habitat and location after both 1 h and 24 h (Latitude×Habitat:  $p = 0.099$  and  $p = 0.499$ , respectively). There was no effect of depth, distance to ocean, and time of day after 1 h (Depth:  $p = 0.827$ ; Distance:  $p = 0.404$ ; Time [midday]:  $p = 0.281$ ; Time [morning]:  $p = 0.116$ ). After 24 h, there was also no effect of distance to ocean or benthos type (Distance:  $p = 0.645$ ; Benthos [seagrass]:  $p = 0.176$ ; Benthos [sand]:  $p = 0.258$ ). While there was a weak effect of depth on consumption after 24 h ( $\beta = 0.965 \pm 0.376$ ,  $p = 0.010$ ), visual inspection and exclusion of depth showed that depth contributed little to explaining regional patterns ( $\Delta R^2$  upon exclusion of depth  $< 0.01$ ) and appeared to be spuriously related to within-site patterns of consumption across depth (see Table S1 in the Supplement).

Despite limited success of the predator census methods, the predator communities exhibited clear differences across locations (Table 2). Florida was dominated by the families Haemulidae and Lutjanidae, North Carolina was dominated by the Sparidae and Serranidae, Massachusetts was dominated by the Sparidae and Labridae, and Maine was dominated by the Gadidae. White grunts *Haemulon plumierii* were detected in 29% of videos in Florida, but no other predatory species was seen in more than 1 video. In North Carolina, pinfish *Lagodon rhomboides* were observed in 50% of videos. Scups *Stenotomus chrysops* were seen in 66% of videos in Massachusetts; however, striped bass *Morone saxatilis* were also frequently observed (55%) at this location. Videos from Maine showed only 1 dominant species: pollock *Pollachius virens* were seen in 40% of videos, but no other predator species was seen in more than 1 video. The MDS ordination of species composition showed clear differences among locations, with a weak overlap between Florida and Maine due to the

Table 2. Families and species of fish observed in the underwater videos. Numbers in parentheses represent the proportion of videos in which the species was observed at each location

Location/Most common families	Species
<b>Florida</b>	
Haemulidae, Lutjanidae	<i>Haemulon plumierii</i> (0.29)
	<i>Lutjanus griseus</i> (0.21)
	<i>Diplodus holbrooki</i> (0.21)
	<i>Menidia menidia</i> (0.21)
	<i>Chaetodinterus faber</i> (0.14)
	<i>Lutjanus mahogoni</i> (0.14)
	<i>Centropomus undecimalis</i> (0.14)
	<i>Lutjanus synagris</i> (0.14)
	<i>Sphyraena barracuda</i> (0.07)
	<i>Pomacanthus arcuatus</i> (0.07)
	<i>Archosargus probatocephalus</i> (0.07)
	<i>Kyphosus sectatrix</i> (0.07)
	<i>Eugerres plumierii</i> (0.07)
<i>Ariopsis felis</i> (0.07)	
<i>Dasyatis sabina</i> (0.07)	
<b>North Carolina</b>	
Sparidae, Serranidae	<i>Lagodon rhomboides</i> (0.50)
	<i>Centropristis striata</i> (0.17)
	<i>Chaetodipterus faber</i> (0.17)
	<i>Anguilla rostrata</i> (0.08)
	<i>Fundulus</i> sp. (0.08)
<i>Sphoeroides maculatus</i> (0.08)	
<b>Massachusetts</b>	
Sparidae, Labridae	<i>Stenotomus chrysops</i> (0.66)
	<i>Morone saxatilis</i> (0.55)
	<i>Tautoga onitis</i> (0.44)
	<i>Centropristis striata</i> (0.44)
	<i>Tautoglabrus adspersus</i> (0.44)
	<i>Brevoortia tyrannus</i> (0.11)
<b>Maine</b>	
Gadidae	<i>Pollachius virens</i> (0.40)
	<i>Menidia menidia</i> (0.20)
	<i>Morone saxatilis</i> (0.10)
	<i>Centropristis striata</i> (0.10)
	<i>Doryteuthis pealeii</i> (0.10)
<i>Tautoglabrus adspersus</i> (0.10)	

presence of silversides *Menidia menidia* at both locations (Fig. 4).

## DISCUSSION

We used a standardized, large-scale experiment to investigate consumption across a latitudinal gradient and between an artificial and adjacent natural habitat. After deploying 1205 squidpops, consumption varied significantly across latitude, with a clear increase towards the tropics. These findings are consis-

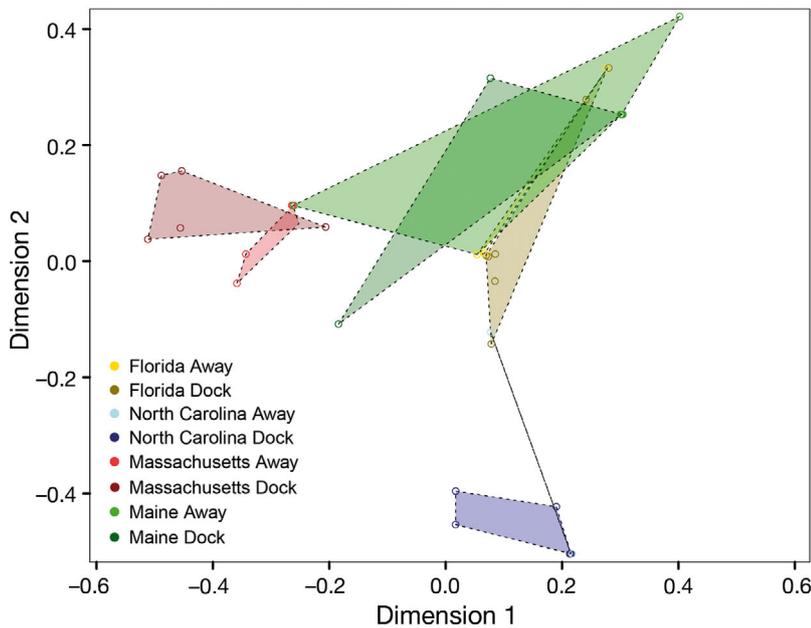


Fig. 4. Community composition differences in mobile consumers across locations and habitat types, as represented by a multidimensional scaling ordination with each open circle representing a specific site. Different shaded colors and dashed lines encompass all of the sites in specific locations and habitats (Dock: underneath dock; Away: 10–15 m away from dock) at the eastern US coast

tent with the growing literature base that asserts that species interactions are stronger at lower latitudes (Schemske et al. 2009, Freestone et al. 2011). Furthermore, we found that the amount of bait consumed away from docks was significantly (21%) higher than under docks after 24 h, suggesting that consumption pressure is lower under docks. While our findings may suggest differences in the biotic communities of natural versus artificial habitats, the lack of an interaction effect between habitat and location suggests that artificial habitats follow broad ecological paradigms, making them a potentially suitable model habitat for macroecological investigations.

### Consumption across latitude

We found a significant latitudinal gradient in consumption, supporting the BIH as a potential explanation for the LDG. Due to the relatively large latitudinal range of this study, several factors may have affected the observed consumption patterns. Biodiversity influences numerous ecosystem processes and has the capacity to affect predation rates in many systems (Ives et al. 2005), but its effects can be context specific. For example, an increase in predator diversity may promote intraguild competition and reduce predation pressure on lower trophic levels at

local scales (Finke & Denno 2004, Guidetti 2007). However, the opportunistic nature of foraging on squid-pops may temporarily release predators from competition because the prey is easily obtained; therefore, in this instance, higher biodiversity may provide a greater chance of consumption. It has long been documented that biodiversity increases at lower latitudes (reviewed by Gaston 2000), and this paradigm parallels the observed consumption rates found in this study.

Another factor that may affect consumption pressure are climatic differences. Our study spans 2 different climate zones: humid subtropical (Florida and North Carolina) and humid continental (Massachusetts and Maine). After 24 h, the locations in the humid subtropical climate had a consumption rate of >90% while the locations in the humid continental climate had a much lower consumption

rate (40–50%), which highlights the potential importance of climate and, most likely, temperature. Temperature is positively correlated with fish metabolism and fish richness (Gillooly et al. 2001, Bailly et al. 2014). In fact, Clarke & Johnston (1999) found that the metabolic rate (measured via resting oxygen consumption) of a tropical fish at 30°C is 6 times greater than that of a polar fish at 0°C. A lower metabolism means that less energy is required to perform vital activities, and therefore necessitates a lower amount of food (and predatory activity) to survive, which may contribute to the lower consumption rates observed in northern locations despite equal or higher abundance of consumer species.

In addition to spanning 2 climate zones, our study consists of areas in 2 Large Marine Ecosystems (LME) (Northeast United States Continental Shelf and Southeast United States Continental Shelf) as well as 3 ecoregions (Gulf of Maine, Virginian, and Floridian, with the Duke University Marine Laboratory on the border between the Virginian and the Carolinian ecoregions; Spalding et al. 2007, Fautin et al. 2010). Climate zones and ecoregions are due to physical differences in climate, currents, seafloor, and various other factors, and they substantially impact the species composition of a region. For example, within the Northeast United States Continental Shelf LME, the Virginian ecoregion shares only 40%

of its species with the Gulf of Maine ecoregion (Fautin et al. 2010). As observed in our underwater videos, each location harbors a distinct community of predators with different ecological requirements and feeding habits. Therefore, the diversity of life histories characterizing the consumer communities in these regions may have led to the variation in consumption rates. However, there was no significant difference in consumption rates between Maine and Massachusetts despite the different composition of consumer communities in the respective locations, and this suggests that many other factors contribute to the variation in consumption pressure across latitudes. Overall, our findings are largely consistent with the prevailing hypotheses concerning consumption rates across latitudes and indicate that the variation among locations is driven by a variety of abiotic and biotic factors that could be further disentangled in future studies.

### **Consumption between a natural and artificial habitat**

Our study provides the first standardized, large-scale comparison of consumption rates between an artificial habitat (docks) and a nearby natural habitat. Interest in artificial marine habitats is increasing due to the burgeoning abundance of these structures worldwide (Seaman & Sprague 1991). However, investigations into the ecological properties of anthropogenic structures only began in the late 1990s (e.g. Able et al. 1998, Connell & Glasby 1999), and many ecological differences between natural and man-made habitats remain unquantified beyond local assessments. In line with our initial hypothesis and much of the available evidence from studies on docks (Able et al. 2013, Simkanin et al. 2013, Rogers et al. 2016), we found a consistently lower consumption rate under docks compared to habitats away from docks across latitudes after 24 h. However, this provides results in contrast to the potential attraction of large, predatory fish to anthropogenic structures (Claisse et al. 2014). While there is support for higher consumption rates under docks due to an increased abundance of predatory species (Rilov & Benayahu 1998), our findings support previous evidence for reduced ecological activity, such as predation, under docks compared to natural habitats (Simkanin et al. 2013, Rogers et al. 2016). Specifically, 2 local studies found that fish abundance and diversity were reduced under piers in the Pacific Northwest and in the northeastern USA (Able et al. 2013, Munsch et al.

2014). Furthermore, in one of those studies, fish abundance was highest around the edges of the dock, approximately where the natural habitat squidpops were located (Munsch et al. 2014). We have demonstrated that the apparent reduction in consumer pressure under docks is consistent beyond local scales, which suggests generality in the observed disparity. While the effect for the 24 h period was relatively weak and there was no significant difference between artificial and natural habitats after 1 h, our data suggest that effects may be stronger if a higher frequency of monitoring the squidpops were employed. Specifically, Florida exhibited a higher consumption rate in the natural habitat compared to the artificial habitat after 1 h while the other 3 sites exhibited the same trend after 24 h. This disparity is rooted in the resolution provided by the 1 and 24 h time points. Floridian sites lost 50% of the bait after 1 h, which suggests that most of the bait was consumed within 2 h of deployment. Therefore, differences after 24 h would be indiscernible. In contrast, almost no bait was consumed in either habitat after 1 h at the 2 northernmost sites, which again prevents the detection of habitat-specific differences. However, the effect after 24 h at these northern sites was relatively robust.

The lower consumption rate underneath docks may be due to specific aspects of docks that influence ambient conditions. Docks (or any overhead structure) reduce the availability of light (Able et al. 1998, 2013) and block incoming photosynthetically active radiation, therefore inhibiting growth of benthic primary producers (Glasby 1999b, Pagliosa et al. 2012). The lack of submerged aquatic vegetation and macroalgae reduces the benthic complexity, which effectively reduces the amount of habitat and, consequently, the abundance of prey and consumers (Pagliosa et al. 2012). Furthermore, Duffy-Anderson & Able (1999) used the growth rates of juvenile fish to determine that foraging conditions under docks are suboptimal due to reduced foraging efficiency and increased prey-handling time, primarily due to the sparsity of light (Able et al. 1998, 2013). Another factor to consider is artificial lighting around docks. Artificial lighting at night (ALAN) has been shown to influence trophic interactions, causing reduced fish density but higher predation pressure (Bolton et al. 2017). Given that many docks are subject to ALAN, it is possible that introduced lighting in the vicinity of docks may have influenced the slight disparity between the 1 and 24 h time points (i.e. significantly lower predation directly underneath docks only after 24 h). While changes in light regimes are likely to be

important, the novelty of overhead structures may also deter fish. Edifices such as docks do not exist in nature; therefore, fish may be wary to swim underneath these structures during the day despite their attraction to submerged overhead structures in natural habitats (Toft et al. 2007, Kerry & Bellwood 2015). The different responses to docks compared to natural overhead structures may be rooted in the fact that docks are relatively high above the benthos. As a result, as compared to submerged overhead structures such as tabular corals, docks provide little shelter from avian and piscine predators and leave prey species exposed in the water column. In this context, we note that pollock *Pollachius virens*, which are usually found in deeper water (Cargnelli et al. 1999), were seen in our study feeding in the relatively shallow bays of Maine. Yet, when observed via underwater video, 75% of the sightings were away from the dock, suggesting a possible aversion to docks due to reduced light or the presence of a novel structure and again supporting a peak in abundance in the vicinity, rather than directly underneath docks (Munsch et al. 2014).

### Evaluating the applied methods

Squidpops are designed to 'provide reliable, standardized data within 24 h on relative rates of feeding by common generalist predators' (Duffy et al. 2015, p. 15). Our study supports this statement; a clear, overarching pattern in consumption was found across latitudes as well as a significant distinction among habitats at the end of deployment. However, our results also show extreme site-specific variability. Although some of this variability may be induced by site-specific abiotic or biotic factors that are unquantified in the present study (e.g. predator density, habitat-specific light regimes, pollution, fishing pressure), some of the variability is likely also attributable to the method itself. For example, the presence of a single fish may determine the fate of the bait on many squidpops in an assay. Two sites in North Carolina experienced unusually high rates of bait loss (>90%) after the first hour. Corresponding with the high consumption measurement was the presence of the northern puffer *Sphoeroides maculatus*, seen both through video and visual observations. *S. maculatus* is known to be an extremely opportunistic feeder that has strong, parrot-like jaws and prefers a sand bottom (Sibunka & Pacheco 1981, Fraser et al. 2012). The benthic composition of these 2 sites was sandier than the other sites in North Carolina (Table 1). Furthermore, the fishing

line used to secure the squid bait was cut at one of the sites, which suggests that a single individual *S. maculatus* may have been responsible for at least part of the high rates of consumption. In addition, 2 *Haemulon plumieri* were seen consuming at least 4 squidpops at 1 site in Florida. While these anecdotal observations along with the high site-specific variability suggests that subtle, site-specific patterns in consumption may be difficult to disentangle using squidpops, our results clearly show that the high level of noise present at single sites is easily overridden by large-scale geographic patterns, especially if adequate statistical techniques that allow for the specification of site-level random effects are employed.

While stochasticity of the squidpop method is difficult to reduce, but can be addressed through analytical means, sufficient replication, and possibly a more detailed quantification of the prevailing biotic and abiotic conditions at each site, there are several other techniques that may increase the robustness of measurements taken. However, we note that none of these improvements is likely to make squidpops a panacea to disentangling predation strength. An increased frequency of monitoring would provide results on a finer scale and potentially parse out random variability based on physical factors, but strongly decreases the user-friendliness of the squidpop method. Varying bait size may also improve the method. Duffy et al. (2015) stated that it is very difficult for smaller fish (<10 cm in size) to remove the bait from a squidpop. If smaller bait was used along with the normal bait size, feeding rates of smaller as well as larger fish can be included and lead to a better understanding of the overall consumption pressure. Finally, the bait could be attached at varying heights on the garden stake to measure consumption intensity of multiple predation types. In Maine, the abundance of benthic invertebrate predators seen on the underwater video was considerably higher than at the other 3 locations. Therefore, it is possible that benthic invertebrates play a much more significant role in the food web at higher latitudes. Adding a piece of bait to the bottom of the stake would potentially allow for a quantification of the role of these species. However, it is possible that both methods will simply cause species already feeding on the squidpops to consume more.

In terms of assessing predator communities, both of the underwater video methods were unsuccessful and only yielded qualitatively valuable data. This may be due to a variety of factors, including visibility and species interactions. Visibility was relatively low at sites of BRUV deployment (North Carolina and Florida)

and could have resulted in the low numbers of fish seen. Similarly, in the northern latitudes where the squidpop video was deployed (Massachusetts and Maine), little to no consumption took place within the first hour and therefore resulted in a low number of fish seen. Furthermore, Lowry et al. (2012) suggested that fast-acting species may 'colonize' the bait early on, which may exclude other species from interacting with the BRUV. The minimal results may also be a consequence of the randomness of mobile marine predators. Developing a 'game camera' apparatus might improve this method. Peterson et al. (2001) developed an underwater design for a chronographic tethering device that was able to record the exact time that a piece of tethered bait was taken through the completion of an electrical circuit. This same concept could be used to create a photographic device that records the identity of a consumer when the bait from a squidpop is taken. While this technique may be expensive and technologically difficult due to the limitation of waterproofing, the data provided would more accurately depict the diversity of species feeding on squidpops. Other potential methods of quantifying the predator community would be underwater visual censuses and angling, although these methods also have inherent biases (Willis et al. 2000).

### Conclusion

Our results show that consumption pressure strongly and predictably varies across 17° of latitude along the US east coast, which supports the biotic interactions hypothesis. We further demonstrate that consumption rates are consistently lower under docks compared to nearby undeveloped areas, which suggests generality in the locally reported differences between docks and natural habitats in terms of ecosystem functioning. Given the increasing prevalence of large-scale, anthropogenic disturbances on ecosystems, global studies are becoming more and more essential to our understanding of ecological patterns and processes, as well as the effects of human influence on the biosphere. While not without limitations, the methods and results presented in the present study may provide a good stepping stone for future standardized, reproducible studies over a large geographic scale. In addition, we suggest that the future investigation of artificial habitats such as docks may aid our understanding of anthropogenic impacts on ecological processes, as these habitats are often situated in environments where anthropogenic pressure is high and ever-increasing.

**Acknowledgements.** The study was funded by the Tennenbaum Marine Observatories Network (S.J.B.) and Northeastern University (J.R.R.). We thank the staff of the Smithsonian Marine Station at Fort Pierce, Duke University Marine Laboratory, the Marine Biological Laboratory in Woods Hole, and the Darling Marine Center for field support, S. Broadhurst, W. Grossman, C. Rigaud, S. Reed, and E. Beltt for field assistance, and J. E. Duffy, J. M. Casey, G. Marafino, and 3 anonymous reviewers for comments on earlier drafts of the manuscript. S.J.B. was supported by a MarineGEO postdoctoral fellowship. This is contribution 14 from the Smithsonian's MarineGEO Network.

### LITERATURE CITED

- Able KW, Manderson JP, Studholme AL (1998) The distribution of shallow water juvenile fishes in an urban estuary: the effects of manmade structures in the lower Hudson River. *Estuaries* 21:731–744
- Able KW, Grothues TM, Kemp IM (2013) Fine-scale distribution of pelagic fishes relative to a large urban pier. *Mar Ecol Prog Ser* 476:185–198
- Airolidi L, Turon X, Perkol-Finkel S, Rius M (2015) Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Divers Distrib* 21:755–768
- Bacchiocchi F, Airolidi L (2003) Distribution and dynamics of epibiota on hard structures for coastal protection. *Estuar Coast Shelf Sci* 56:1157–1166
- Bailly D, Cassemiro FA, Agostinho CS, Marques EE, Agostinho AA (2014) The metabolic theory of ecology convincingly explains the latitudinal diversity gradient of Neotropical freshwater fish. *Ecology* 95:553–562
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Software* 67:1–48
- Becerra JX (2015) On the factors that promote the diversity of herbivorous insects and plants in tropical forests. *Proc Natl Acad Sci USA* 112:6098–6103
- Bertness MD, Garrity SD, Levings SC (1981) Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution* 35:995–1007
- Bolton D, Mayer-Pinto M, Clark G, Dafforn K, Brassil W, Becker A, Johnston E (2017) Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. *Sci Total Environ* 576:1–9
- Borer ET, Halpern BS, Seabloom EW (2006) Asymmetry in community regulation: effects of predators and productivity. *Ecology* 87:2813–2820
- Bulleri F, Chapman M (2004) Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. *Mar Biol* 145:381–391
- Cargnelli L, Griesbach SJ, Packer DB, Berrien PL, Johnson DL, Morse WW (1999) Essential fish habitat source document: pollock, *Pollachius virens*, life history and habitat characteristics. Tech Memo NMFS-NE 131. Northeast Fisheries Science Center, Woods Hole, MA
- Claissie JT, Pondella DJ, Love M, Zahn LA, Williams CM, Williams JP, Bull AS (2014) Oil platforms off California are among the most productive marine fish habitats globally. *Proc Natl Acad Sci USA* 111:15462–15467
- Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *J Anim Ecol* 68:893–905
- Clynick B, Chapman M, Underwood A (2008) Fish assem-

- blages associated with urban structures and natural reefs in Sydney, Australia. *Austral Ecol* 33:140–150
- ✦ Coley PD, Barone J (1996) Herbivory and plant defenses in tropical forests. *Annu Rev Ecol Syst* 27:305–335
- ✦ Connell SD (2001) Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. *Mar Environ Res* 52:115–125
- Connell SD, Glasby TM (1999) Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. *Mar Environ Res* 47:373–387
- ✦ Duffy JE, Ziegler SL, Campbell JE, Bippus PM, Lefcheck JS (2015) Squidpops: a simple tool to crowdsource a global map of marine predation intensity. *PLOS ONE* 10: e0142994
- ✦ Duffy-Anderson JT, Able KW (1999) Effects of municipal piers on the growth of juvenile fishes in the Hudson River estuary: a study across a pier edge. *Mar Biol* 133:409–418
- ✦ Dumont CP, Harris LG, Gaymer CF (2011) Anthropogenic structures as a spatial refuge from predation for the invasive bryozoan *Bugula neritina*. *Mar Ecol Prog Ser* 427: 95–103
- ✦ Elser JJ, Bracken ME, Cleland EE, Gruner DS and others (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* 10:1135–1142
- ✦ Fautin D, Dalton P, Incze LS, Leong JAC and others (2010) An overview of marine biodiversity in United States waters. *PLOS ONE* 5:e11914
- ✦ Ferrario F, Iveša L, Jaklin A, Perkol Finkel S, Airoidi L (2016) The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. *J Appl Ecol* 53:16–24
- ✦ Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240
- ✦ Finke DL, Denno RF (2004) Predator diversity dampens trophic cascades. *Nature* 429:407–410
- ✦ Fraser GJ, Britz R, Hall A, Johanson Z, Smith MM (2012) Replacing the first-generation dentition in pufferfish with a unique beak. *Proc Natl Acad Sci USA* 109: 8179–8184
- Freestone AL, Osman RW (2011) Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity. *Ecology* 92:208–217
- ✦ Freestone AL, Osman RW, Ruiz GM, Torchin ME (2011) Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology* 92:983–993
- ✦ Freestone AL, Ruiz GM, Torchin ME (2013) Stronger biotic resistance in tropics relative to temperate zone: effects of predation on marine invasion dynamics. *Ecology* 94: 1370–1377
- ✦ Gaston KJ (2000) Global patterns in biodiversity. *Nature* 405:220–227
- ✦ Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293:2248–2251
- Glasby T (1999a) Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. *Estuar Coast Shelf Sci* 48:281–290
- ✦ Glasby T (1999b) Effects of shading on subtidal epibiotic assemblages. *J Exp Mar Biol Ecol* 234:275–290
- ✦ Glasby TM, Connell SD, Holloway MG, Hewitt CL (2007) Nonindigenous biota on artificial structures: Could habitat creation facilitate biological invasions? *Mar Biol* 151: 887–895
- ✦ Grothues TM, Rackovan JL, Able KW (2016) Modification of nektonic fish distribution by piers and pile fields in an urban estuary. *J Exp Mar Biol Ecol* 485:47–56
- ✦ Guidetti P (2007) Predator diversity and density affect levels of predation upon strongly interactive species in temperate rocky reefs. *Oecologia* 154:513–520
- ✦ Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425
- ✦ Harper EM, Peck LS (2016) Latitudinal and depth gradients in marine predation pressure. *Glob Ecol Biogeogr* 25: 670–678
- ✦ Heck KL, Wilson KA (1987) Predation rates on decapod crustaceans in latitudinally separated seagrass communities: a study of spatial and temporal variation using tethering techniques. *J Exp Mar Biol Ecol* 107:87–100
- ✦ Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163:192–211
- ✦ Ives AR, Cardinale BJ, Snyder WE (2005) A synthesis of sub-disciplines: predator–prey interactions, and biodiversity and ecosystem functioning. *Ecol Lett* 8:102–116
- ✦ Jablonski D, Roy K, Valentine JW (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106
- ✦ Jeanne RL (1979) A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1224
- ✦ Kerry J, Bellwood D (2015) Do tabular corals constitute keystone structures for fishes on coral reefs? *Coral Reefs* 34: 41–50
- ✦ Knowles J, Frederick C (2016) merTools: tools for analyzing mixed effect regression models. R package version 0.3.0. <https://CRAN.R-project.org/package=merTools>
- ✦ Lefcheck JS, Brandl SJ, Reynolds PL, Smyth AR, Meyer ST (2016) Extending rapid ecosystem function assessments to marine ecosystems: a reply to Meyer. *Trends Ecol Evol* 31:251–253
- ✦ Lowry M, Folpp H, Gregson M, Suthers I (2012) Comparison of baited remote underwater video (BRUV) and underwater visual census (UVC) for assessment of artificial reefs in estuaries. *J Exp Mar Biol Ecol* 416–417:243–253
- ✦ Menge BA, Lubchenco J (1981) Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol Monogr* 51:429–450
- ✦ Merino S, Moreno J, Vásquez RA, Martínez J and others (2008) Haematozoa in forest birds from southern Chile: latitudinal gradients in prevalence and parasite lineage richness. *Austral Ecol* 33:329–340
- ✦ Meyer ST, Koch C, Weisser WW (2015) Towards a standardized Rapid Ecosystem Function Assessment (REFA). *Trends Ecol Evol* 30:390–397
- ✦ Mittelbach GG, Schemske DW, Cornell HV, Allen AP and others (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol Lett* 10:315–331
- Moles AT, Ollerton J (2016) Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica* 48:141–145
- ✦ Moles AT, Bonser SP, Poore AG, Wallis IR, Foley WJ (2011) Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Funct Ecol* 25:380–388
- ✦ Moore JC, McCann K, Setälä H, De Ruiter PC (2003) Top-down is bottom-up: Does predation in the rhizosphere

- regulate aboveground dynamics? *Ecology* 84:846–857
- ✦ Munsch SH, Cordell JR, Toft JD, Morgan EE (2014) Effects of seawalls and piers on fish assemblages and juvenile salmon feeding behavior. *N Am J Fish Manag* 34: 814–827
- ✦ Oksanen J, Kindt R, Legendre P, O'Hara B and others (2016) *Vegan: community ecology package 10*. R package version 2.4-1. <https://CRAN.R-project.org/package=vegan>
- ✦ Pagliosa PR, Cantor M, Scherner F, Otegui MBP and others (2012) Influence of piers on functional groups of benthic primary producers and consumers in the channel of a subtropical coastal lagoon. *Braz J Oceanogr* 60:65–73
- ✦ Palmer AR (1979) Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* 33:697–713
- ✦ Pennings SC, Silliman BR (2005) Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. *Ecology* 86:2310–2319
- ✦ Peterson BJ, Thompson KR, Cowan JH Jr, Heck KL Jr (2001) Comparison of predation pressure in temperate and subtropical seagrass habitats based on chronographic tethering. *Mar Ecol Prog Ser* 224:77–85
- ✦ Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. *Am Nat* 100:33–46
- R Core Team (2016) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. [www.r-project.org/](http://www.r-project.org/)
- ✦ Regal PJ (1982) Pollination by wind and animals: ecology of geographic patterns. *Annu Rev Ecol Syst* 13:497–524
- ✦ Richmond RH (1993) Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *Am Zool* 33:524–536
- ✦ Rilov G, Benayahu Y (1998) Vertical artificial structures as an alternative habitat for coral reef fishes in disturbed environments. *Mar Environ Res* 45:431–451
- ✦ Rogers TL, Byrnes JE, Stachowicz JJ (2016) Native predators limit invasion of benthic invertebrate communities in Bodega Harbor, California, USA. *Mar Ecol Prog Ser* 545: 161–173
- ✦ Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H (2004) A continuous satellite-derived measure of global terrestrial primary production. *Bioscience* 54:547–560
- Schemske DW (2002) Ecological and evolutionary perspectives on the origins of tropical diversity. In: Chazdon RL, Whitmore TC (eds) *Foundations of tropical forest biology: classic papers with commentaries*. The University of Chicago Press, Chicago, IL, p 163–173
- Schemske D (2009) Biotic interactions and speciation in the tropics. In: Butlin RK, Bridle JR, Schuller D (eds) *Speciation and patterns of diversity*. Cambridge University Press, Cambridge, p 219–239
- ✦ Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annu Rev Ecol Evol Syst* 40: 245–269
- Seaman W, Sprague LM (1991) *Artificial habitats for marine and freshwater fisheries*. Academic Press, San Diego, CA
- ✦ Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* 132:131–142
- ✦ Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc R Soc Lond B Biol Sci* 273:1–9
- Sibunka J, Pacheco A (1981) Biological and fisheries data on northern puffer, *Sphoeroides maculatus* (Bloch & Schneider). Tech Ser Rep 26. Northeast Fisheries Center, NMFS, NOAA, US Department of Commerce, Highlands, NJ
- ✦ Simkanin C, Davidson IC, Dower JF, Jamieson G, Therriault TW (2012) Anthropogenic structures and the infiltration of natural benthos by invasive ascidians. *Mar Ecol* 33: 499–511
- ✦ Simkanin C, Dower JF, Filip N, Jamieson G, Therriault TW (2013) Biotic resistance to the infiltration of natural benthic habitats: examining the role of predation in the distribution of the invasive ascidian *Botrylloides violaceus*. *J Exp Mar Biol Ecol* 439:76–83
- ✦ Spalding MD, Fox HE, Allen GR, Davidson N and others (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57:573–583
- ✦ Toft JD, Cordell JR, Simenstad CA, Stamatidou LA (2007) Fish distribution, abundance, and behavior along city shoreline types in Puget Sound. *N Am J Fish Manag* 27: 465–480
- ✦ Torchin ME, Miura O, Hechinger RF (2015) Parasite species richness and intensity of interspecific interactions increase with latitude in two wide ranging hosts. *Ecology* 96:3033–3042
- ✦ Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu Rev Ecol Evol Syst* 34:273–309
- ✦ Willis TJ, Millar RB, Babcock RC (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Mar Ecol Prog Ser* 198:249–260

Editorial responsibility: Konstantinos Stergiou, Thessaloniki, Greece

Submitted: November 17, 2016; Accepted: April 19, 2017  
Proofs received from author(s): June 17, 2017