

Consistent spatial patterns in multiple trophic levels occur around artificial habitats

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ABSTRACT: With increasing global rates of urbanization, it is important to understand the ecological functions of artificial structures. One way to assess the ecological functions of such structures is to test whether they function similarly to natural habitats. In marine systems, naturally occurring structured habitats, such as coral reefs and rocky reefs, support aggregations of planktivorous fish, often inducing spatial patterns in prey and predators. Whether similar spatial patterns occur around submerged artificial structures, which often have more abrupt topographies than natural habitats, remains less well understood. We tested whether consistent spatial patterns in planktivorous fish, their prey (zooplankton), and their predators (piscivorous fish) were present around artificial structures. We first documented spatial distributions of these 3 trophic groups around 15 marine artificial structures (shipwrecks) using acoustic surveys and then asked how spatial distributions of each trophic group relate to the others. We found that the center of planktivorous fish aggregations occurred an average of 39 m from habitat edges. Zooplankton prey were detected throughout nearly 25 % of surveyed areas around habitats. Piscivorous fish predators concentrated closest to habitats. Further analyses revealed that these patterns sometimes related to environmental factors, such as water current magnitude and direction. Because spatial distributions of planktivorous fish, their prey, and their predators were consistent across sampled artificial structures, our findings suggest that artificial structures influence spatial patterns across adjacent trophic levels. This finding adds to a growing body of evidence that artificial habitats provide important ecological functions.

KEY WORDS: Artificial structure · Artificial reef · Reef fish · Fisheries acoustics · Shipwreck · Splitbeam echosounder · Trophic ecology

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1. INTRODUCTION

Global rates of urbanization are increasing (Seto et al. 2012), and coastlines experience particularly concentrated development because one-third of humans reside within 100 km of coasts (Dugan et al. 2012).

However, urbanization is no longer restricted to terrestrial and shoreline environments and now extends beneath the ocean surface, a phenomenon known as 'marine urbanization' or 'ocean sprawl' (Bulleri & Chapman 2010, Dafforn et al. 2015), characterized by introduction of urban or artificial structures to coastal

waters. These artificial structures range from wind turbines and oil and gas rigs to artificial reefs and shipwrecks. Introducing artificial structures to marine environments can drive ecological changes (Buleri & Chapman 2010), such as altering habitat connectivity, which can change the spatial arrangement and movement of organisms (Bishop et al. 2017). As such, understanding ecological functions of artificial structures is timely and important.

One way to assess ecological functions of such artificial structures is to test whether they function similarly to natural habitats. Many marine artificial structures emerge off the seafloor well into, or extending throughout, the water column and create 'abrupt topographies' (Genin 2004), which can be compared to naturally abrupt topographies. On naturally abrupt topographies, such as coral reefs (Hamner et al. 1988, 2007) and rocky reefs (Bray 1980, Gaines & Roughgarden 1987), aggregations of planktivorous fish consistently occur. Here, we use 'aggregation' to refer to groups of animals formed by any mechanism, whether passive or active (Simard et al. 1986). Aggregations of planktivorous fish spatially associate with zooplankton prey (Hamner et al. 1988, Genin 2004). For example, on coral reefs, planktivorous fish can form a 'wall of mouths' by concentrating in large schools near up-current sections of reefs, consuming zooplankton transported towards reefs (Hamner et al. 1988, 2007). Similarly, on rocky topographies with kelp forests, planktivorous fish, such as juvenile rockfishes, consume zooplankton transported towards kelp forests (Gaines & Roughgarden 1987). In both coral reefs and rocky reefs, zooplankton become depleted after reaching dense schools of planktivorous fish that consume zooplankton (Gaines & Roughgarden 1987, Hamner et al. 1988); this depletion can lead to 'holes' in zooplankton biomass, creating increased patchiness (Genin et al. 1988). Similar spatial patterns occur near deeper abrupt topographies, such as seamounts, shelf breaks, and canyons, where aggregations of planktivorous fish consume zooplankton, often generating spatial gradients in zooplankton distribution (Genin 2004). Aggregations of planktivorous fish near both shallow and deep naturally occurring, structured habitats also have effects that propagate up food webs because piscivorous fish and other common predators, such as marine mammals, are attracted to and actively prey on planktivorous fish (by Genin 2004, Prairie et al. 2012).

Multiple mechanisms, including predator-prey dynamics and physical forcing (e.g. water currents), have been proposed to explain why elevated concentrations of planktivorous fish occur around habitats

classified as naturally abrupt topographies (Genin 2004, Genin et al. 2005). In shallow natural habitats, where zooplankton vertical migration is often less pronounced than in deep habitats, the most widely accepted explanation for elevated densities of planktivorous fish is that as water currents transport zooplankton towards both unstructured and structured habitats, planktivorous fish are attracted to structured habitats because they can both feed on incoming zooplankton and use structure for refuge (Genin 2004). While it can be competitively advantageous for planktivorous fish to feed as far into the oncoming stream of zooplankton as possible, there is a tradeoff between acquiring prey and seeking refuge from predators, with planktivorous fish experiencing higher foraging success but also reduced protection at greater distances from structured habitats (Bray 1980). Planktivorous fish may also experience a tradeoff as a function of water current strength. When water currents are too strong, planktivorous fish are unable to hold their position within the water column and often retreat to find refuge in holes and crevices located closer to the seafloor (Liao 2007, Johansen et al. 2008).

Because artificial structures offer similarly abrupt, or in some cases more abrupt, topographies than coral reefs, rocky reefs, and other types of emergent natural habitats, planktivorous fish would be expected to also aggregate near artificial structures. This expectation is supported by observations of planktivorous fish aggregations near artificial reefs (Rilov & Benayahu 1998, Champion et al. 2015). Comparisons of numbers of planktivorous fish between artificial reefs and nearby natural reefs suggest that sizes and likely effects of aggregations on artificial structures may exceed those around naturally occurring reefs (Arena et al. 2007, Simon et al. 2013). Zooplanktivory has been estimated to place artificial reefs among habitats with the highest global fish production (Champion et al. 2015, Smith et al. 2016). Despite documented prevalence of planktivorous fish on artificial structures, it is unknown whether spatial patterns in planktivorous fish occur consistently on artificial structures and how aggregations of planktivorous fish relate to spatial distributions of other trophic groups.

The goal of this study was to document spatial patterns in planktivorous fish, their prey (zooplankton), and their predators (piscivorous fish) around artificial structures. We specifically addressed the following questions: (1) where are planktivorous fish, their zooplankton prey, and their piscivorous predators relative to artificial structures and (2) how are spatial distributions of planktivorous fish, zooplankton, and

piscivorous fish related to each other around artificial structures? Answering these questions will determine whether patterns in planktivorous fish distributions and distributions of adjacent trophic levels occur consistently around artificial structures, potentially providing a key ecological function.

2. MATERIALS AND METHODS

2.1. Site selection

The artificial structures used in this study are 15 shipwrecks that rest on the continental shelf of North Carolina (NC), USA (Fig. 1; see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m611p189_supp.pdf), an area known as the ‘Graveyard of the Atlantic’ (Hoyt et al. 2014). Each shipwreck was selected because it has been submerged for over 50 yr in shallow water (<100 m) on the continental shelf of NC. Because the selected shipwrecks, which rest at depths between 18.9 and 98.6 m and sank between 1862 and 1957, are distributed haphazardly across the continental shelf and also form reefs that support a diversity of fishes (Paxton et al. 2017), they provide an opportunity to quantify planktivorous fish, zooplankton, and piscivorous fish distributions on artificial structures.

2.2. Surveys

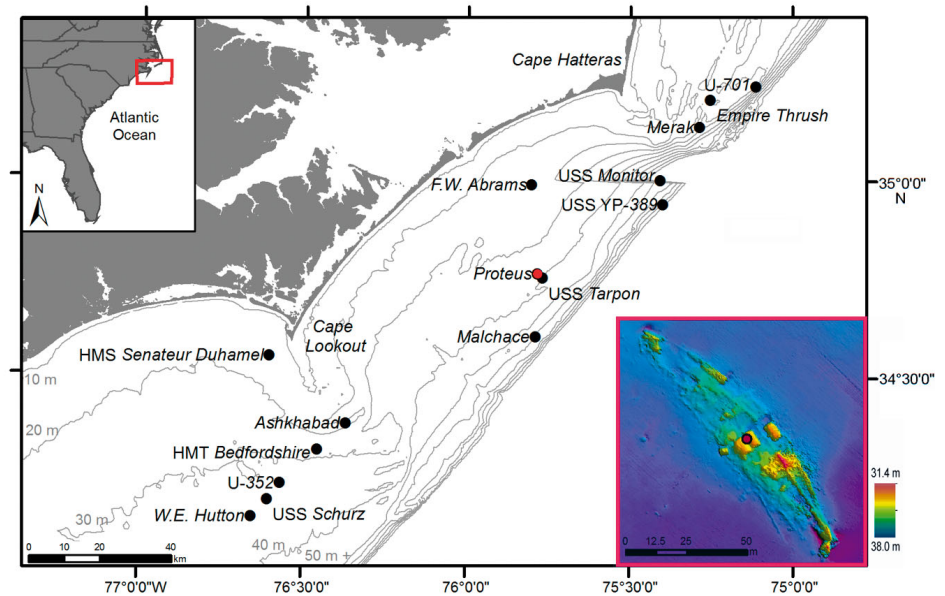
The 15 artificial structures were surveyed onboard the NOAA ship ‘Nancy Foster’ from 1–6 November 2016 and 5–14 July 2017 using hull-mounted instruments that measured bathymetry, zooplankton, several size classes of fish, and currents (Table S2 in Supplement 1). Each structure was surveyed at least once. During the November

cruise, 12 of the 15 artificial structures were each surveyed once using splitbeam echosounder (SBES) to measure zooplankton concentration and fish densities, and multibeam echosounder (MBES) to measure bathymetry. During July 2017, 5 artificial structures, including some of those previously surveyed in November 2016, were surveyed using not only SBES and MBES but also an acoustic Doppler current profiler (ADCP) to measure currents. During the July 2017 surveys, several of the 5 artificial structures were surveyed multiple times to examine whether structure-specific patterns occurred repeatedly. Twenty surveys were conducted in total, all during the daytime between sunrise and sunset. The survey vessel traveled at a speed of about 7 knots during the surveys, and position was logged using differential GPS and an Applanix POS M/V motion sensor. All data were spatially referenced to North American Datum 1983 Universal Transverse Mercator Zone 18 North.

2.3. Mapping shipwrecks

MBES (Reson 7125 SV2, 400 kHz) collected multi-beam bathymetry of each artificial structure at fine resolution (<1 m). Resolution was determined based on structure size and depth to ensure optimal coverage; this resulted in resolutions ranging from 0.15–0.40 m (Table S2 in Supplement 1). MBES operated with a 130° beam angle, emitting 512 beams downward into the water column. MBES data were corrected for changes in the speed of sound throughout

Fig. 1. Locations of 15 shipwrecks surveyed on the continental shelf of North Carolina, USA. Gray lines and corresponding text indicate water depth in 10 m increments. Insert shows multibeam bathymetry of the shipwreck ‘Proteus,’ with warm colors indicating shallower depths and cooler colors indicating deeper depths



the water, as well as tidal influence, static draft, latency, roll, pitch, yaw, and sensor offsets. Bathymetry data for each artificial structure were processed within ArcMAP version 10.5 (ESRI) using functions from the Spatial Analyst Extension to manually delineate each structure from the surrounding sand as a polygon and also identify the centroid. The resulting polygon and centroid data were exported as shapefiles used to determine distances of organisms to structure edges and the structure center, respectively.

Bathymetry maps of each artificial structure were also used onboard the survey vessel to create acoustic survey transect lines along which zooplankton, fish, and water currents would be measured later. Transect lines were created overlying the bathymetry maps in HYPACK version 16.0 (Xylem) so that multiple transect lines extended parallel to the major axis of each structure. Perpendicular to major-axis lines, we established cross lines along the minor axis of each structure. Spacing among lines and the lengths of the major- and minor-axis lines were determined based on the size of the structure as visible in bathymetry maps to ensure high spatial coverage necessary for quantifying zooplankton and fish using the SBES with a narrow beam angle for each individual structure (Fig. S1 in Supplement 1).

2.4. Quantifying fish and zooplankton

Fish and zooplankton were measured along the transect lines determined from multibeam bathymetry using SBES (SIMRAD EK60; 7° beam angle). SBES emitted sound pulses downwards into the water at 3 frequencies (38, 120, and 200 kHz) to detect zooplankton, fish, shipwreck structure, and the surrounding seafloor. For the 38 kHz frequency, the pulse length was 0.256 μ s, whereas for the 120 and 200 kHz frequencies, the pulse length was 0.128 μ s. To reduce acoustic interference among sonar transducers, SBES emitted pings when triggered by MBES so that the SBES ping rate was determined by MBES settings. SBES was calibrated using a tungsten carbide sphere to enable accurate measurements of fish size (Foote et al. 1987). SBES data, displayed as echograms, were processed with Echoview version 8.0 (Echoview Software Pty 2017, version 8.0) to quantify the spatial distributions of zooplankton and fish around each shipwreck (Supplement 1).

Within Echoview, individual fish and schools of fish were identified from the 120 kHz SBES data. Individual fish were identified with a fish tracking algorithm

that classified sequential acoustic targets as discrete fish (Echoview Alpha-Beta fish tracking algorithm). Schools of fish were delineated using a school detection algorithm (Barange 1994). Single acoustic targets corresponding to fish in school perimeters, where fish were loosely aggregated and visible as discrete individuals, were also identified using an acoustic threshold, which permitted calculation of fish size for schools. This method assumes that fish in the periphery of schools are the same species and same size as those within the center of schools.

Data for individual fish and fish schools were exported from Echoview in cells measuring 5 m (horizontal) \times 1 m (vertical, depth) using a threshold of -65 dB. Exported data were processed within R version 3.3.2 (R Core Team 2016) to calculate individual and schooling fish density per cell on a linear scale. Resulting individual fish and schooling fish densities were summed to obtain total fish density, as well as densities corresponding to 3 fish size classes: small (<11 cm length), medium (11–29 cm), and large (>29 cm). Size classes were selected based on observations from previous visual surveys (Paxton et al. 2017). While fisheries acoustics cannot discriminate species, we assume that the fishes detected belong to representative fish species also observed by Paxton et al. (2017) in a nearby study area (Table S3 in Supplement 1). Size classes were assigned using the general logarithmic equation for the relationship between mean target strength (TS_{mean}) and fish total length (L_{fish} , cm) based on Love (1977):

$$L_{\text{fish}} = 10^{(TS_{\text{mean}} + 64.0035)/19.2} \quad (1)$$

Resulting data included per cell values for densities of both total fish and fish separated by size classes (fish m^{-3}). See Supplement 2 for additional details on delineating and quantifying fish.

Zooplankton were identified from SBES data using decibel differencing by comparing mean volume backscattering strength (S_v) detected by echosounders operating at multiple discrete frequencies (Higginbottom et al. 2000, Korneliusson & Ona 2003). Decibel differencing was conducted in Echoview using data from the 38 and 120 kHz transducers. Prior to decibel differencing, 120 kHz data were resampled so that their pulse length matched the pulse length of 38 kHz transducer data. Zooplankton were delineated from 38 kHz data as areas where acoustic signatures from 38 kHz data were less than corresponding acoustic signatures from 120 kHz data. Following decibel differencing, zooplankton delineated in 38 kHz data were exported from Echoview in 5 m (horizontal) \times 1 m (vertical, depth) cells using a

–65 dB threshold. Within R, zooplankton data were converted from logarithmic form (dB re 1 m⁻¹) to linear form (m⁻¹) to calculate the volume backscattering coefficient (s_v) of zooplankton per cell, which we refer to as zooplankton concentration. See Supplement 2 for additional details.

2.5. Quantifying water currents

The hull-mounted ADCP (Teledyne RDI Ocean Surveyor 150 kHz) recorded magnitude and direction of water currents in 2 m vertical bins above and around artificial structures. ADCP data were processed in Matlab v. 2017b (The Mathworks) by separately averaging east–west and north–south velocity components throughout the entire water column and across the spatial extent of the ADCP survey to obtain mean velocity components for each survey. These depth-averaged mean velocity components were used to calculate current magnitude and direction for each survey. See Supplement 3 for additional details.

2.6. Data analyses

Fish, zooplankton, and current data were analyzed in R. Per cell values of zooplankton relative concentration (m⁻¹), small fish density (fish m⁻³), medium fish density (fish m⁻³), and large fish density (fish m⁻³) were each summed vertically across the water column. The resulting depth-collapsed values for each (zooplankton area concentration [m²] and fish area density [m²] per size class) were used for spatial analyses. Here, we call ‘small fish’ planktivorous, and we call ‘medium’ and ‘large fish’ piscivorous. Assigning fish size classes to trophic groups assumes that fish outside of the specified trophic groups would be more difficult to detect and thus would not bias these trophic classifications. For example, small fish in trophic groups that are highly associated with structure would often be difficult to distinguish from the structure itself, as would medium and large demersal fish that are also more highly associated with the structure. Additionally, our classifications assume that planktivorous fish are mainly <11 cm, which is supported by prior visual surveys in the same study location (Paxton et al. 2017). Similarly, our visual surveys indicate that medium and large fish likely to be easily detectable with fisheries acoustics are primarily piscivores. Of the planktivores and piscivores, select species are likely to be detected with fisheries

acoustics because their habitat association is more pelagic than demersal (Table S3 in Supplement 1). The demersal species usually remain close to the seafloor or structure and are difficult to distinguish using fisheries acoustics. These assumptions are all inherent to fisheries acoustic surveys, including ours. We report medium fish separately from large fish because the 2 different size classes help distinguish between candidate piscivorous fish species. Analyses were conducted for the organism groups for each of the 20 surveys with α values of 0.05 for statistical tests, unless otherwise noted. Many analyses included calculation of spatial indicators developed specifically for geostatistical data like our fisheries acoustics data that inherently contain autocorrelation (Woiillez et al. 2007, 2009). See Supplement 4 for additional details.

2.6.1. Spatial location

To describe spatial locations of zooplankton and small, medium, and large fish around artificial structures, we first calculated the area surveyed where each organismal group was present (Table 1, area of presence [positive area, PA]), which we scaled to account for differing total areas among structure surveys (Table S2 in Supplement 1). Second, we calculated the fine-scale irregularity in group distributions (Table 1, microstructure). Third, we calculated the mean center of each group’s spatial distribution, as well as dispersion around the center (Table 1, center of gravity [CG] and inertia [I], respectively). These indicators were calculated using equations and corresponding functions from Woiillez et al. (2007, 2009; Table 1). We tested differences among the mean center and dispersion around the center for organismal groups using 1-way analyses of variance (ANOVAs) followed by post hoc Tukey HSD tests, both using the ‘stats’ base package within R. We used Levene’s test implemented in the ‘car’ package (Fox & Weisberg 2011) to confirm that data met the assumption of homogeneity of variance and examined normal quantile plots to test the assumption of normality. The assumption of normality was violated, as there was a heavy-tailed residual pattern indicating that the residuals had a longer upper tail than predicted by a normal distribution. Given the very low p-values, the amount of error introduced to the calculated p-values from the violation of normality would not have been sufficient to make the results nonsignificant, so we proceeded with models using untransformed data.

Table 1. Definitions and equations for indicators to quantify spatial distributions of individual groups of organisms and spatial relationships between organism pairs. z_i : fish density or zooplankton concentration at sample position x_i ; s_i : area of influence of the sample at position x_i , which is the area of points in space that are closer to this sample than to others; g : transitive covariogram (Bez & Rivoirard 2001); h_0 : mean lag between samples; and l : number of samples where organism 1 (l_1), organism 2 (l_2), or both organisms ($l_{1,2}$) are present

Spatial indicator	Description	Equation	Reference
Spatial distribution of one organism group			
Positive area (PA)	Area surveyed where organism is present	$PA = \sum_i s_i 1_{z_i > 0}$ [m ²]	Woillez et al. (2007, 2009)
Microstructure (MI)	Fine-scale variability in organism distribution	$MI = \frac{[(g(0) - g(h_0))]}{g(0)}$ [0,1] where: if MI = 0, well structured distribution if MI = 1, poorly structured distribution	Woillez et al. (2007, 2009)
Mean center of gravity (CG)	Weighted mean center of organism distribution	$CG = \frac{\sum_{i=1}^N x_i s_i z_i}{\sum_{i=1}^N s_i z_i}$ [coordinates]	Woillez et al. (2007, 2009)
Inertia (I)	Dispersion of organism around mean center	$I = \frac{\sum_{i=1}^N (x_i - CG)^2 s_i z_i}{\sum_{i=1}^N s_i z_i}$ [m ²]	Woillez et al. (2007, 2009)
Spatial relationships between pairs of organism groups			
Global index of collocation (GIC)	Index of collocation between 2 organisms at global scale of survey	$GIG = 1 - \frac{\Delta CG^2}{\Delta CG^2 + l_1 + l_2}$ [0,1] where: if GIC = 0, different CGs and 0 inertia if GIC = 1, coinciding CGs with positive inertia	Woillez et al. (2007, 2009)
Co-occurrence (CO)	Index of collocation between presence of 2 organisms at local scale of sampling points	$CO = \frac{l_{1,2}}{l_1 + l_2}$ [0,1] where: if CO = 0, no co-occurrence at sample locations if CO = 1, co-occurrence at all sample locations	Saraux et al. (2014)

We also identified clusters of high density ('hot spots') and low density ('cold spots') for each organismal group. Hot and cold spots were detected using the Getis-Ord G_i^* statistic (Getis & Ord 1992, Ord & Getis 1995), calculated based on k -nearest neighbors using the 'localG' function within the 'spdep' package (Bivand & Piras 2015). Resulting z -values indicated whether and where statistically significant hot spots (z -value > 1.96) or cold spots ($z < -1.96$) occurred.

2.6.2. Spatial relationships

We quantified spatial relationships between group pairs (e.g. zooplankton and small fish; small fish and medium fish; etc.) at the global scale and the local scale. Global scale refers to the scale of each survey, whereas local scale refers to the scale of each sample point. At the global scale, we calculated the global index of collocation (GIC, Table 1). To complement the GIC, we calculated a localized collocation metric, the percentage of sample points where group pairs co-occurred (CO, Table 1). Because the global metric compared group distribution over the entire extent of

each survey, whereas the local metric assessed overlap at the level of each sample (e.g. 5 m × 1 m depth-collapsed sample), these 2 metrics provide complementary means to interpret relationships between 2 groups that were appropriate for fisheries acoustics data like ours with inherent autocorrelation (Bez & Rivoirard 2000, Woillez et al. 2009, Saraux et al. 2014). To ensure that the calculated values were not extreme, we bootstrapped the global and local metrics for each organism pair for each of the 20 surveys. We then verified that the mean of each metric for each organism pair across the 20 surveys approximated the mean obtained from bootstrapping with 1000 samples.

2.6.3. Water current

We used linear regressions to investigate relationships between fish location and current magnitude. First, we regressed distances between the mean center of the spatial distribution of each fish size class and the nearest structure edge against current magnitude. Second, because small fish were unrelated to water current magnitude and given prior research suggesting that predator-prey dynamics influence

Table 2. Spatial indicators (mean \pm SE) for distributions of zooplankton and fish around shipwrecks. PA: positive area, where values are percentages of the total area surveyed that each indicator occupies. For example, if the total area surveyed around a shipwreck was 100 000 m², and the indicator occurred in 25 000 m², then the PA would be 25%. Inertia is not reported for zooplankton because their high PA suggests that inertia is influenced by sampling extent ($I = NA$). $N = 20$ surveys; definitions for MI and I are given in Table 1

Organism	PA (%)	MI [0–1]	I [m ²]
Zooplankton	23.9 \pm 13.1	0.84 \pm 0.04	NA
Small fish	2.4 \pm 0.7	0.95 \pm 0.03	14210 \pm 2670
Medium fish	2.7 \pm 0.3	0.82 \pm 0.02	6600 \pm 2680
Large fish	2.2 \pm 0.5	0.84 \pm 0.03	3540 \pm 920

planktivorous fish aggregations (Holzman et al. 2005), we fit additional linear regressions investigating relationships between the distance of small fish from structure edges and predictor variables representing apparent predation risk. Predictor variables for apparent predation risk were the number of medium, large, and both medium and large fish present within the structure (designated as the manually delineated polygon corresponding to the artificial structure) and 5 m outward of the delineated structure. We conducted assessments of fit by comparing observed distances of small fish from structure edges to those of the estimated distribution. To determine how water current direction influenced small fish density, we visualized the location of the mean center of small fish relative to upstream and downstream portions of artificial structures. We also calculated the total density of small fish located upstream and downstream on each survey and fit beta regressions using the ‘betareg’ package (Cribari-Neto & Zeileis 2010) to examine whether the proportion of fish located upstream or downstream related to current magnitude. Since the upstream and downstream fish were classified based on orientation relative to current direction, these tests incorporated current direction and magnitude.

Table 3. ANOVA results for response variables representing spatial metrics as a function of organism group (e.g. zooplankton and small, medium, and large fish)

Response variable	Source	df	SS	MS	<i>F</i>	<i>p</i>
Distance between mean center of fish and structure edges	Organism group	2	10893	5446.4	5.93	0.004
	Residuals	57	52377	918.9		
Inertia	Organism group	2	1.21 $\times 10^9$	6.03 $\times 10^8$	5.98	0.004
	Residuals	57	5.76 $\times 10^9$	1.10 $\times 10^7$		
Distance of all sample cells containing fish to structure edges	Organism group	2	39493	19746.5	10.72	<0.001
	Residuals	57	105030	1842.6		

3. RESULTS

3.1. Spatial location

Zooplankton were detected throughout nearly 25% of each survey, resulting in high spatial area of zooplankton presence (Table 2, positive area). Even with zooplankton present at nearly 1 in 4 sampling locations, zooplankton concentrations were variable and irregularly structured across the survey (Table 2, microstructure), indicating underlying finer-scale spatial patterns in their distribution. Because of the large fraction of the total survey area occupied by zooplankton, the mean center and variance in zooplankton spatial distribution were influenced by survey extent, so we do not report these statistics but instead revisit their finer-scale spatial patterns below. Fish of all size classes were present across 2–3% of surveyed areas (Table 2, positive area). For all size classes of fish, spatial structures of their distributions were irregular and unstructured, suggesting that fine-scale variability occurred (Table 2, microstructure).

Because spatial indicators demonstrated that fish occurred over a small fraction (2–3%, positive area) of the surveyed areas, the location of the organism’s mean center (center of gravity) and the dispersion (inertia) around the center could be meaningful for fish. Distances between the mean center and structure edges differed by fish size class (ANOVA, $p < 0.01$; Table 3, Figs. 2 & 3). The mean center of small fish distribution occurred further from structure edges than either medium or large fish (Fig. 2a; Fig. S2a in Supplement 1; 39.1 \pm 8.2 m, mean \pm SE; Tukey HSD, $p < 0.01$ small vs. medium, $p = 0.04$ small vs. large). The mean center of medium fish was located more than twice as close to structure edges as small fish (Fig. 2a; Fig. S2b in Supplement 1; 15.1 \pm 7.5 m). The mean center of large fish occurred more than 5 times closer to structure edges than small fish. While the mean center of large fish was nearly twice as close to structure edges than medium fish, this difference was not statistically significant (Fig. 2a;

Fig. S2c in Supplement 1; 7.5 ± 3.8 m; Tukey HSD, $p = 0.71$).

Dispersion of fish around their mean center also differed by fish size class (ANOVA, $p < 0.01$; Tables 2 & 3, Fig. 3). Small fish were highly dispersed around their mean center ($14\,210 \pm 2670$ m). Medium and large fish were less dispersed around their mean centers than small fish (medium = 6600 ± 2680 m, large = 3540 ± 920 m). Small fish dispersion was statistically different from that of large fish dispersion (Tukey HSD, $p < 0.01$). Medium fish dispersion was marginally significantly different from small fish dispersion (Tukey HSD, $p = 0.05$), but not significantly different from large fish dispersion (Tukey HSD, $p = 0.65$).

Because some size classes of fish were more dispersed around their mean center than others, we also examined the average distance of each sampling cell containing fish of a particular size class from structure edges. We found that when examining all fish, rather than the mean center of fish distributions, fish were on average further from structure edges. Nonetheless, the same pattern remained where small fish were fur-

thest from the structure followed by medium and then large fish (Fig. 2b; Fig. S2d–f in Supplement 1; Table 3; ANOVA, $p < 0.001$).

When we quantified organismal group patchiness by detecting statistically significant clusters of high concentrations (hot spots) and low concentrations (cold spots), general patterns emerged (Fig. 4; Fig. S3 in Supplement 1). For fish of all size classes, statistically significant hot spots were present ($z > 1.96$), but significant cold spots were absent. Because the Getis-Ord G_i^* is calculated as the ratio of the local average to the global average of density, the lack of significant cold spots ($z < -1.96$) suggests that whereas fish density is globally low, it is high in localized areas, which means that areas without fish are no different than global lows and so are not cold spots (Fortin & Dale 2005). Hot spots corresponding to small fish were located further from artificial structures than hot spots of medium or large fish (Fig. 4b–d; 17 of 20 surveys).

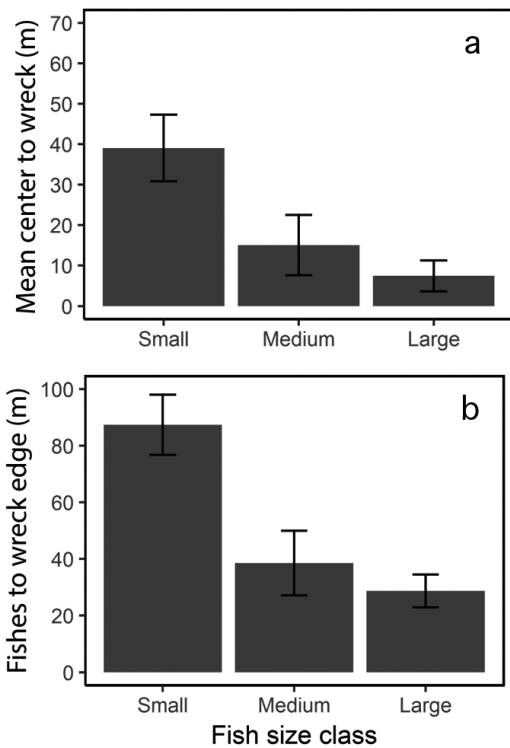


Fig. 2. Distance (mean \pm SE) of fish from nearest structure edges. (a) Distance between the mean center of fish size classes and structure edges. (b) Distance of all sampling cells containing fish to structure edges for small, medium, and large fish. $N = 20$ surveys

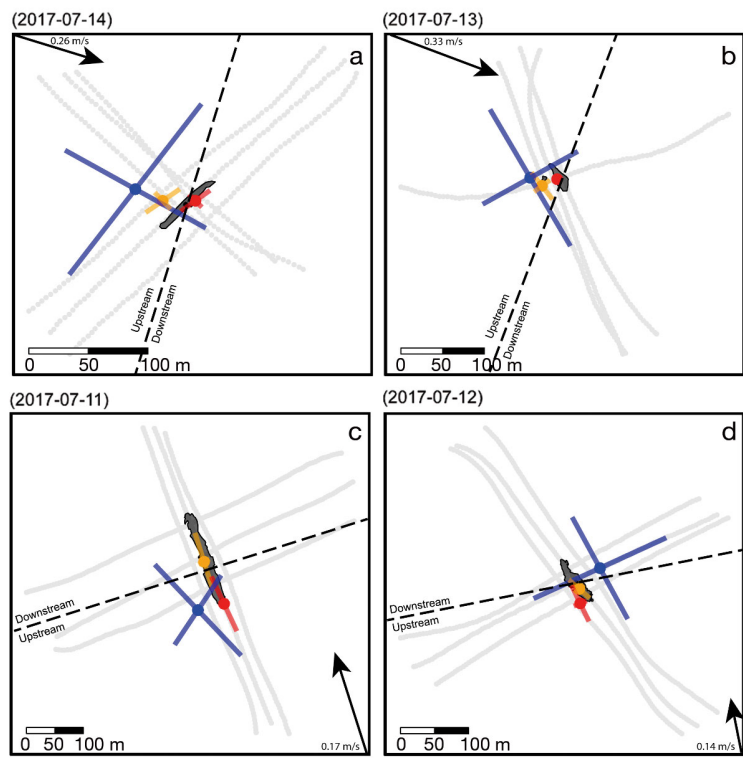


Fig. 3. Spatial location of small fish (blue; planktivores), medium fish (orange; piscivores), and large fish (red; piscivores) relative to 4 shipwrecks (black outlines; see Fig. 1 for their locations): (a) U-352, (b) HMT *Bedfordshire*, (c) *W.E. Hutton*, and (d) USS *Schurz*. Circles represent the weighted mean center of each organism’s distribution (center of gravity; CG). Solid colored lines represent the dispersion around the center (inertia). Gray dotted lines indicate the sampling extent of each survey. Current vector (black arrow) displays the current direction (orientation of vector) and magnitude (length of vector). Black dashed line divides survey into upstream or downstream components. The date surveyed (yyyy-mm-dd) is displayed

Medium and large fish exhibited high densities towards the center of artificial structures (Fig. 4d; 20 out of 20 surveys). All reported hot spots are statistically significant because z -values were >1.96 .

Even though zooplankton were present over nearly 25% of each surveyed area, the Getis-Ord G_i^* method for cluster detection was appropriate because it accounted for variations in low and high zooplankton concentrations. As for fish, the Getis-Ord G_i^* values indicated that zooplankton occurred in hot spots but not cold spots (Fig. 4a; Fig. S3 in Supplement 1). Zooplankton hot spots were usually located on one side of artificial structures (19 of 20 surveys), either on the opposite side from small-fish hot spots (9 of 20 surveys) or between small-fish hot spots and artificial structures (10 of 20 surveys; Fig. 4a,b; Fig. S3 in Supplement 1). If zooplankton and small fish occurred in the exact same location within a sampling cell, however, we would be able to detect fish but not zooplankton, which could affect our interpretation of these results.

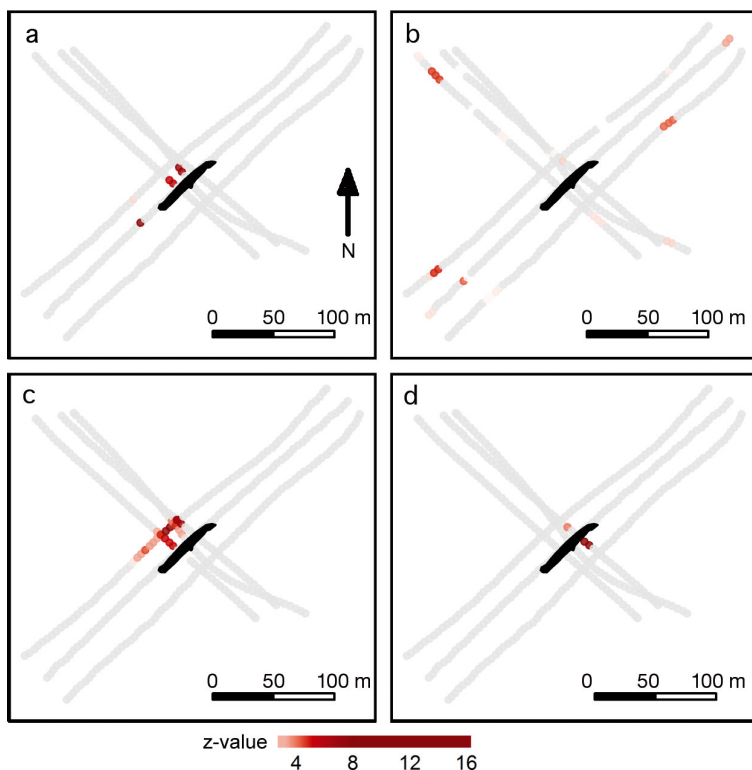


Fig. 4. Spatial clusters of (a) zooplankton, (b) small fish, (c) medium fish, and (d) large fish around the 'U-352' shipwreck. Colors correspond to the Getis-Ord G_i^* z -value. Gray points are locations along the survey where data were collected but the Getis-Ord G_i^* z -value was not significant, so they represent neither hot nor cold spots. The shipwreck structure is shown in black, and data are from 14 July 2017. Results from cluster analysis on other artificial structures are given in Fig. S3 in Supplement 1

3.2. Spatial relationships

At the scale of each survey, known as the global scale, when the spatial distribution was characterized entirely by an organism's mean center and associated dispersion, spatial distributions of all trophic groups highly overlapped (Figs. 3 & 5a; global collocation ≥ 0.77). This is not surprising because zooplankton occupied most of the survey area, and the ellipse describing the spread of the small fish distribution usually included the artificial structure, where larger fish were concentrated. At the local scale of sampling points within surveys, small fish and zooplankton co-occurred at $9.2 \pm <0.1\%$ of the sampling points where at least 1 of the 2 taxa was present (Fig. 5b). Fish co-occurrence was similar, with small and medium fish presence co-occurring locally at a rate of $6.1 \pm <0.1\%$, and medium and large fish at $8.9 \pm <0.1\%$. Small and large fish co-occurred at a lower rate of $3.1 \pm 0.2\%$. Means for organism global collocation and local co-occurrence metrics matched the center of respective distributions from the bootstrapping procedure, indicating that the values presented here are representative (Fig. S4 in Supplement 1).

3.3. Water current

Distances from the mean center of small fish and medium fish distributions to structure edges each displayed no pattern with current magnitude ($p > 0.05$; Fig. S5a,b in Supplement 1). Distances from the mean position of large fish to structure edges, however, related to current magnitude ($p = 0.04$; Fig. S5c in Supplement 1). The center of large fish distributions occurred closer to structure edges, and in some cases, directly above artificial structures with stronger currents. With weaker currents, the center of the large fish distribution was located further from structure edges. Distances of small fish from structure edges showed no pattern relative to densities of predators (medium, large, medium and large fish) residing on structures and 5 m outward of structures ($p > 0.05$; Fig. S5d in Supplement 1). There is high leverage in these linear regressions because extreme values drive 3 of the regressions (Fig. S5a,b,d in Supplement 1). When we examined relationships between small fish and current direction, we found that the

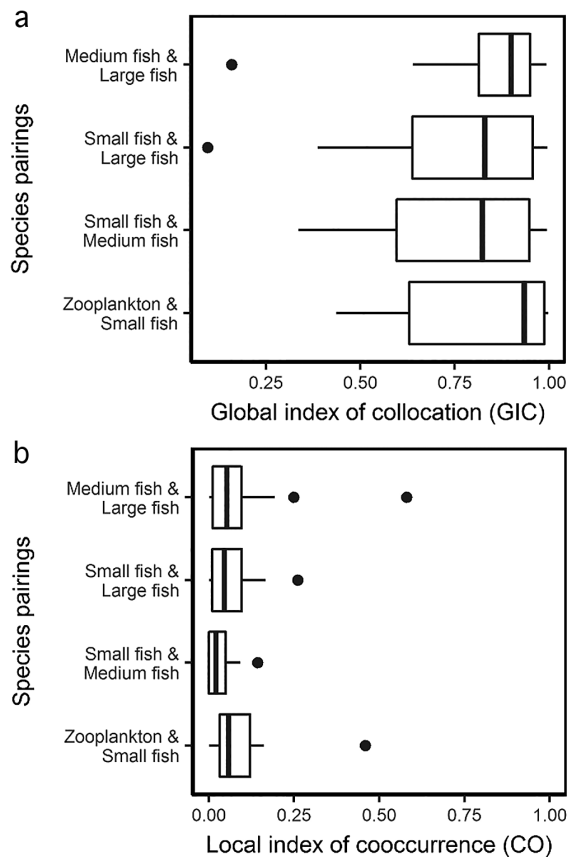


Fig. 5. Global and local spatial relationships between pairwise groupings of zooplankton and small, medium, and large fish. (a) The global index of collocation is a spatial statistic that ranges from 0–1, with 1 representing identical distributional centers. (b) The local index of co-occurrence is based on presence–absence and ranges from 0–1, with 1 representing co-occurrence. The line represents the median; the box represents the lower and upper quartiles. Whiskers extend past the lower and upper quartiles to the smallest or largest values. Points are individual outliers beyond the whiskers

mean center of small fish generally occurred upstream of artificial structures (6 out of 9 surveys, 1 survey without small fish; Fig. 3), but there was no relationship between proportions of fish located upstream or downstream of artificial structures and current magnitude (beta-regressions, $p > 0.05$).

4. DISCUSSION

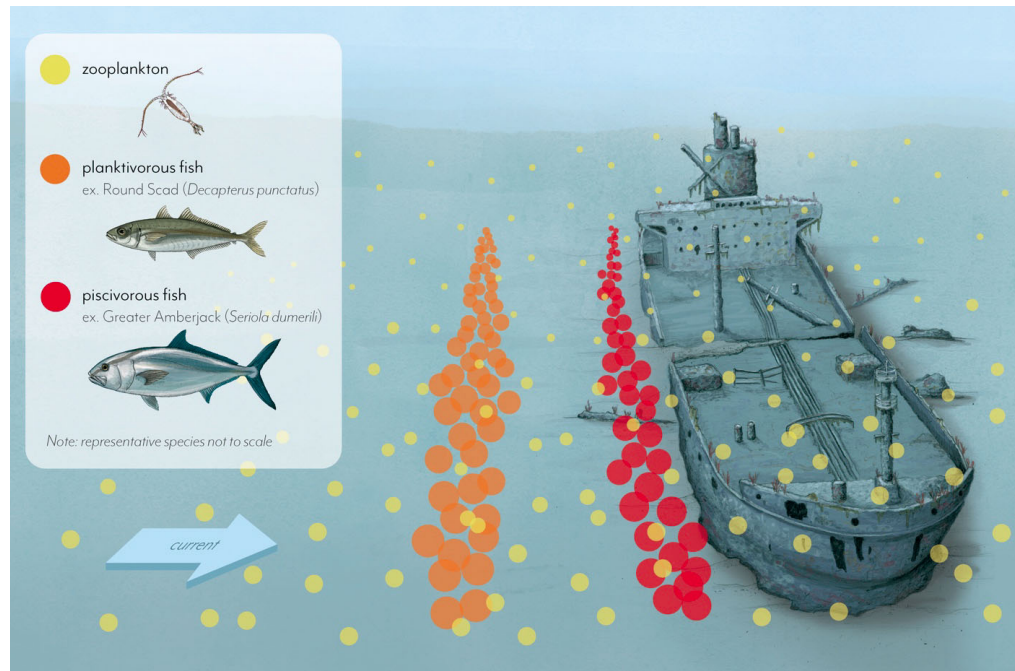
We observed planktivorous fish aggregations consistently around artificial structures surveyed in this study. The center of planktivorous fish aggregations occurred an average of 39 m from structure edges. Despite zooplankton detections throughout nearly

25% of surveyed areas around artificial structures, aggregations of planktivorous fish were spatially distinct from high concentrations of zooplankton prey. Aggregations of planktivorous fish did not co-occur with piscivorous fish, which concentrated closer to structures, especially with stronger water currents. More than half of the time, planktivorous fish aggregations resided on upstream sides of artificial structures, but their position was unrelated to current magnitude. Because spatial patterns in planktivorous fish, their prey (zooplankton), and predators (piscivorous fish) occurred around artificial structures, our findings suggest that these novel structures influence spatial patterns across multiple trophic levels in a consistent way (Fig. 6).

Our finding that planktivorous fish occupied localized patches positioned on average 39 m (mean center) from structure edges is consistent with expectations that artificial structures aggregate planktivorous fish. This distance between planktivorous fish and artificial structures is similar to distances found previously on artificial reefs near our study sites where the fish community, of which the most abundant species was a partially planktivorous species (tomtate *Haemulon aurolineatum*), resided close (77% within 30 m) to artificial structures (Rosemond et al. 2018). Similarly, in Australia, a coastal planktivore (yellowtail scad *Trachurus novaezelandiae*) displayed elevated abundances at approximately 50 m from reef structure (Smith et al. 2017). Other Australian planktivorous fishes exhibit similarly dense aggregations, although 1 species (mado *Atypichthys strigatus*) forages a maximum of 4 m from reef structure (Champion et al. 2015). This discrepancy in distances of planktivorous fish from artificial structures is likely a product of differing species-specific foraging ranges associated with their natural histories. Regardless of exact distances away from artificial structures, repeated high densities of planktivorous fish that we documented adds to a growing body of evidence that artificial structures support high planktivore densities (Arena et al. 2007, Champion et al. 2015).

Our finding that at local scales, zooplankton were detected either between their planktivorous fish predators and artificial structures or on the opposite side of artificial structures from planktivorous fish has at least 2 implications. First, this finding indicates that low to normal background concentrations of zooplankton co-occur with planktivorous fish. Second, it demonstrates that zooplankton concentrations depend on spatial scale because marked patches of high zooplankton concentration emerged at fine spatial reso-

Fig. 6. Conceptual model of distributions of multiple trophic levels documented around artificial structures. Examples of representative zooplankton, planktivorous fish, and piscivorous fish detected by acoustics are provided. Fish inside the wreck or close to the wreck structure are not illustrated. These distributions are dynamic. Illustration ©Alex Boersma (www.alexboersma.com)



lution but were obscured at broader resolutions where zooplankton appeared more ubiquitous. Previous models have demonstrated, and empirical data have supported, the notion that artificial reefs in Australia can support high levels of zooplanktivory (Champion et al. 2015). Considering that we sampled multiple shipwrecks, similar to artificial reefs, our study suggests that artificial structures located in NC, USA, with differing fish communities than in Australia, host patchy distributions of zooplankton that planktivorous fish require.

Dense schools of planktivorous fish on artificial structures have the potential to be prey resources for piscivorous fish. In our study, piscivorous fish predators clustered near structures. Similar activity where predators remain close to edges has been observed on piers, likely because predators can hide in shade provided by pier structure and then attack prey (Able et al. 2013). A similar phenomenon may occur on shipwrecks because predatory fish located closer to structures could hide in overhangs and interiors. Similarly, piscivores could physically hide behind emergent artificial structures. This supports the notion that piscivorous fish may enhance foraging success by lurking near structures to hide from and surprise potential prey fish. Alternatively, piscivorous fish may occur close to artificial structures to hide from their predators or to seek protection from currents.

Elevated densities of planktivorous fish occurred at the same locations as low concentrations of zooplankton, suggesting that patterns in planktivorous fish may influence lower trophic groups to create spatial gradients in zooplankton. Based on similar studies on naturally occurring reefs with abrupt topographies (e.g. Hamner et al. 1988, 2007), we expected that relationships between zooplankton and planktivorous fish would be more pronounced near artificial structures, such that 'holes' in zooplankton concentration would be evident. While patterns existed at local scales, we posit that the magnitude of the relationship was obscured at broader scales because indicators of zooplankton distributions, such as mean center and dispersion, were dependent on sampling extent. Extending transects and associated sampling efforts further away from artificial structures could provide more rigorous evaluations of spatial scales at which spatial relationships between zooplankton and planktivorous fish are most pronounced. The localized trend that we documented between these organisms on 20 surveys across 15 shipwrecks is consistent with stable isotope findings from 4 artificial reefs in the Mediterranean that artificial structures host pelagic pathways between zooplankton and planktivorous fish (Cresson et al. 2014), as well as a model and field data from an Australian artificial reef that zooplanktivory is a key process on artificial structures (Champion et al. 2015).

Our finding that planktivorous fish occurred in the same global vicinity (e.g. survey scale) as their piscivorous fish predators, but that these 2 trophic groups did not co-occur locally (e.g. sample scale), hinges on our classification of piscivorous fish including both medium and large fish. We caution that because fisheries acoustics data do not yet allow species discrimination, these size classes of fish may include not only piscivores but also other larger fish with different trophic ecologies. We assume, however, that inclusion of other trophic groups as large fish is unlikely given our knowledge of reef fish communities in NC, because fish in the large size class (>29 cm) are mainly piscivores (Whitfield et al. 2014, Paxton et al. 2017). Fish in the medium size class (11–29 cm) may include more species from other trophic groups: many medium-sized fish from other trophic groups actively forage on benthic invertebrates and other bottom-dwelling organisms. Because of close association with the bottom, these fish can be difficult to differentiate from surrounding structures and the seafloor with SBES, which likely minimizes their detectability in our study and is a potentially confounding effect. Similarly, we are confident in our classification of small fish as planktivores because other small fish that are not planktivorous but instead are more demersal in nature would also be difficult to distinguish from the artificial structure and surrounding seafloor, again likely reducing a potentially confounding effect. We acknowledge, however, that there could be planktivorous fish larger than 11 cm. Additionally, size estimations of fish hinge upon the intensity of reflected sound. While in fish with swim bladders, the target strength is largely a function of fish size, fish without swim bladders may have a target strength more similar to that of a smaller fish. This could bias our interpretation of fish size and thus trophic groups. These assumptions are inherent to fisheries acoustics studies.

Relationships between fish distributions and water current were complex. Here, we synthesize our 3 main findings about relationships between fish and currents. First, on 67% of surveys where we collected current measurements, the mean center of planktivorous fish aggregations occurred upstream of artificial structures. This is consistent with findings on coral reefs that planktivorous fish aggregate on the leading edge of reef structures (Hamner et al. 1988). Second, the distance of planktivorous fish from structure edges was unrelated to current magnitude. Because most planktivorous fish have streamlined bodies with forked caudal fins that enable them to hold position in currents without high energetic costs (Hobson

1991), the lack of relationship was unsurprising. We hypothesize that once current magnitude exceeds a particular threshold, it becomes energetically costly for planktivorous fish to hold their position, so these fish would retreat towards structures to find refuge from currents (Liao 2007). Since our observations were not indicative of this 'flow-refuging' behavior, the magnitude of this current threshold likely exceeds the highest current magnitude (0.33 m s^{-1}) that we measured. Third, in contrast to planktivorous fish, piscivorous fish remained closer to artificial structures when currents were stronger. This pattern may reflect high energetic costs incurred by large fish trying to hold their position in currents (Johansen et al. 2008). These results should be interpreted cautiously since they are based on measurements from the 9 surveys where we collected current measurements and because some analyses indicated an effect of currents on fish whereas others did not. Relationships between fish locations relative to artificial structures and currents, and tradeoffs between energetic costs of swimming against currents and predation risk, are interesting and complex problems requiring further investigation.

Spatial patterns in planktivorous fish, zooplankton, and piscivorous fish distributions that we documented on artificial structures are similar to phenomena documented on natural reefs characterized by abrupt topographies. Despite apparent similarities, functional effects of these processes occurring on artificial versus natural structured habitats remain to be tested. Artificial and natural habitats are known to differ in many characteristics, including structural complexity and fish community composition (Paxton et al. 2017), as well as trophic structure (Simon et al. 2013), so investigating differences in the magnitude of the zooplankton–planktivore–piscivore relationship on both reef types is an important question to address. Regardless of similarities and differences in zooplanktivory and associated processes on artificial versus natural habitats, artificial structures certainly provide habitat for aggregations of planktivores and their prey and predators (Fig. 6). Effects from artificial structures could continue to influence spatial patterns at other top trophic levels, such as marine mammals, seabirds, and humans, and trophic levels lower than zooplankton, such as phytoplankton. These findings add to a growing body of evidence that artificial structures provide important ecological benefits.

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