

Space size relative to prey width (Sp/Py) influences macrofaunal colonization of artificial structures

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ABSTRACT: We tested an index of habitat complexity, Sp/Py (inter-structural space size/prey body width), by deploying artificial structures on a coral reef near Dibba, United Arab Emirates. The structures were polyethylene tube bundles with tube diameters of 3, 12 and 24 mm and a mixed treatment composed of all 3 tube sizes. We counted and identified mobile macrofauna that colonized the interior of the tubes and divided them into 3 body width categories: small (<3 mm), medium (3–12 mm) and large (>12 mm). Medium and large fauna were excluded from 3 mm tubes, and large fauna were excluded from 12 mm tubes. Small fauna were significantly more abundant in 24 mm tubes compared with 3 mm tubes, with intermediate abundance in 12 mm tubes. A second experiment determined that small fauna probably responded positively to tube interior volume, or responded to differences in hydrodynamic properties between the treatments. Medium fauna were more likely to be found in 12 mm tubes that matched their own body width than in 24 mm tubes. Species richness was significantly lower in the 3 mm tubes compared with the other treatments, in part because errant polychaetes, gastropods, caprellid amphipods and crabs were less likely to be found in the 3 mm tubes. These results indicate that habitats with very narrow inter-structural space sizes may be 'too complex' and may exclude certain fauna, resulting in decreased species richness. Also, some fauna may prefer habitats with intermediate space sizes that match their own body width.

KEY WORDS: Complexity · Structure · Habitat · Predator · Prey · Refuge · Macrofauna

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INTRODUCTION

Habitats that contain structure almost invariably have greater faunal abundance associated with them compared with nearby unstructured habitats, in part due to the refuges from predation that the structure provides to prey species (Orth et al. 1984, Hall & Bell 1988, Heck & Crowder 1991). Other processes besides predation can also lead to increased abundance in complex habitats, including increased recruitment, increased food and space availability and active habitat choice (Orth et al. 1984, Bell & Westoby 1985). Structures within complex habitats provide prey with refuges from predation. Ecologists have demonstrated this in a wide variety of terrestrial (Mullin & Cooper 2000, Finke & Denno 2001), freshwater (Savino & Stein 1982, Jordan et al. 1996) and marine habitats (Graham et al. 1998, Moksnes et al. 1998) and for prey

of various sizes from small meiofauna (Coull & Wells 1983) to large mammals (Sweitzer 1996). However, there are certainly exceptions to this rule (Marinelli & Coull 1987). Predators may use structure to interfere with the stereotyped escape behavior of prey, thus increasing the likelihood of prey capture (Cermak 2002). Structure may benefit ambush predators more than their prey by providing them with cover to attack from (James & Heck 1994, Flynn & Ritz 1999). Prey may prefer less complex habitats if structure decreases their ability to escape predators (Hill et al. 2004), and structure may interfere with a prey's movement more than their predators' movement, thus decreasing prey survivorship in more complex habitats (Drolet et al. 2004).

Structure in complex habitats can interfere with a predator's ability to see or otherwise sense prey (Savino & Stein 1982, Main 1987, Bartholomew 2002a),

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and it can interfere with a predator's ability to maneuver through the spaces in the habitat in search of, or in pursuit of, prey that are usually smaller than the predator itself (Ryer 1988, Bartholomew et al. 2000, Ryer et al. 2004). A given habitat may have a high refuge value for some prey, but poor refuge value for other prey of a different size, depending upon whether the prey can use the spaces within the habitat as refuge, and whether the prey's predators can maneuver through the spaces of the habitat.

Bartholomew et al. (2000) and Bartholomew (2002b) suggest that prey may be excluded from very complex habitats in which space size (Sp), on average, was smaller than prey body width (Py). Prey survivorship and faunal abundance under these circumstances may be low, as prey simply cannot use the spaces within the habitat as refuge (the habitat is 'too complex' for them). Prey survivorship may also be low at high Sp/Py values, since the large spaces would enable the prey's larger predators to move through the habitat easily in search of, or in pursuit of, the prey. Habitats that have intermediate complexity, with inter-structural spaces matching Py (Sp/Py slightly greater than 1), may be ideal for prey as refuges, since prey could move through the spaces in the habitat, but their predators could not (Bartholomew 2002b, their Fig. 1). Overall, prey survivorship should be highest in habitats with spaces that match their own body width.

There are several examples of prey inhabiting spaces that match their own body size. Vytopil & Willis (2001) found a significant relationship between *Tetralia* spp. crab size and the interbranch space size of the *Acropora* spp. coral they inhabit, and suggested that these crabs migrate between coral species as they grow larger relative to the spaces provided by the corals. Steger (1987) also noted a significant relationship between the size of a stomatopod inhabiting a cavity and the size of the cavity itself. Friedlander & Parrish (1998) noted a significant relationship between the average size of coral reef fish and average hole size available in the area. For fauna in complex habitats it may be advantageous to be narrow, all else being equal. Being narrow would enable them to maneuver more easily through the small spaces in the habitat, and narrower individuals could fit into more spaces than wider individuals (Steger 1987). Therefore, narrower individuals could utilize more of the spaces within the habitat as potential refuges (Lipcius et al. 1998). Buchheim & Hixon (1992) and Wahle & Steneck (1991) suggest that shelter holes or appropriate habitat can be a limiting resource for fauna.

Researchers have also found that habitats can be 'too complex' for prey. Eklov & Hamrin (1989) found that juvenile perch *Perca fluviatilis* mortality was higher in a high complexity treatment than in a less complex

treatment when preyed upon by pike *Esox lucius*. The perch used vegetated and unvegetated areas in the low complexity treatment, but used unvegetated areas and the sparsely vegetated edges in the higher complexity treatment. Kelaher (2003) found a significant negative relationship between frond density of coralline algae turf and gastropod abundance in low rocky shore areas. He also found that several larger species of gastropods were not found in a high density artificial turf treatment, perhaps because they were excluded by the small inter-structural space size of the high density treatments. Snickars et al. (2004) found that a low proportion of juvenile perch *P. fluviatilis* used the densest treatments in the presence of pike *E. lucius* predators, perhaps because the spaces between the dowels used were too small for the perch. Bartholomew (2002b) found that high complexity artificial seagrass plots did not exclude fauna that were larger than the inter-structural space sizes in the habitat, since the structures were flexible, and large fauna could simply push them aside. Flexible structures may be less effective than rigid structures for excluding predators (Coull & Wells 1983).

Researchers have also found higher prey densities or higher prey survivorship in habitats with intermediate complexity. Pihl et al. (1995) found that epifaunal biomass increased with increasing filamentous algae biomass from 0 to 50% cover on sandy sediment, but that further increases of filamentous algae to 90% cover decreased epifaunal biomass. They also found dramatic differences in epifaunal communities due to differences in filamentous algae cover. Eklov (1997) found the greatest density of perch *Perca fluviatilis* in intermediate vegetation density. Grenouillet et al. (2002) found greatest juvenile fish abundance in vegetation of intermediate complexity. Moksnes et al. (1998) found that sand and low complexity algae *Ulva lactuca* provided poor refuge for first instar shore crabs *Carcinus maenas* preyed upon by brown shrimp *Crangon crangon*. Intermediate complexity algae *Enteromorpha compressa*, *Enteromorpha clathrata* and *Cladophora* sp. provided good refuges for the crabs, as the crabs could move in between the filaments, whereas the shrimp often became entangled. High complexity algae *Ectocarpus siliculosus* provided poor refuge for the crabs, as they could not move in between the filaments. Hedvall et al. (1998) found that shore crab megalopae selected against settling in this high complexity algae compared with the other less complex algal species.

Bartholomew et al. (2000) and Bartholomew (2002a,b) proposed and tested novel dimensionless indices of habitat complexity that can potentially be applied to any habitat type and at any scale. These indices measure habitat parameters that directly affect

a predator's ability to sense prey and maneuver through the spaces within the habitat. One index presented by Bartholomew et al. (2000) and explored by Bartholomew (2002b) is Sp/Py. Sp/Py is the average space size within the habitat divided by prey body width. This index looks at the refuge value of complex habitats from the prey's perspective. It is important to note that with the Sp/Py index the 'complexity' of the habitat depends, in part, upon the width of the organism, which makes sense biologically.

We performed 2 experiments with small artificial structures with different tube diameters in a coral reef habitat to determine if Sp (space size = tube inner diameter) affected the species richness of the colonizing mobile macrofauna. We also determined if mobile macrofauna of different Py responded differently to the different-sized tubes in a predictable manner.

MATERIALS AND METHODS

For both experiments we deployed artificial structures on a small coral reef close to 'Snoopy Island' (Jazirat Al Ghubba) located south of Dibba, United Arab Emirates (25° 29' 29" N, 56° 21' 59" E). We chose this area because it is a marine reserve, and it has small, fairly healthy coral reefs that are easily accessible from shore.

For both experiments we deployed the structures in coral rubble/sand habitat directly adjacent to living coral forming a small fringing reef at approximately 6.7 m depth. We deployed them within 1 m of a reef-sand interface which made the structures easy to find and recover without damaging living coral. We deployed individual structures with at least one end close to (within approximately 5 cm) an upright piece of coral rubble or living coral to encourage faunal colonization from the surrounding habitat. We never deployed individual structures more than 0.5 m away from living coral, and structures were usually much closer than this. We deployed the structures haphazardly, and an individual structure was never closer than 2 m away from another structure.

For the first experiment, the structures consisted of 6 polyethylene tubes in a bundle, tightly secured to bricks by fishing line such that the ends of the tubes rested on the middle of the brick. The tubes were approximately 44 cm long. The bricks were octagonal, with a diameter of 20 cm and a height of 6 cm. The bricks were used to anchor the tubes and to raise them above the sediment surface so that the mouths of the tubes would not become buried. The different treatments consisted of 6 tubes of 3, 12 or 24 mm inner diameter. We chose these sizes based upon the sizes of common fauna we collected in pilot studies conducted

before the first experiment. We also deployed a 'mixed' treatment consisting of 2 tubes of each size bundled together. The mixed treatment was deployed to determine if increasing heterogeneity of space sizes affected the species richness of colonizing fauna. Individual tubes were completely wrapped in duct tape, so as to block sunlight from shining through the sides of the tubes. Individual tubes in a bundle were trimmed as necessary to ensure that the ends of the tubes all lined up during deployment.

For the first experiment we had 6 deployments in 2005–2006: 22 June to 6 July, 14 to 21 August, 9 to 23 September, 7 to 21 October, 4 to 18 November and 12 to 27 January. All of these deployments had 2 of each type of structure deployed. On 2 separate occasions we lost a mixed treatment, so we had a final deployment from 14 to 28 April in which we deployed 1 each of small, medium and large diameter treatments and 3 mixed treatments to make up for those that were lost previously.

For the second experiment we deployed 2 different treatments: single polyethylene tubes of 18.5 mm in diameter and 12 cm in length and single tubes of 6 mm in diameter and 37 cm in length. These treatments each had the same internal surface area. The 12 cm tubes were attached to a single brick, whereas the 37 cm tubes were attached to 2 bricks, such that both tube openings rested atop a brick. For the second experiment we had 1 deployment with 6 replicates of each treatment. The deployment occurred from 3 to 17 February 2007.

For both experiments we collected fauna by simultaneously plugging up both ends of a tube with sponge pieces cut to the appropriate size. No fauna were observed escaping from the tubes of a structure as we did this. The outside of each tube was thoroughly rinsed in the lab prior to opening the tubes to ensure that no fauna outside the tube interiors was counted during data collection. Tubes were then opened, and tube contents were sieved on 0.5 mm sieves. Fauna were preserved in 10% buffered formalin. Fauna were counted and identified to the lowest taxonomic classification possible using a dissecting microscope. Only mobile species were counted and identified. Bivalves, tube-dwelling polychaetes, barnacles, hydroids, etc. were not counted or identified. For mixed treatments we recorded whether individual fauna came from the small, medium or large tubes.

For the first experiment, fauna were also classified into 4 Py categories: <3, 3–12, 12–24 and >24 mm. Py is the longest linear distance perpendicular to the organism's normal direction of movement that would limit the prey's ability to fit into a tube. Flexible body parts that an organism could bend in order to fit into a tube were not included in measuring Py. The following

are examples of Py measurements: crabs were measured from anterior to posterior end (since they move sideways); shrimp were measured from dorsal to ventral side of the carapace, not including the flexible legs; the width of the central disk was measured in brittle stars; the largest distance from dorsal to ventral surface (depth of body) was measured in damselfish, not including the flexible fins, since they are laterally compressed; and in gobies, the distance from operculum to operculum was measured, since they are dorso-ventrally compressed. For the second experiment we did not measure or categorize fauna according to size.

For the first experiment we tested whether there was a difference in species richness of the fauna that colonized the different treatments using ANCOVA. Faunal abundance and species richness were log transformed to meet the assumptions of ANCOVA. Treatment type was the main factor, abundance was the covariate and species richness was the dependent variable. The interaction between treatment and abundance was not significant ($p = 0.58$), so the interaction term was dropped from the final analysis. We tested which treatments were significantly different from each other using Tukey's multiple comparisons.

For the first experiment we tested whether there was a significant difference in abundance of small fauna between the small, medium and large tube treatments using ANOVA. We used Bartlett's test to verify homogeneity of variance. We used Tukey's multiple comparisons to determine which treatments were significantly different from each other. Fisher's exact test (2-tailed) was used to test whether there was a difference in the likelihood of finding one or more medium fauna in the medium or large tube treatments because of low organism count for medium fauna. Chi-squared analysis was used to test for differences in the likelihood of finding different types of fauna in the 4 different treat-

Table 1. Percent composition of mobile macrofauna collected in Expts 1 and 2 combined. Total number of fauna counted was 1499

Fauna	%
Non-caprellid amphipods and isopods	58
Gastropods	10
Shrimp	8
Caprellid amphipods	6
Polychaetes	5
Ostrocods	3
Crabs	1
Fish	1
Other	8

Table 2. ANCOVA: Log mobile fauna abundance is the covariate, structure treatment is the independent variable and log faunal species richness is the dependent variable

Source	df	Seq. SS	Adj. SS	Adj. MS	F	p
Log abundance	1	2.01977	1.01813	1.01813	70.34	<0.0005
Treatment	3	0.26773	0.26773	0.08924	6.17	0.001
Error	47	0.68034	0.68034	0.01448		
Total	51	2.96784				

ments. We combined individual species into broader taxonomic groups so that the results could be analyzed statistically, as most individual species occurred rarely. The faunal groups that we tested were: caprellid amphipods, non-caprellid amphipods and isopods, shrimp, gastropods, errant polychaetes, ostrocods, crabs and fish.

For the second experiment we tested whether there was a significant difference in total colonizing fauna between the 2 treatments using a 2-tailed *t*-test.

RESULTS

In the first experiment, we counted 945 individuals. In the second experiment, we counted 554 individuals. In both experiments, small crustaceans dominated numerically, particularly amphipods (Table 1).

In the first experiment, we collected 18 medium individuals, and none of them were found in small tubes. We also collected 15 large individuals and none of them were found in small or medium tubes. One individual gastropod (*Thais alouina* with a Py of 25 mm due to its projecting spines) was found tightly wedged into a large 24 mm tube.

There was a difference in species richness between treatments in the first experiment, after controlling for the effect of faunal abundance on species richness. The covariate faunal abundance was highly significant (ANCOVA: $p < 0.0005$), as was treatment ($p = 0.001$), with the small tubes having significantly less species richness compared with the other treatments, which were all equal (Table 2, Fig. 1).

There was a significant difference in the abundance of small fauna between treatments in the first experiment (ANOVA: $p = 0.041$), with large tubes having significantly more small fauna than small tubes and medium tubes having intermediate small fauna abundance, not significantly different from either the large or small tube treatments (Table 3, Fig. 2).

Medium fauna were found in 1 out of 13 large tube treatments and 6 out of 13 medium tube treatments in the first experiment. These results indicate a non-significant trend of having a greater chance of finding

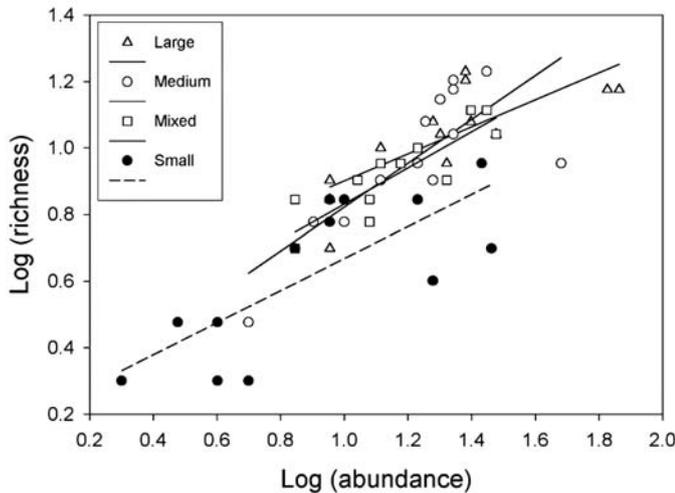


Fig. 1. Log abundance of mobile fauna colonizing a structure versus log species richness found on the structure. ANCOVA revealed that small treatments had significantly less species richness than the other 3 treatment types with log abundance as the covariate

one or more medium individuals in medium tubes compared with large tubes (Fisher's exact test [2-tailed]: $p = 0.073$). In the mixed structure treatments, medium fauna were not found in large tubes, but were found in medium tubes 5 of 13 times. We could not include the results from the mixed treatments in the statistical analysis, since, in some cases, the medium and large tubes were part of the same structure, and therefore were not independent. However, if you combine the non-significant trend (above) with these results from the mixed tubes, it is clear that medium fauna were more likely to be found in medium tubes compared with large tubes for the first experiment as a whole. Note that 11 of the 18 medium individuals we collected were crabs, so the observed pattern for medium fauna was largely driven by crab colonization.

For the first experiment there was a significantly decreased likelihood of finding one or more errant polychaetes and gastropods in small tube treatments compared with the other 3 treatment types (chi-squared: $p = 0.012$ and 0.042 , respectively, $df = 3$). There was a non-significant trend of having a reduced likelihood of finding one or more crabs in small tube

Table 3. ANOVA: Small (<3 mm width) faunal abundance is the dependent variable and structure treatment is the independent variable

Source	df	SS	MS	F	p
Treatment	2	1433	716	3.48	0.041
Error	36	7405	206		
Total	38	8838			

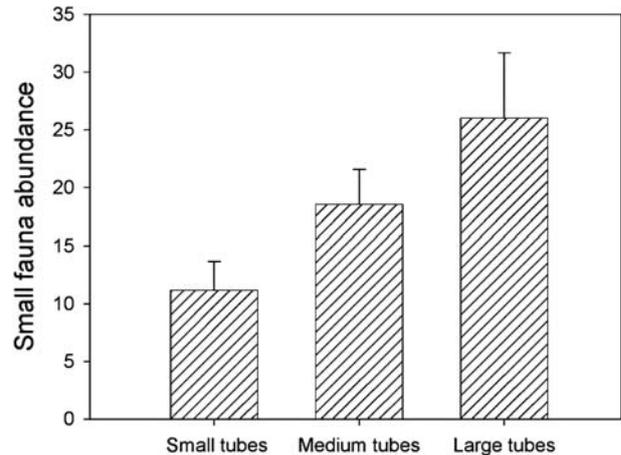


Fig. 2. Abundance of small fauna (<3 mm width) in the small, medium and large tube diameter structures. Large tubes had significantly more small fauna than small tubes, and medium tubes were not significantly different than large or small tubes (Tukey's multiple comparisons). Error bars represent SE

treatments compared with the other 3 treatment types ($p = 0.051$, $df = 3$). There was non-significant trend of having a reduced likelihood of finding one or more caprellid amphipods in small and medium tube treatments compared with the other 2 treatment types ($p = 0.064$, $df = 3$). There were no differences in the likelihood of finding one or more ostracods, non-caprellid amphipods and isopods, shrimp or fish between the different treatments. Note that no fish were found in the small tube treatments and fish were found in all 3 of the other treatments, but not frequently enough to result in a significant difference between these 3 treatments and the small tube treatment.

For the second experiment there were significantly more fauna collected in the large tube treatments compared with the smaller tube treatments (2-tailed t -test: $t = 3.79$, $p = 0.009$, $df = 6$). The average number of fauna in the small tube treatments was 15.7 (SE = 6); the average number of fauna in the large tube treatments was 76.7 (SE = 15). Almost all of the fauna collected in the second experiment had a width <3 mm, and therefore would have been classified as 'small' in the first experiment.

DISCUSSION

We found that only 1 individual gastropod inhabiting the deployed tubes had an Sp/Py value <1 (Sp/Py = 0.96); therefore, measuring Sp/Py values may be useful in determining whether a given space can be used as a refuge or inhabited by a given organism. Our results support the idea that certain habitats with small inter-structural space sizes may be 'too complex', may exclude

certain larger-width fauna, and may therefore not be useful refuges or living spaces for these fauna. It is important to point out that various researchers have found that complex habitats with small inter-structural space sizes appeared to exclude some larger fauna (Moksnes et al. 1998, Kelaher 2003, Almany 2004, Snickars et al. 2004), and many other researchers have found or suggested that space size relative to faunal body size is important to consider when explaining faunal habitat use patterns and/or prey survivorship patterns (see Steger 1987, Hacker & Steneck 1990, Hixon & Beets 1993, Friedlander & Parrish 1998, McAbendroth et al. 2005).

Bartholomew (2002b) predicted that fauna should be excluded from spaces when $Sp/Py < 1$ and that prey survivorship and abundance should be low under these circumstances as a result. Bartholomew (2002b) found that flexible structures (artificial seagrass) certainly did not exclude larger fauna from smaller spaces; the present study supports this prediction with inflexible structures, with the exception of 1 gastropod.

If certain larger species are excluded from habitats with small inter-structural space sizes, these habitats may have reduced species richness relative to less complex habitats. The results of this experiment support this idea, as small tube treatments had significantly reduced species richness after controlling for the effect of faunal abundance on species richness. Other researchers have found that macrofaunal species diversity declines as inter-structural space size decreases. Kelaher (2003) found that gastropod species richness declined with increasing coralline algae frond density in mid rocky shore areas, and similarly he found reduced gastropod species richness in a higher density artificial turf treatment. The evidence presented by Kelaher (2003) suggests that larger gastropod species, such as predatory whelks, were excluded from the higher density turf treatment, contributing to this reduction in species richness. Further research should be performed to determine whether decreased macrofaunal species richness in very complex habitats is an unusual phenomenon. It should be noted that the small tube treatments in the present study had uniformly small spaces formed by inflexible structures, similar to the artificial turf used by Kelaher (2003). A habitat that was heterogeneous, with mostly small spaces but a few larger ones, may have some large fauna inhabiting these larger spaces, leading to increased species richness compared to a habitat with uniformly small spaces. In general, space size heterogeneity may promote increased species richness in a habitat; however, this idea is not supported by the results of the present study, since the mixed treatment that combined the 3 tube sizes into one treatment did not have greater species richness than the uniformly medium or large tube treatments.

In the present study various fauna were less likely to be found in the small tube treatments, including errant polychaetes, gastropods, crabs and caprellid amphipods. Fish were also completely excluded from the small tube treatments. All errant polychaetes and caprellid amphipods collected in this experiment were classified as 'small' fauna, as were most gastropods collected. This indicates that even though they could physically fit into the spaces of the small tubes they were less likely to inhabit them.

Bartholomew (2002b) predicted that fauna should have decreasing survivorship as Sp/Py increases from 1 onwards. Note that the present study did not explicitly test faunal survivorship, but rather simply observed faunal abundance for 3 different size classes of fauna. Abundance in the tubes could have been influenced by several factors other than prey survival, including inter- and intraspecific competitive interactions, differences in hydrodynamic factors that affect faunal movement into and around the tubes and faunal choice. Choice may be affected by factors such as food availability, hydrodynamic factors, feeding ability within the tubes, and perceived refuge value of the tubes.

Small fauna in the first experiment had increased faunal abundance associated with the larger tube size treatments compared with the smaller tube size treatments, with intermediate abundance in medium tubes. This indicates that small faunal abundance responded positively to either the increased surface area or the increased volume of space available in the larger tubes, or they responded to differences in hydrodynamic forces associated with the different treatments. This is despite the fact that large tubes had poorer refuge value for these small fauna due to their larger Sp/Py values. The tubes of the second experiment had different diameters and different volumes, but had the same interior surface areas. The fauna were more abundant in the large tube treatments, again despite the decreased refuge value of these tubes. The results of the 2 experiments suggest that small fauna were responding positively to the increased volume of space within the larger diameter tubes in these 2 experiments, or to differences in hydrodynamic forces around or within the tubes that encouraged greater supply to and/or settlement in the larger diameter tubes. These results suggest that tube diameter and interior surface area were less important or not important in the observed patterns of small fauna abundance.

Medium fauna in the present study were excluded from small tubes and were more likely to be found in medium tubes than large tubes. This abundance pattern is consistent with greater survivorship, or faunal choice based on perceived better survivorship (Bell & Westoby 1986), in medium tubes compared with larger

tubes. The medium fauna in the present study were excluded from spaces smaller than their body size ($Sp/Py < 1$), were at higher abundance in spaces matching their own body size (Sp/Py slightly greater than 1), and were at lower abundance in spaces much larger than their body size (Sp/Py much greater than 1). This abundance pattern is consistent with the prediction of Bartholomew (2002b, their Fig. 1) if prey abundance is greatly affected by prey survivorship. The present study is the first to explicitly test and subsequently verify this prediction. These results should be interpreted with caution, however, since only 18 medium individuals were collected in the first experiment, and most were crabs.

A single given habitat may have different refuge values to different prey depending upon the size of the prey. A given habitat may provide ideal refuge spaces for medium-width prey, for example, if these prey can fit through the spaces in the habitat, but all or most of their large predators cannot fit through the spaces in the habitat to search for or pursue them (assuming the predator's width [Pr] is larger than the prey's). Under these circumstances, Sp/Py would be high, but Sp/Pr would be low, and the structures in the habitat would interfere with the predator's ability to move through the habitat (Bartholomew et al. 2000). The structures would also probably provide cover for the prey to hide behind as well (Bartholomew et al. 2000, Bartholomew 2002a).

This same given habitat may provide less-than-ideal refuge for smaller width prey. These smaller prey may be able to move through the spaces in the habitat easily, but their medium-width predators may be able to do the same to search for and pursue these small prey. Under these circumstances, both Sp/Py and Sp/Pr would be high. The structures would still provide some cover for the small prey to hide behind which would lead to increased prey survivorship relative to habitats with little or no cover at all. Studies suggest that an increase in structure from nothing to a small amount of cover can result in a rapid increase in prey survivorship by interfering with a predator's ability to detect prey, even though there is not enough structure to interfere with predator movement (Isaksson et al. 1994, Graham et al. 1998, Lipcius et al. 1998, Bartholomew 2002a, Hovel & Fonseca 2005).

This same given habitat may provide less-than-ideal refuge for large-width prey. If these prey are too large to fit into the spaces of the habitat ($Sp/Py < 1$) then these large prey are excluded from using the spaces of the habitat as refuge and may be vulnerable to their predators (Bartholomew et al. 2000, Bartholomew 2002b).

It is clearly important to consider the size of the organisms concerned when considering whether a

given 'complex' habitat provides prey with good refuge spaces from predators, and both Sp/Py and Sp/Pr incorporate animal size into the complexity indices themselves. The results of this study indicate that the Sp/Py index may be important when examining faunal habitat use patterns in nature. Specifically, this index may be useful in determining which fauna would be excluded from using a habitat space. It can also be useful because some fauna may be more likely to be found in spaces that match their own body width. This study also demonstrates that habitats with uniformly small spaces may have less species richness than habitats that include at least some larger spaces, as larger taxa may be excluded from using habitats that only have small spaces. This possibility needs to be explored further.

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