Abundance, size and habitat relation of reef fish on biogenic structures (structure-forming invertebrates) at Anacapa Island, southern California

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A biogenic structure ecosystem of extensive worm tubes of Chaetopterus *sp. harbouring different fish species was investigated at Anacapa Island, southern California to determine the numerical abundance, species composition, body size, and seasonality of the ichthyofauna associated, and their relation with the worm patch size. Bimonthly, a 30-m swimming transect and a quadrat-based survey estimated the length of each fish, the type of habitat it occupied, and the worm tube patch size-class. Larger worm mats harboured higher densities of fish, mainly the dominants* Rhinogobiops nicholsii *and* Chaenopsis alepidota, *which live inside the worm tube patches. Fish population density varied between the 'inside' and 'edge' of* Chaetopterus *beds as smaller and younger individuals were hindered from reaching the middle of the patch by larger, older and territorial individuals. The prevalence of positive and significant correlations between the abundance of smaller individuals of* R. nicholsii *and specific habitat features (e.g. edge) suggests that the abundance and distribution of juveniles might be habitat-dependent besides intraspecific competition between older and younger individuals. There was a decreasing density of* R. nicholsii *at greater than 20 cm away from worm tubes and there were no individuals beyond 6 m away from structure.* Chaenopsis alepidota *was not recorded when the patch size was less than 50% tube coverage. Our results revealed that complex habitat structure had a positive influence on the abundance of juvenile and adult of* C. alepidota *and* R. nicholsii, *and suggest that these structured areas are preferentially utilized, which contributes to its patchy distribution pattern. The presence of biological structures in low-relief sedimentary habitats can have critical functional significance even for reef fish. These important habitat features may need to be identified and protected.*

Keywords: reef fish, biogenic structure, habitat selection, *Chaetopteus* beds, *Chaenopsis*, *Rhinogobiops*, southern California

INTRODUCTION

Many of the fish communities of the Southern California Bight have been well studied. This is particularly true of shallow rocky reefs and sediment sea floors (Horn, 1980; Allen, 1985). However, with the exception of some plant beds (such as that of giant kelp *Macrocystis pyrifera*) the fish assemblages of biogenic structures are poorly known.

Sand-dwelling polychaete worms of the genus *Chaetopterus* produce calcareous tubes that are a conspicuous feature of shallow water southern California sand flats. Densities of worms on these biogenic reefs can reach several hundred individuals per m² (Zühlke, 2001; Shucksmith *et al.*, 2006). It is known that sediments around animal tubes can have greater abundances of bacteria (Eckman, 1985), diatoms (Sanders, 1962), meiofauna (Eckman, 1983) and macrofauna (Woodin, 1978) than surrounding sediments lacking structures. Since the biota associated with tubes can

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alter sediment stability, the effects include both the direct hydrodynamic consequences of flow alterations and the indirect effects of biogenic changes (Luckenbach, 1986). Research in other parts of the world (Van Dolah *et al.*, 1987; Zühlke, 2001; Thrush *et al.*, 2002) indicates that these biogenic structures represent ecological islands hosting a different and often more diverse and abundant community than surrounding sandflats and hence contribute to a patchy distribution pattern of the benthic community. Understanding the role of habitat structure for fish on the continental shelf is important because the physical structures created by sessile invertebrates and sediment surface features can be impacted by fishing gear and other human activities (Collie *et al.*, 1997; Freese *et al.*, 1999; Kaiser *et al.*, 1999; McConnaughey & Smith, 2000; Stoner & Tigten, 2003). However, despite their potential importance to some fish species, no research off the Pacific coast has been done on the fish assemblages of the worm tube structure.

Casual observations made while SCUBA diving around Anacapa Island, located in the north-western part of the Southern California Bight, demonstrated that the island's shallow sandy fringe is surrounded by kelp beds, sandy habitat and a biogenic structure ecosystem of extensive

worm tubes (*Chaetopterus* sp.) harbouring different fish species. These fish rest near or hide inside these biological structures and are well camouflaged; when disturbed, they retreat into local hiding places. Structurally complex benthic habitats have been demonstrated to alleviate predation risk for a wide variety of organisms in diverse systems, providing shelter and also abundant food resources for small fish (Ryer, 1988; Stoner & Titgen, 2003; Ryer *et al.*, 2004). *Chaetopterus* qualifies as an 'ecosystem engineer' in that it changes and/or creates a habitat, which affects other organisms (Jones *et al.*, 1997). It is not clear if some of these species depend on this ecosystem (e.g. food, shelter and/or nursery grounds), and how related they are to the patchiness of this enriching biogenic feature. In many cases, the survivorship of juvenile fish is higher in structurally complex habitats, although results vary with different habitats levels of complexity, and behavioural interactions between species (Bradshaw *et al.*, 2003).

This study represents the first attempt to determine the: (1) numerical abundance; (2) species composition; (3) body size; and (4) seasonality of the ichthyofauna associated with *Chaetopterus* worm beds of the north-east Pacific, and their relation with the worm patch size. In this study we tested the prediction that across *Chaetopterus* beds there would be a positive relationship between habitat structure and fish abundance, and that this relationship resulted from different aspects of the habitat structure.

MATERIALS AND METHODS

Study area

Anacapa is the eastern-most island of the northern Channel Islands and is located at approximately 34°00′N and 119°25′W, 19 km from the southern California mainland in the Southern California Bight (SCB). Anacapa Island is about 8 km long and is formed of three small islets (Figure 1). Waters in the SCB originate both from the California Current and northwards-flowing currents of

subtropical origin. Seasonal warming of water in the Bight is from atmospheric heating (Brink & Muench, 1986; Hickey, 1992). Circulation within the Santa Barbara Channel (SBC) is highly variable in time and space and is determined by the relative strengths of wind stress and a deep-water pressure gradient through the channel (Harms & Winant, 1998; Washburn *et al.*, 1999). Generally, warm water from the Southern California Bight enters the SBC's east entrance and flows westward along the channel's northern boundary, and cool water flows through the southern portion of the west entrance then eastward along the islands. Compared to the three islands to the west, waters around Anacapa are relatively warm and less saline, particularly during summer months (Nishimoto, 2000; Blanchette *et al.*, 2006).

The survey was conducted on the north side of east Anacapa Island on a biogenic structure ecosystem of worm tubes (*Chaetopterus* sp.) scattered in 12–15 m of water on a sand bottom. The surveys lay within the Anacapa Island State Marine Conservation Area, where fishing (except for pelagic fish and lobsters) is prohibited.

FIELD SAMPLING

Fish surveys were conducted at approximately two-month (bimonthly) intervals from September 2007 to July 2008 by two of us (I.R.Z. and M.M.).

Upon arrival at the survey site, an anchor was dropped and the divers swam down the anchor line. The first transect was conducted (beginning about 1 m from the anchor) in a northerly direction that went into deeper waters. In the first of two surveys, a diver (about 1 m above the sea floor) swam along a 30-m transect (laying out a measuring tape as he swam). All of the fish seen within 1 m on either side of the diver were identified, and thus the transect area was 60 m². We estimated the length of each fish and noted what type of habitat it occupied. We delineated three habitat types: (1) worm tubes; (2) sand; and (3) tube edge. Tube edge was defined as a worm tube within 20 cm of sand. A second diver followed the first and conducted a quadrat-based survey. In this survey, a 1m² PVC quadrat was placed every 4 m along the tape laid out by the first diver, and thus the quadrat sampled area was 7 m². The second diver then waited a few minutes and returned to the first deployed quadrat and identified and estimated the length of each fish observed. This diver also estimated what fraction of the quadrat was occupied by worm tubes (WT) on a scale of 0%, 25%, 50%, 75% and 100% WT, which corresponded to the worm tube patch size-class. This dual approach ensured that species more likely to swim away due to an observer were the first ones to be counted and allowed for more precise density estimations of all species (Aburto-Oropeza & Balart, 2001; Floeter *et al.*, 2007). This process was then repeated in both a westerly direction (along the depth contour) and a southerly direction.

Data analyses

We normalized for the area counted so as not to be misleading between the methods. We used a fixed-factor one-way analysis of variance (ANOVA) and tested for: (1) among-month differences; (2) among-WT patch size differences by quadrat sampling technique; and (3) among-habitat type by swimming sampling technique in mean density and size structure of the most abundant fish species sampled during the one-year study. The fish density of variable length-class across WT

Fig. 1. Map of Channel Islands (Santa Barbara Channel) showing Anacapa Island and the study site.

patch sizes, habitat type and between months was examined for each species with a 2-factor ANOVA. The transformed fish density was the dependent variable, with month, WT patch size and habitat type as independent variables. Significant effects ($P < 0.05$) were examined using Tukey's HSD *post hoc* multiple-comparison test. Whether WT patch size correlated with fish density and fish length, and with the fish density of each length, was tested with Pearson's product-moment correlation coefficient. When necessary, density data were transformed (log x + 1) to stabilize variances and meet normality and heterogeneity assumptions (Underwood, 1997; Zar, 1999).

ANOVA and product-moment correlation tests were performed with GraphPad Instat3.

RESULTS

A total number of 7 species and 290.11 fish/m² were sampled at Anacapa Island from August 2007 to July 2008 (N = 8 sample dates) through swimming and quadrat sampling techniques, 41.26 and 248.85 fish/m², respectively (Table 1). The quadrat technique sampled a higher number of individuals including the dominant species *Rhinogobiops nicholsii* (black-eye goby) and *Chaenopsis alepidota* (orangethroat pike-blenny), which lives inside the worm tube patches.

Quadrat sampling technique

Four species were sampled by the quadrat technique: *Rhinogobiops nicholsii*, *Chaenopsis alepidota*, *Citharichthys stigmaeus* (speckled sanddab) and *Heterodontus francisci* (horn shark) (Table 1). The two most abundant species *R. nicholsii* and *C. alepidota*, were analysed for among-WT patch size and among-month differences in mean density/m² and size structure during the one-year period study.

Chaenopsis alepidota showed a significantly higher number of individuals ($>60\%$) on larger patch size on all studied months (Figure 2; Table 2). Throughout the study, all sizes of *C. alepidota* were observed preferentially on larger patches with significantly higher numbers of the larger ones on 100% and 75% WT. Smaller individuals were significantly more abundant on $>50\%$ WT in August 2007, November

2007 and January 2008 (Table 2). In March 2008 all the patch sizes were smaller than 50% WT and the sampled individuals were the larger fish (Figure 2). In August 2007, November 2007, January 2008 and July 2008, the number of smaller individuals was higher than the larger ones, while in March, April, May and June 2008 the number of the larger individuals was higher (Figure 2).

Significant temporal differences among months occurred on total mean density and on smaller length-class density of *Chaenopsis alepidota* with the lowest values in March 2008 and April 2008 (Table 2). The highest mean densities occurred in August 2007 and November 2007 and then decreased in January 2008 followed by March and April 2008 with less than 0.86 inds/m² (Table 2). From May 2008 on, the densities of *C. alepidota* increased again with higher values, mainly on 100% and 75% WT. The smaller patch sizes ($<50\%$ WT) showed a lower temporal variation. Considering all studied months, fish density differences among-WT patch sizes revealed significant higher numbers on 100% and 75% WT for total mean density and for bigger length-class individuals (Table 2).

The WT patch size showed a very significant and positive correlation with the total mean fish density, with the fish density of each length-class, and with the fish length of each individual on almost all studied months except March 2008, and also with all months together (N = 31.14 inds/m²) (Table 3). All sizes of *Chaenopsis alepidota* individuals preferred larger worm tube patches.

Throughout the study, densities of *Rhinogobiops nicholsii* were highest on larger WT patch sizes (Figure 3), with significantly lower densities mainly on 0% and 25% WT (Table 4). In March 2008, the patch sizes were all smaller than 50% WT and there were higher densities of larger individuals on 50% WT and of smaller ones on 25% WT (Figure 3). Larger individuals were present in significantly higher numbers primarily on 100–75% WT, while smaller fish were equally present on both the largest and intermediate sized patches (Table 4).

Considering all studied months, fish density differences among-WT patch sizes revealed significantly higher numbers on 100%, 75% and 50% WT for total mean density and for larger length-class individual number, while the smaller ones did not differ among worm tube patch sizes (Table 4).

Table 1. Sampled species, density, size-range, habitat related to the worm tube patch (E, edge; M, middle; S, sand) and occurrence months through each sampling technique.

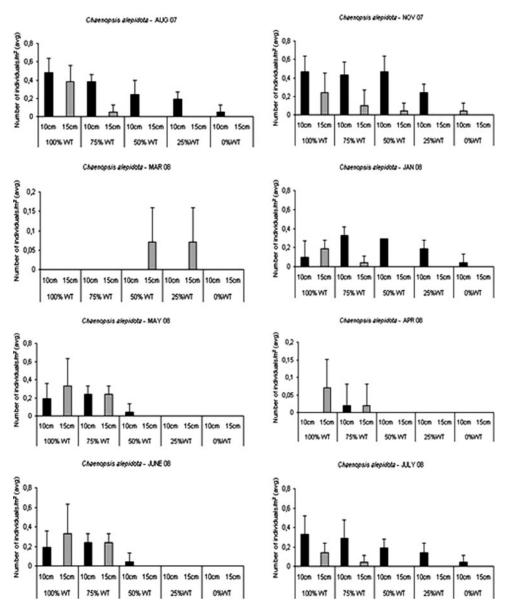| Species	Fish/m²	Size-range (cm)	Habitat	Months	Sampling technique
Rhinogobiops nicholsii	40.12	5–10	E > M > S	August 2007, January–March–April–May-June–July 2008	Swimming
Chaenopsis alepidota	0.70	10–20	E > S > M	August 2007, March–April–May–June–July 2008	Swimming
Citharichthys stigmaeus	0.36	5–10	E > S	August 2007, March–April–May–June–July 2008	Swimming
Alloclinus holderi	0.02	5–10	E	August 2007	Swimming
Heterodontus francisci	0.02	25–30	E	August 2007	Swimming
Squatina californica	0.02	180	E	June 2008	Swimming
Myliobatis californica	0.02	150	E	July 2008	Swimming
Rhinogobiops nicholsii	215.43	5–10	E > S > M	August–November 2007, January–March–April–May–June–July 2008	Quadrat
Chaenopsis alepidota	31.14	10–20	M > E > S	August–November 2007, January–March–April–May–June–July 2008	Quadrat
Citharichthys stigmaeus	2.14	5–10	E > S	Auguat 2007, January–March–April–May–June 2008	Quadrat
Heterodontus francisci	0.14	30–35	E	April 2008	Quadrat

Fig. 2. Average number of individuals/m² and standard deviation of *Chaenopsis alepidota* of each size-class and worm tube patch size sampled by the quadrat technique on every studied month (N = 6 transects/month).

Total mean density of *R. nicholsii* was positively correlated to WT patch size (Table 5). Larger individuals preferred larger patches. The negative and the non-significant correlation values of the WT patch sizes with the smaller individuals showed their preference for 50% and 25% WT patch sizes (Table 5).

SWIMMING SAMPLING TECHNIQUE

Seven species were observed in the swimming technique survey (Table 1). The dominant species, *R. nicholsii*, demonstrated a significantly higher number of individuals (60–95%) on the edge habitat than on the middle of the worm tube patches or on the nearby sand (Figure 4; Table 6). All sizes of individuals preferred the edge habitat, but larger fish showed consistently significant higher differences between the habitats (Table 6). In most months, larger fish tended to inhabit patch edge and middle, and smaller fish were found on the surrounding sand (Figure 4). Considering all studied

months, fish density differences among-habitat type revealed significant higher numbers on the edge for total mean density and both length-class individual numbers (Table 6).

The edge and middle habitats showed a positive and significant ($P < 0.05$) correlation with the total mean fish density ($r = 0.52$, $r = 0.54$, respectively), while the sand habitat fraction was negatively correlated ($r = -0.32$) (Figure 5). Relatively few *R. nicholsii* were present more than 20 cm away from worm tubes and none were seen beyond 6 m (Figure 5).

DISCUSSION

In this study we tested the prediction that fish median density and size varied with the worm tube (WT) patch size and were different between WT patch habitat, edge habitat and sand habitat. In general, larger worm mats harboured higher

Table 2. ANOVA and Tukey's HSD *post hoc* multiple-comparison results among-worm tube (WT) patch size differences in total mean density and size structure of *Chaenopsis alepidota* (smaller and bigger length-class) on each studied month, among-month differences and with all studied months by quadrat sampling technique.

Among-WT patch size differences	Total mean density	Fish density of smaller length-class	Fish density of bigger length-class
August 2007	$P = 0.0001$ 100% $\neq (75-50-25-0\%$ WT)	$P = 0.0125$ (100-75-50%) $\neq (25-0\%$ WT)	$P = 0.0001$ 100% $\neq (75-50-25-0\%$ WT)
November 2007	$P < 0.0001$ (100-75-50%) $\neq (25-0\%$ WT)	$P = 0.0102$ (100-75-50%) $\neq (25-0\%$ WT)	$P = 0.0271$ 100% $\neq (75-50-25-0\%$ WT)
January 2008	$P = 0.0371$ (100-75-50%) $\neq (25-0\%$ WT)	$P = 0.0223$ (75-50%) $\neq (100-25-0\%$ WT)	$P = 0.0046$ 100% $\neq (75-50-25-0\%$ WT)
March 2008	NS	No smaller indiduals	NS
April 2008	$P < 0.0001$ (100-75%) $\neq (50-25-0\%$ WT)	NS	$P < 0.0001$ (100-75%) $\neq (50-25-0\%$ WT)
May 2008	$P = 0.0066$ (100-75%) $\neq 50\%$ WT	NS	$P = 0.0066$ (100-75%) $\neq 50\%$ WT
June 2008	$P = 0.0002$ (100-75%) $\neq (50-25-0\%$ WT)	NS	$P = 0.0024$ (100-75%) $\neq (50-25-0\%$ WT)
July 2008	$P = 0.0004$ (100-75%) $\neq (50-25-0\%$ WT)	NS	$P = 0.0018$ (100-75%) $\neq (50-25-0\%$ WT)
Among-months	$P = 0.0017$ (August–November 2007– January–May–June–July 2008) $\neq$ (March–April 2008)	$P = 0.0001$ (August–November 2007– January 2008) $\neq$ (March–April–May– June 2008)	NS
Among-WT patch sizes (all months)	$P = 0.0004$ (100-75%) $\neq (25-0\%)$ WT	NS	$P = 0.0006$ 100% $\neq (50-25-0\%$ WT) 75% $\neq (25-0\%)$

densities of fish, although there were some intraspecific differences. For example, while larger *Chaenopsis* were almost absent from small mats, smaller individuals could still be found. The occurrence of smaller size fish on habitat of lower prey resource value might be related to intraspecific competition with the larger individuals occupying prime feeding or sheltering habitats.

The abundance of *R. nicholsii* was also significantly higher with high coverage of habitat (defined as WT patch size) but only for larger individuals. According to Steele (1997) and Andrews & Anderson (2004), recruitment of the blackeye goby increases with the amount of habitat in the form of rocky substratum at a small scale and our results generally do not support these previous works, considering the *Chaetopterus* beds as small units of complex reefs. It was

observed that the blackeye goby had similarly higher densities of smaller individuals in habitat with both intermediate and high coverage of *Chaetopterus* tube habitat. This may indicate that there is no further advantage conveyed by greater amounts of habitat, but might depend on the magnitude of recruitment.

Rhinogobiops nicholsii is a small (<100 mm standard length (SL)) reef fish that is common along the Pacific coast of North America (Miller & Lea, 1972). The species is territorial, but territories overlap, the greatest overlap occurring between individuals that differ considerably in size (Cole, 1984). The fish population density of *R. nicholsii* differed significantly between worm tube patch, edge and sand habitat. Although all size-classes preferred the edge habitat on the *Chaetopterus* bed, in general, larger individuals occupied this

Table 3. Pearson's product-moment correlation coefficient between worm tube (WT) patch size with *Chaenopsis alepidota* total average density and with the density of each length-class, and with individual length-class by quadrat sampling technique on each studied month and altogether. Density data were $\log x + 1$ transformed.

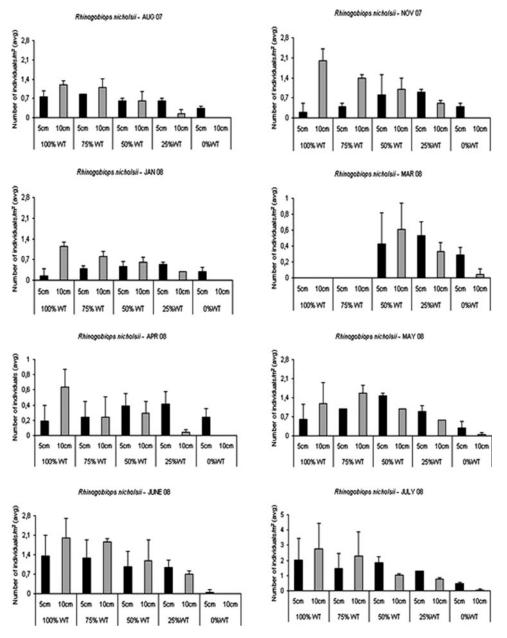| Correlation WT patch size versus	Total mean fish number	Fish number of smaller length-class	Fish number of bigger length-class	Fish individual length-class
August 2007	$r = 0.88$ ($P < 0.0001$)	$r = 0.83$ ($P = 0.0002$)	$r = 0.74$ ($P < 0.0016$)	$r = 0.44$ ($P = 0.0109$)
November 2007	$r = 0.92$ ($P < 0.0001$)	$r = 0.74$ ($P = 0.0016$)	$r = 0.60$ ($P < 0.0203$)	$r = 0.41$ ($P = 0.0466$)
January 2008	$r = 0.65$ ($P = 0.0083$)	$r = 0.25$ NS	$r = 0.69$ ($P = 0.0041$)	$r = 0.55$ ($P = 0.0047$)
March 2008	$r = 0.31$ NS	No smaller inds	$r = 0.31$ NS	$r = 0.43$ NS
April 2008	$r = 0.51$ ($P = 0.0043$)	$r = 0.13$ NS	$r = 0.49$ ($P = 0.0066$)	$r = 0.51$ ($P = 0.0037$)
May 2008	$r = 0.73$ ($P = 0.0019$)	$r = 0.71$ ($P = 0.0033$)	$r = 0.71$ ($P = 0.0035$)	$r = 0.34$ ($P = 0.0410$)
June 2008	$r = 0.82$ ($P = 0.0001$)	$r = 0.33$ NS	$r = 0.73$ ($P = 0.0002$)	$r = 0.39$ ($P = 0.0270$)
July 2008	$r = 0.90$ ($P < 0.0001$)	$r = 0.88$ ($P = 0.0001$)	$r = 0.74$ ($P = 0.0041$)	$r = 0.57$ ($P = 0.0028$)
Altogether	$r = 0.63$ ($P < 0.0001$)	$r = 0.37$ ($P < 0.0001$)	$r = 0.56$ ($P < 0.0001$)	$r = 0.25$ ($P = 0.0003$)

Fig. 3. Average number of individuals/m² and standard deviation of *Rhinogobiops nicholsii* of each size-class and worm tube patch size sampled by the quadrat technique on every studied month (N = 6 transects/month).

habitat. According to Cole (1982) and Breitburg (1987), social organization and territory size is based upon dominance relationships that are determined largely by body size. Population density varied between the 'inside' and 'edge' of *Chaetopterus* beds, where the smaller (<5 cm SL) and younger individuals were hindered in reaching the middle of the patch by larger, older individuals that maintained the territories.

The distribution and abundance of organisms depends to some extent on spatial variation in the physical structure of the available habitat (Bell *et al.*, 1991; Rotenberry & Wiens, 1998). Habitat structure is important in predicting the abundance and distribution of many taxa. Such relationships are particularly evident in the early life stage of reef fish in that recently settled individuals often appear to select complex habitats (Roberts & Ormond, 1987; Tupper & Boutilier,

1997). At Anacapa Island the prevalence of positive and significant correlations between the abundance of smaller individuals of the dominant species *R. nicholsii* and specific habitat features (e.g. edge) suggests that the abundance and distribution of juveniles might be habitat-dependent (Carr, 1991, 1994; Levin, 1991; Tolimieri, 1995; Steele, 1999; Holbrook *et al.*, 2000). Sources of variation in recruitment can be modified by particular habitat features. It is largely unknown whether recruitment of reef fish differs substantially between the edge and the inside of reefs; however, juvenile señorita *Oxyjulis californica* have been found at higher densities on the ecotone of artificial reefs (Anderson *et al.*, 1989) and the recruitment of some rockfish occur at the edges of rocky reefs (Carr, 1991). At the scale of individual reefs, the 'edge' and the 'inside' of a reef may affect the abundance of reef fish populations differently, analogous to the

Table 4. ANOVA and Tukey's HSD *post hoc* multiple-comparison results among-worm tube (WT) patch size differences in total mean density and size structure of *Rhinogobiops nicholsii* (large versus small size-class) in each month, among-month differences, and with all studied months by quadrat sampling technique.

Among-WT patch size differences	Total mean density	Fish density of smaller length-class	Fish density of bigger length-class
August 2007	$P = 0.0001$ $(100-75-50\%) \neq (25-0\% \text{ WT})$	$P = 0.0028$ $(100-75-50-25\%) \neq (0\% \text{ WT})$	$P = 0.0002$ $(100-75-50\%) \neq (25-0\% \text{ WT})$
November 2007	$P = 0.0001$ $(100-75-50\%) \neq (25-0\% \text{ WT})$	NS	$P = 0.0001$ $(100-75\%) \neq (25-0\% \text{ WT})$
January 2008	$P = 0.0008$ $(100-75-50-25\%) \neq 0\% \text{ WT}$	NS	$P = 0.0001$ $(100-75-50\%) \neq (25-0\% \text{ WT})$
March 2008	$P = 0.0206$ $(50-25\%) \neq 0\% \text{ WT}$	NS	$P = 0.0010$ $(50-25\%) \neq 0\% \text{ WT}$
April 2008	$P = 0.0297$ $(100-75-50-25\%) \neq 0\% \text{ WT}$	NS	$P = 0.0148$ $(100-75-50\%) \neq (25-0\% \text{ WT})$
May 2008	$P = 0.0251$ $(100-75-50-25\%) \neq 0\% \text{ WT}$	$P = 0.0052$ $50\% \neq (100\%-0\% \text{ WT})$	$P = 0.0277$ $(100-75\%) \neq (25-0\% \text{ WT})$
June 2008	$P = 0.0003$ $(100-75\%) \neq (25-0\% \text{ WT})$	$P = 0.0015$ $(100-75-50-25\%) \neq (0\% \text{ WT})$	$P = 0.0001$ $(100-75\%) \neq (25-0\% \text{ WT})$
July 2008	$P = 0.0001$ $(100-75\%) \neq (25-0\% \text{ WT})$	$P = 0.0008$ $100\% \neq (25-0\% \text{ WT})$	$P = 0.0001$ $(100-75\%) \neq (50-25-0\% \text{ WT})$
Among-months	$P = 0.0067$ (March–April 2008) $\neq$ (June–July 2008)	$P = 0.0003$ July 2008 $\neq$ all months (January–March–April 2008) $\neq$ (May–June 2008)	$P = 0.0107$ (March–April 2008) $\neq$ (June–July 2008)
Among-WT patch sizes (all months)	$P = 0.0066$ $(100-75-50\%) \neq 0\% \text{ WT}$	NS	$P = 0.0001$ $(100-75\%) \neq (25-0\% \text{ WT})$ $50\% \neq 0\% \text{ WT}$

effect of the habitat fragmentation in many terrestrial populations (Temple, 1986; Paton, 1994; Tewksbury *et al.*, 1998). The effects of ecotone are topical because of increased interest in habitat fragmentation and in how variability in the perimeter-to-area ratio may affect the demography of populations (Temple, 1986; Paton, 1994; Tewksbury *et al.*, 1998; Hovel & Lipcius, 2001). The distribution of newly settled fish among different types of habitats within a reef may result from food availability (Levin *et al.*, 1997) and the distribution of predators (Hixon, 1991). It is important to add intraspecific competition between older and younger individuals of *R. nicholsii*, as observed here.

Affinity for structured habitat in the field could be also related to availability of foods. *Chaenopsis* and *Rhinogobiops* consume primarily motile crustaceans such as mysids, amphipods, cumaceans and small shrimps (Kotrschal & Thomson, 1986). Small crustaceans such as these are often most abundant in structurally complex habitats (Orth *et al.*, 1984; Bostroem & Mattila, 1999). While there were no food cues

in our study, fish may choose habitats that typically carry large numbers of appropriate prey.

Describing fish–habitat relationships and understanding the underlying mechanisms is complicated by ontogenetic changes in habitat requirements and the spatial scales over which mobile individuals integrate habitats (Thrush *et al.*, 2002). As a first step to identifying the relationship between benthic habitat and fish, we aim to determine the importance of habitat structure in influencing the fish abundance. By determining the relationship between the fish abundance and the small-scale elements of habitat structure, we can identify the need for future work to elucidate mechanisms as well as providing information to resource managers on the importance of habitat diversity for different life stages of exploited and non-exploited populations.

Emergent structures may play an important role in the ecology of some juvenile flatfish and it is suggested that the removal of these biological structures by towed fishing gear and other anthropogenic and/or natural disturbance may

Table 5. Pearson's product-moment correlation coefficient between worm tube (WT) patch size with *Rhinogobiops nicholsii* total average density and with the density of each length-class, and with individual length-class by quadrat sampling technique on each studied month and altogether. Density data were log x +1 transformed.

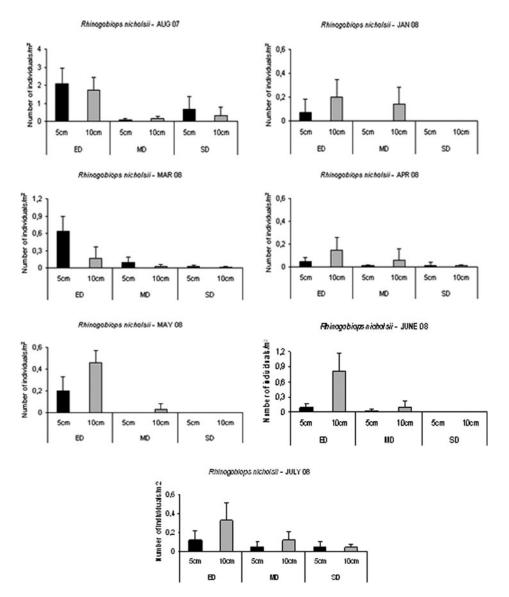| Correlation WT patch size versus	Total meanfish number	Fish number of smaller length-class	Fish number of bigger length-class	Fish individual length-class
August 2007	$r = 0.91$ $(P < 0.0001)$	$r = 0.37$ NS	$r = 0.92$ $(P < 0.0001)$	$r = 0.32$ $(P = 0.0002)$
November 2007	$r = 0.89$ $(P < 0.0001)$	$r = -0.35$ NS	$r = 0.96$ $(P < 0.0001)$	$r = 0.52$ $(P < 0.0001)$
January 2008	$r = 0.85$ $(P < 0.0001)$	$r = -0.33$ NS	$r = 0.97$ $(P < 0.0001)$	$r = 0.48$ $(P < 0.0001)$
March 2008	$r = 0.60$ $(P = 0.0079)$	$r = 0.23$ NS	$r = 0.77$ $(P = 0.0002)$	$r = 0.32$ $(P = 0.0019)$
April 2008	$r = 0.36$ $(P = 0.0049)$	$r = -0.15$ NS	$r = 0.53$ $(P = 0.0027)$	$r = 0.52$ $(P < 0.0001)$
May 2008	$r = 0.89$ $(P < 0.0001)$	$r = 0.39$ NS	$r = 0.96$ $(P < 0.0001)$	$r = 0.27$ $(P = 0.0021)$
June 2008	$r = 0.93$ $(P < 0.0001)$	$r = 0.79$ $(P < 0.0001)$	$r = 0.95$ $(P < 0.0001)$	$r = 0.15$ $(P = 0.0020)$
July 2008	$r = 0.98$ $(P < 0.0001)$	$r = 0.96$ $(P < 0.0001)$	$r = 0.95$ $(P < 0.0001)$	$r = 0.23$ $(P < 0.0001)$
Altogether	$r = 0.51$ $(P < 0.0001)$	$r = 0.11$ NS	$r = 0.65$ $(P < 0.0001)$	$r = 0.31$ $(P = 0.0002)$

Fig. 4. Average number of individuals/m² and standard deviation of *Rhinogobiops nicholsii* of each size-class and habitat type (ED, edge; MD. middle; SD, sand) related to the worm tube patches sampled by the swimming technique on every studied month (N = 6 transects/month).

Table 6. ANOVA and Tukey's HSD *post hoc* multiple-comparison results among-habitat type differences in total mean density and size structure of *Rhinogobiops nicholsii* (smaller and bigger length-class) on each studied month, among-month differences and with all studied months by swimming sampling technique (ED, edge; MD, middle, SD, sand).

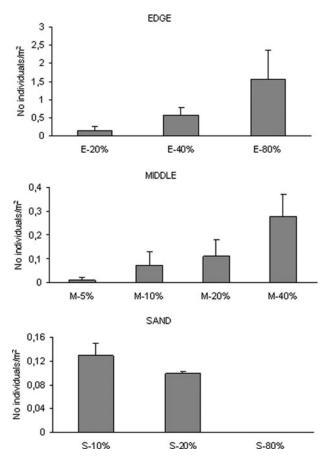| Among-habitat type differences	Total mean density	Fish density of smaller length-class	Fish density of bigger length-class
August 2007	$P = 0.0168$ ED > (MD ∼ SD)	$P = 0.0147$ ED > MD	$P = 0.0234$ ED > (MD ∼ SD)
January 2008	NS	Exclusively on edge	NS
March 2008	$P < 0.0001$ ED > (MD ∼ SD)	$P < 0.0001$ ED > (MD ∼ SD)	$P = 0.05$ ED > (MD ∼ SD)
April 2008	$P = 0.0496$ ED > SD	NS	$P = 0.048$ ED > SD
May 2008	$P = 0.0376$ ED > MD	Exclusively on edge	$P = 0.0217$ ED > MD
June 2008	$P = 0.0022$ ED > MD	NS	$P = 0.0210$ ED > MD
July 2008	$P = 0.0034$ ED > (MD ∼ SD)	NS	$P = 0.0036$ ED > (MD ∼ SD)
Among-months	$P = 0.0004$ (ED) (August 2007 – June 2008) ≠ (January–March–April–May–July 2008)	$P < 0.0001$ (ED) August 2007 ≠ (January–April–May–June–July 2008)	$P = 0.0016$ (ED) (August 2007 – June 2008) ≠ (January–March–April–May–July 2008)
Among-habitat types (all months)	$P = 0.0002$ ED > (MD ∼ SD)	$P = 0.0088$ ED > (SD > MD)	$P < 0.0001$ ED > (MD > SD)

Fig. 5. Average individual number/m² and standard deviation of *Rhinogobiops nicholsii* on the sampled transect fraction of each habitat type related to the worm tube patches by swimming sampling technique on all studied months (N = 6 transects/month).

influence their distribution patterns as fish redistribute to less preferred habitat (Stoner & Tigten, 2003; Ryer *et al.*, 2004). Biogenic structures contribute to marine habitat complexity by increasing the three-dimensional relief of seabed topography (Peatlle & Hoare, 1981). Dredging and other types of bottom fishing reduces habitat complexity by impacting sessile epifauna species, and by extension their associated organisms (Auster, 1998; Jennings & Kaiser, 1998; Kaiser *et al.*, 2002; Bradshaw *et al.*, 2003). The implications of this disturbance could be a decrease of biodiversity and/or species abundance (including commercial species) by removing upright epifauna (Bradshaw *et al.*, 2003). Our results revealed that complex habitat structure had a positive influence on the abundance of juvenile and adult *C. alepidota* and *R. nicholsii*, and suggest that these structured areas are preferentially utilized. This finding highlights the potential for disturbance of such structures (by, for example, trawling or dredging) to affect the abundance of those fish. Small changes in habitat complexity can have significant effects on survivorship.

Rhinogobiops nicholsii seldom ventured more than about 0.5 m away from rocky substrate because they use associated crevices and excavated burrows to hide from predators. At Anacapa Island, there was a sharp drop in density of *R. nicholsii* at greater than 20 cm away from worm tubes, and no *R. nicholsii* beyond 6 m away from structure.

Chaenopsis alepidota, that inhabits *Chaetopterus* tubes in quiet sand flats (Stephens *et al.*, 1989), was not recorded at Anacapa Island when the patch size was less than 50% tube coverage.

The tubiculous, suspension feeding polychaete, *Chaetopterus* cf. *variopedatus* of southern Chesapeake Bay, Virginia recruits in the summer and grows rapidly (Thompson & Schaffner, 2001), while Florida populations of reef-building tube worms may spawn semi-continuously, without a seasonal trend, throughout most of the year (Zale & Merrifield, 1989). At Anacapa Island, we anchored in nearly the same spot each sampling time and there was a clear seasonal trend in tube coverage, with more worm tubes in summer/autumn than winter/spring. *Chaenopsis alepidota* and *R. nicholsii* density followed this temporal trend with higher values during summer and lowest ones in winter and this pattern remained consistent among different tube coverage. The results further demonstrate that temporal variation in population dynamics might lead to significant temporal variability in the relative importance of benthic suspension feeder effects for ecosystem function (Thompson & Schaffner, 2001).

This study demonstrates a high degree of association between two reef fish and *Chaetopterus* beds. At the small scales studied (i.e. centimetres to metres) positive associations were more common than negative ones. These biogenic habitat structures represent ecological islands hosting a different and often more diverse and abundant community than surrounding sandflats. Reef fish richness and abundance of the two most abundant species *C. alepidota* and *R. nicholsii* were higher among tube aggregations with more than 25% of WT patch coverage. All sizes of *C. alepidota* and the largest *R. nicholsii* individuals preferred heavier WT patch sizes (>75% WT), while the smaller *R. nicholsii* preferred smaller patches (<50% WT). Hence, it is concluded that *Chaetopterus* tubes act as a habitat engineer that alters the composition and abundance of some reef fish species and contributes to its patchy distribution pattern. The study supports an accumulating body of evidence that emergent structure, in otherwise low-relief benthic habitats, may play an important role in the ecology of some reef fish species.

We suggest that *Chaetopterus* beds can be thought of as a keystone species (*sensu* Dame, 1996 in Thompson & Schaffner, 2001) and should be included in future studies or models of the Channel Islands. The importance of benthic habitats is now being taken in account in recent conservation and fisheries legislation in the United States, where areas of 'essential fish habitats' must now be identified and protected (Bradshaw *et al.*, 2003).

Links between habitat structure and growth, survivorship and recruitment of fish to fisheries need to be explored. However, our study on habitat preference makes it clear that the presence of biological structures in low-relief sedimentary habitats can have critical functional significance even for reef fish. These important habitat features may need to be identified and protected.

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