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Mobile 'reefs' in the northeastern Gulf of California: aggregations of black murex snails *Hexaplex nigritus* as habitat for invertebrates

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ABSTRACT: We documented positive interactions created by aggregations of black murex snail *Hexaplex nigritus* that support an epifaunal community annually. We examined abundance, species richness, and species composition of epifauna associated with aggregations, sampling snails from 12 aggregations and collecting epifauna from snails. We estimated 49 100 organisms (±7400) within a 25 m^2 area of an aggregation, many of which were juvenile invertebrates, and 193 species (95% CI 178–224) representing at least 7 trophic guilds. Epifauna occur on *H. nigritus* because shell structure provides benthic habitat heterogeneity, although biological characteristics of this foundation species may influence the associated composition of epifauna. To test this hypothesis, we anchored artificial reefs constructed of black murex shells and compared epifaunal communities that developed on them to those on aggregations. Abundance of epifauna was not different between aggregations and artificial reefs ($p = 0.4$); however, species composition was different ($p = 0.005$, $R = 0.7$). Epifaunal communities of aggregations had higher numbers of filter feeders and grazers than artificial reefs. Black murex snails illustrate that mobile benthic organisms can function as a foundation species and that biological characteristics of a foundation species may influence the associated composition of species. This system is ephemeral in nature, and epifauna that occur each spring and summer on snails may vary considerably. Loss of large *H. nigritus* aggregations has been documented due to overfishing, and declines in black murex populations result in the loss of a benthic substrate.

KEY WORDS: Benthic diversity · Biogenic reefs · Black murex · *Hexaplex nigritus* · Epifauna · Gulf of California · Foundation species · Habitat modifier

INTRODUCTION

Many marine benthic communities are generated by habitat-modifying species or foundation species (Dayton 1972, Bruno & Bertness 2001), which create spatial refuge from environmental stress and predation simply by their presence (Dayton 1975, Bruno & Bertness 2001). Foundation species such as kelps, corals, and oysters can facilitate communities by providing a site of attachment for sessile organisms (Witman 1985, Duggins et al. 1990) and enhancing propagule supply or retention (Carr 1989). They can also increase food supply to associated organisms by altering water flow and raising benthic organisms into the water column (Duggins et al. 1990, Irlandi & Peterson 1991, Harvey et al. 1993). These foundation species can transform a 2-dimensional landscape into a complex 3-dimensional landscape (Bruno & Bertness 2001) and increase species richness on a local scale (Heck & Wetstone 1977, Thompson et al. 1996).

In the benthic environment of the northeastern Gulf of California, strips of rocky reef are a limited substrate for rocky reef invertebrates and fish and are separated by vast sandy plains. Consequently, as in other locations, it is thought that there is intense competition for space on these hard substrates (Dayton 1971, Jackson

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1977). However, from April to August, the amount of hard substrate available at certain locations increases as large aggregations of hundreds to thousands of black murex snails (*Hexaplex nigritus* = *Muricanthus nigritus*) gather on sandy bottoms some distance from rocky reefs (Fig. 1).

Hexaplex nigritus, a predatory snail and Gulf of California endemic, aggregates to breed; females lay egg capsules on the shells of other conspecifics, and 1 snail can carry several hundred egg capsules on its shell (Cudney-Bueno et al. in press). Aggregations vary in size and number of snails by location and over the course of the aggregation. Snails are typically found on the surface of the seafloor during warm-water months, and bury themselves into sediments during cold-water months (Cudney-Bueno et al. in press). They have well-developed varices, which create ridges and spines across the shell, giving it a complex shape. Although these snails are mobile, Olabarria (2000) found that they function as habitat for a diverse mollusk epibiont community. When the snails aggregate, they increase benthic habitat complexity over a large area and likely influence local hydrodynamic processes, much like sessile reef structures do (Lenihan 1999, Monismith 2007).

Since the early 1990s, commercial divers have heavily harvested snails for their meat, shells, and opercula during aggregation periods (Cudney-Bueno 2000). Harvesting has resulted in the fishery's rapid decline, prompting community-based resource management, including season closures and harvest refugia (Cudney-Bueno 2007). Loss of large snail aggregations has been documented (Cudney-Bueno et al. in press), and declines in black murex populations may result in the loss of a benthic substrate and a settlement substrate (Prescott et al. 2007).

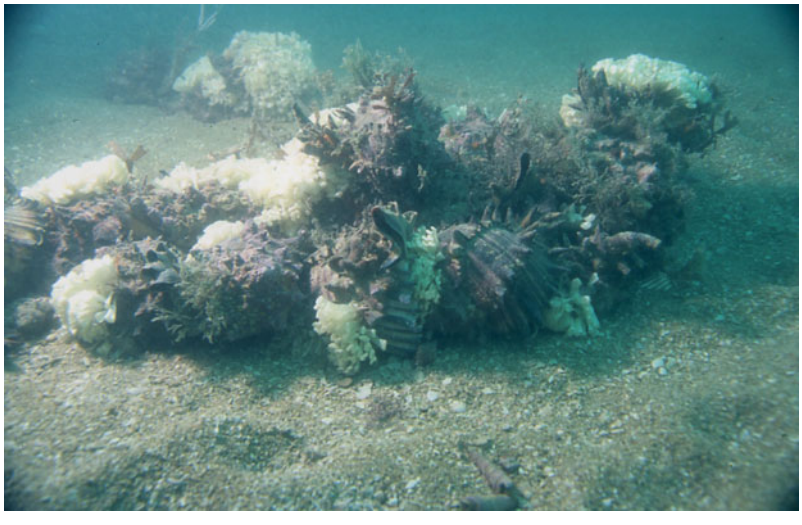

Fig. 1. *Hexaplex nigritus*. Beginning of an aggregation (individuals have egg capsules on shells), depth of 10 m (photo by Doug Moon)

In the present study, we documented the mobile and sedentary invertebrate epifaunal community associated with breeding aggregations of *Hexaplex nigritus*. Specifically, we estimated epifaunal abundance and species richness, and we assessed variation in species composition of epifauna on snails from aggregations at different sites. We also evaluated factors that influenced abundance of epifauna on snails, including site, number of egg capsules on the shell, and the time of year when snails were collected. Finally, we evaluated whether epifaunal organisms use black murex simply because they provide benthic structure, and whether biological and behavioral characteristics associated with living snails, such as movement, influence community composition. To evaluate these hypotheses, we constructed and anchored artificial reefs made of *H. nigritus* shells. We then compared the epifaunal community that developed on artificial reefs to epifaunal communities of aggregations. If relatively similar epifaunal abundance and species composition developed on artificial reefs as on aggregations, then this would suggest that *H. nigritus* simply provides habitat heterogeneity, and biological characteristics of live snails do not influence epifaunal communities.

MATERIALS AND METHODS

Study sites. Breeding aggregations of black murex were sampled along the northeastern coast of the Gulf of California from 4 subtidal sites: La Cholla, Sandy, Las Conchas, and Los Tanques (Fig. 2). La Cholla's benthic topography has many flat rocky reefs (tepetates), with a depth of 20 to 25 m. Sandy has rubble substrates with basalt and granite boulders near shore. Las Conchas and Los Tanques have isolated tepetates separated by fine grain sands. Sandy, Las Conchas, and Los Tanques range from 10 to 15 m in depth; however, all sites vary in depth and currents because of extremely large tides (maximum annual change in water height is 8 m; Thomson et al. 2000). The annual sea-surface temperatures range from <10°C to >32°C (Thomson et al. 2000).

Aggregation measurements and collection of snails. We located and sampled 12 aggregations during May, June, and July of 2003 and 2004 with the assistance of commercial divers. We marked the center of each aggregation with PVC pipe and an underwater buoy. We measured the size of each aggregation by recording 1 length measurement and 2 width measurements,

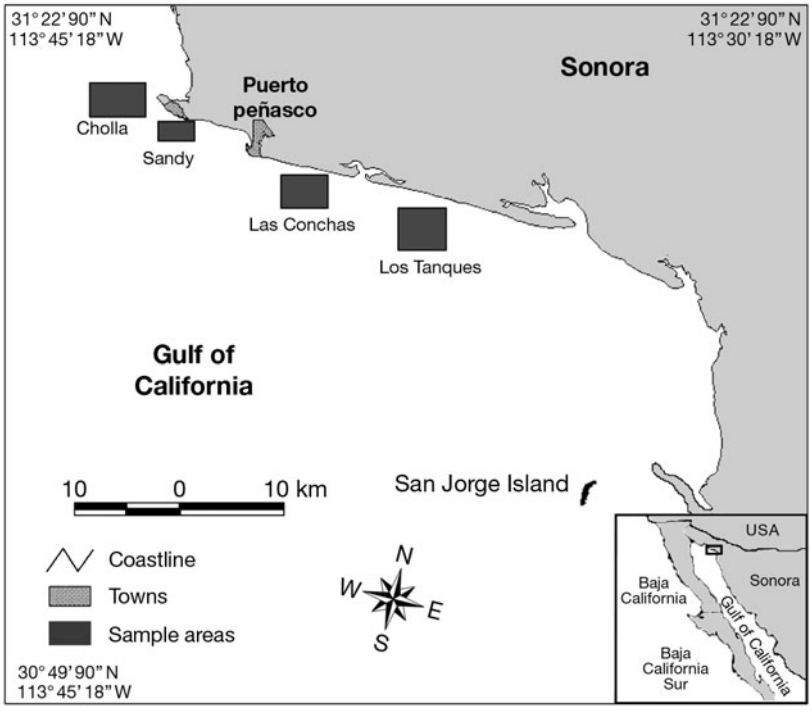

Fig. 2. Northeastern coast of the Gulf of California with 4 sites where snail aggregations were sampled

as width varied considerably along the length of each aggregation. We then averaged the width measurements.

To estimate density of snails in an aggregation and to collect epifauna from snails, we swam 6 transects of 5 to 10 m long from the center of each aggregation. The direction of the first transect was randomly selected, and the other 5 transects were placed in 30° intervals from the direction of the first transect. Along these transects, we placed 0.25 m^2 quadrats at 1, 3, and 5 m, recorded the number of snails in each quadrat, and then collected 1 to 5 snails randomly from each quadrat. If we could not collect at least 5 snails along a 5 m transect, we continued the transect lines out to 10 m. We collected ~30 snails from each aggregation, some of which were without egg capsules on their shells.

As we gathered snails from aggregations, we placed them in separate 3.8 l plastic bags (Ziploc) while underwater to keep mobile epifauna from escaping. Once we returned to a local laboratory, we placed the plastic bags containing snails into tanks filled with seawater for subsequent collection of mobile epifauna and to keep the snails and epifauna alive.

Identification and collection of epifauna. We removed the snails from the plastic bags and rinsed them with saltwater over 3 sieves, sizes 4 mm, 2 mm, and 63 µm, to collect mobile epifauna. Plastic bags were also rinsed over sieves. We then carefully examined the snails for organisms that were still present on shells by searching between egg capsules and on exposed surfaces of the shell. We preserved mobile epifauna from each snail (n = 295 snails; 1 sample = 1 snail) in individual jars containing 70% alcohol. Epifauna were selected for identification and abundance estimation by dividing the contents of a sample into 4 quadrants in a 10 cm diameter Petri dish, and randomly selecting all organisms within 1 quadrant. We then counted and identified epifauna in the subsample to the lowest taxonomic level possible, grouping morphologically similar organisms. Counts of epifauna from subsamples were multiplied by 4 to estimate a total count of organisms per snail. For 50 samples, we counted all organisms in the sample, and compared these counts to our abundance estimates from subsamples. All abundance estimates given in the results are based on subsample calculations. Voucher specimens of epifauna were placed in the University of Arizona's Invertebrate Collection and at the Universidad Autónoma de Baja California collection in Ensenada, Mexico.

We did not collect sessile epibiota, but recorded the percentage of epibiota cover on snails without egg capsules by visually inspecting the surface of the shell. If egg capsules were present on the snail, we counted the number of egg capsules. We measured the total length (apex to the anterior end), aperture length (top of aperture to anterior end), mass, and number of varices of each snail. Snails were kept in tanks until they could be returned to the location where they were collected.

We searched 10 of 30 snails from each aggregation more thoroughly to estimate our ability to detect epifauna on snails. We removed all egg capsules from the shell and carefully searched the entire shell and egg capsules for epifauna. Using this double-sampling method, we determined the percentage of organisms detected by calculating the ratio of the number of organisms collected under each sampling method. Detectability estimates were then applied to all subsample counts of epifauna.

Artificial reef sampling. To investigate the physical and biological characteristics that attract epifauna to *Hexaplex nigritus*, we anchored 3 artificial reefs in La Cholla in July 2003 and 3 in Las Conchas during May 2004 at 250 m intervals east of known snail aggregation

sites. We left reefs for 3 mo on the seafloor. Artificial reefs consisted of a 1 × 3 m sheet of poultry netting with 100 black murex shells attached with zip ties to the poultry netting in random locations. We had previously cleaned shells and filled the inside of each shell with concrete, adding weight and to close the space that would have been taken by the snail if it were alive. Out of the 6 artificial reefs, 4 were sampled using the same methods as those used for sampling aggregations that were collected from the seafloor. One artificial reef from Las Conchas and 1 from La Cholla were never found. We did not place artificial reefs within breeding aggregations or fasten live black murex to artificial reefs, as local conservation efforts with this species were ongoing at the time of study.

Data analysis. We determined mean abundance of epifauna on snails from aggregations and artificial reefs (JMP software, SAS Institute). To estimate species richness, we used the Chao 1 estimator (Chao 1984, Magurran 2004). Estimates of species richness were calculated by randomizing our samples 50 times and averaging the estimates (EstimateS software, University of Connecticut). Chao 1, a rarefaction-based estimator, provides a lower bound estimate of species richness (Magurran 2004). All species richness estimates were generated using subsamples of epifauna per snail.

We evaluated the relationship between abundance of epifauna (ln + 1 transformed) on aggregations and artificial reefs with several explanatory variables in an ANOVA framework. Explanatory variables included site, depth of water, month collected, number of varices, surface area of murex shell (ln-transformed), total area of aggregation, presence/absence of egg capsules, number of egg capsules (ln-transformed), and percentage cover of epibiota on murex snails. Snails without egg capsules were defined as those snails with 0 to 20 egg capsules (n = 131) because individuals with few egg capsules had most of their shell exposed. We defined snails with egg capsules present as snails with 21 or more egg capsules (n = 164). We report means and SEs from untransformed data adjusted for detectability. To determine the average surface area of a black murex shell, we used the surface area equations of 2 cones (bases of cones placed together). We also created 3D images of 5 shells (SolidWorks software), generating more accurate estimates of surface area (R. Prescott unpubl.). We then compared our estimates using cone equations with estimates from 3D images.

Species composition of epifauna among sites and artificial reefs was also examined. First, we 4th-root transformed all species abundances so resulting multivariate ordinations were not determined by the dominant species (Clarke & Warwick 2001). We then calculated Bray-Curtis similarity coefficients from transformed species' abundance data (Bray & Curtis 1957, Field et al. 1982, Clarke & Green 1988; PRIMER software). The resulting matrices were ordinated with nonmetric multidimensional scaling (NMDS; Kruskal 1964). NMDS plots display the multivariate species composition data of the 12 aggregations and 4 artificial reefs as points in 2 dimensions, and the relative distances between points represent how similar or dissimilar aggregations and artificial reefs are in terms of species composition.

Using Bray-Curtis similarity coefficients between samples, the test statistic R (1-way analysis of similarities [ANOSIM]; Clarke & Green 1988) for both aggregations and artificial reefs was calculated under the null hypothesis of no difference between sites or between aggregations and artificial reefs. Last, we used similarity percentages (SIMPER; Clarke 1993) based on the Bray-Curtis similarity coefficients between samples to determine the taxa most responsible for differences in epifaunal composition. SIMPER analysis determines the average contribution of each species to the overall similarity or dissimilarity between groups and within groups.

RESULTS

Structure of black murex breeding aggregations

Black murex snail aggregations averaged 16 ± 3.9 m by 9 ± 1.3 m and ranged from as small as 5 × 5 m to as large as 41 × 16 m. Within a 25 m^2 central square area of each aggregation, density of snails averaged 31 ± 1.0 snails m^{-2}, yielding 769 ± 154 snails in a 25 m^2 area.

Epifaunal community of aggregations

Based on the double sampling procedures described in the methods, we determined that a single sampling procedure without removing egg capsules from shells detected 90% of the mobile epifauna present on snails. We also determined that our estimates of total abundance of epifauna/snail using our subsampling method were correlated with total counts of organisms from samples (r^2 = 0.87, n = 50). Therefore, we proceeded to use subsample data for all further analyses.

The average number of total organisms found on an individual black murex snail was 71 ± 3.4 (Table 1). We estimated 2000 ± 255 epifaunal organisms m^{-2} within an aggregation and 49 100 ± 7400 epifaunal organisms in a 25 m^2 area of an aggregation. We also determined that on average, the surface area of a murex shell was 273.3 ± 7.9 cm^2 and the density of epifauna per snail was 0.27 ± 0.03 individuals cm^{-2}. Surface area esti-

Table 1. Mean abundance of epifauna per murex snail and artificial reefs (AR) for factors associated with abundance

Factor	Mean	SE	N
All sites	*71*	*3.4*	*295*
Cholla	71	4.7	63
Sandy	83	7.4	87
Conchas	78	7.2	75
Tanques	51	5.2	70
No eggs	59	4.8	131
Eggs present	82	4.5	164
Collected June 2003	73	3.9	184
Collected July 2003	91	9.3	52
Collected May 2004	46	6.6	59
AR (*both sites*)	*48*	*5.9*	*106*
Cholla	6	0.7	47
Conchas	81	3.5	59

mates using the equation of 2 cones were determined sufficient, as precise area estimates using 3D images of 5 shells yielded similar measurements (mean surface area = 253.1 cm^2; $r^2 = 0.81$).

Abundance of epifauna on aggregations varied with site, time collected, area of shell, and number of egg capsules ($p < 0.0001$, $F_{7,284} = 19.4$; Table 2). We did not find any relationships among other variables (such as water depth and size of aggregation) and abundance. Mean abundance of epifauna per snail differed between snails with egg capsules (82 ± 4.5) and without egg capsules on their shells (59 ± 4.8; Table 1), after accounting for month collected, site, and area of shell ($p < 0.0001$, $t = 4.76$; from linear contrast). Mean abundance of epifauna was also associated with the month and year snails were collected, after accounting for area of shell, site, and presence/absence of egg capsules ($p < 0.0001$, $F_{2,284} = 33.2$; Tables 1 & 2). Snails collected in May 2004 had lower estimates of abundance than snails collected in June and July 2003 ($p < 0.00001$, $t = 8.14$ from linear contrast; Table 1).

Table 2. ANOVA of abundance of epifauna from aggregations with site, month collected, area of shell, and number of egg capsules as factors; abundance of epifauna on artificial reefs (AR) vs. aggregations. Abundance estimates generated using subsampling methods

Source	df	MS	*F*	p
Abundance on aggregations (whole-model test)	7	9.53	19.44	<0.0001
Site	3	5.83	11.90	<0.0001
Month collected	2	16.30	33.24	<0.0001
Area of murex shell (ln)	1	9.85	20.09	<0.0001
Number of egg capsules	1	11.10	22.65	<0.0001
Error	284	0.49		
Abundance on AR vs. aggregations (whole-model test)	6	41.04	80.60	<0.0001
Site	1	1.59	3.13	0.08
Month collected	3	31.50	61.90	<0.0001
Area of murex shell (ln)	1	4.03	7.92	0.005
Artificial reef effect	1	0.31	0.60	0.438
Error	236	0.51		

Of the 166 morphologically similar organisms observed in subsamples, 69% were mollusks, 12% were arthropods, and 5% were echinoderms (see Appendix 1 for list of all species, available as Supplementary Material at: www.int-res.com/articles/suppl/m367p185_app.pdf). Polychaetes, nematodes, and peanut worms were also abundant (14%). We collected grazers, filter feeders, suspension feeders, predators, scavengers, ectoparasites, and deposit feeders. Fish comprised a small percentage of the total taxa (0.1%), with 1 species collected, the Redlight goby *Coryphopterus urospilus*. Other species of fish were observed on or near aggregations (see Prescott 2006). Overall, an aggregation had an average of 42 ± 4.0 species; however, we estimated 193 species (95% CI 178–224) for all aggregations (Table 3).

Epifaunal species composition of aggregations was more similar within sites than between sites ($p = 0.004$, global $R = 0.377$ from ANOSIM; Fig. 3, Table 4). Pairwise comparisons found that sites were 32.6 to 49.9% similar (from average Bray-Curtis dissimilarity percentages, SIMPER analysis; Table 4). Aggregations at La Cholla, the deepest site with 20 to 25 m depth, differed most from all other sites with the greatest R values (Table 4), especially from Las Conchas ($R = 0.67$).

Using SIMPER analysis, we found that abundance of *Hexaplex nigritus* protoconchs, 2 species of Columbellidae (grazers), slipper limpets (*Crepidula arenta*), worms (phyla Platyhelminthes, Annelida, Sipuncula, and Nematoda), 2 ectoparasitic gastropods (Pyramidellidae), and Pacific calico scallops (*Argopecten ventricosus*) were responsible for most of the differences between epifaunal assemblages among sites. Large numbers of *Ophiactis simplex*, a brittle star, *A. ventricosus*, and several phyla of worms (Platyhelminthes, Annelida, Sipuncula, Nematoda) accounted for much of the difference between La Cholla and all other sites.

Epifauna on artificial reefs vs. aggregations

Mean abundance of organisms did not differ between artificial reefs (48 ± 5.9) and aggregations (71 ± 3.4), after accounting for differences in month collected, site, and area of shell ($p = 0.4$, $t = 0.6$; Tables 1 & 2). However, abundance of epifauna from artificial reefs in La Cholla averaged only 6 ± 0.7 organisms per

Table 3. Observed number of species and estimates of species richness (Chao 1) for all sites and artificial reefs (AR)

Location	No. of species observed	Species richness estimate	(95% CI)
All sites	*166*	*193*	(*178–224*)
Cholla	64	106	(80–172)
Sandy	96	172	(127–282)
Conchas	97	122	(108–155)
Tanques	72	115	(89–176)
AR (*both sites*)	*108*	*146*	(*126–186*)
AR Conchas	80	107	(91–143)
AR Cholla	47	55	(49–71)

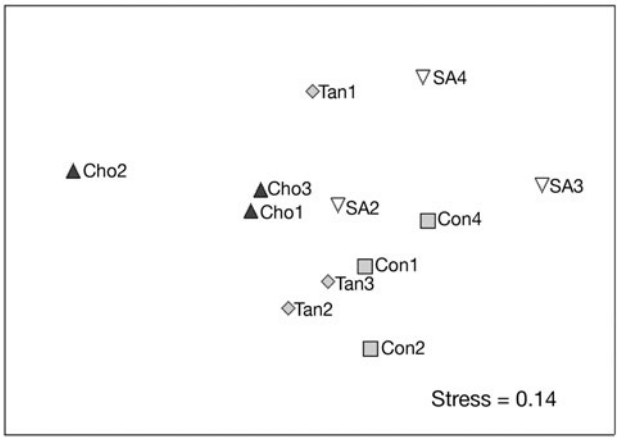

Fig. 3. NMDS plot comparing epifaunal assemblages from aggregations among La Cholla (Cho, ▲), Sandy (SA, ∇), Las Conchas (Con, ■) and Los Tanques (Tan, ◆). Distances between points indicate relative similarity between epifaunal communities of aggregations

Table 4. R and p-values for ANOSIM results and Bray-Curtis dissimilarity percentages from SIMPER analyses comparing species composition among sites and between artificial reefs (AR) and aggregations. na: not applicable

Site pairs	R	p	Average Bray-Curtis dissimilarity %
Global R (*all sites*)	*0.377*	*0.004*	*na*
Cholla-Sandy	0.44	0.10	67.41
Cholla-Conchas	0.67	0.10	65.28
Sandy-Conchas	0.22	0.20	62.7
Cholla-Tanques	0.41	0.20	62.24
Sandy-Tanques	0.22	0.30	60.74
Conchas-Tanques	0.33	0.10	50.1
Global R (*Aggregations-AR*)	*0.675*	*0.005*	*na*

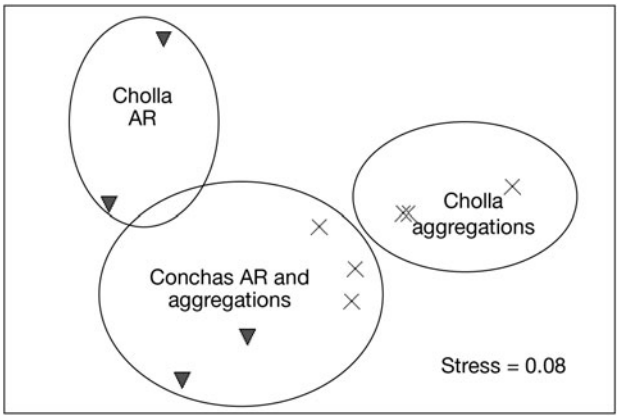

Fig. 4. NMDS plot comparing epifaunal assemblages between aggregations (×) and artificial reefs (AR, ▼). Distances between points indicate relative similarity between epifaunal communities of aggregations and artificial reefs

snail and was much lower than epifaunal abundance from artificial reefs in Las Conchas (81 ± 3.5; Table 1). We observed 108 species and estimated a total of 146 species (95% CI 126–186) from all artificial reefs, a lower number of species than that estimated for aggregations (Table 3). We found that epifauna consisted of 82% mollusks, 8% arthropods, 6% echinoderms, and 9% worms from several phyla.

Epifauna were more similar within aggregations than to epifauna of artificial reefs ($p = 0.005$, global $R = 0.675$ from ANOSIM; Fig. 4), and epifaunal communities that developed on artificial reefs supported only 10% similar species with aggregations. Using SIMPER analysis, we found that most of the differences in epifaunal communities on artificial reefs versus aggregations were explained by 1 species of ectoparasitic gastropod (Pyramidellidae sp.) that was dominant on artificial reefs and 1 species of grazing gastropod (*Anachis* sp.) that was dominant on aggregations.

DISCUSSION

Black murex aggregations are large in size relative to the epifauna they facilitate, and may cover a significant area of the sea bottom annually (see Cudney-Bueno et al. in press). Although these aggregations only occur from April through August each year, we suggest that aggregations function as mobile reefs and as a foundation species. The present study found that black murex aggregations cover >100 m^2 on average, provide topographic relief, and create a unique habitat for thousands of mobile and sessile invertebrates, including juveniles and commercial bivalves. However, these aggregations are currently fished with little to no management of the fishery (Cudney-Bueno et al. in press). If the abundance of black murex snails declines to very low numbers, they could become ecologically extinct, and will no longer have significant

impact on the community as a predator or as a foundation species.

We used subsample counts to estimate species richness and abundance of epifauna, and the Chao 1 estimator of species richness is a conservative estimator (Magurran 2004). It is, therefore, likely that the number of species associated with black murex aggregations may be higher than we estimated, although species richness rarefaction curves for all sites except Sandy were beginning to reach asymptotes (R. Prescott unpubl. data). Sandy also had the largest aggregation sampled (41 × 16 m), and larger aggregations may attract more organisms and more species. The present study could not determine whether there was a relationship between aggregation size and epifaunal abundance or species richness due to confounding variables, and further data would be needed to determine whether this relationship exists.

The shell and egg capsules of *Hexaplex nigritus* create habitat heterogeneity in sandy bottoms areas, which is supported by results from artificial reefs where similar numbers of organisms colonized murex shells. However, epifaunal communities that developed on artificial reefs supported only 10% similar species with aggregations. These differences may be due to (1) differences in location of artificial reefs and aggregations, (2) time differences between collection of reefs and sampling of aggregations, and (3) differences in the length of time underwater between artificial reef shells and living snails. Overall, an ectoparasitic gastropod (Pyramidellidae sp.) dominated on artificial reefs, possibly feeding on numerous tube-building polychaetes that settled on shells. Grazers, suspension feeding brittle stars, and filter feeders dominated on aggregations, with 1 Columbellidae snail (*Anachis* sp.) being the most common. Grazers may have been more common on aggregations because live snails, having been underwater for more than a year at minimum, had well-developed algal communities on their shells for grazers to feed on. Artificial reef shells had been in the sun prior to artificial reef construction and were underwater for only 3 mo. Many sessile animals and algae had settled on the shells, but the composition of epibiota may have been different.

Species composition differences between artificial reefs and aggregations may illustrate another difference; black murex snail aggregations are alive and mobile, thereby generating a different microenvironment than our sessile artificial reefs (see Glasby 2001). Artificial reefs mimicked the structural attributes of aggregations (although without egg capsules), but could not recreate the biological and chemical attributes of aggregations. For example, black murex snails do not become covered by sediments during aggregation periods. Epifauna that do not tolerate large amounts of sedimentation, a process that is common in the northern Gulf because of swift tidal currents, may select black murex as habitat over other sessile structures that are more likely to become silted.

Further research

Due to the ephemeral nature of this system, as snails leave aggregations and bury into the sediments during cold-water months (Cudney-Bueno et al. in press), the epifaunal community of aggregations may develop each year and change dramatically from year to year. New propagules may recolonize aggregations and individual snails each spring. We suspect that only a few epifaunal species remain on black murex through winter as snails that were found buried in sediments during the winter did not appear to have many epifaunal organisms (authors' pers. obs.). We also observed a decrease in epifaunal abundance between July 2003 and May 2004, which may be a seasonal or year difference, and will require further study. However, if seasonal patterns do exist, long-term sampling of aggregations may provide data regarding propagule availability and invertebrate diversity in the region. Aggregations may also decrease genetic isolation and increase fertilization success (see Coma & Lasker 1997) by reducing the distance between mobile, sedentary, and sessile organisms that are broadcast spawners.

One species of scallop, *Argopecten ventricosus*, has been found to settle on black murex snails when given other settlement options (Prescott et al. 2007). It is possible that aggregations function as nursery grounds for some species. Previous studies have found that juveniles of motile benthic organisms are concentrated in structurally complex environments that provide refuge from predation (Pohle et al. 1991, Gosselin & Chia 1995, Mosksnes et al. 1998). The soft, flexible egg capsules and complex shell structure of murex aggregations may give refuge from predators and environmental stress. Further studies determining the survival rate of individuals that settle on black murex aggregations could help better define their ecological role.

Defining the multiple roles of marine benthic organisms is essential to understanding and predicting benthic community dynamics. This includes both positive and negative interactions. Few researchers have focused on the positive interactions created by foundation species (Bruno & Bertness 2001), and their studies have generally focused on sessile, permanent biogenic structures. Black murex snail aggregations represent how a mobile organism may function in the same role as a sessile reef-building organism and as a habitat facilitator.

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LITERATURE CITED

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecol Monogr 27: 325–349

Bruno JF, Bertness MD (2001) Habitat modification and facilitation in benthic marine communities. In: Bertness MD, Gaines SD, Hay ME (eds) Marine community ecology. Sinauer Associates, Sunderland, MA, p 201–218

Carr MH (1989) Effects of macroalgae assemblages on the recruitment of temperate zone reef fishes. J Exp Mar Biol Ecol 126:59–76

Chao A (1984) Non-parametric estimation of the number of classes in a population. Scand J Stat 11:265–270

Clarke KR (1993) Non-parametric multivariate analyses on changes in community structure. Aust J Ecol 18:117–143

Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effects' study. Mar Ecol Prog Ser 46: 213–226

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edn. PRIMER-E Software, Plymouth

Coma R, Lasker HR (1997) Small-scale heterogeneity of fertilization success in a broadcast spawning octocoral. J Exp Mar Biol Ecol 214:107–120

Cudney-Bueno R (2000) Management and conservation of benthic resources harvested by small-scale hookah divers in the northern Gulf of California, Mexico: the Black murex snail fishery. MS thesis, University of Arizona, Tucson

Cudney-Bueno R (2007) Marine reserves, community based management, and small-scale benthic fisheries in the Gulf of California, Mexico. PhD dissertation, University of Arizona, Tucson, AZ

Cudney-Bueno R, Prescott R, Hinojosa-Huerta O (in press) Reproductive ecology and breeding aggregations of the black murex snail, *Hexaplex nigritus* (Mollusca, Muricidae) in the Gulf of California, Mexico. Bull Mar Sci

Dayton PK (1971) Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol Monogr 41: 351–389

Dayton PK (1972) Toward an understanding or community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC. Proc Colloq Conserv Problems Antarctica, Virginia Polytechnic Institute, Blacksburg, VA, p 81–96

Dayton PK (1975) Experimental evaluation of ecological dominance in a rocky intertidal community. Ecol Monogr 45: 137–159

Duggins DO, Eckman JE, Sewell AT (1990) Ecology of understory kelp environments. II. Effects of kelps on recruitment of benthic invertebrates. J Exp Mar Biol Ecol 143:27–45

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analyzing multispecies distribution patterns. Mar Ecol Prog Ser 8:37–52

Glasby TM (2001) Development of sessile marine assemblages on fixed versus moving substrata. Mar Ecol Prog Ser 215:37–47

Gosselin LA, Chia FS (1995) Distribution and dispersal of early juvenile snails: effectiveness of intertidal microhabitats as refuges and food sources. Mar Ecol Prog Ser 128:213–223

Harvey M, Bourget E, Miron G (1993) Settlement of Iceland scallop *Chalamys islandica* spat in response to hydroids and filamentous red algae: field observations and laboratory experiments. Mar Ecol Prog Ser 99:283–292

Heck KL, Wetstone GS (1977) Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. J Biogeogr 4:135–142

Irlandi EA, Peterson CH (1991) Modification of animal habitats by large plants: mechanisms by which seagrass influence clam growth. Oecologia 87:307–318

Jackson JBC (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Am Nat 111:743–767

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115–129

Lenihan HS (1999) Physical-biological coupling on oyster reefs: how habitat structure influences individual production. Ecol Monogr 69:251–275

Magurran AE (2004) Measuring biological diversity. Blackwell Publishing, Oxford

Monismith SG (2007) Hydrodynamics of coral reefs. Annu Rev Fluid Mech 39:37–55

Moksnes PO, Pihl L, Montfrans J van (1998) Predation on postlarvae and juveniles of the shore crab *Carcinus maenus*: importance of shelter, size and cannibalism. Mar Ecol Prog Ser 166:211–225

Olabarria C (2000) Epibiont molluscs on neogastropod shells from sandy bottoms, Pacific coast of Mexico. J Mar Biol Assoc UK 80:291–298

Pohle DG, Bricelj MV, Garcia-Esquivel Z (1991) The eelgrass canopy: an above-bottom refuge from benthic predators for juvenile bay scallops, *Argopecten irradians*. Mar Ecol Prog Ser 74:47–59

Prescott R (2006) An epifaunal community associated with aggregations of Black murex snails (*Hexaplex nigritus*): living reefs in the northeastern Gulf of California. MS thesis, University of Arizona, Tucson, AZ

Prescott R, Koch V, Yingling C, Verdugo CR (2007) Settlement of Pacific calico scallop larvae (*Argopecten ventricosus*, Sowerby II, 1842) on their predator, the black murex snail (*Hexaplex nigritus*, Philippi, 1845). J Shellfish Res 26:1065–1070

Thompson RC, Wilson BJ, Tobin ML, Hill AS, Hawkins SJ (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. J Exp Mar Biol Ecol 202:73–82

Thomson DA, Findley LT, Kerstitch AN (2000) Reef fishes of the Sea of Cortez. University of Texas Press, Austin

Witman JD (1985) Refuges, biological disturbance, and rocky subtidal community structure. New Eng Ecol Monogr 55:421–445

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