The Thesis Committee for Courtney Burke Abshire
Certifies that this is the approved version of the following thesis:

Effects of Local Environmental Factors and Spatial Habitat Characteristics on the Density of a Marine Gastropod, *Megastraea undosa* (Wood 1828)

APPROVED BY
SUPERVISING COMMITTEE:

Supervisor:

Timothy H. Keitt

Co-supervisor:

Laura González-Guzmán

Effects of Local Environmental Factors and Spatial Habitat Characteristics on the Density of a Marine Gastropod, *Megastraea undosa* (Wood 1828)

by

Courtney Burke Abshire, B.S.

Thesis

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Abstract

Effects of Local Environmental Factors and Spatial Habitat Characteristics on the Density of a Marine Gastropod, *Megastraea undosa* (Wood 1828)

Courtney Burke Abshire, M.A.
The University of Texas at Austin, 2010

Supervisors: Timothy H. Keitt, Laura González-Guzmán

The ability to identify and define factors which affect the abundance of marine species has been a primary goal of many ecologists. The need to accurately quantify the relationship between an organism and its environment is of critical importance in cases where that organism is the object of commercial harvest and tied to the economic well being of communities. This is especially evident for communities located along the Pacific coast of the Baja California peninsula where local fishing cooperative and their associated communities are dependent on the continuing successful harvest of a limited number of marine species, one of these being the marine gastropod *Megastraea undosa* (Wood, 1828). I conducted a multi-scale observational study investigating the effects of scale and selected local environmental and regional habitat characteristics of subtidal rocky reefs on the density of *M. undosa.* The study showed that *M. undosa* density varied significantly at two scales: quadrat (m^2) and reef (100s m^2). At the reef level, area and percent total cover were found to have a significant positive relationship with *M. undosa* density. No measured variable showed a significant association to *M. undosa* density at the quadrat level. Results suggest that both local and regional factors combine to affect *M. undosa* density and that their impacts on *M. undosa* density warrants further study.

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Introduction

Identifying and defining factors that influence the abundance of a species represent major questions in ecology. The ability and need to identify these factors are of critical importance in commercially harvested species because of their relationship to the economic well-being of a community. In this study I examine abundance variation at different spatial scales of a harvested benthic resource subjected to similar management across a widespread region of the Pacific coast of Baja California (Mexico) and selected factors that may explain this variation.

Abiotic and biotic factors can influence individuals and populations based on conditions present within a given environment (Wiens 1976). Many studies have been conducted to investigate the effects of a wide range of biotic factors which could influence the density of individuals in benthic marine communities. Local factors include predation (Watanabe 1984, Navarrete 1996, Navarrete and Menge 1996, Alfaro and Carpenter 1999, Moran et al 2009), competition (Underwood 1984, Watanabe 1984, Alfaro and Carpenter 1999), substrate characteristics (Underwood 2004, Toohey 2007, Alexander et al 2009) and habitat complexity (Beck 2000, Chapman 2000, Kostylev et al. 2005, Entrambasaguas et al. 2008).

Regional factors can influence dispersal and recruitment of species. Density at the regional level can be influenced by variation in the habitat matrix related to current flow (Carpenter and Williams 1993, Wahl 1997, Alfaro and Carpenter 1999, Gaylord et al 2007), temperature regimes (Zacherl et al. 2003, Sanford et al. 2006, Kuo and Sanford 2009) and the availability and spatial configuration of habitat patches (With 1995, González-Guzman and Mehlman 2001).

Species abundance may not only vary across sites within a region but also show significant variation across large spatial scales. Many ecologists state that the ability to identify the spatial scale at which various ecological processes operate is critical to the determination and understanding of the patterns of individuals seen in nature (Weins 1989, Levin 1992, Bocard et al. 2004, Denny et al. 2004). The issue of spatial scale is especially evident in marine environments. Processes such as recruitment (Lagos et al. 2007, Broitman et al. 2008), predation (Wieters et al. 2008) and variation associated with physical characteristics of the environment (Schoch and Dethier 1996, Fraschetti et al. 2005) can influence abundance depending on the scale at which they are considered. Failure to correctly identify these relationships can affect management decisions potentially leading to overexploitation of marine resources (Castilla and Defeo 2001, Lorenzen et al. 2010).

In the present study I use an observational approach to determine the spatial scales at which abundance varies and environmental factors that may explain this variation in the Wavy Turban snail *Megastraea undosa* (Wood, 1828), a harvested benthic species inhabiting the Vizcaino peninsula of Baja California Sur. The Vizcaino region presents sharp environmental transitions and varying degrees of coastal upwelling (Zaytsev et al. 2003). *M. undosa* is a good system to study as previous information exists on factors defining its abundance along the coast of southern California. In addition, this species is subject to harvest by similar methods which are practiced by the fishing cooperatives associated in the Federación Regional de Sociedades Cooperativas de la Industria Pesquera Baja California (FEDECOOP), a federation of local cooperatives. Similar management practices and the biotic variability associated with the environment provide an opportunity to observe significant variation in *M. undosa* abundance and evaluate potential explanatory factors at different spatial scales.

Materials and Methods

Study Site

The coastal region of the Vizcaino Peninsula possesses an especially rich and varied marine ecosystem. The region is dominated by seasonal upwelling, the movement of cold nutrient rich waters from depths to shallower waters along the coast, driven by offshore surface currents resultant from seasonal along-shore winds. The seasonal influx of nutrients coupled with effects from shoreline topography result in temporal and spatial synchrony of high primary production (Broitman and Kinlan 2006) and overall rates of larval supply at large spatial scales (Navarette et al. 2008). This high primary productivity in turn supports an abundance of herbivores (Nielsen and Navarrete 2004) which feed on the algae which are a dominant feature of the tidal and subtidal habitats. The subtidal habitat consists of distinct reef patches which mirror the mountainous topography of the nearby shoreline. The two sites selected for study, Bahía Tortugas and Bahía Asunción, are located along the northern coastal portion of the Vizcaino peninsula which is part of Baja California Sur (southern portion of the Baja California Peninsula), México (Figure 1).

Local fishing cooperatives organized within the FEDECOOP capitalize on regional marine resources such as abalone, lobster, marine snails, and sea cucumber, among others. The FEDECOOP is a federation of local cooperatives formed during the 1930’s in order to organize fishing activities and to use the revenues generated to improve local infrastructure and community services (Shester 2008). Cooperatives have exclusive fishing rights within selected geographic coastal boundaries established by the Mexican federal government. This local control enables cooperatives to monitor and establish limits over the marine resources harvested. In regards to *M. undosa*, reefs within cooperatives are surveyed for abundance and individual quotas are established for each reef. A minimum size limit of 90 mm (basal diameter) has been established for *M. undosa* harvest across the Vizcaino region (Gluyas-Millan et al. 2000).

Species description

Megastraea undosa is a marine gastropod which inhabits sub-tidal rocky reefs as well as low intertidal rocks ranging from Point Conception (Santa Barbara Co., California) in the north to Isla Asunción (Baja California, Mexico) in the south (Morris et al. 1980). Like many marine invertebrates *M. undosa* are free spawners with external fertilization (Salas-Garza et al. 2009). Individuals release unfertilized gametes into the water column where fertilization ultimately occurs. After fertilization, new individuals exist in a planktonic larval developmental stage lasting for approximately 7 days (Guzman del Proo et al. 2003) after which individuals settle out of the water column onto solid substrate to continue further development. *M. undosa* are opportunistic herbivores which graze upon the various marine algae species present in tidal and subtidal habitat (Cox and Murray 2006). Individuals can reach sizes up to 15 cm basal diameter (Morris et al. 1980). Their relatively large size and ease of harvest combine to make *M. undosa* an important commercial species for small community centered fishing cooperatives located along the western coast of Baja California Mexico.

Sampling regimes

I established a hierarchical sampling regime to allow for the analysis of scale effects on the variation of *M. undosa* density along the Vizcaino peninsula. Both sample sites contain similar marine habitat characterized by the presence of patchily distributed rocky reefs. I randomly selected 11 reefs; six at Bahía Tortugas and 5 at Bahía Asunción. Within each reef, I conducted quadrat surveys to assess biotic and abiotic conditions. Surveys were conducted between 15 May 2008 and 27 May 2008 using SCUBA. All reefs sampled were rocky reefs ranging in depth from 4.7 to 15.5m and located 0.04 to 0.545 km offshore.

Density

In order to determine *M. undosa* density 1 m^2 quadrats were haphazardly placed within each sampled reef resulting in 16 to 36 quadrats per reef for a total of 243 quadrats. All individuals present within the quadrat were counted and the basal diameter was measured to the nearest half-centimeter.

Scale of variation

The sampling regime of this study creates three distinct scales: quadrat (m^2), reef (100s m^2) and site (km). In terms of the effect of spatial scale I chose to compare *M. undosa* density and overall habitat characteristics at the levels of quadrat, reef and site. The sampling of quadrats within individually defined reefs present within distinct sites creates a nested sampling design which allows for the ability to determine which scale, quadrat, individual reef or overall site, is more useful in describing the variation seen in *M. undosa* density.

Local correlates of density

Macroalgal species presence and percent cover

Algal presence and percent cover was visually determined within the quadrats being surveyed for *M. undosa* density. Classification and estimation was based on functional group with all "fleshy" algal forms incorporated into one functional group as put forth by Steneck and Dethier (1994). Crustose coralline and articulated corallines were classified as separate functional groups. Steneck and Detheir (1994) state that algal-dominated communities, such as those found along the Pacific coast, are more stable and predictable when considered at the functional group level rather than at the individual species level. This classification method allows for simplified analysis on possible effects of algal presence on *M. undosa* density. Total percent cover was calculated by aggregating the above aforementioned functional groups.

Substrate topography and composition

Percent substrate composition was visually quantified within the 1 m^2 quadrats used to survey *M. undosa* density. Substrate was classified as sand, cobble ($\leq$ 10 cm diameter), boulder (10 cm – 1 m diameter) or bedrock ($\geq$ 1 m diameter). Average reef and site substrate composition was determined using individual quadrat estimates.

Rugosity was used as a measure of topographic complexity of reef substrate. Rugosity was determined in situ using a similar method as Martone (2009). The method consisted of laying a chain diagonally across the 1 m^2 quadrat taking care to closely follow the contours of the reef. The length of the chain was then measured to the nearest 10 cm. A longer chain length is obtained as structural complexity of the reef increases therefore a higher measure of rugosity corresponds to a higher level of topographic complexity. Average rugosity was calculated for each reef and site.

Regional Correlates of density

In order to address the possible impact of the availability and configuration of habitats on snail abundance, I characterized size, shape and degree of isolation for each sampled reef. Boundaries of reefs at both sites were delineated using a combination of on-site boundary determination using GPS and remote satellite imagery. Accessible reef boundaries were determined on-site by tracing the boundaries of visible kelp (*Macrocystis pyrifera*) canopies associated with reefs via boat while marking these boundaries with a handheld GPS receiver (Garmin Foretrex 101™). Any reefs not accessible or missed during on-site surveys were identified using satellite imagery accessed via Google Earth (©2010 Google). Program tools available within Google Earth were used to delineate reef boundaries based on visible kelp canopy. GPS data was processed with EasyGPS (©1998-2010 TopoGrafix) in order to create a file format which could then be used for analysis in a geographic information system.

Boundary files from both sources were combined in ArcMap™ ver. 9.3 (©1995-2010 ESRI) to provide boundary data for all reefs identified. Boundary delineation resulted in a total of 39 reefs identified at Bahía Asunción and 55 reefs at Bahía Tortugas. Three meter resolution raster files of reef and coastal boundaries were created and converted to ASCII format for use in the spatial pattern analysis program FRAGSTATS (©2002 McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene). FRAGSTATS is a program which computes various landscape metrics for categorical map data. I used

FRAGSTATS to calculate the following spatial metrics: reef area, fractal dimension and Euclidian nearest neighbor and proximity.

Area (AREA) is simply the total area in hectares within a given reef boundary and gives a metric by which to compare reefs by size. Fractal dimension (FRAC) is a measure of shape complexity which can vary in value from 1 to 2 with values greater than one indicating a departure from Euclidian geometry. An increasing value of FRAC indicates a more complex shape geometry and denotes a larger ratio of edge to reef interior area. Proximity (PROX) measures the neighborhood density of reefs surrounding a focal reef. Proximity takes into account both the area and distance to all reefs surrounding a focal reef within a given search radius. An increase in PROX from 0 (no neighbors) indicates the neighborhood is becoming increasingly populated by reefs that are larger and more closely situated. A search radius of 500 m was chosen for proximity calculations based on a comparison of proximity values acquired for incrementally increasing radii which showed no appreciable change beyond 500 m. Euclidian nearest neighbor (ENN) is the straight line edge-to-edge distance from a focal reef to its nearest neighboring reef. Together, proximity and Euclidian nearest neighbor describe the degree of isolation of any particular reef. The specific formulas used in calculating these metrics can be viewed by accessing the online documentation available at: http://www.umass.edu/landeco/research/fragstats/documents/fragstats_documents.html.

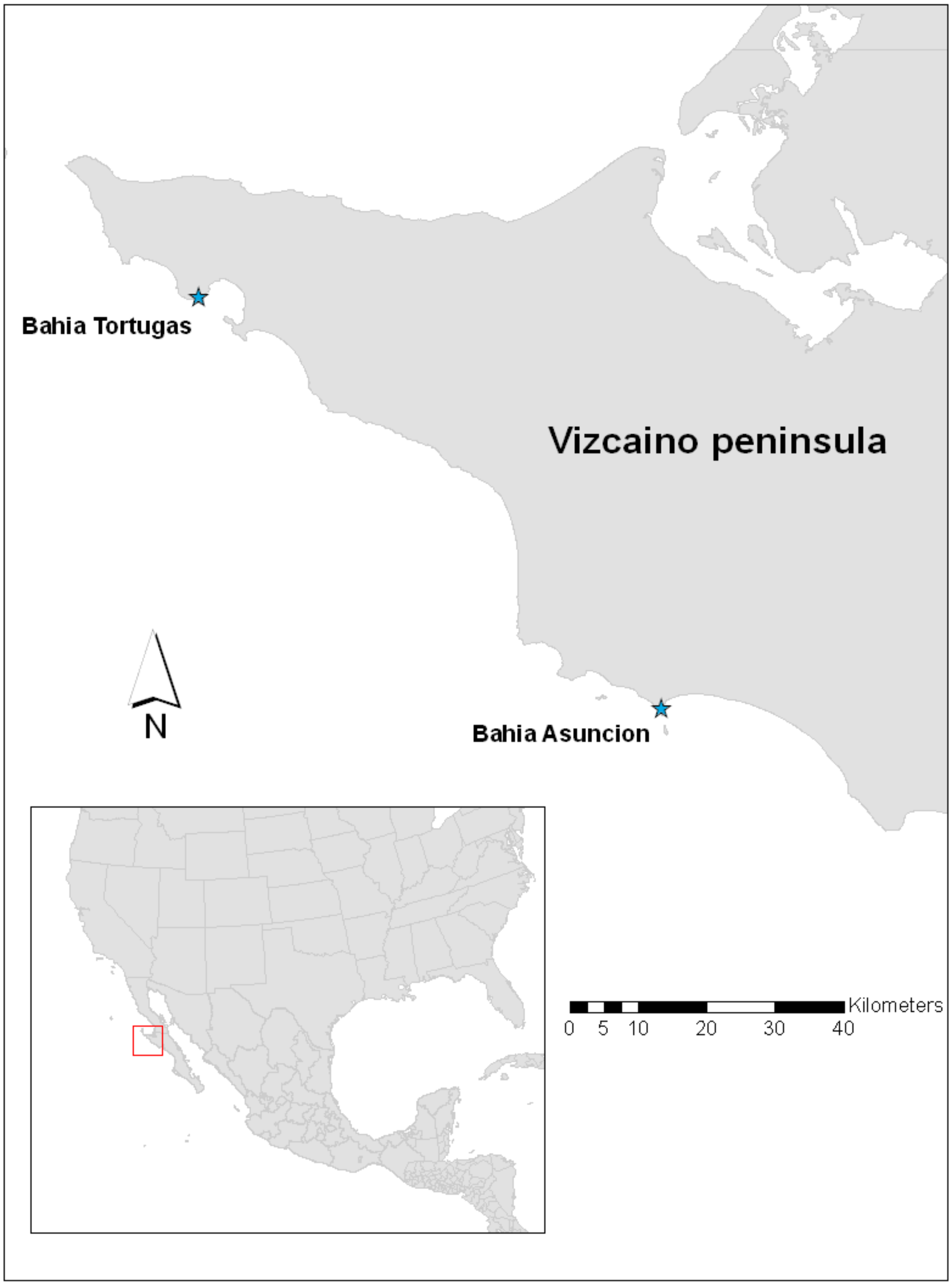

Figure 1. Map of the Vizcaino Peninsula showing the location of fishing cooperatives Bahía Tortugas and Bahía Asunción. Inset shows location of peninsula in relation to Baja California, Mexico.

Statistical analysis

Scale of variation in Megastraea undosa density

To determine the significant spatial scales of variation in abundance of *M. undosa*, I conducted a two-factor nested Analysis of Variance (ANOVA). Site was treated as a fixed factor with two levels while reef was treated as a random factor nested within site (11 levels). The remaining variation not accounted for by these two factors can be attributed to small-scale variation associated with quadrat measurements and an associated error. Magnitude of effect for site, reef and quadrat will be calculated using eta-squared (η^2). Eta-squared is a ratio of the sum of squares for each factor divided by the total sum of squares and is a measure of the strength of the relationship between each factor and the variation in *M. undosa* density. This analysis and all subsequent analyses were conducted using the statistical software program SPSS 16.0 (© SPSS Inc. 2010).

Local and regional correlates of density

Once the relevant scale and/or scales of variation in *M. undosa* density were determined I used GLM and linear regression to investigate which measured correlates may drive any significant variation seen in *M. undosa* density. At the quadrat scale I examined the effects of the measured local biotic and abiotic variables on *M. undosa* density. At the reef scale, I analyzed a combination of regional spatial habitat metrics along with mean values of local biotic and abiotic correlates to determine any potential relationship to *M. undosa* density. Regional habitat spatial metrics were not considered in the initial quadrat level analysis of biotic and abiotic factors. Inclusion of spatial metrics at the quadrat level analysis resulted in artificially inflated degrees of freedom due to repeated values of spatial metrics being associated with individual quadrat measurements for any given reef. This potential inflation of degrees of freedom precluded their inclusion in the fine scale analysis. Regional spatial and local biotic and abiotic correlates were also investigated for significant relationships at the site level.

Results

Scale of variation in Megastraea undosa density

Nested analysis of variance shows that density of *M. undosa* varied significantly at both the reef scale and the finer quadrat scale but not at the broadest scale of site. This is indicated by the significant p-value for quadrats and reefs and the correspondingly higher magnitude of effect estimates (η^2) (see Table 1). A majority of the variation (84.4%) was attributed to fine scale variation associated with quadrats while 15.5% of the variation in *M. undosa* density was explained by differences between reefs. Site level differences failed to explain any of the variation seen in density.

Table 1. Results from Nested Analysis of Variance of *Megastraea undosa* density

Source	**df**	**SS**	**F**	**P**	**η^2**
Site	1	0.003	51.242	0.978	0
Reef	9	37.595	0.001	<0.001	0.155
Quadrat & error	1	204.373	5.416	<0.001	0.844

Local correlates of density

To investigate the potential causes of variation in *M. undosa* density present at the quadrat level I conducted a GLM regression analysis to identify possible significant relationships of local correlates to density. To assess their effect on *M. undosa* density the following biotic and abiotic correlates were used as variables in the regression analysis; percent cover estimates of fleshy algae, articulated coralline algae, crustose coralline and total algal cover, *M. pyrifera* and *E. arborea* presence and rugosity. Due to issues with non-normality *M. pyrifera* and *E. arborea* percentages were not used but a binary categorical variable was created for each to represent presence/absence and treated as random factors in the regression model to assess possible influences on density of snails. A single variable, rugosity, was chosen to represent substrate complexity as the remaining substrate composition variables (rock, boulder, cobble and sand) were not included in the analysis due to their continued departure from normality even after transformation. GLM regression analysis of macroalgal and substrate correlates show no significant interactions as evidenced by the lack of significance in individual correlate p-values (see Table 2).

Table 2. GLM regression summary of *M. undosa* density against macroalgal and substrate correlates.

Source	**df**	**SS**	**F**	**P**	**η^2**
intercept	1	0.52	0.53	0.468	0.004
Macrocystis presence	1	0.342	0.348	0.557	0.003
Eisenia presence	1	0.964	0.98	0.324	0.008
Fleshy algae	1	0.705	0.716	0.399	0.006
Articulated coralline	1	0.366	0.372	0.543	0.003
Crustose coralline	1	0.633	0.644	0.424	0.005
Rugosity	1	0.005	0.005	0.943	0

Regional correlates of density

Reef level analysis

To examine the effects of regional scale correlates on *M. undosa* density I used linear regression analysis to investigate whether habitat availability and configuration in combination with the associated mean values of biotic and abiotic correlates explain the variation in snail abundance at the reef level.

The following variables were considered for selection in regression analysis: proximity, area, fractal dimension, Euclidian nearest neighbor, average rugosity and average total percent algal cover. Initially all variables were input as possible correlates and evaluated based on partial correlation to snail density. Variables were sequentially removed until no variables remained that met the removal criterion (probability of F statistic ≤ 0.1). This method results in significant beta coefficients that may not be reliable due to the fact that removal of variables is based on calculations from the previous model generated during the elimination phase. Essentially the model is fit to the data which can result in p-values for remaining variables that are difficult to interpret. While influential in their explanatory power the remaining variables may not possess truly significant beta coefficients. To eliminate this issue I chose the remaining variables from the backward selection as inputs into a new unbiased regression.

Linear regression analysis of *M. undosa* density against area and total cover resulted in a model which was significant with a p-value of 0.049 and $r^2 = 0.529$. Area and total cover were both significant with p-values < 0.05 (Table 3). Regression estimates for reef area and total cover indicate a positive correlation with *M. undosa* density.

Table 3. Model coefficients and ANOVA table summary for linear regression of reef level biotic and habitat spatial correlate effects on *M. undosa* density.

Coefficient summary	**Beta**	**SE**	**t**	**P**
Area	0.333	0.113	2.948	0.018
Total cover	6.035	2.275	2.65	0.029
(constant)	-27.342	10.414	-2.625	0.03

ANOVA summary	**SS**	**df**	**MS**	**F**	**P**
model	2.005	2	1.002	4.501	0.049
residual	1.782	8	0.223		

Several biotic and abiotic factors were not considered in this analysis due to issues pertaining to non-normality. Although these variables were not included in the regression analysis I investigated the variability of these correlates between reefs. To accomplish this I used the non-parametric Kruskal-Wallace analysis of variance to compare individual reefs. The results of this test showed that 7 of the 11 variables differed significantly at the reef level as well as a significant difference in the distribution of *M. undosa* density (see Table 4). These results show that there exists a high level of variability in the internal characteristics of reefs.

Table 4. Kruskal-Wallis non-parametric analysis of variance comparing distributions of macroalgal, substrate composition and topography variables for reefs sampled at Bahía Tortugas (BT) and Bahía Asunción (AS).

Reef	Mean Rank											
		Macroalgal percent composition						Substrate percent composition				
	M.undosa density	*M. pyrifera*	*E. arborea*	Fleshy	Articulated	Crustose	Total Cover	Rock	Boulder	Cobble	Sand	Rugosity
BT1	87.29	74.75	49.00	73.43	46.50	71.07	65.54	47.36	83.29	63.00	42.79	126.52
BT2	153.63	68.82	52.50	60.00	78.14	62.93	63.21	54.32	49.04	63.64	77.75	134.65
BT3	81.02	65.14	49.00	75.21	70.68	47.39	72.11	57.79	69.04	59.07	75.89	171.32
BT4	165.74	62.77	49.00	75.82	49.73	72.95	62.59	83.68	44.27	80.86	61.41	99.20
BT5	132.09	61.27	49.00	106.45	41.91	39.27	66.50	57.95	74.09	51.86	60.55	100.20
BT6	110.56	66.31	49.00	41.15	93.04	87.42	62.38	73.38	50.54	80.15	68.58	62.69
AS1	137.94	80.44	114.69	45.81	68.56	36.94	91.19	71.13	71.75	44.50	62.75	176.38
AS2	110.65	55.33	72.00	83.44	56.67	59.00	45.28	87.11	50.83	60.39	59.39	115.10
AS3	111.31	41.00	120.21	84.64	27.86	44.21	103.57	52.79	84.29	44.50	52.64	78.06
AS4	118.18	67.94	59.03	34.17	68.94	75.33	36.39	67.44	67.19	67.22	64.14	113.11
AS5	157.03	41.00	94.81	42.75	85.19	90.69	63.44	55.88	64.88	75.63	73.19	154.38
χ^2	37.463	13.197	92.508	44.428	30.079	29.44	26.271	19.69	19.901	17.273	12.692	59.074
Df	10	10	10	10	10	10	10	10	10	10	10	10
P	<0.001	0.213	<0.001	<0.001	<0.001	0.001	0.003	0.032	0.057	0.069	0.241	<0.001

Site level analysis

Even though no significant variation in *M. undosa* density exists between sites I chose to characterize the differences that exist between sites in regards to the local and regional correlates measured for this study.

An average density of 1.93 snails/m^2 was observed at Bahía Tortugas (BT) while Bahía Asunción (AS) exhibited an average of 1.48 snails/m^2. T-test analysis of site level means for biotic correlates showed that fleshy algae and crustose coralline presence was significantly higher in Bahía Tortugas (Figure 3, Table 5). Mann-Whitney U test of *Macrocystis pyrifera* and *Eisenia arborea* cover showed that *E. arborea* cover was significantly different with a higher average presence in Bahía Asunción (Figure 3, Table 6). Articulated coralline, *Macrocystis pyrifera* and Total Cover did not significantly differ between sites. Overall, Fleshy algae showed the highest percent occurrence with *Macrocystis pyrifera* being the least contributor to overall cover.

Mann-Whitney non-parametric analysis of substrate composition showed no significant difference in the distribution of classification categories between sites (see Table 7, Figure 4). T-test comparison of rugosity also showed no significant difference in mean values between sites (mean BT=3.691 n=135, AS=3.719 n=104; t=-0.467 df=237 p=0.641).

T-test comparison of regional spatial habit characteristics for all reefs present at both sites shows that average reef area is higher in Bahía Tortugas although not significantly so (Tables 8 and 9). Reefs at Bahía Asunción, on average, have a slightly more complex perimeter shape (FRAC >1) than those at Bahía Tortugas but not to a significant degree (Tables 8 and 9). Proximity and Euclidian-nearest-neighbor distance show a significant difference between sites (Table 9). Reefs at Bahía Tortugas are closer to each other on average as evidenced by a smaller value of ENN and the general arrangement of reefs is less fragmented as indicated by a larger value of Proximity (Table 8).

Figure 3. Mean percent cover of algal and kelp species including total aggregate cover (± SE) for Bahía Tortugas (n=76) and Bahía Asunción (n=50).

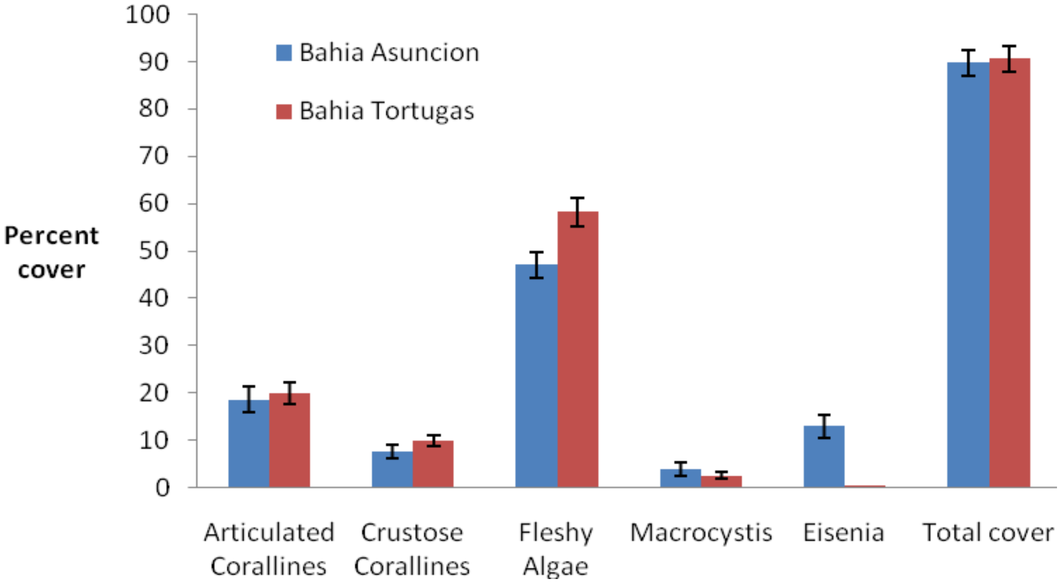

Table 5. T-test comparison of site level means for understory algae and total percent cover.

Source	T	Df	P
Fleshy Algae	-2.62	125	0.007
Articulated Corallines	-0.315	125	0.753
Crustose Corallines	-2.584	125	0.016
Total Cover	-0.22	124	0.826

Table 6. Mann-Whitney non-parametric rank test for comparison of percent kelp cover between sites (BT n=76, AS n=50)

Source	Mann-Whitney U	Wilcoxon W	Z	P
Macrocystis pyrifera	1704.5	2979.5	-1.267	0.205
Eisenia arborea	847.0	3773.0	-7.122	<0.001

Table 7. Mann-Whitney non-parametric rank test for comparison of substrate composition between sites (BT n=76, AS n=50).

Source	Mann-Whitney U	Wilcoxon W	Z	P
Rock	1741.5.00	4744.50	-1.091	0.275
Boulder	1775.00	4778.00	-0.0785	0.432
Cobble	1751.00	3026.00	-1.052	0.293
Sand	1870.00	3145.00	-0.310	0.757

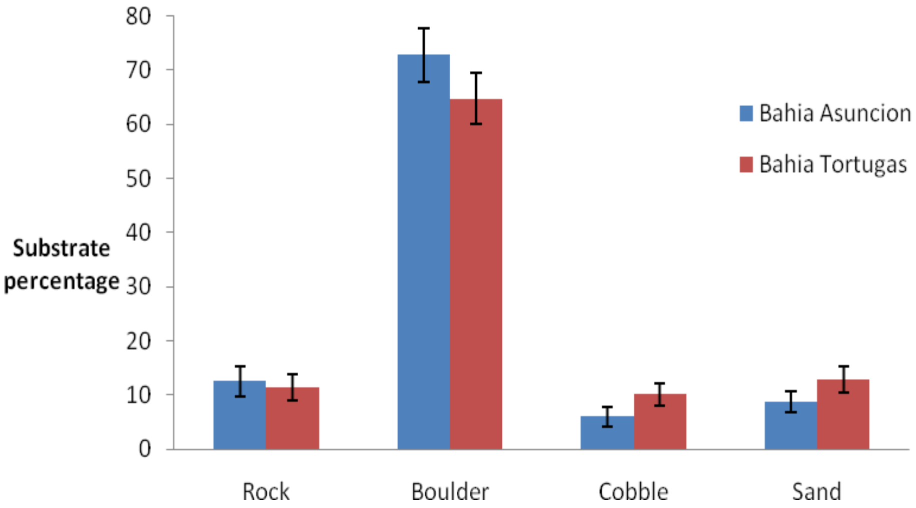

Figure 4. Mean substrate composition percentages for Bahía Asunción and Bahía Tortugas. Values are percentage presence + SE.

Table 8. Summary of spatial habitat correlate means for Bahía Asunción (AS) and Bahía Tortugas (BT)

	Site	**n**	**Mean**	**SE**
Area	AS	39	6.304 ha	2.279 ha
	BT	55	10.875 ha	2.527 ha
Fractal dimension (FRAC)	AS	39	1.102	0.007
	BT	55	1.095	0.005
Euclidian nearest neighbor (ENN)	AS	39	134.34 m	42.677 m
	BT	55	50.82 m	8.229 m
Proximity (PROX)	AS	39	166.718	57.188
	BT	55	877.172	386.077

Table 9. T-test comparison of spatial habitat correlate means for Bahía Asunción and Bahía Tortugas.

Source	t	Df	p
Area	-1.215	92	0.228
Fractal dimension	0.766	92	0.446
Euclidian nearest neighbor	2.156	92	0.034
Proximity	-2.621	92	0.01

Discussion

The goal of my study was to determine the scale of variation in abundance of a harvested marine gastropod *Megastraea undosa* and to investigate local and regional environmental factors which may influence abundance. I found that *M. undosa* density exhibited significant variation at the scale of meters (quadrat level) and at a larger scale of 100's of meters (reef level) but not at the largest scale of km's (site level). At the reef level, density of *M. undosa* showed a significant positive correlation to total algal cover and reef area. At the quadrat level none of the variables measured showed a significant association with abundance.

The lack of significant variation in abundance at the site level is puzzling and may be the result of sampling after harvesting one of the two sites. Comparison of size class distribution of *M. undosa* at both sample sites shows a higher number of large individuals present at Bahía Asunción. Historic data indicate a higher productivity for Bahía Tortugas (Valdez and Diaz 1996) and as such I would expect to find a significantly higher abundance of *M. undosa* to be present. Thus, the lack of significant variation may be the result of harvesting of large individuals (> 90 mm) that took place at the Bahía Tortugas site prior to sampling. This condition may have confounded my results at the level of site because of the absence of the largest size class of the population. Nevertheless, Martone (2009) also found no significant difference in *M. undosa* densities between these sites. Even though abundance did not significantly vary across sites, I did find that sites exhibit significant variation in the spatial distribution of habitat (proximity and Euclidian-nearest-neighbor) as well as in several categories of algal cover (fleshy algae, crustose and *E. arborea* observed also by Martone 2009). To my knowledge no other study has quantified the spatial distribution of reef habitat along the Vizcaino coastal region. The significant differences seen with regard to habitat distribution are tantalizing and encourage further study as to their potential influence on *M. undosa* density across sites.

At the reef scale, the significant positive relationship between *M. undosa* density to area and total cover may be a result of the effect of these two factors on colonization, recruitment and resource utilization. A larger reef provides more space for colonization by algae as well as *M. undosa*. Previous studies of terrestrial species have shown a positive relationship between population densities and patch area (Connor et al. 2000, Yamaura et al. 2008). Explanations for this relationship involve decreased predation pressure and the concentration of a critical resource (Connor et al. 2000) as well as benefits to species restricted to patch interiors (Yamaura et al. 2008). As adults, *M. undosa* are restricted to rocky substrate and larger reefs may provide more contiguous traversable substrate enabling internal migration of *M. undosa* individuals thus improving their ability to respond to local adverse conditions such as reduced food availability or increased predation. There is additional evidence that the size of a reef can influence current regimes, with large reefs experiencing lower rates of internal flow (Jackson 1998, Gaylord et al. 2007). Any reduction in flow within a large reef could favor retention of planktonic *M. undosa* larvae by increasing the probability of finding suitable substrate and ultimately increasing the number of individuals present. Further study is needed to determine whether all the mentioned mechanisms are important in defining snail abundance at the reef scale. This is important as my site level comparison of reef area shows that Bahía Tortugas has a higher average reef area compared to Bahía Asunción and may be a factor in explaining the historically higher productivity seen at Tortugas.

The significant variation in density observed at the quadrat level was not explained by any of the measured biotic and abiotic factors. Substrate composition and rugosity have been found to explain abundance for other species. For instance, Underwood (2004) conducted a study to investigate small-scale variability of substrate topography on settlement of juvenile gastropods and found a positive relationship to gastropod density. In another study encompassing the Vizcaino coastal region, Martone (2009) found rugosity and percentage of boulder habitat to be influential in explaining subtidal benthic invertebrate assemblages in the Vizcaino region. It is possible that rugosity and substrate composition may not be as important to more mobile *M. undosa* individuals and play more of a role in regards to recruitment and survival of juveniles (Underwood 2004). In the case of biotic factors, the non-significant relationship between *M. undosa* density and algal cover categories may be linked to diet preferences of *M. undosa*. Although previous studies on this species have shown contradictory results about dietary preference (Cox and Murray 2005, Leighton 1966, Rosas et al. 1990), *M. undosa* is considered a generalist and opportunistic grazer which can feed on different algal species. Martone (2009) found non-significant correlations between herbivore biomass (of which *M. undosa* was a substantial contributor) and algal functional groups along the Vizcaino coast. Food availability therefore may not be a limiting factor for *M. undosa* within the Vizcaino region. It is also possible that other factors not investigated in this study, such as predation, may be important in explaining *M. undosa* abundance at the quadrat level in the Vizcaino region. For example, Alfaro and Carpenter (1999) found that predation had an important effect on *M. undosa* abundance along southern California reefs dependent upon the zones of algal cover present.

M. undosa density was shown to significantly vary at the scale of meters (quadrats) and hundreds of meters (reefs). The emergence of significant correlation of *M. undosa* density to total cover and individual reef area when considered at the scale of reefs suggest that both local and regional factors combine to influence *M. undosa* density within the Vizcaino region. The significant variability of *M. undosa* density seen at the quadrat level suggests that fine scale environmental heterogeneity is highly influential, however none of the variables measured at the quadrat level showed a significant relationship to density. Fine scale factors affecting the rate and scale of movement of individuals could potentially be influencing observed densities. Chapman (2000) found that densities of several intertidal gastropods varied dependent on the effects of substrate complexity on movement and the temporal window of observation. As of yet no studies have addressed the movement of *M. undosa* adults. Also, I would encourage continued investigation of the variables pertaining to the overall level of fragmentation exhibited by reef networks as well as quantification of current flow within the region. Guzman-Del Proo et al. (2000) conducted a study to investigate the effects of current on dispersal of larval abalone within the Bahía Tortugas region. Their results suggest that kelp bed presence and arrangement can influence the retention of recruits through modification of current flow. Abalone shares similar juvenile life history traits with *M. undosa* in that both species spend approximately 5 to 7 days in the water column prior to settlement. As such *M. undosa* may experience similar impacts from local currents. Information pertaining to these ecological processes can only contribute to the ability of local cooperatives to improve management decisions related to *M. undosa*.

Bibliography

Alexander, T. J., Barrett, N., Haddon, M. and Edgar, G. 2009. Relationships between mobile macroinvertebrates and reef structure in a temperate marine reserve. Marine Ecology Progress Series 389: 31-44.

Alfaro, A. C. and Carpenter, R. C. 1999. Physical and biological processes influencing zonation patterns of a subtidal population of the marine snail, Astraea (Lithopoma) undosa Wood 1828. Journal of Experimental Marine Biology and Ecology 240:259-283.

Beck, M. W. 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. Journal of Experimental Marine Biology and Ecology 249:29-49.

Borcard, D., Legendre, P., Avois-Jacquet, C. and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology 85: 1826-1832.

Broitman, B. R. and Kinlan, B. P. 2006. Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. Marine Ecology Progress Series 327:15-25.

Broitman, B. R., Blanchette, C. A., Mengie, B. A., Lubchenco, J., Krenz, C., Foley, M., Raimondi, P. T., Lohse, D. and Gaines, S. D. 2008. Spatial and temporal patterns of invertebrate recruitment along the west coast of the United States. Ecological Monographs 78:403-421.

Carpenter, R. C. and Williams, S. L. 1993. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnology and Oceanography 38:687-694.

Castilla, J. C. and Defeo, O. 2001. Latin American benthic shellfisheries: emphasis on co-management and experimental practices. Reviews in Fish Biology and Fisheries 11: 1-30.

Chapman, M. G. 2000. A comparative study of differences among species and patches of habitat on movement of three species of intertidal gastropods. Journal of Experimental Marine Biology and Ecology 244: 181-201.

Cox, E. T. and Murray, S. N. 2006. Feeding preferences and the relationships between food choice and assimilation efficiency in the herbivorous marine snail *Lithopoma undosum* (Turbinidae). Marine Biology 148:1295-1306.

Denny, M. W., Helmuth, B., Leornard, G. H., Harley, C. D. G., Hunt, L. J. H. and Nelson, E. 2004. Quantifying scale in ecology: Lessons from a wave-swept shore. Ecological Monographs 74: 513-532.

Entrambasaguas, L., Perez-Ruzafa, A., Garcia-Charton, J. A., Stobart, B. and Bacallado, J. J. 2008. Abundance, spatial distribution and habitat relationships of echinoderms in the Cabo Verde Archipelago (eastern Atlantic). Marine and Freshwater Research 59: 477-488.

ESRI (Environmental Systems Research Institute) Inc. 2008. ArcView 9. 3 GIS Geostatistical Analyst. ESRI, Redlands, CA, USA.

Fraschetti, S., Terlizzi, A. and Beneditti-Cecchi, L. 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. Marine Ecology Progress Series 296: 13-29.

Gaylord, B., Rosman, J. H., Reed, D. C., Koseff, J. R., Fram, J., MacIntyre, S., Arkema, K., McDonald, C., Brezezinski, M. A., Largier, J. L., Monismith, S. G., Raimondi, P. T. and Mardian, B. 2007. Spatial patterns of flow and their modification within and around a giant kelp forest. Limnology and Oceanography 52:1838-1852.

Gluyas-Millan, M. G., Quinonez-Velazquez, C. and Talavera-Maya, J. 2000. Population parameters of the snail Astraea undosa (Wood, 1828) from the west coast of the Baja California Peninsula. Ciencias Marinas 26: 643-658.

Gonzalez-Guzman, L. I. and Mehlman, D. W. 2001. Developmental stability across the breeding distribution of the scissor-tailed flycatcher (*Tyrannus forficatus*). Ecology Letters 4: 444-452.

Guzman del Proo, S. A., Salinas, F., Zaytsev, O., Belmar-Perez, J. and Carrillo-Laguna, J. 2000. Potential dispersion of reproductive products and larval stages of abalone (Haliotis spp.) as a function of the hydrodynamics of Bahía Tortugas, Mexico. Journal of Shellfish Research 19: 869-881.

Guzman del Proo, S. A., Reynoso-Granados, T., Monsalvo-Spencer, P., and Serviere-Zaragoza, E. 2003. Larval and early juvenile development of the wavy turban snail, Megastraea undosa (Wood, 1828) (Gastropoda: Turbinidae). The Veliger 46:320-324.

Jackson, G. A. 1998. Currents in the high drag environment of a coastal kelp stand off California. Continental Shelf Research 17:1913-1928.

Kostylev V. E., Erlandsson, J., Ming, M. Y. and Williams, G. A. 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: Fractal application on rocky shores. Ecological Complexity 2: 272-286.

Kuo, E. S. L. and Sanford, E. 2009. Geographic variation in the upper thermal limits of an intertidal snail: implications for climate envelope models. Marine Ecology Progress Series 388: 137-146.

Lagos, N. A., Tapia, F. J., Navarrette, S. A. and Castilla, J. C. 2007. Spatial synchrony in the recruitment of intertidal invertebrates along the coast of central Chile. Marine Ecology Progress Series 350: 29-39.

Leighton, D. L. 1966. Studies of food preference in algivorous invertebrates of southern California kelp beds. Pacific Science 20: 104-113.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Lorenzen, K., Steneck, R. S., Warner, R. R, Parma, A. M, Coleman, F. C. and Leber, K. M. 2010. The spatial dimensions of fisheries: putting it all in place. Bulletin of Marine Science 86: 169-177.

Martone, R. L. G. 2009. Geographic variation in species demography and community structure in temperate rocky reefs. Doctoral dissertation. Stanford University, 2009.

McGarigal, K., Cushman, S. A., Neel, M. C. and Ene, E. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps (Version 3.3) [software]. Available from http://www.umass.edu/landeco/research/fragstats/fragstats.html

Moran, E. R., Reynolds, P. L., Ladwig, L. M., O'Connor, M. I., Long, Z. T. and Bruno, J. F. 2009. Predation intensity is negatively related to plant species richness in a benthic marine community. Marine Ecology Progress Series 400: 277-282.

Morris, R. H., Abbott, D. P. and Haderlie, E. C. 1980. Intertidal Invertebrates of California. Stanford University Press, Stanford, California, USA.

Navarrete, S. A. 1996. Variable predation: effects of whelks on a mid-intertidal successional community. Ecological Monograph 66: 301-321.

Navarrete, S. A. and Menge, B. A. 1996. Keystone predation and interaction strength: Interactive effects of predators on their main prey. Ecological Monographs 66: 409-429.

Nielsen, K. J. and Navarette, S. A. 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecology Letters 7: 31-41.

Rosas, R. A., Moye, G. T. and Heredia, A. A. 1990. Qualitative analysis of the macroalgal diet of the snail Astraea undosa Wood 1828, in Punta Banda, Baja California, Mexico. Ciencias Marinas 16: 111-120.

Salas-Garza, A., Pares-Sierra, G., Gomez-Rigalt, R. and Carpizo-Itu, E. 2009. The Larval Development, Metamorphosis and Juvenile Growth of the Turban Snail Lithopoma (Astraea) undosa (Wood, 1828) (Gastropoda: Turbinidae). Journal of The World Aquaculture Society 40:460-471.

Sanford, E., Holzman, S. B., Haney, R. A., Rand, D. M. Bertness, M. D. 2006. Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. Ecology 87: 2882-2894.

Schoch, G. C. and Dethier, M. N. 1996. Scaling up: the statistical linkage between organismal abundance and geomorphology on rocky intertidal shorelines. Journal of Experimental Marine Biology and Ecology 201: 37-72.

Shester, G. 2008. Sustainability in smale-scale fisheries: An analysis of ecosystem impacts, fishing behavior, and spatial management using participatory research methods. PhD dissertation, Stanford University.

SPSS for Windows, Rel. 16.0.2. 2008. Chicago: SPSS Inc.

Steneck, R. S. and Dethier, M. N. 1994. A functional approach to the structure of algal dominated communities. OIKOS 69: 476-498.

Toohey, B. D. 2007. The relationship between physical variables on the topographically simple and complex reefs and algal assemblage structure beneath an Ecklonia radiata canopy. Estuarine Coastal and Shelf Science 71: 232-240.

Tuya, F., Wernberg, T. and Thomsen, M. S. 2008. The spatial arrangement of reefs alters the ecological patterns of fauna between interspersed algal habitats. Estuarine, Coastal and Shelf Science 78:774-782.

Underwood, A. J. 2004. Landing on one’s foot: small-scale topographic features of habitat and the dispersion of juvenile intertidal gastropods. Marine Ecology Progress Series 268:173-182.

Valdez, M. C. and Ponce Diaz, G. 1996. Estudio del Potentcial Pesquero y Acuicola de Baja California Sur.

Wahl, M. 1997. Increased drag reduces growth of snails: comparison of flume and in situ experiments. Marine Ecology Progress Series 151: 291-293.

Watanabe, J. M. 1984. The influence of recruitment, competition, and benthic predation on spatial distributions of three species of kelp forest gastropods (Trochidae: Tegula). Ecology 65:920-936.

Wieters, E. A, Gaines, S. D. Navarrete, S. A., Blanchette, C. A. and Menge, B. A. 2008. Scales of Dispersal and the Biogeography of Marine Predator-Prey Interactions. The American Naturalist 171: 405-417.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81-120.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

With, K. A. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

Yamaura, Y., Kawahara, T., Iida, S. and Ozaki K. 2008. Relative importance of the area and shape of patches to the diversity of multiple taxa 22: 1513-1522.

Zacherl, D., Gaines, S. D. and Lonhart, S. I. 2003. The limits to biogeographical distributions: insights from the northward range extension of the marine snail, Kelletia kelletii (Forbes, 1852). Journal of Biogeography 30: 913-924.

Zaytsev, O., Cervantes-Duarte, R., Montante, O. and Gallegos-Garcia, A. 2003. Coastal Upwelling Activity on the Pacific Shelf of the Baja California Peninsula. Journal of Oceanography 59: 498-502.

Vita

Courtney Burke Abshire received his B. S. in Biology from the University of Texas at Austin in 2007 and continued on directly with his studies ultimately receiving his M. A. in Biology in 2010 from U. T. Austin. Courtney's master's thesis evolved from his participation in the Baja Bio-complexity Project under the guidance of Dr. Laura González-Guzmán. The Baja Bio-complexity Project is an multi-national, multi-institutional interdisciplinary study investigating the linkage between socio-economic and ecosystem factors of fisheries located along the western coast of the Vizcaino Peninsula. Information regarding the products of this study can be found at http://www.bajacaliforniabiocomplexity.org/.

Permanent address: 2412 Roehampton Drive, Austin, Texas 78745
This thesis was typed by the author.