TEMPORAL AND SPATIAL VARIABILITY OF BLENNY (PERCIFORMES: LABRISOMIDAE AND BLENNIIDAE) ASSEMBLAGES ON TEXAS JETTIES

A Thesis

by

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Structured, hard-bottom habitats and associated cryptic fish species were effectively absent from the northwestern Gulf of Mexico coast prior to jetty construction 120 years ago. Fishes in the Families Labrisomidae and Blenniidae now distributed across the northwest Gulf may have been influenced by jetty construction. Little is known about the species composition, population dynamics, or origin(s) of blenny assemblages on Texas jetties. In this study, blennies were dipnetted monthly from jetty habitats at Galveston, Port Aransas, and South Padre Island, Texas, during May 2000 through August 2001; and in Florida, once during December 2001 to characterize assemblage structure. All specimens (n=4555) were identified, enumerated, and measured and a subsample taken for otolith microstructure analysis (n=99) and mtDNA sequencing (n=67). Four blenniid species (*Hypleurochilus geminatus*, *Hypsoblennius hentzi*, *Hypsoblennius ionthas*, and *Scartella cristata*) and one labrisomid (*Labrisomus nuchipinnis*) contributed to spatially distinct assemblages differing significantly in species composition, diversity and evenness across sampling sites. Galveston exhibited the highest diversity index values while Port Aransas yielded the most species (4). Temperature appears to be the driving factor behind species composition over time at each sampling site. *Scartella cristata* dominated blenny assemblages on Texas jetties regardless of local environmental conditions and was found to be a short-lived species with an extended spawning period. The Galveston population of *S. cristata* exhibited the statistically highest mean total length and age and demonstrated a close affinity to Florida conspecifics, thus indicating the eastern Gulf to be a likely source. *Scartella cristata* on the lower and middle Texas coast originated from at least two sources, suggesting two genetically distinct populations may exist in the Gulf. Jetty construction on the Texas coast has allowed these two populations to mix.
DEDICATION

This work is dedicated to the three special women in my life. To my grandmother, Dolores, who always taught me to be true to myself and though she is gone will never be forgotten. To my mother, Jane, who has never faltered in her belief in me. And to my wife, Laura, who is a source of constant inspiration because she looks upon this world with a sense of wonder and amazement that I envy. I succeed because of what each of you gives to me.
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Fishes of the Families Blenniidae and Labrisomidae are cryptic residents of structured inshore and offshore marine habitats worldwide (Bond 1996). Blenniidae is a varied and speciose family with 345 species in 53 genera, the majority of which occur in the Indo-Pacific (Nelson 1994). Because blenniids are typically restricted to structurally complex, hard-bottomed substrates such as reefs and rocky shorelines, the Texas Gulf shore probably represented a historical gap in their range prior to construction of jetties. Nevertheless, ten species in the Family Blenniidae occur on nearshore jetties, groins, and pilings; offshore oil platforms, banks, and reefs; and estuarine oyster reefs in the northwestern Gulf of Mexico (Britton and Morton 1989, Hoese and Moore 1998). Two of these, striped blenny, *Chasmodes bosquianus* (Lacepède) and Florida blenny, *Chasmodes saburrae* Jordan and Gilbert, are restricted to low salinity, estuarine habitats (Springer 1959) and are not likely residents of nearshore or offshore waters. Additionally, *C. saburrae* is thought to be restricted to parts of Florida where there is a gap in the range of *C. bosquianus* (Hoese 1958, Springer 1959). Two other species, barred blenny, *Hypleurochilus bermudensis* Bebee and Tee-Van, and feather blenny, *Hypsoblennius hentz* (Lesueur), are not commonly encountered along the Texas coast (Hubbs 1939, Randall 1966, Hoese and Moore 1998). The only known records of *Hypleurochilus bermudensis* in the northwestern Gulf come from the West Flower Garden Banks (Randall 1966, Bright and Cashman 1974, Hoese and Moore 1998). *Hypsoblennius hentz* is somewhat more common, occurring on soft mud bottoms in south Texas bays rather than along jetties of the middle and upper Texas coast (Hubbs 1939, Smith-Vaniz 1980, Hoese and Moore 1998). Three other species, tessellated blenny, *Hypsoblennius invemar* Smith-Vaniz and Acero, redlip blenny, *Ophioblennius atlanticus* (Valenciennes), and seaweed blenny, *Parablennius marmoreus* (Poey), are frequently found on offshore reefs and production platforms but are uncommon in nearshore habitats (Bright and Cashman 1974, Hoese and Moore 1998). Molly miller, *Scartella cristata* (Linneaus), and crested blenny, *Hypleurochilus geminatus* (Wood) are common on jetties and groins but have been known to occur on structured habitats in estuarine systems (Lindquist and Chandler 1978, Hoese and Moore 1998). Hoese

This thesis follows the style of Marine Ecology Progress Series.
and Moore (1998) indicate that *Hypleurochilus geminatus* is the most frequently encountered blenny on the lower Texas coast and imply that *Scartella cristata* is relatively scarce on the middle and upper coast. The freckled blenny, *Hypsoblennius ionthas* (Jordan and Gilbert), also is a typical inhabitant of jetties and groins but occurs more frequently on estuarine oyster reefs (Hubbs 1939, Clarke 1979, Smith-Vaniz 1980, Hoese and Moore 1998).


Blennies have been the focus of diverse research efforts ranging from behavior to aquatic toxicology. However, existing information on population dynamics of blennies in the northwestern Gulf of Mexico is limited, particularly when compared to that of counterparts in the Caribbean, Mediterranean, and northeast Atlantic Ocean. These studies tend to focus on a single species and not multi-species systems where differences in biology of constituent species can be determining factors in assemblage structure. The Texas coast encompasses a wide range of environmental and climatic regimes (Britton and Morton 1989) that have the potential of influencing growth. Growth is an important aspect in structuring species assemblages (Jones 1991); however, there is no information available on the growth rates of Gulf of Mexico blennies. Therefore an attempt to characterize these assemblages would be incomplete without recognizing the importance of an age and growth component.

**Blennies and the “New” Texas Coast**

The Texas coast has historically been an unbroken 650 km stretch of sandy beaches. Rocky shore habitats are practically absent in nearshore waters of the northwest Gulf, with the nearest natural rocky shores occurring at Punta Jerez in Tamaulipas, Mexico (Britton and Morton 1989). There is significantly more hard-bottom habitat in offshore waters of the northwest Gulf but these areas are relatively small, low
relief features isolated from each other by large expanses of flat mud bottoms (Bright 1977, Dennis and Bright 1988). With the exception of the Flower Gardens Banks and other smaller associated banks, few if any of these naturally occurring hard-bottom habitats are suitable for blenny colonization as a result of the Gulf’s oceanographic and bathymetric characteristics (Rezak et al. 1985). Other structure-dependent fishes such as lutjanids and serranids flourish not only on banks and reefs of the northwestern Gulf but on low relief features, such as shell ridges, while blenniids are absent from these habitats (Rezak et al. 1985, Harper 2002). Sediment input from the Mississippi River creates a sunlight-blocking layer of suspended material known as the nephloid layer that effectively limits the depth to which algae can grow on nearshore features of the northwest Gulf. Consequently, the distribution of herbivorous blenniid species is restricted to features that extend above the nephloid layer. Extensive oyster reefs located in primary and secondary bays behind barrier islands are the only other naturally occurring hard-bottom habitats along the Texas coast. However, fluctuations in temperature and salinity associated with these estuarine environments limit blenny assemblages to species such as Chasmodes and Hypsoblennius spp. that tolerate these changing conditions (Springer 1957, Crabtree and Middaugh 1982, Britton and Morton 1989, Hoese and Moore 1998).

Human activities have altered the physical nature of the Texas coast dramatically over the past 140 years. Ensuring the flow of commerce and protecting beaches have resulted in the creation of a limited amount of rocky shore habitat in the form of jetties and groins. Jetty construction along the Texas coast began in 1868 and continued into the 1920’s (Alperin 1977). Currently seven major passes are protected by jetties: Sabine Pass, Bolivar Roads, Freeport Ship Channel, Matagorda Ship Channel, Aransas Pass, Mansfield Cut, and Brazos Santiago Pass. Many other small jetties and groins such as those at Fish Pass on Mustang Island, Texas and at Veracruz and Tampico, Mexico protect passes and shoreline along the western Gulf. Groins were constructed along the Galveston Island beachfront in the 1930’s to protect both the beach and seawall (Alperin 1977).

Jetties represent structurally stable and permanent habitats to associated fauna in contrast to a coastline characterized by shifting sand and bottoms of unconsolidated muds and sands (Bohnsack et al. 1991). Texas jetties are essentially new “islands” in the Gulf of Mexico where planktonic spores, eggs,
and larvae of organisms that must settle on solid substrate to survive have suitable habitat on which to recruit. Many fish species probably are still colonizing and establishing new populations on Texas jetties but unfortunately no comprehensive study of these processes has been undertaken. Due to jetties’ recent construction and relative isolation, their biotic community may be impoverished when compared to that of naturally occurring rocky shores and reefs of the eastern Gulf, southern Gulf, and Caribbean as well as estuarine oyster reefs (Britton and Morton 1989).

Blennies are recent arrivals to the Texas Gulf coast, utilizing jetties as surrogate habitat. The blenniid species found on the Texas coast have probably closed a gap in their historic range by colonizing jetties (Hoese and Moore 1998, Britton and Morton 1989); yet their original source population(s) of individuals comprising this recruitment has not been identified. It also is unknown if blennies have established self-maintaining populations—a possibility in light of self-recruitment in reef fish populations (Stobutzki and Bellwood 1997, Jones et al. 1999, Swearer et al. 1999), or if their persistence is dependent upon recruitment from outside sources.

The three components of the present study (habitat and assemblage characterization; age and growth; population genetics) enabled broad questions regarding the past, present, and future of these assemblages to be addressed. The history of blenny assemblages on Texas jetties was reconstructed using molecular techniques and focused on the question: do assemblages present on Texas jetties today represent an extension from a single source or a convergence of multiple populations? The current status of blenny assemblages was documented through collections along the Texas coast and focused on the question: how are blenny assemblages on jetties structured along the Texas coast? Combining these data with characterization of jetty habitat and age and growth of the dominant species allowed questions regarding the underlying reasons for observed patterns to be raised. The future of blenny assemblages on Texas jetties also was considered including the long-term impact jetties may have on the genetic structure of blenny populations in the Gulf and potential practical applications of this study to conservation and management of marine resources.
OBJECTIVES

1.) Characterize blenny assemblages on Texas jetties and groins.
   a. Document the species composition and size structure of these assemblages and assess their spatial and temporal variability.
   b. Determine the species diversity and evenness of these assemblages.
   c. Identify hydrographic parameters critical to observed distribution.

2.) Characterize age and growth patterns of the dominant blenny species on Texas jetties.
   a. Compare mean age of local populations across sampling sites.
   b. Determine growth rates across sampling sites.
   c. Assess spawning periodicity of conspecifics across sampling sites.

3.) Document the genetic structure of the dominant blenny species on Texas jetties.
   a. Determine the genetic interaction/differentiation among sites in Texas.
   b. Determine the genetic interaction/differentiation among sites in Texas and Florida.
   c. Identify the most likely origin(s) of recruits to Texas jetties.
**METHODS**

**Study Areas**

Blenny assemblages of Texas jetties were characterized at upper, middle, and lower coast locations (Fig. 1). The upper coast study area consisted of an 8 km stretch of beachfront on Galveston Island in Galveston County, Texas (Fig. 2). Ten groins, each extending gulfward from the Galveston beachfront for approximately 50 m, collectively comprised the only sampling station on the upper coast (Table 1). Groins were sampled in Galveston as opposed to the South Jetty at Bolivar Roads on the east end of the island due to safety concerns. Surf conditions and currents at the South Jetty were typically much more severe than those at the groins. Integrating the 10 smaller groins into one station was designed to reduce mortality associated with repeated sampling at these sites. Although the majority of effort was concentrated on two groins (the 44th and 49th Street groins), samples taken from other groins did not differ in CPUE, species composition, or size of individuals from those taken from more heavily fished counterparts during the same month.

The South Jetty bordering Aransas Pass in Port Aransas, Nueces County, was the middle coast study area (Fig. 2). This jetty runs extends gulfward in a south-southeast direction for approximately 2000 m. Two collection stations were established at the South Jetty, station 2 on the north or Aransas Pass side and station 3 on the south or Gulf side. Both stations were sampled concurrently whenever possible, but wind and surf conditions frequently rendered monthly samples possible at only one station.

Lower Texas coast collections were made at the North Jetty protecting Brazos Santiago Pass on South Padre Island, Cameron County (Fig. 2). This jetty extends east-west into the Gulf for approximately 2000 m. Like those for the middle coast, two collection stations were established at the North Jetty-station 4 on the north or Gulf side and station 5 on the south or channel side near a protected cove (Dolphin Cove).

**Characterization of Blenny Habitat**

Blenny habitat was characterized by describing two distinct aspects of the jetty environment: hydrographic conditions and substrate complexity. Hydrographic characterization was based on water
Fig. 1. Map of upper, middle, and lower coast study areas used to characterize blenny assemblages on Texas jetties from May 2000 to August 2001. Highlighted boxes represent study areas shown in greater detail in Fig. 2.
Fig. 2. Collection stations at Galveston (STATION 1), Port Aransas (STATIONS 2 and 3) and South Padre Island (STATIONS 4 and 5), TX study areas.
temperature, salinity, and turbidity measurements made prior to each sampling event. Surface water temperature was measured to the nearest degree Celsius using an alcohol-filled thermometer. Salinity was measured to the nearest part per thousand using an optical refractometer. Turbidity was measured to the nearest 0.1 centimeter using a 0.26-m diameter secchi disc.

Substrate complexity of each collection site was assessed by measuring rugosity of the constituent jetty surface. Rugosity was measured with 1-m lengths of 20-gauge stainless steel wire molded to the surface of the jetty below the water line. The shortest straight-line distance between the two ends after the wire was molded to the jetty’s surface was then measured. The inverse ratio of this distance to the original length of the wire yielded an index value of rugosity. Rugosity was measured at three different locations chosen at random along the length the 15-m transects established for sampling after each collection effort. The structural complexity of blenny habitat also was assessed qualitatively through visual examination by noting fouling community coverage and species composition as well as general jetty construction (i.e. small vs. large boulders, placements of boulders, occurrence of crevices).

**Characterization of Blenny Assemblages**

Surf conditions permitting, three collections were conducted monthly at each upper, middle, lower coast station from May 2000 through August 2001 (July 2000 to August 2001 for South Padre Island). Blennies were captured in a 25.4 x 17.5 cm rectangular dipnet randomly swept along a 15-m transect against the jetty. Each collection was based on approximately 60 minutes of sampling for a total of 3 hours of effort expended at respective stations every month. If more than one collector was present,

<table>
<thead>
<tr>
<th>STATION</th>
<th>NAME</th>
<th>MONTH(S) SAMPLED</th>
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<tr>
<td>1A</td>
<td>19th Street groin</td>
<td>DEC 00</td>
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<td>1B</td>
<td>21st Street groin</td>
<td>JUL 00</td>
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<td>1C</td>
<td>24th Street groin</td>
<td>OCT 00, JUN 01</td>
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<td>1D</td>
<td>27th Street groin</td>
<td>JUN 00, JUN 01</td>
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<tr>
<td>1E</td>
<td>33rd Street groin</td>
<td>MAY 00, JUN 00</td>
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<td>1F</td>
<td>37th Street groin</td>
<td>MAR 00</td>
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<td>1G</td>
<td>40th Street groin</td>
<td>JUL 00</td>
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<td>1H</td>
<td>44th Street groin</td>
<td>APR 00, AUG 00, APR 01</td>
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<tr>
<td>1I</td>
<td>49th Street groin</td>
<td>JUN-NOV 00, JAN 01-MAR 01, MAY 01-AUG 01</td>
</tr>
<tr>
<td>1J</td>
<td>51st Street groin</td>
<td>MAR 01, APR 01</td>
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each worked a different 15-m transect for the same amount of time with their efforts considered two
distinct collections. A paired sample t-test indicated no significant difference between collections made
by different collectors at the same time and station. Depth of capture ranged between that of algae mats at
the supralittoral fringe to approximately 1.5 m below the surface; however, water depth at most stations
was considerably deeper than the area within reach of the sampling gear. Captured blennies were held in
aerated 18.9-L buckets until completion of the collection. Other captured fishes were noted and released.
Blennies were then sacrificed by immersion in MS-222, rinsed, and stored in 70% ethanol. Blennies were
identified to species, enumerated, and measured (total length) to the nearest millimeter.

**Mark and Recapture Studies**

A mark-recapture study was conducted at respective locations to estimate relative abundance of
constituent blenny species. Three mark-recapture experiments based on a minimum of 50 blennies
collected from 10-m transects were conducted at each location. Each collection was initially placed in an
aerated 18.9-L bucket and eventually transferred to another 18.9-L bucket containing seawater and the fish
anesthetic quinaldine. Anesthetized fish were identified to species and marked using visible fluorescent
elastomer injected subdermally above the anal fin (Guy *et al.* 1996, Gibson 1999). Marked fish were
placed into another aerated 18.9-L bucket and allowed to recover before being released near their capture
site. The same 10-m transects of jetty at each location were re-sampled 24 hours later and the number of
marked and unmarked blennies within respective species recorded. Blennies captured in this second
collection were sacrificed and used in the protocols described under Characterization of Blenny
Assemblages (p. 10).

**Otolith Microstructure Analysis**

Sagittal otoliths were removed from *Scartella cristata* (n=106) captured from Galveston, Port
Aransas, and South Padre Island from May through September 2000. *S. cristata* was chosen because it
was encountered across all three localities. Individuals representing the range of sizes and collection dates
were selected for further analysis. Otoliths were prepared following the protocols outlined by Secor *et al.*
(1991) and Rooker and Holt (1997). Otoliths were individually mounted in blocks of Spurr resin and
sectioned using an Isomet™ isometric saw (Buehler, Lake Bluff, IL). Each section was then attached to a
microscope slide with Crystal Bond glue (Aremco Products Inc., Ossining, NY) and polished to the core on both sides using 240, 320, 400, and 600 grit Carbimet™ paper discs, Microcloth™ polishing cloth, and Micropolish™ 0.3 micron alpha alumina (Buehler, Lake Bluff, IL). Age of each individual was then determined by counting daily growth increments from the core to the post rostrum (Fig. 3) under a compound light microscope using OPTIMAS® version 6.0 image analysis software (Media Cybernetics, Inc., Silver Spring, MD).

Daily increment formation was validated by marking otoliths with alizarin complexone. Thirty-four *Scartella cristata* were held in a 250 mg/L alizarin complexone-seawater solution for approximately 60 minutes to stain their otoliths. Individuals were then maintained in 75.8-L aquariums and sacrificed after 10 days (n=14), 17 days (n=6), and 30 days (n=14). Sagittal otoliths were removed from these specimens and prepared as outlined above. Both the number of growth increments and distance between the alizarin complexone mark and otolith’s post-rostral edge were measured. Least squares linear regression and ANOVA were performed to evaluate the relationship between the amount of otolith growth and time. The validation model was confirmed through analysis of covariance (ANCOVA) comparing 10-20 day increments measured at randomly chosen positions on the otolith to increment widths calculated.
for the same time period by the model. The validation trial confirmed that one ring represented one day’s growth but there was some uncertainty in reading the most recent rings on the otolith’s edge. Based on the alizarin complexone marking, otoliths grew at the rate of 0.33 \( \mu \text{m/day} \). The validation model was compared to a least squares regression of a series of readings along short transects on the otolith surface (Fig. 4). While not a perfect match, ANCOVA validated the regression estimates of growth rate \((p=0.943)\) and size-at-hatching \((p=0.171)\).

Age-length relationships were used to estimate growth of *Scartella cristata*. Hatch dates for all *S. cristata* captured under 270 mm TL were calculated by subtracting the estimated age in days from the date of capture. Individuals that exceeded 270 days old were excluded from the analysis due to an inability to discern their daily growth rings. No attempt was made to weigh large individuals during analysis to account for the cumulative effect of mortality on an age class because no published estimate of blenny mortality was found.

![Validation model graph](image)
Mitochondrial DNA D-Loop Analysis

Genetic analysis was performed on a subsample of *Scartella cristata* to identify relationships between sample sites and determine the origin(s) of individuals on Texas jetties. The null hypothesis that Texas jetties represented a single undifferentiated population originating from a single source population was tested. To this end, individuals ranging from 40 to 50 mm TL were selected from Galveston (*n*=20), Port Aransas (*n*=19), and South Padre Island (*n*=19) samples to minimize variation that may occur between age classes (Fig. 4). An additional nine individuals were collected from Gulf Islands National Seashore on Santa Rosa Island, Florida in December 2001 for use in this analysis (Fig. 5). DNA was extracted from these individuals following protocols described by Greig (2000) with minor modification.

![Fig. 5. Capture locations of Scartella cristata used in mtDNA analysis.](image)

Briefly, approximately 0.05 g of epaxial muscle tissue was added to a labeled 1.5 μL microfuge tube with 200 μL of TENS solution (50 mM Tris-HCl [pH 8.0], 100 mM EDTA, 100 mM NaCl, 1.0% SDS) and 20
μL of Proteinase K (10mg/ml) and incubated 10-12 hours at 55 C on a heat block. Nucleic acids were precipitated by adding 20 μL of 5 M NaCl and then spun at 14,000 g for 10 minutes. The sample supernatant was pipetted into a second microfuge tube and approximately 400 μL of 100% cold ethanol was added to precipitate DNA. The sample was spun again at 14,000 g for 10 minutes and the resulting supernatant discarded. DNA pellets were washed by adding 300 μL of 70% cold ethanol, spun again at 14,000 g, and the resulting supernatant was discarded. Pellets were allowed to air-dry overnight. The DNA was resuspended in 100 μL of TE buffer (10 mM Tris-HCl [pH 8.0], 1 mM EDTA) and placed on a heat block at 65 C until the pellet fully dissolved. The presence and quality of extracted DNA was verified by electrophoresis of 3 μL of resuspended DNA through a 1.0% agarose gel at 100 V for approximately 30 minutes. DNA was visualized using ethidium bromide.

Polymerase chain reaction (PCR) was performed to amplify a 380 base pair segment of the mtDNA D-loop region using the heavy strand primer CSBD-H (5’-CCGGTCTGAACACTCACGT-3’) and light strand primer L15998-PRO (5’-TACCCCAAACTCCCAAAGCTA-3’). PCR was conducted in Eppendorf Mastercycle Gradient (Brinkmann Instruments Inc., Westbury, NY) with the following reaction profile: initial denaturation for 2 minutes at 94.0 C followed by 35 cycles (denaturation, 30 seconds at 94.0 C; annealing, 45 seconds at 50.0 C; extension, 1 minute at 72.0 C) and a final extension for 3 minutes at 72.0 C. Electrophoresis through a 1.2 % agarose gel at 100 V for approximately 30 minutes was used to examine the quality of PCR product and check for contamination. Again, ethidium bromide was used for visualization. Upon successful PCR, the product was cleaned of excess dNTP, primers, and AmpliTaq® using ExoSAPIT® (USB Corporation, Cleveland, OH) following manufacturer’s recommendations. Clean PCR products were prepared for cycle sequencing using a BigDye® terminator cycle sequencing ready reaction kit (Applied Biosystems, Foster City, CA). Cycle sequencing was performed in an Eppendorf Mastercycler Gradient with the following reaction profile: 25 cycles (denaturation, 10 seconds at 96.0 C; annealing, 5 seconds at 50.0 C; extension, 4 minutes at 60.0 C). Upon completion of cycle sequencing, the product was cleaned using RapXtract® II dye terminator removal kit (Prolinx, Bothell, WA) and diluted in 30 μL of dd H2O. Single strand nucleotide sequences were obtained
using the ABI Prism 310 Genetic Analyzer (Applied Biosystems, Foster City, CA) at the Molecular Ecology and Fisheries Genetics Laboratory at Texas A&M University at Galveston.

**Data Analysis**

With the exception of DNA sequence data, all data analysis and statistical tests were performed using SPSS for Windows version 10.0.1 (SPSS Inc., Chicago, IL). Means are reported ± 1 standard deviation unless otherwise noted. The assumptions of parametric testing (normality, equality of variance, etc.) were validated and transformations were conducted when necessary. In the cases where a violation of assumptions could not be reconciled through transformation, the data (salinity and turbidity) were log transformed to minimize any effects of excessive variability and the appropriate test performed (Underwood 1981, 1997).

**Habitat characterization:** Hydrographic measurements were grouped by season for analysis and a mean calculated for each parameter during summer (June-August), autumn (September-November), winter (December-February), and spring (March-May). Means for respective parameters were compared across seasons within a given location and between localities during each season using one-way analysis of variance (ANOVA). Significant differences (α=0.05) were identified with the Tukey post-hoc test. Turbidity data were log transformed to meet ANOVA’s assumption of equal variance.

Mean rugosity for each location was compared using a one-way ANOVA and Tukey post-hoc test to determine if substrate complexity of collection sites at upper, middle, and lower coast jetties differed significantly from one another (α=0.05). Log transformation was necessary to satisfy the assumption of equal variance. Qualitative data were used to validate rugosity measures and to account for any observed differences.

**Blenny assemblage characterization:** Species diversity was measured for each collection using the Shannon-Wiener diversity index,

\[
H' = n \log n - \sum_{i=1}^{k} f_i \log f_i
\]
where \( n \) is the total number of blennies captured and \( f \) represents the number of individuals of each blenny species (Zar 1996). Species evenness, \( J' \), was calculated as

\[
J' = \frac{H'}{H'_{\text{max}}}
\]

where \( H'_{\text{max}} = \log k \) and \( k \) represents the number of blenny species (Zar 1996). The mean monthly values of \( H' \) and \( J' \) for upper, middle, and lower coast stations were calculated and compared using one-way ANOVAs with Tukey post-hoc tests to identify significant differences (\( \alpha = 0.05 \)).

Catch per unit effort (CPUE), defined as the number of blennies per sampling-hour, was calculated for constituent species in each collection while mean seasonal CPUE was calculated for each species. Mean seasonal CPUE was compared across sites and among seasons at each locality with ANOVA and Tukey post-hoc tests. Analysis of covariance (ANCOVA) was used to determine if temperature, salinity, turbidity, date, or location correlated with CPUE. Inverse transformation (transformed CPUE=CPUE\(^{-1}\)) allowed for all assumptions to be met.

The monthly and overall mean total length were calculated for each species and compared within locations over time and between locations using ANOVA with Tukey post-hoc tests or \( t \)-tests where appropriate (\( \alpha = 0.05 \)). Length-frequency distributions also were generated for constituent species in each collection. The total length data could not be reconciled with the assumptions of parametric testing. All analysis was conducted with log-transformed data.

**Mark and recapture:** Population size within respective species was estimated using the Petersen equation,

\[
N = \frac{M(C+1)}{R+1}
\]

where \( N \) is the population estimate, \( M \) is the number of blennies initially marked, \( R \) is the number of marked blennies recaptured, and \( C \) is the total number of fish captured in the second sampling effort (Guy *et al.* 1996).

**Age and growth:** Differences in growth rates of *Scartella cristata* among the three study sites were determined through linear regression and ANCOVA. Age-length relationships generated for each site
were used to estimate the age of every *Scartella cristata* captured from that site during the study. Overall mean age at each site was calculated and compared among locations using ANOVA with Tukey *post-hoc* tests.

**Genetic analysis:** DNA sequences were visually aligned and edited using BioEdit Sequence Alignment Editor version 5.0.7 (Hall 1999). DNA polymorphisms in the aligned sequences and genetic variation within samples were assessed through calculations of nucleotide diversity ($\pi$) and haplotype diversity ($h$) using DnaSP version 3.51 (Rozas and Rozas 1999). Genetic distances were estimated using the Tamura-Nei model with pairwise deletion, and a neighbor-joining tree with 500 bootstrap replicates was constructed using MEGA version 2.1 (Kumar *et al.* 2001). TCS version 1.13 (Clement *et al.* 2000) was used to identify haplotypes and determine haplotype relationships. Analysis of molecular variance (AMOVA) was performed using Arlequin version 2.000 (Schneider *et al.* 2000) to determine the proportion of genetic diversity within and among sample sites ($\Phi_{ST}$). AMOVA calculates the difference between mean heterozygosity among population subdivisions and potential frequency of heterozygotes using a modification of Wright’s $F$-statistic (Excoffier *et al.* 1992). It operates under the assumptions that: individuals in the sample are selected independently and at random; individuals within the population can interbreed randomly and non-assortatively; and there is no inbreeding within the population (Excoffier 1992). The number of migrants per generation ($N_m$) among samples sites also was estimated using Arlequin. Mismatch distributions of the frequency of a given number of pairwise differences were generated for each location with Arlequin. These distributions were compared to a Poisson distribution with the same mean as the using chi-square test. Distributions that differed significantly ($\alpha=0.05$) from the Poisson distribution indicated samples were taken from a population of constant size, whereas failure to reject the null hypothesis suggested the population has been growing exponentially for an extended period of time (Slatkin and Hudson 1991). Mantel’s test with 1000 permutations was performed using TFPGA version 1.3 (Miller 1997) to determine if a significant relationship existed between genetic distances and geographical distances among locations.
RESULTS

Habitat Characterization

Water temperature at the three study sites was similar (Fig. 6). Temperatures peaked in late summer and early fall (Galveston: 32.0°C; Port Aransas: 31.0°C; South Padre Island: 31.7°C) and then declined to their minimum in December and January (Galveston: 13.0°C; Port Aransas: 14.0°C; South Padre Island: 14.0°C). Overall mean water temperature from spring 2000 to summer 2001 was 23.1±6.7, 25.0±6.1, and 24.1±4.9°C for Galveston, Port Aransas, and South Padre Island, respectively. Significant seasonal differences in temperature were observed at each study site (Galveston: \( p < 0.001 \); Port Aransas: \( p < 0.001 \); South Padre Island: \( p = 0.007 \)). Mean summer water temperature at Galveston (Fig. 6) was significantly higher in both 2000 (31.4±1.9°C) and 2001 (30.1±2.4°C) than that of other seasons (spring 2000: 25.0°C; fall 2000: 18.7±3.2°C; winter 2000-01: 15.0±2.0°C; spring 2001: 20.5±4.9°C). Winter 2000-01 (15.0±1.0°C) produced the only significant within site comparison at Port Aransas, being cooler than the other seasons (spring 2000: 25.0°C; summer 2000: 30.5±1.5°C; fall 2000: 26.5±3.5°C; spring 2001: 25.0±3.5°C; summer 2001: 30.2±1.3°C), while the winter 2000-01 (17.0±3.0°C) and spring 2001 (23.0±2.6°C) means were significantly lower than those of all other seasons at South Padre Island (summer 2000: 28.3±1.1°C; fall 2000: 28.0±4.2°C; summer 2001: 26.9±1.2°C) (Fig. 6). There were no significant differences among the three sites in mean seasonal water temperature (\( p = 0.736 \)) or in the overall mean water temperature (\( p = 0.732 \)); however winter water temperatures tended to be warmer on the middle and lower coasts while their summer counterparts were warmer on the upper and middle coasts.

Salinity remained relatively constant throughout the year at all three study sites (Galveston: 24.0-34.3‰; Port Aransas: 29.9-36.0‰; South Padre Island: 31.3-35.0‰) (Fig. 6). Overall mean salinity was 28.3±6.7, 32.3±5.9, and 33.0±4.9‰ for Galveston, Port Aransas, and South Padre Island, respectively. Seasonally there were no significant differences at any site (Galveston: \( p = 0.206 \); Port Aransas: \( p = 0.128 \); South Padre Island: \( p = 0.433 \)), but a trend toward lower salinities in winter increasing through the summer did exist. While there were no significant differences in mean seasonal salinity among sites (\( p = 0.236 \)), there was a significant difference in overall mean salinity (\( p = 0.004 \)). Salinity tended both to be higher and
less variable from north to south along the coast. Galveston had significantly lower overall mean salinity than did Port Aransas \( (p=0.016) \) and South Padre Island \( (p=0.007) \). There was no significant difference between Port Aransas and South Padre Island \( (p=0.92) \).

Turbidity, as estimated by secchi disc measurements, remained relatively constant in Galveston (25-55 cm) during the study period. In Port Aransas turbidity peaked in spring 2001 (40 cm) and was lowest in summer 2001 (144 cm) while that at South Padre Island ranged from 135 cm in fall 2000 to 51 cm in summer 2000. Turbidity typically decreased from north to south, with overall mean estimates for Galveston, Port Aransas, and South Padre Island being 34.2±11.4, 79.7±52.6, and 88.0±54.8 cm, respectively. Galveston yielded significantly higher overall mean turbidity \( (p<0.001) \) than did Port Aransas \( (p=0.002) \) and South Padre Island \( (p<0.001) \). Mean seasonal turbidity in Galveston during summer 2000 (55.3±4.2 cm) and winter 2000-01 (37.3±8.3 cm) differed significantly \( (summer: p=0.035; \ winter: p=0.026) \) from those of other seasons (Fig. 6). Seasonal turbidity at Port Aransas also differed statistically \( (p=0.023) \), with summer 2001 estimates (143.6±62.9 cm) being lower than those of either winter 2000-01 \( (p=0.031; \ mean=40.2±9.2 \ cm) \) or spring 2001 \( (p=0.038; \ mean=36.9±10.6 \ cm) \). South Padre Island failed to yield significant differences \( (p=0.434) \) in mean seasonal turbidity. However, its mean estimates were significantly lower than those of Galveston \( (p=0.045) \) during fall 2000 and of Galveston \( (p=0.003) \) and Port Aransas \( (p=0.027) \) during winter 2000-01.

There were small but significant differences in rugosity or structural complexity across the study sites. Mean values were 1.15±0.1, 1.15±0.08, and 1.21±0.08 for Galveston, Port Aransas, and South Padre Island, respectively (Fig. 7). ANOVA indicated significant differences in mean rugosity among sites \( (p=0.029) \). Galveston had significantly lower rugosity than did South Padre Island \( (p=0.043) \). Groins on
the Galveston beachfront were largely bare rock with a poorly developed fouling community of barnacles, oysters, and filamentous epilithic algae. While the rocks of the South Jetty at Aransas Pass did not appear to differ structurally from those of Galveston, the biological complexity of their fouling community was much greater. The South Jetty was mostly covered by dense mats of filamentous and foliose epilithic algae.

![Graph showing seasonal water temperature, salinity, and Secchi disc readings at Galveston, Port Aransas, and South Padre Island, TX from Spring 2000 to Summer 2001. Error bars represent standard error.]

- **Temperature (°C)**: Ranges from approximately 10°C to 30°C with slight seasonal variations.
- **Salinity (ppt)**: Shows similar trends to temperature, with slight deviations.
- **Secchi disc reading (cm)**: Displays varying turbidity levels, with some seasons showing clearer water and others more turbid.

**Fig. 6.** Mean seasonal water temperature, salinity, and Secchi disc estimates of turbidity at Galveston, Port Aransas, and South Padre Island, TX from Spring 2000 to Summer 2001. Error bars represent standard error.
algae that often grew on extensive beds of mussels and barnacles. The North Jetty at Brazos Santiago Pass exhibited little difference in the structural complexity of the rocks, but the arrangement of the rocks on the channel side of the jetty created habitats that were similar to tide pools. Its rocks also were almost completely covered by thick epilithic algae mats comprised of structurally complex species in the genera *Caulerpa* and *Padina*. In places, calcareous remains of *Padina* formed growths resembling hermatypic coral. Density and distribution of mussel and barnacle beds on the North Jetty were more restricted than that at the other two sites (Fig. 7).

**Characterization of Blenny Assemblages**

![Bar graph showing mean rugosity indices for Galveston, Port Aransas, and South Padre Island.](image)

![Images of typical development of the jetty fouling community.](image)

**Fig. 7.** Comparison of quantitative and qualitative measures of habitat complexity at Texas groins and jetties. (A) Mean rugosity indices for the groins/jetties at Galveston, Port Aransas, and South Padre Island. Error bars represent standard error. (B) Examples of the typical development of the jetty fouling community.
Species Composition

A total of 4555 blennies representing five species (Labrisomus nuchipinnis, Hypleurochilus geminatus, Hypsoblennius hentz, Hypsoblennius ionthas, and Scartella cristata) was captured from the three study sites during May 2000 through August 2001. Catch statistics for these species and study sites are summarized in Table 2. Catch per unit effort (CPUE) of blennies and species composition varied temporally and spatially. Temperature ($p<0.001$), location ($p=0.005$), and their interaction ($p=0.017$) had a significant effect on CPUE, yielding a coefficient of determination of 0.596. ANCOVA indicated that turbidity ($p=0.526$), date ($p=0.774$), and salinity ($p=0.936$) had no significant effects on CPUE, despite $r^2=0.572$ when all environmental parameters were factored into the analysis.

| Table 2. Total blenny catch from groins/jetties at Galveston, Port Aransas, and South Padre Island, TX during May 2000 through August 2001. |
|-----------------|-----------|----------|---------------|-----------|
| **Species**      | **Galveston** | **Port Aransas** | **South Padre Island** | **TOTAL** |
| Labrisomus nuchipinnis | 0         | 9        | 80             | 89        |
| Hypleurochilus geminatus | 199       | 65       | 24             | 288       |
| Hypsoblennius hentz | 0         | 6        | 0              | 6         |
| Hypsoblennius ionthas | 59        | 0        | 0              | 59        |
| Scartella cristata | 194       | 1867     | 2052           | 4113      |
| **TOTAL**        | 452       | 1947     | 2156           | 4555      |

Collections in Galveston consisted primarily of Hypleurochilus geminatus and Scartella cristata that were caught in statistically similar numbers ($p=0.519$) during the study. *Hypleurochilus geminatus’* CPUE ranged from 0 to 10.2 to produce an overall mean of 3.2±3.7. Monthly CPUE of this species peaked during early summer and again secondarily in August 2000 but declined through the fall and winter (Fig. 8). Overall mean CPUE of *S. cristata* was 3.6±3.3, with monthly catch rates ranging from 0 to 12.0. *Scartella cristata* CPUE peaked in mid to late summer and declined through January before increasing again by early spring (Fig. 8). *Hypsoblennius ionthas* also was captured at Galveston during spring and summer 2000, with CPUE peaking at 14.1 in May 2000 (Fig. 8). Thereafter, they were only encountered again in May 2001 in low numbers (0.4) to yield an overall mean CPUE of 1.3±3.5. Overall mean CPUE for all species at Galveston was 8.1±7.7.

Four blenny species, *Labrisomus nuchipinnis, Hypleurochilus geminatus, Hypsoblennius hentz,* and *Scartella cristata,* were captured at Port Aransas. For all species combined, overall mean CPUE was
Scartella cristata was the dominant blenny with CPUE ranging from 0.7 to 141.9 and an overall mean of 33.9±42.9. CPUE remained relatively high throughout the year but peaked in late summer.

Fig. 8. Blenny catch per unit effort (CPUE), salinity (ppt) and water temperature (C) at groins on the Galveston Island, TX beachfront during May 2000 through August 2001.

Fig. 10. Blenny catch per unit effort (CPUE), salinity (ppt) and water temperature (C) at the North Jetty on South Padre Island, TX during May 2000 through August 2001.
and declined quickly by mid winter (Fig. 9). Except for one *Hypleurochilus geminatus*, *S. cristata* was the only species captured on the Gulf side of the jetty (station 3) where its overall mean CPUE was 96.8±94.9. Although *S. cristata* also dominated blenny catches on the channel side of the jetty (station 2), its overall mean CPUE (10.8±9.9) was significantly lower (*p*<0.001) at station 2 than that of station 3.

*Hypleurochilus geminatus* had an overall mean CPUE of 1.2±1.1 and monthly means ranging from 0 to 3.8. Catches of *Hypleurochilus geminatus* peaked during late spring and summer (July in 2000; May in 2001) and declined until early spring (Fig. 9). Port Aransas was the northernmost capture site for *L. nuchipinnis* where it exhibited an overall mean CPUE of 0.2±0.4. Monthly mean CPUE ranged from 0 to 1.6, with catch following a temperature related pattern (Fig. 9). The six *Hypsohennius hentz* captured at Port Aransas in May 2000 (CPUE=0.78) were the only representatives encountered during this study.

Only *Labrisomus nuchipinnis*, *Hypleurochilus geminatus*, and *Scartella cristata* were captured at South Padre Island with an overall mean CPUE of 46.4±68.0. *Scartella cristata* was clearly the dominant blenny (Fig. 10), exhibiting an overall mean CPUE of 44.1±65.6 and monthly mean CPUE ranging from

![Graph showing catch per unit effort (CPUE), salinity (ppt) and temperature (C) at the South Jetty in Port Aransas, TX during May 2000 through August 2001. Hypsohennius hentz is not shown in this figure. It was captured in May 2000 with a CPUE of 0.78 individuals/hour.](image)
1.7 to 237.7. CPUE did not differ significantly (p=0.882) from Gulf side (station 4: 48.0±67.7) to the channel side (station 5: 53.5±82.4) of the jetty. It peaked in summer and early fall then declined during winter (Fig. 10). Labrisomus nuchipinnis’ monthly mean CPUE ranged from 0 to 6.0 with an overall mean CPUE of 1.7±1.9. No significant difference (p=0.69) was found between its overall mean CPUE on the Gulf side (1.1±2.3) and that on the channel side (1.9±1.8). CPUE for this species peaked in mid to late summer and declined through fall (Fig. 10). Hypleurochilus geminatus, caught at South Padre Island only in spring-early summer of 2001, exhibited a relatively low overall mean CPUE (0.7±2.0) with monthly catch rates ranging from 0 to 9.6.

Size Structure

Total length (TL) of Scartella cristata captured ranged from 8 to 115 mm with site means at Galveston, Port Aransas and South Padre Island being 51.9±22.3, 36.1±15.9, and 36.3±15.9 mm, respectively (Table 3, Fig. 11). Mean TL of S. cristata in Galveston was significantly larger than that from South Padre Island (p<0.001) despite the largest individuals being captured at South Padre (115 mm TL) and Port Aransas (p<0.001). This species’ mean TL increased through the winter but declined suddenly with the recruitment of young of year appearance of new recruits in early spring (Fig. 12). Nonetheless, individuals in the 0-10 and 11-20 mm size classes were captured less frequently at Galveston than at other sites (Appendix A).

<table>
<thead>
<tr>
<th>Species</th>
<th>Galveston</th>
<th>Port Aransas</th>
<th>South Padre Island</th>
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<tr>
<td></td>
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<td>mean TL (mm)</td>
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<td>Labrisomus nuchipinnis</td>
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<td>Hypsoblennius ionthas</td>
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<td>26.41</td>
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</tr>
<tr>
<td>Scartella cristata</td>
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<td>51.93</td>
<td>1867</td>
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</table>
Hypleurochilus geminatus ranged from 15 to 94 mm TL with the largest size classes (81-90 and 91-100 mm) collected only in Galveston (Appendix A). Overall mean TL for conspecifics from Galveston, Port Aransas, and South Padre Island was 37.49, 40.94, and 22.17 mm, respectively (Table 3, Fig. 13). Port Aransas yielded the largest individuals (Galveston: $t=-3.344$, $p=0.001$; South Padre Island: $t=6.880$, $p<0.001$). This species’ mean monthly TL generally increased through winter and declined as younger individuals recruited to the jetties in early spring (Fig. 12). An exception to this trend occurred at South Padre Island where $H.\ geminatus$ was encountered only in spring and early summer 2001 as small, immature (<40 mm TL) individuals.

Although Labrisomus nuchipinnis was only captured once in the samples from September to April, anglers consistently captured large individuals (>100 mm TL) at Port Aransas and South Padre Island throughout the study. Angler-caught conspecifics were not included in statistical analysis but these captures indicate $L.\ nuchipinnis$ was present on the middle and lower coast throughout the year.

$Labrisomus\ nuchipinnis$, ranging in size from 22 to 167 mm TL, displayed no significant size difference ($p=0.879$) between constituents taken at Port Aransas (59.00 mm) and South Padre Island (60.49 mm) (Table 3, Fig. 14). Monthly mean TL of $L.\ nuchipinnis$ remained relatively constant during this study.
(Fig. 12) as a result of no recruitment pulses. Individuals less than 40 mm TL were captured only during summer (Appendix A).

![Graph showing monthly mean total length (TL) and its standard error for five blenny species at Galveston (G), Port Aransas (PA) and South Padre Island (SPI), TX from May 2000 to August 2001.](image)

**Fig. 12.** Monthly mean total length (TL) and its standard error for five blenny species at Galveston (G), Port Aransas (PA) and South Padre Island (SPI), TX from May 2000 to August 2001.
Hypsooblennius hentz and Hypsoblennius ionthas did not exhibit seasonal size trends. Both species were captured across relatively narrow size ranges and at similar mean TL (H. hentz: 22-31 mm TL, mean=25.83 mm; H. ionthas: 12-50 mm TL, mean=26.41 mm) (Table 3, Fig. 12). Length frequency distributions indicated relatively strong recruitment of H. ionthas at Galveston in late spring of 2000, with those cohorts persisting through August and virtually absent thereafter (Fig. 12, Appendix A).

Fig. 13. Mean total length (TL) and its standard error for Hypleurochilus geminatus at Galveston, Port Aransas, and South Padre Island, TX from May 2000 to August 2001. n represents the number of individuals sampled from each location.
Species Diversity and Evenness

Monthly mean blenny diversity ($H'$) was 0.23±0.02, 0.11±0.11, and 0.09±0.08 for Galveston, Port Aransas, and South Padre Island, respectively (Fig. 15). Galveston had significantly higher diversity than did other sites ($p=0.001$). Monthly diversity never exceeded 0.4 at any site and was never greater than 0.22 at South Padre Island. Although highly variable, diversity generally peaked in late spring, declined through summer and fall, and increased by late winter. This pattern was best defined at Port Aransas (Fig. 16).

Evenness values of 0.64±0.37, 0.29±0.30, and 0.30±0.26 were observed for Galveston, Port Aransas, and South Padre Island respectively (Fig. 15). Galveston also exhibited a significantly higher evenness value ($p=0.001$) than did other sites. Evenness at Galveston remained fairly high throughout summer and fall (0.60-0.98), declined dramatically in winter and was relatively low (0.00-0.40) through spring. Evenness at Port Aransas mirrored species diversity by peaking in spring and diminishing through fall. The only pattern in species evenness at South Padre Island was values in 2000 were considerably higher than those in 2001 (Fig. 16).
Estimate of *Scartella cristata* Population Density

*Scartella cristata* was chosen for mark recapture studies because of its dominance and apparent high population density on Texas jetties. Three complete mark-recapture collections were performed at Port Aransas in June 2001 and were the basis for population estimates ranging from 158 to 281 individuals/linear meter of jetty. These estimates yielded an overall mean of 214 individuals/linear meter of jetty and standard error of 36. CPUE data generated at the same station concurrent to mark recapture experiments and converted to number of individuals per linear meter of jetty estimated mean density to be 11.2 with a standard error of 3.2—approximately 5.2% of the density estimated through mark-recapture trials.

Age Structure of *Scartella cristata* Along the Texas Coast

Microstructure analysis of otoliths indicated *Scartella cristata* ranged in age from 47 (12 mm TL) to 466 days (78 mm TL). Mean age-at-capture for Galveston, Port Aransas, and South Padre Island individuals was 213.0±114.1, 131.6±81.7, and 132.7±81.7 days, respectively. These means differed...
Figure 16. Monthly mean Shannon-Wiener diversity index ($H'$) and species evenness ($J'$) and their standard errors for blenny assemblages at Galveston (G), Port Aransas (PA) and South Padre Island (SPI), TX from May 2000 to August 2001.
Mean age of individuals from the middle and lower coast was statistically similar ($p=0.91$).

Hatch-date distributions were generated for the three sites using age-length keys. While *Scartella cristata* hatch throughout the year on the Texas coast, 48.2% of hatchings occurred between January and March with an additional 29.9% taking place in April and May (Fig. 17). The majority of individuals (67.5%) captured in Galveston hatched between January and May (Fig. 18) with activity peaking in January and March. Hatch-date distributions were more protracted in Port Aransas, lasting from January to early July and peaking between April and June (Fig. 19). South Padre Island was the site of year-round, low level hatching activity that peaked October to March (Fig. 20).

*Scartella cristata* grew at a rate of 0.25 ($r^2=0.69$), 0.26 ($r^2=0.51$), and 0.20 ($r^2=0.34$) mm/day at Galveston, Port Aransas, and South Padre Island, respectively (Fig. 21). Growth rate among sites was statistically similar ($p=0.252$) and yielded a composite value of 0.2 ($r^2=0.44$) mm/day.
Fig. 18. Hatch date distribution of *Scartella cristata* collected from Galveston, TX between May 2000 and August 2001. No estimates of mortality were incorporated into this dataset. Only individuals whose age was calculated at or less than 270 days were used to generate this distribution due to difficulty in reading daily growth increments beyond that age.
Fig. 19. Hatch date distribution of *Scartella cristata* collected from Port Aransas, TX between May 2000 and August 2001. No estimates of mortality were incorporated into this dataset. Only individuals whose age was calculated at or less than 270 days were used to generate this distribution due to difficulty in reading daily growth increments beyond that age.
Fig. 20. Hatch date distribution of *Scartella cristata* collected from South Padre Island, TX between July 2000 and August 2001. No estimates of mortality were incorporated into this dataset. Only individuals whose age was calculated at or less than 270 days were used to generate this distribution due to difficulty in reading daily growth increments beyond that age.
Genetic Structure and Origins of *Scartella cristata* on the Texas Coast

Comparison of mtDNA D-loop sequences performed for *Scartella cristata* revealed 30 aplotypes distinguished by 22 variable sites. Polymorphic sites corresponded to 11 transitions, 10 transversions, and a single nucleotide attributable to an insertion/deletion event. Sequences for each haplotype characterized appear in Appendix B. Haplotype diversity ($h$) within each sample was high, being 0.833, 0.805, 0.959, and 0.977 at Florida, Galveston, Port Aransas, and South Padre Island,

![Graph showing age-length relationship for *Scartella cristata* captured at Galveston, Port Aransas, and South Padre Island, TX jetties from May through September 2000. Individuals older than 270 days are excluded from this analysis due to difficulty in reading daily growth increments beyond that age.](image)

**Figure 21.** Age-length relationship for *Scartella cristata* captured at Galveston, Port Aransas, and South Padre Island, TX jetties from May through September 2000. Individuals older than 270 days are excluded from this analysis due to difficulty in reading daily growth increments beyond that age.

### Table 4. Sample size, haplotype diversity ($h$), and nucleotide diversity ($\pi$) for *Scartella cristata* from sample sites in the Gulf of Mexico.

<table>
<thead>
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<th>LOCATION</th>
<th>$n$</th>
<th>$h$</th>
<th>$\pi$</th>
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<td>South Padre Island</td>
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respectively (Table 4). Nucleotide diversity ($\pi$) varied from low levels in Florida (0.004) and Galveston (0.005) samples to more intermediate levels in those from Port Aransas (0.010) and South Padre Island (0.011) (Table 4). Most haplotypes represented in Florida and Galveston samples were shared between the two sites, whereas more than half of those found in Port Aransas and South Padre Island samples were unique to either site (Table 5). Only one haplotype (D) was shared across all four sites (Table 5). The Florida sample was dominated by one haplotype (B) accounting for 44% of its constituents. Three closely

<table>
<thead>
<tr>
<th>Haplotype</th>
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elated haplotypes (B, D, E) accounted for 80% of the individuals in the Galveston sample whereas no single haplotype was dominant at Port Aransas or South Padre Island (Table 5, Fig. 22, 23).

There was little genetic distance among samples (Fig. 24). Genetic distances ranged from 0.005 between Florida-Galveston to 0.011 between Galveston-Port Aransas and Port Aransas-South Padre Island (Table 6) and averaged 0.009 (S.E.=0.003). Mantel’s test generated a correlation coefficient of -0.217, to indicate no significant relationship ($p\geq0.658$) between genetic distance and geographic distance. AMOVA revealed that samples from Florida and Galveston were statistically similar ($p>0.58$) as were Port Aransas and South Padre Island ($p>0.23$). No such similarity ($p\leq0.01$) was found between Florida or Galveston samples and those of Port Aransas and South Padre Island (Table 6). While the majority of variance (80%) could be accounted for within samples, a significant portion (20%) was attributed to among group variance ($\Phi_{ST}$) corresponding to the differentiation between Florida-Galveston and Port Aransas-South Padre Island. The $\Phi_{ST}$ values, in ranging from –0.24 to 0.30, indicated low levels of population structure (Table 6). Number of migrants per generation ($N_m$) was high between Florida-Galveston ($\infty$) and Port Aransas-South Padre Island (55.6) but an order of magnitude lower among other site comparisons that ranged from 3.8 for Galveston-South Padre Island to 1.2 between Florida-Port Aransas (Table 6). This gene flow did not prevent Florida and Galveston samples from exhibiting a haplotype frequency distinct from those in south Texas (Fig. 22, 23).

Mismatch distributions for *Scartella cristata* sequences tended to visually resemble the Poisson distribution at all locations (Fig. 25) while chi-square analysis indicated significant differences from this expected distribution (Florida: $p=0.003$; Galveston: $p=0.007$; Port Aransas: $p=0.029$; South Padre Island: $p=0.018$). This suggests that the effective population size of *Scartella cristata* is at long-term equilibrium in the Gulf.

### Table 6. Genetic isolation of *Scartella cristata* at Gulf of Mexico study sites relative to geographic distance between sites.

Linear distances (km) between pairs of study sites, Tamura-Nei genetic distance ($d$), the among-group component of genetic variation ($\Phi_{ST}$), a statistical test based on haplotype frequency shifts and an estimate of gene flow in terms of the number of migrants per generation ($N_m$) are presented.

<table>
<thead>
<tr>
<th>LOCATIONS</th>
<th>DISTANCE (km)</th>
<th>$d$</th>
<th>$\Phi_{ST}$</th>
<th>EXACT TEST</th>
<th>$N_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Florida-Galveston</td>
<td>689</td>
<td>0.005</td>
<td>-0.24</td>
<td>($p&gt;0.58$)</td>
<td>8</td>
</tr>
<tr>
<td>Florida-Port Aransas</td>
<td>763</td>
<td>0.011</td>
<td>0.30</td>
<td>($p&lt;0.01$)</td>
<td>1.2</td>
</tr>
<tr>
<td>Florida-South Padre Island</td>
<td>948</td>
<td>0.010</td>
<td>0.17</td>
<td>($p&lt;0.01$)</td>
<td>2.4</td>
</tr>
<tr>
<td>Galveston-Port Aransas</td>
<td>272</td>
<td>0.010</td>
<td>0.24</td>
<td>($p&lt;0.01$)</td>
<td>1.6</td>
</tr>
<tr>
<td>Galveston-South Padre Island</td>
<td>416</td>
<td>0.009</td>
<td>0.12</td>
<td>($p&lt;0.01$)</td>
<td>3.8</td>
</tr>
<tr>
<td>Port Aransas-South Padre Island</td>
<td>196</td>
<td>0.011</td>
<td>0.09</td>
<td>($p&gt;0.23$)</td>
<td>55.6</td>
</tr>
</tbody>
</table>
Fig. 22. Composite haplotype distribution of mtDNA D-loop sequences of Scartella cristata from Florida, Galveston, Port Aransas and South Padre Island, TX. Diameter of each circle represents frequency of occurrence of that haplotype within a site. The division of each circle represents percent of individuals from a particular site exhibiting that haplotype. Empty circles represent hypothesized intermediates. Alternative linkages are represented by dotted lines.
Fig. 23. Haplotype distributions of mtDNA D-loop sequences of *Scartella cristata* from Florida, Galveston, Port Aransas and South Padre Island, TX. Empty circles represent hypothesized intermediates. Alternative linkages are represented as dotted lines.
Fig. 24. Genetic distances between *Scartella cristata* from Florida, Galveston, Port Aransas, and South Padre Island, TX.
DISCUSSION AND CONCLUSION

Structure and Composition of Blenny Assemblages on Texas Jetties

Variability in Species Composition

The data suggests that blenny assemblages are different in species composition, diversity and evenness among the locations sampled. Assemblages on the upper Texas coast at Galveston were dominated to similar extents by *Hypleurochilus geminatus* and *Scartella cristata*. *Hypsoblennius ionthas* also occurred sporadically on these jetties. Four blenny species were captured on jetties from the middle Texas coast at Port Aransas. *Scartella cristata* was the dominant species, but *H. geminatus* and *Labrisomus nuchipinnis* were taken regularly. *Hypsoblennius hentz* was a fourth but rare inhabitant of jetties in this area. Differences between Port Aransas stations 2 and 3 suggest that these sites may not encompass the range of variability blenny assemblages encounter on a jetty. Despite exhibiting similar
diversity and evenness values, Port Aransas and lower Texas coast at South Padre Island yielded blenny assemblages with distinct species composition. The blenny assemblages at South Padre Island were dominated by *S. cristata*. *Labrisomus nuchipinnis* occurred with greater frequency here than on the middle Texas coast. *Hypeurochilus geminatus* was rarely encountered and only as small individuals (<40 mm TL) thus suggesting its recruitment to lower coast jetties is infrequent and short-term. With the exception of *Hypsoblennius ionthas* in Galveston, *Hypsoblennius hentz* in Port Aransas, and *Hypeurochilus geminatus* at South Padre Island, species composition was predictable and relatively stable at a given location.

Blenny assemblages on Texas jetties also demonstrated temporal variability. Blenny species underwent seasonal shifts in relative abundance at all three study areas. Although numerous factors could account for this variability, the ultimate cause is likely seasonal temperature fluctuations and differential thermal preferences or tolerances of constituent species. Thermal preferences/tolerances have been demonstrated to be important in the determining the composition and structure of fish communities in intertidal habitats (Zander et al. 1999, Davis 2000, Faria and Almada 2001). For example, CPUE of *Scartella cristata*, typically considered a tropical/subtropical species (Hoese and Moore 1998), peaked in early to mid summer while the maximum CPUE of a more temperate counterpart, *Hypleurochilus geminatus*, occurred in mid to late spring. Spring and summer peaks of *H. geminatus* and *S. cristata* respectively, exhibited higher CPUE than did other seasons due to influx of new recruits to Texas jetties as illustrated by both hatch-date analysis and length-frequency data. This pattern suggests a stable adult component of blenny assemblages with observed variability due to the timing of spawning and subsequent recruitment, which is often linked to temperature (Clarke 1979, Faria and Almada 1999). Faria and Almada (1999, 2001) in Portugal and Davis (2000) in California found that relative abundance of similar species in rocky intertidal fish assemblages was closely tied to temperature.

The majority of individuals captured during these peaks in CPUE were small, new recruits while the relative numbers of adults remained constant, this pattern has also been described in *Hypsoblennius ionthas* populations in Mobile Bay (Clarke 1979). Many rocky shore fishes exhibit little relationship between the variability of their recruitment pulses and adult population size, despite significant mortality.

Blenny catches on Texas jetties tended to vary with changes in water temperature; however, selectivity of sampling gear and blenny behavior during winter months may have accounted for temporal variability in CPUE. For example, blenny CPUE declined during winter 2000-01 from higher fall and spring levels at all three sites. It is likely that winter conditions (*i.e.* cold temperatures and rough surf) result in blenny mortality (Santos and Nash 1996) thereby impacting CPUE; however, blennies also probably have behavioral responses to low temperatures (Murdy *et al.* 1997). Responses such as reduced activity levels or moving to deeper, more thermally stable water, a pattern seen in many fish (Neill 1979), may coincidentally enhance gear avoidance. Higher CPUEs in 2001 than in 2000 may have resulted from increased proficiency and experience with collection techniques. For example, CPUE at South Padre Island increased dramatically in May 2001 due to the discovery of large numbers of blennies in the supralittoral fringe. Previous collections had not sampled this area because it was not expected that blennies would be out of the water.

Salinity and turbidity did not seem to influence monthly blenny CPUE. Blenny CPUE during low beachfront salinities (15‰) at Galveston following Tropical Storm Alison in June 2001 was not lower compared to June 2000. Low turbidity was anticipated to enhance gear avoidance at Port Aransas and South Padre Island; however, no discernable effect was noted. CPUE on the middle and lower coast was consistently higher than in more turbid waters on the upper coast.

Results of the present study appear to indicate that blenny assemblages on the Texas coast could be divided into three distinct groups based on regional species composition, species diversity, and evenness with these distinctions being driven primarily by temperature. However, expansion of this study to other jetty systems in Texas would enable a better assessment of the distinctiveness of blenny
assemblages and their habitat requirements across the upper, middle and lower Texas coast and to what degree Galveston, Port Aransas, and South Padre Island are representative of these features. Expansion to cover a greater amount of potential blenny habitat would allow assessment of how effective stations used in the present study represent Texas’ jetty system as a whole.

Size Structure

Total length of *Scartella cristata* and *Hypleurochilus geminatus* was significantly higher on jetties on the upper and middle Texas coast than on those of the lower coast. Mean total length was highest at Port Aransas in the case of *H. geminatus* and at Galveston for *S. cristata*. There are several possible explanations for this pattern in *S. cristata*. The total $n$ for the Galveston collections was an order of magnitude lower than that of the other two sites; therefore, any bias toward larger individuals would have a greater impact on the mean. It is also possible density-dependent effects, such as competition for food or shelter, might be operating at a reduced level, thus allowing *S. cristata* to reach a larger size at Galveston because the density was lower than that at the other two sites. The amount of shelter available to smaller individuals may be limiting and thereby favor larger individuals because the structural complexity of the habitat at Galveston was less than that at the other sites. Shelter availability and size was found to be a determining factor in the size structure of blenny populations in rocky littoral zones of the western Mediterranean (Patzner 1999), the rocky intertidal zone of California (Stephens *et al.* 1970), and on oyster reefs along the east coast of the United States (Swearer and Phillips and Swears 1979, Crabtree and Middaugh 1982). The precise role of rugosity on the composition and structure of blenny assemblages is not conclusive. The location with the lowest structural complexity, Galveston, exhibited the highest species diversity, evenness, and mean TL. There also is the possibility that large *S. cristata* were present at Port Aransas and South Padre Island but were concentrated in deeper reaches of the jetty not sampled during this study.

Stability of Blenny Assemblages

How stable is the structure and composition of blenny assemblages on Texas jetties? The only other studies that documented blenny assemblages on jetties focused on newly constructed jetties in the Florida panhandle (Hastings 1979) and South Carolina (Van Dolah *et al.* 1984, 1987) Blenny assemblages
on these jetties exhibited a fair degree of stability. *Hypleurochilus geminatus* was the first blenny to recruit to both locales and although other species (*Hypsoblennius* spp.) eventually arrived during these studies, *H. geminatus* never relinquished dominance (Hastings 1979, Van Dolah *et al.* 1984, 1987). While this study is consistent with the findings of Hastings (1979) and Van Dolah *et al.* (1984, 1987) indicating that blenny assemblages are relatively stable, long-term surveys of a larger percentage of Texas jetties with an ecosystem focus should be undertaken. Of particular importance would be establishing sampling stations across the entire reach and depth of the jetty habitat and incorporating complete faunal and floral surveys of these habitats. The blenny species on Texas jetties may be a series of metapopulations undergoing local extinctions and re-colonizations on a regular basis and acting as sources or sinks for each other (Pulliam 1988). The sampling design of this study left large expanses of the jetty uncharacterized (deep water, end of the jetty, intermediate stations) from which to resolve uncertainties regarding temporal and spatial variability. The present study made no attempt to characterize other biotic components of the jetty community. Future studies need to characterize changes in the fauna and flora of Texas jetties. Population dynamics of organisms such as epilithic algae and invertebrates upon which blennies depend for food and shelter or potential predators such as birds and larger fishes could impact the composition of blenny assemblages on Texas jetties. Kevern *et al.* (1985) reported an “explosive” colonization of sculpins on a newly constructed artificial reef in Lake Michigan that eventually declined due to shifts in the population structure of predators that fed on sculpins. Concurrent shifts in the size structure of local sculpin populations were also observed (Kevern *et al.* 1985). Little is known about predators and prey of blennies and thus changes in their populations may precipitate major shifts in blenny assemblage structure without apparent cause.

Differences in CPUE, species composition, size structure, diversity, and evenness may be due to this study’s experimental design. Due to safety concerns, sampling frequently was not conducted evenly between stations at study sites on a monthly basis. The significant difference in CPUE and species composition between stations 2 and 3 at Port Aransas is also problematic, indicating potential differences between microhabitats and suggesting that sampling was not representative of the entire jetty. As previously mentioned, increasing the number of stations at a study site to include areas not covered in this
study as well as increasing the number of study sites would alleviate many of these problems. It would also be desirable to establish paired stations (i.e. on the north and south jetty at each site) enabling better replication of sampling effort.

**Age and Growth of *Scartella cristata* on Texas Jetties**

*Age and Growth*

*Scartella cristata* appears to be a fast growing, short-lived resident on Texas jetties. It was found to grow at 0.2 mm/day, live about 1.5 years, and spawn from January to June. While no previous work has been published on age and growth of *S. cristata*, Eyeberg (1984) found similar results in a South African congener, *Scartella emarginata*. The latter grows quickly, up to 0.26 mm/day under laboratory conditions, reaches sexual maturity at 36 mm total length, rarely lives past 2 years, and spawns year round (Eyeberg 1984). This pattern is seen in small, short-lived reef fishes such as gobies (Kritzer 2002); however, whether it holds true for all subtropical/tropical blenniids or only for the Genus *Scartella* is unclear. Nonetheless, temperate blennies exhibit a life history pattern almost completely opposite that of *Scartella*. *Hypsoblennius* species along the California coast are long-lived (7+ years) and grow quickly (0.12 mm/day) for their first year prior to slowing (0.03 mm/day) considerably (Stephens *et al.* 1970). *Blennius gattorugine* and *Blennius pholis* live up to 9 years in Ireland, grow quickly (no rate reported) for the first 2 years, then slow considerably (Dunne and Byrne 1979). These temperate species also spawned within discrete seasons, usually spring through early summer (Stephens *et al.* 1970, Dunne and Byrne 1979). Estuarine species of blennies also appear to exhibit a different life history pattern. *Hypsoblennius hentz* was found to grow at over double the rate (0.5 mm/day) of *Scartella* in estuaries of the mid-Atlantic Bight (Able and Fahay 1998). This may be due to estuarine species of *Hypsoblennius* being longer-lived and slower to mature (Clarke 1979) than *Scartella*, thus allowing them to dedicate more energy toward somatic growth.

Growth rates of *Scartella cristata* appear consistent with those of *S. emarginata*, the only published value for *Scartella*; however, estimated size-at-hatching is somewhat problematic because at 10.42 mm it greatly exceeds published accounts of hatch sizes for Blenniidae; *Chasmodes bosquianus*=3.56-3.78 mm (Fritzsche 1978), *Hypsoblennius hentz*=2.6-2.8 (Fritzsche 1978),
Hypsoblennius ionthas = 2.82 mm (Clarke 1979), Ophioblennius atlanticus = 1.3-1.5 mm (Labell and Nursall 1985), Scartella emarginata = 3.5 mm (Eyeberg 1984). However, published estimates of size-at-hatching were all acquired by direct observation while current estimates for S. cristata were inferred from the regression model. This difference illustrates one limitation in using size-at-age relationships to estimate hatch size. In addition, y-intercept estimates in this study are misleading due to the lack of small specimens examined.

Patterns of Dominance

Four blenniid species—Hypleurochilus geminatus, Hypsoblennius hentz, Hypsoblennius ionthas, and Scartella cristata—potentially recruit to Texas jetties but their coexistence at any given time is rare. Post-recruitment resource partitioning on both large and small temporal and spatial scales allows blenniid to coexist and leads to assemblage stability (Stephens et al. 1970, Clarke 1989). Differences in interspecific dietary preferences (Eyeberg 1984, O’Farrel and Fives 1990), dietary preferences between sexes or age classes within a species (Clarke 1979, Osenberg et al. 1992, Goncalves and Almada 1997), metabolic rates (Clarke 1992), or feeding morphology (Lindquist and Dillman 1986) may be significant factors isolating species into niches and thereby determining the composition of blenny assemblages. Shelter availability (Stephens et al. 1970, Phillips and Swears 1979, Crabtree and Middaugh 1982), territoriality (Stephens et al. 1970, Goncalves and Almada 1998, Wilson 2000), water temperature preferences (Zander et al. 1999), and recruitment patterns are other influences on assemblage structure. These interspecific and intraspecific interactions plus those between individuals and their habitats are key to predicting changes in population structure (Jones 1991). Because these blenniid species share similar habitat requirements and differ only slightly in dietary requirements (Lindquist and Dillaman 1986), it is much more common for assemblages to be dominated by one or two species.

Scartella cristata is the dominant blenniid species on the Texas jetties sampled during this study regardless of local conditions. This is contrary to previous accounts by Hoese and Moore (1998) who assigned dominant status to Hypleurochilus geminatus. These previous accounts may have been based upon incomplete or inaccurate data, as there is little published literature describing ichthyofauna of Texas jetties. However, it is possible blenny assemblages have undergone major shifts in species composition as
the biotic community continues to evolve on Texas jetties. Other studies on Florida and South Carolina jetties have noted dominance of *H. geminatus* (Hastings 1979, Van Dolah 1984, 1987), but may not have been sufficient in duration to observe the colonization of *S. cristata*. The latter species appears to be tolerant of the entire spectrum of environmental conditions (temperature, salinity, turbidity, and habitat complexity) along the Texas coast. A lack of more detailed information on the biology of other constituent species for comparison, particularly *H. geminatus*, makes it difficult to explain why *S. cristata* is so successful on Texas jetties.

*Scartella cristata*’s total dominance of other blenniids through competitive exclusion may be possible only under the environmental conditions and habitat quality of the central and lower Texas coast. Woodland (1999) found this type of exclusion and dominance based on differences in local condition demonstrated by the Family Signidae, a family of herbivorous reef fishes in the western Pacific. Conversely, the more temperate species such as *Hypeurochilus geminatus* may not compete as well as *Scartella cristata* in the more subtropical waters of the central and lower Texas coast. Clarke (1989, 1992) found that the higher metabolic rate of *Acanthemblemaria spinosa*, a tube dwelling chaenopsid blenny, allowed it to displace a congener, *Acanthemblemaria aspera*, from preferred, higher quality habitat and facilitating a higher growth rate in *A. spinosa*. A more tropical species, such as *S. cristata*, may have a higher metabolic rate giving it an advantage in agonistic interactions as seen in *A. spinosa* (Clarke 1992).

Differential growth rates between species may be an important underlying explanation for why certain species dominate (Jones 1991) or a result of competitive interactions between species (Clarke 1992). With growth, fishes typically decrease their vulnerability to predation, increase their fecundity, and, in territorial species such as blennies, increase the size of territory they can or need to defend (Stephens *et al.* 1970, Phillips and Swears 1979, Jones 1991, Goncalves and Almada 1998). A blenniid species reaching a large size quicker than a competing species has the edge in not only holding more territory, but also producing more offspring. Consequently, a faster growing species has the potential to exclude a slower growing species from a given area over time. Further work with additional blenniid species, particularly *Hypeurochilus geminatus*, will determine if this is the case on Texas jetties.

**The Genetic Structure of *Scartella cristata* on Texas Jetties**
*Scartella cristata* is a wide-ranging species occurring on nearshore reefs and rocky shores throughout the tropical Atlantic, Caribbean, Gulf of Mexico, and Mediterranean. The Texas Gulf coast likely represented a gap in the distribution of this species due to a lack of suitable habitat. With initiation of jetty construction in Texas during the 1880’s, *S. cristata* larvae that historically would pass the Texas coast found new habitat to colonize in state waters. The genetic structure of local populations on Texas jetties reflects the history of this colonization. Haplotype diversity (*h*) of *S. cristata* across Florida, Galveston, Port Aransas, and South Padre Island was high; however, nucleotide diversity (*π*) was low to moderate. While these results indicate a large number of different haplotypes exist in the *S. cristata* population, low nucleotide diversity suggests they are closely related and effective population size is relatively small. This relationship between *h* and *π* is consistent with findings by Muss *et al.* (2001) for another wide ranging blenniid, *Ophioblennius atlanticus*, and appears to be a common theme among many marine fishes (Palumbi 1994, Grant and Bowen 1998).

Both haplotype and nucleotide diversity were greater for conspecifics from the middle and lower Texas coast than that for their upper coast and Florida cohorts. This suggests that the source population of *Scartella cristata* for Port Aransas and South Padre Island is more diverse and possibly older or larger than that for Galveston and Florida. Whether or not Florida is the source population for Galveston cannot be answered definitively based on the limited number of sample sites and small number of individuals from the former. It is clear that if Florida is not the source population for Galveston then the two share the same origins. Similarities in haplotype distribution and among group component of variation (*Φ*<sub>ST</sub>), low genetic distances between sites (0.005), and high level of gene flow per generation link the two sites despite the large geographic distance (689 km) and the Mississippi River plume that separates them. This linkage is accomplished through predominant nearshore currents in the Gulf, which would tend to carry larvae from east to west throughout the year (Fig. 26).

Transport of *Scartella cristata* larvae to Texas jetties from either Mexico or Florida is plausible. Although not known for *S. cristata*, the larval duration of *Hypsoblennius ionthas* lasts from 6 to 8 weeks (Clarke 1979). Longshore currents along the Texas coast range in velocity from 12 (Fox and Davis 1976) to 21.5 cm/s (Smith 1975) under typical conditions, while larvae entrained in a boundary current such as
the Mexican Current can be carried at 70-100 cm/s (Sturges and Blaha 1976). These features put Texas jetties within reach of larvae traveling from the eastern or southern Gulf or Mexico even if larval duration is only 30 days. A small amount of one-way gene flow (N_m<4.0) from Galveston-Florida to Port Aransas and South Padre Island may facilitated by prevailing currents (Fig. 26), but this does not appear to be the primary source of *S. cristata* to these southerly sites. Current flow in the Gulf and on the Texas-Louisiana shelf suggests the hard shores and nearshore reefs of southern Gulf or western Caribbean as a primary

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**Fig. 26. Direction of current flow in the Gulf of Mexico (a,c) and on the Texas-Louisiana shelf (b, d) during non summer (a, b) and summer months (c, d).** Black and white triangles represent northerly and southerly flow, respectively, in b and d. Black circles represent sample sites. Gulf of Mexico currents adapted from Britton and Morton (1989) and Texas-Louisiana shelf currents from Cho et al (1998).
source for Port Aransas and South Padre Island (Fig. 26) due to the northerly current flow during summer
middle and lower coast have similar haplotype distribution, no difference in the among group component
of variation (\( \Phi_{ST} \)), and exchange a large number of migrants per generation (\( N_m=55.6 \)). These similarities
suggest they share the same source population(s); however, the two sites are separated by a genetic
distance (0.011) comparable to that of most other sites (Table 6). Since mismatch distributions indicate
Port Aransas and South Padre Island samples were large enough to encompass the variability at each
locality, it seems these sites may be in the process of evolving distinct subpopulations. Overall, this study
indicates that \( S. cristata \) on Texas jetties are not yet isolated from their possible sources but are extensions
of them. This is contrary to work on red drum (\( Sciaenops ocellatus \)) and red snapper (\( Lutjanus
campechanus \)) that indicates a single population of each species within the Gulf (Gold et al. 1999, Heist
and Gold 2000, Gold et al. 2001). Comparisons of these species with \( Scartella cristata \) should be made
cautiously as both red drum and red snapper have greater potential for mixing/migrating and a greater
abundance of suitable habitat throughout the Gulf.

Even though larval blennies have high dispersal potential (Hunte and Côté 1989, Riginos 2000,
Riginos and Nachman 2001), spatial and temporal heterogeneity of coastal habitats and nearshore Gulf
waters may act to partially isolate \( Scartella cristata \) on Texas jetties both from each other and their source
populations. Palumbi (1994) predicts that larvae of marine organisms probably do not “see” the marine
environment as a homogenous habitat. The traditional interpretation is that this results in development of
genetically structured populations in areas that do not appear isolated from one another (Palumbi 1994,
Debenham et al. 2000). This does not explain low levels of genetic variation found in \( Ophioblennius \)
populations throughout the Atlantic basin (Muss et al. 2001) or in intertidal sculpins on the Pacific coast of
North America (Yoshiyama and Sassaman 1993). Both of these groups inhabit areas exhibiting spatial
and temporal heterogeneity. Studies examining population genetics of \( Ophioblennius atlanticus \) have
found that a gap in a species’ range due to lack of habitat is not sufficient to form distinct populations;
whereas, a similar gap with a barrier such as a large river is (Muss et al. 2001). A similar phenomenon
was observed in the blenny, \( Axoclinus nigriceps \), which exhibits distinct populations separated by less
than 200-km of unsuitable habitat in the Gulf of California (Riginos and Nachman 2001). The Texas coast prior to jetty construction represented such a gap between *S. cristata* populations in the eastern Gulf of Mexico and the southern Gulf/western Caribbean. This gap was a result of the mud and sand shores of Louisiana, Texas, and northeastern Mexico and the Mississippi River plume. Establishment of suitable habitat in the form of jetties and groins along the Texas coast seems to have removed any barriers to the exchange of individuals between the eastern and western Gulf and raises questions regarding the role of the Mississippi River in separating populations.

The Mississippi River plume may never have been a barrier to blenniid larval dispersal. Govoni (1993) found that larval fishes were able to cross frontal boundaries such as the Mississippi River plume; a finding supported by high levels of gene flow observed in this study between Florida and Galveston. Larvae of many reef fish species, including blenniids, typically have a much broader geographical range than do their adult counterparts (Leis 1991), which suggests the availability of suitable adult habitat plays a major role in the genetic structure of these species. This appears to have been the case in *Scartella cristata*. At least two distinct populations of *S. cristata* exist in the Gulf that were kept separate more by the lack of suitable habitat in the northwestern Gulf and prevailing currents than by the Mississippi River plume. Distribution of larvae from these populations may have overlapped along the Texas coast, but a lack of suitable habitat prevented their interbreeding. It is unclear what impact jetty construction on the Texas coast will have on the genetic structure of *S. cristata*. Jetties have facilitated these populations mixing to a degree but current patterns appear to be an isolating mechanism by preventing homogenization as evidenced by the distinction between Galveston and Port Aransas-South Padre Island. Further testing of this hypothesis should be undertaken by examining recruits from multiple spawning events throughout the year. As indicated through hatch-date analysis, *S. cristata* has the potential to spawn throughout the year; however, the individuals selected for this analysis were all within the winter 1999-2000 cohort. This means sites such as Port Aransas have the potential to undergo shifts in genetic composition with seasonal changes in current patterns. The mismatch distributions tend to suggest otherwise, but these data may be representative of the larger source populations and not reflect the full diversity that potentially occur in local populations.
The subpopulations *Scartella cristata* on Texas jetties also need to be examined as metapopulations. Blenny assemblages on Texas jetties could be sinks for their respective source populations as described in terrestrial systems by Pulliam (1988) or they may interact together as their own metapopulation in which an upstream jetty acts a source for a downstream sink and so on along the coast. The data suggest this is not the case. Mismatch distributions indicate that *S. cristata* populations in the Gulf have been stable for some time. This is opposite the pattern expected in populations structured as metapopulations. The same holds true if *S. cristata* was recruiting to jetties from estuarine oyster reefs. Even though it is known to occur on oyster reefs (Britton and Morton 1989, Hoese and Moore 1998), *S. cristata* does not appear to be a dominant species in estuarine habitats (*personal observation*). Jetty populations established from estuarine sources would be expected to exhibit a mismatch distribution indicating exponential population growth. Data on possible interactions between jetty subpopulations and their source population(s) are critical to understanding the population dynamics of blenny assemblages on Texas jetties.

The genetic structure of *Scartella cristata* also has the potential to reveal historical patterns of distribution of nearshore fishes in the Gulf of Mexico. There is a great deal of significance to the large number of haplotypes present at Port Aransas and South Padre Island relative to that at Galveston and Florida, as it is probably a result of the impact of Pleistocene glaciations. Prior to the last glaciation, Florida was flooded allowing the movement of fishes out of the Gulf to the Atlantic coast (Briggs 1974), but potentially reducing the amount of rocky shore habitat on the Florida peninsula. The Wisconsin glacial period dropped sea level and temperature and probably forced the range of *S. cristata* south. The rise in temperature and sea level associated with the end of the Wisconsin glaciation enabled *S. cristata* to re-colonize this habitat, thus creating a founder effect (Strickberger 1996) that reduced genetic diversity of individuals living in the eastern Gulf and subsequently the upper Texas coast. *S. cristata* populations along the Mexican coast and throughout the Caribbean probably did not experience a dramatic impact from glaciation, and were able to maintain higher genetic diversity. While this scenario is supported by differences in haplotype diversity between locations, the disparity between the mismatch and Poisson distribution suggests that *S. cristata*’s effective population sizes have been stable for an extended period of
time. A similar pattern has been observed in demographically distinct local populations of the parrotfish *Chlorurus sordidus* from widespread locations on Australia’s Great Barrier Reef (Dudgeon *et al.* 2000). Analysis of blennies from a larger number of sample sites will be needed to fully explore the plausibility of this scenario.

**Biogeography of Blennies on Texas Jetties**

A transition in the species composition of blenny assemblages appears to occur on the middle Texas coast. This area may represent a biogeographic break for several blenny species due to current patterns and environmental tolerances of these taxa. The Texas coast receives a convergence of northward and southward flowing longshore currents (Fig. 25). The exact location of this convergence varies by season; it is located near Matagorda Bay in summer and near the mouth of the Rio Grande throughout the rest of the year (Cochrane and Kelly 1986, Britton and Morton 1989, Cho *et al.* 1998). The Texas coast also provides transition between subtropical and temperate climatic regimes (Britton and Morton 1989).

Two species, *Labrisomus nuchipinnis* and *Hypleurochilus geminatus*, appear to reach the limits of their distribution on the Texas coast near Port Aransas. Failure to encounter *L. nuchipinnis* north of Port Aransas conforms to previous descriptions (Springer 1958, Hoese and Moore 1998) of this tropical-subtropical species’ range. *H. geminatus*, a more temperate species (Hoese and Moore 1998), was rarely encountered south of Port Aransas. These distributional patterns may be indicative of these species’ environmental tolerances and/or probable sources of initial recruits to Texas jetties. Even though *L. nuchipinnis* occur on hard shores of the eastern Gulf, they are more typically associated with warmer waters of the Caribbean and southern Atlantic (Hoese and Moore 1998). Their observed distribution on Texas jetties suggests that the original source population(s) is located in the southern Gulf or Caribbean. Whether environmental conditions are favorable to this species’ colonization north of Port Aransas may be irrelevant if prevailing current patterns prevent transport of their larvae. *H. geminatus* is common along the southeastern U.S. coast (Lindquist and Chandler 1978, Hoese and Moore 1998) and is a frequent inhabitant of Florida jetties (Hastings 1979). Based upon its distribution on Texas jetties, the most probable source population for *H. geminatus* would be from the eastern Gulf of Mexico. If *H. geminatus* recruits to Texas jetties originated in the southern Gulf or Caribbean then South Padre Island should host a
more robust population. The catch of small individuals at South Padre only during the late spring and early summer suggests these individuals were transported from the eastern Gulf before current flow shifted for the summer.

The distribution pattern observed for two *Hypsoblennius* species found on Texas jetties does not appear to be impacted by a biogeographical break. *Hypsoblennius hentz* and *H. ionthas* are commonly found on estuarine oyster reefs (Hubbs 1939, Clarke 1979, Smith-Vaniz 1980, Hoese and Moore 1998) and usually are not common on Texas jetties except for newly settled individuals in the late spring/early summer. This distributional pattern leads to the conclusion these species probably colonized jetties from bays. It is difficult to explain why *H. ionthas* was virtually absent from Galveston collections in 2001 after being relatively common during spring and early summer 2000. It is possible that some environmental condition favored a large-scale export of larvae from the bay to groins on the beachfront. Few, if any, of these individuals were able to reach maturity in the Gulf as evidenced by there being no individuals >40 mm TL. Conditions that favored larval transport in 2000 may not have occurred in 2001. It also is possible that the scenario represented by 2000 is typical for *H. ionthas* on the upper coast and 2001 represents an aberration. Additional surveys of both beachfront groins and estuarine oyster reefs would clarify the status of *Hypsoblennius* species on Texas jetties.

*Scartella cristata* may play a unique role in determining the composition of blenny assemblages on Texas jetties. Even though *S. cristata* was found at each study site, there was a difference in the abundance and dominance corresponding to the biogeographical break described above. *S. cristata* on the Texas coast originated from at least two different source populations, the eastern Gulf and another source likely the southern Gulf and/or western Caribbean. There also appears to be differential recruitment from these sources. The lower and middle coast receives a large influx of recruits during the summer and lesser numbers throughout the year at South Padre Island (Appendix A). Recruitment pulses in Galveston do not seem to be as strong (Appendix A). This could be the underlying reason for lower densities seen on the upper coast. The difference in population density of *S. cristata* may impact the other blenniid populations through both direct and indirect competitive interactions. More information describing the nature of
interactions between constituent species of blenny assemblages on Texas jetties is needed to evaluate this hypothesis.

**Blennies and Fisheries Management**

No only do blennies serve as excellent models for testing theories of ecology, biogeography, and population genetics but they may also be useful to fisheries biologists. Pressures placed on fisheries resources by human populations have increased dramatically during the past century, resulting in the eventual collapse of various “inexhaustible” stocks. Resource managers around the world are scrambling to maintain sustainable fisheries and still meet the needs of burgeoning populations that utilize them. The tragedy of the commons as described by Hardin (1969), in which individuals or nations use a common resource to its exhaustion for their own gain because the costs are shared by all, is a specter that has not been eliminated at the dawn of the 21st Century. It has become more prevalent then ever as more participants compete for dwindling fishery resources. The biggest challenge facing resource managers and society over the next 100 years will be balancing needs of human populations and those of not only fishes, but also the marine environment as a whole.

Artificial reefs are one of many management tools used along the Texas coast to conserve fish stocks under pressure from the competing interests of commercial and recreational fishermen. Humans have used artificial reefs for hundreds of years to increase their catch (Mottet 1985, Stone 1985). The ability of some organisms to recruit to and establish populations on artificial substrates has been well documented. Passage of the Artificial Reef Act by the Texas State Legislature in 1989 required the Texas Parks and Wildlife Department (TPWD) to deploy, monitor, and manage artificial reefs in state waters (Stephan et al. 1990). Although TPWD’s artificial reef plan recognizes jetties, groins, and other similar structures as artificial reef habitat (Stephan et al. 1990), the plan’s primary reliance on decommissioned petroleum production platforms as artificial reefs has negated the development of monitoring or management programs for other substrates including jetties. This may change in light of recent findings that rock jetties serve as a nursery habitat for structurally dependent, economically important fishes such as lutjanids and sparids in the absence of other suitable substrate (Hernandez et al. 2001).
The last comprehensive survey in the northwest Gulf of finfish landings from jetties, groins, and piers was conducted in 1973. It indicated that 288,000 recreational anglers from the Mississippi River delta to Brownsville captured 15 million kg of fish in 1970 from jetties, piers, and bridges on both the Gulf and the bays (Deuel 1973). For the small amount of area represented by jetties on the shores of the northwest Gulf, this seems to be a disproportionately large number of anglers. It appears that jetties not only attract and concentrate fishes but anglers as well. TPWD surveys indicate that spotted seatrout, *Cynoscion nebulosus*; red drum, *Sciaenops ocellatus*; black drum, *Pogonias cromis*; southern flounder, *Paralichthys lethostigma*; sheepshead, *Archosargus probatocephalus*; Atlantic croaker, *Micropogonias undulatus*; sand seatrout, *Cynoscion arenarius*; and gafftopsail catfish, *Bagre marinus*, constitute the majority of fishes caught off Gulf jetties and piers (McEachron 1980). Though these fishes are not taken in sufficient numbers off jetties and piers to significantly impact their populations (McEachron 1980), no recent studies examine the role jetties play in enhancing shore-based fisheries for these species.

The evaluation of jetties or any other artificial reef’s enhancement of fish populations is a significant issue in its use as a fisheries management tool. Although there is little consensus whether artificial reefs enhance fisheries or merely concentrate existing fishes, recent research suggests that location plays a major role in how the reef impacts fish populations. Deployment of artificial reefs adjacent to abundant, natural rocky substrate attracts fishes from natural habitats; whereas, those placed in areas without natural structure, such as the Texas coast, probably enhances fisheries (Grossman *et al.* 1997, Bortone 1998, Shipp 1999). One key in addressing the aggregation-enhancement issue and evaluating performance of artificial reefs will be to determine how closely they function ecologically in comparison to natural counterparts. This necessitates that resource managers change their focus, as the community structure of non-game fishes likely provides a better assessment of the functional equivalency of artificial habitats than does that of game fishes (Topolski and Szédlmayer 2000). Blennies have potential to be excellent indicators to measure the functional equivalency of artificial habitats, such as jetties and petroleum production platforms, to their natural counterparts (Topolski and Szédlmayer 2000) due to their sedentary nature, relative ease of capture, great abundance, and hardiness. In many regards, blennies are the ideal measure for functional equivalency in these habitats because they are sensitive to
changes in the composition of the fouling community (Topolski and Szedlmayer 2000). The structure of blenny assemblages also may indicate the development an artificial habitat functionally equivalent to a natural one (Topolski and Szedlmayer 2000).

Blennies also may serve as important indicators of environmental quality due to their habit of establishing populations in close proximity to human impacts on the marine environment. Viviparous blennies, Zoarces viviparous, have been found to be useful indicators of petroleum contamination from oil platforms (Celander et al. 1994) and industrial chemical effluents (Vetemaa et al. 1997) in the North Sea. Blennies may be useful environmental indicators of jetty habitats on the Texas coast as well as oil platforms. Over 13,000 commercial vessels and an even larger number of smaller recreational and fishing boats annually pass through channels protected by jetties at the three sites utilized in the study (Port of Houston Authority 2001, Port of Corpus Christi Authority 2001). More than 1,000 of these commercial vessels were tankers carrying 75.5 million tons of petroleum and 1.94 million tons of assorted chemicals through Aransas Pass alone (Port of Corpus Christi Authority 2001). Blennies on jetties may be useful as models to study the chronic effects of long-term sub-lethal exposures to petroleum and other chemicals. The data presented in this study should serve as the foundation for continued examination of the utility of blennies to fisheries biologists and resource managers.

Conclusions

The major findings of the present study are as follows:

- Four species of blenniid and one labrisomid species reside on Texas jetties. These species formed geographically distinct assemblages at the three study sites but further work is needed to determine if these sites are representative of the Texas coast.
- The blenny assemblages at each site appeared to be relatively stable in species composition over time. Observed fluctuations in CPUE were driven primarily by temperature and may be an artifact of sampling bias.
- Scartella cristata is the dominant blenny on Texas jetties. It is a short-lived species that spawns throughout most of the year. Further research questions should focus
on why this species is so abundant on Texas jetties by addressing information voids on growth rates of other blenny species; physiological tolerances and requirements; and interactions between *S. cristata* and other constituent species.

- Texas jetties represent a convergence of at least two genetically distinct populations of *Scartella cristata*. The local population of *S. cristata* at Galveston had close ties with Florida indicating its origins lie in the eastern Gulf. Port Aransas and South Padre Island do not share this affinity with Florida. These local populations were closely related to each other suggesting a source population in the southern Gulf or Caribbean. Future work should include samples from a wider geographical range and incorporate investigations into cohort effects on the genetic structure of local populations.
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Fig. A-1. Monthly length-frequency distributions for *Scartella cristata* captured at Galveston, Texas from May 2000 to August 2001. Months in which *S. cristata* were not captured are omitted from this figure. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-1. CONTINUED

**Histograms showing the distribution of TL (mm) for different months in 2000 and 2001.**

- **November 2000**
  - Total individuals: 7
  - Distribution:
    - 0-10: 1
    - 11-20: 1
    - 21-30: 2
    - 31-40: 1
    - 41-50: 1
    - 51-60: 1
    - 61-70: 1
    - 71-80: 1
    - 81-90: 1
    - 91-100: 1
    - 101-110: 1
    - 111-120: 1

- **December 2000**
  - Total individuals: 3
  - Distribution:
    - 0-10: 1
    - 11-20: 1
    - 21-30: 1
    - 31-40: 0
    - 41-50: 0
    - 51-60: 0
    - 61-70: 0
    - 71-80: 0
    - 81-90: 0
    - 91-100: 0
    - 101-110: 0
    - 111-120: 0

- **March 2001**
  - Total individuals: 6
  - Distribution:
    - 0-10: 2
    - 11-20: 2
    - 21-30: 1
    - 31-40: 0
    - 41-50: 0
    - 51-60: 0
    - 61-70: 0
    - 71-80: 0
    - 81-90: 0
    - 91-100: 0
    - 101-110: 0
    - 111-120: 0

- **April 2001**
  - Total individuals: 20
  - Distribution:
    - 0-10: 1
    - 11-20: 2
    - 21-30: 2
    - 31-40: 2
    - 41-50: 2
    - 51-60: 2
    - 61-70: 2
    - 71-80: 2
    - 81-90: 2
    - 91-100: 2
    - 101-110: 2
    - 111-120: 2

- **May 2001**
  - Total individuals: 12
  - Distribution:
    - 0-10: 2
    - 11-20: 2
    - 21-30: 2
    - 31-40: 2
    - 41-50: 2
    - 51-60: 2
    - 61-70: 2
    - 71-80: 2
    - 81-90: 2
    - 91-100: 2
    - 101-110: 2
    - 111-120: 2

- **June 2001**
  - Total individuals: 25
  - Distribution:
    - 0-10: 2
    - 11-20: 2
    - 21-30: 2
    - 31-40: 2
    - 41-50: 2
    - 51-60: 2
    - 61-70: 2
    - 71-80: 2
    - 81-90: 2
    - 91-100: 2
    - 101-110: 2
    - 111-120: 2

- **July 2001**
  - Total individuals: 33
  - Distribution:
    - 0-10: 2
    - 11-20: 2
    - 21-30: 2
    - 31-40: 2
    - 41-50: 2
    - 51-60: 2
    - 61-70: 2
    - 71-80: 2
    - 81-90: 2
    - 91-100: 2
    - 101-110: 2
    - 111-120: 2

- **August 2001**
  - Total individuals: 11
  - Distribution:
    - 0-10: 2
    - 11-20: 2
    - 21-30: 2
    - 31-40: 2
    - 41-50: 2
    - 51-60: 2
    - 61-70: 2
    - 71-80: 2
    - 81-90: 2
    - 91-100: 2
    - 101-110: 2
    - 111-120: 2
Fig. A-2. Monthly length-frequency distributions for *Hypleurochilus geminatus* captured at Galveston, Texas from May 2000 to August 2001. Months in which *H. geminatus* were not captured are omitted from this figure. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-2. CONTINUED
Fig. A-3. Monthly length-frequency distributions for *Hypsoblennius ionthas* captured at Galveston, Texas from May 2000 to August 2001. Months in which *H. ionthas* were not captured are omitted from this figure. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-4. Monthly length-frequency distributions for *Scartella cristata* captured at Port Aransas, Texas from May 2000 to August 2001. *S. cristata* was captured every month except for November 2000 when no collection effort was made. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-4. CONTINUED
Fig. A-4. CONTINUED
Fig. A-5. Monthly length-frequency distributions for *Hypleurochilus geminatus* captured at Port Aransas, Texas from May 2000 to August 2001. Months in which *H. geminatus* were not captured are omitted from this figure except for November 2000 when no collection effort was made. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-5. CONTINUED
Fig. A-6. Monthly length-frequency distributions for *Labrisomus nuchipinnis* captured at Port Aransas, Texas from May 2000 to August 2001. Months in which *L. nuchipinnis* were not captured are omitted from this figure except for November 2000 when no collection effort was made. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-7. Monthly length-frequency distributions for Scartella cristata captured at South Padre Island, Texas from July 2000 to August 2001. *S. cristata* was captured every month except for November 2000 when no collection effort was made. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-7. CONTINUED
Fig. A-8. Monthly length-frequency distributions for *Hypleurochilus geminatus* captured at South Padre Island, Texas from July 2000 to August 2001. Months in which *H. geminatus* were not captured are omitted from this figure except for November 2000 when no collection effort was made. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 111-120 mm.
Fig. A-9. Monthly length-frequency distributions for *Labrisomus nuchipinnis* captured at South Padre Island, Texas from July 2000 to August 2001. Months in which *L. nuchipinnis* were not captured are omitted from this figure except for November 2000 when no collection effort was made. Axes are standardized across each month. Y-axis is percent of monthly catch in 25% intervals. X-axis is 10 mm size classes starting with 0-10 mm and ending with 131-140 mm.
Fig. A-9. CONTINUED
APPENDIX B
### APPENDIX B. Sequences for each haplotype characterized at Florida and Texas localities. Underscores ( _ ) represent alignment gaps.

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AAGGTTATTGATGGTCAGGGGACAAATTATTGTGGGAGGGGTTTCACTTTAATGAAACTATTCTCGGCA
TCTGGTTC

HAPLOTYPE L
CCGAC_TTGAAAGTTGGGAGTGCACAT_GTATGTATTAACCCATAAATTTATATATATATACCATT
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ATATAACACATTTAAGGTTATACACATACCCATTTAATATATATATACACAAACAAAGATTAA
CCAGAAATCTCCATAACTCATAAGAAGATAGGCTCCAAGGCATTTATACACGTGCATTCAC
ATCCACCCACCTGAAATATACATACCCAAATAGAAGACAGGACACATCAGTTGATATCTCTAATGCC
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TCTGGTTC

HAPLOTYPE M
CTGCCATTGAAAGTTGGGAGTGCACAT_GTATGTATTAACCCATAAATTTATATATATATACCATT
AATTCATAGTATTAAGTACATTAGATATAACACATACCATACATAATATACACATCAAGG
ATATAACACATTTAAGGTTATACACATACCCATTTAATATATATATACACAAACAAAGATTAA
CCAGAAATCTCCATAACTCATAAGAAGATAGGCTCCAAGGCATTTATACACGTGCATTCAC
ATCCACCCACCTGAAATATACATACCCAAATAGAAGACAGGACACATCAGTTGATATCTCTAATGCC
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TCTGGTTC

HAPLOTYPE N
CTGCCATTGAAAGTTGGGAGTGCACAT_GTATGTATTAACCCATAAATTTATATATATATACCATT
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ATATAACACATTTAAGGTTATACACATACCCATTTAATATATATATACACAAACAAAGATTAA
CCAGAAATCTCCATAACTCATAAGAAGATAGGCTCCAAGGCATTTATACACGTGCATTCAC
ATCCACCCACCTGAAATATACATACCCAAATAGAAGACAGGACACATCAGTTGATATCTCTAATGCC
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TCTGGTTC

HAPLOTYPE O
CTGCCATTGAAAGTTGGGAGTGCACAT_GTATGTATTAACCCATAAATTTATATATATATACCATT
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CCAGAAATCTCCATAACTCATAAGAAGATAGGCTCCAAGGCATTTATACACGTGCATTCAC
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TCTGGTTC

HAPLOTYPE P
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CCAGAAATCTCCATAACTCATAAGAAGATAGGCTCCAAGGCATTTATACACGTGCATTCAC
ATCCACCCACCTGAAATATACATACCCAAATAGAAGACAGGACACATCAGTTGATATCTCTAATGCC
AAGGTTATTGATGGTCAGGGGACAAATTATTGTGGGAGGGGTTTCACTTTAATGAAACTATTCTCGGCA
TCTGGTTC
HAPLOTYPE Q
CCGAC_TTGAAAAAGTGGGGATGTACAT_GTATGTATTAACACCATAAAATTTATATTAACCATT
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TCTGGTTC

HAPLOTYPE R
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TCTGGTTC

HAPLOTYPE S
CTGCC_TTGAAAAAGTGGGGATGTACAT_GTATGTATTAACACCATAAAATTTATATTAACCATT
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TCTGGTTC

HAPLOTYPE T
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TCTGGTTC

HAPLOTYPE U
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TCTGGTTC
HAPLOTYPE V
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HAPLOTYPE W
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TCCACCACCATGAAATATACATTACCCAAATAGAACCAGGACCCTCATGTGATATCTTTAATGCCA
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HAPLOTYPE X
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HAPLOTYPE Y
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HAPLOTYPE Z
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HAPLOTYPE AA
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TCCACCACCATGAAATATACATTACCCAAATAGAACCAGGACCCTCATGTGATATCTTTAATGCCA
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HAPLOTYPE AB
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HAPLOTYPE AC
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HAPLOTYPE AD
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