Community Structure and Habitat Preferences of Intertidal Fishes of the Eastern Canary Islands: Fuerteventura, Gran Canaria, and Lanzarote, With a Behavioral Description of Mauligobius Maderensis (Osteichthyes: Gobiidae).

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COMMUNITY STRUCTURE AND HABITAT PREFERENCES OF INTERTIDAL FISHES OF THE EASTERN CANARY ISLANDS: FUERTEVENTURA, GRAN CANARIA, AND LANZAROTE, WITH A BEHAVIORAL DESCRIPTION OF MAULIGOBUS MADERENSIS (OSTEICHTHYES: GOBIIDAE)

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

The Department of Zoology and Physiology

by

Richard P. Cody
B.S., University College Dublin, 1984
M.S., University of West Florida, 1989
May, 1996
DEDICATION

This study is dedicated to the memory of Annette Cody (1937 - 1991).

The Lake Isle of Innisfree

I will arise and go now, and go to Innisfree,
And a small cabin build there, of clay and wattles made:
Nine bean-rows will I have there, a hive for the honey-bee,
And live alone in the bee-loud glade.

And I shall have some peace there, for peace comes dropping slow,
Dropping from the veils of the morning to where the cricket sings;
There midnight’s all a glimmer, and noon a purple glow,
And evening full of the linnet’s wings.

I will arise and go now, for always night and day
I hear lake water lapping with low sounds by the shore;
While I stand on the roadway, or on the pavements grey,
I hear it in the deep heart’s core.

W.B. Yeats
ACKNOWLEDGMENTS

I would like to thank my Major Professor, Dr. J.M. Fitzsimons, who steadfastly believed in the completion of this work. My committee members, Dr. J. Geaghan (Minor Professor), Dr. J. Lynn, Dr. H. Silverman, Dr. M.S. Hafner, Dr. R.W. Hastings, and Dr. E. Turner (Graduate School) deserve credit for not allowing me to lose sight of the importance of all fields of research. I would especially like to thank Dr. S.A. Bortone who introduced me to the Canary Islands, and thereby provided the opportunity to learn something about its fishes.

My family in Ireland and the U.S. have been supportive throughout with words of encouragement when I most needed them. Sadly, my mother, Annette Cody who was always proud of my accomplishments, even when I had little to show for it, passed away before I completed this work. This work is dedicated to her memory.

I could not have completed this study without the support of friends and colleagues. A special thanks is due to Dr. A. Brito, Dr. K.S. Cole, J.W. Demastes, J.M. Falcon, M. Marin, Drs. J.P. and L.A. O'Neill, H.G. Oulton, Dr. S. Southerland, Dr. C.K. Swing, J. Tamplin, T.F. Tomas, J.L. VanTassell, and all the Earthwatch staff and volunteers (1990-1993). Forgive me if I omitted names. The study was completed with support from Earthwatch, U.S.A., Lerner-Grey Marine Science Fund, and the Society of Sigma-Xi.
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ABSTRACT

Community structure and relative habitat preferences of intertidal fishes from the eastern Canary Islands of Fuerteventura, Gran Canaria, and Lanzarote were examined in a study of 354 tidepools at 33 localities. Habitat use and behavior of the most abundant fish Mauligobius maderensis were examined on Gran Canaria and Lanzarote.

Of the 27 species encountered, 11 were common to each of the islands. The most abundant species were: M. maderensis, Parablennius parvicornis, Gobius paganellus, Coryphoblennius galerita, and Chelon labrosus. In a Two-way indicator species analysis Fuerteventura and Lanzarote localities clustered together. The same analysis differentiated between species that inhabited the upper intertidal shore and those that associated with lower shore pools. Canonical Correspondence Analysis revealed a weak relationship between abundant species and habitat preference variables. Transient species (e.g., Abudefduf luridus, Scorpaena maderensis, and Tripterygion delaisi) showed a greater affinity with variables: mean standard length (SL), number of species, pool depth, shelter, and volume.

When habitat use of M. maderensis was assessed in terms of body size, larger individuals showed an affinity for downshore pools. A general downshore movement associated with increasing size was evident from the elevational distribution of size classes of M. maderensis and provides a mechanism by which the habitat heterogeneity of the rocky shore may be
exploited by *M. maderensis*. Although the abundance and broad intertidal distribution of *M. maderensis* are consistent with a generalist strategy, differential habitat use by the size classes of *M. maderensis* supports the hypothesis that habitat use is constrained by size.

Males of *M. maderensis* were territorial. Territoriality was associated solely with reproduction and did not involve the defense of food resources. In territorial encounters between resident males and intruding males, resident fish were never displaced. An intruding male decreased its probability of being displaced by responding to the defensive displays of the resident male with a "face-away" posture. Males were the sole participants in nest-guarding.
INTRODUCTION

The rocky shore environment of the Canarian Archipelago, created largely by tidal weathering of its volcanic substrate, provides a diversity of habitats for intertidal teleosts. The relative ages of the predominantly "A'ā" and "Pāhoehoe" rocky shores, the degree of physical modification attributable to climate and wave action, coupled with the geographic proximity of the Canary Islands to continental Africa, Mediterranean Europe, and islands of the mid-Atlantic ridge have provided some of the exceptional factors that have influenced the evolutionary history of the biota of the archipelago. Many teleost fishes associated with the intertidal zone of these islands are encountered elsewhere in the northeastern Atlantic (Wheeler, 1969) and Mediterranean oceans (Miller, 1986; Zander 1986). However, a number of species are restricted in their distributions to the rocky shores of islands contained in the temperate Macaronesian Chain (Miller, 1984), collectively, consisting only of the Azores, Madeira, and the Canary Islands. The syntopic association of endemic and more broadly distributed teleost species presents a rare perspective for the study of intertidal ecology of fishes.

Coincident with the potential of the Islands for the study of evolutionary dynamics is a more "urgent" conservation-driven necessity to acquire an understanding of the functioning of the intertidal teleost community at the levels of the community and the individual populations comprising that community. With the exception of Gomera and Hierro, the most remote of
the major islands, tourism is a major industry of each of the Canary Islands. Gran Canaria, Lanzarote, Fuerteventura, and Tenerife are visited by over 2,000,000 tourists each year (Gobierna Las Canarias, in Bortone et al., 1991).

Associated with these seasonal population fluctuations are a number of problems such as increased fishing pressure (increased demand for traditional cuisine) and pollution. Although the decline in local fisheries has led to concern from the Canarian government (Franquet, in press), attention thus far has focused on the status of inshore fish populations affected directly (Bortone et al., 1991). The construction and deployment of artificial reefs off Gran Canaria (Bacallado et al., 1989), together with ongoing visual censuses of inshore teleost populations off Hierro, Gran Canaria, Tenerife, Lanzarote, and Fuerteventura, represent two approaches taken to examine factors that affect the composition and abundances of inshore fish assemblages. However, absent from this research agenda is an assessment of littoral fish populations. Despite suggestive evidence from numerous reports of occasional and transient occupation of the intertidal zone by inshore or infralittoral species (e.g., Hiatt and Strasburg, 1960; Rice, 1962; Gibson, 1968; 1973; Brito, 1991; Mata et al., in press), the significance of the rocky intertidal zone as a habitat for the postlarvae and juveniles of inshore fishes is largely unknown. The occurrence of “transient” inshore species in intertidal areas supports the hypothesis that the littoral zone functions to some extent as a nursery or as a refuge for juveniles of commercially important inshore species and forage
species. As the Canary Islands receive little precipitation, there are no natural permanent freshwater bodies or brackish water habitats where juveniles of inshore species can forage and/or avoid predation. For juveniles of inshore fishes, habitat is largely restricted infralittorally to volcanic reefs and steep ledges, and littorally to the intertidal rocky shores and lagoons surrounding the islands. Some of the predators that occupy infralittoral areas include moray eels (*Muraena helena*), groupers and basses (*Epinephelus marginatus, Mycteroperca rubra, Serranus atrocauda, S. cabrilla*), scorpion fishes (*Scorpaena scrofa*), and lizard fishes (*Synodus saurus* and *S. synodus*) (Bortone et al., 1991; Brito, 1991). Littoral rocky shores of the Canary Islands are characteristically narrow with diverse but patchy resources in terms of both shelter and food. However, the littoral zone has the advantage of limited accessibility to inshore predators. Presently, knowledge of the intertidal teleost community structure of the Canary Islands and the extent of resource use by intertidal fishes, transient and obligate, remains unknown and therefore presents dilemmas for conservation and coastal management. The present study addressed the questions of community structure and resource use among intertidal fishes in terms of relative habitat preferences because ultimately the success of conservation and coastal management strategies will depend on the completeness of our understanding of community function.

The predominant intertidal teleost in the Canarian Archipelago is the caboso negro, *Mauligobius maderensis*. This species is endemic to Madeira and
the Canary Islands where they are abundant in tidepools (Miller, 1984, Brito, 1991). Studies of the biology of this species have been limited to taxonomic characterizations (Miller, 1984) and incidental habitat and locality descriptions (e.g., Mata et al., in press). In contrast, studies of gobies endemic to the Hawaiian Archipelago (e.g., Ego, 1956; Timbol et al., 1980; Nishimoto and Fitzsimons, 1986; Tate et al., 1991; Fitzsimons et al., 1993; Fitzsimons and Nishimoto, 1995), have yielded valuable information not only on those species but also on island biogeography and gobiid behavioral ecology in general.

The first approach of this study was to describe the littoral teleost community structure for the three major easternmost Canary Islands, Fuerteventura, Gran Canaria, and Lanzarote. Description of community structure involved three main objectives: identification and enumeration of intertidal teleosts, determination of species associations, and description of the relative habitat preferences of occupant fishes. This information was used concurrently to lend validity to interpretations of the behavior of *M. maderensis*. In turn, the behavioral ecology of *M. maderensis* was seen as integral to the understanding of intertidal community structure on the Canary Islands for three main reasons. First, the endemic nature of *M. maderensis* strongly suggests a degree of specialization to the set of environmental conditions that characterize rocky intertidal shores of the Canary Islands. Second, the abundance of *M. maderensis* reflects its ecological
importance in the intertidal rocky shore, and lastly, its status as a “true intertidal inhabitant” increases the probability that most factors affecting the distribution of individuals of this species can be identified from the rocky littoral zone. As a result, the well-being of the rocky intertidal shore of the Canary Islands in terms of environmental conditions is more likely to be reflected in both the behavior and patterns of abundance of individuals of *M. maderensis*.

The study represents the most intensive sampling of any intertidal teleost community undertaken over a four-year (four summer field seasons) period. Moreover, until the present study, examination of community structure and behavioral ecology of intertidal fishes of the Canary Islands had not been attempted on such a large scale. As the study represents the first time intertidal community structure of fishes of the area was examined in detail, care was taken in the development of generalizations, and in the scope of inferences made concerning the role of interspecific biological interactions such as competition and predation as factors influencing community structure. Instead, generation of plausible hypotheses was seen as a fundamental step in the encouragement of future study of the intertidal fishes of the Canary Islands.
MATERIALS AND METHODS

SAMPLING PROCEDURE

Three hundred fifty four tidepools from 33 sites located on the three major easternmost islands of the Canarian Archipelago were sampled during June - August, 1990-1993 (Fig.1). Ten, 12, and 11 localities were selected from Fuerteventura, Gran Canaria, and Lanzarote respectively. Locality names are listed below for each of the islands sampled. Corresponding site numbers, with abbreviated island names (for simplicity of understanding) and number of pools sampled at each locality are listed in parentheses. Fuerteventura (FV) localities included: Playa Corralejo North (FV-1, 7); Corralejo South (FV-2, 26); Punta de Tivas North (FV-3, 12); Punta de Tivas South (FV-4, 5); Caleta de Bajo (FV-5, 6); Pozo Negro, Playa de los chopos (FV-6, 9); Morro del Jable, Cuchillo del Ciervo (FV-7, 5); Casas de Joros (FV-8, 3); Ajuy, Punta del Cantil (FV-9, 4); and El Cotillo, Playa del Castillo (FV-10, 10) (Fig. 2). Localities sampled on Gran Canaria (GC) included: Arinaga, Bahía de Formas (GC-1, 4); Morro del Pasito Blanco (GC-2, 12); Las Meloneras East (GC-3, 2); Las Meloneras West (GC-4, 29); Montaña la Arena (GC-5, 12); Bahía de Santa Agueda West (GC-6, 21); Punta de Puerto Rico East (GC-7, 38); Punta de Puerto Rico West (GC-8, 11); Punta Cruz de Piedra (GC-9, 23); El Taurito (GC-10, 15); Tititana (GC-11, 22); Sardina, Punta de Gáldar (GC-12, 6) (Fig. 3). On Lanzarote (LZ), the localities were: Orzola, Playa de la Cantería (LZ-1, 4); Charca de la Laja (LZ-2, 4); Arrieta, El Cortijo (LZ-3, 13); Arrieta, Playa de la Garita (LZ-4, 3);
Riscos de Lajero (LZ-5, 9); Mala (LZ-6, 6); Puerto del Carmen, Casa de los Mojones (LZ-7, 5); Puerto Calero, Playa Quemada (LZ-8, 7); Punta del Jurado, El Golfo (LZ-9, 8); Punta Ganada/Los Lomillos (LZ-10, 8); Caleta del Rio (LZ-11, 5) (Fig. 4).

Detailed scale maps (maximum resolution of 1 cm = 5 cm and minimum resolution of 1 cm = 40 cm) of each pool were made prior to collection of data on pool parameters. A tape measure was placed along the longest axis of the pool. Measurements to the pool edge were then made at right angles to the longest axis at 5-20 cm intervals and plotted on water resistant graph paper (1 mm resolution). The positions and sizes of major features such as boulders, crevices, caves, algal mats, and foreign objects were noted and included on each scale map. Pool surface areas were then calculated from the average of three measurements of pool maps made with a Keuffel and Essel (KE) polar planimeter.

Variables measured on site at each pool included: pool elevation (cm below mean high tide [bmht] as determined by the upper limits of the barnacle zone), volume (liters), maximum depth (cm, at the deepest part of the pool), substrate type (1 = rock, 2 = rock/cobble, 3 = cobble, 4 = cobble/pebble/sand, 5 = pebble/sand), shelter (1 = a shelter in ≤ 20% of pool bottom surface, 2 = 20% < shelter ≤ 40%, 40% < shelter ≤ 60%, 60% < shelter ≤ 80%, shelter in > 80% of bottom surface area), algal cover (1 = cover ≤ 20%, 2 = 20% < cover ≤ 40%, 3 = 40% < cover ≤ 60%, 4 = 60% < cover ≤ 80%, 5 = cover >
80%), air temperature in the shade (°C), water temperature at the deepest shaded part of the pool (°C), salinity (‰), dissolved O₂ (ppm), number of species, and number of fish. Total biomass of fishes per pool was estimated by extrapolating from a loge-linear regression model of preserved weights on standard lengths of preserved specimens (LogₑW = Logₑa + b LogₑL) where W = weight (g), L = SL (mm), a = slope, and b = W/L intercept (Appendix A).

Fishes were collected from pools by the administration of the anesthetic Quinaldine (20% solution in Acetone, Gibson, 1967a) directly into crevices, caves, and under ledges to flush fishes from positions where they were not readily accessible. To assist pool recovery and limit the effects of sampling, pools were rinsed and refilled with seawater after the removal of fishes and the completion of data collection. Fishes were immediately fixed in a 10% formalin solution for subsequent identification of species and measurement of standard length (SL). Specimens collected from Fuerteventura localities were placed in the catalogued ichthyology collections of the American Museum of Natural History (AMNH) and Louisiana State University Museum of Natural Science (LSUMNS). Specimens collected on Gran Canaria and Lanzarote were placed exclusively in the catalogued and uncatalogued ichthyology collections of LSUMNS. The sex of specimens of Mauligobius maderensis was determined by examination of genital papilla morphology with a magnifying glass. In female gobioïd fishes, the papilla is short and the opening wide and fimbriate whereas in males, the papilla is
longate and conical (Arai, 1964; McDowall, 1965). In addition, the papillae of preserved male *M. maderensis* are pigmented even in small specimens (30 mm SL).

**BEHAVIORAL OBSERVATIONS**

Inpool (proximate) and remote observations of *Mauligobius maderensis* were made at low tide. Remote observations were made at a distance of 1-3 m from the pool's edge with the aid of Bausch and Lomb polarized glasses. Inpool observations, limited to large pools able to accommodate a submerged observer, were made with mask (1.5 X magnification) and snorkel. In both methods, fish were allowed to acclimate to the presence of the observer for a period of at least five minutes before observations were recorded. Pools containing high numbers of the blenny *Parablemmius parvicornis* and the wrasse, *Thalassoma pavo* were avoided to reduce the level of interspecific interference of behavioral sequences. Remote and proximate methods of observation were used also at high tide. At high tide, proximate observations were made by snorkeling at a distance of 1-3 meters from the subjects. Remote observations were made at a distance of 1-3 meters shoreward of advancing and retreating tidal fronts. Observation distances varied more at high tide due to turbidity and the effects of wave action on observer movement. Although observations were made throughout Gran Canaria and Lanzarote, most behavioral data were collected at seven localities: Las Meloneras (GC-4), and, Montaña la Arena (GC-5) on Gran Canaria, and Arrieta (LZ-3, 4, 5), Mala
(LZ-6), and El Golfo (LZ-9) on Lanzarote. Locality selection was based on the amount of human traffic (that might interfere with behavioral observations), accessibility to repeated observation, and ease of observation and data recording. In addition, the localities covered a diversity of substrates from predominantly Pāhoehoe rocky shores at GC-5 LZ-3, LZ-4, and LZ-6 sites to pools containing cobble and loose rock at GC-4 and LZ-9 and Aā substrate pools at LZ-5.

ANALYSES

Statistical analyses were done with PC-SAS (SAS Inst., 1985) Cornell Ecology Program Series (CEPS) CANOCO ver. 3.12 (ter Braak, 1987-1992), CEPS TWINSPLAN (Hill, 1979) for IBM compatibles, Statview II for the Macintosh. Loge transformations were made of community structure data (environmental variables and species abundance data) which were examined by using Canonical Correspondence Analysis (CCA), and multiple regression. Locality and species data were analyzed by using a Two Way Indicator Species Analysis (TWINSPLAN), a "polythetic divisive" clustering technique (Hill, 1979). The technique has the advantage of objectivity over other clustering techniques. Data are first ordinated by reciprocal averaging (RA). Samples are polarized by species representing RA ordination axis extremes. Two initial clusters are produced by dividing the axis at or near the middle. A reclassification of species based on their ability to polarize samples is then used to improve the sample division. The process is repeated on the two
initial clusters to produce four, then eight, etc. (Jongman et al., 1987). To facilitate TWINSPLAN ordinations and clustering of species and pools, species abundances were summarized by locality, i.e., species abundances represented overall mean abundances per pool at each locality. Species abundances were expressed as a percentage of the total number of fishes at each locality and evenly scaled so that no value < 1.0 was used.

Multiple regression, and analysis of variance (ANOVA) were used to model *M. maderensis* social structure/habitat utilization. Loge transformations of elevation, algal cover, substrate, and shelter were performed. Size-distributional data in which shore elevation was categorized as four consecutive elevational zones (Upper = 20 cm and higher above mht, 20 cm < Upr-Mid ≤ 60 cm, 60 cm < Lwr-Mid ≤ 100 cm, Lower > 100 cm) and was examined in a Kruskall-Wallis test.
Figure 1. The Canary Islands. The islands of Fuerteventura, Gran Canaria, and Lanzarote are three easternmost major islands.
Figure 2. The island of Fuerteventura. Tidepool localities are denoted by numbers 1-10.
Figure 3. The island of Gran Canaria. Tidepool localities are denoted by numbers 1-12.
Figure 4. The island of Lanzarote. Tidepool localities are denoted by numbers 1-11.
RESULTS AND DISCUSSION

INTERTIDAL COMMUNITY STRUCTURE

SPECIES COMPOSITION

Twenty-seven species representing 14 teleost families were collected from pools on Fuerteventura, Gran Canaria, and Lanzarote. Five blenniid genera accounted for 29.6% of tidepool teleost species whereas gobiids and sparids each comprised 11.1% of the species. Fuerteventura, Gran Canaria, and Lanzarote pools accounted for 16, 21 and 20 species respectively (Table 1). Of the 27 species encountered, 11 were common to the three islands. In decreasing order of total abundance, these shared species included:

*Mauligobius maderensis, Parablennius parvicornis, Gobius paganellus, Coryphoblennius galerita, Chelon labrosus, Thalassoma pavo, Scartella cristata, Lepadogaster lepadogaster, Ophioblennius atlanticus, Lipophrys trigloides, and Epinephelus marginatus* (Table 1). Both Gran Canaria and Lanzarote pools contained three unique species, *Apogon imberbis, Boops boops, and Centrolabrus trutta* on Gran Canaria and *Atherina presbyter, Chromogobius britoi, and Lepadogaster zebrina* on Lanzarote. Species unique to Fuerteventura pools included: *Lipophrys pholis* and *Muraena helena*. The most abundant species in terms of both mean abundance per pool, and % pools occupied were *M. maderensis, P. parvicornis, G. paganellus, C. galerita* and *C. labrosus* respectively (Table 2). Other estimates of abundance: overall (combined island) abundance (Fig. 5) and overall numerical predominance (Fig. 6) revealed similar findings
with the notable exception that *C. galeria* was the numerically predominant species in 18% of the pools while accounting for < 10% of the total number of individuals. *Gobius paganellus* accounted for 18.4% of the total number of fishes and was numerically predominant in 13% of the total number of pools.

In addition to those species collected, a number of occupant species was noted in unsampled pools. On Fuerteventura, *Abudedefduf luridus* (FV-10), *Canthigaster rostata* (FV-1), *Centrolabrus trutta* (FV-3) and *Thorogobius ephippiatus* (FV-9) were observed but not collected. On Gran Canaria, specimens of *Canthigaster rostrata* (GC-3, 10), *Chromis limbatis* (GC-10) and *Macrorhamphosus scolopax* (GC-7) were collected. *Chromis limbatis* and *Centrolabrus trutta* (LZ-8), and *Oblada melanura* (LZ-7) were present at Lanzarote localities. These observations were excluded from abundance and diversity measurements because no data on pool parameters or species composition were collected.

Comparative data on Canarian intertidal fishes are scant. However, in a preliminary examination of the intertidal fishes from 41 pools (Volume = 7-3100 liters) on the island of Alegranza, a few km to the north of Lanzarote (Fig. 4), Mata et al. (in press) found 15 species representative of eight teleost families. All species encountered by Mata et al. (in press), with the exception of *Liza aurata* (Mugilidae), were also found in the present study. Only 16 individuals of *L. aurata* were found in Alegranza pools. Due to the similar appearance of juveniles of *L. aurata* and *C. labrosus*, and problems associated with mullet taxonomy, it was possible that *C. labrosus* was confused with *L.*
aurata. However, four species (and one questionable record of Oedalechilus \textit{labeo}) have been recorded from Canarian waters of which, \textit{C. labrosus} was listed as the most abundant, and \textit{L. aurata} was described as common (Brito, 1991). In addition, \textit{C. labrosus} and \textit{L. aurata} have been encountered littorally (Brito, 1991). In the present study, \textit{C. labrosus} was abundant (n = 83) while \textit{L. aurata} was entirely absent from Lanzarote pools. The community structure of the Alegranza pools was remarkably similar to Lanzarote pools. Species found in the present study that were not encountered by Mata et al. (in press) included \textit{Atherina presbyter} (Atherinidae), \textit{Chromogobius britoi} (Gobiidae), \textit{Labrisomus nuchipinnis} (Labrisomidae), \textit{C. labrosus} ? (Mugilidae), \textit{Diplodus sargus} (Sparidae), and \textit{Tripterygion delaisi} (Tripterygidae). The sand smelt, \textit{A. presbyter} which prefers inshore areas but has been caught in pools over tidal flats (Wheeler, 1969), the endemic goby, \textit{C. britoi}, often associated with sublittoral caves (VanTassell, pers. comm.) but reported intertidally (Brito, 1991), and the sargo blanco, \textit{D. sargus}, which has been found over rocky and sandy bottoms at all depths to 200 m, were limited to single occurrences (i.e., associated with one pool from a single locality).

The most abundant fish in Alegranza pools was \textit{P. parvicornis}, which, accounted for almost 43.1% of all fishes (Mata et al., in press). Three other blennies, \textit{C. galera}, \textit{L. trigloides}, and \textit{L. pholis}, were the next three most abundant fishes (14.6%, 11.24%, and 9.51%), followed by the endemic goby, \textit{M. maderensis} at 8.1%. At first examination, the paucity of individuals of \textit{M.}
*maderensis* appeared inconsistent with abundances reported herein from Lanzarote localities. However, only two localities were investigated in the Alegranza study (El Veril on the southern coast, and El Bermujo to the north of the island) and whereas *M. maderensis* comprised less than 2% of the fishes from EL Veril, it accounted for approximately 33% of fishes at El Bermujo. In a comparison of the closest sites (LZ-1, 2, 10, 11) on Lanzarote with the Alegranza localities, *M. maderensis* was the most abundant species at LZ-1, LZ-2, and LZ-11. However, *C. galerita* was numerically dominant at LZ-10.

Consistent with the abundances reported by Mata et al. (in press) for Alegranza sites, *L. trigloides* was next most abundant at LZ-10.

An extensive visual census of inshore fishes at 18 localities off the island of Hierro included 47 species in 369 samples (Bortone et al., 1991). Of those 47 species, 46 were teleosts of which 13 (28%) were encountered in tidepool samples in the present study. The amount of species in common increased to 33% when tidepool observations of *Canthigaster rostrata* and *Chromis limbatus* were also included. The real overlap may be higher as the five-minute radius surveys used in the visual census of inshore fishes may be biased toward the detection of larger species. During the surveys, the divers remained stationary at the center of the sample area (Bortone et al., 1991). The detection of smaller cryptic benthic species may require more time and movement by the diver to be more effective (Falcon, pers comm.). Although the island of Hierro represents the extreme west of the Canarian Archipelago,
the proportion of species common to both sublittoral areas along its coast and to the intertidal pools of Fuerteventura, Gran Canaria and Lanzarote provides strong evidence of the importance of the intertidal zone as habitat for life history stages of inshore species.

**SPECIES ASSOCIATIONS**

Patterns in the relative abundances and the distribution of species have been used to infer mechanisms that structure communities (Pielou, 1978). However, the use of descriptive work as an end to the examination of community structure has been criticized, as has the lack of consensus among ecologists as to the design of methods that can appropriately distinguish the factors (biotic or otherwise) responsible for community organization (Werner, 1984). The present study assessed species associations from relative abundances of fishes at 33 localities on the three islands. In turn, the affinities of species for particular localities (and islands) provided an indication of habitat preferences on a large scale.

The Initial dichotomy produced with Two-way indicator species analysis (TWINSPAN) resulted in clusters of 19 species (A) and eight species (B) (Fig. 7). Cluster A was dominated by transient and facultative intertidal inhabitants. Of these species, *O. atlanticus, T. pavo, E. marginatus, L. lepadogaster,* and *T. delaisi* were among the more abundant intertidal inhabitants overall (Table 3). In addition, rare species that were recorded in low numbers in
Table 1. Mean species abundances (calculated as the total number of individuals divided by the total number of pools) at each locality for the islands of Fuerteventura, Gran Canaria, and Lanzarote. Numbers aligned with species show mean abundance at a locality. Standard deviations are shown in parentheses directly below mean abundances.

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### Fuerteventura Localities

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| Mugilidae  
*Chelon labrosus* | 0.71 | 0.08 | 0.08 | _    | _    | 0.2  | 0.33 | _    | _    | _     |
|                   | (1.89)| (0.29)| (0.29)| _    | _    | (0.45)| (0.58)| _    | _    | _     |
| Muraenidae  
*Muraena helena*  | _    | 0.2  | _    | _    | _    | _    | _    | _    | _    | _     |
| Pomacentridae  
*Abudefduf luridus* | _    | _    | _    | _    | _    | _    | _    | _    | _    | _     |
| Scorpaenidae  
*Scorpaena maderensis* | _    | _    | _    | _    | _    | _    | _    | _    | _    | _     |
| Serranidae  
*Epinephelus marginatus* | 0.14 | _    | _    | _    | _    | _    | _    | _    | _    | _     |
|                   | (0.38)| _    | _    | _    | _    | _    | _    | _    | _    | _     |
| Sparidae  
*Boops boops* | _    | _    | _    | _    | _    | _    | _    | _    | _    | _     |
| Diplodidae  
*Diplodus annularis* | _    | _    | _    | _    | _    | _    | _    | _    | _    | _     |
| Diplodidae  
*Diplodus sargus* | _    | _    | _    | _    | _    | _    | _    | _    | _    | _     |
| Tripterygiidae  
*Tripterygion delaisi* | _    | _    | _    | _    | _    | _    | 0.4  | _    | _    | _     |
|                   |      |      |      |      |      |      | (0.89)| _    | _    | _     |
| Number of pools  | 7    | 26   | 12   | 5    | 6    | 9    | 5    | 3    | 4    | 10    |
|                   | (table con'd) |
### Gran Canaria Localities

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(Lanzarote Localities)

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Table 2. Mean species abundances summarized for each of the islands. Number in parentheses = number of pools, sd = standard deviation, Max = maximum number per pool, % Occur = percentage overall abundance at the locality where the maximum number was recorded.

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<th>Gran Canaria (n = 194)</th>
<th>Lanzarote (n = 72)</th>
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<th>Lanzarote (n = 72)</th>
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Figure 5. Species abundances for the islands of Fuerteventura, Gran Canaria, and Lanzarote. Abundance is expressed as a percentage of the total abundance for each of the islands.
Figure 6. Percentage numerical predominance. Overall abundance is expressed as percent of the total number of pools in which a species was most abundant.
single pools (e.g., A. presbyter, B. boops, C. britoi, and M. helena) were grouped in cluster A. Conversely, cluster B was characterized mostly by true intertidal species. Chelon labrosus (cluster B1) and D. sargus (cluster B4) were the only transient inhabitants, represented in the intertidal zone by juveniles. Mauligobius maderensis, G. paganellus, and P. parvicornis (cluster B3) were the three most abundant species on each of the three islands (Table 3). They were found together in 14.7% (n = 52) of all pools and 79% (n = 26) of localities examined. The three species co-occurred in 12.5% of pools on Fuerteventura, 12.9% of the pools from Gran Canaria, and 22% of pools on Lanzarote. Only 18% (n = 6) of the localities did not contain two of the three species. Of clusters B4 and B5, only one half of the dichotomy allowed a meaningful interpretation. Diplodus sargus, L. pholis, and L. trigloides (cluster B4) were among the least encountered species. As a consequence, their association may have reflected their low respective abundances. In contrast, the relatively abundant blennies, C. galerita and S. cristata were contained in cluster B5. The occurrence of S. cristata at all localities (with the exception of LZ-3) coincided with the presence of the more abundant C. galerita. However, within a locality, S. cristata and C. galerita, were not always present in the same pools. Of the 29 pools that contained S. cristata, 55% did not contain any individuals of C. galerita. Scartella cristata was numerically dominant in only two of those pools. In a study of intertidal blennies on the Mediterranean coast of the Iberian peninsula, Nieder (1988) also found C. galerita and S. cristata together,
but at only four of 10 sites examined. Although *S. cristata* was far more abundant overall than *C. galera*, neither species, when found together, was particularly abundant.

The primary level clusters of localities produced with TWINSPLAN allowed meaningful interpretations. The first major dichotomy resulted groups of 23 localities (Fig. 8, cluster A) and 10 localities (cluster B) (Fig. 8). *Thalassoma pavo, M. maderensis,* and *L. lepadogaster* (indicator species) were important in the determination of cluster A, whereas *C. galera* and *S. cristata* acted as indicator species for cluster B. Eight of the 10 Fuerteventura localities and nine of the 11 Lanzarote localities were placed in cluster A. The second level dichotomy of cluster A resulted in clusters (A1 and A2) of 10 and 13 localities, respectively. Of the 10 localities in cluster A1, 7 localities were low in species diversity (≤ 6 species). In addition, *M. maderensis* was the most abundant species at each of the ten localities represented by cluster A1 (Tables 1, 3). In contrast, cluster A2 was composed predominantly of localities characterized by relatively high species richness. Ten of the 13 localities in cluster A2 were inhabited by eight or more species while no locality was occupied by less than 6 species.

Although Gran Canaria localities were distributed among the two major clusters A and B, cluster B was dominated by Gran Canaria localities. Six of the 10 localities in this cluster were Gran Canaria localities. *Thalassoma pavo* was a notable absentee from all of the localities in cluster B (Tables 1, 3). In
general, Gran Canaria localities were characterized by low diversity. Pools at the localities GC-7 and GC-10 (which were heavily sampled, n = 38, n = 15 respectively) were small, topographically homogeneous, and contained very few species. The immediate subtidal area was densely inhabited by *T. pavo* which suggested that suitable habitat was unavailable intertidally even for occasional inhabitation by *T. pavo*. Cluster B produced clusters B1 (4 localities) and B2 (6 localities) at the next level. Although Cluster B1 was composed exclusively of localities from Gran Canaria, each of the three islands were equally represented in cluster B2. *Chelon labrosus* was absent from all of these localities while they were present in B1 localities, hence the designation (using TWINSPLAN) of indicator species at the node B (Fig. 8).

Perhaps the most obvious pattern evident from the data was the widespread distribution of *M. maderensis* and *P. parvicornis* throughout the rocky intertidal shores of the islands of Fuerteventura, Gran Canaria, and Lanzarote. These two species numerically dominated the pools on each island and they cohabited = 40% of the pools. Of those pools in which *P. parvicornis* and *M. maderensis* coexisted, 52 contained more individuals of the former while 63 contained more *M. maderensis*. *Mauligobius maderensis* were present in 88 pools that did not contain any individual of *P. parvicornis*. By comparison, *P. parvicornis* existed in the absence of *M. maderensis* in 70 pools. No patterns emerge until we look at the distribution of these mutually exclusive pools. Of the 70 pools that did not contain any *M. maderensis*, 55
were located on Gran Canaria. Topographically, intertidal rocky shores of Gran Canaria were characteristically narrow and formed on eroded volcanic basalt ledges beneath steep cliffs. In general, pools lacked the macroporosity of pools on pāhoehoe shores which were more typical of Lanzarote and Fuerteventura localities. Cover largely consisted of loose spherical cobble (10cm to 50cm, diameter). Spawning aggregations of *P. parvicornis* have been found in pools containing cobble (Cody, 1993). On Gran Canaria, *G. paganellus* was also more abundant than on Lanzarote or Fuerteventura. This species is a common intertidal inhabitant as far north as the northern British Isles (Holt and Byrne, 1903), and it is found also on Mediterranean rocky shores (Miller, 1986). In more northern portions of its distribution, *G. paganellus* is often found on shores occupied by the giant goby, *Gobius cobitis* (Gibson, 1972). Although overlap occurred in the elevational distributions of these species, *G. paganellus* showed a distinct preference for upper shore pools on both exposed and sheltered shores, whereas *G. cobitis* was more abundant below mean tide level (MTL) on sheltered shores (Gibson, 1972). *Gobius cobitis* was not encountered on exposed shores. The greater abundances of *G. paganellus* in Gran Canaria pools may reflect adaptation to more exposed environments.

**HABITAT**

Rocky shores have long been described in terms of tidal levels. Stephenson and Stephenson (1972), in their classic treatment of intertidal zonation, divided the rocky intertidal shore into three main areas or bands.
At the most landward extreme was the supralittoral fringe. This area represented the boundary between the intertidal and supralittoral areas. The infralittoral fringe referred to the boundary between the intertidal and infralittoral (sublittoral) zones. Between these two boundary layers was the midlittoral zone. Although many sedentary organisms show affinities for particular tidal levels or the macroalgae associated with those levels, the patterns are by no means universal (e.g., Broekhuysen, 1940; deSilva, 1962; Williams, 1964; Dayton, 1971). Stephenson and Stephenson (1972) attributed this to variation in tidal height, even over a short distance, and physical characteristics of the shores. In general, the lower intertidal is considered more stable and heterogeneous than the upper littoral zone (Newell, 1979). Associated with this increased stability and habitat heterogeneity is a tendency toward niche specialization and higher species diversity. Evidence indicates that competition and predation are the most important biological factors in the determination of the abundances of species in this zone (e.g., Dayton, 1971, Paine, 1974). In contrast, the upper limits of distribution of organisms in the intertidal have been attributed to physical tolerances (e.g., Connell, 1972, 1975). In general, physical conditions of the upper intertidal zone are more extreme and the habitat is less heterogeneous than on the lower intertidal zone. Casual acceptance of these generalizations has been criticized by Underwood and Denley (1984), who advocate thorough testing of the
Figure 7. TWINSPLAN species tree. The tree was generated from the relative abundances of 27 species collected from pools at 33 localities on the islands of Fuerteventura, Gran Canaria, and Lanzarote. Scale refers to level at which a dichotomy occurred.
Figure 8. TWINSPLAN locality tree. The tree was generated from the relative abundances of 27 species collected from pools at 33 localities on the islands of Fuerteventura, Gran Canaria, and Lanzarote. Species listed at the nodes (indicator species) on the tree are those that were important in determining the groupings of localities, +/- refer to the polarity of the RA axes. Scale refers to level at which a dichotomy occurred.
Table 3. Two-way ordered species/locality matrix generated from TWINSPLAN output. Numbers reflect relative abundances on a 1-5 scale, where 1 = least abundant and 5 = most abundant. The absence of a species at a locality is represented by a "-". Column headers indicate island study sites.

| Species                        | F | V | C | Z | V | Z | C | Z | V | Z | C | C | C | V | Z | V | C | Z | C |
| Ophioblennius atlanticus       |   |   |   |   |   | 1 | 3 | 4 | 10| 1  | 2 | 1 | 3 | 7 | 7 | 10| 11| 9 | 6 | 8 |
| Chomogobius britoi             |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 | 1 |   |   |   |   |   |
| Abudefdufl luridus             |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Boops boops                    |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Centrolabrus trutta            |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Thalassoma pavo                |   |   |   |   |   |   |   |   |   |   |   | 1  | 3 | 4 | 4 | 5 |   |   |   |   |   |
| Apogon imberbis                |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Scorpaena maderensis           |   |   |   |   |   |   |   |   |   |   |   |   |   | 1 | 1 |   | 3 | 2 |   |   |   |
| Lepadogaster zebra             |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Lepadogaster lepadogaster      |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 2  |
| Tripterygion delaisi           |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 1  |
| Labrisomus mucipinnis          |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Diplodus annularis             |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Parablennius pilicornis        |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 3  |
| Muraena helena                 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Atherina presbyter             |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Lipophrys parvus               |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Epinephelus marginatus         |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Mauligobius maderensis         |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Gobius paganus                 |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Parablennius parvocorinns      |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Chelon labrosus                |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Diplodus sargus                |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Lipophrys trigloides           |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 2  |
| Coryphoblennius galerita       |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   | 4  |
| Lipophrys pholis               |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |
| Scartella cristata             |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |   |

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hypothesis through experimentation rather than the invocation of biological and physical factors to explain species abundances. The applicability of these generalizations to fishes may be even more susceptible to criticism as most were derived from studies of the invertebrate and vegetative components of communities (Connell, 1972). An examination of habitat preferences in intertidal fishes must also take into consideration fish mobility which allows a fish to traverse less than optimal habitat (and relatively long distances) quickly and may affect the accuracy of sampling by producing distributional data which do not necessarily reflect habitat preferences. Unlike many invertebrates associated with macroalgal zones, fishes are largely restricted to pools at low tide. Pools may vary considerably within a narrow tidal band, and, hypothetically, two competing species may occur within the same locality but remain mutually exclusive by differential occupation of the pools. Gibson (1972) was able to explain only about 30% of the variation in abundances of *G. paganellus, G. cobitis,* and *L. pholis* on sheltered and exposed Atlantic rocky intertidal shores of France by using the variables shore level, percent cover, and surface area. However, Gibson (1972) was able to distinguish three groups of tidepool fishes based on shore level preferences: those widely distributed throughout the intertidal zone, those found in the upper intertidal zone, and those occupying the lower zone only. The importance of "site-specific conditions" such as local physiography as determinants of abundance and distribution patterns was demonstrated by
Littler (1980) for macrophyte and macroinvertebrate communities of a southern Californian rocky intertidal ecosystem. In contrast to Gibson (1972), Littler (1980) used a large number of descriptive parameters to characterize sites. As my sample unit was the intertidal pool, the potential of the effect of site specific conditions could not be ignored. Therefore, pool descriptions were as exhaustive as conditions would permit. In addition, the work of Gibson (1972) suggested that abundance patterns of the numerically dominant species may be influenced by a number of factors, some of which were not obvious to Gibson. A description of variables used in the analysis of habitat preferences follows:

**Elevation**

Pools were distributed from 55 cm above mean high tide (mht) to 207 cm below mht (Table 4). The species with the widest distribution ranges included *P. parvicornis* (-51 to 207 cm below mht), *M. maderensis* (-55 to 181 cm bmht), *C. galerita* (-45 to 207 cm bmht), and *C. labrosus* (-18 to 151 cm bmht). Although most species had broad elevational distributions, a distinction could be made between those showing an affinity for upper shore pools (approximately 0 to 60 cm bmht) and those preferring the lower intertidal zone (approximately 60 to 180 cm bmht). Among the fishes showing an affinity for upper shore pools (group A) were *G. paganellus, M. maderensis, P. parvicornis, C. galerita, and C. labrosus* which were the most abundant tidepool fishes. Middle to lower shore inhabitants (group B) were dominated by species often found sublittorally or
in open waters, e.g., *T. pavo*, *O. atlanticus*, *D. annularis*, *D. sargus*, *A. imberbis*, *A. luridus*, and *E. marginatus* (Fig. 9). However, the lower intertidal zone was not limited to transient inhabitants or species generally associated with the sublittoral zone. The intertidal blenniids, *L. pholis*, *L. trigloides*, *P. pilicornis*, and *S. cristata* were concentrated in mid-lower shore pools.

**Surface area**

Mean pool surface areas for the three islands were comparable at approximately 1.41 m². However, surface areas varied from less than 0.22 m² to greater than 5 m² (Table 4). The pools with the largest and the smallest surface areas were located on Fuerteventura at FV-2, and Gran Canaria at GC-6, respectively. The former contained 121 fish representing 5 species while the latter contained two representatives of a single species.

**Volume**

Pool volume varied dramatically within and between localities (Table 4). The largest pool was on Lanzarote at the Puerto Calero (LZ-8) locality. Sea water inundated the pool before volume was measured completely. The volume recorded was not a true measurement as volume measurement was halted prematurely due to tidal inundation at 3860 liters and estimated at approximately 4000 liters. The smallest pool occupied by a single fish (1.2 liters) was on Gran Canaria at Punta de Puerto Rico East (GC-7).
Maximum pool depth

The deepest pool occurred on Gran Canaria at GC-11, and had a maximum depth of 102 cm. The shallowest pool (5 cm) also occurred on Gran Canaria at GC-10. Overall, Fuerteventura pools had the smallest mean maximum depth at 25.58 cm (Table 4).

Algal cover

Algal cover was highest in Fuerteventura pools with an average of between 60-80% cover. Pools from Gran Canaria and Lanzarote both averaged between 40-60% cover (Table 4). Interisland differences between pools for algal cover were also revealed through a comparison of the frequency distribution of the scale values (1-5) that represented increasing amounts of algal cover (Fig. 10). The overall mode was 1 = less than 20% cover. Thirty-one percent of all pools fell into this category. Thirty-seven percent (mode = 1) of Gran Canaria pools contained less than 20% cover while 33% (mode = 1) of Lanzarote pools had less than 20% cover. Only 13% of Fuerteventura pools contained less than 20% algal cover. In contrast, 40% of pools on Fuerteventura contained greater than 80% cover (mode = 5). The predominant algal forms included *Caulerpa webbiana*, *Cympolia barbata*, *Cystoseira* spp., *Dictyota dichotoma*, *Halopteris scorparia*, and *Padina pavonica*. Cover, in terms of refuge was provided best by the branching algae, *Cystoseira compressa* and *D. dichotoma*. 
Substrate

Although the bed for all the pools on each of the three islands was volcanic basalt, pools varied in the quantity and composition of loose substrate. Pools on Gran Canaria and Lanzarote tended toward bare rock substrate with large boulders and cobble whereas pools on Fuerteventura, on average, contained greater amounts of smaller, loose substrate such as cobble, gravel, and sand (Table 4). The composition of pools in terms of the relative frequencies of substrate types (1-5) was similar for each of the islands. Pools formed on rock substrate that contained little or no loose substrate (scale =1) was the most common category on each of the three islands (Fig. 10).

Shelter

Mean shelter was greatest for pools on Fuerteventura (Table 4). On average, shelter-forming structures other than algae occurred over approximately 60% of the pool bed. On Gran Canaria and Lanzarote, shelter was available over approximately 50% of the average pool. The modes for Fuerteventura, Gran Canaria, and Lanzarote were 3, 2, and 1, respectively. No tidepool on Lanzarote was considered to have shelter on greater than 80% of its bed (Table 4, Fig. 10). This value is somewhat misleading as it does not take into account the macroporosity of a pool. A single cave entrance could conceivably have led to a complex of tunnels and caves in the volcanic basalt that formed the base for every pool.
Salinity

Although salinity varied 11% between pools (Table 4), over 71% of the pools had salinities of at least 37%. The modal salinity was 37% which accounted for 25.7% of the pools. The pool with the lowest salinity (30%) occurred at Famara (LZ-10) on Lanzarote. The pool contained two individuals of *C. galerita*. There was freshwater seepage in the area from a steep cliff area which rose to over 650 meters above the beach. The peaks were usually clouded over and although there was no noticeable precipitation, rock surfaces remained wet due to the high moisture content of the air. It is possible that moist conditions may have affected salinity at LZ-10 and LZ-11 sites. In addition, freshwater seepage from abandoned mines in the cliff face may also have contributed freshwater to these sites. Two pools (both on Gran Canaria) had salinities of 41%. The pools located at GC-1 and GC-7 were both inhabited by *P. parvicornis*. The GC-1 site also contained a single specimen of *M. maderensis*.

Temperature

Both air and water temperatures varied considerably depending on the time of day and the tide. The range of water temperature on Fuerteventura was 7 °C, but on Gran Canaria, the range was 17 °C, and on Lanzarote, 12 °C (Table 4). The highest water temperature (36 °C) was recorded at GC-11 at 14:17, August 17, 1991, the lowest water temperatures (19.5 °C) were at GC-6 at 08:45, August 11, 1991, and LZ-3 at 08:30, August 18, 1993. Air temperatures on
rocky shores were recorded at 39 °C, but sampling at these temperatures was avoided for safety reasons. Hence, it is probable that at times water temperatures exceeded 36 °C in shallow upper shore pools with a black pāhoehoe substrate at times.

**Biomass**

Estimates of biomass included mean SL and extrapolated biomass. The smallest mean SL per pool was recorded on Gran Canaria at GC-4. The pool contained two juveniles of *M. maderensis*. The pool with the largest mean SL also occurred on Gran Canaria at GC-7. This pool contained a male and female of *P. parvicornis* in spawning condition. Pools on Lanzarote tended to be inhabited by larger fishes than either Fuerteventura or Gran Canaria. The occurrence of the pool with the largest mean SL on Gran Canaria was atypical of intertidal pools on that island which were characterized by fishes of smaller sizes than pools of the other two islands (Table 4).

Differences in calculated biomass per pool were more pronounced than differences in mean SL. Mean biomass of fishes from pools on Lanzarote was over twice that of values obtained from pools on Fuerteventura and Gran Canaria. The pool with the highest biomass of teleost fishes (712.8 g) was located at LZ-9 and contained 130 fish representing nine species. The pool with the lowest biomass (0.07 g) was found at GC-4.
Species diversity

Lanzarote had the highest species richness in terms of mean number of species per pool (Table 4). However, the maximum number of species occupying a single pool occurred at GC-4 on Gran Canaria. The pool contained 43 fishes representing 10 species. Species diversity Indices (D) for the three islands were calculated for localities rather than individual pools. Values ranged from a minimum of $D = 0.121$ on Fuerteventura at FV-5 to $D = 0.988$ at GC-4. Fifteen species were collected from GC-4 whereas only three species were found at FV-5 (Table 1). Three species were also found at an adjacent site, FV-4, but the numbers of fish per species were higher and more uniform, resulting in higher overall diversity at this site.

HABITAT PREFERENCES

Relative habitat preferences were assessed in terms of the variables described in the previous section. However the variables, island, Locality, and Dominant Species were included in the examination of relative habitat preferences. Relative habitat preferences of intertidal fishes were examined by using Canonical Correspondence Analysis (CCA) (Ter Braak, 1986, 1987). The sum of all eigenvalues (Total inertia) = 5.056, while the sum of constrained canonical eigenvalues = 1.281. The species/pool variables correlations for the first two canonical axes were $R_1 = 0.803$ and $R_2 = 0.786$. The cumulative variance of the species/pool variables relation explained by the first four canonical axes were 30.3%, 49.5%, 64.9%, and 75.2%. Pool
variables highly correlated with the first species canonical ordination axis included: Dominant species ($R = 0.604$), Number of species ($R = 0.447$), Volume ($R = 0.37$), Substrate ($R = 0.362$), Shelter ($R = 0.3524$), Number of fish ($R = 0.34$), Biomass ($R = 0.322$), and Surface area ($R = 0.308$). Variables highly correlated with the second species ordination axis included: Mean SL ($R = 0.536$), Pool depth ($R = 0.471$), Elevation ($R = 0.41$), Number of species ($R = 0.381$), and Volume ($R = 0.331$). The position and lengths of variable vectors relative to the ordination axes reflect their influence on the axes (Fig 11). In turn, the positions of the species (also plotted on the same axes) relative to the variable vectors are measures of the relationship between the species and the variables characterizing the pools occupied by those species. Additionally, the closer a species occurs to the origin of the two axes, the weaker the association between species and variables.

The canonical ordination biplot of the relationship between the Canarian intertidal species and pool variables did not reveal a strong relationship between species in general and specific variables (Fig. 11). The most abundant species, *M. maderensis* (MMAD), *P. parvicornis* (PPAR), *G. paganellus* (GPAG), *C. labrosus* (CLAB), and *Coryphoblennius galerita* (CGAL) did not show a strong affinity with any variable. Accordingly, they are clustered close to the origin. However, a number of clusters of species associated with a variable or group of variables were clear. *Abudefduf luridus* (ALUR), *Apogon imberbis* (AIMB),
Table 4. A summary of tidepool descriptive parameters for the islands of Fuerteventura, Gran Canaria, and Lanzarote. Numbers in parentheses refer to the number of pools sampled on each island, sd = standard deviation, Min and Max = minimum and maximum values obtained from pools. Species diversity (D) = Simpson’s Index of diversity

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Fuerteventura (n = 87)</th>
<th>Gran Canaria (n = 195)</th>
<th>Lanzarote (n = 72)</th>
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<tr>
<td></td>
<td>mean</td>
<td>sd</td>
<td>Min</td>
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<tr>
<td>Elevation (cm below mht)</td>
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<td>Mean SL (mm)</td>
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Figure 9. Box plot of elevational distributions of species. Distributions are based on pool elevations from all three islands. Mean = ■, 25th and 75th percentiles are represented by the short sides of the box, 95% Confidence intervals = horizontal line through bow, mht = Mean high tide line. Vertical line through box = median value.
Figure 10. Distribution of pools (% total number) based on the amount of algal cover, substrate type, and shelter. Modes for algal cover, substrate, and shelter on each of the islands are indicated by a triangle.
Labrisomus nuchipinnis (LNUC), O. atlanticus (OATL), Scorpaena maderensis (SMAD), and Tripterygion delaisi (TDEL) comprised a cluster of species that showed a strong affinity to pool depth and/or pool volume. In general, these species were found in large pools. The cardinal fish, A. imberbis (AIMB) preferred pools with an overhanging ledge or a large cave. Thalassoma pavo (TPAV) was associated with number of species and pool volume. A similar tight relationship was found between Boops boops (BBOO), Chromogobius britoi (CBRI), C. trutta (CTRU), and S. cristata (SCRI) and the variables, pool depth and mean SL. The distribution of Lepadogaster lepadogaster (LLEP) was influenced by shelter while area was found important to Muraena helena (MHEL).

The efficacy of short-term studies of population patterns as a means of studying the relationships of species in variable environments has been questioned by Wiens (1977), who found that the ecological relationships between species of breeding birds varied over distances of less than 100 m. In addition, Wiens (1977) was not able to attribute this variation in bird communities to biological and physical characteristics of the sites or to body size or bill size. Intertidal rocky shore ecosystems exemplify the term “variable habitat” on both a spatial and temporal scale. The role, therefore, of the present study was not to infer processes such as competition and predation from abundance patterns of species but to relate abundance patterns to general habitat use. The lack of a strong association between abundant
Figure 11. Ordination biplot generated from Canonical Correspondence Analysis of the species abundances/habitat variables. Species names are abbreviated (first letter of genus name followed by first three letters of species name).
species, in particular, *G. paganellus*, *M. maderensis*, and *P. parvicornis* and any of the habitat variables (Fig. 11) concurred with similar (but less comprehensive) findings of Gibson (1972) for *G. cobitis*, *G. paganellus* and *L. pholus*. Inherent in their numerical dominance is resilience to heterogeneous conditions. Hence, a weak relationship between these species and habitat variables may reflect a generalist habit. This inference also finds support from the stronger association between more restricted species (*A. imberbis*, *S. maderensis*, *L. nuchipinnis*, and *T. delaisi*) and variables, mean SL, pool depth, volume, and number of species. A generalist habit does not preclude the possibility that resources are being partitioned intraspecifically by size or sex. This possibility deserves consideration for future study.

**POPULATION STRUCTURE OF MAULIGOBILUS MADERENSI**

Observations of *M. maderensis* were restricted to the islands of Gran Canaria and Lanzarote. The ratio of females to males was 1.1:1 on Gran Canaria and 1:1 on Lanzarote. However, the mean SLs of females and males were considerably lower on Gran Canaria, at 49.26 mm and 49.21 mm, respectively as opposed to 62.61 mm and 65.15 mm for Lanzarote fish. The lower mean size of Gran Canaria individuals did not reflect earlier maturity of Gran Canaria fish as indicated by size ranges of each of the three classes: juveniles, males, and females (Fig. 12). The smallest male identified through gross visual examination of the genital papillae measured 15.8 mm on Lanzarote, less than 3 mm smaller than the smallest male on Gran Canaria.
Figure 12. Size distributions (SL) of Gran Canaria and Lanzarote population samples of *Mauligobius maderensis.*
The smallest female (18.1 mm) was collected from Gran Canaria pools and measured 9 mm less than the smallest Lanzarote female. Juveniles made up 44.3% of Gran Canaria individuals and 27.9% of Lanzarote fish. Mean SLs of juveniles were similar on both Gran Canaria and Lanzarote at 19.49 mm and 20.82 mm respectively.

Population parameters such as sex ratios and size distributions of the sexes often provide pertinent information on the social structure of populations and reproductive modes (Hoffman, 1985). In sequentially hermaphroditic species, the final sex will always be less plentiful than the original sex due to age/size-related mortality. In the protogynous goby Coryphopterus nicholsi, males are less abundant than females and tend to be larger (Cole 1982). Both size and sex have been demonstrated to affect the outcome of agonistic encounters in territorial fishes (Fitzsimons and Seok, 1989). In populations where nest defense depends on size, natural selection would be expected to favor large size in males. The underlying assumption made in the presentation of such sex ratio and size distribution data is that the data represent a valid population sample (i.e., the sampling procedure does not favor one sex or size class). In the presentation of a natural selection model for the control of sex-ratio in spatially heterogeneous environments, Charnov et al. (1981) acknowledged that for animals other than protogynous fishes, "which sex gains relatively more by being large" remained undemonstrated. Hence, at best, population parameters can effectively be
used only in support of other forms of biological data and in the generation of hypotheses for studies concerning the evolutionary and behavioral ecology of a population.

The administration of the anesthetic quinaldine as a fish collection technique is probably less biased than netting or trapping, which are designed to target particular size classes. The approximately uniform sex ratio of *M. maderensis* coupled with highly overlapping size distributions suggested a gonochoristic habit. However, the relatively greater maximum size of males was consistent with a territorial habit in *M. maderensis*.

**HABITAT SELECTION BY MAULIGOBIIUS MADERENSIS**

Differential habitat use by conspecific fishes has been widely reported (Keast, 1977; Laughlin and Werner, 1980; Schlosser, 1982). Consistent with size distribution data that showed differences in the relative abundances of the size classes, there also were differences in the percentage of pools occupied by *M. maderensis* on Gran Canaria and Lanzarote. *Mauligobius maderensis* was present in 73.6% of the pools on Lanzarote and 50.5% of the pools on Gran Canaria. Although individuals of *M. maderensis* comprised similar proportions of the tidepool fishes on both islands, pools on Lanzarote contained over twice the number of fish found in pools on Gran Canaria. (Table 5). As pools on Lanzarote were larger than those on Gran Canaria, contained greater numbers of fishes in general, and occurred farther downshore, it was hypothesized that the lack of concordance between the two
islands in abundance parameters (% *M. maderensis* and numbers of *M. maderensis*) was attributable to differences in the habitat preferences of the size classes rather than to a major shift in habitat use of *M. maderensis* between the two islands. This rationale formed the basis for the approach to the assessment of habitat preferences.

In the assessment of habitat preferences, numbers of fish per pool, mean SL, and biomass of fish were used as response variables. Variables used to predict habitat preferences represented a subset of the variables used to examine relative habitat preferences of species comprising the intertidal teleost community. With the incorporation of an additional habitat variable, dissolved O$_2$, these variables included elevation, surface area, volume, algal cover, substrate, shelter, water temperature, salinity, and maximum pool depth. All the variables were log$_e$ transformed. As collinearity was detected in initial analyses, volume was discarded as an independent variable from regression models in which either biomass or number of fish were the response variables. Results of multiple regression analyses demonstrated the effectiveness of the habitat variables as predictors of number of *M. maderensis*, Mean SL, and Biomass (Table 6). Not unexpectedly, several habitat variables were significant contributors to two or more of the three models. These variables included maximum pool depth, water temperature, surface area, and salinity. Maximum pool depth was negatively correlated with number of fish (R = -0.241), but was positively correlated with biomass (R = 0.226) and
mean SL (R = 0.306). Water temperature and salinity were both negatively correlated with biomass (R = -0.295, R = -0.323, respectively) and mean SL (R = -0.220, R = -0.223 respectively). Surface area was positively correlated with number of fish (R = 0.425) and biomass (0.280). Specific predictor variables of significance (predictor variables that were significant for a single model) included shelter which was positively correlated with number of fish (R = 0.308), elevation which was negatively correlated with mean SL (R = -0.322), and dissolved O₂ (positively correlated with biomass, R = 0.226).

The relationship of habitat variables and the habitat preference response variables (number of fish, biomass, and mean SL) suggested specific habitat preferences of *M. maderensis* existed and also that these preferences were size-related. Larger individuals occurred in deeper pools and avoided conditions of high salinity, low dissolved O₂, and high water temperature. Increased size associated with decreased shore elevation strongly suggested a size-related downshore movement. The apparently contradictory relationship suggested by the negative correlation between maximum pool depth and number of fish appears counterintuitive to the positive correlation between maximum pool depth and biomass. However, an increase in biomass may solely reflect an increase in fish size rather than an increase in abundance as was suggested from the positive relationship between pool depth and mean SL. Hence, an increase in biomass may be accompanied by a decrease in the numbers of individuals. From the relative habitat preferences of the species
that comprised the intertidal community structure, it was already
demonstrated that *M. maderensis* (among other species) showed a general
preference for the upper intertidal zone. In addition, it was shown that the
mid-lower intertidal zone was inhabited by a greater number of species than
the upper rocky shore (Fig. 9). Most of those species were transient or
facultative intertidal inhabitants. Whereas large size in the lower intertidal
area may afford a degree of safety from predation, competition for limited
space, predation, and natural mortality may constrain the downshore
abundance of *M. maderensis*. Another factor that affected the abundance of
larger-sized *M. maderensis* in lower shore pools may have been the availability
of suitable habitat. Shelter was positively correlated with number of fish (R =
0.308) but had a weak negative correlation with mean SL (p = 0.061). An
explanation of this relationship may lie in the way shelter was measured in
pools. Measurement of shelter was based on the proportion of the pool bed
that contained a structure. No reference was made to the quality of shelter. A
negative correlation between size and shelter probably does not reflect a
preference by larger fish for low-shelter pools, but rather an increased space
requirement associated with an increase in size.

Habitat shifts have been widely reported for marine and freshwater
teleosts (eg., Keast, 1977; Laughlin and Werner, 1980). When elevation was
categorized as four contiguous zones and fishes were assigned to four classes
(small, medium, medium-large, and large), the general preference for the
upper-mid littoral zone was still evident. However, a steady increase in the abundance of smaller fish towards the upper littoral zone was clear (Fig. 13). A Kruskal-Wallis rank test corrected for ties (df = 3, H = 100.07, p = 0.0001) revealed a significant trend of increase in size of *M. maderensis* associated with a decrease in shore elevation (cm < mht). When pool profiles were presented for each elevational category, there was an increase in algal cover, shelter, and maximum depth in the direction of the lower shore that suggested a habitat shift as *M. maderensis* increased in size and moved downshore (Table 7). The development of patterns in a species' use of resources with increase in size has been defined as its “ontogenetic niche” by Werner and Gilliam (1984).

The movement downshore by *M. maderensis* represents an ontogenetic niche shift within the intertidal zone that effectively segregates size classes spatially. Intrapool evidence of spatial segregation or habitat partitioning was found in larger pools which, as a consequence of size, contained larger numbers and a wider size range of individuals (probably accounting for some of the noise in the elevation/mean SL relationship). In large pools containing fish larger than 60 mm SL, juveniles and smaller fish (< 30 mm SL) occupied the shallowest portions of the pools (< 30 mm depth). These areas were restricted to ledges and accessory- or side-pools separated from the main pool by an obstructive lip. Large fish (> 60 mm SL) did not forage in these areas at low tide, but occasionally larger specimens traversed narrow shallow channels between pools by a combination of swimming, flipping, and crawling, while
avoiding the wider ledges. In a transfer experiment, four fish, 18, 23, 28, and 32 mm SL were introduced to a small pool with two shallow side pools (22, 24 mm depth). A male, 65 mm SL, occupied the main body of the pool. After a period of 25 mins., the two smallest fish had entered a side pool, while the others took cover in *Padina* clumps close to the surface of the pool. Shallow cover and relatively inaccessible side pools may have afforded some degree of safety for small fish from predation, some of which can be attributed to conspecific cannibalism. Large *M. maderensis* (> 80 mm SL) were frequently observed in pursuit of fish that were smaller than 30 mm SL in open water in large pools. It is unlikely that these smaller fish were pursued for courtship or because they posed a territorial threat. More significantly, successful intraspecific predation or cannibalism was also observed. Although at first the occurrence of mixed size classes within a single pool appears contradictory to the overall pattern of increasing size and decreasing shore elevation, large pools, by virtue of size alone, are more heterogeneous than more typical small pools. The strength of the relationship between size and elevational distribution would probably improve if large pools were omitted and sampling concentrated on smaller pools more typical of a particular locality. I would hypothesize also that the relationship between and elevational distribution will be strongest in wider shores where zonation is less compressed and more pools may be sampled at a given elevation.
Table 5. A summary of descriptive variables for tidepools occupied by *Mauligobius maderensis* on the islands of Gran Canaria and Lanzarote. \( n \) = number of pools where data were collected, \( se \) = standard error.

<table>
<thead>
<tr>
<th></th>
<th>Gran Canaria</th>
<th>Lanzarote</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( n )</td>
<td>Mean</td>
</tr>
<tr>
<td>Elevation</td>
<td>97</td>
<td>36.53</td>
</tr>
<tr>
<td>Surface Area</td>
<td>96</td>
<td>20507</td>
</tr>
<tr>
<td>Volume</td>
<td>98</td>
<td>359.6</td>
</tr>
<tr>
<td>Pool Depth</td>
<td>97</td>
<td>29.49</td>
</tr>
<tr>
<td>Algal Cover</td>
<td>96</td>
<td>2.28</td>
</tr>
<tr>
<td>Substrate</td>
<td>96</td>
<td>2.32</td>
</tr>
<tr>
<td>Shelter</td>
<td>96</td>
<td>2.63</td>
</tr>
<tr>
<td>Dissolved Oxygen</td>
<td>36</td>
<td>8.83</td>
</tr>
<tr>
<td>Species</td>
<td>98</td>
<td>2.99</td>
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<tr>
<td>Fishes</td>
<td>98</td>
<td>12.76</td>
</tr>
<tr>
<td><em>Mauligobius maderensis</em></td>
<td>98</td>
<td>3.3</td>
</tr>
<tr>
<td>% <em>M. maderensis</em></td>
<td>98</td>
<td>42.06</td>
</tr>
</tbody>
</table>
Table 6. Summary of multiple regression analysis of habitat preference variables. Listed predictor variables are those that were significant contributors to the models. \( n \) = number of pools occupied by *Mauli gobius maderensis* where data were obtained, \( R \) square = the amount of variance explained by the complete models, \( p \) = levels of significance for the models and for individual variables.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>( n )</th>
<th>R square</th>
<th>F</th>
<th>p</th>
<th>Predictor</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of fish</td>
<td>77</td>
<td>0.27</td>
<td>4.085</td>
<td>0.003</td>
<td>Surface area</td>
<td>3.927</td>
<td>0.0002</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Shelter</td>
<td>2.494</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Max. depth</td>
<td>2.161</td>
<td>0.034</td>
</tr>
<tr>
<td>Mean SL</td>
<td>76</td>
<td>0.47</td>
<td>7.632</td>
<td>0.0001</td>
<td>Elevation</td>
<td>3.423</td>
<td>0.0011</td>
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<td></td>
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<td></td>
<td>Water temp.</td>
<td>3.272</td>
<td>0.0017</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Salinity</td>
<td>2.562</td>
<td>0.0127</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Max. depth</td>
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<td>0.0121</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Diss. Oxygen</td>
<td>2.223</td>
<td>0.0297</td>
</tr>
<tr>
<td>Biomass</td>
<td>77</td>
<td>0.42</td>
<td>7.025</td>
<td>0.0001</td>
<td>Surface area</td>
<td>2.897</td>
<td>0.0051</td>
</tr>
<tr>
<td></td>
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<td>Water temp.</td>
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<td>0.0038</td>
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<tr>
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<td></td>
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<td></td>
<td></td>
<td>Diss. Oxygen</td>
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<td>0.0065</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Max. depth</td>
<td>2.271</td>
<td>0.0264</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Salinity</td>
<td>2.406</td>
<td>0.0189</td>
</tr>
</tbody>
</table>
Table 7. A summary of tidepool variable means for pools inhabited by *Mauligobius maderensis*. Pools are categorized into four elevational zones, Upper, Upper-Mid, Lower-Mid, and Lower. sd = standard deviation.

<table>
<thead>
<tr>
<th></th>
<th>Upper</th>
<th>Upper-Mid</th>
<th>Lower-Mid</th>
<th>Lower</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>sd</td>
<td>sd</td>
<td>sd</td>
<td>sd</td>
</tr>
<tr>
<td>Surface Area (sq. cm)</td>
<td>17506</td>
<td>25621</td>
<td>31440</td>
<td>15153</td>
</tr>
<tr>
<td>Volume (liters)</td>
<td>191.8</td>
<td>426.2</td>
<td>663.4</td>
<td>466.6</td>
</tr>
<tr>
<td>Pool Depth (cm)</td>
<td>23.84</td>
<td>31.4</td>
<td>16.64</td>
<td>736.2</td>
</tr>
<tr>
<td>Substrate (1-5)</td>
<td>2.13</td>
<td>2.13</td>
<td>2.13</td>
<td>2.5</td>
</tr>
<tr>
<td>Shelter (1-5)</td>
<td>2.33</td>
<td>2.57</td>
<td>2.82</td>
<td>2.5</td>
</tr>
<tr>
<td>Algal Cover (1-5)</td>
<td>1.77</td>
<td>2.42</td>
<td>2.39</td>
<td>2.6</td>
</tr>
<tr>
<td>Salinity (0/00)</td>
<td>36.5</td>
<td>36.7</td>
<td>36.14</td>
<td>35.1</td>
</tr>
<tr>
<td>Dissolved Oxygen (ppm)*</td>
<td>8.9</td>
<td>9.4</td>
<td>9.16</td>
<td>9.95</td>
</tr>
<tr>
<td>Mean SL (mm)</td>
<td>29.5</td>
<td>42.3</td>
<td>50.35</td>
<td>60.7</td>
</tr>
<tr>
<td>Species</td>
<td>2.22</td>
<td>3.1</td>
<td>3.9</td>
<td>3.3</td>
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<tr>
<td>Fishes</td>
<td>10.22</td>
<td>14.97</td>
<td>20</td>
<td>16.8</td>
</tr>
<tr>
<td><em>Mauligobius maderensis</em></td>
<td>5.83</td>
<td>5.05</td>
<td>3.6</td>
<td>4.8</td>
</tr>
</tbody>
</table>

*Dissolved Oxygen subsampled only*
Figure 13. Distribution of size classes of *Mauligobius maderensis* by elevational categories. Pools are categorized into four elevational zones, Upper, Upper-Mid, Lower-Mid, and Lower.
BEHAVIOR OF **MAULIGOBIUS MADERENSIS**

MALE AND FEMALE COLORATION

In tidepools, individuals of *M. maderensis* were recognizable by a conspicuous "checkerboard" pattern. Fish typically exhibited alternating black and white blotches in two rows on each side of the body. The checkerboard pattern was usually replaced in preserved specimens, larger than 60 mm SL, by 12 narrow vertical bars, but persisted in younger fish (< 60 mm SL).

Variation in caudal-peduncle pigmentation (usually attributable to scarring) facilitated recognition of large individuals (> ~ 60 mm SL) that were included in qualitative behavioral descriptions. With the exception of the pectorals, all other fins were heavily pigmented. The smallest individual with basic adult pigmentation was a postlarva of 8 mm SL. Three distinct color phases were recognizable from the degree of pigmentation: (1) Cryptic - in this phase, pigmentation was faint and usually matched the substrate; the checkerboard pattern remained discernable but decidedly faint; (2) Dark - the checkerboard patterning was lost, the entire body became darkened, and the edge of the dorsal fin became vivid lemon-white in large males (the dark phase pigmentation was usually associated with agonistic interactions); (3) Typical - the predominant checkerboard pattern.

Subtle differences in pigmentation between the sexes occurred in courting fish. Courted females (< ~ 60 mm SL) exhibited a faint orange tinge on their pectoral fins. With the exception that male genital papillae were often black
in both preserved and live fish (which was extremely helpful in behavioral observations), *M. maderensis* exhibited very little evidence of sexual dichromatism. Color differences were most pronounced between size classes. The first dorsal fin of fish smaller than 60 mm SL, approximately, appeared vivid cobalt blue with a 1 mm to 2 mm orange border that extended between the I - VI spines. Dorsal fin pigmentation was most intense during lateral displays. In contrast, the pigmentation of the first dorsal of large specimens was variable. Males went from having a sparsely pigmented, mottled pattern in the typical checkerboard phase coloration to vivid black with a lemon fringe (also extending from the I spine to the VI spine) in the dark phase condition. In addition, the pattern was repeated on the second dorsal of these fish. Although dark phase females were observed with dorsal-edge pigmentation similar to males, the dorsal pigmentation was relatively faint. The checkerboard pattern was more distinct in smaller fish, and the dark phase pigmentation was not observed in specimens smaller than approximately 60 mm SL.

**MOVEMENT WITHIN THE INTERTIDAL ZONE**

On wide, gently sloping rocky shores characterized by low energy wave action, heterospecific schools of *M. maderensis, P. parvicornis*, and *Chelon labrosus* migrated upshore with each tidal inundation. At high tide, *M. maderensis* 50 - 110 mm SL routinely ventured from their low-tide tidepool positions into pools and channels upshore at or (on occasion) above mht within the
supralittoral fringe. Foraging aggregations of 4-8 *M. maderensis* individuals spaced apart at < 20 cm remained parallel to, and 50-100 cm behind, the tidal front. *Chelon labrosus* and *P. parvicornis* displayed a similar foraging strategy and often outnumbered foraging *M. maderensis*. The largest heterospecific aggregation occurred on Lanzarote at Arrieta (LZ-3) and contained 82 fish: 19, 38, and 25 individuals of *M. maderensis*, *P. parvicornis*, and *C. labrosus*, respectively. Fish fed primarily on items associated with the substrate, but material suspended by wave action was also taken by each species. Despite a tendency toward territoriality among male *M. maderensis* while occupying tidepools at low tide, no agonistic interactions between foraging fish (conspecific or otherwise) occurred. Although migrations were primarily vertical with respect to shore elevation, *M. maderensis* routinely made lateral foraging excursions while advancing and retreating. For example, a 90 mm individual made a lateral excursion of > 4 m where it came into contact with a 60 mm fish. Both fish remained in close proximity for several minutes near a loose boulder before rejoining the foraging group. No courtship or agonistic (territorial) behaviors were noted. In general, the multispecies aggregations disintegrated as the tide receded. In contrast to the deliberate upshore movement of foraging fishes, downshore movement of *M. maderensis* was erratic. Intraspecific agonistic interactions such as chasing and biting were common among migrating *M. maderensis* as they moved downshore between channels and pools.
In addition to the regular upshore foraging movement, prior to upshore migrations, *M. maderensis* made brief downshore excursions that lasted 2-3 wave cycles. Similarly, groups of 2-10 *P. parvicornis* consistently made downshore trips. However, *M. maderensis* was either solitary or in groups of 2-3 individuals. In large pools, as many as nine *M. maderensis* formed loosely associated aggregations at the area of the pool where initial tidal inundation occurred. As waves flooded the pool, fish moved with the backsurge downshore and reentered the pool immediately on the next tidal surge. This same mode of movement in which fish were carried by the tidal surge and backsurge was used by *P. parvicornis*. Individuals of *M. maderensis* made 2-3 trips although not every fish left the original pool to venture downshore. When their pool of origin was completely filled with seawater, these fish oriented with the incoming waves and began their upshore foraging trips in heterospecific aggregations.

Short-range movement within the intertidal zone has been described for a number littoral teleosts (Goldsmith, 1905, Beebe, 1931; Richkus, 1978; Milton, 1983). In general, descriptions of movement have been limited to reports of short-range foraging excursions at high tide. In a study of the biology of three intertidal blennies, *Coryphoblennius galera*, *Lipophrys pholis*, and *Parablennius gattorugine*, Milton (1983) remarked that each left their respective pools at high tide to forage. With little elaboration, Milton (1983) inferred that movement was probably very restricted, the shortest trips attributable to the
smallest fishes. In addition, no reference was made to schooling behavior among the three blennies. Heterospecific schooling associated with intertidal movement on sandy beaches was noted for juvenile plaice, *Pleuronectes platessa* (Gibson, 1973). Vertical migration occurred along the beach with each tidal inundation. However, migrations were limited to transient intertidal and inshore sandy bottom species. A widely distributed tidepool fish in tropical and subtropical waters of the western North Atlantic, the frill-finned goby *Bathygobius soporator* demonstrated an affinity for their original pools even when displaced a few meters to other pools (Beebe, 1931). Learning ability was hypothesized for *B. soporator* by Aronson (1951) who found that in general fish had little difficulty in locating alternative escape routes when regular avenues of movement had been blocked intentionally. In addition, Aronson (1951) also found that movement between pools often entailed overland jumping between distinct pools. Memory of shore topography was suggested also by movements of the inshore reef blenny, *Meiacanthus nigrolineatus*, which displayed little difficulty in finding its shelter even when movement involved distances of some meters from the shelter (Fishelson, 1975).

Consistent with observations of other intertidal fishes, short-range movement was a characteristic component of habitat use by *M. maderensis*. The formation of heterospecific migratory schools immediately behind the tidal front represents a foraging strategy constrained by tidal action in which
the participant species apparently share resources. However, tidal inundation presents a very limited window of time for foraging fishes to exploit intertidal resources outside the confines of the tidepools to which they are restricted during low tide. Effective exploitation of resources may require that individuals devote their energies toward foraging rather than to the exclusion of competing species. In addition, the formation of heterospecific schools may provide a greater degree of safety from predation. A parallel kind of symbiotic resource sharing has been demonstrated in fishes occupying coral reefs (Robertson and Polunin, 1981). However, conclusions concerning the complexity of the relationship between component species of foraging schools of intertidal fishes, based on observations reported herein, would amount to speculation. With the approach of high tide on some shores, inshore predators may be able to gain access temporarily to the pools inhabited by *M. maderensis* and other littoral fishes. Evidence of upshore littoral movement by inshore predators was provided by the collection of a 50 cm individual of *Muraena helena* from a pool at the FV-1 locality. Although occupation of crevices and caves by *M. maderensis* can provide refuge from more visible inshore predators (serranids, sparids), the same strategy may increase the risk of predation from morays. In addition, octopuses, frequently encountered inhabitants of intertidal pools, also have access to caves and crevices at low tide. By retreating upshore with the advancing tide, intertidal inhabitants reduce their susceptibility to inshore predators. Few if any
inshore predators can negotiate the wave action or the shallow water associated with the tidal front.

Repeated, brief downshore movements of some individuals suggested a function other than foraging or predator avoidance. Brief exploratory excursions to downshore pools facilitates assessment of the habitability of other pools and provides a possible mechanism by which size-related downshore movement can be effected with a minimum of intraspecific interaction among territorial fishes. If we accept the thesis that a primary function of territoriality is the reduction of conspecific agonistic interaction, a fish trapped (or remaining) in a downshore pool not only increases the probability of agonistic interaction but also risks losing a territory in its original pool. A brief exploratory excursion to the downshore pool can provide a rapid assessment of the potential for habitation. In addition, brief repeated downshore movements may provide insights into the behavioral mechanism by which intertidal fishes such as *B. soporator* gain familiarity with local shore topography.

**TERRITORIAL BEHAVIOR**

**Behavioral Elements of Territoriality**

Many littoral fishes of the families Blenniidae, Clinidae, and Gobiidae exhibit social structure (Gibson, 1969) of which territoriality is a major determinant. Territorial (and reproductive) behavior is characteristically comprised of sequences of stereotypic behavioral elements (Qasim, 1956;
Wickler, 1957; Fishelson, 1963; Abel, 1964). However, there is evidence to suggest that the behavior of littoral fishes may not be as rigid as their freshwater and marine relatives (Cody, 1993). A number of distinct, recurrent behavioral elements consistent with a territorial existence were identified. These behavioral elements were integral to territorial defense in M. maderensis. The following elements were distinguished in M. maderensis.

**Perching**

Most tidepool fishes are benthic. Individuals of M. maderensis came to rest within a pool at specific points designated herein as perches. In particular, these resting points were visited regularly and exclusively by males occupying a territory (i.e., resident territorial males). Conspecific fish never came to rest on a perch occupied by territorial fish. Moreover, a fish other than a territorial fish was rarely observed on a perch. Perches consisted of open areas such as widenings in channels, sandy bottoms (devoid of algal growth), shallow ledges (overhangs), or (in larger pools) the exposed surfaces of medium to large sized cobble or rocks (> 20 cm min. length). The size and type of perch preferred by a fish was influenced by the physical characteristics of the pool and the size of the fish. In general, smaller fish occurred in more exposed shallow pools of the upper shore. These pools contained few submerged boulders. As a consequence, fish made use almost exclusively of open areas (channel widenings) as perches. Another difference between large and small males was the manner in which they perched on boulders. Large
males (> 60 mm) conformed to the convex shape of the boulders by arching dorsoventrally (draping). Draping by Hawaiian freshwater gobies may achieve a reduction of resistance to flow in torrential streams (Fitzsimons, pers. comm.). It is possible that draping may serve a similar function in \textit{M. maderensis} at periods of tidal movement.

Although perches within any territory were visited regularly by the occupant male, visiting order was without obvious sequence or pattern. Perching times varied from 10 secs. to 19 mins., but on average lasted less than 1 min. Large males (> 80 mm SL) had greater perching intervals and were less active than smaller males; i.e., males larger than 80 mm SL spent less time patrolling than did smaller males. The individual (= 90 mm SL) that perched for 19 mins. had successfully preyed on a conspecific fish (= 40 mm SL). The predator fish remained at the perch until the prey was completely ingested.

\textbf{Patrolling}

Patrolling included movement of a territorial male within its territory that ultimately resulted in conspecific encounters. The consistent use of perching spots as rest stations by the territorial resident male was characteristic of patrolling activity. Movement between perches varied and was either a direct darting motion or an indirect "amble" that included foraging stops.
Lateral display

In this behavior, the displaying male turned broadside to the recipient of the display, hence the designation "lateral display." Such lateral presentations by males of *M. maderensis* characteristically involved the erection of both dorsal fins. Dorsal fin erection was always accompanied by flaring of caudal and anal fins. In addition, the displaying fish raised its body by lowering the pelvic fins. The pectoral and anal fins functioned as a "tripod" in this position. The genital papilla, usually not visible during perching or while the fish is resting, also became visible.

Lateral orientation

Although laterally displaying fish were always separated by a body length, their initial orientation with respect to each other was either in the same (parallel) or the opposite (anti-parallel) direction. An adjustment to the lateral display ensued only when fish were parallel. In conspecific territorial encounters, the intruder rapidly reoriented its body so that it was anti-parallel to the displaying resident male. The resident male did not adjust its posture \((n = 39)\). The significance of lateral orientation was that it acted as a cue for a change in the level of intensity of the lateral display. At this point, the characteristic checkerboard pigmentation patterns were replaced by a uniform black/dark brown pigmentation. In large fish \((> 60 \text{ mm SL})\), the dorsal fringe became a vivid lime/white. In fish smaller than 60 mm SL, the first dorsal appeared cobalt blue with an orange fringe. The caudal and anal fins were
flared so that the second dorsal, caudal, and anal fins appeared continuous. Although difficult to observe in small fish, the genital papilla of large males became more visible during lateral display by becoming erected and darkly pigmented.

**Face-away**

In this posture, the body of one fish was positioned anti-perpendicularly (along the substrate) to another (laterally displaying) fish. The tail of the former was closest to the laterally displaying fish (i.e., facing directly away from the display). In addition, the dorsal fins previously raised during lateral display, were lowered slowly as the fish faced away from the displaying fish. When both fish engaged in lateral displays, the intruder always ceased displaying laterally before the occupant. Cessation of a lateral display was marked by a 90° “about turn” by the conspecific intruder so that it faced away from the laterally displaying resident fish. The occupant fish either remained in this position or turned 90° so that it faced the same direction as the intruder. The distance maintained between the two fish was approximately one body length. The face-away posture was accompanied by a return to the typical checkerboard pigmentation pattern.

**Chasing**

In territorial chases, conspecific pursuit by the resident male was maintained for a distance of at least 30 cm. However, pursuits of greater than 1 meter were observed in larger channelized pools that contained more than
one territory and where *T. pavo* and *P. parvicornis* were generally absent. In a larger pool (at GC-3), where a number of contiguous territories existed, the pursuit of an intruding male designated B₁ by a territorial male A₁ resulted in a cascade of conspecific interaction. The expelled intruder B₁ chased and attempted to bite the next-nearest conspecific male B₂ while in flight. This agonistic behavior was repeated by B₂ on another fish B₃ (B₁ > B₂ > B₃ >...). Six fish were involved in a single cascade which suggested a dominance hierarchy.

**Biting**

Biting was associated with chasing and withdrawal, with bites directed toward the median and paired fins. Characteristically, bites were executed by rotating the body laterally about 90° while in pursuit. Pursued and withdrawing fish directed bites toward the substrate or toward conspecifics, if present.

**Withdrawal**

Withdrawal involved movement of a conspecific territorial intruder to a distance that did not elicit a response from the resident fish. This distance in all observations was 30 cm or greater but appeared to be determined by pool topography. In pools with highly varied topography, such as those containing large numbers of channels, boulders, and cobble, fish generally retreated to a position where they were obscured from view of the nest of the territorial
resident. Hence, withdrawal did not necessarily entail complete withdrawal from a territory.

In pools containing abundant algal cover, withdrawing fish grasped tufts of algae while in flight by momentarily flipping (approximately 90°) to one side and then the other while in motion. At least some of the contents of the fish's mouth were then ejected and reengulfed. In an approximate distance of 50 cm, a fish of 70 mm was able to grasp material three times while in motion. The grasping motion was similar to biting behavior in that it involved a momentary 90° lateral flip of the body.

**Circling/Gaping**

Circling involved two laterally displaying males that had oriented anti-parallel with respect to each other. The two participating fish flexed their bodies laterally and concave with respect to each other. The distance separating the head of one fish from the tail of the other was a little under a body length. In synchrony, both males slowly arched their heads upward and began to gape. The two participant fish then went into a circling motion while remaining approximately one body length apart at the trunk (heads and caudal fins were closer). Gaping was not maintained continuously while circling; rather, mouths were closed and opened slowly but regularly. In two observations, each fish, in synchrony, opened and closed its mouth four times per rotation. During circling movements, the opercular flaps of the two fish were flared open and closed at the same rate. Fish paused briefly after rotating
180° before completing each rotation. Circular movement recommenced after
each pause with a brisk snap of the posterior body and tail. A maximum of
five complete rotations (10 pauses) were observed for two fish (80 mm SL
Intruder, 85 mm SL Resident). Circling occurred only twice where all the
behavioral components leading to, and following circling were completed. In
both cases, the intruder discontinued circling first and was immediately
ejected (chased) from the vicinity. An interesting effect of circling behavior,
which facilitated identification of high activity pools, was sediment
disturbance. In sandy bottom pools, sediment became waterborne due to
movements of the fish. In both completed territorial sequences, a circular
track remained. These circular tracks were conspicuous in large pools dusted
with sand at Las Meloneras (GC-3) Gran Canaria.

**Territory**

Few generalizations can be made concerning the physical characteristics of
the territories inhabited by males of *M. maderensis*. The only constant feature
was the presence of at least one shelter structure that also functioned as a
nest-site. Consistent with their widespread distribution throughout localities
that included a variety of habitat types, territories reflected the habitat
characteristics of the particular pool and surrounding rocky shore. The size
of the territory was constrained by the size and the physical characteristics of
the tidepool in which it was established. Pools with as many as five
contiguous territories were found at Las Meloneras (GC-3). In general, these
pools were large and structurally complex; shelter was abundant, as were perching spots. Pool size and structural complexity may have been factors that influenced the number of territories in a pool, but the presence of predators, territorial defensibility from conspecific intruders, potential for nest construction, male size, and population density probably influenced the numbers and sizes of territories at a locality. At the same site (GC-3), a single pool estimated at 5,000 liters formed the territory of a single male (> 100 mm SL). The pool contained abundant shelter for nest construction, but equally as important was the presence of eight perching spots which facilitated territorial defense. A distinct dorsal scar on the mid-caudal peduncle of the male allowed identification of this individual in the same pool for the duration of behavioral observations (1991-1993). Single-territory pools, occupied by males 60 - 80 mm SL, were much smaller (mean Volume < 400 liters) at GC-3, GC-5, GC-6, GC-7, LZ-5 sites. In contrast to the pools at these sites, the Orzolo site LZ-2 contained the largest concentration of individuals of *M. maderensis* in a single pool. A single pool contained 86 individuals (mean SL = 37.1 mm), of which, 21 were identified as males, 22 as females and 43 as juveniles. The measured volume of this pool was 970 liters. In addition, no other teleost species was found in the pool. Shelter in this pool was largely limited to cracks and crevices in the volcanic substrate. Much of the pool's volume was contained within these cracks and crevices and was not visible from the surface.
In marine and freshwater environments occupied by territorial fishes, only occasionally can territory size be characterized in terms of fish size (Fitzsimons et al., 1993) and number of fish (Larson, 1980). In most examples, factors such as habitat type (Warner, 1991), population density (Warner and Hoffman, 1980), predation (Stephens et al., 1970), and feeding patterns (Choat and Bellwood, 1985) may be important in the selection of a territory. Despite the spatial heterogeneity of the intertidal habitat occupied by *M. maderensis*, classical indications of territorial delineation (Roberts, 1986) were evident. These included exclusive perching spots, locations of agonistic interactions (disturbed substrate), and the localization of the individual to a particular area (e.g., nest-site). However, the establishment of territories may depend on habitat type as suggested from huge variation in the numbers of fish per pool. Whereas the high cover pools at Las Meloneras (GC-3) and Montaña la Arena (GC-4) facilitated the establishment and maintenance of territories by male *M. maderensis*, the highly macroporous pools at Orzolo (LZ-2) may have been better suited to a different life history strategy in which territories were either greatly reduced in size or did not exist at all.

**Territorial Defense**

Territorial behavior of male *M. maderensis* consisted of a sequence of distinct and stereotyped behavioral elements. However, each behavioral element was not included in every territorial behavior sequence (Table 8). Specifically, the outcome was variable (Fig. 14). A complete territorial
sequence is represented diagrammatically in Fig. 15. In the absence of a conspecific intruder (male or female), the territorial male divided its time between patrolling, perching, and foraging of which the latter was the least observed. The introduction of a conspecific intruder into the territory of the resident male resulted immediately in one of three responses by the resident. These were immediate chase, lateral display, or the resumption of perching, patrolling or foraging (previous activity). In turn, a laterally displaying resident elicited one of three immediate responses from the intruding conspecific male. These included lateral display, face-away, or withdrawal. In general, when the intruder either responded by adopting a face-away posture or by withdrawing from the immediate vicinity, the resident returned to previous activities (foraging, patrolling and perching) (Table 8). However, fish that exhibited the face-away posture were occasionally chased (Table 8). When both fish were positioned anti-parallel with respect to each other, a lateral display by the intruder led to the initiation of circling behavior by the resident. Adjustment of the lateral display by the intruder occurred only when both fish faced in the same direction (parallel). Almost in synchrony, both fish circled, gaped and paused at each half rotation. A space equivalent to one body length apart was maintained throughout the rotation. When the intruder ceased circling, the response of the resident was to chase and to bite at the intruder as it withdrew. A resident fish never withdrew from its territory or was chased by an intruder (Table 8).
It is clear that the territorial behavior of *M. maderensis* involved an ordered sequence of stereotyped behavioral elements (Figs. 14 and 15). Exclusive use and defense of resources within a territory are implicit in the classical definition of territoriality. The varied response by territorial males to conspecific intruders raises a question concerning this definition. As was evident from the success of intruding conspecific fish that foraged within the territorial boundaries often within view of the resident male, exclusivity of use among territorial individuals of *M. maderensis* did not include food resources. By and large, territorial males spent less time foraging than did conspecific intruders. In general, the foraging activity of territorial fishes was largely limited to periods of tidal inundation and restricted to areas of the shore above the home pool (containing its territory).

Although territorial behavior did not involve the defense of food resources, the behavioral repertoire of *M. maderensis* was consistent with that of other territorial gobiids with the exception of the face-away posture. Face-away or an equivalent posture has not been described for gobiids and as such may represent an adaptation to conditions in the rocky intertidal pools of the islands of Macaronesian chain to which *M. maderensis* is endemic. A prolonged pause by the defeated intruder prior to withdrawal may be selectively advantageous if it increased the probability of a cessation of agonistic interactions, thereby increasing the time available to forage and the
relative safety of the foraging individual. In addition, at some sites the whole pool was included in the territory of a single male of *M. maderensis*. Escape would have entailed potentially hazardous out-of-water movement without the assurance of escape to a safer pool. Conversely, a reduced territorial response by the resident fish is selectively advantageous to the territorial fish if the cost associated with allowing an intruder to remain within the territory was less than that associated with excluding an intruder. Energy expended in territorial defense could be redirected to growth, courtship and gamete production. The evolution of the face-away posture suggested a dominance relationship in which prior residence is a factor in the outcome of agonistic interactions as is the case with the naked goby, *Gobiosoma bosci*. In aquarial territorial disputes involving individuals of one sex, the prior resident (regardless of size) always succeeded in occupying a provided shelter when two fish were introduced simultaneously to the aquarium (Fitzsimons and Seok, 1989). Regardless of size in *M. maderensis*, prior occupancy was the major determinant in the outcome of territorial encounters (Table 8). In addition, if a dominance hierarchy existed among *M. maderensis* within a particular pool or group of pools, one would expect an unfamiliar intruding fish to elicit a relatively elevated response from the resident male. Furthermore, an unfamiliar intruding conspecific may also be more inclined to challenge a fish that it had not encountered previously. Familiarity may
explain why some intruding *M. maderensis* responded to the lateral display of a territorial fish by facing away rather than challenging the territorial fish. The varied territorial interaction of intruder and territorial resident coupled with the relationship between shore elevation and fish size provides the basis for a simple size-dependent model of social structure. As indicated earlier, a general downshore movement associated with increasing size in *M. maderensis* can be reliably inferred from the elevational distribution of individuals of *M. maderensis*. Although habitat partitioning or niche shift based on size is common among fishes (Laughlin and Werner, 1980), predation and interspecific competition are mostly advocated to explain temporal and spatial distributions of the size classes in fishes (Werner, 1984). The relationship between size-dependent habitat shifts and reproductive fitness remains largely unexplored. A general downshore shift in habitat preference associated with increasing size not only allows *M. maderensis* to exploit differentially the spatial heterogeneity of the rocky shore but also to constrain conspecific interactions between individuals based on size. The hierarchical nature of conspecific interactions was strongly suggested by (redirected) agonistic behavior of a pursued intruder as it withdrew from the territory. The pursued intruder either briefly chased another conspecific fish, which resulted in a cascade of agonistic behavior among individuals, or (when conspecific fish were absent) grasped algal clumps while withdrawing.
Table 8. Territorial behavior in *Mauligobius maderensis*. A summary of observations from the islands of Gran Canaria and Lanzarote. Numbers in parentheses show calculation of number of observations. Symbols show where numbers originated.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>No. Obs.</th>
<th>% No. Obs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conspecific encounters (Orientation of occupant male)</td>
<td>92</td>
<td>100</td>
</tr>
<tr>
<td>Initial lateral display by occupant</td>
<td>75</td>
<td>81.5</td>
</tr>
<tr>
<td>Initial lateral display by intruder</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Intruder elicits no response after initial orientation by occupant +</td>
<td>6</td>
<td>6.5</td>
</tr>
<tr>
<td>Intruder withdrawal (no chase)</td>
<td>6</td>
<td>6.5</td>
</tr>
<tr>
<td>Intruder chased prior to display ^</td>
<td>5</td>
<td>5.4</td>
</tr>
<tr>
<td>Intruders eliciting a response from occupant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intruder lateral display (response)</td>
<td>39</td>
<td>42.4</td>
</tr>
<tr>
<td>Occupant face-away</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Intruder face-away*</td>
<td>47</td>
<td>51</td>
</tr>
<tr>
<td>Face-off (dual lateral display)</td>
<td>14</td>
<td>15.2</td>
</tr>
<tr>
<td>Circling/gaping</td>
<td>2</td>
<td>2.2</td>
</tr>
<tr>
<td>Intruder chased after displaying ^</td>
<td>36</td>
<td>44.6</td>
</tr>
<tr>
<td>Intruder remaining in territory</td>
<td>45</td>
<td>48.9</td>
</tr>
<tr>
<td>No face-away</td>
<td>6</td>
<td>13.3</td>
</tr>
<tr>
<td>Face-away</td>
<td>39</td>
<td>82.8</td>
</tr>
<tr>
<td>Intruders chased</td>
<td>41</td>
<td>100</td>
</tr>
<tr>
<td>No face-away</td>
<td>33</td>
<td>80.5</td>
</tr>
<tr>
<td>Face-away</td>
<td>8</td>
<td>19.5</td>
</tr>
</tbody>
</table>
Figure 14. Territorial behavior of *Mauligobius maderensis*. Solid lines with arrows refer to the sequence of behaviors. Dashed lines refer to behaviors that apparently elicited a response from the individual towards which the behavior was directed.
Figure 15. A diagrammatic presentation of a complete sequence of territorial behavior. Large arrows refer to the direction of the sequence whereas thin arrows indicate movement of the participant fish.
REPRODUCTIVE BEHAVIOR

Behavioral Elements of Courtship and Spawning

As with territorial behavior, courtship and spawning were comprised of a number of repeated behavioral elements. Of these behavioral elements, a number were common to both territorial and reproductive behavior sequences. However, courtship also contained specific elements.

Perching

Perching was restricted to a 50-cm radius around the nest during courtship and nest guarding. Nest-guarding males restricted their perching to ledges above the nest entrance and to areas directly in front of the entrance.

Patrolling

Nest-guarding males typically did not patrol a territory in the same manner as did males that had not recently spawned at a particular nest site (prior spawnings may have occurred at other sites). In large pools where nest sites were at a distance greater than 1.5 m from the nearest perimeter of the pool, excursions were short (<1m) and brief (<30 secs.). Hence, intermittent perching activity concentrated either in or around the nest entrance (<30 cm from the nest entrance). Foraging activity was restricted to a 20-50 cm radius from the nest. At the GC-3 locality where algal mats of Caulerpa spp. were distributed within pools, nest guarders were easily recognized by vigorous short feeding trips to the algal mats followed by immediate return to the nest.
Lateral display

In courtship displays as in territorial displays, the dorsal fins were erected. However, the tripod stance characteristic of the lateral territorial display was replaced by a perching stance in which the body of the displaying male remained closer to the substrate. However, the genital papilla of the male remained visible despite its proximity to the substrate.

Face-away

In this posture, the body of the female was positioned anti-perpendicularly (along the substrate) to the laterally displaying male. The tail of the female was closest to the male at a distance of approximately one body length. Unlike the face-away posture of intruding conspecific males in which the dorsal fins were lowered, the dorsal fins of the female were not noticeably lowered during face-away.

Chasing

Two forms of pursuit associated with courtship and spawning were distinguished. Unreceptive females were either chased from the vicinity of the nest (30-50 cm) after an unsuccessful courtship sequence or were pursued as a continuance of courtship activity.

Withdrawal

Withdrawal by the female to a distance that did not elicit a response from the resident male was direct (i.e., without pauses). Similar to territorial withdrawal, the distance at which the male ceased responding to the presence
of the female varied with pool topography. Unlike withdrawing males, females did not grasp at algal tufts.

**Circling**

A distinction between circling motion associated with territorial defense and with spawning was apparent. Unlike territorial circling where the two males circled in synchrony, during courtship the male circled a stationary female during courtship. In addition, no gaping or pausing occurred, and movement was in a tighter circle. The male rounded the female, and the motion culminated in the parallel positioning of the male's body with respect to the stationary female. Although the male was parallel to the female, it came to rest approximately a head length behind the female. A distance of less than one pectoral extension was maintained between the fish.

**Showing/leading**

Showing/leading was used to describe movement of the male toward the nest during courtship. The male broke away from a lateral display temporarily and darted around the stationary female toward the nest entrance. As the male passed the female brief lateral contact was made. At the nest entrance, the male paused and turned briefly toward the female. The male then moved from the nest entrance and resumed its lateral display. This behavior was repeated at least twice. On each occasion, the location of the lateral display prior to and subsequent to showing/leading remained the same.
**Nudging/touching**

Nudging was a behavior exclusively associated with reproductive behavior. The action involved momentary contact between the male and female prior to entering the nest. If receptive, the female entered the nest slightly in front of and in contact with the male. Repetitive nudging (referred to herein as shunting) was witnessed in pools containing a single pair of individuals. The movement was similar to nudging but more rapid. The female entered the nest in contact with, and slightly in front of the male but exited immediately. The male circled the female and nudged her towards the nest which she reentered. On one occasion, the process was repeated six times without interruption at a LZ-5 pool.

**Quivering/spawning**

As male and female (in contact) entered the nest, both fish initiated a quivering movement. The motion consisted of rapid lateral shaking of the fishes bodies and caudal fins that resulted in the suspension of sediment in the nest entrance. It was only possible to observe movement of the posterior half of both fishes as quivering occurred partially inside the nest entrance.

**Nest-Site**

A single nest-site was located within each territory. The position of the nest-site was variable. The undersides of large cobbles (> 20 cm diameter) with limited access (i.e., a single entrance), cracks, and crevices in the lava substrate were preferred sites. In pools containing a light covering of
sediment and pebbles, nest modification and maintenance that involved a minimum of construction was observed regularly. Nest maintenance entailed rapid tail movement and circling within the nest (in the absence of a female). The fanning motion aided in expelling light sediment from the nest interior.

A number of gobioid fishes are reported to construct nests. The intertidal mudskipper *Periophthalmus sobrinus* builds an elaborate U-shaped burrow with accessory chambers and raised entrances (chimneys) in uncanopied mud flat beaches (Stebbins and Kalk, 1961). Members of the genus *Taenioides* also construct complex burrows (Rao, 1939). In contrast, the sand goby, *Pomatoschistus minutus*, also a soft-substrate inhabitant, first selects an area covered by hard objects such as shells (Lindström, 1988), the nest is then excavated underneath the objects. Breder (1942) found the eggs of *Gobiosoma robustum* on the undersides of shells and sponges, but males guarded eggs attached to exposed surfaces of clam shells in aquaria. Extensive excavation by *M. maderensis* was witnessed once only, in a large (= 3.3 m², surface area), moderately exposed pool (40-60% structural cover) at the GC-3 locality at dusk. A male (70 mm SL) located a site at the edge of a pool channel in approximately 25 cm of water. Prior to the construction of the nest the male began to establish a territory by chasing conspecific males and females that came within a 25-30 cm radius of the chosen site. The prevailing pool substrate consisted of eroded A‘ä base covered with a layer of sand (= 5 mm
thickness). Tufts of *Caulerpa webbiana* occurred in the shallower areas of the pool and extended into pool channels where the alga was fastened to small rocks 10-20 mm (max. length) embedded in the sand. Dead alga was infiltrated with sand and behaved as "plugs" in pool crevices. The nesting male grasped mouthfuls of sediment and displaced them to a single pile at a distance of = 25 cm from the site. After each return to the nest, the fish paused for several seconds before grasping the next mouthful and leaving the site. Forty-two excavation trips were observed until light conditions did not permit further observation. The presence, however, of the same fish in the entrance of the new nest two low tide periods later, confirmed the function of the excavation behavior.

**Courtship and Spawning**

Seven instances of courtship were observed (involving different pairs of males and females), of which two resulted in spawning (Table 9). These observations provided an adequate outline from which the reproductive behavioral sequence of *M. maderensis* was constructed (Fig. 16). In its initial stages, this sequence of behavioral components comprising courtship and spawning was similar in many respects to territorial defense (Fig. 14).

In the absence of a female, the male partitioned its time between perching and patrolling. As the male and female encountered each other, the male began to display laterally as it did when a conspecific male intruder entered the area. During the lateral courtship display, the genital papilla of the male
became erect and darkly-pigmented. The face-away posture adopted by initially unreceptive females did not result in the male returning to its previous activities as it often did in territorial encounters (Table 8). In contrast, when the female faced away, the male rounded the female and displayed laterally again (Fig. 16). Movement of the female from the vicinity of the nest was necessary before a courting male would cease displaying laterally. In one case (at GC-4), a male (60 mm SL) pursued a female (80 mm SL) away from the nest site over a distance of at least 1 m. During this period, the male made seven attempts to display laterally to the female, who remained in flight throughout, albeit interrupted by the displays of the persistent and unsuccessful male. This observation was included once only in the enumeration of behavioral elements as it involved multiple unsuccessful courtship attempts between the same two fish. Similarly to a challenging male intruder, females receptive to the lateral display of the courting male responded by also displaying laterally. During the lateral display, the female faced in the opposite direction (anti-parallel) to the male and remained a body-length apart.

Unlike territorial encounters, in which both laterally displaying males engaged in circular movement (Fig. 15), the female remained stationary while the male initiated circular motion (Fig. 17). The male rounded the female so that both fish were parallel. As the male rounded the female, it brushed the female laterally. The male paused for less than a second as it contacted the
female and then continued in the direction of the nest entrance. Following a 180° turn in the nest entrance, the male paused briefly (< 1 sec.) and circled the female again. On this occasion, contact between the male and female consisted of a lateral nudge by the male that resulted in movement of the pair toward the nest. Both fish remained in contact, the female about a head length in front of the male as they entered the nest (Fig. 17). A single nest with a wide entrance and shallow interior provided the only view of a pair as they entered the nest. The partially visible posterior halves of both fish quivered in synchrony within the nest. The quivering motion, which caused sediment and particles to become water-borne, was particularly pronounced in the caudal fins of both fish. The female disappeared from view first due to her position slightly in front of the male. After a period of less than 30 secs., the pair exited the nest. Although the female remained in front of the male, the pair were now separated by a body length. Following a brief pause at the nest entrance, the female, which had assumed a face-away posture, was chased from the nest-site and departed the vicinity (= 30-50 cm radius). The male, however, returned to the entrance and alternated perching activity between the mouth of the nest and a ledge above the nest entrance.

Participation by the female in parental care (nest-guarding) was suggested from a number of "joint occupancies" (Table 9), where for one low-tide period of the tidal cycle both a male and a female occupied a nest site simultaneously. However, on occasions where the male departed the nest
and was replaced by the female, defensive actions (such as perching, lateral display, or pursuit of a conspecific fish) by the female were not observed. Careful monitoring of nest sites in which a female was noted at the previous low tide revealed that joint occupancy was not maintained through to the following low tide. Departure of a female (60 mm SL) from a nest in a GC-3 pool immediately following a successful spawning with a male (60 mm SL) resulted in increased activity from other pool inhabitants, namely, *P. parvicornis* (*n* = 10) and *T. pavo* (*n* = 2). Both species briefly invaded the nest (2 mins. duration) and displaced the resident male *M. maderensis*. Although the female returned to the nest during this period, only the male attempted to chase and bite swarming individuals of *P. parvicornis* and *T. pavo*. Throughout the nest-raid, the female remained within 15 cm of the nest entrance in a resting position (median fins lowered, ventral side in contact with the substrate). Within 15 secs. of the departure of the last nest-raider, the male resumed perching activity above the nest entrance. Although the female remained near the nest (< 30 cm away), no courtship occurred again during the same tidal cycle. Hence, the reproductive behavior of *M. maderensis* was consistent with the general model for territorial benthic teleosts in which the male is the sole participant in nest-guarding and territorial defense (e.g., Breder, 1942; Fishelson, 1963; Breder and Rosen, 1966; Moore, 1970; Nishimoto and Fitzsimons, 1986; Fitzsimons et al., 1993). Within the
territory, a single nest site was maintained at least during the reproductive season by the resident male. Females that entered the area of the nest were courted, and spawning occurred within the nest. In terms of behavioral elements that were specific to courtship and reproduction in *M. maderensis*, repeated nudging of the female (shunting) warrants consideration. Repeated nudging may have evolved as an adaptation to the spatially restricted environment of tidepools where a previously courted, unreceptive female cannot easily escape the attentions of a courting male. Just as escape to a new pool by a pursued male intruder cannot ensure greater safety from conspecific agonistic encounters, movement to a new pool by the female does not ensure successful spawning. The strategy (which in this instance may represent the optimal strategy) may simply be to "place all her eggs in one basket." A female that repeatedly spawns with the same male may at least realize some genetic return for the energetic investment associated with egg production. Similarly, for the male, the energetic costs associated with courtship, nest establishment, maintenance, and defense will yield some return for the energy expended. The interpretation of repeated nudging as an adaptation to tidepool spawning is further supported by the omission of the behavioral steps leading up to nudging and ultimately the reentrance of the nest by the female (Fig. 17).
Table 9. Reproductive behavior in *Mauligobius maderensis*. A summary of observations from the islands of Gran Canaria and Lanzarote.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>No. Obs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Courtships</td>
<td>7</td>
</tr>
<tr>
<td>Initial lateral display by male</td>
<td>7</td>
</tr>
<tr>
<td>Female lateral display (positive response)</td>
<td>2</td>
</tr>
<tr>
<td>Female face-away (negative response)</td>
<td>5</td>
</tr>
<tr>
<td>Female chased from territory after face-away</td>
<td>2</td>
</tr>
<tr>
<td>Continued courtship by male after female face-away +</td>
<td>1</td>
</tr>
<tr>
<td>Circling by male</td>
<td>2</td>
</tr>
<tr>
<td>Showing of nest cavity by male</td>
<td>2</td>
</tr>
<tr>
<td>Pursuit by male (in contact)*</td>
<td>2</td>
</tr>
<tr>
<td>Female and male enter nest</td>
<td>2</td>
</tr>
<tr>
<td>Quivering (spawning?)</td>
<td>2</td>
</tr>
<tr>
<td>Female reenters nest#</td>
<td>(2), (5)</td>
</tr>
</tbody>
</table>

+ Male not associated with territory
* Pursuit towards nest (nudging)
# Reentering nest associated with courtship
(Numbers in parentheses refer to number of times a female reentered the nest)
Figure 16. Reproductive behavior of *Mauligobius maderensis*. Solid lines with arrows refer to the sequence of behaviors. Thick dashed lines refer to behaviors that apparently elicited a response from the individual towards which that the behavior was directed. Thin dashed line and arrow denotes truncation of sequence. The shaded area indicates that the behavior occurred within the nest.
Figure 17. A diagrammatic presentation of a reproductive behavior sequence in *Mauligobius maderensis*. Large open arrows refer to the direction of the sequence whereas thin arrows indicate movement of the participant fish.
EVOLUTIONARILY STABLE STRATEGY

Any discussion of the reproductive strategy of *M. maderensis* should necessarily include careful consideration of territoriality. Territorial behavior (defense) is widespread among fishes (Hixon, 1981). Myrberg and Thresher (1974) made the observation that territorial behavior represents "a conspicuous determinant of social organization" in reef fishes. This is also true of fishes from other environments, including the intertidal zone. Within intertidal rocky shores, males of *Lipophrys (Blennius) pavo* defend permanent territories (Fishelson, 1963). Both males and females of *Ophioblenius atlanticus*, a transient intertidal inhabitant, maintain permanent territories in which they feed (Nursall, 1977) although territoriality in *O. atlanticus* has not been observed in the intertidal zone. On tidal mud flats, territorial males of *Periopthalminus sobrinus* exclude conspecific fish (Stebbins and Kalk, 1961).

At a minimum, exclusion of conspecific males (exclusivity of use) is inherent in the classical definition of the territory of an animal as a "defended area" (Noble, 1939; Burt, 1943). Territorial defense among males of *M. maderensis* does not necessarily involve exclusion of conspecific fish and as such is somewhat selective. A reevaluation of the interpretation of territoriality therefore may be in order. Reese (1978) suggested that resource use (and the benefits) should be the focus of attention rather than defense and its associated cost. Food cannot be considered as an exclusive defended
resource as intruders remained to forage within view of the territorial occupant. As previously mentioned for territorial fish and others, foraging effort was concentrated during tidal inundation to the intertidal zone above the home pool. As a result, fishes that occupy the lower shore pools have access to a larger foraging area than those found in upper shore pools. In addition, by virtue of territory (pool) position, lower shore inhabitants also have a greater period of time in which to forage. Although food may not be considered a defended resource, the location of the territory may (incidentally or otherwise) confer foraging benefits on the territorial occupant.

If direct resource use and the associated benefits are the focus of attention, then one of the benefits of territorial behavior to males of *M. maderensis* is exclusive access to the females that enter the territory. Conversely, the benefit to the female will be choice of spawning partner. However, given the patchy distribution of tidepools, their physical heterogeneity, and temporally restricted accessibility to both sexes, the reliance on an inflexible territorial life history strategy may well be maladaptive. The high densities of individuals at LZ-2 pools seem to suggest that an alternative reproductive strategy to territoriality may operate under certain conditions. Although such an evolutionarily stable strategy (ESS) necessitates the abandonment of one strategy in favor of the other as conditions dictate, "switching" of this nature has been noted in other marine fishes. Warner (1991) remarked that Fitch and Shapiro (1990) found only pair-spawning in a habitat that supported low
densities of individuals of the bluehead wrasse *Thalassoma bifasciatum*
whereas both pair-spawning and group-spawning were noted for this species in high density habitats by von Hebring (1988). Nesting aggregations of the intertidal blenny, *Parablennius parvicornis*, were noted where the ratio of males to females varied between sites (Cody, 1993). The topography of these nest pools would have made nest guarding very difficult as the egg-covered undersurfaces of the boulders were accessible to fishes from many directions. In pools that contained isolated boulders, male *P. parvicornis* maintained an exclusive area around the nest-site (in prep.). To exploit the spatial heterogeneity that characterizes the intertidal rocky shore, maximization of reproductive potential may require a higher degree of behavioral flexibility than is required in less variable environments. Male redlip blennies *Ophioblennius atlanticus* experiencing low reproductive success switch from one nest to another between reproductive periods (Côte and Hunte (1989). However, high densities of male *M. maderensis* in a pool does not preclude the possibility of male territoriality. Territorial males frequently encountered non-territorial (intruding) males on their territories (Table 8). The numbers of territories in a pool are more likely to be determined by the number of defensible nest sites. The proportion of territorial males cannot be determined from the population density of males (territorial residents and intruder males) at a pool.
The behavior of many teleost fishes has been generally regarded as inflexible (Breder and Rosen, 1966). However, observations of *M. maderensis* provide considerable evidence of behavioral plasticity. The outcome of territorial contests between intruders and occupants was predictable in that the intruder never won a contest. However, the response of the occupant male varied as did the action of the intruding male or female. Other studies of gobiid behavior can provide a valuable insight into the behavioral ecology of closely and distantly related species. There is a danger that specific or characteristic behaviors may be overlooked if the observer focuses attention on general patterns of behavior or fails to gain the necessary familiarity with the habitat of the subject species. Gibson (1969) pointed out that tidepool fishes often aggregated in a manner that was “inconsistent” with territorial spacing. Gibson (1967b, reiterated in 1969) hypothesized that low levels of intraspecific aggression (territoriality) were indicative of a general reduction in levels of activity during low tide. Perhaps a more valid behavioral hypothesis might have considered the possibility of habitat-specific life-history strategies.

The conclusion arrived at in Gibson’s (1969) review of the behavior of littoral fishes was that “careful observation of individual species in their natural habitat” was required to resolve questions concerning the behavior of intertidal fishes. Our understanding of the behavior of littoral fishes has advanced little since Gibson’s seemingly obvious conclusions more than 25
years ago. Behavioral plasticity in *M. maderensis* may reflect a life-history strategy in which flexibility is key to the effective exploitation of resources. This strategy may be more prevalent among intertidal fishes than is commonly thought.
SUMMARY

The intertidal fish community structure and relative habitat preferences of tidepool fishes of the eastern Canary islands of Fuerteventura, Gran Canaria, and Lanzarote were examined for four field seasons (June-August) from 1990-1993. The behavior and habitat use of the endemic and most abundant fish, *Mauligobius maderensis* was examined on the islands of Gran Canaria and Lanzarote from June-August, 1991-1993.

Twenty-seven species representing 14 teleost families were collected from 33 localities on the three islands. The number of tidepool species increased to 34 species when observations of species were included. Eleven species were common to the three islands, the most abundant of which were: *Mauligobius maderensis, Parablennius parvicornis, Gobius paganellus, Coryphoblennius galerita and Chelon labrosus*. A cluster analysis (TWINSPLAN) of species abundances at the 33 localities distinguished between transient and true intertidal species. This dichotomy was also supported by distributional data that showed a tendency for transient species to associate with lower shore pools whereas true intertidal fishes were associated with pools farther upshore. Two species associations were also noted. Clustering of *M. maderensis, G. paganellus*, and *P. parvicornis* reflected their widespread distribution. In contrast, the association of *C. galerita and Scartella cristata* was indicative of the distributional co-occurrence of *S. cristata* on *C. galerita*. With the exception of LZ-3, *S. cristata* was not found at any locality where *C. galerita* did not occur. Although these
two blennies have overlapping ranges, this relationship has not been noted by other authors. Based on the relative abundances of species and species composition on the three islands, Fuerteventura and Lanzarote localities were most similar. TWINSpan also distinguished between low diversity and high diversity localities. Furthermore, these low diversity sites were in part accounted for by localities that were dominated by *M. maderensis*. The numerical dominance of *M. maderensis* and lack of abundance of the other abundant species in tidepools at these localities suggested habitat differences between localities. This inference was also supported by the displacement of *M. maderensis* on Gran Canaria as the most abundant species by *P. parvicornis*. The rock goby *G. paganellus* which in the Canary Islands is at the southern limits of its range, was more abundant on Gran Canaria than the endemic *M. maderensis*.

Relative habitat preferences were described for the tidepool fish community in terms of the variables elevation, surface area, volume, depth, salinity, temperature, substrate, shelter, and algal cover. The concentration of true or obligate species in pools of the upper rocky shore and the restriction of transient and rare intertidal inhabitants to lower shore pools was the most obvious pattern indicative of a species/habitat association. Habitat preferences of the five most abundant species reflected their "generalist" strategy. Abundance patterns of these species were not strongly associated with any of the habitat preference variables when examined with Canonical
Correspondence Analysis (CCA). However, a number of the less abundant species defined as ecological specialists (e.g., the cardinal fish, *Apogon imberbis*; the hairy blenny, *Labrisomus nuchipinnis*; the skillet fish, *Lepadogaster lepadogaster*) demonstrated clearer habitat associations.

Habitat use and behavior of the most abundant intertidal fish, *M. maderensis* were examined in detail for Gran Canaria and Lanzarote populations. Although *M. maderensis* were associated with low species diversity localities and with the upper intertidal zone, an intraspecific examination of habitat preferences showed that there was differential habitat use by individuals of *M. maderensis* related to body size. In regression models of habitat use, elevational distribution was an important predictor of body size. Larger fish preferred deeper pools with greater shelter and algal cover in the lower shore, whereas small fish were associated with less sheltered pools of the upper shore. Habitat segregation or an ontogenetic niche shift was suggested by size-related differences in habitat use by *M. maderensis* and provides a mechanism for the effective exploitation of the heterogeneous conditions of the rocky intertidal zone.

Descriptions of the appearance and behavior of *M. maderensis* were based on over 200 hrs. of observations of individuals at localities on Gran Canaria and Lanzarote. Three basic color phases were recognized. They included (1) cryptic, (2) dark, and (3) checkerboard or typical. Additional subtle differences in fin coloration between size classes and between the sexes were also noted.
On gently sloping broad A'a type shores, *M. maderensis* migrated upshore with the incoming tide. Occupants of lower shore pools assembled in heterospecific schools and formed foraging lines of fishes immediately behind the tidal front. Brief downshore excursions were made by using the tidal surge to effect movement to and from a pool of origin.

The behavior of *M. maderensis* conformed to the general model of territoriality in gobioid fishes. Males established and maintained a nest site within a territory which was defended from conspecific male intruders. Territoriality was characterized by a specific sequence of stereotyped behaviors. However, territorial intrusion by a conspecific male did not necessarily result in its ejection. Most intruding males remained and foraged within defended territories. The probability of remaining within a territory was greatly improved when an intruder executed a "face-away" posture in response to the territorial defense postures of the occupant male. The face-away posture or an equivalent behavior has not been observed in any other goby and was interpreted as an adaptation to a territorial existence on intertidal rocky shores.

The nest site of *M. maderensis* was located in a crack or crevice or under boulders. Nesting males maintained their nest sites by caudal fanning or sweeping of the nest interior with their caudal fins. This motion resulted in the expulsion of sediment. Nest construction was observed once only, but the persistent and deliberate appearance of construction activity of the nesting
male suggested this behavior is more common. Similar to territorial defense, courtship also consisted of a specific sequence of behaviors. The face-away posture adopted by male territorial intruders was also exercised by unreceptive females. Spawning was inferred from male and female quivering motions as they entered the nest. On two occasions females reentered the nest after spawning. However, males were the sole participants in nest guarding.
CONCLUSIONS

The fishes that inhabit the intertidal rocky shore of the islands of Fuerteventura, Gran Canaria, and Lanzarote can be categorized either as true intertidal or transient species. Among the true intertidal species of the eastern Canary Islands the gobies, Mauligobius maderensis and Gobius paganellus and the blennies, Parablennius parvicornis and Coryphoblennius galerita were the most conspicuous littoral inhabitants. The only transient occupant of significance (in terms of abundance) was the mullet, Chelon labrosus. The abundance of C. labrosus suggested that the intertidal zone functioned at least as a refuge from predation. The participation of mullet in heterospecific schools of foraging littoral fishes provided evidence that the intertidal zone not only functioned as a source of refuge but also as a nursery area. Greater than 50% (n =14) of the intertidal species were accounted for by fishes that were considered as inshore or sublittoral in habit. A pattern that emerged from the examination of relative habitat preferences was the restriction of transient species to pools in the lower intertidal zone while true intertidal fishes predominated in the upper shore pools. The concentration of transient species (some of which were among the more abundant inshore species) in the lower intertidal shore marked a transitional zone where both intertidal fishes and inshore fishes intermingled. Currently, the development of an inshore fishery management/conservation strategy is a major concern of the Canarian Government. A management plan that focuses solely on the
condition or well-being of the sublittoral component of the fish fauna of the Canary Islands ignores the association of sublittoral species with the littoral zone.

The endemic goby *M. maderensis* was the most abundant intertidal fish. Narrow endemism has often been equated with niche specialization (Pielou, 1978). However, in terms of its overall abundance, widespread distribution within the intertidal zone, and lack of an association with particular habitat variables, *M. maderensis* (by definition) cannot be considered an ecological specialist. The success of ecological generalists is measured by their ability to exploit (tolerate) a wide range of conditions. *Mauligobius maderensis* exploits the habitat heterogeneity of the rocky intertidal zone by an ontogenetic shift in habitat preferences (i.e., increase in size of *M. maderensis* is accompanied by downshore movement). Analyses of habitat preferences of species comprising a community are usually based on species abundances or presence/absence at sites indicative of a range of habitat conditions. These analyses may not detect true species/habitat relationships because of a lack of resolution or a failure to consider differential habitat use based on size (or sex). A clear relationship between the abundance patterns and specific habitat variables would therefore be unlikely for *M. maderensis* because of a size-related shift in habitat preferences. In the assessment of relative habitat preferences of fishes that comprised the intertidal community, it is not only necessary to distinguish the relative habitat preferences of species but also to
distinguish intraspecific differential habitat use. This is particularly important for abundant species that occupy a range of habitats and are represented by a relatively broad size distribution. Overall, the blenny *P. parvicornis* was almost as abundant as *M. maderensis* and on the island of Gran Canaria the latter was outnumbered by both *P. parvicornis* and *G. paganellus* outnumbered *M. maderensis*. The true habitat preferences of these species may also have been obscured by the sole consideration of abundance patterns. Zonation patterns based on shore elevation are by no means universal on rocky intertidal areas. However, invertebrate and algal communities generally exhibit species zonation. An increase in size related to shore elevation in *M. maderensis* suggests that zonation patterns among true intertidal fishes is probably more of an intraspecific phenomenon that reflects habitat segregation among conspecific fish of different sizes.

Territorial behavior in *M. maderensis* is similar to territoriality described for other gobiids. However there are behavioral elements that represent adaptations (or preadaptations) to a littoral existence. The face-away posture adopted by an intruding conspecific fish and the non-aggressive response of the territorial male are more subtle behavioral interactions when compared to circling and gaping by challenging males. The inclusion of the face-away behavior and response in the behavioral repertoire of *M. maderensis* could be interpreted as a reduction in territoriality. However, a different conclusion is indicated when constraints imposed on a territorial existence in the intertidal
zone are considered. These constraints are spatial and temporal. Spatially, tidepools are diverse. In pools made up of either a single territory or contiguous territories, safe retreat of a conspecific intruder may not be possible within the pool. At high tide, isolated or discrete pools become connected which greatly facilitates extrapool movement albeit under a threat of predation from opportunistic inshore species. Therefore, a trapped intruder remains confined to a pool only until tidal ingression. The face-away posture and response provide a mechanism whereby territoriality can function as an evolutionarily stable strategy (ESS) under these temporal and spatial constraints. The mechanics of the face-away posture hint at the evolutionary origins. In pools where intruding males were chased from a territory, the intruder always turned away from the territorial fish prior to flight. Face-away probably evolved as a prolonged pause prior to flight. Defense of food resources was not a function of territoriality; territorial fish foraged upshore of their respective pools/territories. The function of the territory was as a location for reproduction. An intruding male that remained within a territory posed little threat to the reproductive potential of the nesting male as long as they were not contesting territorial occupancy. The presence of intruding males within a territory may also ensure the replacement of the occupant male when it grows larger, vacates its territory, and moves downshore.

The primary objective of this study was the integration of both
interspecific and intraspecific components of the relationships of the intertidal fishes on the islands of Fuerteventura, Gran Canaria, and Lanzarote. An understanding of interspecific relationships facilitated a more in depth behavioral study of *M. maderensis*. In turn, the behavior of the most abundant intertidal fish, its status as a "true" intertidal species (as opposed to a transient inhabitant), and narrow endemism were seen as integral to a more complete understanding of the functioning of the intertidal fish community.
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Resultados preliminares de la expedición Aleganza-91. Estudio de las
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Appendix A. Log-linear Length/Weight models used to estimate biomass of tidepool fishes. Specimens belong to the catalogued collections of the American Museum of Natural History, New York. Fish lengths and weights were provided by J.L. VanTassell (Field Associate, AMNH). 

\( n \) = number of fish weighed, \( W = \log_e \) body weight (g), \( L = \log_e \) standard length (mm).

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Model</th>
<th>R \text{ SQ}</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Blenniidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Coryphoblennius galerita</em></td>
<td>382</td>
<td>( W = -11.697 + 3.178 L )</td>
<td>0.98</td>
</tr>
<tr>
<td><em>Lipophrys pavo</em></td>
<td>29</td>
<td>( W = -12.002 + 3.157 L )</td>
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</tr>
<tr>
<td><em>L. trigloides</em></td>
<td>60</td>
<td>( W = -11.014 + 3.031 L )</td>
<td>0.98</td>
</tr>
<tr>
<td><em>Parablennius parvicornis</em></td>
<td>679</td>
<td>( W = -12.198 + 3.278 L )</td>
<td>0.98</td>
</tr>
<tr>
<td><em>Ophioblennius atlanticus</em></td>
<td>36</td>
<td>( W = -10.633 + 2.878 L )</td>
<td>0.97</td>
</tr>
<tr>
<td><strong>Gobiidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gobius paganellus</em></td>
<td>238</td>
<td>( W = -9.676 + 2.719 L )</td>
<td>0.9</td>
</tr>
<tr>
<td><em>Mauligobius maderensis</em></td>
<td>660</td>
<td>( W = -11.893 + 3.273 L )</td>
<td>0.99</td>
</tr>
<tr>
<td><strong>Labridae</strong></td>
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<td><em>Thalassoma pavo</em></td>
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<td>( W = -10.994 + 3.037 L )</td>
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<td><strong>Mugilidae</strong></td>
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<td><em>Chelon labrosus</em></td>
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<td><strong>Serranidae</strong></td>
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<td><em>Epinephelus marginatus</em></td>
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<td>( W = -11.227 + 3.154 L )</td>
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</table>
Appendix B. Raw data matrix for all tidepools sampled on the islands of Fuerteventura, Gran Canaria, and Lanzarote. No. = number of pools, Elev. = elevation (cm bmht), Area = surface area (cm²), Vol. = volume (l), Spp. = number of species, Fish = number of individuals, Alg. = algal cover (1 - 5), Subs. = substrate (1 - 5), Shelt. = shelter (1-5), Temp. = water temperature (°C) Sal. = salinity (%o), Dep. = maximum pool depth (cm), D.O. = dissolved O₂, Mean SL = mean standard length (mm), Biomass = weight of fishes (g), Dom. Sp. = numerically predominant species (first letter = first letter of genus name, last three letters refer to first three letters of species name).

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VITA

Richard P. Cody is currently a Research Associate and Adjunct Instructor at the University of West Florida. The effects of pollutants on the morphology and physiology of freshwater fishes are the focus of his research although he maintains a keen research interest in the behavioral ecology of marine and freshwater fishes. In 1989, R.P. Cody entered the doctoral program in Zoology under the supervision of Dr. J.M. Fitzsimons at Louisiana State University Museum of Natural Science. While a graduate student at L.S.U., R.P. Cody served as an Earthwatch staff member and Coprincipal Investigator of an Earthwatch-funded expedition to the Canary Islands. He assisted in the collection of specimens for L.S.U. Museum of Natural Science and the American Museum of Natural History. In 1993, "Spawning and nest guarding in a Canary Islands population of Parablennius parvicornis" authored by Cody, was published in Copeia (Issue 4, 1151-1154). He earned his M.S. in Biology from the University of West Florida in 1989 where he studied the reproductive modes of sparid fishes. In 1984, He received a B.S. in Zoology from University College, Dublin. Richard P. Cody, a citizen of Ireland, was born in Athlone, Ireland in 1962.
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Richard P. Cody

Major Field: Zoology

Title of Dissertation: Community Structure and Habitat Preferences of Intertidal Fishes of the Eastern Canary Islands: Fuerteventura, Gran Canaria, and Lanzarote with a Behavioral Description of Mauligobius maderensis (Osteichthyes: Gobiidae)

Approved:

[Signature]
Major Professor and Chairman

[Signature]
Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination:

April 8, 1996