

**Abstract**—Rockpools on a tropical flat reef off the southeastern coast of Brazil were sampled to determine the influence of pool morphometry and water characteristics on fish community structure. The pool closest to the inner fringe of the reef had lower salinity and higher temperature due to inflow of groundwater. The other pools varied only with respect to their morphometric characteristics, algal cover, and bottom composition. Species with a strong affinity for estuarine-like waters characterized the pool closest to the beach and distinguished its fish community from that of the other pools. Instead of being strongly structured by the physicochemical setting and position in the reef, fish communities of the other pools were determined by behavioral preferences and intra- and interspecific interactions. Differences in community structure were related to pool size (the larger sizes permitting the permanency of schooling species), to algal cover (which allowed camouflage for large predatory species), to bottom composition (which provided substrate for turf flora available to territorial herbivores), and to ecological effects (e.g., competition, territoriality, and predation). Although distribution patterns of tidepool fishes have previously been related to the availability of niches, independent of pool position in the reef, our results show synergistic interactions between water properties, presence or absence of niches, and ecological relationships in structuring tidepool fish communities.

Manuscript submitted 24 November 2010.  
 Manuscript accepted 6 May 2011.  
 Fish. Bull. 109:305–315 (2011).

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## Distribution patterns of tidepool fishes on a tropical flat reef

Raphael M. Macieira (contact author)

Jean-Christophe Joyeux

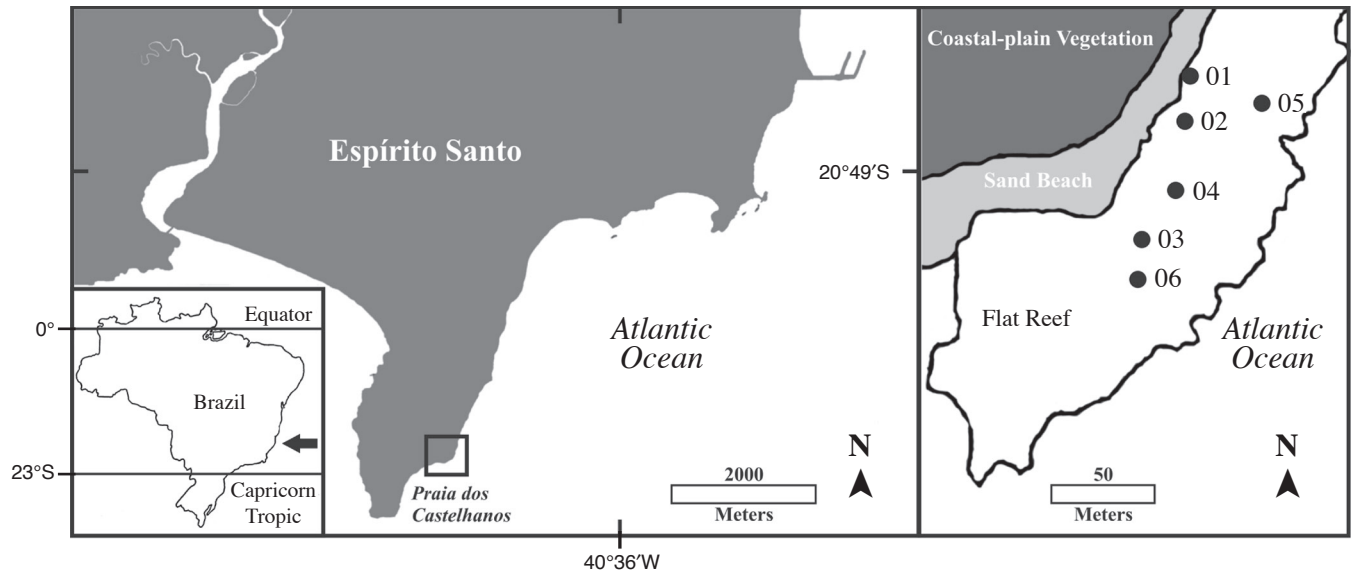
Email address for contact author: raphaelmacieira@hotmail.com

Laboratório de Ictiologia  
 Departamento de Oceanografia e Ecologia  
 Universidade Federal do Espírito Santo  
 Av. Fernando Ferrari, 514  
 Goiabeiras, 29075-910  
 Vitória, Espírito Santo, Brazil

Habitually, at low tide most fishes of the intertidal zone are concentrated in tidepools. There, physicochemical (e.g., temperature and salinity) and biological (e.g., recruitment) variables are inherently related to the duration of pool isolation from the sea (Gibson, 1986). Thus, isolation has been suggested to be a determinant for the establishment and maintenance of a fish community (e.g., Gibson, 1972) and has become one of the “templates” onto which fish distribution patterns are established, either partially or totally (Zander et al., 1999). However, factors such as surface area or water volume also influence community composition and structure (Mahon and Mahon, 1994). For instance, larger, deeper pools allow the permanency of more stenotopic species (Gibson and Yoshiyama, 1999). Therefore, the distribution of fishes is to some extent “azonal” (i.e., pool height within the intertidal zone is not necessarily the single or even the main determinant for fish distribution) because the occurrence of each species is more dependent upon pool characteristics than upon the vertical position of the pool on the rocky shore (Zander et al., 1999). On the other hand, the synergistic effects between pool morphometry and pool isolation have obscured the distinction of their respective contributions to the spatial distribution of fishes (Bennett and Griffiths, 1984). As a consequence, the influence of ecological aspects like competition, predation, or niche availability on shaping tidepool fish distributions may thus far be inadequately evalu-

ated (Faria and Almada, 2001, 2006; Arakaki and Tokeshi, 2010; Rojas and Ojeda, 2010).

In flat reefs, there are no significant differences in vertical position of pools and in wave impact on pools and, consequentially, the duration of isolation from the sea is similar for all pools (e.g., Mahon and Mahon, 1994). In such a situation, pool morphometry probably is the most influential factor on the distribution of fishes. The relative evenness of physicochemical factors among pools enables a standardization of the species filter (i.e., one or more environmental factors that impede species occurrence), and differences among pools will be due more to differences in the availability of resources (e.g., food, mates, space, protection) and microhabitat. However, despite offering an opportunity to study these effects without overly confounding factors, flat reef areas have been little studied in respect to the spatial distribution of their intertidal fishes (Mahon and Mahon, 1994; Zander et al., 1999). Thus, how pool size and shape (depth and volume) and substrate complexity interact to affect community composition remains poorly understood. Therefore, our objectives were to investigate the effects of the physicochemical setting (temperature and salinity) and morphometric characteristics of pools on the structure of fish communities on a flat reef, without the interactive effects caused by differences in the duration of isolation of the rockpools. In comparison with a “classic” rocky shore (with varying duration of isola-



**Figure 1**

Location of study area (Praia dos Castelhanos) off the coast of Espírito Santo, Brazil. The spatial distribution of the rockpools on the reef flat is shown in the map on the right.

tion from the sea; e.g., Gibson, 1972), the abundance and distribution of fishes on a flat reef are expected to be affected by less complex interactions between environmental and ecological variables and that there would be a lower disparity in fish community structure among pools. Such natural simplification of environmental complexity could also shed some light on how the current tendency of habitat homogenization driven by modern anthropogenic activities (Thompson et al., 2002) may affect the divergence of fish communities (Villéger et al., 2010).

## Materials and methods

### Study area

The study was conducted at Praia dos Castelhanos (20°49'S, 40°36'W), in the state of Espírito Santo in southeastern Brazil (Fig. 1). The mean water level relative to the reference datum of zero-level of Brazilian marine charts is 0.82 m. The reef is a complex of carbonate material composed of encrusting coralline algae and stony coral skeletons with sparse lateritic (ferruginous) rocks and is essentially flat. During the ebb tide a large number of pools become isolated. Pool substrates often consist of sand and gravel and pool walls are characteristically irregular, almost vertical, and are covered by algal turf, soft macro-algae, crustose coralline algae, encrusting soft-coral, and a few stony corals.

### Morphological characterizations of tidepools

Six isolated tidepools (without connectivity to the sea or other pools during the ebb tide) were selected: two

located near the sand beach (pools 1 and 2), two in an intermediary position (pools 3 and 4), and two closer to the water edge (pools 5 and 6; Fig. 1). The mean time of exposure to air was about three hours per day. The height of the reef flat was located at about 6 cm (pool 2), 11 cm (pool 3), 10 cm (pool 4), 20 cm (pool 5), and 13 cm (pool 6), below that near pool 1. The pools were characterized on a single occasion relative to their surface area, depth, and bottom rugosity. Surface area was estimated by using a 3×1-m grid of 10×10-cm squares. Depth was measured with a ruler at randomly chosen intersections of the grid. Volume was derived from surface area and mean depth. Rugosity was measured by the chain-and-tape technique (Wilding et al., 2010).

### Sampling

Sampling was conducted every three months between August 2005 and June 2007 ( $n=8$ ) during the mornings of two consecutive days. During the first day, water temperature and salinity were measured with a mercury thermometer (0.5°C precision) and a refractometer (1 psu precision). Measurements were taken at three separate times in each pool: immediately after isolation of the pool from the sea ("beginning"); when the water level fell below reef level ("middle"); and at the time corresponding to the lowest level of the tide and immediately before the pool was connected to the rising sea ("end"). Algal cover and bottom composition were visually estimated on a scale ranging between 0 and 100 (Bennett and Griffiths, 1984). Algal cover was estimated only for pool walls and consolidated bottom areas and refers exclusively to macroalgae. Substrate types were categorized as sand (less than 1 mm diameter), gravel, or rock (diameter greater than 50 mm), and the sum of all categories

**Table 1**

Morphometric characteristics, substrate composition, macroalgae cover, and physicochemical parameters of pools at Praia dos Castelhanos, Espírito Santo, Brazil. Pools were characterized once for depth, surface area, volume, and rugosity and every three months between August 2005 and June 2007 for substrate, cover, and physicochemical parameters ( $n=8$  for all pools except pool 1 where  $n=7$ ). \*=mean (range: minimum–maximum). Depth (max)=mean depth (and maximum depth); area=surface area; vol.=volume; rug.=rugosity.

| Pool | Morphometric characteristics |                        |                        |      | Substrate |             |           | Cover      | Physico-chemical parameters |                  |
|------|------------------------------|------------------------|------------------------|------|-----------|-------------|-----------|------------|-----------------------------|------------------|
|      | Depth (max.)<br>cm           | Area<br>m <sup>2</sup> | Vol.<br>m <sup>3</sup> | Rug. | Sand<br>% | Gravel<br>% | Rock<br>% | Algae<br>% | Temperature*<br>°C          | Salinity*        |
| 1    | 8.30 (20.5)                  | 6.35                   | 0.53                   | 1.11 | 30        | 10          | 60        | 20         | 26.1 (22.5–35.0)            | 28.1 (17.0–35.8) |
| 2    | 22.2 (36.3)                  | 10.15                  | 2.24                   | 1.19 | 80        | 10          | 10        | 40         | 24.4 (21.5–29.6)            | 34.3 (32.0–38.0) |
| 3    | 17.4 (25.5)                  | 1.36                   | 0.24                   | 1.26 | 30        | 60          | 10        | 40         | 24.8 (22.0–30.1)            | 34.3 (31.4–37.0) |
| 4    | 28.2 (49.0)                  | 7.88                   | 2.22                   | 1.30 | 40        | 20          | 40        | 70         | 24.2 (21.8–29.7)            | 34.5 (32.0–37.0) |
| 5    | 23.8 (46.0)                  | 16.12                  | 3.81                   | 1.20 | 10        | 10          | 80        | 30         | 24.7 (22.2–28.0)            | 34.8 (31.3–39.0) |
| 6    | 25.6 (51.0)                  | 6.52                   | 1.67                   | 1.27 | 20        | 50          | 30        | 40         | 24.5 (22.2–24.9)            | 34.7 (31.0–38.0) |

corresponded to 100% of bottom cover. The ichthyofauna was collected on the second sampling day with hand nets and with application of water-based rotenone solution (Polivka and Chotkowski, 1998; Gibson, 1999) and was later fixed in 10% formalin. Due to seasonal variation in beach profile, tidepool 1 was covered by sand during the August 2006 sampling.

### Sample processing

The fishes were measured (total length; TL) to the nearest mm and weighed (individual total wet weight; W) at 0.01 g precision. The species were categorized by their degree of residency in pool habitats (modified from Griffiths, 2003) as permanent residents, opportunists, and transients. Permanent residents (PR) can spend their entire life in pools and are frequently highly adapted for intertidal life. Opportunists (O) spend only part of their life history in pools, usually as juveniles or during high tide feeding excursions, when they are trapped in pools. Transients (T) are species that only occasionally or accidentally enter pools, generally have no specialized adaptations for intertidal life, and normally occur in large rockpools for a short period of time (from a tidal cycle to several weeks). In this study, the assignment of species to categories was based upon frequency of capture, life stage(s) present in pools, species size, and occurrence in the infralittoral zone.

### Data analysis

Temperature and salinity data were tested for normality by the Kolmogorov-Smirnov-Lilliefors test (Zar, 1999) and the data were shown to be normally distributed ( $P>0.05$ ). Variation in temperature and salinity during the ebb tide was tested through repeated-measures ANOVA ( $n=8$ ; except  $n=7$  for tidepool 1), and contrasts of “beginning vs. middle” and “beginning vs. end” were tested. The Mauchly test was used to verify data spher-

icity and the  $F$ -value obtained from the Greenhouse-Geisser test was used when sphericity assumptions were violated. The fish community of each pool was described by the mean number of individuals, number of taxa, Shannon-Wiener index (using  $\log_e$ ), and Pielou's evenness. Friedman nonparametric tests were used to detect differences among pools with significance estimated through Monte Carlo resampling (10,000 runs) (Zar, 1999). The mean length and weight of all individuals were tested among pools by using Kruskal-Wallis nonparametric tests for independent samples with Monte Carlo resampling (10,000 runs).

Nonmetric multidimensional scaling (nMDS) was used to determine the similarity between rockpools by using 1) the morphometric characteristics (4 variables [area, mean depth, volume, rugosity]  $\times$  6 pools), 2) the physicochemical parameters of the water (6 variables [mean, minimum and maximum for temperature and salinity]  $\times$  6 pools), and 3) the fish community structure (64 variables [=taxa]  $\times$  6 pools) by using total abundance and total weight (summed up across the eight sampling events). Data were transformed (fourth<sup>th</sup> root) and matrices were built with the Bray-Curtis coefficient.

## Results

### Characteristics of rockpools

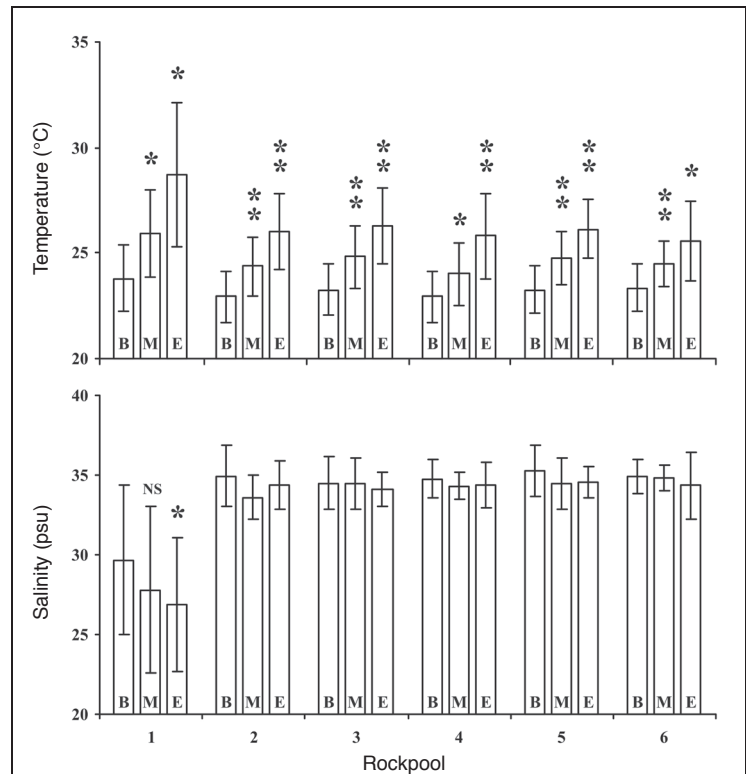
The pools differed in morphometric characteristics but were similar in their physicochemical setting, except for pool 1 (Table 1). Changes during low tide were exacerbated in pool 1 (Fig. 2) because of groundwater inflows (which lowered salinity during the rainy season) and shallowness (which allowed temperature to rise because of the high ratio between area [i.e., insolation] and volume). In extreme cases, a thermopycnocline formed within the pool (without apparent effect on the ichthyofauna; senior author, personal observ.). Besides

being segregated by its physicochemical characteristics (Fig. 3B), pool 1 also differed from other pools (Fig. 3A; Table 1) on account of the smoothness of its bottom. This feature is probably caused by high hydrodynamics and the constant sanding of the rocky substratum by virtue of the pool location in the breaker zone adjacent to the beach. Abrasion also severely limited growth of macroalgae and sessile invertebrates (Table 1). The five other pools separated into three categories: category 1 consisted of pool 3 (very small and filled with gravel), category 2 consisted of pool 5 (of large size with high rock and low sand covers), and category 3 consisted of the remaining pools 2, 4, and 6. The sandiness of pool 2, the depth, rugosity, algal and sand cover of pool 4, and the "graveliness" (coarseness of unconsolidated substrate) of pool 6 were insufficient to differentiate them (Fig. 3A).

### Spatial distribution of fishes

A total of 3448 individuals, representing 64 taxa (58 species) and 27 families, was caught (Table 2). Sixteen of the 58 species, representing 64% of the total number of individuals, were considered permanent residents (PR), 19 (28%) were opportunists (O), and 23 (7.3%) were transients (T). Abundance, richness, diversity, and total wet weight of all fish differed among rockpools, but there were no significant differences in Pielou's evenness or mean length (Fig. 4). Abundance was very high at pool 5 due to *Halichoeres poeyi*, *Stegastes fuscus*, and *Acanthurus bahianus*. Individual mean weight was very high at pool 4 because of rather large and abundant *Labrisomus nuchipinnis* and juveniles of *Sparisoma axillare*. The community indices for pool 1 were characteristic of environments with elevated stress level (e.g., estuaries): high abundance, low diversity, and dominance of few species. Permanent residents were the most representative pool users (above 40% of total) in both number and weight. Proportions of the three user categories varied among pools. Pools 1 to 4 were dominated by permanent residents (above 60% in number and above 80% in weight). In pools 5 and 6 (and in a smaller measure, 2 and 4), although permanent residents remained dominant, the number and weight of opportunists and transients were very representative (Fig. 5).

The ten most-abundant species were either permanent residents or opportunists and showed four different patterns of spatial distribution (Friedman test, Fig. 6). Pattern A, where species were most abundant at pool 5 and rare elsewhere (except pool 6), was displayed by *A. bahianus*, *H. poeyi*, and *S. fuscus*. Species most abundant at pool 1 but rare in other pools, *Bathygobius saporator* and *Ctenogobius boleosoma*, were classified as displaying pattern B. Absence at pool 1 and low abundance at pool 3, as for *Malacoctenus delalandei* and *S.*



**Figure 2**

Mean ( $\pm$  standard deviation) temperature and salinity at the beginning (B), middle (M), and end (E) of isolation of pools from the sea at Praia dos Castelhanos, Espírito Santo, Brazil. Differences in these variables during the period of pool exposure to air were tested by repeated-measure ANOVA models with the Greenhouse-Geisser test (temperature in pools 2, 3, and 5) or the sphericity assumed test (all other models). In significant models (temperature for all pools, with  $P \leq 0.001$ ; salinity in pool 1 with  $P \leq 0.05$ ), results for contrast tests between the beginning and middle periods and the beginning and end periods are indicated above M and E, respectively. For all pools,  $n=8$  except for pool 1, where  $n=7$ . NS=not significant; \*= $P \leq 0.01$ , \*\*= $P \leq 0.001$ .

*axillare*, characterized pattern C. The most abundant species overall, *Bathygobius mystacium* and *L. nuchipinnis*, displayed pattern D where abundance was most expressive at pool 5 but remained relatively high in the other pools. No obvious pattern of spatial distribution was identified for *Abudefduf saxatilis*. Except for *B. saporator* and *C. boleosoma* (pattern B), there was no similarity between abundance and physicochemical characteristics of rockpools. The distribution patterns of mean individual weight (not shown) of these most-abundant species did not present much similarity with those of abundance (Fig. 6). The gobies *C. boleosoma* and (to a lesser degree) *B. mystacium* showed a pattern similar to pattern B detected for abundance. The mean individual weight of *Abudefduf saxatilis* was higher in larger pools (2 and 5) and that of *B. saporator* was lowest in pool 1 which presented the highest abundance. Overall, six of the ten species displayed significant differences in

weight among pools (*B. mystacium*, *L. nuchipinnis*, *C. boleosoma*, *A. saxatilis*, *S. fuscus*, and *A. bahianus*).

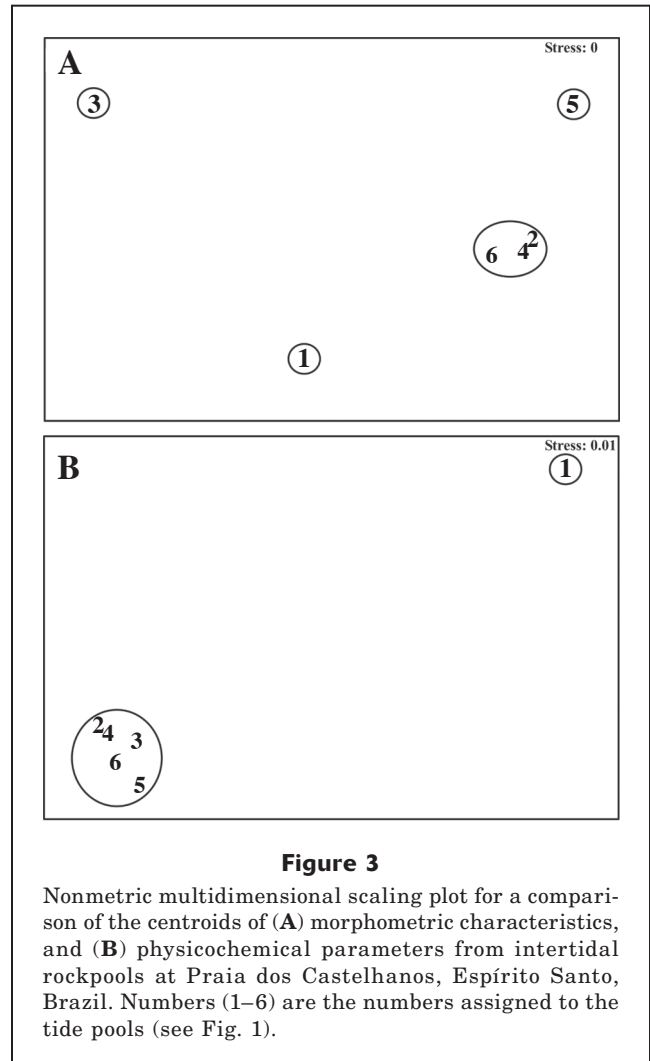
The nMDS ordination analysis on both abundance and mean weight showed that the fish assemblage, when all taxa are considered, is structured differently among pools (Fig. 7). In both cases, pools 1 and 3 were segregated from all others (and each other), 3 because of a low total abundance and a low number of taxa and 1 because of the absence of some common species (*H. poeyi*, *S. axillare*, and *M. delalandei*) and the dominance of *B. saporator* and *C. boleosoma*. The other pools, loosely grouped, shared similar values in number of taxa, Shannon-Weiner diversity, total length (Fig. 4), and higher percentages of opportunist and transitory species (Fig. 5). Although differences in the physicochemical setting of pools were low (except for pool 1), the 10 most abundant taxa presented distinctive distribution patterns for abundance related to the morphometric characteristics of each pool, such as position on the reef, depth, surface area, volume, substrate composition, algal cover and rugosity.

## Discussion

### Spatial distribution of fishes

Species living in intertidal ecosystems are distributed along a vertical gradient according to their tolerance of physical factors and their response to ecological interactions (Raffaelli and Hawkins, 1996). Although the vertical distribution of sessile organisms has been studied for many years, the distribution of fishes and other mobile organisms that take refuge in pools has not been investigated as extensively because it is much more dynamic and thus more difficult to study (Zander et al., 1999; Thompson et al., 2002). The shape and volume of a pool, its degree of isolation from the sea, and its connectivity with other pools determine the amplitude of the fluctuation in physicochemical characteristics of the water (Mahon and Mahon, 1994; Davis, 2000; Castellanos-Galindo et al., 2005). Consequently, the occurrence of each species is dependent more upon pool characteristics than upon vertical position of the pool on the rocky shore, i.e., species occurrence is nearly azonal (Zander et al., 1999). Other factors, such as exposure to waves (Gibson, 1972; Grossman, 1982) and algal cover (Bennett and Griffiths, 1984), have been investigated, but their influence on the distribution of fishes may be secondary.

Habitat heterogeneity is intimately associated with variability in microhabitats and therefore offers the conditions for the coexistence of antagonistic species (Rojas and Ojeda, 2010). Two main microhabitats are available to rockpool fishes (Griffiths et al., 2006): the substratum of the pool where fish can hide and the complex macroalgal cover used by midwater or pelagic species. Rojas and Ojeda (2010) demonstrated that small fishes prefer pools of low structural complexity where there are fewer ambush areas for predators. On the other

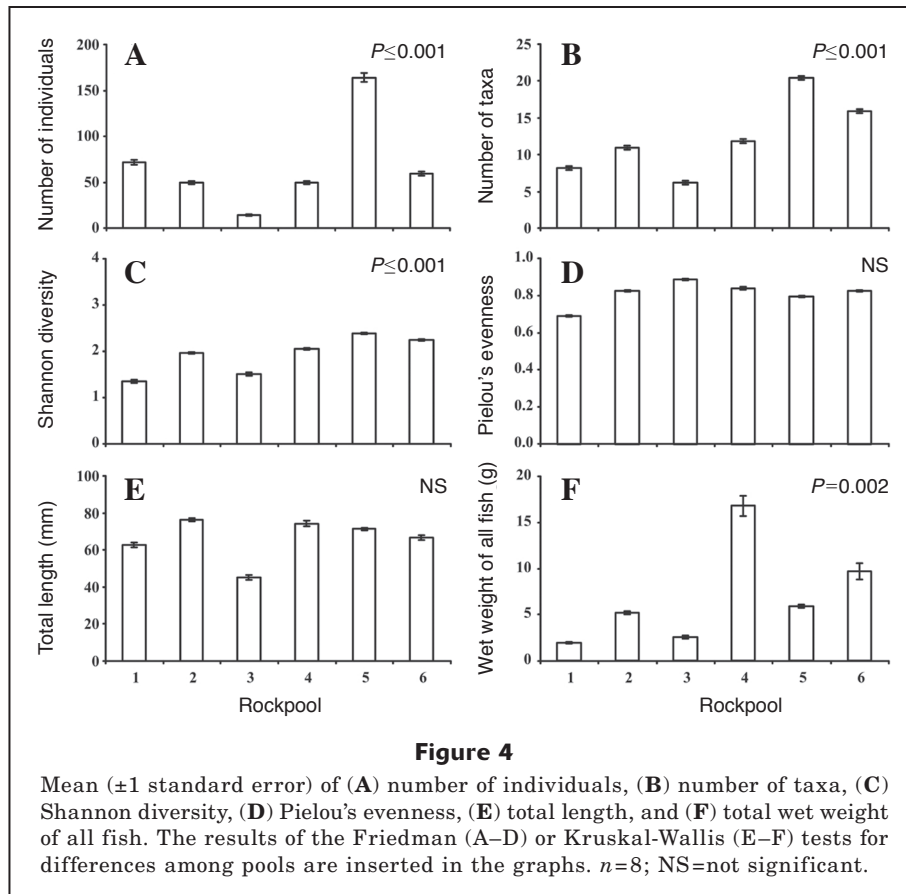


**Figure 3**

Nonmetric multidimensional scaling plot for a comparison of the centroids of (A) morphometric characteristics, and (B) physicochemical parameters from intertidal rockpools at Praia dos Castelhanos, Espírito Santo, Brazil. Numbers (1–6) are the numbers assigned to the tide pools (see Fig. 1).

hand, fish distribution on a rocky shore is also affected by inter-intra specific interactions such as competition and predation (Gibson and Yoshiyama, 1999; Zander et al., 1999) that may lead to microhabitat segregation (Faria and Almada, 2001). Thus, many different physical and ecological factors regulate the distribution and structure of fish community in rockpools (e.g., Gibson, 1972, 1982), and the principal difficulty is to determine the respective contribution of each of these.

There are about three “vertical” ecological pool-zones on a flat, fringing, intertidal rocky reef. The first is located at and just below the upper edge of the reef. This is an area under stronger atmospheric and terrestrial influence and that is subject to shifting conditions from reef to nonreef environment. Permanent residents and a few opportunistic fish that can tolerate the physiologic stress caused by physicochemical changes during the exposure of the reef to the air (Evans et al., 1999), normally dominate this zone. There, B-pattern species, such as the eurythermic and euryhaline *B. saporator* and *C. boleosoma*, probably find resources available and lower predation risk because at low tide



the number of interspecific competitors and predators also is regulated by physiologic stress. Moreover, equivalent-size pools at the reef's higher fringe hold more individuals than those at lower levels because of the overwhelming numerical dominance of thermal and saline stress-adapted species. In that case, low substrate heterogeneity and environmental complexity, held as important factors for community structuring, do not necessarily translate into low fish abundance as commonly thought (Griffiths et al., 2006). Immediately below this upper zone, the middle zone is much less affected by external influences (e.g., groundwater seepage) and consequently even small pools present less extreme and less stressful conditions. Thus, species with little or no adaptation to intertidal life (opportunistic and transient fish) are more common in this zone and differences in fish community structure among pools would be directly related to pool morphometry because it will determine the number of available niches. The last zone (unstudied) is close to the sea, and a high number of pools, if not all, are extensively connected to it through a pipe and cave system; at low tide, water circulation remains intense in these pools because it is driven by waves on the forereef from a meter to tens of meters away. Occurring in these pools are juveniles and small-size adults of infralittoral species not found elsewhere on the reef flat.

According to Mahon and Mahon (1994), large tidepools have higher numbers of individuals, species richness, and biomass because of higher availability of resources and niches. Such a pattern was clearly distinguishable at Praia dos Castelhanos and presented some interesting twists that shed some light on the mechanisms responsible for pool-specific community structure. Instead of being strongly structured by the physicochemical setting, middle zone communities were finely tuned by minor differences in pool characteristics and ecological effects such as competition, predation, and territorialism. In particular, the abundance of territorial species is related to their need to establish territory and, because larger pools provide more space, they also offer an opportunity for a larger number of territories. Nevertheless, for territorial herbivores (such as *S. fuscus*, pattern A) the ultimate factor is sufficient consolidated substrate in sunlit areas for these species to maintain their "gardens". In a similar way, roving herbivores such as *A. bahianus* (pattern A) are particularly abundant in large pools filled with rocks because schooling behavior (schools usually contain 5–20 individuals) and herbivory create a demand for ample space and adequate substrate (Lawson et al., 1999). Finally, a number of discrete and solitary species, such as the roving herbivore *S. axillare* (pattern C) and the carnivores *L. nuchipinnis* (pattern D) and *M. delalandei* (pattern C),

Table 2

Taxonomic list of individual fish species caught in pools at Praia dos Castelhanos, Espírito Santo, Brazil. Family order follows Nelson (2006). Residency status is adapted from Griffiths (2003): permanent resident (PR), opportunist (O), transient (T), indeterminate (I).

| Family and taxa                                  | Residency status | Family and taxa                                   | Residency status |
|--|------------------|---|------------------|
| Muraenidae                                       |                  | Chaetodontidae                                    |                  |
| <i>Gymnothorax funebris</i> Ranzani, 1840        | PR               | <i>Chaetodon striatus</i> Linnaeus, 1758          | O                |
| <i>Gymnothorax moringa</i> (Cuvier, 1829)        | PR               | Pomacentridae                                     |                  |
| <i>Gymnothorax vicinus</i> (Castelnau, 1855)     | PR               | <i>Abudefduf saxatilis</i> (Linnaeus, 1758)       | O                |
| Ophichthidae                                     |                  | <i>Stegastes fuscus</i> (Cuvier, 1830)            | PR               |
| <i>Ahlia egmontis</i> (Jordan, 1884)             | PR               | <i>Stegastes variabilis</i> (Castelnau, 1855)     | O                |
| <i>Letharchus aliculatus</i> McCosker, 1974      | PR               | <i>Stegastes</i> sp. (Unidentified larvae)        | I                |
| <i>Myrichthys breviceps</i> (Richardson, 1848)   | O                | Labridae  |                  |
| <i>Myrichthys ocellatus</i> (Lesueur, 1825)      | O                | <i>Doratonotus megalepis</i> Günther, 1862        | O                |
| <i>Myrophis platyrhynchus</i> Breder, 1927       | PR               | <i>Halichoeres brasiliensis</i> (Bloch, 1791)     | O                |
| Clupeidae  |                  | <i>Halichoeres poeyi</i> (Steindachner, 1867)     | O                |
| Unidentified larvae                              | I                | <i>Halichoeres</i> sp. (Unidentified larvae)      | I                |
| Ophidiidae                                       |                  | <i>Sparisoma axillare</i> (Steindachner, 1878)    | O                |
| <i>Raneya brasiliensis</i> (Kaup, 1856)          | T                | Dactyloscopidae                                   |                  |
| Mugilidae  |                  | <i>Dactyloscopus tridigitatus</i> Gill, 1859      | T                |
| <i>Mugil curema</i> Valenciennes, 1836           | T                | Blenniidae  |                  |
| <i>Mugil liza</i> Valenciennes, 1836             | T                | <i>Parablennius marmoreus</i> (Poey, 1875)        | T                |
| Atherinopsidae                                   |                  | <i>Scartella cristata</i> (Linnaeus, 1758)        | PR               |
| <i>Atherinella brasiliensis</i>                  | T                | Unidentified blenniid larvae                      | I                |
| (Quoy & Gaimard, 1825)                           |                  | Labrisomidae                                      |                  |
| Belonidae  |                  | <i>Labrisomus nuchipinnis</i>                     | PR               |
| <i>Strongylura timucu</i> (Walbaum, 1792)        | T                | (Quoy & Gaimard, 1824)                            |                  |
| Syngnathidae                                     |                  | <i>Malacoctenus delalandei</i>                    | PR               |
| <i>Bryx dunckeri</i> (Metzelaar, 1919)           | T                | (Valenciennes, 1836)                              |                  |
| <i>Micrognathus crinitus</i> (Jenyns, 1842)      | T                | <i>Paraclinus arcaneus</i>                        | T                |
| Scorpaenidae                                     |                  | Guimarães & Bacellar, 2002                        |                  |
| <i>Scorpaena plumieri</i> Bloch, 1789            | O                | Gobiesocidae                                      |                  |
| Epinephelidae                                    |                  | <i>Gobiesox barbatulus</i> Starks, 1913           | O                |
| <i>Rypticus subbifrenatus</i> Gill, 1861         | O                | Gobiidae  |                  |
| Apogonidae                                       |                  | <i>Barbulifer ceuthoecus</i>                      | T                |
| <i>Apogon americanus</i> Castelnau, 1855         | PR               | (Jordan & Gilbert, 1884)                          |                  |
| <i>Phaeoptyx pigmentaria</i> (Poey, 1860)        | PR               | <i>Barbulifer enigmaticus</i> Joyeux, Van Tassell | PR               |
| Carangidae                                       |                  | & Macieira, 2009                                  |                  |
| <i>Carangoides bartholomaei</i> (Cuvier, 1833)   | T                | <i>Bathygobius mystacium</i> Ginsburg, 1947       | PR               |
| <i>Caranx latus</i> Agassiz, 1831                | T                | <i>Bathygobius soporator</i> (Valenciennes, 1837) | PR               |
| Lutjanidae                                       |                  | <i>Bathygobius</i> sp. (Unidentified larvae)      | I                |
| <i>Lutjanus jocu</i> (Bloch & Schneider, 1801)   | O                | <i>Coryphopterus glaucofraenum</i> Gill, 1863     | PR               |
| Gerreidae  |                  | <i>Ctenogobius boleosoma</i>                      | PR               |
| <i>Eucinostomus argenteus</i>                    | T                | (Jordan & Gilbert, 1882)                          |                  |
| Baird & Girard, 1855                             |                  | <i>Ctenogobius saepepallens</i>                   | O                |
| <i>Eucinostomus lefroyi</i> (Goode, 1874)        | T                | (Gilbert & Randall, 1968)                         |                  |
| <i>Eucinostomus melanopterus</i> (Bleeker, 1863) | T                | <i>Gobiosoma hemigymnum</i>                       | PR               |
| <i>Eucinostomus</i> spp. (Unidentified larvae)   | I                | (Eigenmann & Eigenmann, 1888)                     |                  |
| Haemulidae                                       |                  | Acanthuridae                                      |                  |
| <i>Anisotremus virginicus</i> (Linnaeus, 1758)   | T                | <i>Acanthurus bahianus</i> Castelnau, 1855        | O                |
| <i>Haemulon aurolineatum</i> Cuvier, 1830        | O                | <i>Acanthurus chirurgus</i> (Bloch, 1787)         | O                |
| <i>Haemulon parra</i> (Desmarest, 1823)          | O                | Paralichthyidae                                   |                  |
| <i>Haemulon plumieri</i> (Lacepède, 1801)        | T                | <i>Etropus longimanus</i> Norman, 1933            | T                |
| <i>Haemulon steindachneri</i>                    | T                | Tetraodontidae                                    |                  |
| (Jordan & Gilbert, 1882)                         |                  | <i>Sphoeroides greeleyi</i> (Gilbert, 1900)       | T                |
| Sparidae   |                  |   |                  |
| <i>Diplodus argenteus</i> (Valenciennes, 1830)   | T                |   |                  |

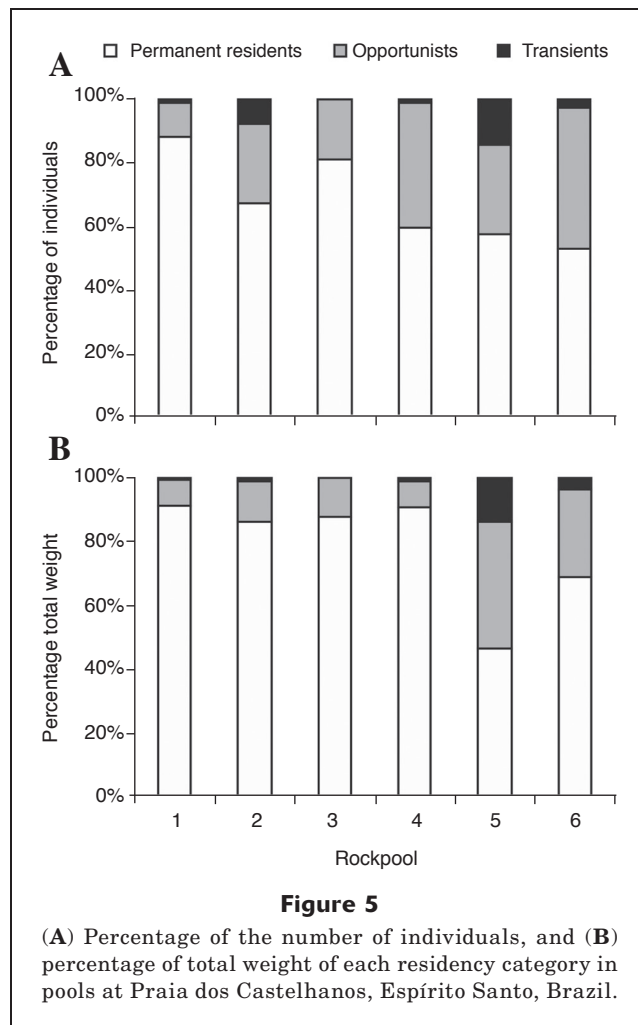
heavily rely on crypsis or camouflage provided by macroalgae and on rugosity for either refuge or ambush.

Large pools near the infralittoral are expected to have a larger proportion of transient fishes (Gibson and Yoshiyama, 1999). However, on low gradient reefs, pool size is probably more important than connectivity to the sea or other pools because many such species are schooling or active swimmers (e.g., families Atherinopsidae, Carangidae, Gerreidae, Haemulidae, Mugilidae, and Sparidae). No distributional pattern clearly linked community structure to distance from the sea and the most suggestive patterns (C, A, and D) probably include the influence of parameters, as yet unaccounted for, that act upon the fauna. Although distance from the forereef may be one of these determinant parameters, we suspect that “aleness” of a tidepool may play an important role in concentrating, at low tide, many fish (herbivores and nonherbivores alike) of large size that were roving over the reef flat at high tide. Thus, if juvenile rovers avoid the forereef, a relatively small pool alone in a large area suitable for roving (i.e., the reef flat at high tide) would at low tide “drain” as many roving transient fish as several large pools dispersed over this same (and now unsuitable) area. Experimental substrate manipulations, such as those proposed by Griffiths (2003) and performed by Griffiths et al. (2006), Arakaki and Tokeshi (2010) and Rojas and Ojeda (2010), would permit evaluation of the importance of each factor in determining the composition and structure of pool communities.

Another factor that could influence the spatial distribution of species is intra- or interspecific resource partitioning, and either of these may cause segregation (Gibson, 1986; Faria and Almada, 1999; Zander et al., 1999; Davis, 2000; Faria and Almada, 2001; Arakaki and Tokeshi, 2010). The sympatric gobiid species *B. saporator* and *C. boleosoma* display frequent intra- and interspecific agonistic behavior. In particular, *B. saporator* feeds on *C. boleosoma* and, occasionally, cannibalizes smaller individuals (senior author, personal observ.). For both species, territoriality explains agonistic behavior between conspecific individuals. The two species share the same preference for eurythermal-euryhaline pools and interspecific interactions result from niche overlap. These interactions could theoretically result in spatial segregation, but there is no clear evidence that such a process occurs at Praia do Castelhanos. Further study is necessary to comprehend the importance of interspecific interactions in the distribution of these species.

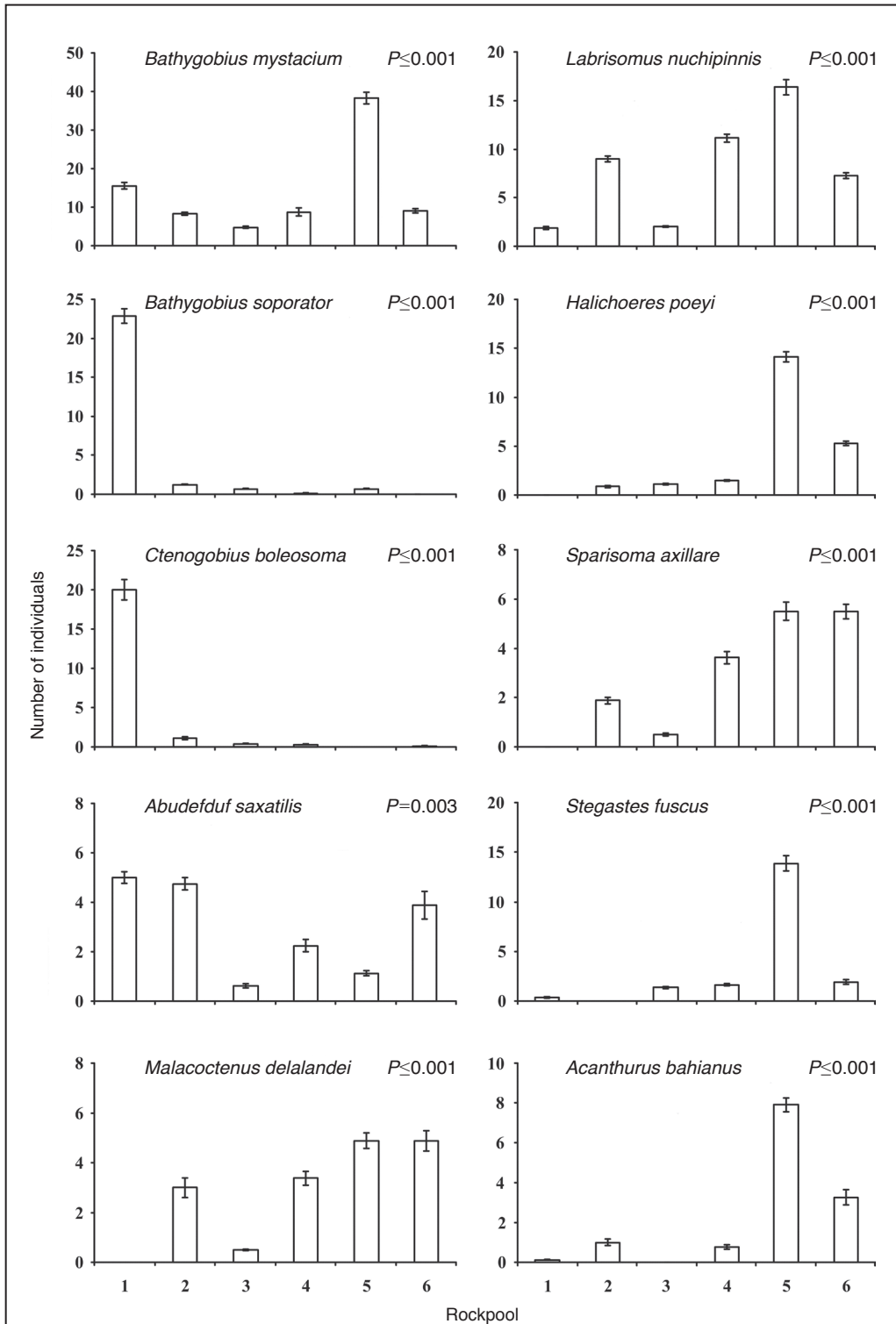
## Conclusions

The main factors structuring intertidal fish communities on rocky shores (e.g., isolation, height, gradient, and exposure of tide pools to waves) were held constant at Praia dos Castelhanos. Spatial distribution of fishes only partially depended upon the physicochemical setting and was apparently independent of distance of the tide pools from the sea. The structure of the fish com-



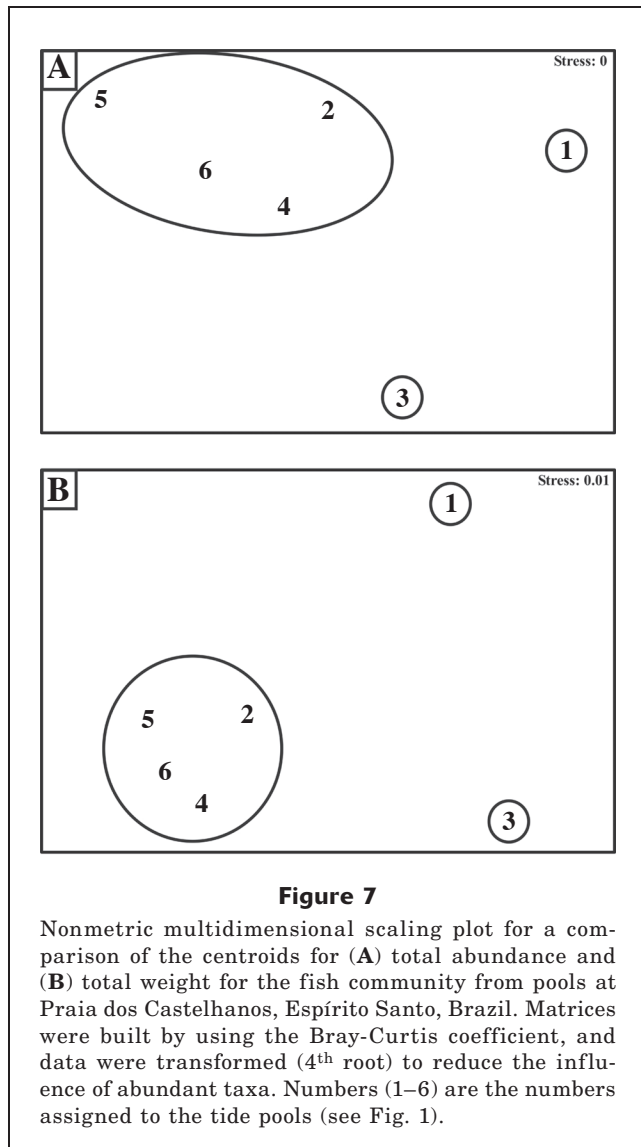
munity within each physicochemical setting principally resulted from the synergistic interaction of niche availability (that directly depends upon pool morphometry) and ecological relationships among species (e.g., competition, territoriality, predation). Mason et al. (2008) suggested that niche complementarity (i.e. niche differences between species) prevents competitive exclusion (when one species outcompetes and displaces another by making a better use of the same critical resource) and can increase ecosystem function. Further studies should focus on niche overlap within and among species for an understanding of the influence of competition in the structuring of intertidal fish communities. Moreover, we hypothesize that pool “aleness” (the concept here includes the degree of connectivity with other pools) influences the interactions within pools at low tide by incorporating into the pool-effect the space and niches available at high tide. The use of out-of-pool space would widely vary between direct pool-to-pool passage (e.g., *B. saporator*; Aronson, 1951) and extensive roving over nonpool space (e.g., Faria and Almada, 2006). The paradigm therefore needs to shift from isolated tidepools to pools integrated into their surroundings (pools and





**Figure 6**

Mean ( $\pm 1$  standard error) number of individuals for the ten most abundant species in pools at Praia dos Castelhanos, Espírito Santo, Brazil. The results of Friedman tests ( $n=8$ ) for differences in number of individuals among pools are inserted in the graphs.



nonpools alike) to incorporate the full complement of species' behavior for a more complete understanding of how intertidal fish species use and survive in a challenging environment.

### Acknowledgments

The authors thank C. Pimentel, J. L. Gasparini, J. Van Tassell, P. Jesus Jr., E. Almeida and E. Stein for their help, A. Martins and C. E. L. Ferreira for their insights and corrections. R. M. acknowledges financial support by Fundação de Amparo a Pesquisa do Espírito Santo (FAPES) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). Biological material was collected with permit 033/05 from Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA).

### Literature cited

- Arakaki, S., and M. Tokeshi.  
2010. Analysis of spatial niche structure in coexisting tidepool fishes: null models based on multi-scale experiments. *J. Anim. Ecol.* 80:137–147. doi: 10.1111/j.1365-2656.2010.01749.x
- Aronson, L. R.  
1951. Orientation and jumping behavior in the gobiid fish *Bathygobius soporator*. *Am. Mus. Nat. Hist.* 1486:1–22.
- Bennett, B. A., and C. L. Griffiths.  
1984. Factors affecting the distribution, abundance and diversity of rock-pool fishes on the Cape Peninsula, South Africa. *S. Afr. J. Zool.* 19:97–104.
- Castellanos-Galindo, G. A., A. Giraldo, and E. A. Rubio.  
2005. Community structure of an assemblage of tide-pool fishes on a tropical eastern Pacific rocky shore, Colombia. *J. Fish. Biol.* 67:392–408.
- Davis, J. L. D.  
2000. Spatial and seasonal patterns of habitat partitioning in a guild of southern California tidepool fishes. *Mar. Ecol. Prog. Ser.* 196:253–268.
- Evans, D. H., J. B. Claiborne, and G. A. Kormanik.  
1999. Osmoregulation, acid-base regulation and nitrogen excretion. *In Intertidal fishes: life in two worlds* (M. H. Horn, K. L. M. Martin, and M. A. Chotkowski, eds.), p. 79–92. Academic Press, San Diego, CA.
- Faria, C., and V. Almada.  
1999. Variation and resilience of rocky intertidal fish in western Portugal. *Mar. Ecol. Prog. Ser.* 184:197–203.  
2001. Microhabitat segregation in three rocky intertidal fish species in Portugal: does it reflect interspecific competition? *J. Fish Biol.* 58:145–159.  
2006. Patterns of spatial distribution and behaviour of fish on a rocky intertidal platform at high tide. *Mar. Ecol. Prog. Ser.* 316:155–164.
- Gibson, R. N.  
1972. The vertical distribution and feeding relationships of intertidal fish on the Atlantic Coast of France. *J. Anim. Ecol.* 41:189–207.  
1982. Recent studies on the biology of intertidal fishes. *Oceanogr. Mar. Biol. Annu. Rev.* 20:363–414.  
1986. Intertidal teleosts: life in a fluctuating environment. *In The behavior of teleosts fishes* (T. I. Pitcher, ed.), p. 388–407. Croom Helm, London.  
1999. Methods for studying intertidal fishes. *In Intertidal fishes: life in two worlds* (M. H. Horn, K. L. M. Martin, and M. A. Chotkowski, eds.), p. 7–25. Academic Press, San Diego, CA.
- Gibson, R. N., and R. M. Yoshiyama.  
1999. Intertidal fishes communities. *In Intertidal fishes: life in two worlds* (M. H. Horn, K. L. M. Martin, and M. A. Chotkowski, eds.), p. 264–296. Academic Press, San Diego, CA.
- Griffiths, S. P.  
2003. Rockpool ichthyofaunas of temperate Australia: species composition, residency and biogeographic patterns. *Estuar. Coast. Shelf Sci.* 58:173–186.
- Griffiths, S. P., A. R. Davis, and R. J. West.  
2006. Role of habitat complexity in structuring temperate rockpool ichthyofaunas. *Mar. Ecol. Prog. Ser.* 313:227–239.
- Grossman, G. D.  
1982. Dynamics and organization of a rocky intertidal fish assemblage: the persistence and resilience of taxocene structure. *Am. Nat.* 119(5):611–637.

- Lawson, G. L., D. L. Kramer, and W. Hunte.  
1999. Size-related habitat and schooling behavior in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. *Environ. Biol. Fishes* 54:19–33.
- Mahon, R., and S. D. Mahon.  
1994. Structure and resilience of a tidepool fish assemblage at Barbados. *Environ. Biol. Fishes* 41:171–190.
- Mason, N. W. H., C. Lanoiselée, D. Mouillot, J. B. Wilson, and C. Argillier.  
2008. Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *J. Anim. Ecol.* 77:661–669.
- Nelson, J. S.  
2006. *Fishes of the world*, 4th ed., 624 p. Wiley, New York.
- Polivka, K. M., and M. A. Chotkowski.  
1998. Recolonization of experimentally defaunated tidepools by Northeast Pacific intertidal fishes. *Copeia* 1998:456–462.
- Raffaelli, D., and S. Hawkins.  
1996. *Intertidal ecology*. Chapman and Hall, London.
- Rojas, J. M., and F. P. Ojeda.  
2010. Spatial distribution of intertidal fishes: a pattern dependent on body size and predation risk? *Environ. Biol. Fishes* 87:175–185.
- Thompson, R. C., T. P. Crowe, and S. J. Hawkins.  
2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environ. Conserv.* 29(2):168–191.
- Villéger, S., J. R. Miranda, D. F. Hernández, and D. Mouillot.  
2010. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* 20:1512–1522.
- Wilding T. A., E. J. L. Palme, and N. V. C. Polunin.  
2010. Comparison of three methods for quantifying topographic complexity on rocky shores. *Mar. Environ. Res.* 69:143–151.
- Zander C. D., J. Nieder, and K. Martin.  
1999. Vertical distribution patterns. *In* *Intertidal fishes: life in two worlds* (M. H. Horn, K. L. M. Martin, and M. A. Chotkowski, eds.), p. 26–53. Academic Press, San Diego, CA.
- Zar, J. H.  
1999. *Biostatistical analysis*, 4th ed. Prentice Hall, New Jersey.