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Cryptobenthic reef fishes: depth distribution and correlations with habitat complexity and sea urchins

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In this study, cryptobenthic fish depth patterns and their correlations with habitat complexity and sea urchin densities were investigated. In general, total density, species richness and diversity were higher in the shallower zones (3 m), while evenness was higher at the 10 m depth zone. Among sites, species density was similar at the 10 m zone, but at the 3 m zone it varied greatly. Species-specific depth preferences were found. Correlation between species density and habitat complexity was usually positive. The influence of sea urchin densities on the cryptobenthic fish assemblage was site and species dependent.

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Key words: Blenniidae; Brazil; community structure; ecosystem engineer; interference visual census; South Atlantic Ocean.

INTRODUCTION

Cryptobenthic fishes comprise small species, which are visually and behaviourally cryptic and live in close association with the substratum (*e.g.* Blenniidae, Labrisomidae and Gobiidae) (La Mesa *et al.*, 2006). Due to their relatively high energetic demands and turnover rates as well as their potential to be preyed upon by piscivorous organisms, they may play significant roles in reef processes (Ackerman & Bellwood, 2000; Ackerman *et al.*, 2004). Despite their numerical abundance and potential importance in marine ecosystem trophodynamics, however, most studies have focused almost entirely on the conspicuous members of the reef fish community (Sale, 1991, 2002), providing very little accurate information on cryptobenthic species, and hence, a poor understanding of their ecology.

The abundance and diversity of cryptobenthic fish assemblages can be remarkably variable, with some species (or families) being much more common in shallower zones, and others being common in one site and rare at another in the same depth (Illich & Kotschal, 1990; La Mesa *et al.*, 2006). Some of the possible reasons are biotic interactions, habitat complexity and depth preferences, which are known to play a major role in determining species distributions and abundances in marine habitats (Patzner, 1999a; Munday *et al.*, 2001; Gratwicke & Speight, 2005; Jones, 2005; Macieira & Joyeux, 2011).

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Habitat structure has a fundamental influence on species distribution. The relationships between fish assemblage variables and habitat complexity has been the focus of attention in numerous studies, which in many cases demonstrated positive correlations between complexity and species richness, diversity and total abundance of the fish assemblage (Luckhurst & Luckhurst, 1978; Gratwicke & Speight, 2005). Furthermore, due to their small home ranges (0.25–2 m²) and benthic behaviour, small cryptic fish assemblages are expected to show even stronger relationships with habitat characteristics (Depczynski & Bellwood, 2004). Depth is another factor that could affect the distribution of cryptobenthic species. Several studies recognized the preference of some species for specific depth ranges (Patzner, 1999a; Orlando-Bonaca & Lipej, 2007) due to a variety of reasons, including resource availability (*e.g.* food and nesting sites) and interspecific competition. The resulting depth segregation reduces the spatial overlap between species with similar ecological requirements (Larson, 1980; Illich & Kotrschal, 1990; Macpherson, 1994).

At the interface between biotic interactions and habitat structure are the ecosystem engineers [*i.e.* organisms that cause physical modification, maintenance or creation of habitats; Jones *et al.* (1997)]. Sea urchins may act as biogenic sources of habitat structure for small reef fishes (Sakashita, 1992; Hartney & Grorud, 2002). Little emphasis, however, has been placed on evaluating the conditions under which positive interactions are relevant when compared to negative forces such as competition and predation.

So far, there have been only a few studies on the distribution patterns of subtidal cryptobenthic species in Brazil (Mendes, 2006; Rangel, 2007), and none on the southern coast. The aim of the present investigation was to explore the ecological processes that could affect the distribution patterns of cryptobenthic fish species on the rocky sublittoral zone of the subtropical southern Brazilian coast. The following questions were addressed: (1) do cryptobenthic fishes have higher richness and density in shallower waters; (2) do species-specific depth preferences exist; (3) is there a positive correlation between cryptobenthic fish density and habitat complexity (including sea urchins)?

MATERIALS AND METHODS

STUDY AREA

The coast of Santa Catarina state, Brazil, is characterized by narrow sandy and gravel beaches surrounded by a granitic rocky shore with intrusive diabase rocks. The predominant wind comes from the north-east, and the less frequent but stronger wind comes from the south. The seasons in the area are well defined, with summer and winter very distinct and autumn and spring with similar characteristics (Koettker & Freire, 2006). This study was carried out at four sites within central Santa Catarina state, Brazil: Farol and Capim Inlets (both at Arvoredo Island), Costão da Barra on Santa Catarina Island and Xavier Island (Fig. 1).

SAMPLING DESIGN AND PROCEDURE

Sampling was done during daylight hours between 20 May and 3 October 2009. Seasonal variations were not considered a variable for analyses because the cryptobenthic fish densities remained similar among these months.

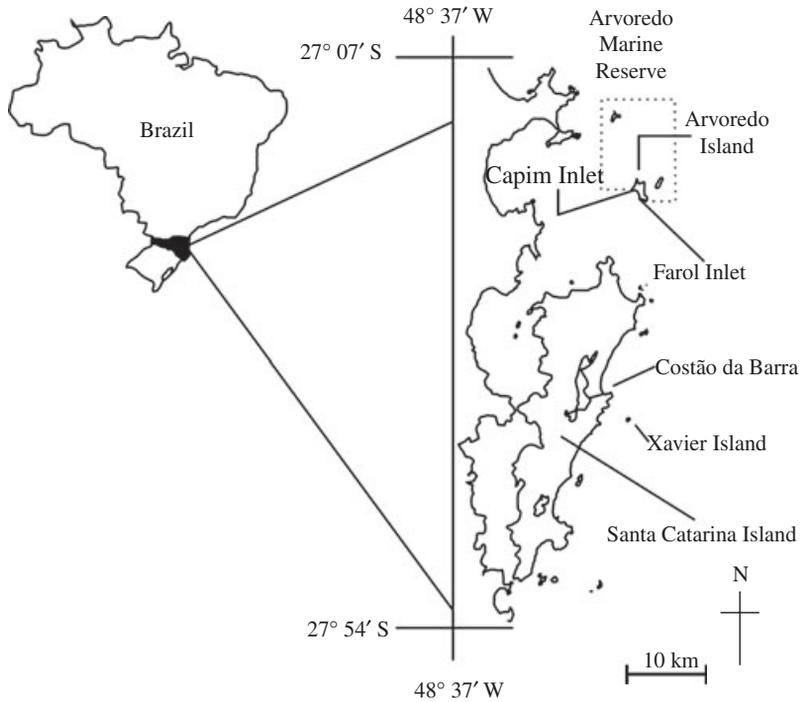


FIG. 1. Map of central Santa Catarina State showing the study sites.

Cryptobenthic fish assemblage was sampled through the interference visual census (IVC) (Beldade & Gonçalves, 2007). The IVC consists of counting not only all visible fishes over the substratum but also performing a systematic search for hidden fishes (*e.g.* under rocks or sea shells and among algae). Replicated randomly placed linear transects of 10×2 m (20 m^2) were distributed over three depth strata (3, 10 and 15 m). Due to the rocky shore inclination and the depth limit of rocky environments, Farol Inlet was the only site that presented all three depth strata ($n = 42$, 17 and 16 transects, respectively). Xavier and Capim had two depth strata (3 and 10 m; $n = 51$ and 31, respectively), while Costão da Barra had only the shallowest depth (3 m; $n = 5$).

Ecological engineers (sea urchins *Echinometra lucunter*) were counted using standardized visual census (VC) following Floeter *et al.* (2007). When sampling, the diver first counted cryptobenthic fishes using the IVC method and then returned over the same line counting the sea urchins with the VC method.

Ferreira *et al.* (2001) indicated that among the many ways to measure habitat complexity, the number and largest diameter of possible refuges (holes) are the best measures for rocky shore environments. The holes were classified into three different sizes classes (1–10, 11–20 and 21–30 cm) and counted on the different depth strata (3, 10 and 15 m) in the same transects as the fishes and urchins. This procedure was replicated eight times at each depth and, because it is very time consuming, it was only done at Farol Inlet.

DATA ANALYSIS

The assemblage structure was assessed by calculating density and the following diversity indices: species richness (S = number of species), evenness (J ; Pielou, 1966) and diversity (H' , Shannon–Wiener index) for each transect. The mean and the median were calculated to determine differences between sites and depths. As expected, the data generated by counts of

individuals did not show a normal distribution. The transformation of the data $\{\sqrt{[\log_{10}(x + 0.5)]}; \log_{10}(x + 1)\}$ was unsuccessful in fixing the normality issue, so non-parametric tests were used.

Kruskal–Wallis ANOVA by ranks was used to compare data (assemblage variables, total and species density) among the sites on the same depth strata and, on Farol Inlet, to compare the three depth strata. Multiple comparisons of mean rank for all groups were done to identify the differences. The Mann–Whitney U -test was used to compare data among depths in the sites with only two strata (Capim Inlet and Xavier Island). Spearman correlation was used to analyse the relationship between the cryptobenthic fish and sea urchins, as well as size and number of holes.

Principal component analysis (PCA) was used to explore the relationships of the nine most abundant cryptobenthic fish species at each site and depth combination. Weighted pair-group method with arithmetic mean cluster analyses (WPGMA; Bray Curtis) were used to identify groups among sites and depths accordingly with species frequency of occurrence. Only species that accounted for at least 5% in some combination of site and depth were included in the analysis involving average density.

RESULTS

SPECIES COMPOSITION

Overall, 1336 individuals and 14 species of cryptobenthic fishes were recorded. Among them, *Callionymus bairdi* Jordan 1888, *Gobiesox barbatulus* Starks 1913, *Scartella cristata* (L. 1758) and *Hypsoblennius invemar* Smith-Vaniz & Acero P. 1980 were rarely seen and not included in further analysis. *Malacoctenus delalandii* (Valenciennes 1836), *Parablennius marmoreus* (Poey 1876), *Parablennius pilicornis* (Cuvier 1829), *Hycleurochilus fissicornis* (Quoy & Gaimard 1824), *Labrisomus nuchipinnis* (Quoy & Gaimard 1824), *Labrisomus cricota* Sazima, Gasparini & Moura 2002, *Coryphopterus glaucofraenum* Gill 1863, *Emblemariopsis signifer* (Ginsburg 1942), *Starksia brasiliensis* (Gilbert 1900) and *Ophioblennius trinitatis* Miranda Ribeiro 1919 were the more representative species accounting for at least 0.5% of the individuals at a given site.

ASSEMBLAGE VARIABLES BETWEEN SITES AND DEPTH

Cryptobenthic assemblage variables changed at the different sites and depths (Fig. 2). The mean species richness (S) per transect (20 m²) was similar between sites [Fig. 2(a)] with the exception of Capim, which was different at 3 m (Kruskal–Wallis, $n = 95$; $P = 0.001$) and 10 m (Kruskal–Wallis, $n = 60$; $P = 0.03$). When comparing average S among depths [Fig. 2(a) and Table I], Farol and Xavier had most species at 3 m. Xavier was the site with highest evenness (J) at 3 m (Kruskal–Wallis, $n = 95$, $P < 0.001$) [Fig. 2(b)]. In all sites, the average J per transect was always higher at 10 m [Fig. 2(b) and Table I]. The mean diversity (H) per transect at 3 m was higher at Xavier and Costão da Barra than at Farol and Capim (Kruskal–Wallis, $n = 95$; $P < 0.001$) [Fig. 2(c)]. Xavier was the only site where diversity was significantly different between depths (Table I). Costão da Barra presented a disproportionately higher density of cryptobenthic fishes than the other sites (Kruskal–Wallis, $n = 98$; $P < 0.001$) and densities always decreased with depth (Table II).

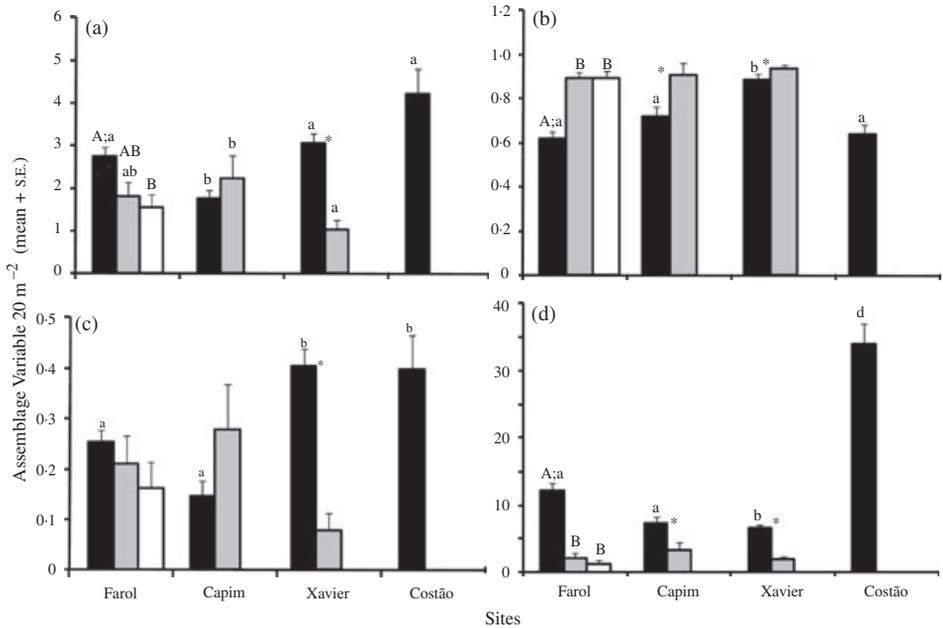


FIG. 2. Cryptobenthic fish assemblage variables (mean + S.E. 20 m^{-2}) observed by site and depth (■, 3 m; ▒, 10 m; □, 15 m). (a) Species richness, (b) evenness, (c) diversity and (d) cryptobenthic fish assemblage density. Letters indicate groups formed by multiple comparisons of mean rank for all groups following Kruskal–Wallis ANOVA by ranks. Upper case letters indicate groups among depths at Farol. Lower case letters indicate groups among sites at the same depth zone. *, significant differences ($P < 0.05$) between depths on the same site (Mann–Whitney U -test).

CORRELATION BETWEEN CRYPTOBENTHIC FISH DENSITIES, FREQUENCY OF OCCURRENCE, SITES AND DEPTHS

Individual species densities varied greatly (Fig. 3). Considering the depth patterns of the nine species involved, four showed negative relationships with depth, *i.e.* higher densities in the shallows (*M. delalandii*, *P. pilicornis*, *Labrisomus* spp. and *H. fissicornis*), three showed positive relationships (*P. marmoratus*, *E. signifer* and *C. glaucofraenum*) (Table II) and only two showed no relationship with depth (*O. trinitatis* and *S. brasiliensis*).

In relation to the distribution of species among sites, some species were exclusive, or at least more abundant, at the northern sites (Farol and Capim) and some at southern sites (Xavier and Costão). *Malacoctenus delalandii*, *C. glaucofraenum*, *E. signifer* and *S. brasiliensis* form a northern group, whereas *P. pilicornis* and *H. fissicornis*, a southern group. Some species were observed at all sites (*P. marmoratus*). Some were only recorded at the islands (*C. glaucofraenum* and *E. signifer*) and some were more abundant at the coastal site, Costão da Barra (*O. trinitatis*, *Labrisomus* spp. and *P. pilicornis*).

To further understand species distributions, species frequency of occurrence at each site and depth was analysed through a principal component analysis and cluster

TABLE I. Statistical tests comparing mean cryptobenthic fish assemblage variables among depths at each site. Only significant values are shown

Assemblage variables	Test	Valid <i>n</i>	Sites
<i>S</i>	Kruskal–Wallis	75	Farol**
	Mann–Whitney <i>U</i>	3 m = 29, 10 m = 23	Xavier***
<i>J</i>	Kruskal–Wallis	75	Farol***
	Mann–Whitney <i>U</i>	3 m = 15, 10 m = 5	Capim*
	Mann–Whitney <i>U</i>	3 m = 29, 10 m = 23	Xavier***
<i>H'</i>	Mann–Whitney <i>U</i>	3 m = 29, 10 m = 23	Xavier***
Density	Kruskal–Wallis	75	Farol**
	Kruskal–Wallis	3 m = 27, 10 m = 8	Capim*
	Mann–Whitney <i>U</i>	3 m = 24, 10 m = 23	Xavier***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *n*, sample size; *S*, mean species richness; *J*, average evenness; *H'*, mean diversity.

analysis (Fig. 4). It was noted that axis 1 was related to the separation of sites by a north–south gradient. Axis 2 was more related to depth. Neighbouring sites with the same depths ended up grouped together in both analyses (Fig. 4).

MICROHABITAT FEATURES (NUMBER AND SIZE OF HOLES), SEA URCHINS AND THEIR RELATIONSHIPS WITH CRYPTOBENTHIC FISH DENSITIES

Sea urchin densities varied among sites and depths (Fig. 5), with higher densities at Arvoredo Island (Farol and Capim) and always higher in shallow waters (3 m). Costão da Barra was excluded of the analyses due to extremely low numbers of urchins.

TABLE II. Statistical tests comparing cryptobenthic fish species densities among depths at each site. Only significant values are shown

Species	Test	Valid <i>n</i>	Sites
<i>Malacoctenus delalandii</i>	Kruskal–Wallis	98	Farol***
	Mann–Whitney <i>U</i>	3 m = 27; 10 m = 8	Capim***
	Mann–Whitney <i>U</i>	3 m = 24; 10 m = 23	Xavier***
<i>Parablennius pilicornis</i>	Mann–Whitney <i>U</i>	3 m = 24; 10 m = 23	Xavier***
<i>Parablennius marmoratus</i>	Mann–Whitney <i>U</i>	3 m = 24; 10 m = 23	Xavier*
<i>Hypleurochilus fissicornis</i>	Mann–Whitney <i>U</i>	3 m = 24; 10 m = 23	Xavier**
<i>Labrisomus</i> spp.	Kruskal–Wallis	75	Farol***
<i>Coryphopterus glaucofraenum</i>	Kruskal–Wallis	75	Farol***
	Mann–Whitney <i>U</i>	3 m = 27; 10 m = 8	Capim**
<i>Emblemariopsis signifer</i>	Mann–Whitney <i>U</i>	3 m = 27; 10 m = 8	Capim**

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; *n*, sample size.

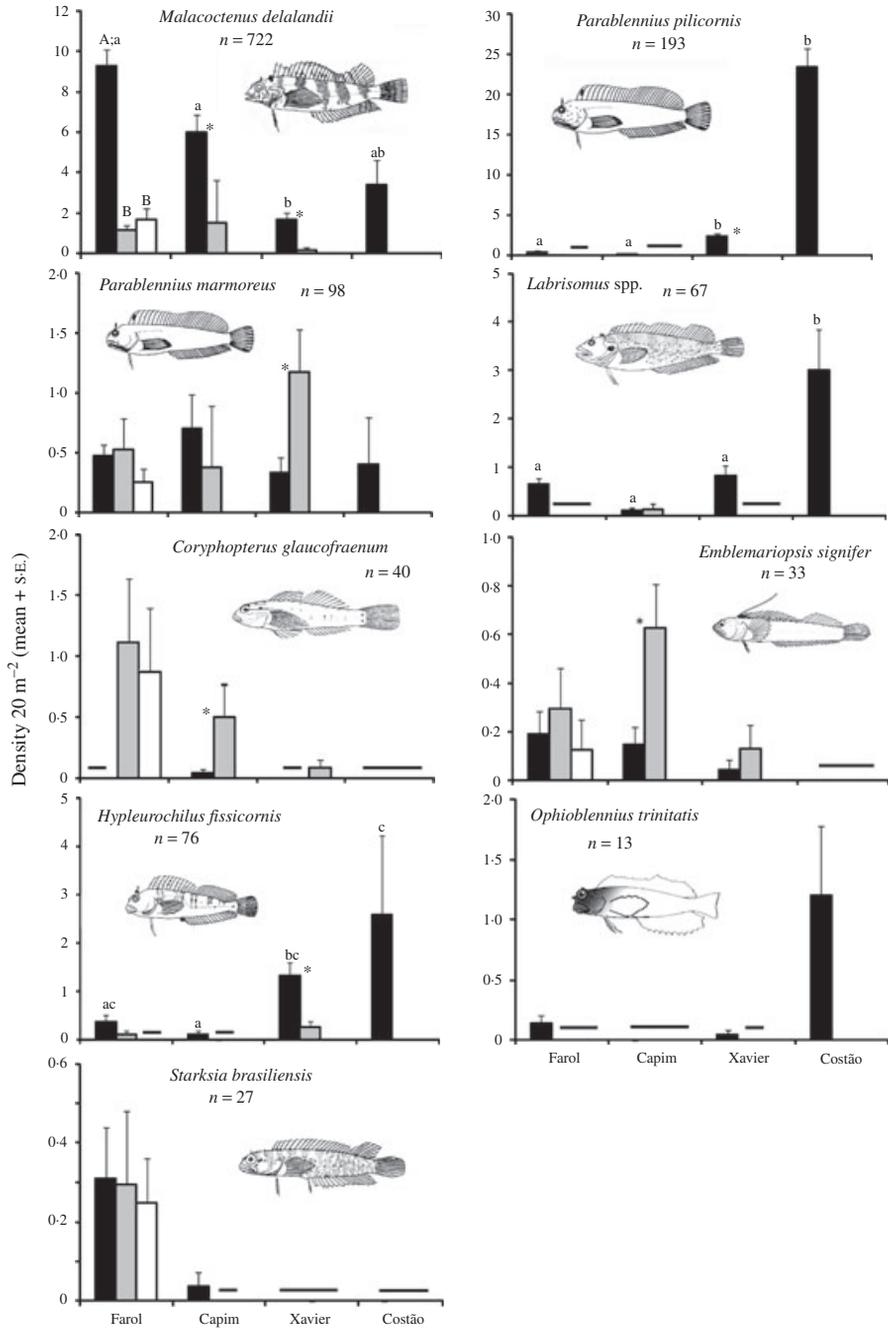


FIG. 3. Cryptobenthic fish species density (mean + s.e. 20 m^{-2}) by site and depth (■, 3 m; □, 10 m, □, 15 m). Letters indicate homogeneous groups formed by multiple comparisons of mean rank for all groups test following Kruskal–Wallis ANOVA by ranks. Upper case letters indicate groups among depths at Farol. Lower case letters indicate groups among sites at the same depth zone. *, significant differences between depths on the same site (Mann–Whitney *U*-test). Note that each histogram has a different density scale. Only species that accounted for at least 5% of the total abundance are included.

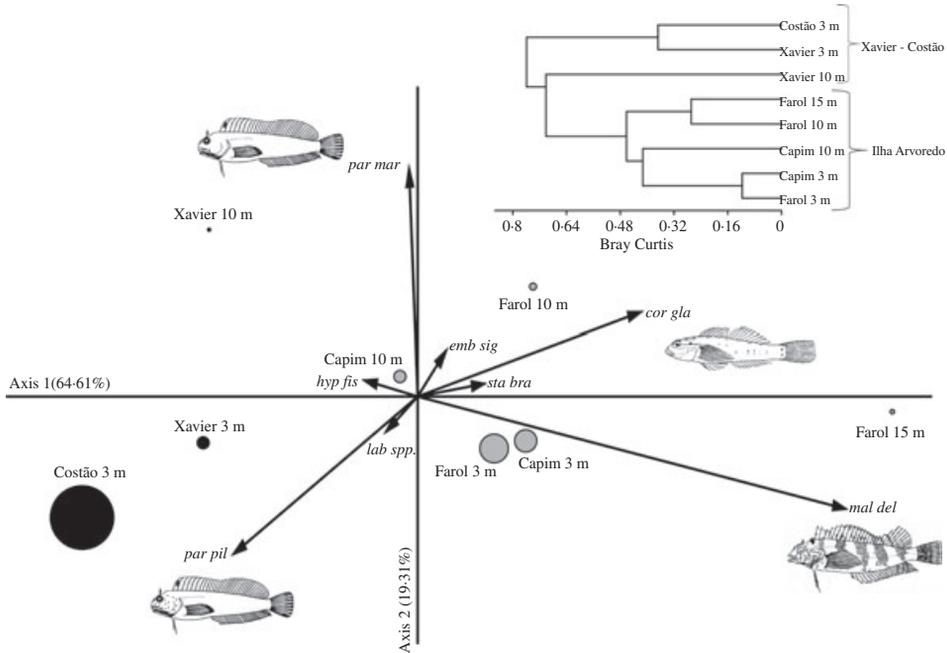


FIG. 4. Principal component analysis and sampling site dissimilarities (Bray Curtis) based on cryptobenthic species frequency of occurrence. Circle size is proportional to total cryptobenthic fish density at each site. (●, south sites; ○, north sites). *mal del*, *Malacoctenus delalandii*; *par pil*, *Parablennius pilicornis*; *par mar*, *Parablennius marmoratus*; *lab spp.*, *Labrisomus* spp.; *cor gla*, *Coryphopterus glucofraenum*; *emb sig*, *Emblemariopsis signifer*; *sta bra*, *Starksia brasiliensis*; *hyp fis*, *Hypleurochilus fissicornis*.

A significant positive correlation was found between the whole cryptobenthic fish assemblage and sea urchin densities at Farol at 3 m ($r = 0.40$, $P < 0.05$). The correlation was mainly driven by *P. marmoratus*, *H. fissicornis* and *S. brasiliensis*. Other species showed no clear pattern.

With respect to microhabitat structural complexity, cryptobenthic fish assemblage mean density was positively correlated with the number of holes, but only in shallow waters (Table III). Specifically at 3 m depth, *M. delalandii* showed a strong correlation with 10–20 cm sized holes. In deeper areas (15 m), *C. glucofraenum* was positively correlated with 20–30 cm sized holes (Table III).

DISCUSSION

ASSEMBLAGE VARIABLES BETWEEN SITES AND DEPTH

The lower species diversity and evenness found at Arvoredo Island (Capim and Farol Inlet), was a reflection of the dominance of *M. delalandii* (representing 80% of cryptobenthic fish density). Moreover, the lower evenness found at Costão da Barra was related to the dominance of *P. pilicornis* (60% of the assemblage). Evenness showed a tendency to increase with depth. This is because the two dominant species (*M. delalandii* and *P. pilicornis*) are less abundant in deeper strata. The general

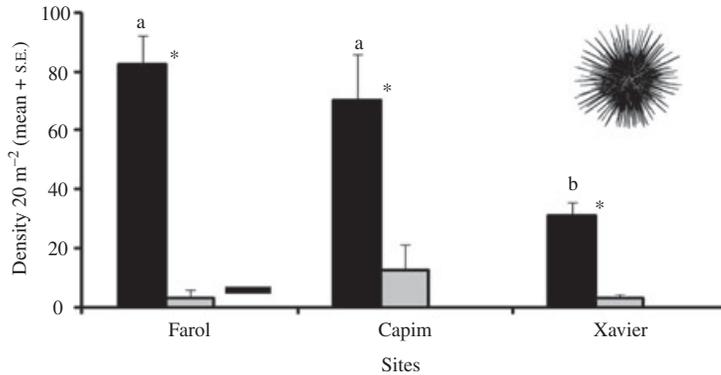


FIG. 5. *Echinometra lucunter* (sea urchin) density (mean + s.e. 20 m⁻²) (■, 3 m; □, 10 m; □, 15 m). Lower case letters indicate homogeneous groups formed by multiple comparisons of mean rank for all groups following Kruskal–Wallis ANOVA by ranks. *, significant differences ($P < 0.05$) between depths on the same site (Mann–Whitney U -test).

decrease of species richness and density with depth was expected, because most cryptobenthic fishes dwell preferentially in the shallow waters (Illich & Kotschal, 1990; Topolski & Szedlmayer, 2004). The exception of this trend at Capim Inlet was due to the appearance of the rock–sand interface at 10 m, the preferred microhabitat for some species like *C. glaucofraenum* and *C. bairdi*.

Due to the inherent limitations of the sampling method the real species richness of cryptobenthic fishes in the rocky shores is probably higher than reported in this study. This is expected because density and diversity of these small and cryptic fishes can be underestimated by visual census methods (Willis, 2001). Despite being the most accurate method, rotenone and anaesthetic samplings often require special permits (Robertson & Smith-Vaniz, 2008). The interference visual census (IVC) method, used in this study, gives a good representation of species relative abundance, rendering better abundance estimates than regular visual census and closest to those that can be obtained with anaesthetics (Beldade & Gonçalves, 2007). The IVC method should be considered as a regular protocol for preliminary assessments of cryptobenthic fishes.

The discrepancy of cryptobenthic fish densities between Costão da Barra and the other sites could be a possible indication of overfishing in the area. This site is very accessible and fishermen can easily reach the water by walking on the rocky shore. As a consequence of intensified fishing on macrocarnivorous fishes, ecological models predict a higher abundance of cryptobenthic fishes (Pinnegar & Polunin, 2004). There are some documented reductions in the cryptobenthic fish density in areas where macrocarnivorous fishes are abundant (*e.g.* groupers) (Macpherson, 1994; Sasal *et al.*, 1996; Prochazka, 1998; La Mesa & Vacchi, 1999; Willis & Anderson, 2003).

The density of cryptobenthic fishes obtained from this study seems to be surprisingly lower when compared with the results obtained by Rangel (2007). In the present study, a maximum of 30 individuals 20 m⁻² was found, whereas Rangel (2007) found 225 individuals 20 m⁻² (750% more than the present study). Part of this difference could be related to the latitudinal gradient, since Rangel's (2007)

TABLE III. Spearman correlation results between cryptobenthic fishes and possible refuge (holes) densities. Only significant values are shown

Species	Depth (m)	Hole size	<i>r</i>
<i>Malacoctenus delalandii</i>	3	10 < holes < 20	0.86*
	3	Total holes	0.77*
<i>Coryphopterus glaucofraenum</i>	15	20 < holes < 30	0.79*
Whole assemblage	3	10 < holes < 20	0.79*
	3	20 < holes < 30	0.71*
		Total holes	0.71*

* $P < 0.05$.

study area is located in Rio de Janeiro state, a lower latitude (22° 59' S) and more diverse region. Another reason may be the use of different methods. Rangel (2007) used clove oil for fish collection and in the present study the IVC method was used. When Rangel (2007) compared both methods, however, the abundance was only 37% lower using the IVC.

CRYPTOBENTHIC FISHES DENSITY BETWEEN SITES AND DEPTH

Considering the relative density of species among depths, it was possible to identify depth preferences for certain species. For example, *M. delalandii*, *Labrisomus* spp., *P. pilicornis* and *H. fissicornis* were more abundant in shallow waters. *Malacoctenus delalandii* and *Labrisomus* spp. belong to the same family (Labrisomidae) and are known to consume Decapoda and Peracarida (Randall, 1967; Pereira & Jacobucci, 2008). Isopods and gammarids, which are both Peracarida crustaceans have tendencies to decrease in density with depth (Jacobucci & Leite, 2002).

It is already known that the zonation of sessile invertebrates creates gradients and patchiness of habitats that affect demersal reef-fish populations (Sale, 1991). *Parablennius pilicornis* and *H. fissicornis* were frequently seen inside empty barnacles (e.g. *Megabalanus tintinabulum*), and Gerhardinger *et al.* (2004) cited the use *Perna perna* empty shells by *H. fissicornis* as nesting sites. *Megabalanus tintinabulum* and *P. perna* are two species with tendencies to occur in very shallow waters and decrease in density with depth (pers. obs.). The preference of *P. pilicornis* for shallow depths is also reported from the north-eastern Atlantic Ocean (Zander, 1988).

Another group was formed by *C. glaucofraenum*, *E. signifer* and *P. marmoreus*, species that at least in some sites, showed higher densities at deeper depths (10 m). For *C. glaucofraenum* the presence of rock-sand interface in deeper areas may be the explanation, because it is the preferred habitat of this species (Mendonça-Neto *et al.*, 2008). *Emblemariopsis signifer* is generally found below 6–10 m elsewhere in Brazilian rocky reefs (pers. obs.). *Parablennius marmoreus* was found in the present study in deeper waters than it is generally found in the Caribbean (Hastings *et al.*, 1976; Greenfield & Johnson, 1981; Rauch, 1996, 2003; Topolski & Szedlmayer, 2004). It is interesting to note that a positive correlation with depth was found for *P. marmoreus* only at Xavier Island, a site with a high frequency of occurrence

of its congeneric, *P. pilicornis*. When co-occurring with *P. pilicornis*, *P. marmoreus* may have its distribution pushed to deeper waters. Moreover, on Costão da Barra, a site where *P. pilicornis* was extremely abundant, the frequency of occurrence of *P. marmoreus* was low. Pastor & Francour (2010) described that the voracity of *P. pilicornis* and its strong territoriality make it a great competitor for other species from the same habitat.

MICROHABITAT FEATURES AND BIOTIC CORRELATIONS

As in other studies (Willis & Anderson, 2003) cryptobenthic fishes were positively correlated with microhabitat complexity, *i.e.* number of holes. Note, however, that *M. delalandii*, was responsible for this positive correlation, since the counting of the number of holes was only performed at Farol Inlet, where this species accounted for 80% of the total abundance. *Coryphopterus glaucofraenum* was positively correlated with large holes (20–30 cm) at 15 m depth, where it was frequently seen inside large holes resting on the sand. Forrester & Steele (2004) demonstrated through a manipulative experiment that intraspecific competition for refuges can be a key agent of mortality for this species.

The relationship between sea urchins and cryptobenthic fishes showed distinct site-dependent patterns. Although *M. delalandii* was sometimes observed behind sea urchins, their densities did not show a positive correlation. *Starksia brasiliensis* was significantly correlated with black sea urchins and was only seen behind or near sea urchins. At Santa Catalina Island (southern California, U.S.A.), manipulative experiments confirmed a causal relationship between the local abundance of a small temperate cryptobenthic fish, *Lythrypnus dalli* Gilbert 1890 and the presence of the sea urchin *Centrostephanus coronatus* (Hartney & Grorud, 2002). Patzner (1999b) also recorded the effect of sea urchins as a hiding place for juvenile benthic fishes in the Mediterranean Sea.

The present research provides the first insight into the cryptobenthic fish assemblage of Santa Catarina, southern Brazil, offering a baseline for future work. The results show that the patterns of dominance of the different species are more similar between neighbouring sites than among distant ones, possibly indicating that some larger scale mechanisms (*e.g.* currents and upwelling) are affecting the cryptobenthic fish assemblages. At a small scale, it was possible to identify depth preference patterns for some species. As expected, cryptobenthic fish densities have a strong positive correlation with habitat complexity (number of holes). No obvious pattern was found between cryptic fishes and sea urchins.

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