

FISH ASSEMBLAGES ON INTERTIDAL SHORES OF THE ISLAND OF FAIAL, AZORES

RICARDO SERRÃO SANTOS, RICHARD D. M. NASH & STEPHEN J. HAWKINS



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In the present paper we describe fish assemblages of rocky intertidal pools and intertidal areas of sandy beaches of the Azores. Blennies (*Parablennius sanguinolentus parvicornis*, *Coryphoblennius galerita* and *Lipophrys trigloides*) constitute the dominant resident fish family in the intertidal pools. Thirteen species were encountered in intertidal pools. Richness is higher in the 3rd quarter of the year with 12 species and lower in the 1st and 2nd quarters with 8 species occurring in the samples. Diversity is also higher in the 3rd quarter. The small variation can mostly be attributed to transient species and juveniles using the shore as a nursery ground. Fifteen species occurred in the intertidal region of the protected shallow sandy beach of Porto Pim. This fish assemblage was dominated by juveniles of transient species. No resident species were present here. Richness and abundance were higher in 3rd and 4th quarters due to recruitment of juveniles, and the occurrence of migrant and transient species.

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No presente artigo descrevemos as associações de peixes das poças do *intertidal* rochoso e do *intertidal* arenoso dos Açores. São treze as espécies que ocorrem nas poças do *intertidal* rochoso. Os blenídeos, com *Parablennius sanguinolentus parvicornis*, *Coryphoblennius galerita* e *Lipophrys trigloides*, constituem a família dominante de peixes residentes das poças do *intertidal* rochoso. A riqueza é maior no 3º trimestre, com 12 espécies, e menor no 1º trimestre com apenas oito espécies a ocorrerem nas poças. A diversidade é também superior no 3º trimestre. O pequeno grau de variação pode ser fundamentalmente atribuído à presença de espécies transientes e de juvenis que utilizam a costa durante as primeiras fases de desenvolvimento. São quinze as espécies que ocorrem na zona *intertidal* da praia arenosa de Porto Pim. A comunidade de peixes é aqui dominada por juvenis de espécies transientes. Não encontramos espécies *intertidais* residentes. A riqueza e abundância são superiores no 3º e 4º trimestre devido ao recrutamento de juvenis, e à ocorrência de espécies migradoras e transientes.

Ricardo Serrão Santos, Universidade dos Açores, Departamento de Oceanografia e Pescas, PT-9900 Horta, Açores, Portugal, and IMAR/Açores, Unidade de Estudos Oceânicos, Cais de Santa Cruz, PT-9900 Horta, Açores, Portugal. - Richard D. M. Nash & Stephen J. Hawkins, University of Liverpool, Port Erin Marine Laboratory, Isle of Man, British Isles.

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INTRODUCTION

Shallow littoral fish communities have been studied in many parts of the world (GIBSON 1982). Rocky intertidal and subtidal zones are rich in both primary (algae) and secondary production (e.g. molluscs, crustaceans and fishes). These habitats are more complex than soft substrata habitats with respect to topography and physical conditions (e.g. water movements, salinity and temperature) and have a greater range in physical conditions than both deeper benthic habitats and the open ocean (STEPHENSON & STEPHENSON 1972, HISCOCK & MITCHELL 1980).

The littoral zone of the Azores is of considerable biological interest as it comprises the most oceanic of North Atlantic archipelagos. There have been numerous studies on the fishes of the Azores (see MARTINS 1990). However, only recently has research been orientated toward studies of the littoral fish assemblages. Most of the shoreline is rocky, but there is a limited number of sandy beaches. Much of the research has been concentrated on the island of Faial, but work has been done around Pico, Santa Maria and Formigas. To date research has covered the composition of rocky shore pool fish assemblages (ARRUDA 1979, 1980), distribution of littoral species (ALMEIDA & VIVIEN 1983, ARRUDA et al. 1992, PATZNER et al. 1992, NASH & SANTOS 1993, PATZNER & SANTOS 1993), diel and seasonal variations in assemblage structure on soft sediments (NASH et al. 1994a, b).

The aim of this study was to examine the intertidal fish assemblages on both sandy and rocky shores of Faial, Azores. The differences in the community structure and life-styles of the species were evaluated with respect to the constraints imposed by rocky and sandy habitats. Due to the differences in the habitat, major differences in the proportions of resident and transient, *sensu* GIBSON (1969), were expected.

MATERIAL AND METHODS

1. Sampling

Different methods were employed to sample fishes from both habitats (see GIBSON 1982 for summary of intertidal fish sampling methodology).

1.1. Rocky intertidal

Intertidal rock pool fishes were sampled during low tide from six different pools at Feteira (Fig. 1), using the anaesthetic Quinaldine (20% solution in acetone) giving a final dosage of approximately 10 ppm in the pools (GIBSON 1967b). The shore of Feteira is a flat basaltic platform facing south. It extends approximately 250 metres east-west and 100 metres north-south. This platform contains shallow intertidal pools of different sizes, but quite similar depths (none deeper than 0.75 metres). Each pool was thoroughly searched and all fishes collected. Sampling in the years of 1987 and 1988 was conducted on a seasonal basis distributed as follows: 18 samples during the first quarter of the year, 16 during the second quarter of the year, 13 during the third quarter of the year and 6 during the last quarter of the year of 1987.

All the anaesthetized fishes caught from the pools were counted and measured. Most fishes were returned to the pools.

1.2. Shallow sandy beach

The sampling site, Porto Pim, is located on the south-east corner of the island of Faial (Fig. 1). The beach is small (approximately 280 m) facing south-west. The southern border is the edge of Monte da Guia. The beach is exposed at low water for approximately 30 metres.

Sampling was undertaken with a 20m beach seine (32mm stretch mesh at the wings reducing through 15mm to 8mm in the centre). Two sets of the beach seine were made at three hour intervals for 24h on each sampling date. Samples

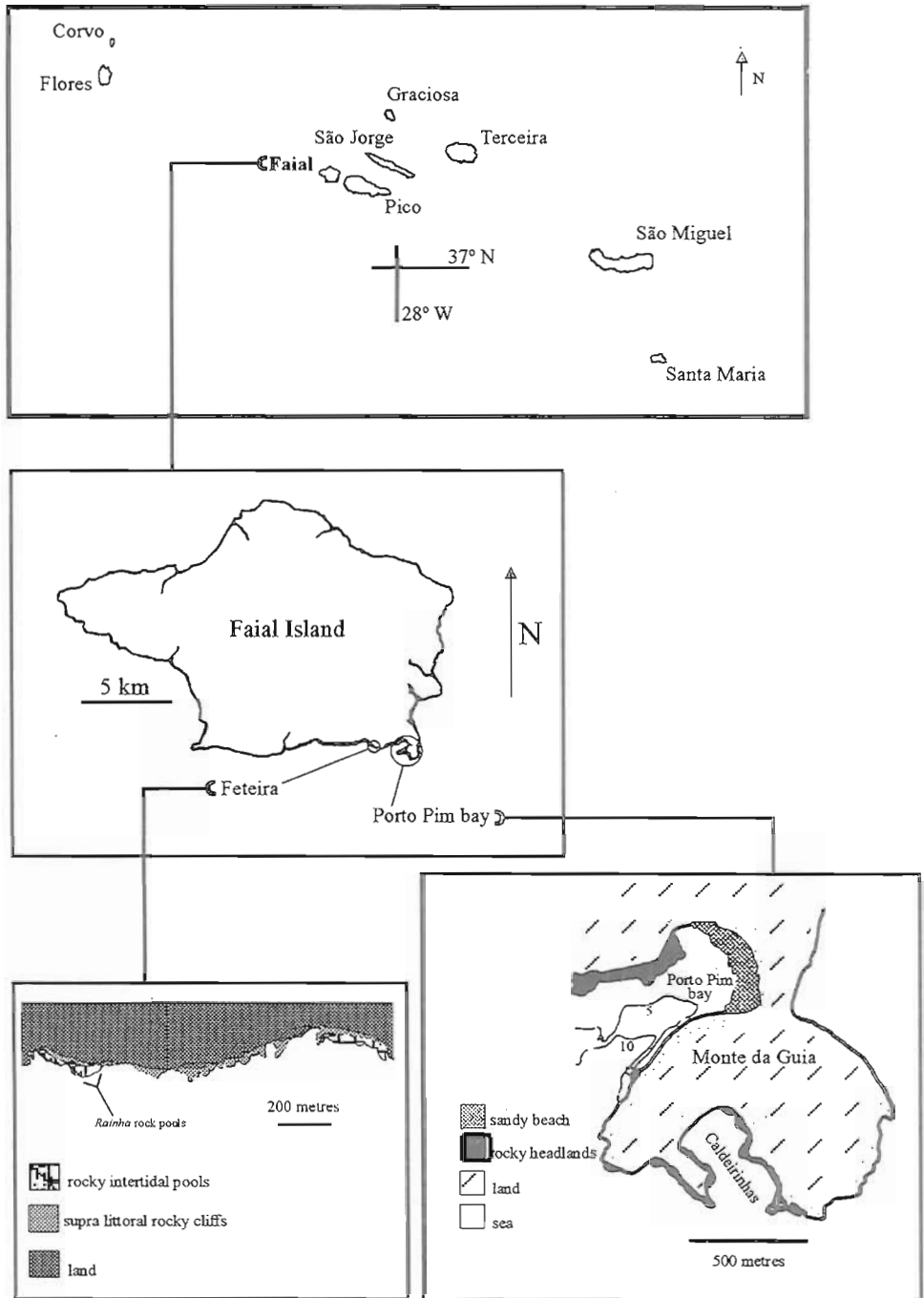


Fig. 1. The archipelago of the Azores, the island of Faial and the two locations where the data were collected: Porto Pim bay - close to Monte da Guia protected landscape -, and *Rainha* rock pools basaltic platform, in Feteira.

were taken once every month, except December, between July 1989 and June 1990. The number of individuals of each species were counted. For other details, not included in the present paper see NASH et al. (1994a,b). For the purpose of this paper only those hauls made at high water -the intertidal area of the beach- are considered.

2. Statistical methods

For the purposes of the analysis the data were rearranged to reflect the four quarters of the year by pooling the data into 1st (January, February and March: mean sea water temperature -mswt- 16.1°C), 2nd (April, May and June: mswt- 17.3°C), 3rd (July, August and September: mswt- 21.4°C) and 4th quarter (October, November and December: mswt- 18.7°C). This arrangement, which gave adequate number of individuals, also reflects adequately the sea temperature cycle. Whenever possible, the data were analyzed with the Statistical Ecology programs package of LUDWIG & REYNOLDS (1988).

2.1. Similarities and associations

The community composition in different quarters of the year was compared through a procedure that considers the relative proportion of species: the Chord Distance (CRD) (LUDWIG & REYNOLDS 1988). The upper limit of CRD is 1.41 and the lower limit is 0.

Similarities in the fish communities between different seasons of the year were also measured with Jaccard's coefficient, based on presence-absence data.

Schoener's index (SCHOENER 1970) of species relative abundance overlap was used to compare interspecific associations. The index varies between 0% and 100%. Cluster analyses were performed on the raw matrix of Schoener's index (SCHOENER 1970) using Ward's method (WARD 1963) and euclidean distances (SNEATH & SOKAL 1973) for dendrogram construction.

2.2. Community diversity and other measures

The fish assemblages in intertidal rocky shore pools and on shallow sandy beaches were examined for diversity and associated parameters (i.e. richness, relative abundance and evenness).

Species richness is a very awkward measure when samples are of different sizes (see comments in LUDWIG & REYNOLDS 1988). Three measures of richness are presented: i. N = total number of species in the community; ii. $E(S_n)$ - the expected number of species in a sample of n individuals taken from the community. This measure is used to overcome the problem of comparison between samples of different sizes, and is based on a rarefaction method (SANDERS 1968, HURLBERT 1971, LUDWIG & REYNOLDS 1988, MAGURRAN 1988). iii. Margalef's index (R) of diversity (MARGALEF 1958).

Diversity was also measured through the Shannon's index (H') (LUDWIG & REYNOLDS 1988).

Evenness indices are measures of species equitability. Two indices were calculated: the Pielou's index (J') (PIELOU 1975, 1977) and the modified Hill's ratio (E) (HILL 1973).

RESULTS

1. Interspecific fish associations

1.1. Intertidal rocky shore pools

The following 13 species occurred in intertidal rocky pools: *Parablennius ruber* (Valenciennes, 1836), *Parablennius incognitus* (Bath, 1968), *Parablennius sanguinolentus parvicornis* (Valenciennes, 1836), *Ophioblennius atlanticus* (Valenciennes, 1836), *Coryphoblennius galerita* (Linnaeus, 1758), *Lipophrys trigloides* (Valenciennes, 1836) [Blenniidae], *Gobius paganellus* (Linnaeus, 1758) [Gobiidae], *Centrolabrus trutta* (Lowe, 1833) [Labridae], *Chelon labrosus* (Risso, 1826) [Mugilidae], *Gaidropsarus guttatus* (Collett, 1890) [Gadidae], *Trachinotus ovatus* (Linnaeus, 1758)

[Carangidae], *Epinephelus marginatus* (Lowe, 1834) [Serranidae] and *Diplodus sargus* (Linnaeus, 1758) [Sparidae].

The highest percentage overlaps (as given by Schoener's index) were observed between four resident shallow upper subtidal species: *P. ruber*, *P. incognitus*, *O. a. atlanticus* and *C. trutta*. The values of Schoener's indices for every possible pair of species are quite high, varying between a minimum of 54% (*C. trutta*/*P. ruber*) and a maximum of 73% (*O. a. atlanticus*/*P. incognitus*). These four species form a distinct cluster (Fig. 2a).

Another cluster is formed, at a higher level of linkage, by five common resident intertidal species (*C. galerita*, *L. trigloides*, *P. s. parvicornis*, *G. paganellus* and *G. guttatus*) and

two of the most common seasonal transient species (*C. labrosus* and *D. sargus*). The percentage overlap of these species is much lower than the one of cluster -A- (Fig. 2), varying from 16% to 42% indicating some differentiation of ecological niches. The two small cryptobenthic blennies (*C. galerita* and *L. trigloides*) are linked at a lower level sub-cluster (Fig. 2b), while the two other species with parental care, *P. s. parvicornis* and *G. paganellus*, are linked in a distinct sub-cluster.

C. labrosus shows a pattern of uniform overlap with other species, centred in most cases at around 35%. This is an opportunistic species which occurs in a great variety of shallow littoral habitats, including pools. *G. guttatus* is the only piscivorous species. Its overlap with *C. galerita*,

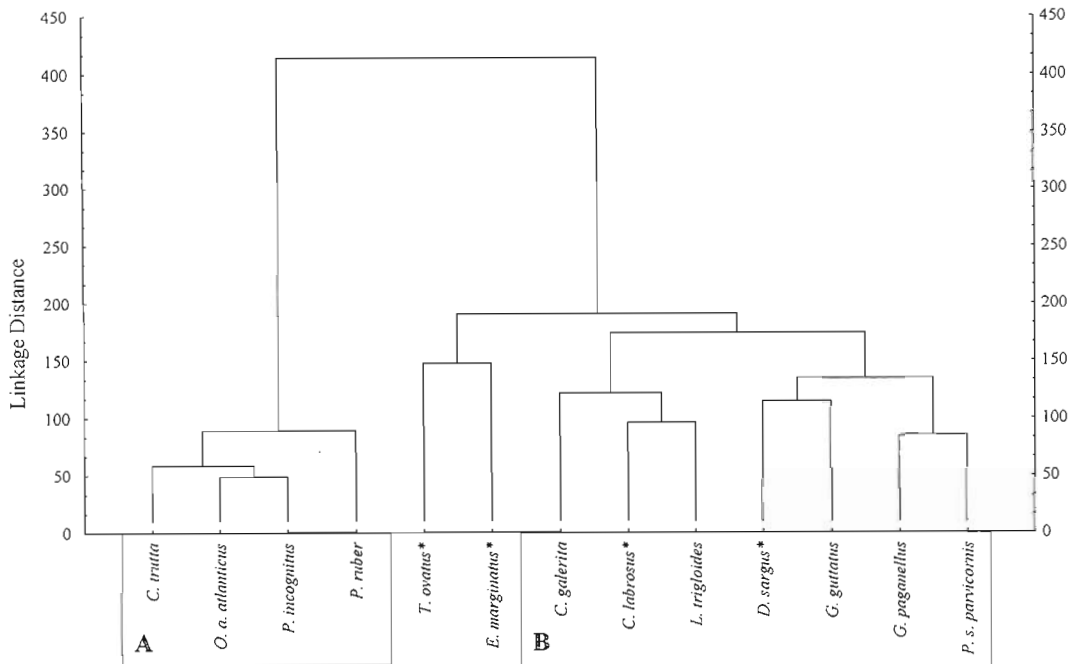


Fig. 2. Dendrogram of all rocky intertidal species caught at Feteira, based on cluster analysis performed on a matrix of Schoener's index. Species marked with * are juveniles of transient species.

L. trigloides, and *P. incognitus* is weak, but it is well associated with *P. s. parvicornis* and *G. paganellus*.

The two remaining species are rare. The occurrence of *T. ovatus* in pools is accidental. *E. marginatus* occurs strictly on a seasonal basis for very short periods; post-metamorphic larvae occur during a week in September, then migrate into deeper waters.

1.2. Shallow sandy beaches

The following fifteen species occurred at high tide in the intertidal region of the beach: *Pagellus bogaraveo* (Brünnich, 1768), *Diplodus sargus*, *Boops boops* (Linnaeus, 1758) [Sparidae], *Chelon labrosus* [Mugilidae], *Trachinotus ovatus*, *Trachurus picturatus* (Bowdich, 1825) [Carangidae], *Mullus*

surmuletus (Linnaeus, 1758) [Mullidae], *Pomatomus saltator* (Linnaeus, 1766) [Pomatomidae], *Echiichthys vipera* (Cuvier, 1829) [Trachinidae], *Dasyatis pastinaca* (Linnaeus, 1758) [Dasyatidae], *Bothus podas* (Delaroche, 1809) [Bothidae], *Sardina pilchardus* (Walbaum, 1792) [Clupeidae], *Belone belone gracilis* Lowe, 1839 [Belonidae], *Syngnathus acus* Linnaeus, 1758 [Syngnathidae] and *Sphoeroides marmoratus* (Lowe, 1839) [Tetraodontidae]. Three species clearly dominated the samples: *P. bogaraveo*, *C. labrosus* and *T. ovatus*, representing 41%, 30% and 19%, respectively, of the total number of individuals of all species. However, their seasonal abundance was irregular. Each of them tended to be most abundant in different seasons (Table 1). Their overlap is thus low. They are not closely clustered (Fig. 3).

Table 1

Rank of most abundant fish species in the sandy beach of Porto Pim at different quarters of the year

Species Rank	1st Quarter		2nd Quarter		3rd Quarter		4th Quarter	
1	<i>T. ovatus</i>	83%	<i>P. bogaraveo</i>	48%	<i>P. bogaraveo</i>	59%	<i>C. labrosus</i>	88%
2	<i>C. labrosus</i>	14%	<i>T. picturatus</i>	25%	<i>C. labrosus</i>	29%	<i>S. pilchardus</i>	6%
3	<i>D. sargus</i>	2%	<i>D. sargus</i>	14%	<i>T. ovatus</i>	9%	<i>T. ovatus</i>	3%
4	<i>P. saltator</i>	1%	<i>T. ovatus</i>	7%				
5			<i>C. labrosus</i>	6%				
No. of individuals	1 205		1 464		4 485		956	

2. Diversity, richness and evenness

2.1. Rocky shore pools

The number of species found in the pools was highest in the 3rd quarter. This is confirmed by both the Margalef's index of species richness ($R=1.7$) and the expected number of species from the rarefaction curve ($E[S_{50}]=9$) (Table 2). The 1st and 2nd quarters of the year were less rich in species, being very similar according to Margalef's index (Table 2), but the rarefaction method gave the second quarter as slightly richer

in species than the 1st quarter. The 4th quarter occupied an intermediate position; although the rarefaction method suggests that species richness were similar in the 2nd and 4th quarter of the year.

Diversity (Shannon's index - H') was at its lowest in the 1st quarter and highest in the 3rd quarter (Table 2). Evenness was low in the 1st quarter, when *P. s. parvicornis* dominated the samples with 72% of the total number of individuals. *C. galerita* was the second most abundant species (11%), and *G. paganellus* the third with 7% of all the individuals (Tables 2 and

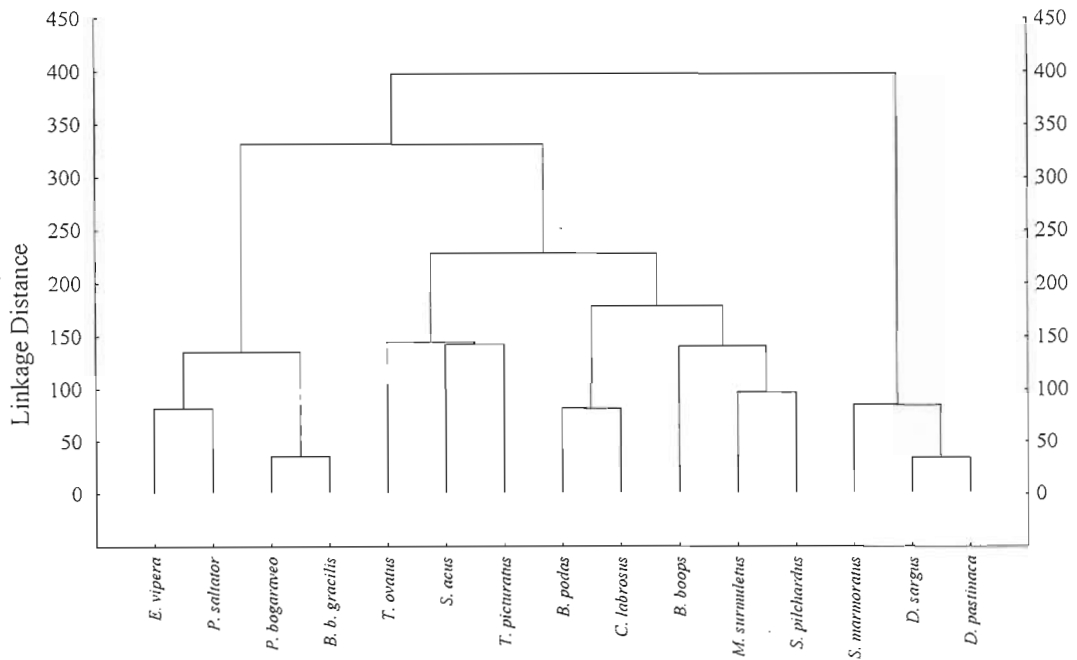


Fig. 3. Dendrogram of all sandy intertidal species caught at Porto Pim, based on cluster analysis performed on a matrix of Schoener's index.

3). Evenness increased in the 2nd quarter. The community was still dominated by *P.s. parvicornis*, which contributed 46% of the number of individuals in the samples, followed by *C. labrosus* (all juveniles) with 35% of the individuals.

Table 2

Quarterly variation in the richness, diversity and evenness of intertidal rock pool fish at Feteira

	Quarters of the year				All
	1st	2nd	3rd	4th	
N. species	8	8	12	10	13
E (S50)	5	6	9	6	8
R	1.19	1.20	1.70	1.62	1.63
H'	0.98	1.33	1.85	1.37	1.66
J'	0.48	0.64	0.74	0.60	0.65
E	0.49	0.68	0.69	0.75	0.65

E(S50)= expected number of species (rarefaction curve);
 R= Margalef's index of richness; J'= Pielou's index of evenness;
 H'= Shannon's index of diversity; E= Hill's index of evenness.

In the 3rd quarter, Hill's index of evenness was slightly higher. At this time *C. labrosus* dominated the community (36% of individuals) followed by *P. s. parvicornis* (23%) and *C. galerita* and *G. paganellus* each with 8% of the individuals in the samples.

According to Hill's index, the highest evenness was in the 4th quarter. In contrast Pielou's index gave a different result, probably due to the recognized sensitivity of the Pielou's index to changes in species richness (PEET 1974, LUDWIG & REYNOLDS 1988). We believe that Hill's index gives a better determination of equitability. During the 4th quarter the community was clearly dominated by three species: *C. labrosus* (44%), *P. s. parvicornis* (25%), and *C. galerita* (22%). The next most abundant species *L. trigloides*, accounted for 3% of the individuals in the samples.

If all seasons are pooled the overall dominant species was *P. s. parvicornis* (39%), followed by *C. labrosus* (30%), *G. paganellus* (6%), *P. ruber* (4%) and *D. sargus* (4%).

Table 3

Rank of most abundant fish species in the intertidal rock pools of Feteira at different quarters of the year

Species Rank	1st Quarter	2nd Quarter	3rd Quarter	4th Quarter
1	<i>P. s. parvicornis</i> 72%	<i>P. s. parvicornis</i> 46%	<i>C. labrosus</i> 36%	<i>C. labrosus</i> 44%
2	<i>C. galerita</i> 11%	<i>C. labrosus</i> 35%	<i>P. s. parvicornis</i> 23%	<i>P. s. parvicornis</i> 25%
3	<i>G. paganellus</i> 7%	<i>P. ruber</i> 5%	<i>C. galerita</i> 8%	<i>C. galerita</i> 22%
4		<i>G. paganellus</i> 4%	<i>G. paganellus</i> 8%	<i>L. trigloides</i> 3%
5			<i>P. ruber</i> 6%	
6			<i>O. a. atlanticus</i> 4%	
No. of individuals	345	337	635	260

2.2. Shallow sandy beaches

The number of species was higher in the 3rd and 4th quarters. This is also shown by both Margalef's index of species richness ($R=1.31$) (Table 4) and the expected number of species from the rarefaction curve ($E[S_{50}]=4$). The first and second quarters were less rich in species, although in the second quarter more species were present.

Table 4

Quarterly variation in the richness, diversity and evenness of the intertidal sandy beach fishes of Porto Pim

	Quarters of the year				
	1st	2nd	3rd	4th	All
N. species	7	9	10	10	15
E (S50)	3	6	4	4	6
R	0.85	1.10	1.31	1.31	1.58
H'	0.57	1.38	1.05	0.53	1.44
J'	0.29	0.63	0.42	0.23	0.53
E	0.54	0.71	0.69	0.40	0.74

$E(S50)$ = expected number of species (rarefaction curve);
 R = Margalef's index of richness; J' = Pielou's index of evenness;
 H' = Shannon's index of diversity; E = Hill's index of evenness.

Diversity (Shannon's index - H') was lower in the 4th quarter and higher in the 2nd quarter (Table 4).

Evenness was low in the 4th quarter, when *C. labrosus* dominated the samples with 88% of the total number of individuals (Tables 1 and 4). Evenness slightly increased in the 1st quarter, reaching a peak in the 2nd quarter ($J'=0.63$; $E=0.71$), when the assemblage was dominated by *P. bogaraveo*, *T. picturatus* and *D. sargus*. The same trend is given both by Pielou's and Hill's indices of evenness (Table 4).

2.3. Between habitats

Overall more species occurred during sampling of the sandy beaches than of the rock pools. Despite this, the seasonal species richness and diversity was, generally, higher in rock pools than on sandy beaches. The only exception was in the 2nd quarter, when sandy beach fish evenness reached its maximum value (Table 4).

3. Seasonal similarities in fish assemblages

3.1. Rocky shore pools

Exactly the same species occurred in the 1st and 2nd quarters of the year ($J=1$) (Table 5). Similarity between the other seasons was also high. The lowest similarity was between fish

assemblages of the 4th quarter and those of the 1st and 2nd quarters ($J=0.64$).

However, if one considers community resemblance between the different seasons using proportions of individuals per species (Chord

distance) the pattern is slightly different (Table 5). Fish communities in the 3rd and 4th quarters showed the greatest resemblance ($CRD=0.37$), while they were the least similar in the 4th and 1st quarters ($CRD=0.94$).

Table 5
Seasonal resemblances of intertidal rocky shore pool and sandy beach fish assemblages

	Rock Pools			Sand Beach		
	Jaccard Coefficient			Jaccard Coefficient		
	2nd quarter	3rd quarter	4th quarter	2nd quarter	3rd quarter	4th quarter
1st quarter	1.00	0.67	0.64	0.46	0.46	0.42
2nd quarter		0.67	0.64		0.62	0.46
3rd quarter			0.69			0.70

	Rock Pools			Sand Beach		
	Chord Distance			Chord Distance		
	2nd quarter	3rd quarter	4th quarter	2nd quarter	3rd quarter	4th quarter
1st quarter	0.60	0.92	0.94	1.31	1.26	1.26
2nd quarter		0.46	0.56		0.61	1.35
3rd quarter			0.37			1.05

3.2. Shallow sandy beaches

Inter-seasonal similarities of species assemblages were low. As measured by Jaccard's coefficient, similarity between the 3rd and 4th quarters was higher ($J'=0.70$). It was lower between the 1st and 4th quarters ($J'=0.42$).

When considering fish assemblage resemblance between the different seasons using proportions of individuals per species, the pattern is again slightly different (Table 5). Higher resemblance was found between fish assemblages in 2nd and 3rd quarters ($CRD=0.61$). The fish assemblages of the 2nd and 4th quarters were the least similar ($CRD=1.35$).

3.3. Between habitats

Inter-season resemblances of fish assemblages were significantly stronger in intertidal rock pool habitats than in sandy beach habitats (Table 2).

DISCUSSION

There are considerable problems in comparing the assemblages on sandy beaches and rocky shores, particularly as different methods with different types of selectivity are used in both. On rocky shores it is quite likely that a very large proportion of the species were sampled, with the possible exception of extremely cryptic species which may remain anaesthetized in crevices. Netting on sandy beaches may miss or be biased against highly mobile visual species present during the day and those species (e.g. gobies) smaller than the mesh size used. These reservations aside it is still possible to compare the assemblage structure, and seasonal variation between the two habitats and compare them with studies elsewhere.

Most of the non-resident species that occur in the intertidal are juveniles. Most of them show no special adaptations and may be trapped in pools that may not be inundated by a high tide during the following days or weeks. Many of

these individuals are unable to escape and often die there (e.g. *Diplodus sargus* and also, under more extreme conditions, *Chelon labrosus*).

Shallow water sandy beach fish of the Azores do not show special adaptations to live in the intertidal. Species like *D. sargus*, *C. labrosus* and *Trachinotus ovatus* make similar use of shallow sandy beaches and rocky intertidal pools, with the difference that they have to leave the sandy intertidal when the tide ebbs. In rock pools they are trapped at ebb tide.

During low tide there are no fishes present in the intertidal zone of sandy beaches of the Azores, since burrowing species (e.g. *Ammodytes* spp. -Ammodytidae-) are absent. At high tide there is an assemblage of species which is characterized by the absence of resident species, contrasting with rocky intertidal pools. The shallow sandy beach fish assemblage is dominated by schools of juveniles of transient species, which use these protected habitats as nurseries. Adults live offshore. Evenness is generally very low reflecting species-specific dominance of the assemblages (*T. ovatus* dominates the assemblage in the 1st quarter, *Pagellus bogaraveo* with *Trachurus picturatus* in 2nd and, with *C. labrosus*, in 3rd quarter, and *C. labrosus* in 4th quarter). Contrasting with that picture, evenness is always high in rocky intertidal pools due to the presence of more than one resident species. Abundance of individual species on sandy beaches is highly seasonal, reflecting the timing of spawning and juvenile recruitment timings. No trend or pattern of species association emerges from the species overlap matrix of intertidal sandy beaches. Few piscivores are present (e.g. *Pomatomus saltator*: 1% in the first quarter).

Species overlap within intertidal rock pools shows an interesting pattern that must be determined by mechanisms of habitat partitioning within the community. The highest proportions of overlap were observed among four species, *Parablennius ruber*, *P. incognitus*, *Ophioblennius a. atlanticus* and *Centrolabrus trutta*, that only represented 6% of the fish

population in the pools (representing 17% of the total sum of percentage of overlap of all species).

These four species are residents in the shallow subtidal, ranging from 0 down to 6 metres. In contrast each of the resident species of intertidal pools (*P. s. parvicornis*, *C. galerita*, *Lipophrys trigloides* and *Gobius paganellus*) shows an evenly distributed overlap with other species. These resident species may occupy separate ecological niches. This could be related both with the exploitation of different food items (they all have different diets: GIBSON 1968; FIVES 1980; TABORSKY & LIMBERGER 1980; CARVALHO 1982) and with mutual segregation during the reproductive season which occurs in the late spring and early summer for all four species. They all belong to the same reproductive guild and have very similar ethology (GIBSON 1969, 1982, 1986), but their size, body shape and ecological traits (e.g. feeding habits, affinity to light) result in different nesting structures.

The most remarkable feature of the sandy beach fish assemblages of the Azores is the almost total absence of adult fishes and the absence of residents. No species reproduce there, nor are there species with demersal eggs. Species which bury in the sand, which are present as adults in the shallow subtidal, e.g. *Apterichthys caecus* (Linnaeus, 1758) [Ophichthidae], were never found in the intertidal area of the sandy beach. *Echiichthys vipera*, *Dasyatis pastinaca* and *Bothus podas*, which are caught in the intertidal area in low numbers, leave the area when the tide falls.

Fish assemblages are greatly reduced in sandy beaches most exposed to wave action and turbulence (LASIAK 1984a,b). Under normal conditions the surf zone of sandy beaches may contain some resident species and be rich in visiting species (BROWN & MCLACHLAN 1990). For the most part these assemblages are comprised of juveniles (MCFARLAND 1963; GIBSON 1973; LASIAK 1981; NASH et al. 1994a, b), and, in some exceptional cases, these occur together with larvae (SENTA & KINOSHITA 1985). For the most part transients tend to breed elsewhere (GIBSON 1967a, 1973, 1988; BECKLEY

1986). Species of *Leuresthes* [Atherinidae] and *Mallotus* (e.g. *M. villosus* (Müller, 1776): TEMPLEMAN 1948) [Osmeridae] are exceptions to this rule. *Leuresthes* spp. spawn on sandy beaches at high spring tide and immediately leave the eggs (THOMPSON & THOMPSON 1919).

In areas with comparable strong wave-action, sandy beaches are far less rich than rocky intertidal habitats in resident species (GIBSON 1969, 1982; BROWN & MCLACHLAN 1990). BROWN & MCLACHLAN (1990) state that true resident fish species in surf-zones of a large set of sandy marine shores varies from 3 to 10% of the total number of visiting species. This percentage is much higher in rocky intertidal shores, where they may represent between 40% and 80% of the species occurring in there, as is the case for the Azores.

Rock pool fish assemblages are relatively homogeneous and similar in species presence across the seasons, with some variation in the proportions of the species in each season. Seasonal fluctuations in the occurrence of recruits of non-resident fishes caught in pools contribute to the large differences between community structure parameters in different seasons. Seasonality of juvenile recruitment was also found to be the main factor contributing to seasonal fluctuations in Californian rocky intertidal pools (THOMSON & LEHNER 1976). Variation in species composition involved replacement by species that are closely related and ecologically similar, a condition that gives persistence to tide pool fish assemblages in general (MORRIS 1962; YOSHIYAMA et al. 1986). Richness is relatively stable. Seasonal similarity of intertidal fish assemblages in sandy beaches are much weaker, thus reflecting the less stable species composition.

Higher species richness in both intertidal habitats during the third and fourth quarters of the year may be attributed to several factors. Many species of littoral fishes in the Azores reproduce in spring and summer, and the recruits occur in shallow waters in summer and autumn. Some of them spend part of their early development, after leaving the plankton, in

shallow habitats, such as rocky intertidal pools. This is the case for *P. bogaraveo*, *T. ovatus*, *C. labrosus*, *D. sargus* and *E. marginatus*. Some of the resident species of the shallow rock subtidal (e.g. *O. a. atlanticus*, *P. incognitus*, *P. ruber* and *C. trutta*), or species that also occupy intertidal rocky surfaces, such as crevices (e.g. *C. galerita* and *L. trigloides*), may seek refuge in the pools as juveniles. This happens with *P. ruber* and *C. galerita*. The increasing occurrence in the pools of what seems to be one year old juveniles of *O. a. atlanticus*, during the summer, could be related to them being driven out by adult conspecifics involved in strong territorial competition to allow mating in the 0.5m to 6m depth band (SANTOS in press), or avoiding predators not resident in pools. The high occurrence of *C. galerita* in the 1st quarter could be due to the fact that they are seeking refuge in the pools, from the very rough sea conditions that affect the exposed rock intertidal surfaces that they otherwise seem to prefer (ALMADA et al. 1983).

It is interesting to note that *C. galerita*, which is able to use rocky shore pools as a refuge under severe sea conditions, represents 11% of the assemblage in the 1st quarter while the dominant species in the 3rd (36%) and 4th (44%) quarters is the transient *C. labrosus*. *Chelon labrosus* which is not so well prepared to cope with these conditions (both anatomically, physiologically and behaviourally) and prefers to retreat to deeper water, is poorly represented in the first quarter.

Seasonal fluctuations are probably related to three main factors: i. refuge from strong wave action; ii. social interactions; iii. recruitment.

In conclusion, intertidal sandy habitats are weakly structured while rocky intertidal habitats are highly complex and structured. This is also reflected in the dynamics and nature of the fish assemblages present in both habitats. Rocky intertidal habitats are dominated by resident species while no resident species are found in intertidal sandy habitats. The dominating species of intertidal sandy fish assemblages, schools of juveniles of transient species, vary from season to

season, which makes interseason resemblance quite low. Despite the fact that transient juveniles seek refuge also in intertidal rock pools, the presence of resident species makes these assemblages more stable with a higher level of similarity between seasons. In both cases species richness increases in the summer and autumn with the input of recruits of transient species. However, diversity is always high and more stable in rocky intertidal pools due to the stabilising effect of residents.

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