Influence of Fishing Activity on Total Species Richness and Abundance Unevenness in Reef Fish Communities: A Case Study in a Brazilian Tropical Coral Complex

Jean Béguinot[1*]

[1]*Société Histoire Naturelle-Bourgogne Nature, 7 bvd H. P. Schneider, 71200, Le Creusot, France.*

Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

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ABSTRACT

The internal organization of reef-fish communities, particularly the species richness and the hierarchical structuring of species abundances, depends on many environmental factors, including fishing intensity and proportion of macroalgal cover which are expected to have determinant influences. However, reported studies on this topic are generally based on incomplete samplings (almost unavoidable in practice when dealing with highly uneven and species-rich communities), so that the derived results can be appreciably skewed. To overcome this difficulty, the incomplete samplings involved in this study were completed numerically through a reliable extrapolation procedure. This precaution provided a safe confirmation that reduced fishing activity and increased macroalgae cover both contribute to enhance the total species richness and to reduce the abundance unevenness in these reef fish communities. Yet, it is shown that this reduction of abundance unevenness is almost entirely attributable to the increase in species richness.

1. INTRODUCTION

Tropical marine ecosystems in shallow waters, particularly those associated with coral reefs, are of major interest, because of their remarkably high levels of diversity and biological complexity [1-5]. *Reef-fish* communities are emblematic examples of these very rich and diverse

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assemblages of species cooccurring at a same location.

Yet tropical marine ecosystems, especially those hosted by coral reefs, are particularly sensitive to either positive or negative environmental conditions, the latter often (but not always) related to human activities, such as over-exploitation, pollution, climate change, etc… [4, 5]. This urges to monitor these remarkably rich communities, aiming to unravel the causes of positive and negative changes that can be detected in their internal organization. Among the environmental factors expected to have influence on reef-fish communities, fishing pressure and the proportion of macro-algal coverage have been reported as potentially important determinants for the internal organization in these fish communities, particularly in terms of species richness and degree of unevenness of species abundance [6-10].

Now, to avoid drawing seriously biased conclusions about the main structural descriptors of reef fish communities (such as total species richness and species abundance unevenness), it is imperative to rely on (sub-) exhaustive inventories [11–14]. However, *incomplete* sampling is almost unavoidable in practice when having to consider species-rich communities having very uneven distribution of abundances, as is most often the case with reef fish communities. Hence the need to supplement the available partial samplings by implementing a reliable *numerical extrapolation* procedure [15] that can provide estimates with a minimized bias regarding the number of species not yet recorded as well as the distribution of the abundances of these unrecorded species. This is all the more important as rare species, which often escape recording in practice, can nevertheless contribute disproportionately to the functional structuring of ecological communities [16–21].

Fortunately, a recently developed *numerical extrapolation* procedure takes these needs into account. As a consequence, this new extrapolating tool invites to revisit the already available reported data based on non-extrapolated partial inventories, in order to critically reconsider the previous interpretations based on these incomplete inventories. The purpose being to tentatively establish more relevant interpretations, based on *numerically completed* samplings. More specifically, once properly numerically completed (and *only* when it is so [13]), the distribution of species

abundances can provide synthetic data, both *qualitative* and *quantitative*, on the underlying process that governs the hierarchical structuring of species abundances within community [22-26].

Hereafter, I compare the internal organizations of two reef fish communities along the northeast coast of Brazil, that differ from each other by the *intensity of fishing activity* and the *proportion of macro-algal coverage*. The available inventories of these two communities being substantially incomplete, the investigations were conducted, as required, after *numerical extrapolation* of samplings, thus providing least-biased estimates of both the number and abundance distribution of the set of unrecorded species. In particular:

(i) I re-evaluate the difference in *species richness* between the two fish communities, taking full account of the *unrecorded* species;
(ii) I address a second major feature of communities' structure, the *unevenness of the species abundance* distribution, while making a clear distinction, in this respect, between the *pattern* of unevenness and the underlying *process* of hierarchical structuring of species abundances;
(iii) Finally, I further carry on the same types of analysis *separately for each of the two feeding guilds*, primary and secondary consumers.

2. MATERIALS AND METHODS

2.1 The Reported Field Data

The present study is based on two partial samplings of fish communities conducted on "Tamandaré" coral reefs, northeast coast of Brazil [27]. All details regarding the precise locations of the compared habitats and the sampling procedure are provided in the open-access reference above and need not being repeated here. The most important point is that the numbers of individual occurrences have been recorded for each species, thus making possible to implement reliable numerical extrapolations. These extrapolations are required because the relatively high proportions (10% - 12%) of species recorded only once ("singletons") suggest that the reported samplings remain substantially incomplete, as was indeed confirmed later. The number N_0 of observed individuals and the number R_0 of recorded species in each of the two communities are provided in Table 1.

Two types of coral-reef fish communities were sampled, respectively located at:

-'*Aver o Mar*', where fishing activity is relatively weak and the algal beds among corals are primarily composed of macroalgae;

-'*Caieiras*', suffering significantly stronger fishing impact and with quite less coverage of macroalgae.

2.2 The Numerical Extrapolation Procedure and its Exploitation

2.2.1 Implementation of the procedure of numerical extrapolation

* Total species richness: The least-biased estimation of the number of still undetected species during partial sampling and the resulting estimation of the total species richness of the partially sampled communities are derived according to the procedure defined in [28-29], on the basis of the numbers f_x of species observed x-times during partial sampling (x = 1 to 5). The same procedure allows to derive the least-biased extrapolation of the Species Accumulation Curve, which, in turn, allows to predict the increase in the number of newly recorded species, R(N), as a function of the growing sampling size N (N: number of currently recorded individuals). In practice, this extrapolation allows to forecast the additional sampling efforts that would be required to obtain any desirable increment in sampling completeness.

* Species Abundance Distribution: As mentioned above, the Species Abundance Distribution ("S.A.D.") is intended to provide the basic data necessary (i) to describe the *pattern* of structuration of species abundances within community and (ii) to qualify and quantify the underlying *process* that governs this structuration. Yet, to accurately exploit its full potential [30, 31], the "S.A.D." requires (i) being *corrected* for the bias resulting from drawing stochasticity during sampling of finite size and, still more importantly, (ii) being *completed* by *numerical extrapolation*, to the extent that sampling is suspected to be incomplete, as revealed by the subsistence of singletons. The appropriate procedure of correction and least-biased numerical extrapolation of the as-recorded partial "S.A.D." is described in details in reference [31] and exemplified in details in Béguinot [32]. Classically, the "S.A.D." is graphically presented with the (log-transformed)

abundances a_i plotted against the rank i of species, the latter being ordered by decreasing values of abundance (with, thus, a_1 and a_{St} respectively standing for the highest and the lowest abundances in a community of S_t species).

2.2.2 Abundance unevenness: the apparent pattern of species abundance structuration

Once numerically completed, the "S.A.D." conveys all the relevant quantitative data required to address the internal organization of species within a local community [33]. In turn, the "S.A.D." can be synthetically summarized focusing on two of its major features: the *total species richness* 'S_t' and the *degree* 'U' *of unevenness* of the abundance distribution. Indeed, following [34], it is the degree of *unevenness* – rather than evenness – that should be preferred to address the hierarchical structuring of species abundances in ecological communities. According to the mode of representation of the "S.A.D.", it goes natural to quantify the degree of abundance unevenness U as the average slope of the log-transformed abundance decrease, as already proposed by [35], that is:

$$U = [\log_{10}(a_1) - \log_{10}(a_{St})]/(S_t - 1)$$
$$= [\log_{10}(a_1/a_{St})] / (S_t - 1) \qquad (1)$$

2.2.3 The underlying process of species abundance structuration

Beyond the unevenness pattern U, the underlying process of hierarchical structuration of abundances is worth considering, in terms of both (i) the kind of *mechanism* involved and (ii) the genuine *intensity* of this structuring process.

Very schematically, the kind of *mechanism* driving the hierarchical structuration of abundances can result either (i) from the major contribution of *one dominant* factor or (ii) from the combined contributions of *many mutually independent factors* acting together. This distinction can be tested by checking the conformity of the "S.A.D." to either the *log-series* model or the *log-normal* model respectively [22, 36-39].

As regards the *genuine intensity* of the process of hierarchical structuration, it should be first emphasized that this intensity is not reliably mirrored by the degree of unevenness U, since the latter is *also* mathematically dependent (negatively) upon the species richness S_t [40-

42]; see also Appendix. Thus, the unevenness *pattern* U cannot relevantly account for the *genuine* intensity of the structuring *process* itself [24,25,43]. To get rid of this mathematical influence of species richness, the genuine intensity of the structuring process can be quantified appropriately by standardizing the average slope, U, of the "S.A.D." to the slope U' of the so-called "broken-stick" distribution [22, 44], computed for the same species richness S_t [45-48]. This standardization is effective precisely because the average slope U' of the "broken-stick" distribution exactly represents the mathematical influence of species richness [22, 46]. Accordingly, the genuine intensity, "I_{str}", of the hierarchical structuring process is relevantly defined by the ratio U/U':

$$I_{str} = [\log_{10}(a_1/a_{St})/(S_t\text{-}1)]/[\log_{10}(a'_1/a'_{St})/(S_t\text{-}1)]$$

that is:

$$I_{str} = \log_{10}(a_1/a_{St}) / \log_{10}(a'_1/a'_{St}) \qquad (2)$$

with a_1 and a_{St} standing for the highest and the lowest abundances in the studied community and a'_1 and a'_{St} standing for the highest and the lowest abundances in the corresponding "broken-stick" distribution computed for the same species richness S_t.

3. RESULTS

3.1 Estimated Total Species Richness of Each Community

The two studied fish communities differ in the level of *recorded* species richness [27], with the communities at 'Aver o mar' and at 'Caieiras' having respectively 57 and 47 *recorded* species (Table 1).

Now, the numerical extrapolation estimates the numbers of unrecorded species: 8 species for 'Aver o mar' and 3 species for 'Caieiras'. Accordingly, the estimated true (total) species richness amounts to 65 and 50 species at 'Aver o mar' and 'Caieiras' respectively (Table 1).

3.2 Taxonomic Dissimilarity between the Two Fish Communities

3.2.1 Evaluation of the Jaccard similarity index

The fish communities at 'Aver o mar' and 'Caieiras' have respectively 57 and 47recorded species, among which 42 are shared in common, 15 species appearing as exclusive to 'Aver o mar' and 5 species appearing as exclusive to 'Caieiras' [27]. Thus the recorded value of the Jaccard similarity index is J = 0.68 (= 42/(57+47– 42)). Yet, considering samplings incompleteness highlighted above, this inference remains *hypothetical* or, at least *ill-defined*, since either all, part or none of the *unrecorded* species, in each community, may be shared by the other community. Fortunately, although the taxonomic identities of the undetected species remain unknown, the numerical extrapolation can partially clear up the issue. Among the 8 unrecorded species in the community 'Aver o mar', from none of them to all of them can possibly be shared with the community 'Caieiras' (in the latter case, the 8 unrecorded species in 'Aver o mar' would identify to the 5 species recorded as exclusive to 'Caieiras' plus the 3 unrecorded species in 'Caieiras'). Thus, the total number of species shared by both communities – including the 42 shared species that were already detected – is comprised between 42 and 50 (= 42+8) species. The extrapolated value of the Jaccard similarity index is therefore comprised between J= 0.58 (= 42/(65+50–42)) and J = 0.77 (= 50/(65+50–50)). Thus, instead of the ill-defined value of J derived from incomplete samplings, it can now be safely concluded that J is, indeed, comprised within the range 0.58 -0.77.

3.2.2 Comparison of the distributions of abundances for the most common species

The distribution of the relative abundances of the ten most common species in each community are provided at Fig. 1. The most striking features that stand out from the comparison are the strong abundance gaps, observed at 'Caieiras', between two important primary feeders: *Stegastes fuscus* (Cuvier 1830) (a) and *Acanthurus bahianus* Castelnau 1855(b), as well as between two important secondary feeders: *Pempheris schomburgkii* Müller & Troschel 1848 (d) and *Halichoeres poeyi* (Steindachner 1867) (e).This pattern is in deep contrast with the relatively similar abundances of all these four species at 'Aver o mar'.

This might probably result from the significantly stronger fishing activity at 'Caieiras', with an unequal - but overall negative - impact among secondary feeders. In turn, the resulting reduced predation pressure upon primary feeders likely enhances the interspecific competition between

Table 1. The number of collected individuals N_0, the number of recorded species R_0, the type of nonparametric estimator (Jackknife) selected as being the least-biased one, the estimated number Δ of unrecorded species, the resulting estimate of the "true" total species richness S_t (= $R_0 + \Delta$), the resulting estimated level of sampling completeness R_0/S_t

Community	'Aver o mar'	'Caieiras'
nb. collected individuals N_0	4858	3381
nb. recorded species $R_0 = R(N_0)$	57	47
selected least-biased estimator	JK-2	JK-2
number unrecorded species Δ	8	3
Total species richness S_t	**65**	**50**
sample completeness R_0/S_t	88%	94%

a - *Stegastes fuscus*
b - *Acanthurus bahianus*
c - *Abudefduf saxatilis*
d - *Pempheris schomb.*
e - *Halichoeres poeyi*
f - *Haemulon aurolin.*
g - *Odontoscion dentex*
h - *Haemulon squami*p.

i - *Sparisoma axillare*
j - *Stegastes variabilis*
k - *Acanthurus coeruleus*
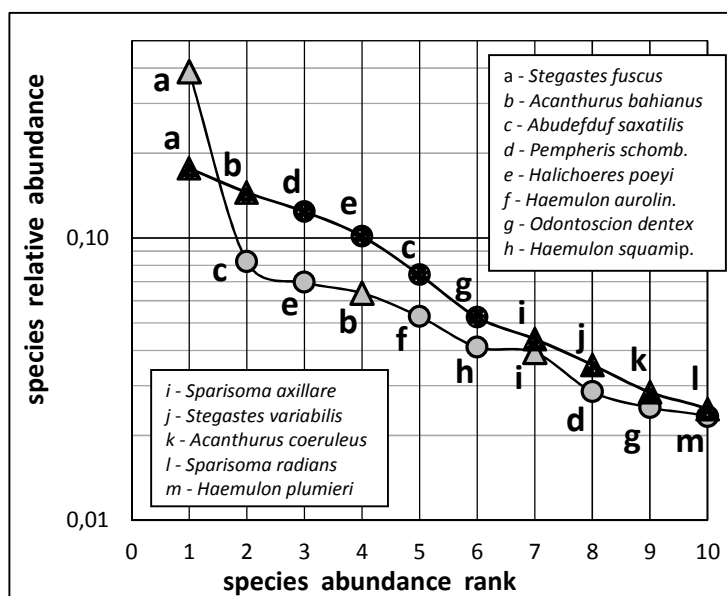l - *Sparisoma radians*
m - *Haemulon plumieri*

Fig. 1. The distribution of relative abundances of the 10 most common species (ranks 1 to 10) in communities at 'Aver o mar' (blackfigures) and at 'Caieiras' (grey figures). Triangles stand for primary feeders; discs stand for secondary feeders. Note, in the community at 'Caieiras', the strong abundance gaps between the primary feeders "a" and "b", as well as between the two secondary feeders "d" and "e" (as compared to the more regular pattern in the community at 'Aver o mar')

Acanthurus bahainus Castelnau 1855   and   *Acanthurus coeruleus* Bloch & Schneider 1801:
two rather common species in the guild of primary feeders   © D Ross Robertson ; © *Brian Gratwicke*

Haemulon plumierii (Lacepède 1801)   and   *Halichoeres poeyi* Steindachner 1867:
two rather common secondary *feeders* © *Laszlo Ilyes;* © *Fernando H. Martin*
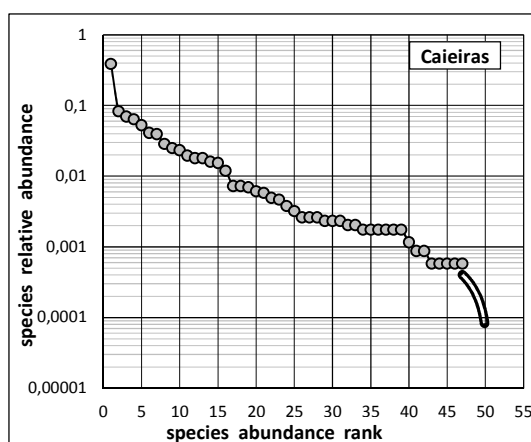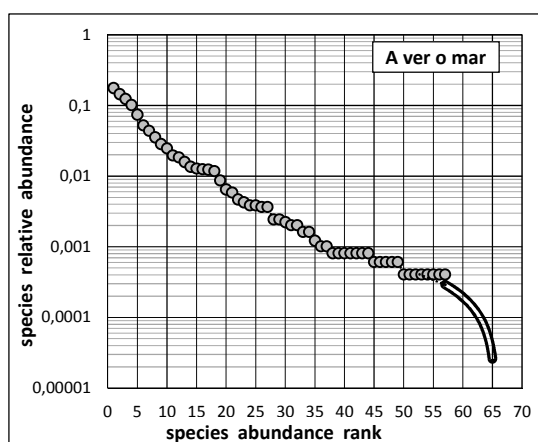
Figs. 2 & 3. The numerically completed species abundance distributions of the two studied fish communities. *Grey circles*: **recorded part of the "S.A.D." after correction for bias.** *Coarse double line*: **least-biased extrapolation of the abundance distribution for the set of species remaining unrecorded.** *Left*: **community at 'Aver o mar' (sampling completeness: 88%);** *right*: **community at 'Caieiras' (sampling completeness: 94%)**

them, in this case for the benefit of *Stegastes fuscus* and at the expense of *Acanthurus bahianus*.

3.3 Comparison of the Completed Species Abundance Distributions of Each Two Communities

The bias-corrected and numerically extrapolated Species Abundance Distributions ("S.A.D.") of the two studied communities are provided in Figs. 2 & 3. The abundances of the *recorded* species are plotted as grey circles, while the *extrapolated* part of the abundance distribution is plotted as a thick double line.

3.4 Testing for the Type of Process Involved in the Structuring of Species Abundances

The numerically completed "S.A.D.s" of both studied communities clearly fit best the "log-normal" model than the "log-series" model (Figs. 5 & 6). Now, focusing more specifically upon the set of more abundant species (say, ranks up to i = 10), a significant discrepancy from the "log-normal" model is highlighted (Figs. 7 & 8), especially for the most abundant species (rank i = 1), *Stegastes fuscus,* in both communities. At 'Aver o mar', the relative abundance of this species is significantly lower than predicted by
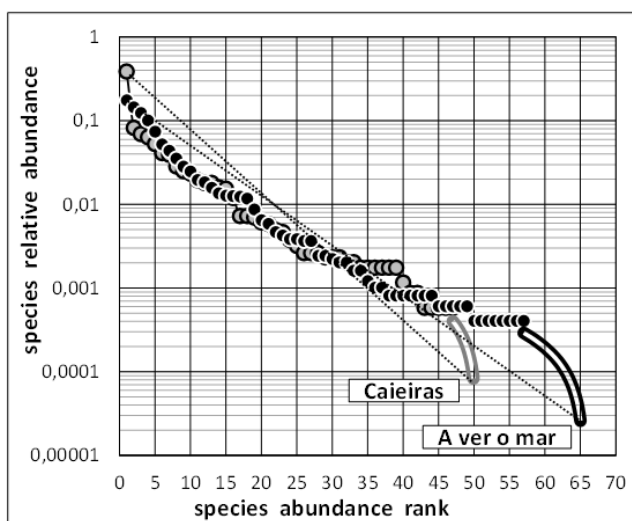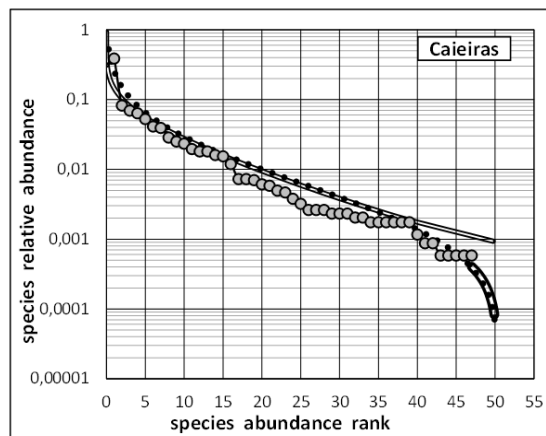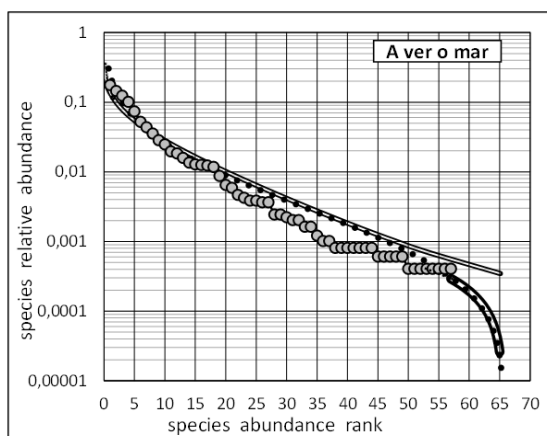
Fig. 4. Direct comparison between the numerically completed species abundance distributions of the two studied communities. Note the slightly steeper average slope for the community at 'Caieiras'

Figs. 5 and 6 – Two classical models: "log-normal" (coarse dotted line) and "log-series" (fine double line) compared to the numerically completed species abundance distributions of each of the two studied communities. Best fit is with the "log-normal" distribution for both communities

Table 2 . A synthetic summary of the main quantitative features of the hierarchical organization of species abundances within community, as derived from the numerically completed "S.A.D.s" : (i) the total species richness S_t of the community ; (ii) the relative abundances a_1 and a_{St} of the most and the least abundant species (species rank 1 and S_t) ; (iii) the same, a'_1 and a'_{St}, for the "broken-stick" model, (iv) the unevenness of abundances U in the community; (v) the unevenness of abundances U' in the corresponding "broken-stick" distribution and, at last, (vi) the genuine intensity of the structuring process I_{str} = U/U'

Site	S_t	a_1	a_{St}	a_1/a_{St}	a'_1	a'_{St}	U	U'	I_{str}
"Aom"	**65**	.1765	.0000260	6788	.0732	.000237	**.0599**	.0389	**1.54**
"Cai"	**50**	.3884	.0000832	4668	.0900	.000400	**.0749**	.0480	**1.56**
"Cai"/"Aom"	*.77*	*2.20*	*3.20*	*.688*	*1.23*	*1.69*	***1.25***	*1.23*	***1.01***

the "log-normal" model, at the benefit of the abundances of the following species (ranks i = 3, 4, 5): Chi^2 test, χ^2 = 78, p << 0.0001. At 'Caieiras', on the contrary, the abundance of *Stegastes fuscus* is significantly higher than predicted by the "log-normal" model, at the expense of the abundances of all the following species (ranks i > 1): Chi^2 test, χ^2 = 244, p << 0.0001.

3.5 Beyond the Apparent Unevenness of Species Abundances, the Genuine Intensity of the Hierarchical Structuring Process

In Figs. 9 and 10, the average slope (U) of the "S.A.D." is compared to the average slope (U') of the corresponding "broken-stick" model (§ 2.2.2 & 2.2.3), from which is derived the genuine intensity of the underlying structuring process I_{str} = U/U' (equation (2)).

The main results derived from this comparison are summarized synthetically in Table 2 which highlights, in particular, the variations of (i) the true total species richness S_t, (ii) the ratio a_1/a_{St} between the abundances of the commonest and the rarest species, (iii) the degree of unevenness U of species abundances and, finally, (iv) the genuine intensity I_{str} of the process driving the hierarchical structuration of species abundances.

The main trends derived from this comparison are graphically highlighted in Fig. 11, where both the apparent unevenness U and the genuine

intensity of the structuring process I_{str} are plotted together against the species richness S_t. While the intensity I_{str} of the structuring process remains constant (only very slightly increasing by only 1%) all along the range of variation of species richness S_t, the degree of unevenness U, on the contrary, strongly decreases by 25%. This discrepancy between the unevenness *pattern* and the intensity of the underlying structuring *process* is entirely due to the already underlined negative mathematical dependence of U upon the species richness S_t (§2.2.3).

3.6 Species Richness and the Hierarchical Structuring of Species Abundances in Each Feeding Guild, Considered Separately

The numerical extrapolation procedure applied above to the entire communities can be implemented for each of the two feeding guilds *separately*: *primary* feeders (herbivores) and *secondary* feeders (carnivores and omnivores): Figs. 12 and 13.

The respective contributions of each feeding guild – in terms of both total species richness and the cumulated number of individuals per guild – are derived accordingly for each community: Table 3. The guild of *secondary* consumers is three to four times more species-rich than is the guild of *primary* consumers, while the cumulated numbers of (recorded) individuals differ quite less sharply between the two guilds.
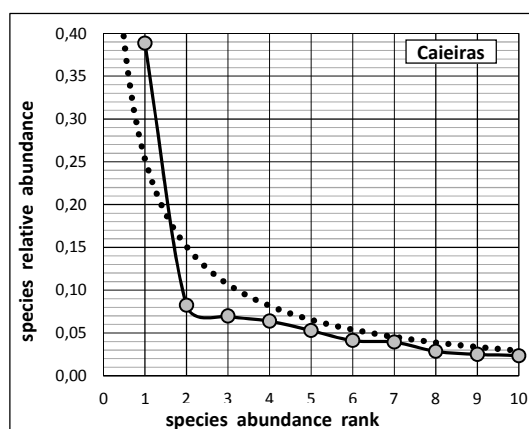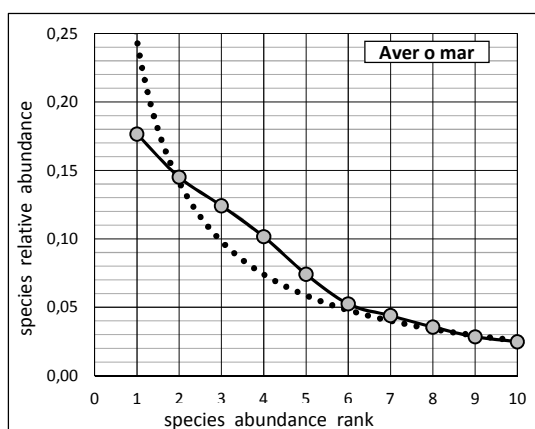
Figs. 7 and 8. Detail of the comparison between the species abundance distributions of the two studied fish communities and the "log-normal" model (coarse dotted line); ordinate with *arithmetic* scale to make the comparison easier. Highlighted are the negative density-dependence at 'Aver o mar' and, on the contrary, the positive density-dependence at 'Caieiras' in favor of the most abundant species (*Stegastes fuscus*, rank 1 in both communities) at the expense of the following species, already highlighted at § 3.2.2
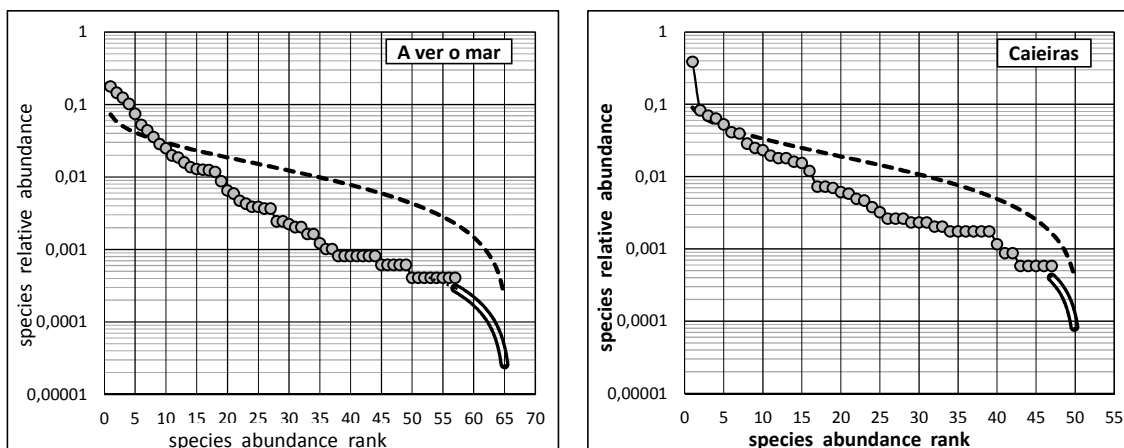
Figs. 9 and 10. The species abundance distributions compared to the corresponding "broken-stick" model (dashed line) for communities at "Aver o mar" and at "Caieiras"
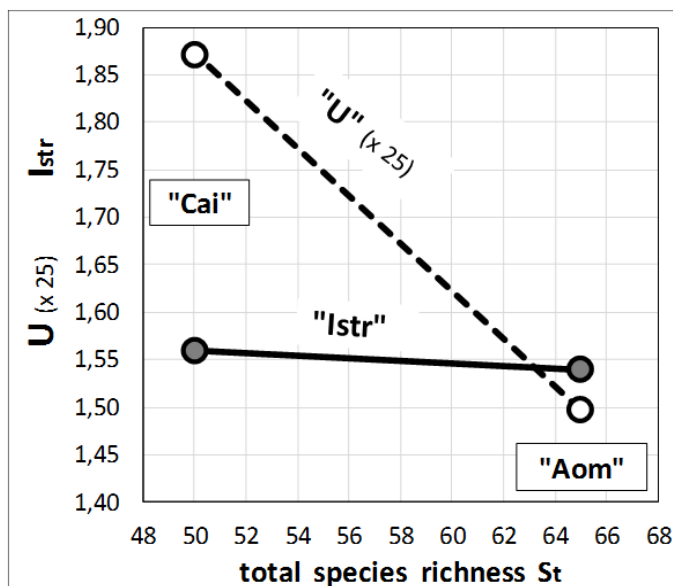

Fig. 11. The degree U of abundance unevenness (*dashed* line) and the intensity I_{str} of the underlying structuring process (*solid* line) plotted against the total species richness St, for the two studied communities

Table 3. Respective contributions of each *feeding guild* (*primary* and *secondary* consumers) to the total species richness and the cumulated numbers of (recorded) individuals

	'Aver o mar'		'Caieiras'	
	Primary	**Secondary**	**Primary**	**Secondary**
nb. recorded indiv. N_0	2350	2508	1951	1430
contrib. to nb.individ. %	*48%*	*52%*	*58%*	*42%*
total species richness S_t	**12.5**	**52.5**	**12.5**	**37.5**
contrib. to sp. richness %	**19%**	**81%**	**25%**	**75%**

As regards the hierarchical structuration of species abundances (Table 4), the intensity I_{str} of the structuring process is clearly stronger for primary feeders than it is for secondary feeders

and the degree of unevenness U is still more strongly contrasted in favor of primary feeders. This was expected since the unevenness pattern depends not only on the intensity of the structuring process but is also mathematically linked (negatively) to the level of species richness, the latter being much weaker in the guild of primary feeders. All these trends, regarding the species richness S_t, the intensity I_{str} of the structuring process and the abundance unevenness U, are consistent at both sites. Even more remarkable is the consistency still maintained when extending the comparison from reef *fish* communities to reef *gastropods* communities [32,47,48]: Figs. 14 and 15.
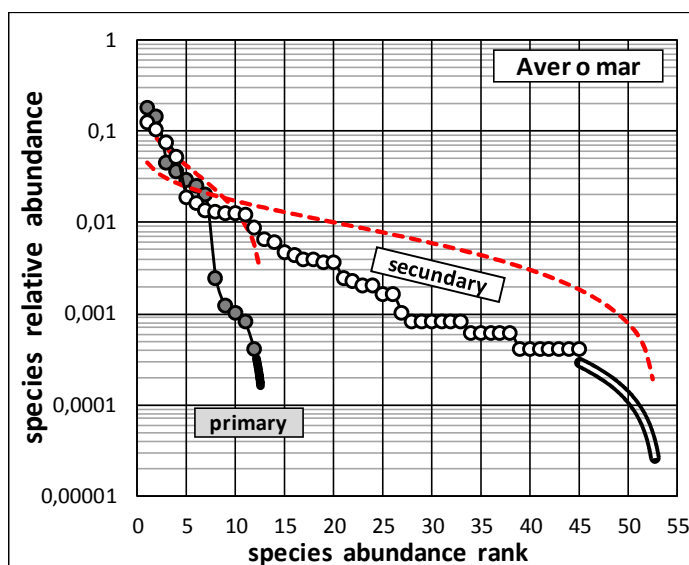

Fig. 12. The bias-corrected and extrapolated "S.A.D.s" for the two feeding guilds (*primary* and *secondary* consumers) in the reef fish community at '*Aver o mar*'; dashed line: the corresponding "broken stick" model
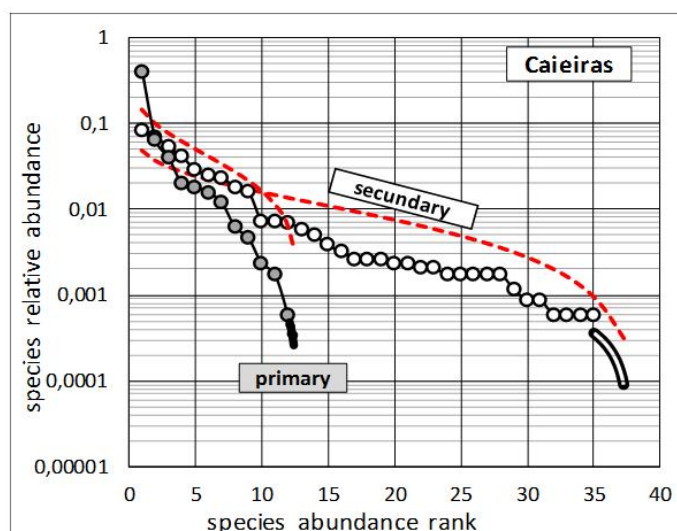

Fig. 13. The bias-corrected and extrapolated "S.A.D.s" for the two feeding guilds (*primary* and *secondary* consumers) in the reef fish community at '*Caieiras*'; dashed line: the corresponding "broken stick" model

Table 4. A synthetic summary of the main quantitative features of the hierarchical organization of species abundances according to feeding guild, as derived from the corresponding numerically completed "S.A.D.s": (i) the total species richness S_t of the community ; (ii) the relative abundances a_1 and a_{St} of the most and least abundant species (species rank 1 and S_t) ; (iii) the unevenness of abundance distribution U and (iv) the genuine intensity of the structuring process I_{str}

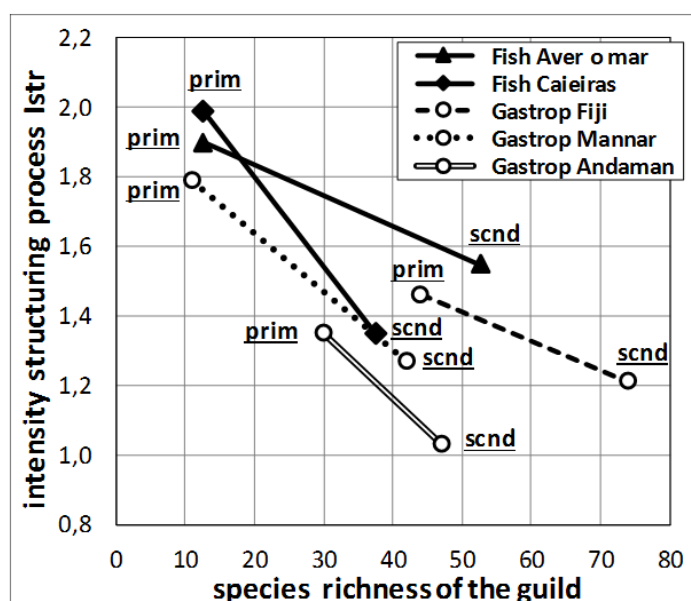| Site	Feeding guild	S_t	a_1	a_{St}	a_1/a_{St}	U	I_{str}
Aver o mar	primary feeders	12.5	0.1765	0.000162	1090	0.264	1.90
	secondary feeders	52.5	0.1241	0.000026	4773	0.071	1.55
	primary / secondary	*0.24*	*1.42*	*6.23*	*0.228*	*3.72*	*1.22*
Caieiras	primary feeders	12.5	0.3884	0.000259	1500	0.279	1.99
	secondary feeders	37.5	0.0824	0.000089	926	0.082	1.35
	primary / secondary	*0.33*	*4.71*	*2.91*	*1.62*	*3.40*	*1.47*

Fig. 14. The intensity I_{str} of the structuring process plotted against the species richness, for each of the two feeding guilds (primary and secondary feeders) in the reef fish communities at 'Aver o mar' and at 'Caieiras': *coarse solid lines*. For comparison, the same figures are provided for three marine gastropod communities at (i) Fiji Islands [48], (ii) Mannar Gulf (India) [47] and (iii) Andaman Islands (India) [32]. The trend for primary consumers to have lower species richness and stronger intensity of the structuring process than have secondary consumers, is common to all five communities

3.7 The Role of Fishing Activity on the Structuration of Each Feeding Guild

The more intense fishing activity at 'Caieiras' results in a slight reduction in the overall abundance of secondary feeders (Fig. 16). More specifically, it is the three most common species which are especially targeted (Fig. 16, species ranks i = 1 to 3), as can be also followed in detail in Figure 1. Fishing activity therefore leads to a positively density-dependent predation on fishes.

In turn, the moderate reduction in the overall abundance of secondary feeders is expected to have some moderate positive consequence on the primary feeders that usually serve as preys. This indeed is highlighted in Fig. 17. Yet, this positive effect seems restricted to the sole benefit of the most common species, a territorial herbivore, *Stegastes fuscus*, with its abundance more than doubling (Fig. 17). In turn, this substantial enhancement of *Stegastes fuscus* abundance (rank i = 1) tends to reinforce the competitive exclusion of the immediately

following species, *Acanthurus bahianus* (rank i = 2), the abundance of which is reduced by a factor three (see Fig. 17 and Fig. 1). Finally, the enhanced impact of *Stegastes fuscus* may arguably contribute to the recorded decrease in macroalgal coverage at 'Caieiras'.
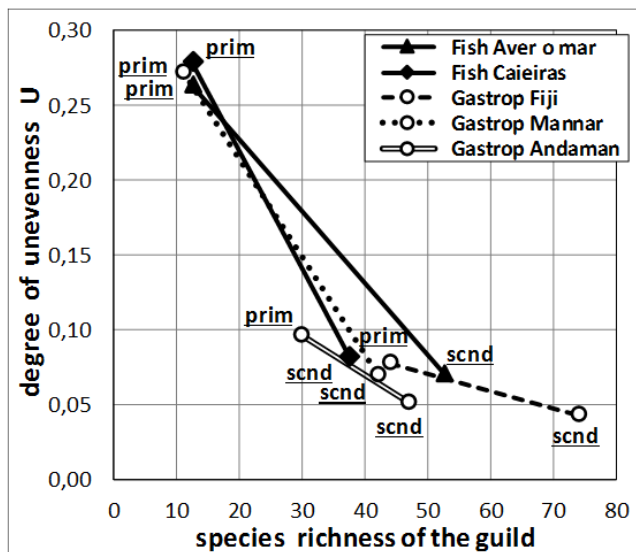

Fig. 15. The degree U of abundance unevenness plotted against the species richness, for each of the two feeding guilds (primary and secondary feeders) in the reef fish communities at 'Aver o mar' and at 'Caieiras': *coarse solid lines.* **For comparison, the same figures are provided for three marine gastropod communities at (i) Fiji Islands [48], (ii) Mannar Gulf (India) [47] and (iii) Andaman Islands (India) [32]. The trend for primary consumers to have lower species richness and much stronger degree of abundance unevenness than have secondary consumers, is common to all five communities**
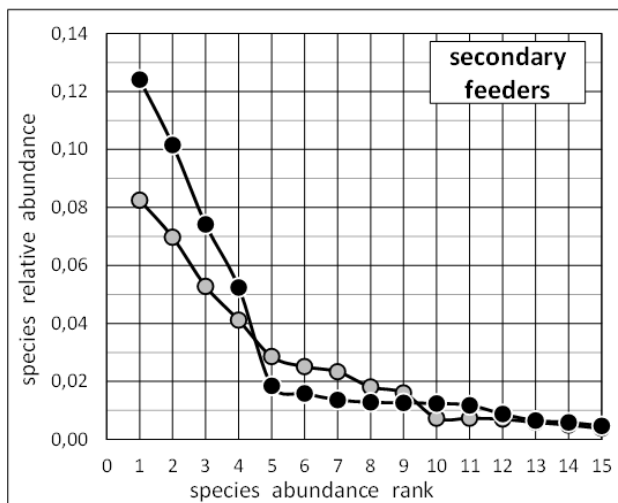

Fig. 16. The distribution of the relative abundances of the 15 most common species of *secondary feeders* **(ranks 1 to 15) in the communities at 'Aver o mar' (black discs) and at 'Caieiras' (grey discs). Note the overall trend for lower abundances of secondary feeders at 'Caieiras', especially sensitive among the most common species, as the likely consequence of stronger fishing activity at this site**
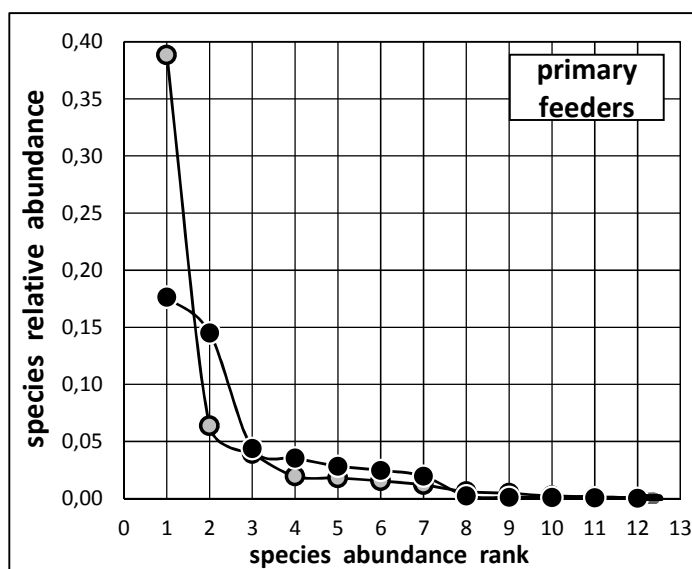
Fig. 17. The distribution of the relative abundances of *primary feeders* in communities at 'Aver o mar' (black discs) and at 'Caieiras' (grey discs). Note the trend for the higher abundances of primary feeders at 'Caieiras', in fact concentrated on the most common species (*Stegastes fuscus*), as the likely consequence of reduced predation pressure from secondary feeders (the latter being less abundant due to stronger fishing activity at this site)

4. DISCUSSION

Fishing activity is usually considered as indirectly enhancing the macroalgal coverage by reducing the abundance of herbivore fishes; the development of macroalgae being, in turn, detrimental to healthy coral settings [7]. Yet, opposite influences of fishing impact have also been reported [9]. Indeed, it seems likely that the outcome of overfishing, regarding algal/coral balance, is dependent upon whether herbivore or carnivore fish species are most collected by fishing, so that re-examining the issue is worth considering at each new offered opportunity. Here, the field data reported by Pereira and coworkers [27] supports the second alternative – macroalgal coverage decreasing with increasing fishing activity, in accordance with reference [9]. Yet, beyond this first observation, the more detailed impact of fishing activity upon the internal organization of reef fish communities – total species richness and the hierarchical structuration of species abundances – remained to be further addressed. This, indeed, is of prime interest, since better highlighting the ins and outs of the internal organization of species within their respective communities is a major way to improve our efficiency in better conserving these interesting reef communities.

Besides, in quite another respect, but still related to feeding guilds, it was also interesting to re-check the hypothesis according to which the primary feeders (herbivores) are remarkably less species-rich with more unevenly distributed abundances than is the case for the secondary feeders (omni-carnivores).

Among the two compared reef fish communities, 'Aver o mar' and 'Caieiras', the latter supports significantly stronger fishing activity than does the former [27], which makes the comparison between them relevant as regards the first issue evoked above. Yet, preliminary to any further analysis, the reported samplings [27] - being substantially incomplete - were completed by an appropriate procedure of numerical extrapolation [28,29,31] providing least-biased estimates of both the *number of unrecorded species* and their *distribution of abundances* for each of the two compared fish communities.

4.1 Species Richness of the Two Fish Communities

According to the numerical extrapolations, 8 and 3 species had remained unrecorded at 'Aver o mar' and at 'Caieiras' respectively, resulting in 'Caieiras' having lower true (total) species richness (St = 50 species) than 'Aver o mar': (St = 65 species): Table 1. That is, a 23% lower true species richness in the more actively fished community.

4.2 Taxonomic Dissimilarity between the Two Fish Communities

Originally ill-defined, due to samplings incompleteness, the value of the Jaccard similarity index between the two communities is best evaluated after numerical extrapolation. This similarity index is thereby safely estimated within the range 0.58 -0.77.

In particular, a striking feature that differentiates the community at 'Caieiras' is the strong abundance gaps that occur (i) between the two primary feeders, *Stegastes fuscus* and *Acanthurus bahianus*, and (ii) between the two secondary feeders *Pempheris schomburgkii* and *Halichoeres poeyi* (Fig. 1). This pattern contrasts deeply with the relatively similar abundances of all these four species at 'Aver o mar', a contrast that might probably result from the significantly stronger fishing activity at 'Caieiras', with an unequal, but overall negative, direct impact among secondary feeders. In turn, the resulting, reduced predation pressure on primary feeders (herbivores) likely enhances the interspecific competition between them, in this case, for the benefit of *Stegastes fuscus* and at the expense of *Acanthurus bahianus*. This leading, at last, to a reduced coverage of macroalgae at site 'Caieiras' [27].

4.3 Process Involved in the Structuring of Species Abundances

After numerical completion, the Species Abundance Distributions of both fish communities clearly fit best the "log-normal" than the "log-series" models (Figs. 5 and 6), thereby suggesting a hierarchical structuring of species abundances governed by the combined influence of many independent factors, rather than by one or very few dominant factor(s). A conclusion that would have been less clearly demonstrated if only the recorded portion of the species abundance distributions had been taken into account. This, once again, underscores the interest of numerical extrapolation of incomplete inventories. The conformity of the Species Abundance Distributions of both communities to the "log-normal" model is not surprising, being rather common in most species-rich communities, at least when they are not subjected to excessively harsh environmental stresses (pollutions, etc …) [36,38,39].

Yet, as shown in Figs. 7 and 8, a significant discrepancy from the "log-normal" model is highlighted – in both communities – as regards the subset of more abundant species, especially the most abundant one, *Stegastes fuscus*. At 'Aver o mar', the relative abundance of this species is significantly lower than what is predicted by the "log-normal" model, at the benefit of the abundances of the following species. At 'Caieiras', on the contrary, the relative abundance of this species is very significantly higher than predicted by the "log-normal" model, at the expense of the abundances of the following species. This contrasted pattern is the expected result from the stronger fishing activity at 'Caieiras'. Thus, *Stegastes fuscus* features as the major herbivore species on the reef settings of these localities, potentially highly competitive and, as such, a very efficient exploiter of the macroalgal resource, to the extent, however, that it is not too much exposed to predatory pressure from carnivore fish species. As argued in more detail in section 3.7, it seems likely that the stronger fishing pressure at 'Caieiras' has markedly reduced the abundances and impact of some carnivore species (Fig. 16, see also Fig. 1), thus leaving free rein to the full potential efficiency of *Stegastes fuscus*. While, on the contrary, the low fishing activity at 'Aver o mar' has let the carnivore fishes being sufficiently abundant to exert a more efficient control on the development of herbivore species, in particular *Stegastes fuscus* (Fig. 17). At last, the higher abundances of herbivore fishes, indirectly allowed at 'Caieiras' by stronger fishing activity, explain the marked decrease in macroalgal coverage at this site.

4.4 The Pattern of Abundance Unevenness and the Genuine Intensity of the Hierarchical Structuring Process

Although species abundance unevenness U is higher at 'Caieiras' than at 'Aver o mar' (Figs. 2,3, 4, 11; Table 2), the genuine intensity I_{str} of the structuring process (i.e. the part of unevenness which is not directly related to species richness: § 2.2.3) remains practically the same in both communities (Figs. 9, 10, 11; Table 2). This invariance of I_{str} suggests that the stronger abundance unevenness at 'Caieiras' is essentially the by-product of the reduction in species richness resulting from the stronger fishing activity at 'Caieiras'.

4.5 The Respective Responses of Each Feeding Guild to Fishing Activity

The two feeding guilds, herbivores and omni/carnivores, show very contrasted structuration in terms of both species richness and abundance hierarchization. As compared to secondary feeders, the primary feeders are characterized by a lower species richness, as already reported in many researchers [32,47-53] and a stronger abundance unevenness, as already reported in many researchers [32,47-49]. In turn, this stronger unevenness partly results from the lower species richness but also from the higher intensity I_{str} of the structuring process, as already reported by many researchers [32,47,48].

Thus, *primary* feeders are three times ('Caieiras') to four times ('Aver o mar') less species-rich than *secondary* feeders, while the cumulated numbers of (recorded) individuals differ quite less sharply between the two guilds. As regards the hierarchical structuration of species abundances (Table 4), the intensity I_{str} of the structuring process is clearly stronger for primary feeders than for secondary feeders (+ 23% for '*Aver o mar*' and + 47% for '*Caieiras*': Figs. 12 and 13, Table 4) and the degree of unevenness U is still more strongly contrasted in favor of primary feeders: Figs. 12 and 13, Table 4).

All these trends, regarding the species richness S_t, the abundance unevenness U and the intensity I_{str} of the structuring process, are common to both sites. Even more remarkable, the same trends are highlighted when considering the gastropod communities associated with coral reefs: Figs. 14 & 15.

On the other hand, what remains common to both guilds, is the *sigmoidal* aspect of the Species Abundances Distributions (Figs. 12 and 13). Both feeding guilds thus conform best to the "log-normal" model, denoting that, even at the level of feeding guilds separately, the structuring process of species abundances remains governed by the combined influence of many independent factors, rather than by one or very few dominant factor(s). Looking more precisely at the detail of the distribution of species abundances (Figs. 15 and 16), some specificity distinguishes 'Caieiras' from 'Aver o mar':

- a slight reduction in the overall abundance of the three most common species among secondary feeders (Fig. 16, see also Fig. 1).

This is likely indicative of some density-dependent increase in predation exerted upon the three most common omni/carnivore fishes;
- quite an opposite figure for the most abundant species among primary feeders (Fig. 17, see also Fig. 1), indicative of some density-dependent reduction in the degree of predation on the most common herbivore fish species.

Both aspects above may possibly be considered as the consequences of the stronger fishing activity reported at 'Caieiras', as far as this activity more readily targets the most common predatory fishes.

4.6 Final Remark Regarding the Process of Hierarchization of Species Abundances

Both the lower species richness and the stronger hierarchical structuring process that characterize the guild of primary feeders (Figs. 12 and 13, Tables 3 and 4) are indicative of a much weaker niche partitioning and a stronger interspecific competition among primary feeders, as compared to secondary feeders [54,55]. The contrary holds true for the guild of secondary feeders, suggesting a quite higher degree of feeding specialization among omnivore and carnivore species which, in turn, can relax the level of competitive exclusion. This is in accordance with their larger species richness and their less acute hierarchical structuration.

5. CONCLUSIONS

The comparative analysis of the internal structuring of two neighboring reef fish communities differently influenced by anthropogenic influences – especially as regards fishing activity – highlights consistent similarities but also conspicuous differences regarding the levels of species richness and the process and pattern of hierarchical structuring of species abundances. Further considering separately each of the two feeding guilds (herbivores and omni/carnivores) still provides additional insight as regards the role of fishing activity on the internal organization in reef-fish communities and the associated consequences on the reef ecosystem, considered more globally.

From a methodological point of view, the success of these analyses relies intimately upon the implementation of an appropriate procedure for

the *numerical extrapolation* of samples, since such uneven and species-rich communities cannot be exhaustively sampled in practice.

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COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX

The trivial ("mechanistic") contribution of the level of species richness to the degree of structuring of species abundances

All things equal otherwise, the larger the species richness, the weaker is the slope of the Species Abundance Distribution.
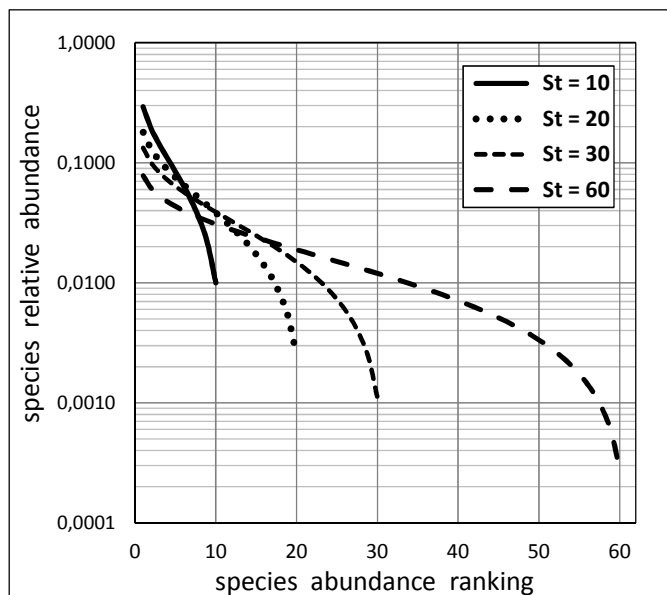

Fig. A1. The "broken-stick" distribution model applied to species communities with increasing species richness S_t = 10, 20, 30, 60. Although the theoretical structuring process involved in the "broken-stick" model remains unchanged (random apportionment of relative abundances among member species), the slope of the species abundance distribution strongly depends upon (and monotonously decreases with) the level of species richness S_t (the relative abundance of the species of rank 'i' is computed as: $(1/S_t).\Sigma_n (1/n)$, with the summation Σ_n on the integer n being extended from n = i to n = S_t, see reference [22]

This can be easily quantified, on a theoretical basis, by considering a theoretically constant structuring process - such as the random distribution of the relative abundances that characterizes the "broken-stick" distribution model. By applying this model successively to a series of communities with increasing species richness, a steady decrease of the slope of abundance distributions is highlighted: Fig. A1