

LIFE-HISTORY STRATEGIES OF FISH ASSEMBLAGES FROM REEFS, SOFT BOTTOM AND MANGROVES FROM NEW CALEDONIA

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Abstract

Life-history strategies were used to describe and compare the fish assemblages of coral reefs, soft bottoms and mangroves. Each habitat was sampled monthly during one year. Each species was classified into one among 6 life-history strategies ranging from r-type species -class 1- (early reproduction, short live...) to K-type species -class 6- (late reproduction, low mortality...). On a yearly basis, the structures of the three fish assemblages were different. On reefs, species composition is dominated by fishes of the classes 2, 3, 4. Class 1 species make a large contribution to the density on reefs despite a low diversity of this group, but most of the density is given by class 2 fishes which make also an important contribution to biomass. However, classes 3 and 5 form also an appreciable part of the biomass on reefs. On soft bottom the species composition is dominated by the 3 first classes. Class 1 fishes contribute the most to density (89 %) and biomass (51 %), with class 5 and 6 making a non negligible part of the biomass. In mangroves the structures at the species and density levels are similar to soft bottom, but for biomass class 3 dominates. There are 2 poles of productivity in mangroves, one due to class 1 fish, the other to class 3 fishes. All 3 communities had different monthly variations. At the species level the structure remained stable for all 3 assemblages. Biomass fluctuated more than density. Most of the variations in density or biomass were due to class 1 and 2 which have a higher turnover. There were also variations in classes 5 and 6 but this is due to the fact that these species are rare and have usually large territories and are not well sampled. From the above data it was possible to outline the major aspects of the functioning of these 3 assemblages. In particular, one would expect reefs to be more resilient to small environmental changes than mangroves or soft bottom and on the opposite, in case of a major environmental change soft bottom and mangroves would react faster than reefs.

Key words : Life-history strategies, fish assemblage

Introduction

Coral reef fish assemblages from the lagoon of New Caledonia have links with other fish assemblages of this lagoon in particular with the soft bottom and mangrove ones (Thollot and Kulbicki 1988; Thollot *et al.* 1991). However, these authors, working on species composition, concluded that these various assemblages function according to different models. In order to demonstrate these differences and to assess their importance in the global functioning of the lagoon fish fauna, it is necessary to investigate these assemblages at a level higher than the species one. The species can be grouped in various ways, usually according to trophic levels (Kulbicki 1991), but other levels are possible such as ecological niches (Harmelin-Vivien 1989) or life-

history strategies (Kulbicki 1991). To our knowledge, the latter classification has never been used to differentiate fish assemblages or to help in understanding their functioning. Most of the work involving life-history strategies has been either theoretical or has considered variations of life-history traits within a species or group of species in order to explain variations in the complexity of ecosystems (for reviews on these matters see Barbault (1981), Blondel (1986) or Frontier and Pichod-Viale (1991) among others). After the publication of MacArthur's theory on island biogeography (MacArthur and Wilson, 1967) and the presentation of the r-K continuum by Pianka (1970) there has been a very important number of publications on these matters but these concepts have seldom been applied to practical problems such as simplifying very complex assemblages. Fisheries models are currently based on population dynamics and cannot take into account the complexity of tropical fish assemblages. Simplifications are mandatory if one wants to build alternative models. This article will try to indicate how the use of life-history strategy classes could be useful in this context.

Material and methods

Study area and sampling

Three different habitats, coral reefs, soft bottom and mangroves, were sampled monthly during 1989. All 3 habitats were chosen in a small area (approximatively 50 km²) in order to reduce geographical variations (Fig. 1).

Coral reefs

Three stations were selected on a coast to reef axis (Fig. 1). On each station 2 permanent transects were set from the top to the bottom of the reef. Each transect was 50 m long and visited monthly by 2 divers, one on each side of the line. Each diver recorded all fish he could see on his side. For all sighting the number of fish, their average size and their distance to the line were recorded. The size of fish was given in 2 cm classes for fish less than 20 cm, in 5 cm classes for fish between 20 and 50 cm and in 10 cm classes for larger sizes. The distance to the line was given in 1 m classes for distances less than 5 m and in 2 m classes beyond. The weight of the fish were estimated from length-weight relationships (Kulbicki *et al.* 1990; Wantiez and Kulbicki 1991). Densities and biomasses were calculated using the distribution of distances to the transect (Burhnam *et al.* 1980). For the present work the results from all 3 stations were pooled.

Soft bottoms

Two trawlable areas exist in the Bay of St. Vincent (Fig. 1), each of them representing a different biotope (Wantiez, 1990). On each area 2 stations were sampled with a shrimp trawl and a fish trawl. The shrimp trawl

had a 14 m head rope, a 2 cm mesh on the cod end and a tickler chain, the towing speed being 2.3 knots. The fish trawl had an 18 m head rope, a 3 cm mesh on the cod end and was towed at 3 knots. The trawling time was 30 min for the shrimp trawl and 23 min for the fish trawl in order to have the same swept area. The number and weight of all fish caught were recorded by species. To calculate the density or the biomass of a given species the maximum value of the two fishing methods was retained for each area. This method is better than averaging because of the complementarity of the two gears (Wantiez 1990) and because trawling always underestimates the real density or biomass (Kulbicki and Wantiez 1990). For technical reasons it was not possible to sample during July 1989. The results of the 2 areas were pooled for the present study.

Mangroves

Two different types of mangroves were selected (Fig. 1). One station was along an estuarine mangrove, the other station on a mangrove bordered by a fringing reef. On each station sampling was performed monthly using 3 different gill nets and one fyke net (Thollot 1992). Each gill net was 70 m long and 3 m high with a mesh of respectively 40, 70 and 80 mm stretched mesh. The gill nets were set at high tide and removed at low tide along the mangrove limit in a manner to block the fish leaving the mangrove with the ebbing tide. Two of these sets were performed during daytime and 2 during nighttime. The fyke net had a 50 m wing and a poach with 3 chambers of 5 m each, the final mesh being 15 mm (stretched mesh). The fyke net was set with the wing perpendicular to the mangrove limit in order to catch fish swimming along the mangrove. This net was sampled twice over a 48 h period simultaneous to the gill net fishing. All fish caught were registered and weighed. Total catch in numbers or weight will be used as density and biomass indices, but since no standardization is possible these values will be only indicative.

Life-history strategies

Each species was classified into one of the 6 life-history categories given in table 1. The biological information used for this classification is derived from the ORSTOM biological data base for lagoon fish (40 000 entries) and the literature. For a number of species there was either no biological information available or the information was too scant. In such cases the taxa were attributed a life-history strategy of the closest species within the genus for which sufficient information was available. Only a limited number of species could not be given a life-history strategy and were not considered in the analysis (15 species on a total of 565).

Results

The classification of the major genera into life-history strategy categories is given in Table 2. With further investigation into the biology of these species it is possible that a number of species would be classified in a

category different from the present one. However, due to the broadness of the classes chosen it is unlikely that major changes would occur. As a consequence, the present work should be regarded as a preliminary investigation, but the main conclusions should remain valid.

A total of 565 species were collected and are distributed as follow : 344 species on coral reef fishes, 232 species on soft bottoms and 140 species on mangroves. The species composition of these assemblages and their temporal variations have been presented in Thollot *et al.* (1991). The distribution of the species among life-history strategy classes along with the density and the biomass of these various classes will be referred as life-history structure. The variations of this structure between assemblages will be presented on a yearly and monthly basis hereafter.

Yearly composition of the life-history structure

The 3 fish assemblages have very different structures (Fig. 2). All three assemblages differ by their species composition (Tab. 3) and reefs and soft bottoms have significantly different structures at the density and biomass level (Tab. 3).

On reefs, the species composition is dominated by fish of the classes 2, 3, 4 with average life-span, medium to high reproductive effort and usually small to medium size. Class 1 species make a large contribution to density on reefs despite a low diversity of this group in this habitat. However, the biomass of these fish is negligible (1.3 %). Most of the reef fish density (53 %) is made of class 2 fishes. These fish make also an important contribution to the biomass of the reef fish assemblages but other groups such as species of class 3 and 5 are also important contributors. These 2 latter groups are fish with longer life-spans, lower reproductive effort and are usually medium to large species. This indicates that the biomass of the reef fish should be rather stable over a long period while density should be more variable at the same scale. These data suggest also that the production of reef fish is dominated by species with an average to rapid turnover but that the larger species may have a non negligible share.

Soft bottom assemblages show a very different picture. The species composition is dominated by the 3 first life-history classes. By far class 1 contributes the most to density (89 %) or to biomass (51 %). This indicates a very fast turnover and certainly a great instability in density or biomass over short periods and likely a greater stability on a long term basis. One notices that classes 5 and 6 species make a non negligible contribution to biomass on soft bottoms. These are essentially large but rare carnivorous bottom dwellers (*Rhynchobatus* spp., *Rhyna* spp., large rays, *Plectorhynchus* spp. ...). These species have certainly rather stable numbers and their growth rate is very slow. Therefore they represent a stable component in the biomass of a community which otherwise is very variable. There seems to be very little utilisation of this important density, biomass and productivity of class 1 species by upper level classes within the benthic part of this assemblage. Most of the predation is done by pelagic fishes (Carangidae, Scombridae, Sphyraenidae, Trichiuridae...) which do not belong exclusively to the soft bottom and can be considered as part of a pelagic fish assemblage for which only scant data are available. This structure may be linked to the influence of

catastrophic climatic events such as cyclones and droughts which may have an important impact on the environmental parameters which influence soft bottom fish assemblages.

The data for mangroves is similar to the observations for soft bottoms. It indicates a dominance of fish of the classes 1, 2 and 3 in the species composition. The abundance is, as for soft bottoms, dominated by species of class 1 (83%). Weights are essentially made of class 3 fishes (44 %), which can be divided into two groups. The major group is made of Mugilidae, Scatophagidae, Platacidae, Siganidae and Ephippidae which are detritus or microalgae feeders. Small Lutjanidae, Lethrinidae and Carangidae, which are carnivores or piscivores, constitute a second and less important group. Fish of the classes 5 and 6, which are large but rare, are also relatively important. In this instance these classes are represented mainly by sharks, rays, large Serranidae and large Muraenidae (*Thyrsoidea* spp.). These large fish, except the Muraenidae, are usually found as juveniles in the mangroves. This suggests that the productivity of mangrove fish assemblages has 2 poles, on one hand short living fishes (mainly Clupeidae, Engraulidae, *Ambassis* spp., Leiognathidae and Atherinidae) with a very high turnover but relatively low biomass and on the other hand class 3 fishes with a slow turnover but a high biomass. The former species are preyed upon essentially by visiting predators from the pelagic fish component and to some extent by demersal carnivorous species of class 3. The detritus and microalgae feeders (essentially from class 3) are mainly resident (except some Mugilidae) and their production is not exported directly to other compartments. On a long period, one would expect mangrove fish assemblages to have a rather stable part (class 3) and two unstable components : class 1 fishes which are very dependant on environmental conditions and classes 5 and 6 which are present mainly as juveniles and as such are subjected to recruitment patterns.

This preliminary functioning diagram show that all three assemblages work according to different models. Soft bottoms and mangroves show the most similarity with a relatively close species distribution and overall, an equivalent role of class 1 species which make most of the productivity in these two assemblages. Reef fish are characterized by a shift of their three patterns of distribution (species, density and biomass) towards higher classes. In other words they have fish which have longer life cycles and lower turnovers and likely less productivity, this being compensated by less fluctuations in the production.

Monthly variations of the life-history structures

Monthly variations of the species composition, diversity and biomass are given (Fig. 3, 4, 5). The number of species sampled each month was of 166-205 species for reefs (total 344 spp.), of 75-100 for soft bottoms (total 232 spp.) and of 54-76 for mangroves (total 140 spp.). In all 3 assemblages the species classification remained stable through time (Fig. 3 a, b, c). However, all 3 communities showed differences in the variability of their species composition except for class 2 species (Tab. 4a). Reefs differed from mangroves and soft bottoms in having a higher variability for fish of the class 4 and 5. On the opposite mangroves and soft bottoms had a higher variability for species of class 6. This indicates that on reefs species of class 4 and 5 and, to a lesser extent, of class 6 may roam over areas which are much larger than what is covered by the

transects. For mangroves and soft bottoms the high variation in species of class 6 could be due to similar reasons such as large trophic migrations.

The density of each class varied more through time than its species composition (Fig. 4). Most of the variation is due to class 1 and 2 as can be expected since these are species with short to medium live-spans. Figure 4 suggests that on soft bottoms and mangroves there is a seasonal increase in class 1 fishes in September-October, this corresponds to the reproduction period of most bait fishes (Conand 1987) and also to the recruitment of *Atherinomorus endrachtensis* and *Ambassis myops* in the mangroves (Thollot 1992). A seasonal increase of class 1 fishes appears on reefs in March-April which corresponds to the recruitment period of most class 1 species (Fig. 4). Table 4 shows that the variability of densities on soft bottoms and reef communities were not statistically different (it is not possible to test density for mangrove communities).

The biomass showed the most important short term variations. This is due to mainly 2 factors. The first one is the rapid change through time of the biomass of class 1 and to a lesser extent class 2 species due to their fast growth and high mortality rates. The second factor is linked to sampling. Very large fishes (mainly class 6) are caught or seen only occasionally but make an important contribution to the biomass. Table 4 shows also that soft bottoms and reef communities differed in their variability for class 1 and 5 species. Class 1 is very important in biomass for soft bottoms and shows a seasonal trend with a peak in September-October (as for density) whereas this class is negligible in biomass for reefs and varies little. Class 5 is very variable on soft bottoms and rather stable on reefs. On soft bottoms this variability is due to the catch of Lutjanidae, large Lethrinidae and Haemulidae which are found in small and highly dispersed schools. On reefs this little variation in biomass of class 5, linked with the high variability in species composition of this class on reefs (Fig. 3) indicates that these large fish roam extensive parts of the reef. Unexpectedly it is the mangrove fish community which is the most stable in terms of biomass (Fig. 5). There is however a seasonal trend for classes 1 and 2, the Leiognathidae which are an important component of class 1 recruit to mangroves in January and leave in July, increasing in biomass during this interval because of growth. On the opposite, there is a migration of *Gerres* spp. (class 2) during the November-February period. This relative stability in the biomass distribution in mangroves could be attributed to a continual flux and influx of species within the same niches.

Discussion

This study has indicated that the three fish assemblages considered show marked differences in their life-history structures. Within each assemblage there were temporal variations but they were generally small compared to those between habitat. Variations at the species level were minimal whereas variations at the density or biomass level were more important, especially for fish of the classes 1 and 2. Some major aspects of the functioning of these 3 assemblages can be outlined from the data presented here. The stability of the structure at the species level in all assemblages suggests that for each assemblage the species pool (Kulbicki 1991) is well defined.

On reefs, class 1 species are not very diverse and do not represent much of the biomass but are an important component of the density. Class 2 species are certainly the most important component of the diversity and density of reef assemblages and their share of the biomass is near 30% of the total. Due to their high productivity these 2 classes of fish certainly make the bulk of the fish production on reefs. The stability in diversity, density and biomass of class 3,4,5 species suggests that these fish form the core of the assemblage. Due to the long life-span of these fish the effects of variations in recruitment on density or biomass have more time to dampen than for classes 1 or 2. Therefore a major change in the structure of these "middle" classes is likely to be a signal of a profound modification of the assemblage. Class 6 fish were not well sampled because these large fish are too scarce or have very large territories. Consequently it is very difficult to monitor accurately modifications of their parameters which is to be deplored because these species are usually the first ones affected by fishing. There are variations across the Pacific in the structure of reef fish assemblages. An analysis of the data presented by Galzin (1985) for French Polynesia indicates some difference in species composition linked to the composition of the species pools of French Polynesia and New Caledonia (Kulbicki, in press), but as in New Caledonia the species composition is dominated by classes 2,3,4. In French Polynesia density is also dominated by species of classes 2 and 3 and to a lesser extent class 1. Galzin (1985) found important differences between reef types, the analysis of his data showing that outer reefs are dominated in density by class 1 fishes. Similar differences between reef types were found in New Caledonia by Kulbicki (1991). However these differences stay minor in comparison with the structures of the soft bottoms or mangroves.

Mangrove and soft bottom assemblages are dominated by class 1 and 2 species especially at the density level. These fish are extremely sensitive to changes in the environment and major variations in their density or biomass may occur over short periods (Conand and Kulbicki 1988; Kulbicki and Wantiez 1990). The production of these species is certainly important but, because of its variability, is not well utilised by the sedentary (mostly benthic) component of these assemblages. Pelagic or midwater predators are the most apt to use this resource because they can travel large distances to find adequate concentrations of this resource. This has been demonstrated for mangrove fishes by Thollot (1992), but unfortunately for soft bottoms we have very little information on these fish due to the lack of appropriate sampling techniques. A second interesting character of the mangrove and soft bottom fish assemblages is the importance of class 5 and 6 fishes in the biomass, despite their low diversity and density. These fish are mainly present as juveniles in the mangroves and as large adults on the soft bottoms, important trophic migrations between these habitats being observed (Thollot 1992). They are certainly the most sensitive species to fishing, but their elimination from the system will likely not affect much the other components of these fish assemblages. There are two reasons for this, first these fish have low densities, second they do not share the same food sources than class 1 or 2 species nor prey much upon the fish of these classes.

In our opinion, the present data suggest that confronted to small environmental variations reefs will have a more resilient structure than mangroves or soft bottom. On the opposite in case of a major environmental change or a catastrophic event, soft bottom and mangroves will react faster than reefs. At the moment there is no clear support of these hypothesis in the literature, but a certain number of indices. In a review on coral

reef fish assemblages, Kulbicki (1991) indicates that most studies found little variations in these assemblages over long terms, but that in case of major changes in the environment significant modifications in the fish assemblages could be detected. In the Bay of St Vincent, Kulbicki and Wantiez (1990) found very important changes in the structure of soft bottom fish assemblages over a three year period (1984-1986), these variations being attributed to climatic disturbances (droughts). Three years later (Wantiez 1990) the characteristics of these assemblages were back to those observed initially (Tab. 5).

The present study indicates that all three assemblages are clearly identifiable from their structure. One should however keep in mind that within each of the biotopes studied there are many different habitats. For instance reefs can be subdivided into fringing, barrier, outer reefs ... There is a variability of the life-history structure of the fish assemblages within each biotope because of habitat type. This is reviewed by Kulbicki (1991) for reefs, illustrated by Thollot (1992) for mangroves and Kulbicki and Wantiez (1990) for the soft bottom in St Vincent Bay. Differences between habitats, within a biotope, are minor at the species level but may become important at the density or biomass level, examples are given in table 5 for soft bottom and other evidences can be found in Kulbicki (1991) for reefs. However, these differences stay minor compared to those between biotopes.

One should notice that the structures which have been outlined in the present article were drawn from the study of relatively large sampling units. Had one considered smaller scales of observation, such as patch reefs, it is likely that no consistent structure could have been identified. This problem of scale is well documented by Harmelin-Vivien (1989) for reefs.

The use of life-history classes has demonstrated that various fish assemblages in the lagoon of New Caledonia have different, identifiable and stable (at the species level) structures. Such identification and stability allow to consider predictability, in other words, how these structures might be affected by changes. To enhance the precision of this predictability it is possible to include other structures such as trophic structure (Kulbicki, 1991) but this is getting beyond the scope of the present article. The use of life-history strategy classes has also allowed a rapid understanding of the main differences in the functioning of these three assemblages. As noted earlier much of the classification used is only tentative. If more accurate results are wanted it will be necessary to launch a major offensive on the life-history traits of Pacific fishes which are for a majority very poorly known.

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Table 1: definition of the 6 life-history strategy classes used for defining structure.
life length can be considered as life expectancy (L50 after recruitment)

Class	Size	Reproduction	Behavior	Growth	Mortality	Life length
1	Small to medium < 30 cm	Very early in life Very high gonado-somatic index	Most species school Simple sexual behavior	Very fast	High	0.5 to 3 years
2	Small to medium < 30 cm	1-3 years old at first reproduction High gonado-somatic index	Often schools may be territorial Sexual behavior may be complex	Rapid initially	Medium	3 to 7 years
3	Medium to large > 30 cm	2-3 years old at first reproduction High gonado-somatic index	Often schools seldom territorial Simple sexual behavior	Rapid initially or through life	Medium	3 to 7 years
4	Small to medium < 30 cm	Late in life Usually > 50 % maximum size at first reproduction Medium gonado-somatic index	Seldom schools Often territorial	Slow after first initial growth often fast	Low	7 to 12 years
5	Medium to large > 30cm usually >50cm	Late in life Usually > 60% maximum size at first reproduction Low gonado-somatic index	Seldom schools Often territorial	Slow after first reproduction Often rapid initial growth	Low	7-12 years
6	Large to very large > 50 cm usually > 1m	Very late in life Usually > 60% maximum size at first reproduction Often ovoviparous Low gonado-somatic index	Almost never schools except for reproduction	Very slow specially after reproduction	Very low	> 12 years

Table 2 : Classification of the major genera into life-history strategies

1	REEFS	small Apogonidae, Atherinidae, small Blenniidae, small <i>Chromis</i> spp., small <i>Chrysiptera</i> spp., Clupeidae, Engraulidae, small Gobiidae, <i>Neopomacentrus</i> spp., <i>Pseudocheilinus</i> spp., <i>Pseudochromis</i> spp., <i>Trimma</i> spp., Trypterigidae
	SOFT BOTTOMS	small Apogonidae, small Bothidae, small Calytonimidae, Carapidae, Clupeidae, small Gobiidae, Leiognathidae, <i>Neopomacentrus</i> spp., <i>Upeneus</i> spp.
	MANGROVES	<i>Ambassis</i> spp., small Apogonidae, Atherinidae, small Blenniidae, Clupeidae, Engraulidae, small Gobiidae, Leiognathidae, <i>Neopomacentrus</i> spp., <i>Upeneus</i> spp.
2	REEFS	small <i>Abudefduf</i> spp., small Acanthuridae, <i>Amphiprion</i> spp., large Apogonidae, Caesionidae, large <i>Chromis</i> spp., large <i>Chrysiptera</i> spp., <i>Dascyllus</i> spp., large Gobiidae, small Labridae (most <i>Anamps</i> , <i>Cirrilabrus</i> , <i>Halichoeres</i> , <i>Labroides</i> , <i>Labropsis</i> , <i>Thalassoma</i> ...), <i>Liopropoma</i> spp., small Lutjanidae, Nemipteridae, <i>Parapercis</i> spp., <i>Parupeneus</i> spp. (except the very large ones), most <i>Pomacentrus</i> spp., small Siganidae, Synodontidae, <i>Neoniphon</i> spp., small Scorpaeidae, most Syngnathidae
	SOFT BOTTOMS	<i>Amblyrhychotes</i> spp., Anthiinae, large Apogonidae, Antennariidae, Caesionidae, medium to large Calytonimidae, <i>Decapterus</i> spp., <i>Canthigaster</i> spp., large Gobiidae and Blenniidae, Gerreidae, small Lethrinidae and Lutjanidae, <i>Parapercis</i> spp., most <i>Parupeneus</i> spp., small Scorpaeidae, small Siganidae, Synodontidae, most Syngnathidae
	MANGROVES	small Acanthuridae, large Apogonidae, large Gobiidae and Blenniidae, Gerreidae, small Lethrinidae and Lutjanidae, <i>Liza</i> spp., <i>Parupeneus</i> spp., small Scorpaeidae, small Siganidae, Synodontidae
3	REEFS	medium Acanthuridae, <i>Calotomus</i> spp., most Carangidae, medium Labridae (<i>Choerodon</i> , <i>Cheilinus</i> , <i>Cheilo</i> , some <i>Halichoeres</i>), medium Lethrinidae and Lutjanidae, plankton feeding <i>Naso</i> spp., most <i>Scarus</i> spp., medium to large Siganidae
	SOFT BOTTOMS	medium <i>Arothron</i> spp., most Carangidae, medium flatfishes, medium Lethrinidae and Lutjanidae, Pomadasytidae, medium Siganidae, <i>Scomberoides</i> spp., medium Sphyraenidae
	MANGROVES	medium <i>Arothron</i> , Belonidae, most Carangidae, <i>Chirocentrus dorab</i> , <i>Elops machnata</i> , Ephippidae, large Hemiramphidae, <i>Kuhlia</i> spp., medium Lethrinidae and Lutjanidae, <i>Mugil cephalus</i> , Platacidae, Scatophagidae, <i>Scarus</i> spp., medium to large Siganidae, medium Spyraenidae, <i>Valamugil</i> spp., <i>Trichiurus lepturus</i>
4	REEFS	large Antennariidae, medium Balistidae, <i>Cantherines</i> spp., large Chaetodontidae, medium Labridae (<i>Coris</i> , <i>Cheilinus</i> , <i>Choerodon</i> , <i>Hologymnosus</i> , <i>Macropharyngodon</i>), small Muraenidae, <i>Myripristis</i> spp., large Pomacentridae (most <i>Abudefduf</i> , <i>Paraglyphidodon</i> , <i>Stegastes</i>), <i>Sargocentron</i> spp., large Scorpaeidae, small Serranidae
	SOFT BOTTOMS	medium Balistidae, medium Labridae, <i>Lactoria</i> spp., small Muraenidae, medium Platyccephalidae, Priacanthidae, medium to large Scorpaeidae, small Serranidae
	MANGROVES	large Chaetodontidae, small Muraenidae, <i>Myripristis</i> spp., medium Platyccephalidae, <i>Sargocentron</i> spp., small Serranidae, medium to large Scorpaeidae
	REEFS	large <i>Acanthurus</i> spp., large Balistidae, largest Carangidae, <i>Cetoscarus bicolor</i> , <i>Diodon</i> spp., large Labridae (some <i>Bodianus</i> , some <i>Choerodon</i>), large Lethrinidae and Lutjanidae, large Muraenidae, macro-algae feeding <i>Naso</i> spp., large <i>Parupeneus</i> , <i>Plectorhynchus</i> spp., <i>Pomacanthus</i> spp., large <i>Scarus</i> spp., large Serranidae

5	SOFT BOTTOMS	large <i>Arothron</i> spp., large Balistidae and Monacanthidae, largest Carangidae, large Congridae and Muraenidae, Dasyatidae, large Lethrinidae and Lutjanidae, large Platyccephalidae, large Serranidae, large Sphyraenidae
	MANGROVES	largest Carangidae, <i>Chanos chanos</i> , Dasyatidae, <i>Diodon</i> spp., large Lethrinidae and Lutjanidae, <i>Megalops cyprinoides</i> , Muraenidae, large <i>Parupeneus</i> , large Platyccephalidae, large Serranidae
	REEFS	largest Balistidae, <i>Bolbometopon muricatum</i> , <i>Cheilinus undulatus</i> , <i>Diagramma pictum</i> , <i>Hippocampus longiceps</i> , <i>Lutjanus sebae</i> , <i>Lethrinus olivaceus</i> , largest Muraenidae, largest <i>Plecterhynchus</i> spp., <i>Scarus gibbus</i> , largest Serranidae, sharks and large rays, <i>Symphorus nematophorus</i>
6	SOFT BOTTOMS	<i>Diagramma pictum</i> , <i>Lutjanus sebae</i> , largest Muraenidae and Congridae, largest <i>Plecterhynchus</i> spp., <i>Rhyna</i> spp., <i>Rhynchobatus</i> spp., largest Serranidae, sharks and large rays, <i>Symphorus nematophorus</i>
	MANGROVES	largest Muraenidae, largest <i>Plecterhynchus</i> spp., largest Serranidae, sharks and large rays

Table 3 : Comparison of the life-history structure between assemblages at the species, density and biomass level.

Two-way ANOVA using a randomized block design on the arcsin (\sqrt{p}), p being the percentage of each class in each assemblage (Sokal and Rohlf, 1981).

For density and biomass only soft bottom and reef fishes are considered.

A : reef B : soft bottom C : mangrove

The underlined numbers are not statistically different between themselves

* : significant at $\alpha \leq 0.05$

** : significant at $\alpha \leq 0.01$

NS : not significant

Life-History class	Species	Density	Biomass
1	** ABC	**	**
2	** ABC	**	**
3	** ABC	**	**
4	** ABC	**	**
5	** ACB	**	*
6	** ABC	**	NS

Table 4 : Comparison of the monthly variability in the life-history structure of the 3 fish assemblages.

The value given are the coefficients of variations. The Fmax test (Sokal and Rohlf, 1981) was performed on the variance of the means (number of species /class; density/class; biomass/class).

Within habitat (coefficient of variations) comparison is only descriptive.

Between habitat (variance of the means) is quantitative. A significant Fmax indicates that all habitats did not have the same variability.

* : significant at $\alpha \leq 0.05$

** : significant at $\alpha \leq 0.01$

NS : not significant

M : mangrove

SB : soft bottom

R : reef

Life-history class	Species				Density				Biomass			
	M	SB	R	Fmax	SB	R	Fmax	SB	R	Fmax		
1	6.6	5.5	6.7	*	7.1	16	NS	23	21	**		
2	5.3	5.8	3.7	NS	22	10	NS	16	17	NS		
3	3.7	8.5	4.4	*	41	15	NS	31	13	NS		
4	56	9.3	4.6	**	33	12	NS	26	16	NS		
5	16	10	4.4	**	41	15	NS	49	16	*		
6	9.6	23	23	*	39	26	NS	45	49	NS		

Table 5 : Life-history structures of soft bottom fish assemblages in New Caledonia.

S : species D : density B : biomass

all numbers are percentages

Life-history		St Vincent Bay 1989			St Vincent Bay 1984			North Lagoon		
class		S	D	B	S	D	B	S	D	B
1		20	89	51	20	90	56	14	51	27
2		34	10	20	38	8	22	44	45	49
3		19	1.1	6	16	.95	7	14	3	4
4		12	.21	1.2	11	.21	7	14	3	4
5		10	.16	8	11	.19	4	11	.73	5
6		5	.05	14	5	.03	9	5	.09	14

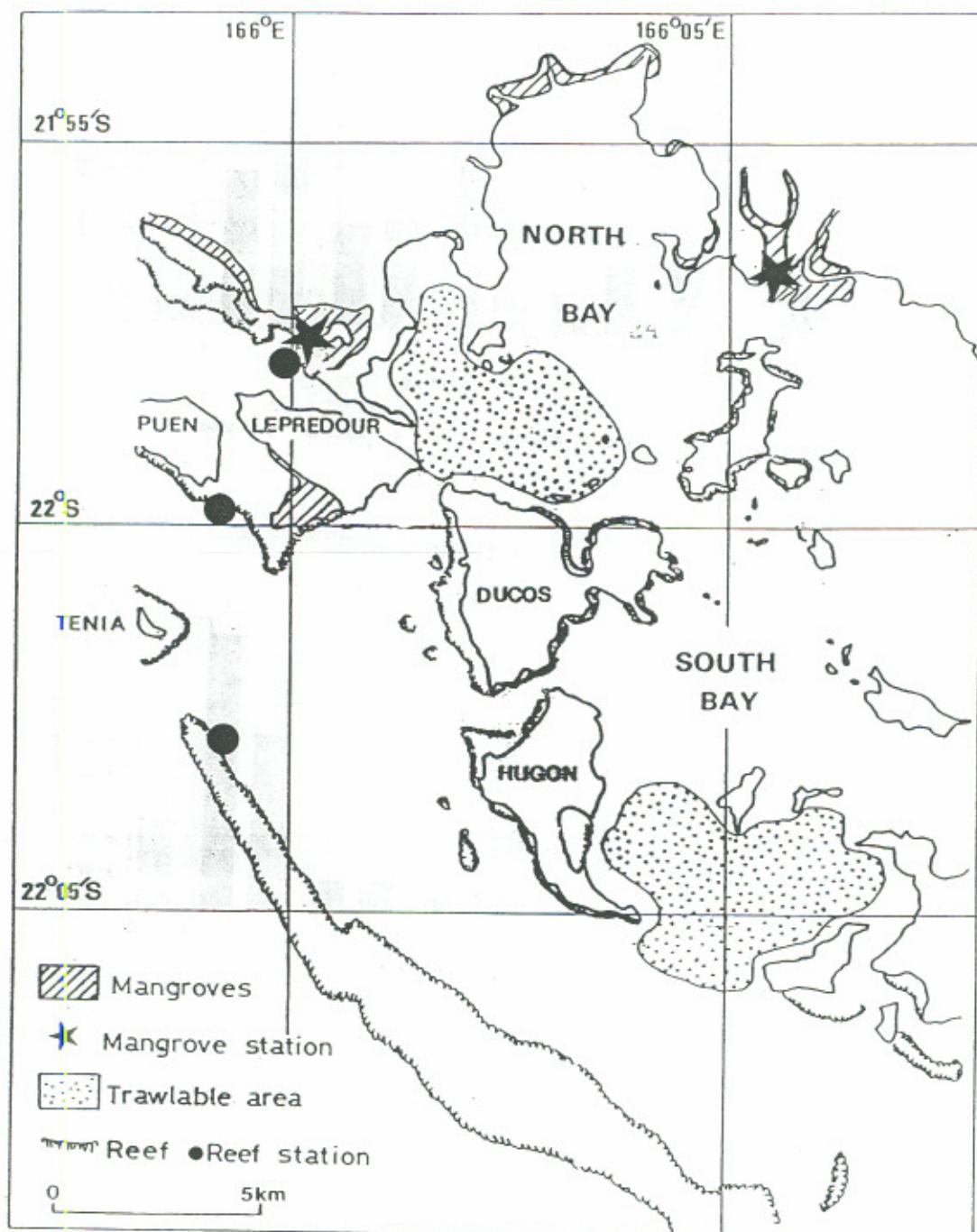
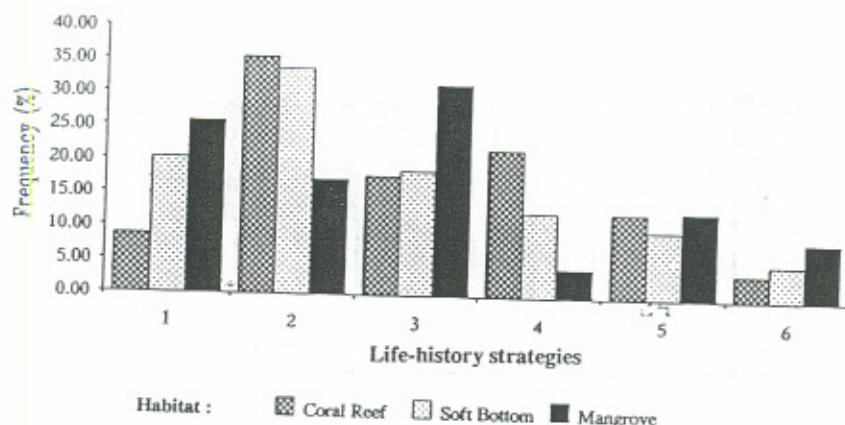
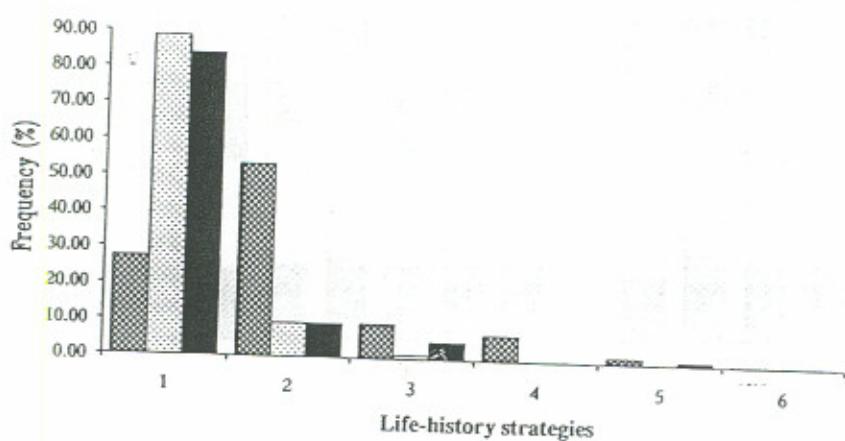


Figure 1 : Location of the sampling sites

SPECIES RICHNESS



DENSITY



BIOMASS

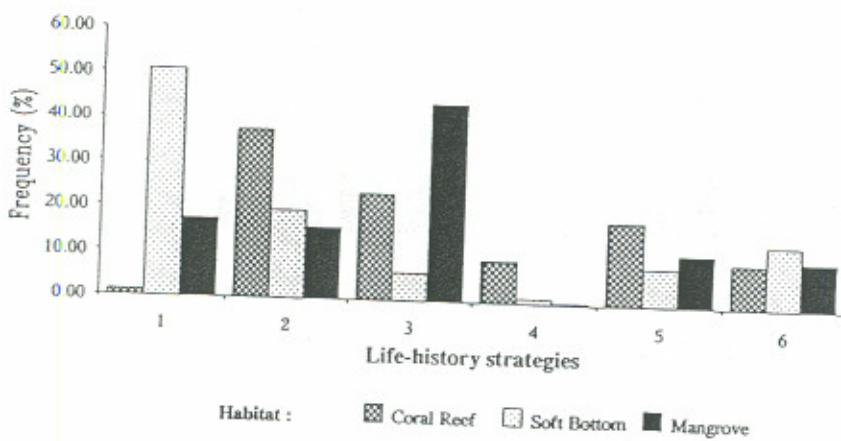
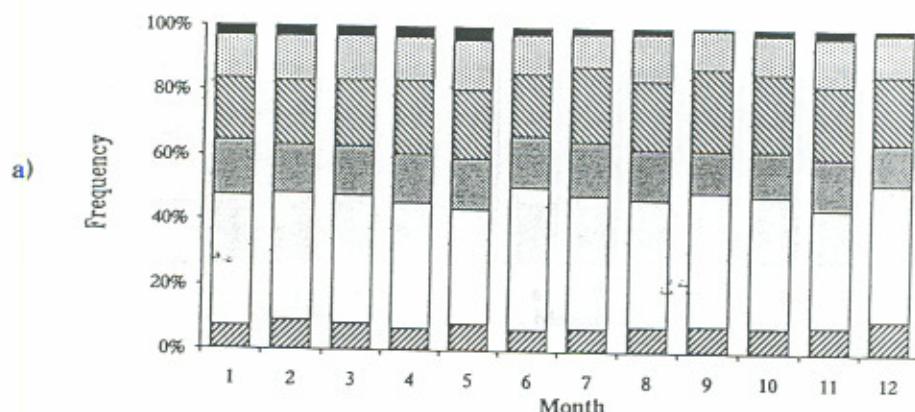
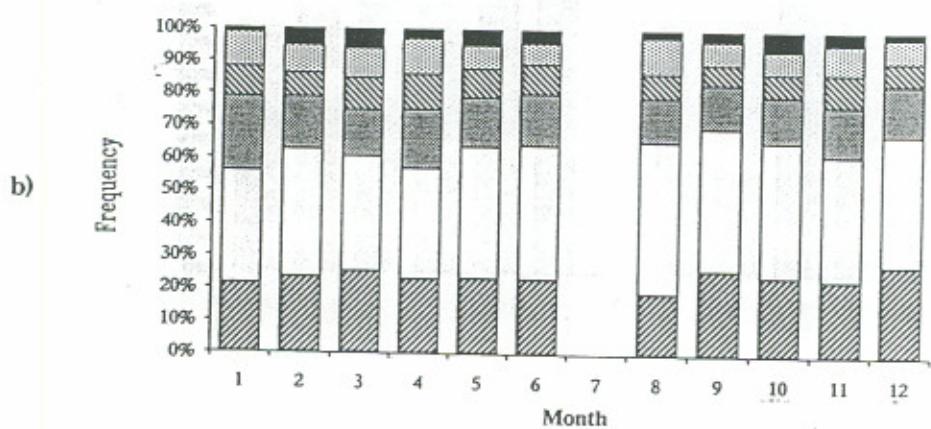


Figure 2 : Distribution of the life-history classes among habitats for species richness, density and biomass

CORAL REEF FISH ASSEMBLAGES



SOFT BOTTOM FISH ASSEMBLAGES



MANGROVE FISH ASSEMBLAGES

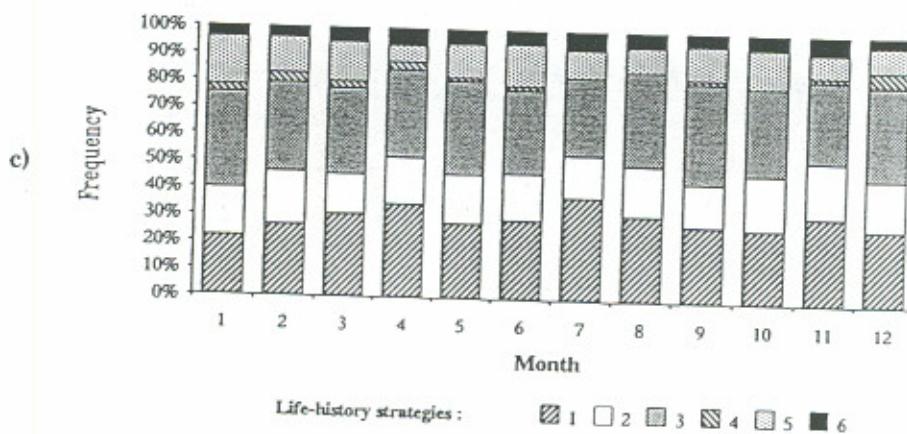
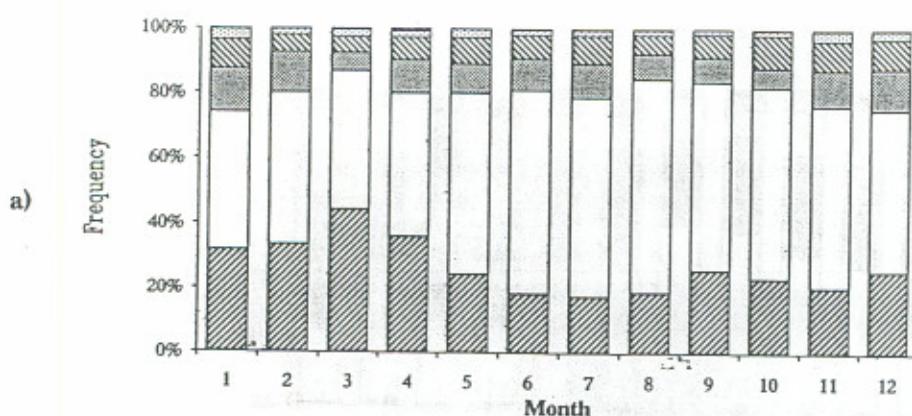
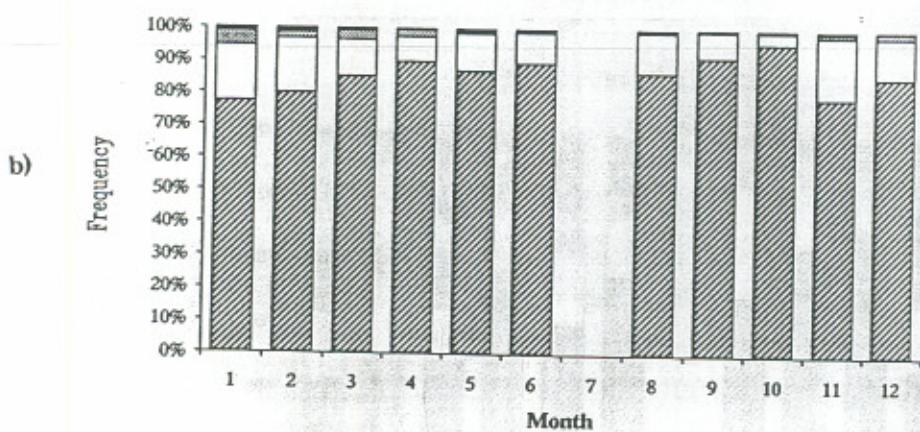


Figure 3 : Monthly distribution of the life-history classes among habitats for species richness

CORAL REEF FISH ASSEMBLAGES



SOFT BOTTOM FISH ASSEMBLAGES



MANGROVE FISH ASSEMBLAGES

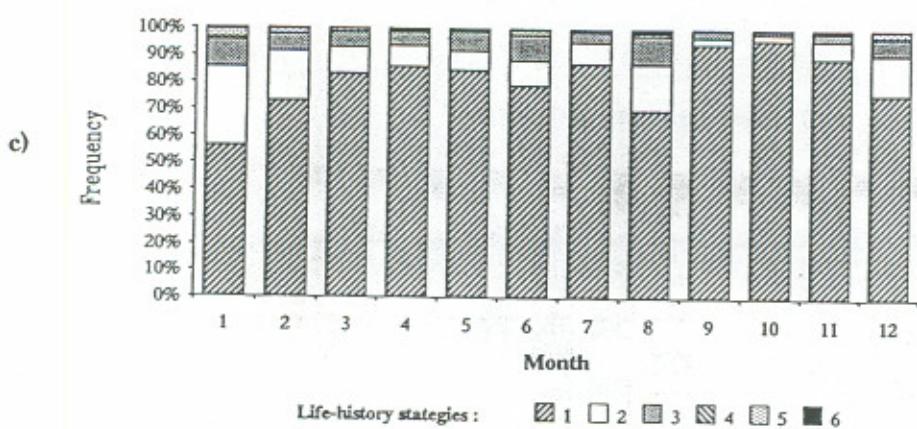
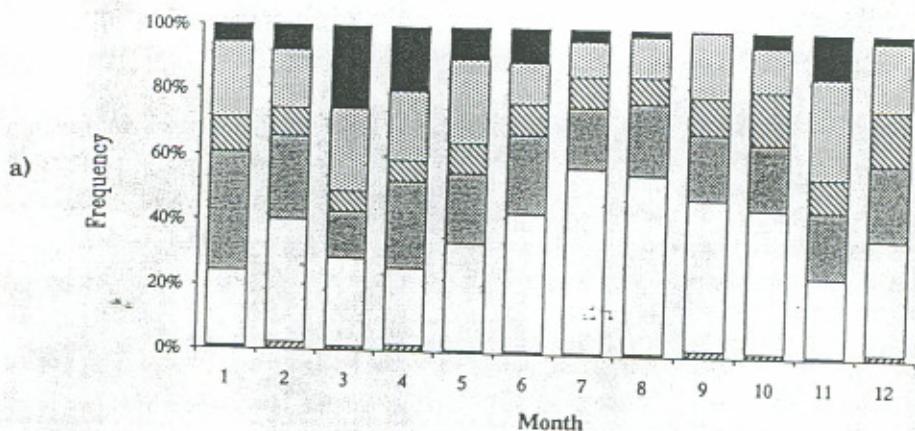
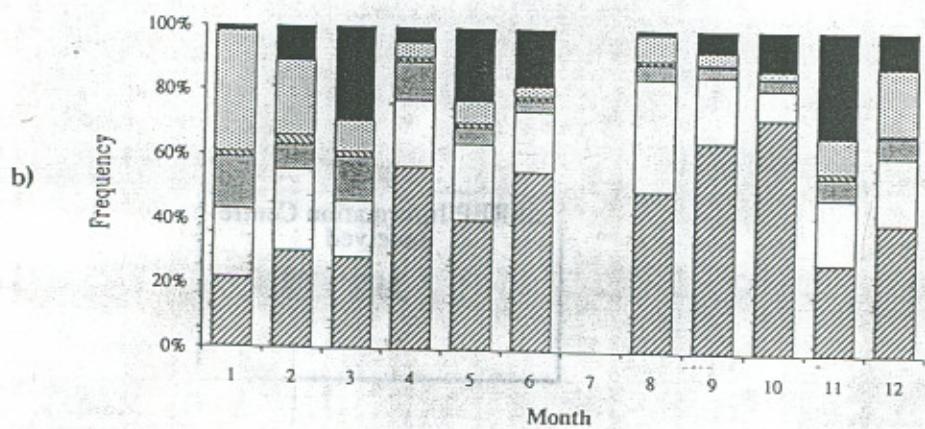


Figure 4 : Monthly distribution of the life-history classes among habitats for density

CORAL REEF FISH ASSEMBLAGES



SOFT BOTTOM FISH ASSEMBLAGES



MANGROVE FISH ASSEMBLAGES

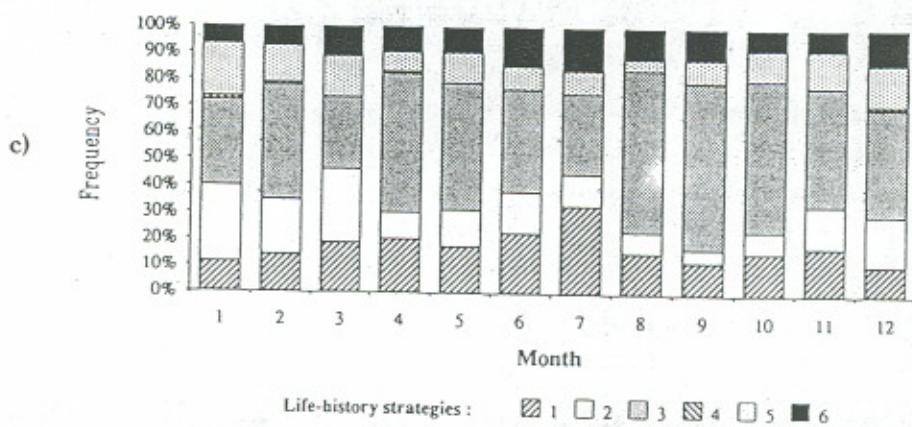


Figure 5 : Monthly distribution of the life-history classes among habitats for biomass