Journal of Fish Biology (1997) **51,** 3–20

Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar

J. Laroche*, E. Baran† and N. B. Rasoanandrasana‡

**ESA CNRS no 5023, Laboratoire d'Ecologie des Eaux Douces et des Grands Fleuves, Université Claude Bernard Lyon I, 43 boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France; †Antenne ORSTOM, Laboratoire d'Ecologie des Eaux Douces et des Grands Fleuves, Université Claude Bernard Lyon I, 43 boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France and ‡Institut Halieutique et des Sciences Marines, BP 141, Tuléar, Madagascar*

(*Received 17 September 1996, Accepted 5 January 1997*)

Gillnet sampling was conducted for a year in a tropical mangrove creek (SW Madagascar), characterized by a limited freshwater influence, a high turbidity and a tidal range up to 3 m. Sixty species of juvenile fishes were caught, 44 species being of commercial interest. Catches were dominated by Gerreidae (27% of total abundance), Teraponidae (16%), Carangidae (13%) and Sparidae (12%). The temporary resident fishes in the mangrove zone represented 50% of the species and 97% of the total abundance, the other species being rare (less than five individuals). The species richness, abundance and biomass per netting were low in the middle of the cool season (July–August). Monthly changes in the fish assemblage were particularly complex, with three species groups displaying a clear seasonal pattern, some species succeeding one another in a rather unstructured way, and three species abundant throughout the year. There was no clear structuring effect of temperature, salinity and turbidity on the fish assemblage. However, tidal, lunar and diel effects on the composition of the fish assemblage were evident. The species overlap between the Sarodrano mangrove fauna and the adjacent coral reef fauna is particularly weak with six species in common and shows that the mangrove plays only a very limited nursery role for coral reef species.

Key words: tropical fish assemblage; mangrove; Madagascar.

INTRODUCTION

The shallow water fish faunas of subtropical and tropical estuaries and coastal waters are often similar within the Indian Ocean Region (Blaber, 1981). Studies on the fish fauna and community structure of SW Indian Ocean estuaries have stressed that the majority of species use these systems as nurseries and/or foraging areas (Whitfield, 1994). Mangrove formations are well developed on the tropical East African coast and cover 19 400 ha in Kenya, Tanzania and Mozambique (MacNae, 1974). These mangroves are characterized by stable salinities and their ichthyofauna is dominated by juveniles (Day, 1974; Little *et al.*, 1988; Ntiba *et al.*, 1991). The mangroves in Madagascar are located mainly on the west coast and cover 330 000 ha. Although their fish faunas have been studied poorly up to now, they appear to be rich in species (Kiener, 1966) with species linking Madagascar with the Indo-West Pacific fish fauna.

This study describes the temporal pattern of fish assemblages in a Madagascar mangrove system characterized by stable salinities similar to those of neighbouring East African tropical mangroves. The influence of salinity, water

0022–1112/97/070003+18 $25.00/0/jb970406

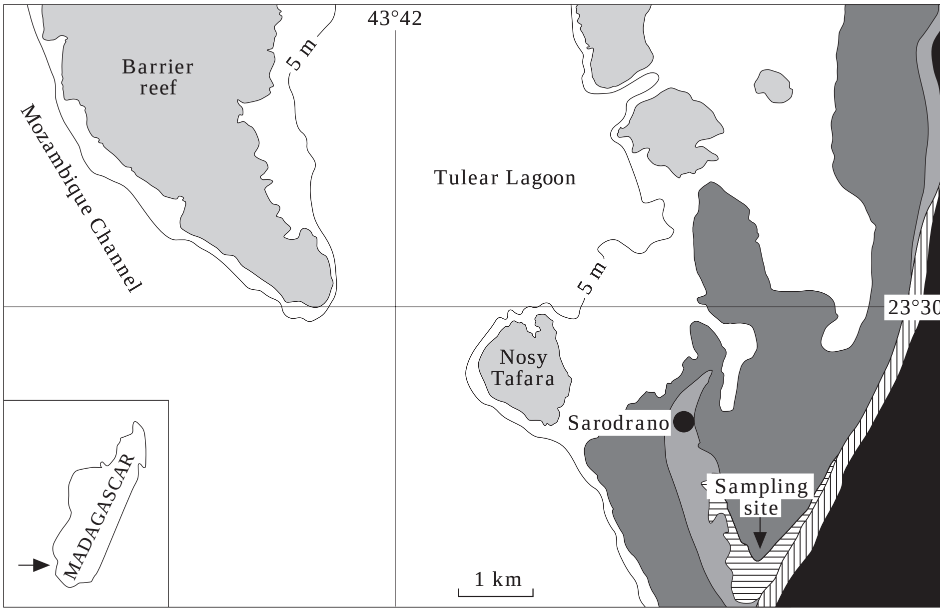

FIG. 1. Sarodrano mangrove in the south of Tulear Lagoon with adjacent habitats. ▩, Reef; ▤, mangrove; □, sand; ▥, cliff; ▧, mud bank.

temperature, tidal range, moon phases and day *v.* night on the fish assemblage was studied. In the mangroves, which are completely drained at low tide, the water height is an especially important parameter influencing the species composition (Laegdsgaard & Johnson, 1995) and the abundance of some species (Davis, 1988; Blaber *et al.*, 1995). Moreover, moon phases can modify species abundance in mangrove zones (Davies, 1988; Rooker & Dennis, 1991). The day/night effect is generally highly pronounced in mangroves where many species show abundance variations linked to their feeding habits (King, 1986; Thollot & Kulbicki, 1988; Rooker & Dennis, 1991; Blaber *et al.*, 1995).

STUDY AREA

The climate of the Tulear region is semiarid with annual rainfall <500 mm year^{-1} (Salomon, 1986). There are two main seasons, the austral summer, a warm and rainy season from November to April, and the austral winter, a cool and dry season from May to October. The Sarodrano mangrove is located in the south of Tulear Lagoon (Fig. 1) and sheltered from the south-west swell by a sandy peninsula and various coral reef formations. The mangrove forest covers about 100 ha and is composed of *Rhizophora mucronata* and *Avicennia marina*. Its inner fringe is bordered by a calcareous cliff with freshwater seepage. Extensive mudflats fringe the outer edge of the mangrove forest.

The tides are semi-diurnal and range from 0·4 to 3 m from neaps to springs. At low tide the forest and mudflats become completely exposed to air. Water turbidity varies seasonally in Tulear harbour with the Secchi disc readings ranging from 4·5 m during the warm season to 6 m during the cool season (Gaudy, 1973; Pichon, 1978). The increased transparency during the cool season is linked to reduced supply of turbid waters from the two rivers entering the bay. In the littoral zone, Tulear Bay waters are constantly turbid because of the resuspension of mud particles by tidal currents. The Secchi disc reading in the waters fringing the Sarodrano mangrove ranges from 0·9 to 1·1 m (Rakotovao, 1991).

MATERIALS AND METHODS

Sampling was undertaken between February 1994 and January 1995, eight times a month to take account of the four different moon/tide phases and day or night changes. The total number of fishing operations was 112.

During each fishing operation, surface salinity was measured with a salinometer and surface temperature with a mercury thermometer. In order to compare mangrove fringe temperatures with lagoon temperatures, the Tulear lagoon surface temperature was measured on a daily basis.

Fishes were collected using three monofilament gillnets of 50, 70 and 80 mm stretch-mesh respectively. Each gillnet was 40 m long (fishing length) and the three nets were set together along the inlet, perpendicular to the mangrove fringe. Each fishing operation began 2 h after high tide and lasted 2 h. Fishes were identified individually and measured (fork length). Gillnet catches were recorded as abundance and biomass per species.

DATA ANALYSIS

Comparisons between the monthly mean species richness, abundance and biomass were carried out using ANOVAs and Student–Newman–Keuls (SNK) analyses (Sokal & Rohlf, 1981). Before processing ANOVAs, data were transformed using Taylor's power law to normalize the distributions and stabilize the variances (Elliott, 1977). After the correlation between abundance and biomass was proven to be highly significant ($n=112$, $r=0{\cdot}998$, $P<0{\cdot}001$), only the biomass data was used. The influence of the environment on the biomass of the principal species was assessed using the Spearman rank-order correlation.

Correspondence analysis (COA) of biomass data (Anderson, 1958; Hill, 1974; Gittins, 1985; Greenacre & Hastie, 1987) was conducted after log transformation (Field & McFarlane, 1967; Clifford & Stephenson, 1975; Kimura, 1981), to investigate the structure of the fish assemblage and particularly its temporal variation. In order to obtain an optimal pattern of months taking species distributions into account, a between-class COA was performed (Benzecri, 1983; Greenacre, 1984). In this type of analysis, each class corresponds to the data of a given month. The averages of the different classes are plotted on the factorial map with the interclass variance maximized, then the sampling units are scattered around each centre of the class they belong to (Doledec & Chessel, 1991). The statistical significance of the dispersion of the averages was tested using a permutation test (Good, 1994). This method consists of repeated random permutations of the rows in the tables (i.e. of samples) followed by re-computation of the interclass variance. Comparing the variance obtained in the original analysis with the variances obtained after permutations provides an estimation of the probability of finding the observed situation in the absence of relationships between classes. Two other between-class correspondence analyses and permutation tests were performed also in order to test the tide/moon effect and the day/night effect on the distributions of species. All the multivariate analyses were performed using the ADE-4 software package (Chessel *et al.*, 1995).

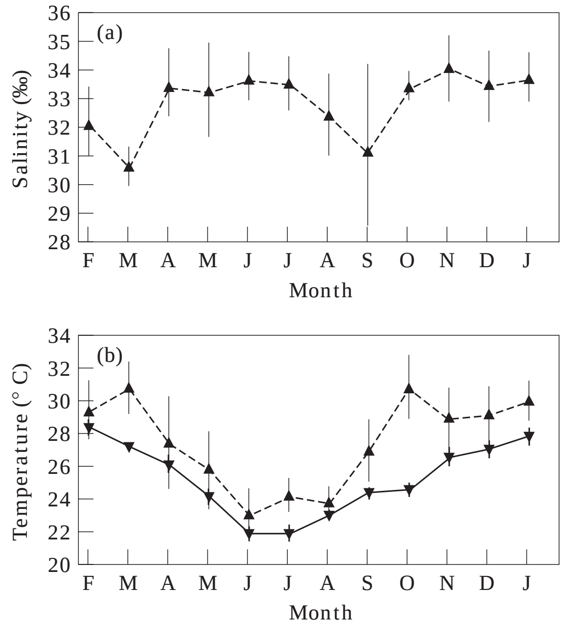

FIG. 2. Monthly average of (a) surface salinity of waters in the Sarodrano mangrove; (b) surface temperature in Tulear lagoon (——) and in the Sarodrano mangrove (– – –). Means ± 95% CL.

RESULTS

PHYSICAL PARAMETERS

During the sampling year, rainfall was typically low for the region (508 mm) and salinity remained high (30·7–34·1‰) with no clear seasonal pattern [Fig. 2(a)]. The annual cycle of surface temperature was clearly defined in Tulear lagoon [Fig. 2(b)]. The average temperature of coastal waters in the mangrove zone followed the same cycle, with temperatures 1–6° C higher than in the lagoon. The extreme temperature values in lagoon waters and the mangrove zone were 20·3–29·9 and 19·0–35·0° C respectively.

GLOBAL APPROACH OF THE ASSEMBLAGE

During the sampling, 60 species (including 44 commercial species) belonging to 35 families were caught (Table I). The total catch amounted to 2018 fishes weighing 128 kg. The most abundant families were Gerreidae (27%), Teraponidae (16%), Carangidae (13%) and Sparidae (12%). *Gerres acinaces* (Bleeker), *Terapon jarbua* (Forsskål), *Caranx papuensis* (Alleyne & Macleay), *Crenidens crenidens* (Forsskål) and *Lutjanus fulviflammus* (Forsskål) were numerically dominant (67%) but represented only 37% of the biomass because of their small size (12 cm average length).

The Sarodrano mangrove was a nursery zone for marine species. As adults, these species are mainly demersal or pelagic within the 20 m isobath. Only a few exceptions were observed with *Acanthopagrus bifasciatus* (Forsskål), *Rhabdosargus sarba* (Forsskål), *Lethrinus harak* (Forsskål) and *L. nebulosus* (Forsskål) recorded down to 50 m depth, *Sphyraena barracuda* (Walbaum) and

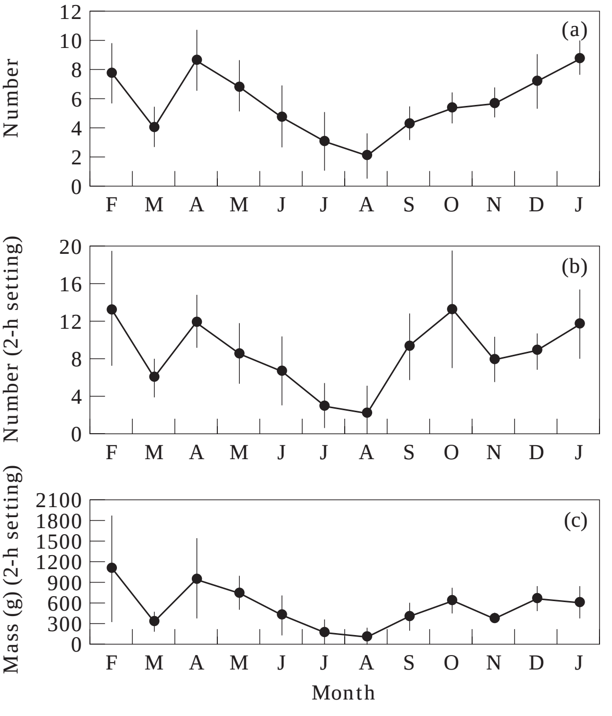

FIG. 3. Monthly average of (a) number of species, (b) abundance and (c) biomass per net. Means ± 95% CL.

Chirocentrus dorab (Forsskål) from the surface to 100 m depth and *Tylosurus acus melanotus* (Bleeker) present in both coastal waters and offshore.

The average number of species per net per month was linked closely to temporal changes in surface temperature of the lagoon except in March [Fig. 3(a)]. The number of fish species overall decreased with water cooling from April to August, and increased with water warming from August to January (SNK test: Jul., Aug., Sep. < Apr., Jan. with $P<0{\cdot}01$). The average abundance and biomass per net varied seasonally in parallel with species richness [Fig. 3(b), SNK test: Jul., Aug. < Apr., Sep. Dec., Jan. with $P<0{\cdot}05$; Fig. 3(c), SNK test: Mar., Jul., Aug. < Feb., Apr., May with $P<0{\cdot}05$].

For the 31 most common species in the catches (occurrence ≥ 3%), the average biomass per net and per month was established (Fig. 4). Only three species were caught throughout the year (*Gerres acinaces*, *Terapon jarbua* and *Sphyraena barracuda*). In the middle of the cool season, many species disappeared from the catches or showed a significant drop in biomass. The species turnover was a complex phenomenon as indicated by the disappearance of up to eight species and the appearance of up to nine species, from one month to the next. ANOVA performed on species biomass revealed a significant month effect for 14 species (Table II). Also the day/night effect was well defined for 10 species whereas the tide/moon effect (four different phases) was significant for only two species. Five species showed a positive relationship between biomass and temperature (Table II). Only one species correlated negatively. The same number of significant

TABLE I. Abundance, biomass, average length and months during which the species is captured, for all fishes sampled at Sarodrano mangrove

Species	Family	Abundance (no.)	Abundance (%)	Biomass (g)	Biomass %	Average length (cm)	Months captured
*Gerres acinaces**	Gerreidae	525	26·02	14 600	11·44	11·0	12
*Terapon jarbua**	Teraponidae	318	15·76	10 910	8·55	13·0	12
*Caranx papuensis**	Carangidae	191	9·46	9338	7·31	12·7	11
*Crenidens crenidens**	Sparidae	175	8·67	7342	5·75	12·1	9
*Lutjanus fulviflammus**	Lutjanidae	153	7·58	5233	4·10	12·1	11
*Valamugil seheli**	Mugilidae	55	2·73	6808	5·33	18·5	8
*Liza melinoptera**	Mugilidae	55	2·73	4127	3·23	16·8	11
*Scomberoides commersonianus**	Carangidae	50	2·48	11 885	9·31	27·2	4
*Sphyraena barracuda**	Sphyraenidae	47	2·33	5633	4·41	25·1	12
*Bothus pantherinus**	Bothidae	44	2·18	1980	1·55	14·7	9
*Rhabdosargus sarba**	Sparidae	36	1·78	813	0·64	10·3	6
Plotosus lineatus (Thunberg)*	Plotosidae	35	1·73	1378	1·08	17·8	6
*Mugil cephalus**	Mugilidae	34	1·68	12 150	9·52	27·3	10
*Tylosurus acus melanotus**	Belonidae	29	1·44	6343	4·97	46·2	9
*Acanthopagrus bifasciatus**	Sparidae	25	1·24	483	0·38	9·0	5
Polynemus plebeius	Polynemidae	22	1·09	3470	2·72	20·1	5
Liza macrolepis (Smith)*	Mugilidae	20	0·99	1618	1·27	17·4	7
*Scomberoides tol**	Carangidae	19	0·94	1308	1·02	17·5	6
*Chirocentrus dorab**	Chirocentridae	19	0·94	7021	5·50	37·6	8
*Gerres oyena**	Gerreidae	19	0·94	485	0·38	11·2	3
*Lethrinus harak**	Lethrinidae	14	0·69	1080	0·85	15·1	4
*Hemiramphus far**	Hemiramphidae	13	0·64	1683	1·32	30·9	3
*Lutjanus russelli**	Lutjanidae	13	0·64	378	0·30	12·4	3
Platax orbicularis	Platacidae	12	0·59	135	0·11	5·8	3
*Lethrinus nebulosus**	Lethrinidae	7	0·35	193	0·15	11·1	1
Silago sihama	Sillaginidae	6	0·30	295	0·23	17·9	5
Monodactylus argenteus	Monodactylidae	6	0·30	183	0·14	10·3	4
*Herklotsichthys quadrimaculatus**	Clupeidae	5	0·25	148	0·12	13·2	3
Sphyraena forsteri (Cuvier)*	Sphyraenidae	5	0·25	749	0·59	27·7	2
Leiognathus equulus	Leiognathidae	5	0·25	70	0·05	8·2	3

TABLE I. *Continued*

Species	Family	Abundance (no.)	Abundance (%)	Biomass (g)	Biomass %	Average length (cm)	Months captured
*Upeneus vittatus**	Mullidae	4	0·20	278	0·22	13·4	2
*Platycephalus longiceps**	Platycephalidae	4	0·20	1005	0·79	32	2
Ctenochaetus striatus (Quoy & Gaimard)	Acanthuridae	3	0·15	285	0·22	13·8	2
Trachinotus blochii (Lacépède)*	Carangidae	3	0·15	278	0·22	14·8	3
*Gerres filamentosus**	Gerreidae	3	0·15	78	0·06	11·2	2
Saurida gracilis	Synodontidae	3	0·15	53	0·04	12·6	3
Scarus ghobban (Forsskål)	Scaridae	3	0·15	200	0·16	13·7	2
Lactoria cornuta (L.)	Ostraciidae	3	0·15	123	0·10	11·7	2
*Platycephalus indicus**	Platycephalidae	3	0·15	850	0·67	33·1	3
Chanos chanos (Forsskål)*	Chanidae	2	0·10	440	0·34	25·0	2
Yongeichthys nebulosus (Forsskål)	Gobiidae	2	0·10	38	0·03	10·2	2
Plectorhinchus plagiodesmus (Fowler)*	Haemulidae	2	0·10	640	0·50	24·3	2
Plactorhinchus gaterinus (Forsskål)*	Haemulidae	2	0·10	190	0·15	17·2	2
Lutjanus argentimaculatus (Forsskål)*	Lutjanidae	2	0·10	333	0·26	21·0	2
Lutjanus fulvus (Schneider)*	Lutjanidae	2	0·10	140	0·11	14·7	2
Rastrelliger kanagurta (Russell)*	Scombridae	2	0·10	240	0·19	20·3	1
Siganus sutor (Valenciennes)*	Siganidae	2	0·10	60	0·05	10·7	2
Megalops cyprinoides (Broussonet)*	Megalopidae	2	0·10	730	0·57	33·9	2
Liza richardsonii (Smith)*	Mugilidae	2	0·10	510	0·40	24·4	1
Acanthopagrus berda (Forsskål)*	Sparidae	2	0·10	188	0·15	12·4	1
Caranx sexfasciatus (Quoy & Gaimard)*	Carangidae	1	0·05	1050	0·82	39·0	1
Scomberoides lysan (Forsskål)*	Carangidae	1	0·05	150	0·12	25·0	1
Carangoides fulvoguttatus (Forsskål)*	Carangidae	1	0·05	1225	0·96	42·0	1
Dactyloptena orientalis (Cuvier)	Dactylopteridae	1	0·05	155	0·12	20·5	1
Kiphosus cinerascens (Forsskål)	Kyphosidae	1	0·05	145	0·11	20·0	1
Lethrinus ramak (Forsskål)*	Lethrinidae	1	0·05	30	0·02	12·0	1
Priacanthus hamrur (Forsskål)	Priacanthidae	1	0·05	270	0·21	26·3	1
Synodus variegatus (Lacépède)	Synodontidae	1	0·05	18	0·01	14·0	1
Sphyraena obtusata (Cuvier)*	Sphyraenidae	1	0·05	118	0·09	31·2	1
Leiognathus dussumieri (Valenciennes)	Leiognathidae	1	0·05	20	0·02	8·3	1

*Commercial species.

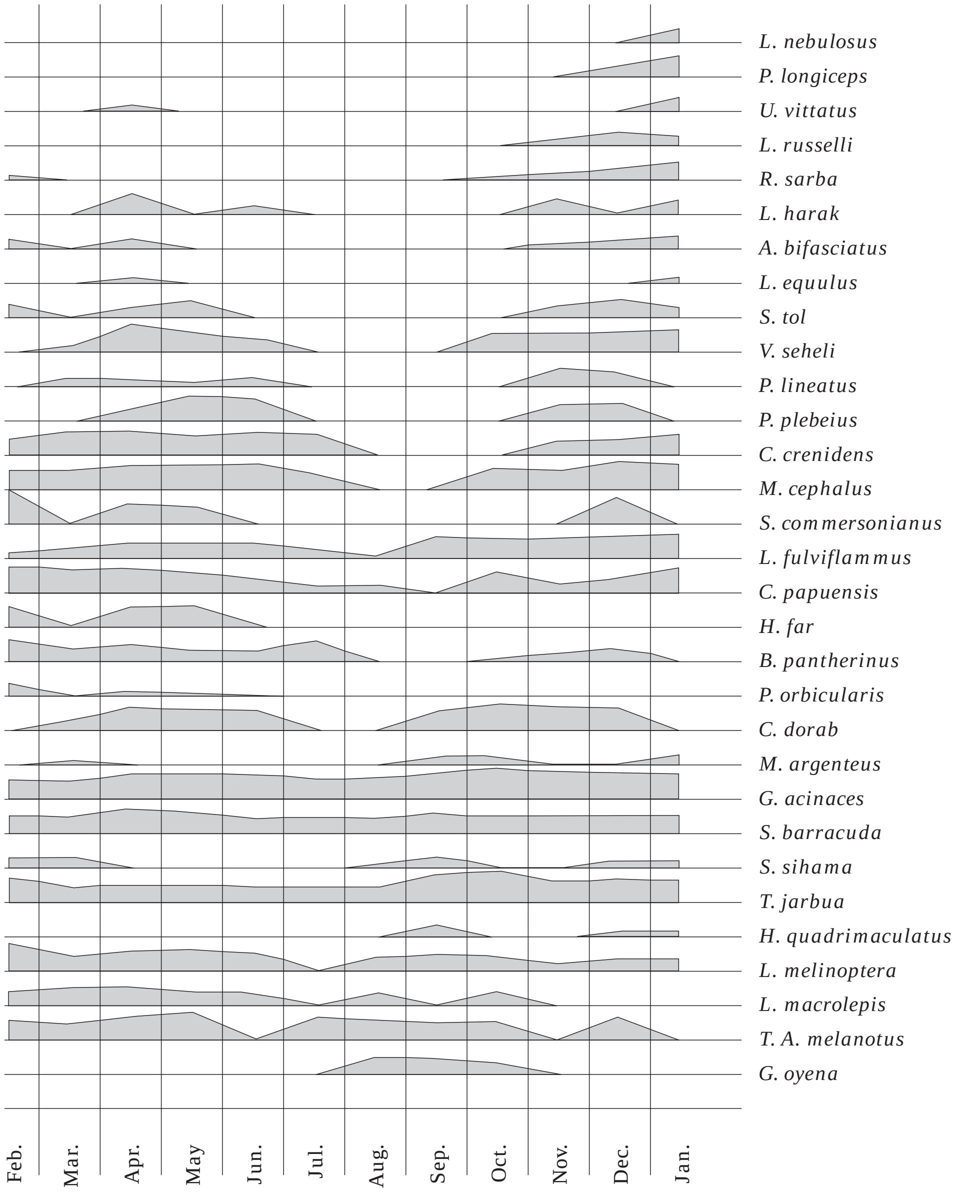

FIG. 4. Average biomass (g) per net and per month for the 31 most common species (log transformed data).

relationships was obtained for the biomass and salinity correlation, but for different species.

STRUCTURAL APPROACH OF THE ASSEMBLAGE

Three between-class COA were performed on biomass data for the 31 principal species. Taking into account the different factors of the sampling design, the month, tide/moon and day/night effects explained respectively 17·7,

TABLE II. Month, diel and moon-tide effects tested by ANOVA performed on species biomass

Species	ANOVA (Significance)			Correlation test (Significance)	
	Month	Day/night	Moon tide	Temperature	Salinity
T. A. melanotus					
B. pantherinus	**	(D)**			
H. quadrimaculatus					
C. papuensis	**			(+)*	
S. commersonianus	**			(+)*	
S. tol					
C. dorab		(N)*	*		
G. acinaces	*	(D)**			(+)*
G. oyena					
H. far					
L. fulviflammus	**				(+)*
L. russelli	*			(+)*	
L. harak					
L. nebulosus	**				
P. plebeius	**	(N)**		(−)*	
P. orbicularis					
S. sihama					
S. barracuda					
L. equulus					(+)*
U. vittatus					
M. argenteus					(−)*
M. cephalus		(N)**			
V. seheli	*	(N)**	**		(+)*
L. macrolepis		(N)*			
L. melinoptera	*	(N)**			
P. lineatus					(+)*
P. longiceps	*				
C. crenidens	**	(D)**			
A. bifasciatus		(D)*			
R. sarba	**			(+)**	
T. jarbua	**			(+)*	

Relation between biomass and environmental parameters tested by Spearman rank correlation (*$P<0{\cdot}05$; **$P<0{\cdot}01$).

3·8 and 3·4% of the total variance. The permutation test showed that the three effects were statistically significant (month effect and day/night effect, $P<0{\cdot}01$; tide/moon effect, $P<0{\cdot}05$).

On the factorial map of the between-month COA (Fig. 5), axes I and II explained 24·5 and 21·2% respectively of the total variance. This analysis confirms the global temporal pattern and also points out three groups of species; *Scomberoides commersonianus* (Lacépède), *Platax orbicularis* (Forsskål) and *Hemiramphus far* (Forsskål), were caught from February to May (end of the austral summer); *Gerres oyena* (Forsskål), *Herklotsichthys quadrimaculatus* (Rüppell) and *Monodactylus argenteus* (L.) were especially common from August

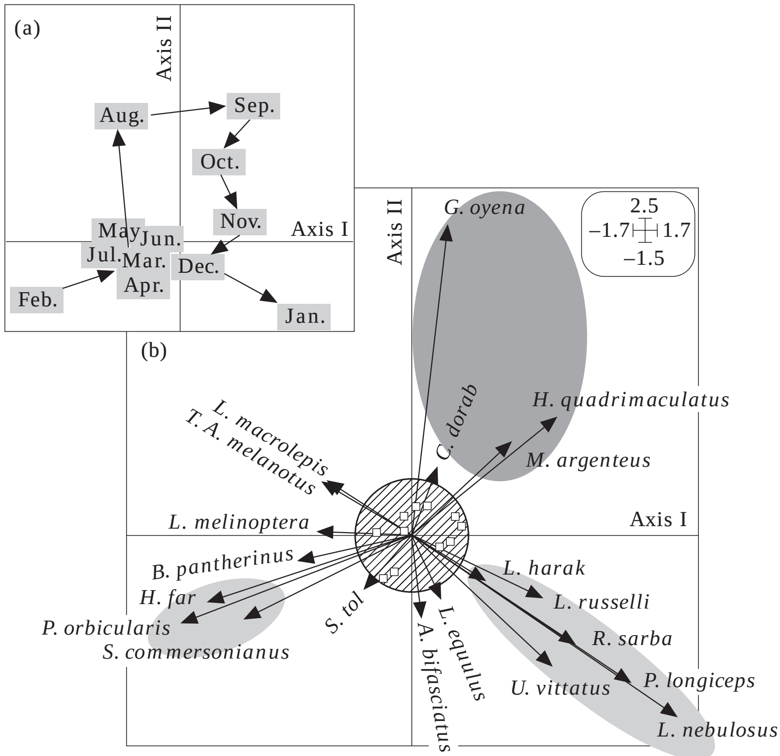

FIG. 5. Factorial map of the between-month correspondence analysis (axes I and II): (a) averages of the different months; (b) most significant species.

to October (end of the austral winter) and *Lutjanus russelli* (Bleeker), *Rhabdosaragus sarba*, *Platycephalus longiceps* (Cuvier), *Lethrinus nebulosus* and *Upeneus vittatus* (Forsskål) were caught mainly from November to January (beginning of the austral summer).

On the first factorial map of the between-moon/tide period COA (Fig. 6) axes I and II explained 47 and 36% of the total variance. Classes were grouped according to the type of tide (spring tides *v.* neap tides) on axis 1 and secondly a lunar pattern on axis 2 [Fig. 6(a)]. Thus the tide effect was more significant than the moon phase effect on the assemblage. From left to right of axis I, the neap tide fish composition [most characteristic species: *Valamugil seheli* (Forsskål), *Lethrinus harak* and the piscivore *Chirocentrus dorab*] contrasted with that of the spring tide [characteristic species: *Sillago sihama* (Forsskål), *Platax orbicularis* and the piscivores, *Scomberoides commersonianus*, *S. tol* (Cuvier) and *Tylosurus acus melanotus*]. Two other piscivores (*Caranx papuensis* and *Sphyraena barracuda*) seemed to be unaffected by the tidal phase. Axis II divided the moon calendar globally into two parts, new moon—first quarter, full moon—last quarter. A few species seemed to be associated with different moon phases: new moon [*Polynemus plebeius* (Broussonet), *Scomberoides tol*, *Acanthopagrus bifasciatus*]; first quarter [*Leiognathus equulus* (Forsskål), *Lethrinus nebulosus*, *Valamugil seheli*]; full moon (*Platax orbicularis*, *Tylosurus acus melanotus*); and last quarter (*Lethrinus harak*, *Monodactylus argenteus*).

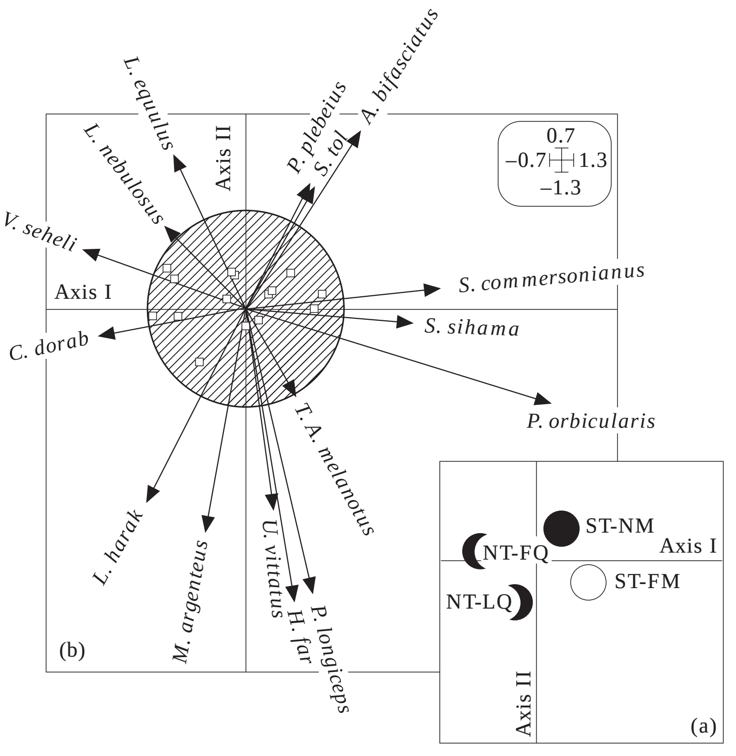

FIG. 6. Factorial map of the between-moon/tide period correspondence analysis (axes I and II): (a) averages of the different moon/tide periods (ST-NM = spring tide, new moon; NT-FQ = neap tide, first quarter); (b) most significant species.

From the species position on the factorial axis I of the between-day/night COA (Fig. 7), two groups of 13 and 10 species respectively were associated with day and night fishing.

The summary of the results (Table III) showed a good agreement between ANOVA and correspondence analysis. COA results confirmed the ANOVA results regarding seasonal and diel patterns (Table III) and provided a more comprehensive insight of the structure of the assemblage. They also revealed a global moon-tide effect due to several species reacting together while ANOVA, considering species one by one, detected a significant effect for two species only.

DISCUSSION

A review of 56 studies in tropical estuarine, coastal and mangrove zones (Baran, 1995) shows that species richness varies from 18 to 197 species, which places the Sarodrano mangrove and its 60 species at an intermediate level. Species richness does not always characterize the fauna adequately because it can depend greatly on the fishing effort, on the use of complementary fishing gears, and on the length of sampling linked to the turnover of species in such open systems (Baran & Poizat, 1994). Thus one artisanal fishing by poisoning observed in Sarodrano led to the identifiation of unrecorded families

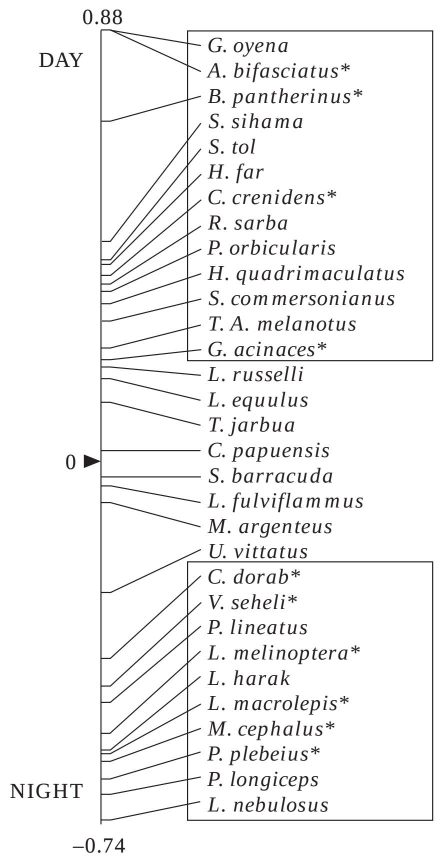

FIG. 7. Species position on the factorial axis I of the between-day/night correspondence analysis (*significant day/night effect tested by ANOVA). Squares stress two species groups significantly associated with day and night respectively.

(Apogonidae, Atherinidae). Using beach seine, fly screen and poisoning, Mauge (1967) also found other families in this mangrove (Syngnathidae, Cichlidae, Periophthalmidae and Ophichthidae). These different families are probably rare in Tulear lagoon as shown by the catch of artisanal beach seines with a stretched mesh-size of 20 mm and a cod-end made of fly screen (Laroche & Ramananarivo, 1995, unpublished).

The ratio of species to families (*S/F*) characterizes the diversity within families. The *S/F* value varies from 1·6 in cool temperate estuaries to 2·0 in warm temperate estuaries and 2·8 in subtropical estuaries in South Africa and reaches 2·8 in tropical estuaries in West Africa (Whitfield, 1994). The *S/F* value for Sarodrano (1·7) is relatively low. This low family diversity also occurred in constant salinity mangrove creeks in Kenya (Little *et al.*, 1988: *S/F* = 2·2; Ntiba *et al.*, 1991: *S/F* = 2·1). In Tulear lagoon, the low *S/F* was probably linked to the high artisanal fishing pressure (Vasseur *et al.*, 1988; Laroche & Ramananarivo, 1995).

Other Indo-Pacific mangrove creeks with a predominant marine influence have 13–24 species in common with Sarodrano mangrove, i.e. 15–29% of their species

TABLE III. Summary of the data analysis

	Month effect	Moon-tide effect	Diel effect	Temperature	Salinity
ANOVA (number of species affected)	5* 9**	1* 1**	3* 7**		
Correspondence analysis					
% of total variance	17·7**	3·8*	3·4**		
Species number according to factorial maps	20	16	23		
Spearman rank correlation (number of species affected)				5* 1**	6*

$^*P<0·05$; $^{**}P<0·01$.

richness (Kenya: Little *et al.*, 1988; Ntiba *et al.*, 1991; Australia: Blaber *et al.*, 1985; New Caledonia: Thollot, 1989). This result provides confirmation of the great similarity of tropical and subtropical fish species composition in the Indo-Pacific (Blaber, 1981; Blaber *et al.*, 1985; Blaber & Milton, 1990). The most common species are: *Terapon jarbua*, *Gerres oyena*, *G. filamentosus* (Cuvier) and *Saurida gracilis* (Quoy & Gaimard). These are distributed widely in the Indo-Pacific, the first two being associated particularly with shallow waters as juveniles (Blaber & Blaber, 1980; Day *et al.*, 1981; Potter *et al.*, 1990; Whitfield, 1994); *Lutjanus fulviflammus* is linked clearly with mangroves as juveniles (Little *et al.*, 1988; Thollot, 1992); *Mugil cephalus* (L.) and *Sphyraena barracuda* are ubiquitous species, the first being common in shallow waters both as juveniles and adults (Wallace, 1975), and the second is common in mangrove zones as juveniles (Fischer & Bianchi, 1984).

Many coastal marine species use estuaries, shallow waters and their associated mangrove formations as nursery areas (Wallace, 1975; Blaber *et al.*, 1985, 1995; Little *et al.*, 1988; Robertson & Duke, 1990; Laegdsgaard & Johnson, 1995). Usually, spawning takes place at sea and is followed by immigration and recruitment of postlarvae and small juveniles 10–60 mm long into coastal zones (Wallace, 1975; Robertson & Duke, 1990). Generally, the juveniles do not stay more than a year in these zones (Wallace *et al.*, 1984; Robertson & Duke, 1990). At low tide, the Sarodrano mangrove forest drains completely, with the result that fishes use the mudflats only as a temporary habitat at high tide (Laegdsgaard & Johnson, 1995). On the basis of a thorough scanning of the literature on their residence status in the coastal zone, the 30 most common Sarodrano species can be described as temporary residents in mangroves (50% of the species and 97% of the abundance), the other species being rare (less than five individuals). Among temporary residents, the long-term residents inhabit mangroves for several consecutive months, notably *Gerres acinaces*, *Terapon jarbua* and *Caranx papuensis*. The short-term residents occupy the mangroves irregularly, for example: *Valamugil seheli*, *Liza melinoptera* (Valenciennes) and *Scomberoides commersonianus*. The nursery role played by the mangrove zone is confirmed here in Sarodrano.

In the Sarodrano mangrove, the fish species richness, abundance and biomass were especially low in the middle of the cool season (July–August). A decrease in the species richness during the cool season is often associated with a decrease in abundance and is a common phenomenon in temperate, subtropical and tropical systems (Loneragan *et al.*, 1986; Robertson & Duke, 1987; Williamson *et al.*, 1994; Laegdsgaard & Johnson, 1995; Tremain & Adams, 1995).

There was no clear structuring effect of temperature and salinity on the fish assemblage. The seasonal patterns for many species were not linked necessarily to these parameters. Unfavourable environmental conditions for some species were probably associated with the lowest temperatures that initiate fish migration towards the sea (Ogren & Brusher, 1977). In the constant salinity systems of Madagascar, there is a rather precise link between penaeid shrimp emigration toward the open sea and falling temperature (Laroche *et al.*, 1995). The reduced availability of some benthic invertebrates, especially shrimps, during the cool season could modify the distribution of dominant benthic invertebrate feeding fish in Sarodrano.

Other factors such as turbidity can play an important role in fish distribution in coastal zones. Turbid areas associated with estuaries or mangrove creeks reduce the effectiveness of visual piscivorous predators and thus are especially attractive to juveniles (Cyrus & Blaber, 1987*a*, *b*; Blaber & Blaber, 1980; Blaber *et al.*, 1995). In the Sarodrano mangrove, the decreasing turbidity gradient from the coastal fringe to the lagoon is relatively stable throughout the year and should not induce great variations in the seasonal distribution of juveniles.

The tidal range in Sarodrano influences the composition or the abundance of species (Davis, 1988; Laegdsgaard & Johnson, 1995). Some piscivores (*Scomberoides commersonianus*, *S. tol*, *Tylosurus acus melantous*) are associated with spring tides and therefore require a minimum water height to enter the mangrove. This result is confirmed for the two first species which are abundant between 2–5 m and rare when water depth is <2 m in the Gulf of Carpentaria (Blaber *et al.*, 1995). The occurrence of other piscivores (*Caranx papuensis*, *Sphyraena barracuda* and *Chirocentrus dorab*) is not related to spring tides. The large tidal range leads to relatively deep waters at high tide in Sarodrano which may increase piscivorous predation on small sized fishes. Piscivores represent 18% of the species composition in Sarodrano (Carangidae, Sphyraenidae, Belonidae, Chirocentridae) and this proportion is much lower than the one observed in the Dampier region (37% of the species composition) which is characterized by a higher tidal range and lower tubidity (Blaber *et al.*, 1985).

Lunar periodicity has a moderate influence on the fish assemblage in Sarodrano, modifying the distribution of 10 species. Moon-phase effects on fish assemblage in mangroves have been little studied; lunar periodicity affected 10 species in Puerto Rico where tidal ranges are low (Rooker & Dennis, 1991). In North Australia three species (Davis, 1988) were affected by lunar phase during spring tides.

The time of day or night had an influence on the Sarodrano fish assemblage. The day association was very marked for some species: e.g. *Bothus pantherinus* (Rüppell), a benthic invertebrate feeder which fed essentially during the day (Harmelin-Vivien, 1979) and the piscivore, *Scomberoides commersonianus* which was particularly active during the day (Fisher & Bianchi, 1984). The fishes of the family Gerreidae probably leave the mangrove before dusk (Rooker & Dennis, 1991). The Sarodrano nocturnal species included one piscivore, *Chirocentrus dorab*, which was particularly active at night (Blaber *et al.*, 1995). The nocturnal feeding trend of some Mugilidae was observed also for *Mugil cephalus* in South Africa (Day *et al.*, 1981) and for *Liza grandisquamis* (Valenciennes) in Nigeria (King, 1986). In Sarodrano, piscivores did not seem to have pronounced nocturnal foraging habits as they do in Australia and New Caledonia (Blaber *et al.*, 1995; Thollot & Kulbicki, 1988).

In Tulear lagoon, the mangrove-associated fauna can be compared to those of adjacent habitats, soft bottoms and coral reefs. Out of the 51 species caught by the artisanal seine fishing on soft bottoms (Laroche & Ramananarivo, 1995, unpublished), 18 species are common to both soft bottoms and mangrove, i.e. respectively 35 and 30% of their species richness. Out of more than 500 species observed by scuba diving in coral reefs (Harmelin-Vivien, 1979), only six large ones are common to both coral reefs and mangrove: *Bothus pantherinus*, *Lethrinus harak*, *Lutjanus fulviflammus*, *Platycephalus indicus* (L.), *Lutjanus russelli* and *Sphyraena barracuda*. In addition, the Sarodrano mangrove is similar to other Indo-Pacific mangroves in that it is not a significant nursery ground for reef species (Quinn & Kojis, 1985; Birkeland & Amesbury, 1987; Little *et al.*, 1988; Parrish, 1989; Blaber & Milton, 1990; Thollot, 1992).

Many thanks to J. E. Thorpe, A. K. Whitfield, P. Gaudin and anonymous referees for useful comments.

References

Anderson, T. W. (1958). *An Introduction to Multivariate Statistical Analysis*. New York: John Wiley.

Baran, E. (1995). Dynamique spatio-temporelle des peuplements de poissons estuariens en Guinée — relations avec le milieu abiotique. Thèse de Doctorat, Available at http://biomserv.univ-lyon1.fr/baran/page-html.html.

Baran, E. & Poizat, G. (1994). Comparaison d'un estuaire et d'un bras de mer en Guinée: abondance et richesse spécifique de l'ichtyofaune. *Revue d'Hydrobiologie Tropicale* **27,** 43–55.

Benzecri, J. P. (1983). Analyse de l'inertie intra-classe par l'analyse d'un tableau de correspondances. *Les Cahiers de l'Analyse des Données* **8,** 351–358.

Birkeland, C. & Amesbury, S. E. (1987). Fish transect surveys to determine the influence of neighbouring habitats on fish community structure in the tropical Pacific. *UNEP Regional Seas Reports and Studies* **97,** 195–202.

Blaber, S. J. M. (1981). The Zoogeographical Affinities of Estuarine Fishes in South-East Africa. *South African Journal of Science* **77,** 305–307.

Blaber, S. J. M. & Blaber, T. G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology* **17,** 143–162.

Blaber, S. J. M. & Milton, D. A. (1990). Species composition, community structure and zoogeography of fishes of mangrove estuaries in the Solomon islands. *Marine Biology* **105,** 259–267.

Blaber, S. J. M., Young, J. W. & Dunning, M. C. (1985). Community structure and zoogeographic affinities of the coastal fishes of the Dampier region of north-western Australia. *Australian Journal of Marine and Freshwater Research* **36,** 247–266.

Blaber, S. J. M., Brewer, D. T. & Salini, J. P. (1995). Fish communities and the nursery role of the shallow inshore waters of a tropical bay in the Gulf of Carpentaria, Australia. *Estuarine, Coastal and Shelf Science* **40,** 177–193.

Chessel, D., Doledec, S. & Thioulouse, J. (1995). *ADE Version 4: HyperCard© Stacks and Programme. Library for the Analysis of Environmental Data*. URA CNRS 1451, Université Lyon 1, 69622 Villeurbanne Cedex. Available at http://biomserv.univ-lyon1.fr/ade-4.html.

Clifford, H. T. & Stephenson, W. (1975). *An Introduction to Numerical Classification*. New York: Academic Press.

Cyrus, D. P. & Blaber, S. J. M. (1987*a*). The influence of turbidity on juvenile marine fishes in estuaries. Part 1. Field studies at Lake St Lucia on the southeastern coast of Africa. *Experimental Marine Biology and Ecology* **109,** 53–70.

Cyrus, D. P. & Blaber, S. J. M. (1987*b*). The influence of turbidity on juvenile marine fishes in estuaries. Part 2. Laboratory studies, comparisons with field data and conclusions. *Experimental Marine Biology and Ecology* **109,** 71–91.

Davies, T. L. O. (1988). Temporal changes in the fish fauna entering a tidal swamp system in tropical Australia. *Environmental Biology of Fishes* **21,** 161–172.

Day, J. H. (1974). The ecology of Morrumbene estuary, Mozambique. *Transaction of the Royal Society of South Africa* **41,** 43–97.

Day, J. H., Blaber, S. J. M. & Wallace, J. H. (1981). Estuarine fishes. In *Estuarine Ecology with Particular Reference to South Africa* (Day, J. H., ed.), pp. 197–223. Rotterdam: Balkema.

Dolédec, S. & Chessel, D. (1991). Recent developments in linear ordination methods for environmental sciences. *Advances in Ecology* **1,** 133–155.

Elliott, J. M. (1977). Some methods for the statistical analysis of samples of benthic invertebrates. *Freshwater Biological Association, Scientific Publication* **25,** 1–156.

Field, J. G. & McFarlane, G. (1967). Numerical methods in marine ecology. I: A quantitative similarity analysis of rocky shores samples in False Bay, South Africa. *Zoologica Africana* **3,** 119–138.

Fischer, W. & Bianchi, G. (1984). *FAO Species Identification Sheets for Fishery Purposes in Western Indian Ocean (Fishing Area 51)*. Rome: FAO.

Gaudy, R. (1973). Les Copépodes pélagiques de la région de Tuléar (Madagascar). 1. L'environnement physique (octobre 1963–juin 1964). *Téthys* **5** (Suppl.), 117–132.

Gittins, R. (1985). *Canonical Analysis, a Review with Applications in Ecology*. Berlin: Springer-Verlag.

Good, P. (1994). *Permutation Tests. Springer Series in Statistics*. New York: Springer-Verlag.

Greenacre, M. (1984). *Theory and Applications of Correspondence Analysis*. London: Academic Press.

Greenacre, M. & Hastie, T. (1987). The geometric interpretation of correspondence analysis. *Journal of the American Statistical Association* **82,** 437–447.

Harmelin-Vivien, M. L. (1979). Ichtyofaune des récifs coralliens de Tuléar (Madagascar). Ecologie et relations trophiques. Thèse de Doctorat d'Etat, Université Aix-Marseille II.

Hill, M. O. (1974). Correspondence analysis: a neglected multivariate method. *Journal of the Royal Statistical Society* **23,** 340–354.

Kiener, A. (1966). Contributions à l'étude écologique et biologique des eaux saumâtres malgaches. Les poissons euryhalins et leur rôle dans le développement des pêches. *Vie et Milieu* **16,** 1013–1149.

Kimura, D. K. (1981). Standardized measures of relative abundance based on modelling log (c.p.u.e.) and their application to Pacific ocean perch (*Sebates alutus*). *Journal du Conseil International d'Exploration de la Mer* **39,** 211–218.

King, R. P. (1986). Observations on *Liza grandisquamis* (Pisces: Mugilidae) in Bonny river, Nigeria. *Revue d'Hydrobiologie tropicale* **19,** 61–66.

Laegdsgaard, P. & Johnson, C. R. (1995). Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Marine Ecology Progress Series* **126,** 67–81.

Laroche, J. & Ramananarivo, N. (1995). A preliminary survey of the artisanal fishery on coral reefs of the Tulear Region (southwest Madagascar). *Coral Reefs* **14,** 193–200.

Laroche, J., Benoely & Siaviri, A. (1995). Biologie et pêche traditionnelle des crevettes pénéides dans l'embouchure d'un fleuve en milieu semi-aride (sud-ouest de Madagascar). *Oceanologica Acta* **18,** 659–670.

Little, M. C., Reay, P. J. & Grove, S. J. (1988). The fish community of an East African mangrove creek. *Journal of Fish Biology* **32,** 729–747.

Loneragan, N. R., Potter, I. C., Lenanton, R. C. J. & Caputi, N. (1986). Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. *Marine Biology* **92,** 575–586.

MacNae, W. (1974). A general account of the fauna and flora of mangrove swamp forests in the Indo-West-Pacific region. *Advances in Marine Biology* **6,** 73–270.

Mauge, L. A. (1967). Contribution préliminaire à l'inventaire ichtyologique de la région de Tuléar. *Recueil des Travaux de la Station Marine d'Endoume* **7** (Suppl.), 101–132.

Ntiba, M. J., Wakwabi, E. O., Okoth, B. K., Mwatha, G. K. & Kimani, E. (1991). A preliminary study on the ichtyo community of the Gazi mangrove creek, Kenya. *Workshop in Tropical Coastal Lagoon Ecosystems, Inhâca Island, Mozambique, Swedish Agency for Research and Cooperation with Developing Countries, Conference Reports*, 127–134.

Ogren, L. H. & Brusher, H. A. (1977). The distribution and abundance of fishes caught with a trawl in the St Andrew Bay system, Florida. *North East Gulf Science* **1,** 83–105.

Parrish, J. D. (1989). Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series* **58,** 143–160.

Pichon, M. (1978). Recherches sur les peuplements à dominance d'Anthozoaires dans les récifs coralliens de Tuléar (Madagascar). *Atoll Research Bulletin* **222,** 1–447.

Potter, I., Beckley, L. E., Whitfield, A. K. & Lenanton, R. C. J. (1990). Comparisons between the roles played by estuaries in the life cycles of fishes in temperate western Australia and southern Africa. *Environmental Biology of Fishes* **28,** 143–178.

Quinn, N. J. & Kojis, B. L. (1985). Does the presence of coral reef in proximity to a tropical estuary affect the estuarine fish assemblage? In *Proceedings of the 5th International Coral Reef Congress,* Tahiti (Gabrie, C. & Saluat, B., eds), Vol. 5, pp. 445–450. Tahiti: Antenne Museum EPHE.

Rakotovao, J. M. (1991). *Contribution à l'étude de l'huitre* Crassostrea cucullata *de la région de Sarodrano (Toliara). Conditions du milieu, bioécologie et croissance.* D.E.A. d'Océanologie Appliquée, Université de Tuléar, Tuléar, Madagascar.

Robertson, A. I. & Duke, N. C. (1987). Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. *Marine Biology* **96,** 193–205.

Robertson, A. I. & Duke, N. C. (1990). Recruitment, growth and resistance time of fishes in a tropical Australian mangrove system. *Estuarine, Coastal and Shelf Science* **31,** 723–743.

Rooker, J. R. & Dennis, G. D. (1991). Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science* **49,** 684–698.

Salomon, J. N. (1986). Le Sud-Ouest de Madagascar, étude de géographie physique. Thèse de Doctorat d'Etat, Université d'Aix-Marseille.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. New York: W. H. Freeman.

Thollot, P. (1989). Les poissons de mangrove de Nouvelle Calédonie: caractérisation du peuplement et relations avec les autres communautés ichtyologiques du lagon. Résultats préliminaires: mangrove de Déama (avril-mai 1987). *ORSTOM-Nouméa, Rapports Scientifiques et Techniques, Sciences de la Mer* **52,** 1–58.

Thollot, P. (1992). Importance of mangroves for Pacific reef fish species, myth or reality? In *Proceedings of the 7th International Coral Reef Symposium*, Guam (Richmond, R. H., ed.), Vol. 2, pp. 934–941. Mangilao: University of Guam Press.

Thollot, P. & Kulbicki, M. (1988). Species overlap between the fish fauna inventories of coral reefs, soft bottoms and mangroves of Saint-Vincent Bay (New Caledonia). In *Proceedings of the 6th International Coral Reef Symposium*, Australia (Choat, J. H., Barnes, D., Borowitzka, M. A., Coll, J. C., Davies, P. J., Flood, P., Hatcher, B. G. & Hopley, D., eds), Vol. 2, pp. 613–618. Townsville, Australia.

Tremain, D. M. & Adams, D. H. (1995). Seasonal variations in species diversity, abundance, and composition of fish communities in the northern indian river lagoon, Florida. *Bulletin of Marine Science* **57,** 171–192.

Vasseur, P., Gabrié, C. & Harmelin-Vivien, M. (1988). State of coral reefs and mangroves of the Tulear region (SW Madagascar): assessment of human activities and suggestions for management. In *Proceedings of the 6th International Coral Reef Symposium*, Australia (Choat, J. H., Barnes, D., Borowitzka, M. A., Coll, J. C., Davies, P. J., Flood, P., Hatcher, B. G. & Hopley, D., eds), Vol. 2, pp. 421–425. Townsville, Australia.

Wallace, J. H. (1975). The estuarine fishes of the east coast of South Africa. Part I: Species composition and length distribution in the estuarine and marine environments. Part II: Seasonal abundance and migrations. *Investigational Report, South African Association for Marine Biological Research* **40,** 1–72.

Wallace, J. H., Kok, H. M., Beckley, L. E., Bennett, B., Blaber, S. J. M. & Whitfield, A. K. (1984). South African estuaries and their importance to fishes. *South African Journal of Science* **80,** 203–207.

Whitfield, A. K. (1994). An estuary-association classification for the fishes of southern Africa. *South African Journal of Science* **90,** 411–417.

Williamson, I., King, C. & Mather, P. B. (1994). A comparison of fish communities in unmodified and modified inshore habitats of Raby Bay, Queensland. *Estuarine, Coastal and Shelf Science* **39,** 401–411.