PART III. REEF FISH COMMUNITIES AND FISHERY YIELDS OF TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)

BY

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INTRODUCTION

Fish communities in the lagoon of the Tikehau atoll were studied by only a few researchers. Harmelin-Vivien (1984) studied the distribution of the main herbivorous families (Scaridae and Acanthuridae) in the lagoon and on the outer slope to 30 m in depth. The total fish community of the outer slope was studied by Galzin (1985, 1987) at 12 m in depth. These studies were carried out in the southwestern part of the atoll. Spatial organization of coral associated fish community was studied throughout the lagoon by Morize *et al.* (1990). Most of the other studies undertaken at Tikehau involved the artisanal fishery (Morize, 1984, 1985 ; Caillart and Morize, 1986, 1988) and the biology of some target species to the exploited stock (Caillart et *al.*, 1986; Caillart, 1988; Morize et Caillart, 1987). It seems worthwhile to present in this special issue of ARB, all the available information on the fish fauna of Tikehau. Furthermore, this overview allows us to compare our results with others in the Indopacific region.

FISH COMMUNITIES OF TIKEHAU ATOLL

METHODS

To study the fish communities of Tikehau, two complementary methods were used : visual census and rotenone poisoning.

Many synthesis (GBRMPA, 1978; Barans and Bortone, 1983; Harmelin-Vivien *et al.*, 1985) describe the method for estimating *in situ* fish communities and populations using visual censuses. These methods, widely used on coral reefs, enable scientists to study fish communities without perturbation. In the Tikehau atoll, visual censuses were carried out by SCUBA diving on 50 m length and 5 m width transects. The transects on the outer slope and the inner reef flat were parallel to the reef. Around the pinnacles, the sampling line was curved around them. In each transect, abundance inside three caregories of size (small - medium - large) were recordered for all species encountered (St. John *et al.*, 1990).

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Fish hidden in reef shelters and in sediment were caught with ichtyotoxic rotenone. Individual fish were measured to the nearest millimeter (standard and total length), weighted to the nearest gram and preserved in a 10% neutral formalin. Length-weight relationships were subsequently computed for all species caught, providing that the sample size was large enough.

The two methods were used to study fish communities in the lagoon, but only visual censuses were used on the outer slope.

FISH COMMUNITIES OF THE OUTER SLOPE

Fish communities of the outer slope are strongly influenced by environmental factors : primary substratum types, slope gradient, level of wind exposure, and magnitude of the 1983 cyclonic damages on coral assemblages. Several surveys of the outer slope fish fauna were carried out on the southwestern outer slope of the atoll (Fig. 1). For the damages induced by the cyclones and the description of the outer slope, see the previous chapter on the environment by Intes and Caillart.

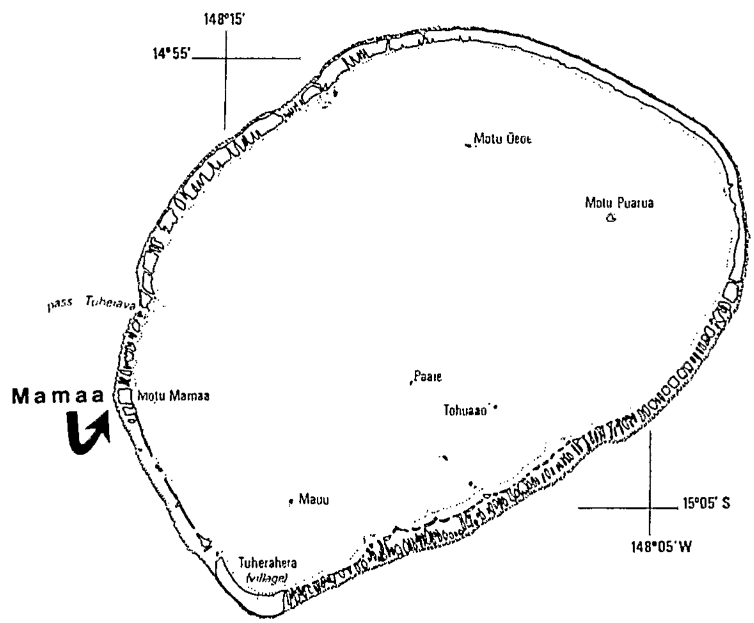

Fig. 1 : Location (*Mamaa*-arrow) of fish community sampling station on the outer slope of the Tikehau atoll .

The fore reef area (0-10 m)

The spur and groove zone is an area of very high fish abundance. In particular surgeonfish *Acanthurus achilles, A. nigroris, A. guttatus, A. lineatus* and parrotfish *Scarus sordidus* , *Scarus sp.* are typical features of this zone. Small coral dependant fish found are Cirrhitidae, small Serranidae (*Cephalopholis urodelus*), Chaetodontidae (*Chaetodon quadrimaculatus*) Pomacanthidae (*Centropyge sp.*), Labridae (*Thalassoma fuscum*), numerous Balistidae (*B. viridescens, B. undulatus* and *Melichthys niger* and *M. vidua* in mid-water). The shark *Carcharhinus melanopterus* and a great variety of Carangidae are also frequentely encountered in this productive and well oxygenated area.

On the fore reef platform (4-10 m), benthic fish fauna (*e.g.* : Gobiidae, Chaetodontidae, Acanthuridae, Serranidae, Labridae) can be distinguished from zooplankton-feeding mid-water fish fauna (*e.g.* : *Anthias* spp., Pomacentridae, nocturnal Holocentridae and *Naso spp.*), and upper-water fish fauna (Balistidae, sharks, tunas and Sphyraenidae).

The outer terrace (10-25 m)

The fish fauna of this zone present a great diversity (more than 100 species), and an abundance of fishes. The most conspicuous families are Holocentridae (genus *Holocentrus, Sargocentron, Myripristis*) numerous around coral patches, Lutjanidae (*Lutjanus bohar, L. gibbus, L. kasmira*) forming schools of several hundred individuals, Acanthuridae (*Ctenochaetus striatus, C. strigosus, Zebrasoma scopas, Acanthurus glaucopareius, A. nubilus* and schools of *Naso spp.*), Serranidae (genus *Variola, Gracila* and the common grouper *Epinephelus microdon*), Chaetodontidae and some Scaridae (*Scarus gibbus, S. niger, Cetoscarus bicolor*).

The deep outer slope (from 25 m)

Abundance and diversity of fish fauna decrease somewhat but a new, more characterized, species assemblage occurs with depth. Holocentridae and Scaridae are less important while the abundance of large Serranidae, some Labridae (genus *Bodianus, Cirrhilabrus*), Zanclidae and *Heniochus* noticeably increase. Among Chaetodontidae still present, species of the genus *Hemithaurichtys* appear. Among the Acanthurid censused are, *Acanthurus bleekeri, A. pyroferus, A. xanthopterus* and large schools of *Naso hexacanthus* and *Naso vlamingii.* Lutjanidae, with large *Lutjanus bohar,* are numerous as well. The abundance of parrotfish decreases rapidly below 30 m.

Fish assemblage was not studied below 40 m on the outer slope of the Tikehau atoll.

Temporal variations of fish communities

Numerous authors working on coral reef ecosytems, and Bell and Galzin (1984) and Galzin *et al.* (1990) in French Polynesia, emphasized that a strong relationship exists between the live coral coverage rate and fish repartition. As shown in Table 1, dramatic changes occured in live coral coverage rate on transect under investigations in five years, inducing a renewal of fish assemblages. Most of these dramatic changes were induced by six cyclones which ravaged french Polynesia during the hot season 1982-83 (Harmelin-Vivien and Laboute, 1986).

Table 1 : Live coral coverage rate of the southwestern outer slope of the Tikehau atoll before, immediatly after and five years after cyclones.

Depth	1982 Before the cyclones (Faure et Laboute, 1984)	1983 After the cyclones (Harmelin-Vivien et Laboute, 1986)	1987 (Galzin et Harmelin-Vivien, unp data)
3 m	5 to 25 %	<5 %	-
5 m	40 to 60 %	20 to 25 %	56 to 62 %
10 m	40 to 60 %	20 to 25 %	42 %
20 m	40 to 60 %	15 %	22 to 24 %
30 m	40 to 60 %	15 %	16 to 24 %

Data displayed in Table 2 permit the assessment of fish fauna temporal variations. Between 1983 and 1987, total number of species on the fore reef area increased from 46 to 56 due to a conspicuous resettlement of Serranidae, Pomacentridae and Labridae. On all other biota of the outer slope, the total number of species decreased between 1983 and 1987. Most of the Scaridae, Acanthuridae and Balistidae left the 10 m depth area whereas most of Holocentridae, Lutjanidae and Mullidae usually encountered around 20 m in depth, moved away. Fish densities at 20 m depth decreased dramatically between 1983 and 1987 (*i.e.* : from 3.4 ind m^{-2} in 1983 to 2.6 ind m^{-2} in 1987 on the average).

Table 2 : Main characteristics of the ichtyological fauna on the outer slope of Tikehau at different depths before, just after, and five years after cyclones of late 1982 - early 1983. Nhs : Number of herbivorous species, Dih : Number of individuals of herbivorous species . 100 m^{-2},Nst : Total number of species, Dsi : Number of all individuals . 100 m^{-2}. (-- : no data).

Depth (m)	1982 Before cyclones				1983 After cyclones				1987			
	Nhs	Dih	Nst	Dsi	Nhs	Dih	Nst	Dsi	Nhs	Dih	Nst	Dsi
5	15	159	--	--	17	213	46	--	19	143	56	--
10	20	188	--	--	21	78	40	337	12	55	69	260
20	21	199	--	--	19	174	78	--	25	152	67	--
30	19	140	--	--	17	101	58	--	22	152	--	--

Herbivorous species were studied in more detail. Data listed in Table 2 and 3 show that for herbivorous fishes the mean number of individuals is relatively constant at 5, 20 and 30 m depths between 1982 and 1987. As previously noticed, the only anomality is found at a 10 m depth where the number of herbivorous species on the outer slope undergo a veritable decrease : 1.7 ind. m^{-2} in 1982, 1.4 ind. m^{-2} in 1983 and 1.2 ind m^{-2} in 1987.

After the cyclones, fish fauna decreased considerably. A great number of cryptic species died with associated corals, another part remained unsheltered and suffered subsequently from higher predation by piscivorous species like *Epinephelus microdon* that became more abundant after the cyclones. Another part of fish fauna escaped toward undamaged reef areas. A re-arrangement of fish fauna was noticed on the outer slope ; a greater number of species were counted in shallow areas.

COMPARISON WITH FISH COMMUNITIES OF OTHER OUTER SLOPES

Galzin (1985) has compared fish communities in the outer slopes of 2 high islands (Moorea, Mehetia) and 3 atolls (Tikehau, Takapoto and Mataiva) of French Polynesia. Qualitative and quantitative studies show that fish communities found at a 12 m depth on atoll outer slopes are different than those found on high island outer slopes (Moorea, Fig. 2).

Out of the 189 species censused in ten sampling stations, 8 (4%) are found exclusively at Tikehau. These are : *Elagatis bipinnulata, Lethrinus elongatus, Lethrinus xanthochilus, Chromis margaritifer, Bodianus loxozonus, Cetoscarus bicolor* and *Scarus niger*. Pomacentrid *Chromis xanthura* is unexpectedly absent from Mataiva and Tikehau outer slopes whereas it is present at the 8 other sampling stations.

Differences in coral coverage can also be a major factor since outer slope sampled at Tikehau and Mataiva have been damaged by cyclones to a greater extent than the southwestern outer slope of Takapoto (Galzin, 1987 ; Harmelin-Vivien and Laboute, 1986). The current state of knowledge does not enable to isolate the major factors influencing fish repartition on atoll outer slopes in French Polynesia.

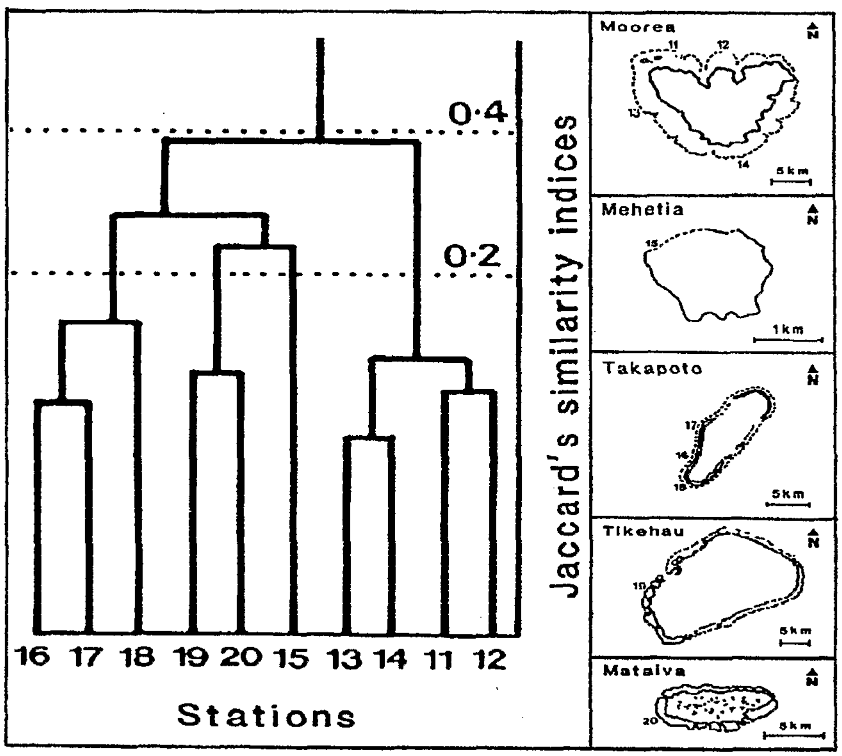

Fig. 2 : Location of sampling stations on each of the five islands and dendrogram derived from similarity matrices. Numbers refer to the 10 sampling sites distributed among the five islands (from Galzin, 1987).

Table 3 : Temporal variability for two families of herbivorous fish (Scaridae and Acanthuridae) on the outer slope of the Tikehau atoll. (number of individuals . 1000 m^{-2})).

	1982				1983				1987			
	-5	-10	-20	-30	-5	-10	-20	-30	-5	-10	-20	-30
SCARIDAE												
Cetoscarus bicolor		7	3	4		2	6	2			2	
Hipposcarus longiceps		1	4			2			11	2		
Scarus altipinnis	5	12	6	7	3	5	4		1		4	1
Scarus forsteri												1
Scarus frenatus	5	9	11		14	2	5	4	1		5	2
Scarus frontalis		8	2		5	1		4				
Scarus ghobban	5	10	4			2	1	4	2	3	4	3
Scarus gibbus	8	13	30	16		1	10	12	3	1	4	
Scarus globiceps					1				4		1	
Scarus niger			1	8	3			16			3	2
Scarus oviceps							1					
Scarus psittacus					2				6		1	
Scarus rubroviolaceus		1			2		1					
Scarus schlegeli		1				9					2	6
Scarus sordidus	27	15	21	17	77	7	50	18	14`	9	13	48
Scarus juv.	15	26	6			10						
Number of species	**6**	**11**	**10**	**5**	**8**	**10**	**8**	**7**	**8**	**4**	**10**	**7**
Number of individuals	**65**	**103**	**88**	**52**	**107**	**41**	**78**	**60**	**42**	**15**	**39**	**63**
ACANTHURIDAE												
Acanthurus achilles	24	8			51				10			
Acanthurus bleekeri				3								
Acanthurus glaucopareius	21	26	111	5	35	2	36	4	6		17	3
Acanthurus guttatus	13				13				4			
Acanthurus nigricauda				1		2	2	4			24	13
Acanthurus nigroris	108	85			145	74			170	75		
Acanthurus nubilus				9			4	14			4	2
Acanthurus olivaceus						11				9	7	8
Acanthurus pyroferus			2	24			46	40			19	37
Acanthurus thompsoni			34	27							3	30
Acanthurus triostegus	2				6	3			86			
Acanthurus xanthopterus			14	60								
Ctenochaetus striatus	90	149	14	16	153	15	72	12	5	14	50	48
Ctenochaetus strigosus	60	63	164	104		2	148	74	2	2	75	50
Naso brevirostris			10	7			7	14			12	5
Naso hexacanthus												8
Naso lituratus	7	13	52	15	12	34	24	6	20	8	23	46
Naso vlamingii				1				6			3	6
Zebrasoma rostratum	8	4	1	6	8	7	1		10	3	13	2
Zebrasoma scopas		17	6	21		3	15	18	1	7	79	59
Zebrasoma veliferum		2	2			1	3		1		8	1
Acanthurus juv.					2					5	4	
Number of species	**9**	**9**	**11**	**14**	**9**	**11**	**11**	**10**	**11**	**8**	**15**	**15**
Number of individuals	**333**	**367**	**410**	**299**	**425**	**154**	**358**	**192**	**315**	**123**	**341**	**318**

FISH COMMUNITIES ASSOCIATED WITH CORAL FORMATIONS

In the lagoon of Tikehau, three main types of biotopes can be distinguished : coral reef formations, sediments and mid-water. Coral reef formations are composed by the inner reef flat, pinnacles and coral patches. They are scattered all over the lagoon but are more numerous in the front of channels (Harmelin-Vivien, 1985). In the southern and western part of the lagoon, the inner reef flat that edges the atoll rim lagoonward does not extend deeper than 5-6 m. Live corals extend down to 15 m depth on pinnacle slopes. Pinnacles are more abundant in the western part of the lagoon, especially between the village and the pass.

Fish abundance on Takapoto's outer slope (4 to 5 ind . m^{-2}) appears to be greater than that on the outer slopes of Tikehau and Mataiva (3 to 4 ind . m^{-2}) (Table 4). However, the difference is not statistically significant. This difference can be explained either by geomorphological considerations (presence/absence of a pass) or by variations in longitudinal position.

Table 4 : Comparative quantitative data for the coral reef fish community at 12 m depth of the outer-slope of 5 islands in French Polynesia. NI : Number of individuals . 100 m^{-2}, NS : Number of species . 100 m^{-2}.

		NI		NS	
	stations	NI	Mean (s.d.)	NI	Mean (s.d.)
	11	575		44	
	12	428		32	
MOOREA	13	220	400	27	35
	14	378	(146)	37	(7)
	16	487		46	
TAKAPOTO	17	435	442	41	45
	18	404	(42)	47	(3)
MEHETIA	15	516		46	
TIKEHAU	19	337	418	43	45
MATAIVA	20	400	(91)	47	(2)

Only the fish community associated with coral formations was studied in detail (Harmelin-Vivien, 1984; Morize *et al.*, 1990). The total fish fauna of the lagoon is obviously richer because soft-bottom and mid-water fish communities were under-sampled (St. John *et al.*, 1990). Lagoon fish communities are divided as follows : 1) fish species remaining in the lagoon during their entire life span after recruitment to the reef, 2) fish species that, at least at one time of their life, live on the outer slope or in ocean water, 3) and species living on the outer slope but that migrate toward the lagoon for reproduction. Species with different life cycles gather especially near the pass.

Structure of the coral associated fish fauna in Tikehau lagoon.

A total of 164 fish species, belonging to 34 families were censused around the coral formations in the Tikehau lagoon : 99 species were observed by visual census and 108 species were caught by rotenone poisoning (Appendix 1). The most diversified families are Labridae (21 spp.), Acanthuridae (20 spp.), Scaridae (14 spp.), Serranidae and Chaetodontidae (7 spp.). All species recorded only by visual census live in mid-water. These species belong to families of Carcharinidae, Fistularidae, Echeneidae, Carangidae, Lutjanidae, Lethrinidae and Zanclidae.

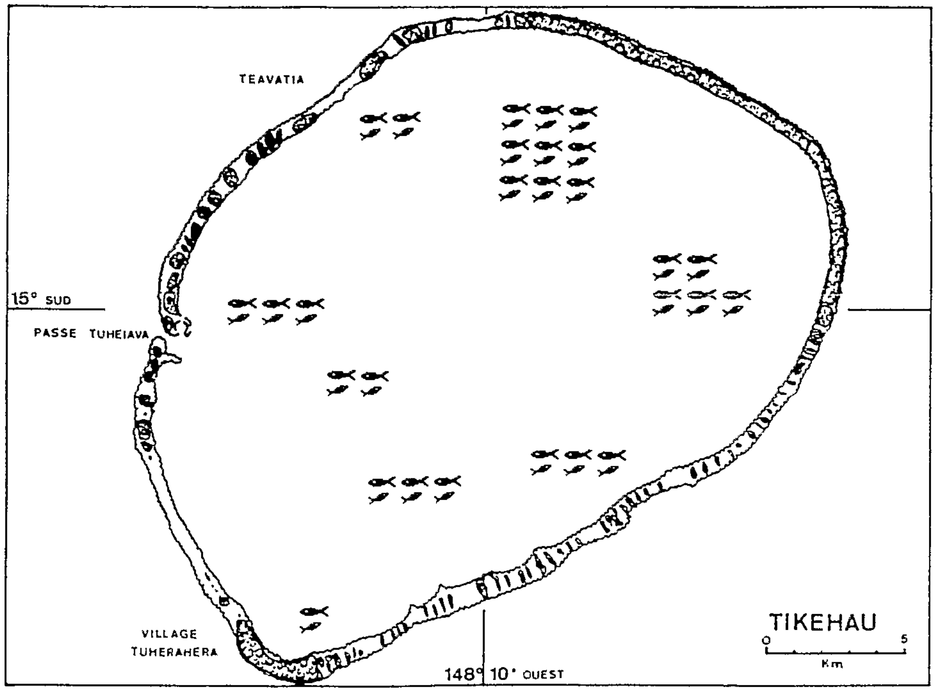

Fig. 3 : Mean fish densities at different sampling stations in the Tikehau lagoon (2 fish : 100 ind . 100 m-2) (Morize *et al.*, 1990).

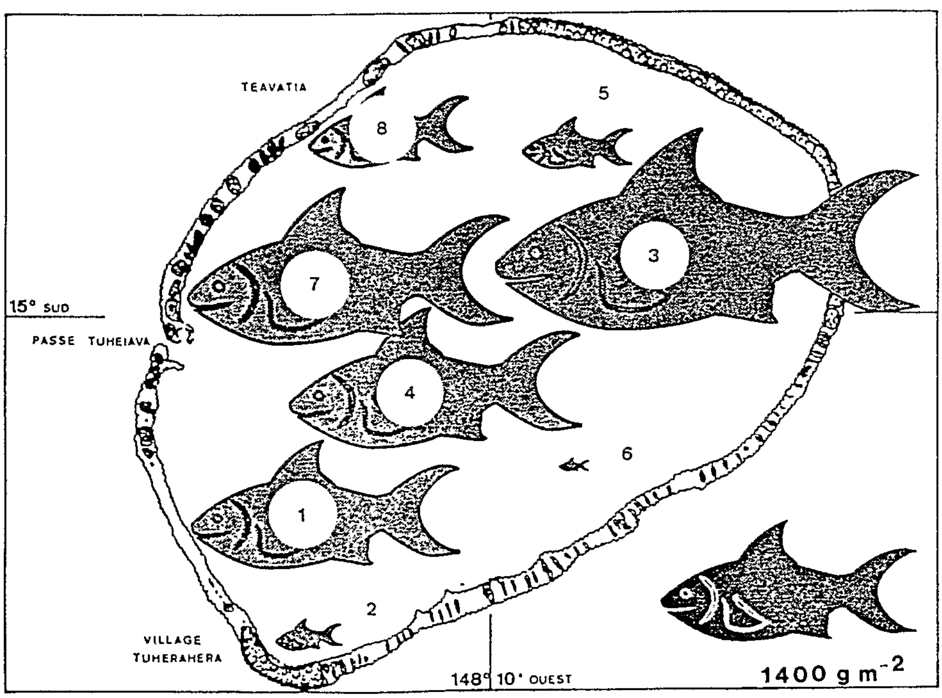

Fig. 4 : Mean fish biomass at different sampling stations (numbers) in the Tikehau Lagoon (modified from Morize *et al.*, 1990).

On the other hand, species recorded only by rotenone poisoning, are cryptic species or live buried in sediments (Congridae, Ophichthidae, Ophidiidae, Scorpaenidae, Blenniidae and Bothidae). Only a part of the fish fauna of coral formations can be recorded by each method (60% by visual census and 67% by rotenone poisoning). Only 30 % of all species are recorded by both methods.

The composition of fish species is relatively homogeneous throughout the whole lagoon. Down to a depth of 15 m, the distribution of species does not show any gradient over the whole lagoon (Morize *et al.*, 1990). The same fish community is found around coral reef patches of the lagoon of Tikehau. On a biomass basis, this community is made up of about 70% of carnivorous species, 14% of omnivorous species and 17% of herbivorous species (Table 5). However the trophic structure of the community observed is different according to the method of sampling. Samples obtained by rotenone poisoning allow to have a better estimation of the abundance of nocturnal plankton feeders, nocturnal carnivores and omnivores. On the other hand, diurnal plankton feeders, sessile invertebrates feeders and herbivorous species are better sampled with visual censuses.

Table 5 : Comparison of trophic structure of fish community in the Tikehau lagoon related to the two assessment methods (expressed as percentage of total number of species).

		Total community	Visual counts	rotenone poisoning
Total number of species		161	97	108
% piscivorous		9.4	8.3	10.2
% other carnivorous	nocturnal	18.7	11.5	20.4
	diurnal	20,6	20,8	22,2
% planktivorous	nocturnal	8.8	4.2	12.0
	diurnal	3.1	5.2	1.9
% sessile invertebrate browsers		9.4	14.6	9.3
% omnivorous		13.7	8.3	18.5
% herbivorous		16.3	27.1	5.5

Spatial distribution of fishes in the Tikehau lagoon

Geographical distribution

The small-scale spatial heterogeneity of fish community in the lagoon is considerable. However the distribution of this community follows a steady pattern all around the pinnacles. On the windward area of the pinnacles, species richness, density, and biomass of fish are always higher (between 1.5 to 4 times) than on leeward ones (Morize *et al.*, 1990).

In spite of a relatively homogeneous distribution of fish in the whole lagoon, densities, biomass and length frequencies of fish of this community present a heterogeneous spatial distribution.

Densities : Depending on the sites, average fish density around pinnacles of the Tikehau lagoon vary from 102 to 1274 fishes per 100 m^2. The highest mean densities are located windward of the atoll (in the northeastern part of the lagoon, Fig. 3).

Biomass : The biomass of the 31 most abundant species varies from 0.8 to 34.4 kg . 100 m^{-2} and display a considerable spatial heterogeneity. The spatial variations of biomass seem to depend in part upon the localisation of studied sites from the reef flat, the village and the pass (Morize *et al.*, 1990). The most important average biomass is recorded near the center of the lagoon and at the pass of the atoll (Fig. 4).

Table 6 : Mean demographic structure of fish populations around coral pinnacles in the Tikehau lagoon (D : mean density of individuals 100 m^{-2} ; % : percentage of each total population size class).

Station	location	Juveniles		Adults		Olds	
		D	%	D	%	D	%
1	S W	12.4	8.0	82.9	53.6	59.3	38.4
2	S W	6.0	12.9	27.2	58.5	13.3	28.6
4	W	20.7	18.4	49.1	43.6	42.8	38.0
7	W	7.9	5.2	103.9	68.9	39.0	25.9
3	E	26.1	10.7	159.0	65.3	58.3	24.0
5	NNE	31.6	6.7	293.9	62.3	146.5	31.0
6	SE	20.5	13.0	93.3	59.2	43.8	27.8
8	N N W	19.8	14.0	76.9	54.6	41.4	29.4

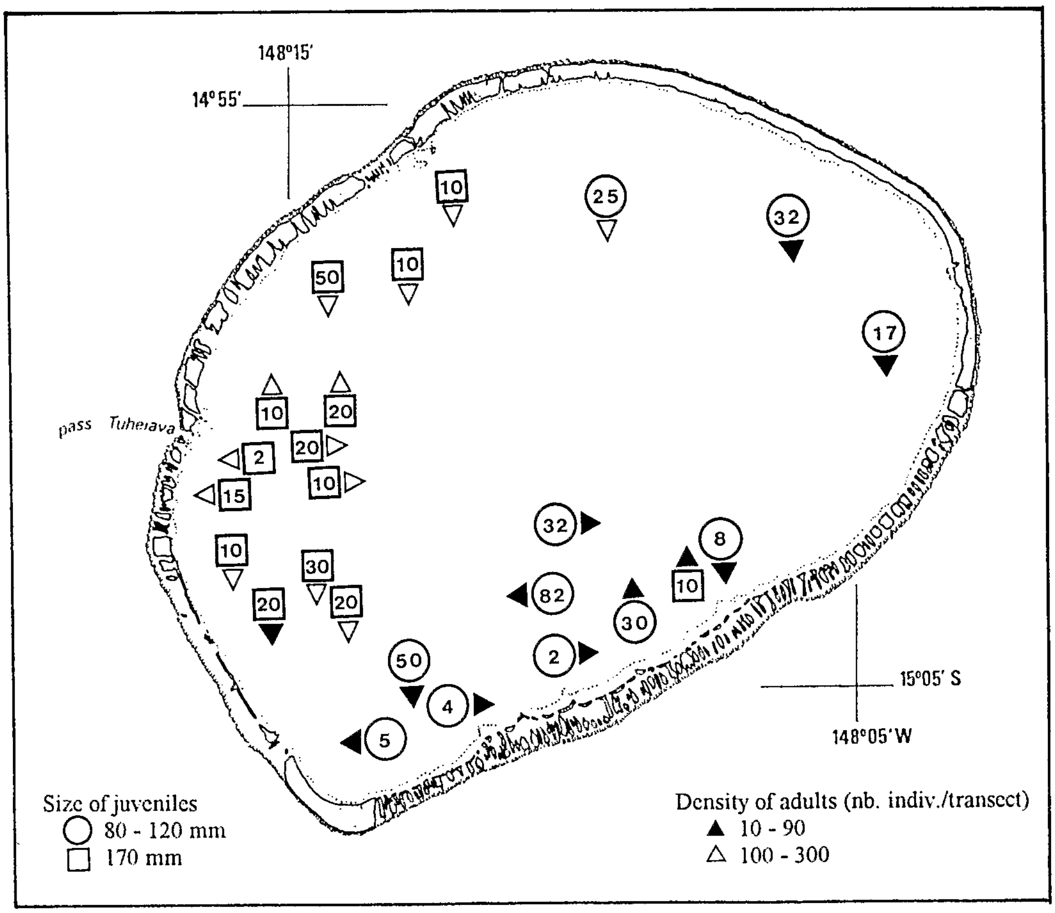

Fig. 5 : Size-class repartition of *Naso brevirostris* in the Tikehau Lagoon. (number : number of juveniles recorded per transect).

Age structure : Generally, middle sized fish are the most numerous and represent from 44 up to 70% of the total number of fish (Table 6). The number of the largest fish varies between one fourth and one third of the total population, while juveniles are less numerous (5 to 8%). The low abundance of juveniles may be due to the fact that they are not easily seen by divers or that they recruit somewhere else to other biotopes. Furthermore, the length frequency distribution throughout the lagoon is not homogeneous. Juveniles are more numerous in northern and eastern parts of the lagoon. These areas receive oceanic water passing over the reef flat through hoa which are particularly numerous. The distribution of length frequencies of *Naso brevirostris* is a good example that shows differences in juvenile and in adult fish distribution (Fig. 5). All small juveniles (80-120 mm) were observed in the eastern part of the lagoon while larger juveniles (170 mm) were seen mostly in the western part (Caillart, 1988). Conversely, the density of adult fishes in the western part, and particularly near the pass, is four time higher than in the eastern part.

Distribution with depth

Specific composition : The species richness of the fish community in the lagoon is greater between 3 and 5 meters depth : 87 species were recorded at these depths by visual censuses. From 10 to 15 m, the community is poorer (only 65 species censused) but is not qualitatively different. Only one species, Gobiidae *Amblygobius phalaena*, appears to be a characteristic species of this deeper zone. Inversely, some Mullidae (*Mulloides spp., Parupaeneus porphyreus*), Pomacanthidae, some Labridae (*Gomphosus varius, Thalassoma amblycephalum*), Scaridae (*Scarus globiceps*) and Acanthuridae (*Acanthurus nigroris, Zebrasoma veliferum*) were not inventoried deeper than 5 m.

Density and biomass : For the whole community, there is no significant difference in mean fish density and biomass between 5 m and 15 m in the Tikehau lagoon (Table 7). However, most species or families are not uniformly distributed with depth : Scaridae and Acanthuridae densities are greater on the inner reef flat and on the top of pinnacles, and decrease with depth (Harmelin-Vivien, 1984). Similarly, Labridae are more numerous near the surface than at 15 m. Conversely, the density of Lutjanidae, Gobiidae and some Pomacentridae, like *Pomacentrus pavo*, are higher at 15 m (Morize *et al.*, 1990).

Table 7 : Mean density and mean biomass of reef fishes estimated from visual census according to depth (number of replicates n=8).

	Density Nd indiv. 100 m^{-2}		Biomass g 100 m^{-2}	
	-5 m	-15 m	-5 m	-15 m
mean	413.5	318.0	11465.6	10236.0
SD	365.5	195.0	10236.0	10109.6

Age structures : The average density of larger fishes on the whole fish community is more important between a depth of 3 to 5 m (Fig. 6). It decreases with depth and on reef flats (Harmelin-vivien, 1984 ; Morize *et al.*, 1990). The average density of juvenile fish is in turn more important at 15 m deep than at 5 m.

Meanwhile, distribution of length classes with depth differs among families. The highest densities of juveniles of Scaridae and Acanthuridae were observed in shallow waters (0-2 m) (Table 8). Conversely, juveniles of Lutjanidae, Labridae and Pomacentridae are more numerous between 10 and 15 m depth.

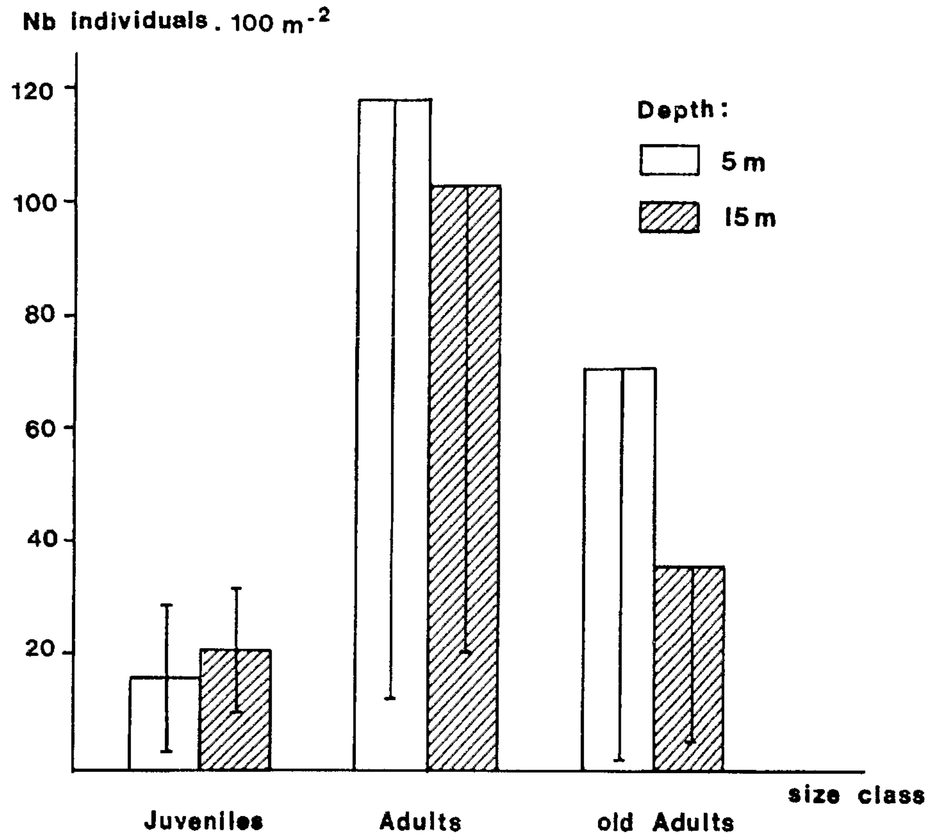

Fig. 6 : Mean demographic structure of fish community at two depths (5 and 15 m) around pinnacle reefs of Tikehau lagoon.

Table 8 : Mean density of juvenile parrotfishes (Scaridae) and juvenile surgeonfishes (Acanthuridae) with depth in Tikehau lagoon (number of individuals . 100 m^{-2}).

		0-2 m	3-5 m	10-15 m
Scaridae	mean	12.3	9.6	7.2
	SD	5.4	8.3	5.6
Acanthuridae	mean	2.9	0.4	0.2
	SD	1.5	0.9	0.2

Comparison with other Tuamotu atolls

The fish communities of atoll lagoons were studied by different authors with a different sampling design in five other Tuamotu atolls, Takapoto, Scilly, Mataiva, Fangataufa and Mururoa (Table 9). Each of these lagoonal communities differs somehow from the other, either by its specific composition or by its average density and biomass, whereas the outer reef slopes look much alike (Galzin, 1987).

Table 9 : Comparison of lagoon fish communities associated with coral formations of six Tuamotu atolls : total number of species and mean density of individuals.

Atoll	Number of fish species	Depth (m)	Density (nb indiv 100 m-2)		reference
			mean	range	
Takapoto	170	0-20	-	-	1
Scilly	180	0-30	-	-	2
Tikehau	161	3-5	414	102-1274	3
		10-15	318	104-612	3
Mataiva	157	0-3	50	3-125	4
Fangataufa	128	0.3	164	54-275	5
Mururoa	230	12	188	56-531	6

References :

1 . Bagnis, Galzin and Bennett, 1979 (28 sites in lagoon, 16 in hoa)

2 . Galzin, Bagnis and Bennett, 1983 (2 transects in lagoon, 2 transects in hoa, 4 transects on outer reef flat).

3 . Morize, Galzin, Harmelin-Vivien and Arnaudin, 1990 (8 sites in lagoon, 4 transects on inner reef flat).

4 . Galzin, Bell and Lefèvre, 1990 (8 sites in lagoon surveyed 4 times in 8 years).

5 . Galzin, unpublished data (7 sites in lagoon).

6 . Galzin, unpublished data (10 sites in lagoon, 6 sites on inner reef slope)

The observed species richness is low in the Fangataufa lagoon (128 spp.), an atoll without a natural pass. It is in turn very high in the Mururoa lagoon (230 spp.), an atoll widely opened to oceanic waters. The number of species recorded in the four other atolls are closely related in spite of differences in morphological structures : Tikehau and Mataiva have a pass whereas Takapoto and Scilly do not.

The mean fish density is very low in the lagoon of Mataiva (Table 9) ; this phenomenon can be explained by a distrophic crisis that seems to affect this atoll (Galzin *et al.*, 1990). On the other hand the mean density of fish is higher in the Tikehau lagoon, in spite of a considerable exploitation of fish stock. At a 12 m depth, the density of fish is lower at Mururoa than at Tikehau. However, the average length of fish is much larger at Mururoa where there is no fishery. The average biomass of fish is probably the same in these two lagoons.

Conclusion

Only one fish community is observed around coral formations (pinnacles) in the lagoon of Tikehau. The mean fish density and biomass do not vary with depth, although the species richness is lower at 15 m deep than between 3 and 5 m. The highest fish densities, characterized by a great proportion of juveniles, are generally found in the northern and eastern parts of the lagoon. Mean biomass per unit area is generally the highest in the southern and particularly the western part of the lagoon, near the pass, characterized by a great proportion of large-sized fishes. The depth *vs* age structure of population relationship varies according to families or species. Juvenile densities are higher in shallow water for some families (Scaridae, Acanthuridae) or in deeper water for other families (Lutjanidae, Labridae, Pomacentridae).

Lagoon - outer slope comparison

Fish community of the outer slope of the Tikehau atoll is more diversified than the lagoonal fish community (Appendix 1). Indeed, twice as many species of fish were recorded on the outer slope as in the lagoon by visual censuses. Around Moorea island, Galzin (1987) recorded also a greater fish species richness on the outer slope than in the lagoon and on reef flats.

Among families, some fish species are more numerous on the outer slope than in the lagoon of Tikehau and vice versa. Serranidae, Cirrhitidae, Carangidae, Lutjanidae, Chaetodontidae and Balistidae species are more numerous on the outer slope (31 spp.) than in the lagoon (24 spp.) (Harmelin-Vivien, 1984). However, the mean Acanthuridae density is higher on the outer slope, whereas Scaridae density is higher in the lagoon (Table 3). Other families, like Lethrinidae and Mullidae are more diversified and their populations are much more abundant in the lagoon as compared to the outer slope.

The distribution of length class, and sex ratio may be also different into or out of the lagoon for a same species or a same family. The most juvenile Scaridae were observed in the lagoon. Immature males and females are more abundant in the lagoon, whereas ripe males are much more numerous on the outer slope (Harmelin-Vivien, 1984).

Fish communities of the outer slope and of the lagoon of the Tikehau atoll are different not only by their species richness and population density, but differ also by their age and trophic structures.

THE EXPLOITED LAGOON RESOURCE : THE FISHERY OF TIKEHAU

The fishery of Tikehau is of artisanal nature, in which fish are sought for commercial and subsistence purpose. It is based principally upon the use of a relatively simple gear : bottom-fixed fish traps. Additionally, an important proportion of fish is occasionally taken with hook and line or spear gun. The fishery of Tikehau was thoroughly studied for four years. Numerous data on the fishery yields and on the biology and behavior of the target species have been gathered in order to assess the reef fish stock for management purposes.

THE FISHERY OF TIKEHAU

The fishing gear

Traditionally, fish traps were built in shallow waters using rocks or coral boulders. Blanchet *et al.* (1985) pointed out that yields were low but satisfactory sufficient to meet the needs of the low-level human population. In the middle of the century, intensive phosphate mining on the neighboring island of Makatea created and kept a high sustained demand of fish to feed the population of workers (about 3,000 in 1962). As a result, the subsistence fishery of Tikehau developed into a commercial fishery by setting traps in more productive areas (in the vicinity of the pass), using modern building materials (wire net, iron stakes) as well as traditionnal wooden stakes. After the close-down of the mining site in 1966, fish trading logically reoriented toward the Tahiti fish market.

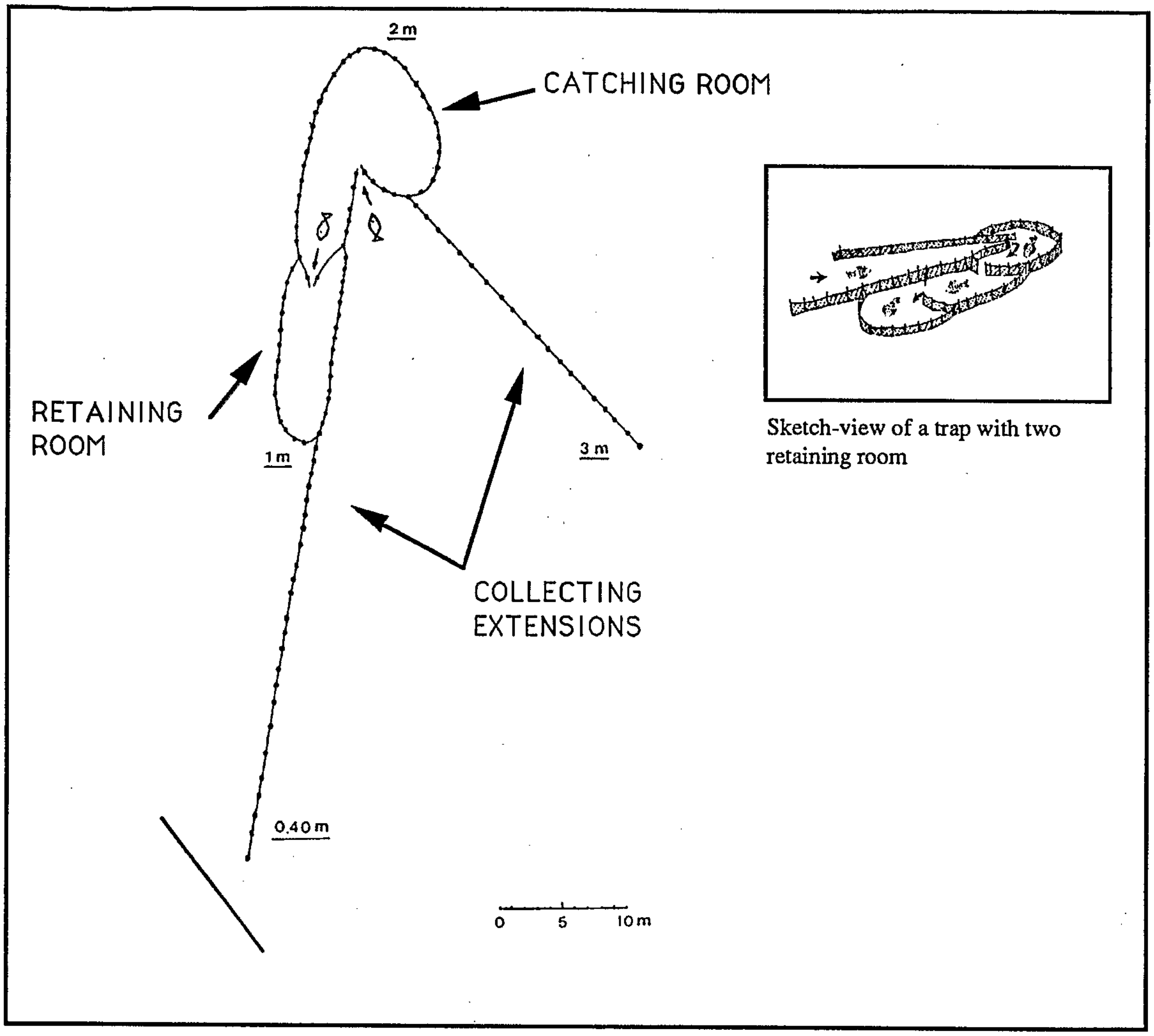

Fig 7 : Diagram of a typical Tikehau fish trap (actually fish-trap n°2, see text for more details). As shown in the framed sketch-view, there can be two retaining rooms. Dotted line : wire-net, underlined number : depth at which the part of the trap is set.

The general shape of a Tikehau fish trap is presented on Fig. 7. A fish - or a school of fish - coming across the large collecting extensions of wire net (locally termed *Rauroa*) are naturally driven toward the catching room (locally called *Aua*) in which they enter through a narrow opening. At least every day, trapped fish are herded off the trap by fishermen banging on the water surface and driven into a first retaining room (*Tipua*) where they can be held alive for a couple of weeks until they are sold. The fish are landed when the small trading vessel, able to load between 12 and 15 metric tons of catches, arrives at Tikehau (usually once a week), and subsequently shipped to Tahiti.

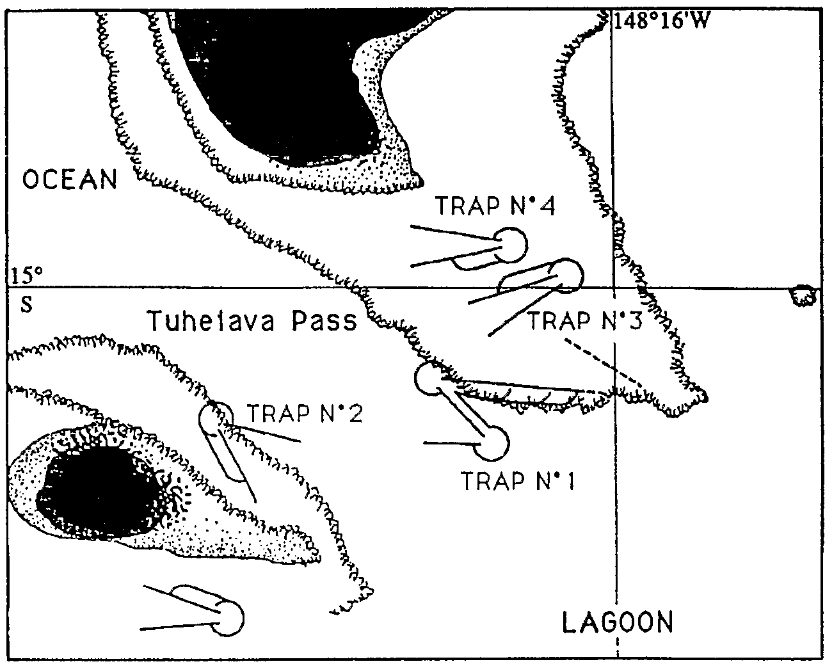

Fig. 8 : Location of fish traps in the pass of Tikehau. Trap n°1 and n°2 located close to the middle of the pass are far more efficient than the two others located lagoonward on the reef flat. Although the origin of a great part of the catches has not been accurately determined, data available indicate that trap n°1 and n°2 yield at least 78 % of the total catches.

The main fishery of Tikehau uses four fish traps, all located in or around the vicinity of the pass. Two traps (trap #1 and #2) are set quite in the middle of the pass by up to a 5 m depth (Fig. 8), and the two others traps (#3 and #4) are located lagoonward on the northern shore of the pass in shallower water (1 to 2 m). When fish is thought to be abundant in the pass and if current speed allows underwater work, a net is set across the pass between trap #1 and trap #2 and a "scare line" driving technique is used to increase catches.

Handlines and spear-guns are used mostly for a subsistence purpose. The use of these kind of gears can however significantly contribute to commercial catches when there are huge concentrations of groupers or emperors in the pass making these species readily available in large quantities. Fishermen retain a portion of their catch for their own use and sell the remainder to the trader.

Fishery yield

In Tikehau, statistical sampling of the catches was done by a local agent who noted down on a log sheet the species composition of the catch, weights sold on a species basis and the number of fish traps that provided the catch. Various information relevant to fishing such as current strength in the pass and weather were also recorded (Morize, 1984). Data were recorded from 1983 to 1987. As fishing activities are maximal by the end of the year and lower by July - August, a fishing year was defined to run from 1st of July to 30th June. Thus, the study of the fishery of Tikehau was carried out upon four fishing years : 83-84, 84-85, 85-86 and 86-87.

Morize (1984) pointed out that fishing effort is somewhat difficult to appraise but since the shape, the number and the location of the traps have not been modified during the study, the fishing effort can be assessed as the number of days with a fully efficient presence of the traps on the fishing grounds. As the level of fishing effort can be estimated to have been constant, variations of catch per unit effort (c.p.u.e.) correspond with variations of catch.

Table 10 gives an inventory list of species caught in Tikehau fish traps (comprehensive studies available in Morize, 1985 ; Caillart and Morize, 1986). Almost fifty species are likely to be trapped, covering a complete trophic spectrum of species ranging from piscivorous to herbivorous species. Although the selectivity of the gear appears to be poor, no more than fourteen species significantly contribute to the catch by accounting for about 85 % of the total landing. These fish include lutjanid *Lutjanus gibbus* and *Lutjanus fulvus*, lethrinid *Lethrinus miniatus*, carangid *Caranx melampygus, Decapterus macarellus* and *Selar crumenophthalmus*, serranid *Epinephelus microdon*, acanthurid *Naso brevirostris* and *Acanthurus xanthopterus*, mullid *Upeneus vittatus* and *Mulloides spp.*, albulid *Albula vulpes*, sphyraenid *Sphyraena forsteri*, and lastly holocentrid *Myripristis spp.*

Table 11 shows that total harvests obtained through trap fishing range from 144 metric tons to 207 metric tons a year with an average value of 165 metric tons. *Lethrinus miniatus* is the principal component of the catches with an average landing of 32 metric tons per year. It is followed by *Lutjanus gibbus, Caranx melampygus* and *Selar crumenophthalmus* representing a yearly average catch of respectively 17, 16 and 14 metric tons. These species can be dubbed target species though fishing activity is not specifically oriented toward them. Landings of the other species are less abundant ranging from 2 to 10 tons a year on the average.

Local consumption of fish is difficult to appraise since every inhabitant of the atoll meets his needs himself. Morize (1984) had estimated that about 150 kg of fish per year and per person are likely to be consumed. Given the total population of Tikehau, an additional 40 metric tons of fish would be landed every year for subsistence. Species readily available to various simple gear (handline, spear) such as groupers, surgeonfish or parrotfish are probably the principal components of this secondary fishery.

Temporal variations of the catch

Although total landings are somewhat homogeneous from year to year (average value of 165 metric tons), with a slight upward trend (Table 11), the relative species abundance in the catches varies considerably. In 1985-86, about 14 tons of *Lethrinus miniatus* have been fished whereas more than 50 tons were caught the next year with the same fishing effort applied to the stock. At the same time, *Epinephelus microdon* yield changed from 5 to about 50 tons and that of *Naso brevirostris* dropped from 19 to 2 tons. These variations are extremes but in general, only a handful of minor species are equally harvested from year to year. For most of the target species, yield can double or conversely, be reduced by half from year to year without any predictive signs. However, the great number of species available to the traps tend to buffer large fluctuations in total catches by changes in recruited population levels of individual species.

Table 10: Check-list of species (italic) caught in Tikehau fish traps with indicative figures of their diet (P : piscivorous, I : invertebrate feeders, H : herbivorous) and indications on their relative abundance in the catches (* : low, erratic catches generally less than 1 % of the total catches; ** : medium abundance, species often fished but representing less than 5 % of the annual total catches ; *** : high abundance, species regularly catched accounting for more than 5 % of the total).

Family	Species	Diet	Harvest
Holocentrid	*Sargocentron spiniferum*	I	*
	Myripristis sp.	I	**
Sphyraenid	*Sphyraena forsteri*	P	**
Siganid	*Siganus argenteus*	H	*
Serranid	*Epinephelus merra*	P,I	*
	Epinephelus microdon	P,I	***
Priacanthid	*Priacanthus cruentatus*	I	*
Carangid	*Alectis indicus*	P	*
	Carangoides orthogrammus	P	*
	Caranx ignobilis	P	*
	Caranx lugubris	P	*
	Caranx melampygus	P	***
	Caranx sp.	P	*
	Decapterus macarellus	P	**
	Elagatis bipinnulata	P	*
	Scomberoides lysan	P	*
	Selar crumenophthalmus	P	***
Lutjanid	*Lutjanus fulvus*	P,I	***
	Lutjanus gibbus	P,I	***
Mullid	*Mulloides flavolineatus*	I	***
	Mulloides vanicolensis	I	***
	Parupeneus barberinus	I	*
	Upeneus vittatus	I	**
Mugillid	*Mugil cephalus*	I	*
	Liza vaigiensis	I	*
Chanid	*Chanos chanos*	I	*
Lethrinid	*Lethrinus mahsena*	P,I	*
	Lethrinus miniatus	P,I	***
	Monotaxis grandoculis	I	**
Chaetodontid	*Chaetodon auriga*	I,H	**
Albulid	*Albula vulpes*	I	**
Kyphosid	*Kyphosus cinerascens*	H	*
Scarid	*Scarus gibbus*	H	*
	Scarus sp.	H	*
Acanthurid	*Acanthurus xanthopterus*	H	**
	Ctenochaetus striatus	H	*
	Naso brevirostris	I,H	***
	Naso lituratus	I,H	*
	Naso unicornis	I,H	*
	Naso vlamingii	I,H	*
Balistid	*Balistoides viridescens*	I	*

Table 11 : Yearly total weight landed (kg) of the fourteen main species caught by Tikehau fish traps and yearly total (kg) including all species. Mean year calculated by averaging data of the four year.

	83-84	84-85	85-86	86-87	Mean
Lethrinus miniatus	34,812	29,923	13,961	50,983	32,419
Lutjanus gibbus	8,152	11,371	24,374	24,354	17,062
Caranx melampygus	24,357	21,332	10,213	11,214	16779
Selar crumenophthalmus	8,337	14,201	17,133	16,063	13,933
Epinephelus microdon	180	810	5,183	48,902	13,786
Lutjanus fulvus	11,226	15,962	13,050	7,694	11,983
Naso brevirostris	3,036	15,299	19,374	2,293	10,000
Mulloides sp.	9,593	8,506	11,066	5,359	8,631
Albula vulpes	12,292	7,889	6,391	5,099	7,918
Upeneus vittatus	9,454	882	6,206	1,085	4,406
Sphyraena forsteri	2,835	2,835	5,085	2,954	3,427
Acanthurus xanthopterus	2,085	6,229	307	1,661	2,270
Myripristis sp.	2,475	1,559	2,931	1,851	2,204
Decapterus pinnulatus	m.d.	1,424	3,580	1,582	2,195
Other species	15,484	15,974	16,152	26,348	18,489
total	**144,318**	**154,236**	**155,006**	**207,442**	**165,250**

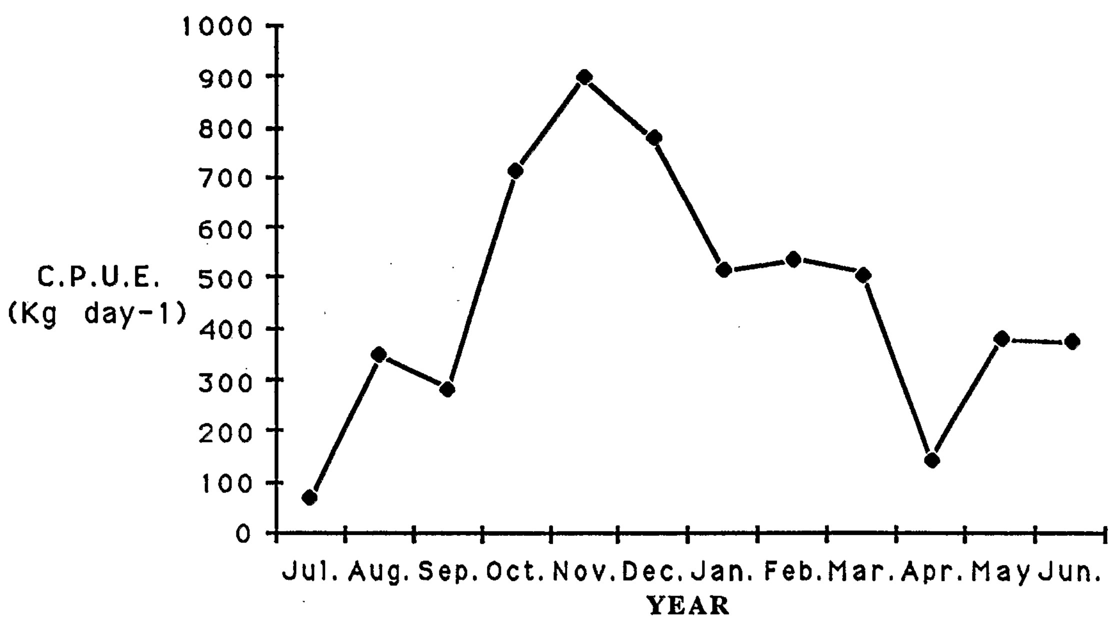

Fig.9 : Temporal variations of Catch per Unit Effort (C.P.U.E.) over an average year in the fishery of Tikehau.

Fig. 9 shows fairly wide fluctuations in the overall monthly catch per unit effort through an average year. Yield ranges from 68 kg per day in July to 898 kg per day in November. The highest productivity of the fishery occurs from October through January and the lowest from April through August. Individual yields of the overwhelming majority of the target species follow these variations but maximal c.p.u.e. of a few species are reached at a different time of the year. Noteworthy is the example of *Epinephelus microdon* in which the presence on the fishing ground peaks in April. Behind these strong seasonal fluctuations, c.p.u.e.s have a clear relationship depending on the time of the lunar month. Yields of the target species noticeably increase the week prior to the new moon and drop around the full moon.

Obviously, yields of the target species are strongly related to seasonal spawning aggregations in the vicinity of the pass. Biological sampling of landed fish carried out every month of the study confirmed that all fish trapped are adult fish, most of them having ripe gonads. Such spawning movements in other tropical areas are also well documented in numerous published observations reviewed by Johannes (1978). Thus temporal variations of c.p.u.e.s of the fishery of Tikehau would have a strong relationship with the time of the breeding period of the major components of the catches as emphasized by Caillart and Morize (1988).

BIOLOGY AND ECOLOGY OF TARGET SPECIES

The biology of the main species caught by fish traps in Tikehau has been studied. The overwhelming majority of the fish sampled was collected in the fishery landing. Additionally, some fish were collected by experimental fishing in the lagoon or on the outer slope using a handline or spear gun. The biological study presented hereafter is restricted to the seven major species : lethrinid *Lethrinus miniatus*, carangid *Caranx melampygus*, serranid *Epinephelus microdon*, lutjanids *Lutjanus gibbus* and *Lutjanus fulvus* and acanthurids *Acanthurus xanthopterus* and *Naso brevirostris*.

Reproduction

Reproductive patterns of the target species were followed throughout the year on a monthly basis. For all samples taken, gonosomatic indices (GSI) were calculated for individual males and/or females as GSI = 100xgonad wt/fish wt.

Fig. 10 summarizes the observations gathered on the time of spawning of the target species. At Tikehau, fish typically have extended breeding seasons with more or less conspicuous seasonal peaks in breeding activity. For *Lethrinus miniatus*, spawning is virtually confined from September to December with most spawning through September. The snappers *Lutjanus fulvus* and *Lutjanus gibbus* appear to spawn between October and June with two seasonal peaks that occur in November and in March. The average GSI remain however at significant levels all year round suggesting that some individual spawning may occur at an odd time. The data for *Caranx melampygus* indicates that spawning occurs throughout the year with slight peaks in July, October and February. Lastly, spawning of *Epinephelus microdon* and *Naso brevirostris* is virtually confined to a short period of three months. The records for *Epinephelus microdon* show a maximum in the period between March and May with the greatest proportion of ripe fish found in April. The surgeonfish *Naso brevirostris* spawns between December and February with most spawning in December. For this last species, the time of spawning was confirmed by two additional methods : maturity stages assigned to female fish using a five stage scale and a study of frequency distributions of egg size within ovaries over the year (Caillart, 1988). Patterns in fecundity of *Naso brevirostris* were drawn from this last meaningful method. A female would spawn about 160,000 eggs, on the average, within a breeding season. Batch fecundity averaged over the complete breeding season, about 221 eggs g^{-1} body weight, indicated that each female *N. brevirostris* must release its eggs in about three times, providing that discrete spawning occurs (Caillart, 1988).

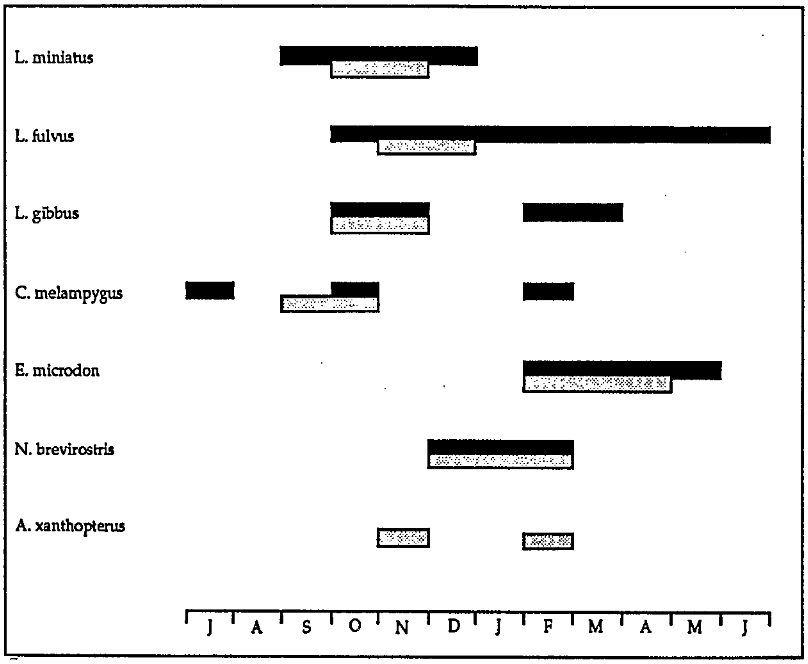

Fig. 10 : Summary of information on time of spawning of the target species of the fishery of Tikehau drawn from GSI variation study, and relationship with time of maximum catch per unit effort (cpue) over an average year (dark bars : breeding season, dotted bars : cpue). No data available to determine the breeding season of *A. xanthopterus* .

For most species, occasional individual spawning is likely to happen in all months, but maximum activity takes place in the earlier months of the year. However, the sole study of GSI variations only gives general trends and is probably insufficient to accurately provide estimates of the occurrence of breeding seasons in the tropics.

Table 12 : Fork-length at first reproduction (mm) of the target species of the fishery of Tikehau obtained from length-frequency data of the catches in fish traps. (* : length-frequency data inadequate to calculate length for both sexes ; ** : relevant data available only for females).

Species	Male	Female
Lethrinus miniatus	410	370
Lutjanus gibbus	220	210
Caranx melampygus	270	250
Epinephelus microdon	m.d.	310 **
Lutjanus fulvus	200	200
Acanthurus xanthopterus	320 *	320 *
Naso brevirostris	260	220

Length at first reproduction was determined under the assumption that the relationship between fishery yields and spawning activity does exist. The first group in the length-frequency distributions of the catch is assumed to actually represent the earlier migrating spawner group (*i.e.* : fish newly recruited to the fishery). Therefore length at first reproduction was calculated as the length in which summed length-frequency reaches 50 % of the total number of fish in the first cohort (Table 12).

Growth

Information on the age and growth of fishes is a central element in fishery management analysis. Common biological characteristics of fishes of Tikehau such as a missing seasonal growth and an extended breeding season throughout the year, have made growth rate determination difficult. Basically, three approaches to the determination of age and growth of the target species were attempted. These were 1) modal progression analysis in a time series of length-frequency histograms ; 2) tag-recapture study and 3) the aging of individuals on the basis of regular periodic (daily) markers in otoliths.

The growth rate of fishes has been described by the Von Bertalanffy Growth formula (hereafter expressed VBGF) because it fits most of the data obtained on fish growth and it can be readily incorporated into models of stock assessment. The VBGF expression is :

$$L(t) = L_\infty (1 - \exp(-k(t-t_0))$$

where L(t) is the length at time t, L_∞ is the asymptotic length, k the rate at which the fish approaches the asymptotic length and t_0 the origin of the growth curve. All length measurements presented herein are fork lengths in mm unless stated otherwise.

Table 13 : VBGF growth parameter estimations for the main species caught in the fishery of Tikehau. L_∞ is given in mm, k and t_0 on a year basis. (σ : standard deviation of relevant parameter when available, Meth : method used ; 1 : modal progression analysis of length-frequency histograms, 2 : tag-recapture study and 3 : otolith microstructure examination).

	L_∞	σ_{L_∞}	k	σ_k	t_0	σ_{t0}	Meth
Lethrinus miniatus	560	110	0.42	0.32	-0.49	1.09	1
Lutjanus gibbus	360	70	0.60	0.26	-0.59	0.83	1
Lutjanus fulvus	280	---	0.89	---	-0.05	---	3
Caranx melampygus	610	367	0.20	0.30	-1.80	1.50	1
Epinephelus microdon	610	---	0.35	---	---	---	2
Epinephelus microdon	690	301	0.31	0.03	0.22	0.08	1
Acanthurus xanthopterus	490	---	0.30	---	-0.00	---	1
Naso brevirostris (male)	380	---	0.33	---	-0.39	---	1
Naso brevirostris (female)	350	---	0.26	---	-0.80	---	1

Length-frequency histograms were examined. A random length sample of the main target species was taken serially, whenever possible. For species in which spawning season is confined to a short period (*Lethrinus miniatus, Lutjanus gibbus, Epinephelus microdon* and *Naso brevirostris*), analysis was carried out under the assumption that cohorts are separated by a time interval of one year. The VBGF parameter estimations presented in Table 13 probably lack robustness but figures generated correspond to some extent to growth parameters reviewed by Munro and Williams (1985) and can be considered as reliable. Several limitations arise on the results presented on *Caranx melampygus* and *Acanthurus xanthopterus* because breeding seasons tend to be prolonged over several months and as a result, age classes are not readily separable from one another. In that case, mode discrimination involves a large part of subjectivity.

A tag-recapture study was undertaken on grouper *Epinephelus microdon* (Morize and Caillart, 1987). Between 1984 and 1987, over one thousand tags were released all over the lagoon. Most recoveries occurred within one month of tagging and very close to the point of release but there is a tendency for at least a part of the population to seasonally migrate toward the pass since a few fish tagged in various locations of the lagoon were recaptured in the vicinity of the pass during the breeding season (*i.e.* : April). For growth rate estimation purposes, all tagged fish were measured upon release and fishermen were asked to provide information on the length of fish recaptured. Out of the thousand tags released, only 47 tags recovered met this basic requirement. Data were fitted to the VBGF using the method of Fabens. The VBGF parameter estimations are presented in Table 13.

Otoliths are structures that are commonly used to age tropical fishes (Panella, 1971). The relatively new finding that many fish deposit otolith growth increments with a daily periodicity appeared to offer a method of assessing age and growth with greater accuracy than was previously possible through other classical methods. Otolith microstructures of the target species of the fishery of Tikehau were examined (Caillart *et al.*, 1986 ; Caillart, 1988) for *Lethrinus miniatus, Lutjanus gibbus, Caranx melampygus* and *Naso brevirostris.* Ages determinated through increment counts appeared to be obviously underestimated although the actual age-increment discrepancy has not been measured. Tetracycline injected into adult *Epinephelus microdon* reared for more than one year was used to verify the periodicity of increment deposition (Caillart and Morize, 1989). For this species held in captivity, one ring was laid down every two days on an average. If this result applies to *Epinephelus microdon* in their natural environment, aging fishes under the assumption that otolith increments are daily, would have lead to underestimate the actual age by a factor of two.

In spite of all the limitations raised by the foregoing discussion, growth parameters of *Lutjanus fulvus* were calculated by fitting the VBGF to the results of otolith increment counts because either the length-frequency histograms method or the tag-recapture operation failed to give results (Table 13).

Table 14 : Length (in mm) at age (in year) of the target species of the fishery of Tikehau during the exploited phase (data backcalculated with VBGF growth parameters presented in table 13). (*) : Data backcalculated with the tag-recapture VBGF, (**) : Data backcalculated with the modal progression analysis VBGF.

Age	*L. miniatus*	*L. gibbus*	*L. fulvus*	*C. melampygus*	*E. microdon* (*)	*E. microdon* (**)	*A. xanthopterus*	*N. brevirostris* male	*N. brevirostris* female
1		221		262					
1.5		257	210	295	249				
2	363	284	235	325	307	293			
2.5	400	304	251	352	356	350		234	
3	431			376	397	399		256	220
3.5	455				431	440		275	236
4	475				460	476	342	291	250
4.5	491				484		363	304	262
5	504				504		381	316	273
5.5	515						396	326	282
6							409		
6.5							420		
7							430		
7.5							438		

Lengths at age back calculated from the VBGF growth parameters are presented in Table 14. Only the portion of the growth curve covering the range of data used to establish the predictive equation was taken into account. Since this range of data corresponds with the exploited phase of the fishes, Table 14 gives insight into the duration of the phase. Certain patterns emerge pertaining to the main species and can be summarized as follows : the duration of the exploited phase is generally short ranging from three years (*Naso brevirostris, Caranx melampygus*) to four years (*Lethrinus miniatus, Epinephelus microdon* and *Acanthurus xanthopterus*). In the case of lutjanids, the vulnerability to fishing gear appears to last two years. Data furthermore suggest that fishes are fully recruited to the fishery at an average age of three years for acanthurids, and two years for the others. It is most likely that fishes disappear from the fishing ground due to a dramatic mortality rate since experimental fishing carried out in various locations of the lagoon and off the reef yielded a very few fish beyond the maximal size recorded in the catches. *Caranx melampygus* is however an exception. The adult population of this species shifts later in its life-cycle toward the pelagic environment of the outer slope, out of the reach of fishing gears.

Length-weight relationships

The relation of weight (W in g) to the fork length (Lf in mm) was calculated for the seven target species. The parameters a and b of the formula :

$$W = aL^b$$

are listed in Table 15 (Morize, unpublished data). For all species under investigation, samples of a few hundred fish taken in the catches were used to derive the regression equations. Correlation coefficients r obtained ranged from 0.95 to 0.99.

ASSESSMENT OF THE FISHERY OF TIKEHAU

The problem of stock assessment in the fishery of Tikehau mostly relates to the fact that it is based upon at least fourteen species in which none of them is overwhelmingly dominant. Given the set of data obtained on the fishery (catch statistics, common biological parameters of individual species), two techniques are available for appraising potential harvests. Firstly, assessment can be based upon a comparison with known harvests per unit area taken by fisheries of a similar environment. Secondly, analytical models requiring reliable estimates of either biological or fishery parameters can be used in order to model the response of the stock to exploitation.

Table 15 : Length-weight relationship for the main species caught in Tikehau fish-traps (a and b, parameters of the equation $W=aL^b$ where W = weight in g, L = fork length in mm).

	a ($.10^{-5}$)	b
Lethrinus miniatus	3.4	2.8
Lutjanus gibbus	2.1	3.0
Lutjanus fulvus	11.0	2.8
Caranx melampygus	6.4	2.8
Epinephelus microdon	0.5	3.2
Acanthurus xanthopterus	9.3	2.8
Naso brevirostris	3.8	2.8

Yield per unit area

On the average, 200 metric tons of finfishes per year are caught in the main fishery of Tikehau. Additionally, 40 metric tons are taken for subsistence and another 40 tons are fished by occasional fishermen for commercial purposes (Morize, 1984 ; Morize, 1985). That is, the fishery of Tikehau produces an average of 280 tons per year (table 16). The area covered by the lagoon of the Tikehau atoll is about 420 km^2 and the annual harvest per unit area of 0.7 tons . km^{-2}. Marshall (1980) pointed out that a finfish harvest of 3 to 5 tons . km^{-2} may be upheld as a generalization for the potential fishery yields of coral reefs and adjacent shallow water environments. Although records presented in Table 16 fall far below the suggested potential, data are somewhat homogeneous, ranging from 0.6 tons . km^{-2} in the fishery of Ontong Java to 1.3 tons . km^{-2} in the fishery of Mataiva with the noticeable exception of Rangiroa where fishery harvests reach only 0,2 tons . km^{-2}. However a limitation arises to permit the comparison of the different harvests per unit area recorded.

Table 16 : Harvests per unit area for a selection of exploited coral atolls (for the Tuamotu coral atolls, groups included in catch statistics are only finfishes. For Kapingamarangi and Ontong Java, composition of the catches is unknown),

	Total catch (metric tons)	Lagoon area (square kilometers)	Harvest per unit area (Tons/km2)	Ref.
Kapingamarangi (Caroline islands)	280	400	0.7	1
Ontong Java (Solomon islands)	122	79	0.6	2
Rangiroa (Tuamotu)	350	1600	0.2	3
Kaukura (Tuamotu)	500	500	1.0	3
Mataiva (Tuamotu)	63	50	1.3	3
Tikehau (Tuamotu)	280	420	0.7	4

Reference

1- Stevenson and Marshall (1974) ; 2 - Munro and Williams (1985)

3 - Galzin *et al.* (1989) ; 4 - Caillart (1988)

As a reef fishery is generally a patchwork of coral reef patches (which are highly productive) and sandy bottoms (which is not that productive) ; the yield per unit area can very much depend upon the area and the percentage of area that is actually covered by hard coral substrate. Some fishery records like these of Rangiroa cover a large area, only part of which is actually covered by coral, whereas other records of fish yield apply to very small areas like Mataiva or Ontong Java where a hard substrate coverage is much greater. Moreover the potential fish yield from a given area cannot be inferred from sole catch records without even a rough reference to the fishing effort. In Rangiroa and Mataiva, the level of exploitation applied to the stock is low with regard to fishing effort in Tikehau or Kaukura.

Information on yield assessment and management in the fishery of Tikehau can be drawn from the comparison with the neighboring atoll of Kaukura. These two atolls have a comparable surface and morphology. In Tikehau, the fishery is based on bottom fixed fish traps all located in the vicinity of the pass. Yield relies on the behavior of species most prone to migrate for spawning. These fish are primarily carnivorous species as indicated by the specific composition of the catches. In Kaukura, bottom fixed fish traps are set not only in the vicinity of the pass but also all around the atoll rim, on the shallow inner reef flat.

Species caught are for a great percentage non territorial herbivorous species which wander to seek for food (Stein, *in* Galzin *et al.*, 1989). So, higher yields in Tikehau could probably be achieved by setting traps in various locations of the lagoon which in turn would probably exploit the food chain more efficiently. The total harvest of the Tikehau fishery could also be increased by diversifying the fishing gears, and setting classical bottom free fish traps around the numerous coral knolls scattered in the lagoon. Although we believe that it would be quite impossible to reach the potential yield suggested by Marshall (1980) (*i.e.* : 3 to 5 tons . km^{-2}), it would be at least possible to attain a harvest of 1 ton . km^{-2} recorded at Kaukura. This would result in a substantial increase of the catch of about 140 tons.

If this simple but nevertheless useful approach can be used to set a likely estimate of the potential fish yield of Tikehau, it is obvious that more thorough evaluations must be undertaken in order to focus management issues not only on optimum yield but also on preferred species.

Analytical assessment models

Analytical assessment models have been widely used in temperate water fisheries but they have been applied to coral reef fisheries in a limited number of cases. If these models cannot take into account the numerous and intricate relationships between all the components of the multi-species fishery, they are nevertheless of great value in giving an insight into the state of the fishery. There were two means used to provide estimates of the status of the fishery of Tikehau. One mean was a length converted catch-curve analysis (*in* Ricker, 1980). The other mean was to use yield per recruit estimates in a length structured model in which fishing mortality vector (F) is obtained from a length cohort analysis (Jones, 1974).

No adequate data sets on Tikehau fish stocks exist for an accurate determination of natural mortality (M). This parameter was estimated by two empirical formulas (Hoenig, 1984 and Pauly, 1980) that provided rough estimates of the value of M (Table 17). The real value of M is expected to lie in between these two estimates.

The specific exploitation rate E is given by :

$$E = \frac{F}{F+M}$$

where F is the fishing mortality. E estimated through length-converted catch curve analysis is found greater than 0.5 for *Lutjanus gibbus, L. fulvus, Caranx melampygus* and *Epinephelus microdon*, and less than 0.5 for *Lethrinus miniatus, Acanthurus xanthopterus* and *Naso brevirostris*. Gulland (1973) pointed out that a value of 0.5 of the exploitation rate can be roughly set as a limit below which a fish stock is lightly exploited and over which over-fishing may occur.

Table 17 : A range of values of natural mortality M (yr^{-1}) chosen for Tikehau target species. Mmin is given by Hoenig (1984) empirical formula, Mmax by Pauly (1980) equation.

Species	M min	M max
Lethrinus miniatus	0.43	0.66
Lutjanus gibbus	0.57	0.96
Lutjanus fulvus	0.46	0.88
Caranx melampygus	0.43	0.72
Epinephelus microdon	0.61	0.88
Acanthurus xanthopterus	0.43	0.72
Naso brevirostris	0.60	0.80

Yield per recruit model results listed in Table 18 are strongly related to the estimate of M chosen and have considerable different responses to F variations with respect to the species under investigation. For *Lethrinus miniatus, Acanthurus xanthopterus* and *Naso brevirostris,* a substantial increase of yield per recruit (more than 10% on the average) can be achieved if the fishing mortality vector is 50% or 100% higher. The snapper *Lutjanus gibbus* and *L. fulvus* yield per recruit estimates appears to be poorly increased (5% on the average) when fishing mortality vector increases. Lastly, yield per recruit estimates of *Epinephelus microdon* and *Caranx melampygus* do not significantly increase and can even decrease if an attempt to increase F is made.

Table 18 : Range of yield per recruit variations of the target species of Tikehau fishery (in % of present yield per recruit) in response to variations of fishing effort (μF : Fishing mortality coefficient, lowest value of yield per recruit correspond to the highest natural mortality figure).

Species	μF = 0.5	μF = 1	μF = 1.5	μF = 2
Lethrinus miniatus	-30 / -20	0	+20 / +8	+27 / +10
Lutjanus gibbus	-30 / -15	0	+12 / +3	+20 / +3
Lutjanus fulvus	-25 / -12	0	+10 / +2	+15 / +2
Caranx melampygus	-25 / -8	0	+10 / 0	+20 / -1
Epinephelus microdon	-15 / -6	0	+6 / -1	+8 / -2
Acanthurus xanthopterus	-40 / -30	0	+20 / +10	+40 / +20
Naso brevirostris		0	+19 / +26	+32 / +20

According to the foregoing results, the Tikehau fishery appears to be well fitted to carnivorous fish stock exploitation. The evidence from these analytical models suggests that Tikehau fish stocks are being fished at or near the Maximum Sustainable Yield (MSY). No major change in the direction of the present trap fishing strategy (increases or decreases in effort) is justifiable, although yield per recruit of certain species (emperors, surgeonfishes and snappers to a lesser extent) could be improved by a moderate increase of fishing effort. And it is unlikely that the grouper and jack fisheries could tolerate a heavy effort increase.

Higher harvests of carnivorous species could probably be achieved by using more selective fishing gears. For instance, the abundant stock of *Lethrinus miniatus* could provide substantial additional catches if handlines were more heavily used when the fish are abundant in the pass and hence, readily available. It has been mentioned that the herbivorous fish stock at Tikehau is very lightly exploited. The principal management issue would probably be to orient fishing pressure toward this part of the resource by setting traps on shallow areas all around the atoll rim where availability of herbivorous species is greater.

CONCLUSION

A total of 276 species belonging to 47 families have been recorded on the Tikehau atoll (Appendix 1). The real number of species is obviously under-estimated since rotenone poisonning was not used in all sites, and only one transect was regularly studied on the outer slope. The number of species censused in the lagoon was 167, 39 in the pass and 180 on the outer slope.

Only 17 species (6.2% of the total richness species) were encountered in the three environments : *Sargocentron spiniferum, Epinephelus merra, Epinephelus microdon, Caranx melampygus, Lutjanus gibbus, Lutjanus fulvus, Lethrinus miniatus, Monotaxis grandoculis, Mulloides vanicolensis, Chaetodon auriga, Scarus gibbus, Acanthurus xanthopterus, Ctenochaetus striatus, Naso lituratus, Naso unicornis, Naso vlamingii* and *Balistoides viridescens.* An unusual paucity of Carcharhinidae, Synodontidae, Apogonidae, Mugilidae, Sphyraenidae, Caesionidae and Tetraodontidae was noted while fish of the families of Holocentridae, Serranidae, Carangidae, Lutjanidae, Lethrinidae, Mullidae, Chaetodontidae, Pomacanthidae, Pomacentridae, Labridae, Scaridae, Acanthuridae and Balistidae were abundant.

A key question in fishery management is the correspondence between adult stock size and the number of each new cohort reaching the mean size of capture by the fishing gear. Recruitment to the fishery is preceded by a pre-recruit phase from birth to recruitment to the ecosystem and followed by a post recruit phase consisting of a pre-exploited phase. No study of larval recruitment was carried out at Tikehau though the knowledge of this part of the life-cycle is critical for understanding the dynamics of reef fish populations. Recruitment processes in coral reef fishes are however well documented (reviews in Munro and Williams, 1985 ; Richards and Lindeman, 1987) and much of the findings can apply to Tikehau.

Most reef fishes spawn externally in the water column above hard bottom structures. Off-shore larval dispersal is thought to be an evolutionary response to intense predation pressure in the adult habitat (Johannes, 1978). Fish community studies at Tikehau suggest that, adult fishes of various species gather off or in the pass to release their offspring in oceanic water. Larvae or fertilized eggs subsequently undergo oceanic advection and diffusion and juveniles enter the lagoon through shallow channels of the eastern coast. Most coral reef fishes characteristically present a two part life-cycle ; a pelagic larval phase during which extensive dispersal is possible and a relatively site-attached phase during in which movements are somewhat restricted. According to relevant data presented by Brothers *et al.* (1983), the duration of the pelagic stage of the main families exploited in Tikehau is estimated to range from about one month (Lethrinidae, Lutjanidae) to over three months in the case of *Naso sp.* (Acanthuridae). Absolute survivalship during planktonic life stages is a function of highly complex interactions among predation, oceanographic processes, growth and food availability. Mortality rates through this phase are subject to tremendous variations which considerably affect the availability of recruits to the atoll fish community. Although of a lesser order of magnitude, additional losses in subsequent post-settlement life due to innapropriate habitat and predation can in turn impact the number of recruit to the fishery. Variations in recruitment can also contribute to significant shifts in species composition within the exploited stock as it does occur in Tikehau.

Knowledge on the extent of fish population exchange between islands through the pelagic phase is of particular importance to effectively manage a fishery. The management strategy will vary greatly depending on the extent to which recruitment to the atoll is derived from within the fished population or is spawned outside the system. Due to the close-spacing pattern of the atoll of the Tuamotu archipelago, it might be expected that the stocks of species having a long pelagic larval stage occurring in a given atoll may be recruited from parent stocks living in areas further upstream. If the exploited stock of Tikehau is recruited largely from atolls located upstream like Rangiroa and Arutua, regulations for the conservation of the spawning stock will be ineffective and will be of benefit only to islands lying downstream (Mataiva). We have yet insufficient information to determine any general patterns, but there is an urgent need for further studies aiming to determine the potential limits of stock exchanges between atolls and the unit stock of a given species.

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Literature cited

BAGNIS (R.), GALZIN (R.), BENNETT (J.) - 1979 - Poissons de Takapoto. **J. Soc. Océanistes,** 62 (35) : 69-74

BARANS (C.A.), BORTONE (S.A.), Eds. - 1983 - The visual assessment of fish populations in the Southeastern United States, **1982 Workshop, South Carolina Sea Grant Consortium, Techn. Rep.,** 1 : 52 p

BELL (J.), GALZIN (R.) - 1984 - Influence of live coral cover on coral reef fish communities. **Mar. Ecol. Prog. Ser.,** 15 : 265-274

BLANCHET (G.), CAILLAUD (L.), PAOAAFAITE (J.) - 1985 - Un aspect de la pêche artisanale en Polynésie Française, les pièges à poissons de Tikehau. **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 25 : 116 p

BROTHERS (E.B.), WILLIAMS (D.McB.), SALE (P.F.) - 1983 - Length of larval life in twelve families of fishes at "One tree lagoon", Great Barrier Reef, Australia. **Mar. Biol.,** 76 : 319-324

CAILLART (B.) - 1988 - Etude d'une pêcherie artisanale de l'archipel des Tuamotu (Polynésie Française). Biologie, ethologie et dynamique des populations d'une espèce caractéristique : *Naso brevirostris* (Poissons-Acanthuridae). **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 38 : 235 p

CAILLART (B.), FRANC DE FERRIERE (M.), MORIZE (E.) - 1986 - Croissance de deux espèces du lagon, *Lethrinus miniatus* (Schneider) et *Lutjanus fulvus* (Schneider), évaluée par la lecture des otolithes. *in* : Contribution à l'étude de l'atoll de Tikehau, III. **ORSTOM Tahiti, Notes et doc. Océanogr.,** 30 : 1-44

CAILLART (B.), MORIZE (E.) - 1986 - La production de la pêcherie de l'atoll en 1985. *In* : Contribution à l'étude de l'atoll de Tikehau, III. **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 30 : 45-71

CAILLART (B.), MORIZE (E.) - 1988 - Biology and reproduction strategy of *Naso brevirostris* and relationships with fishery yields. **Workshop on Pacific Inshore Fishery Resource, Noumea, New Caledonia, March 1988 :** 10 p

CAILLART (B.), MORIZE (E.) - 1989 - Etude du rythme de dépôt des microstries sur les otolithes d'un serranidae tropical, *Epinephelus microdon* (Bleeker) à l'aide d'un marqueur fluorescent : l'oxytetracycline. **Aquat. Living Resour.,** 2 : 255-261

FABENS (A.J.) - 1965 - Properties and fitting of the Von Bertalanffy growth curve. **Growth,** 29 : 265-289

FAURE (G.), LABOUTE (P.) - 1984 - Formations récifales de Tikehau : I - Définition des unités récifales et distribution des principaux peuplements de Scléractiniaires.*In* : L'atoll de Tikehau (Archipel des Tuamotu, Polynésie Française), premiers résultats. **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 22 : 108-136

GALZIN (R.) - 1985 - Ecologie des poissons récifaux de Polynésie française. **Thèse Doc. ès-Sciences, Univ. Montpellier,** 195 p

GALZIN (R.) - 1987 - Structure of fish communities of French Polynesian coral reefs. 1- Spatial scales. **Mar. Ecol. Prog. Ser.,** 41 : 129-136

GALZIN (R.), BAGNIS (R.), BENNETT (J.) - 1983 - Premier inventaire et distribution de la faune ichtyologique de l'atoll de Scilly (Polynésie française). **J. Soc. Océanistes,** 77 (34) : 17-28

GALZIN (R.), BELL (J.D)., LEFEVRE (A). - 1990 - Etude interannuelle du peuplement ichtyologique du lagon de l'atoll de Mataiva en Polynésie française. **Cybium,** 14 (4) : 313-322

GALZIN (R.), MORIZE (E.), STEIN (A.), CONTE (E.) - 1989 - Dégradations naturelles et anthropiques en zones côtières intertropicales et répercussions possibles sur l'économie des pêches : le cas des récifs coralliens. **Action CORDET, Rapport antenne EPHE-Museum, 1989, RA 32** : 135 p

GBRMPA - 1978 - Great Barrier Reef Marine Park Authority workshop on reef fish assessment and monitoring. **Workshop Series 1, Heron Island, Australia :** 64 p

GULLAND (J.A.) - 1973 - Fish stock assessment. A manual of basic methods. J. Wiley & Sons, Chichester : 223 p

HARMELIN-VIVIEN (M.L.) - 1984 - Distribution quantitative des poissons herbivores dans les formations coralliennes de Tikehau (Polynésie française). *In* : L'atoll de Tikehau (Archipel des Tuamotu, Polynésie Française), premiers résultats. **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 22 : 81-107

HARMELIN-VIVIEN (M.L.) - 1985 - Tikehau atoll, Tuamotu archipelago. **Proceeding of the Fifth International Coral Reef Congress, Tahiti,** 1985, 1 : 211-266

HARMELIN-VIVIEN (M.L.), LABOUTE (P.) - 1986 - Catastrophic impact of hurricanes on atoll outer reef slopes in the Tuamotu (French Polynesia). **Coral Reefs,** 5 : 55-62

HARMELIN-VIVIEN (M.L.) and al. (11 authors) - 1985 - Evaluation visuelle des peuplements et populations de poissons. Méthodes et problèmes. **Rev. Ecol. (Terre Vie),** 40 : 467-539

HOENIG (J.M.) - 1984 - Empirical use of longevity data to estimate mortality rates. **Fish. Bull.,** 82 (1) : 898-902

JOHANNES (R.E.) - 1978 - Reproductive strategies of coastal marine fishes in the tropics. **Env. Biol. Fish.,** 3 (1) : 65-84

JONES (R.) - 1974 - Assessing the long term effects of changes in fishing effort and mesh size from length composition data. **CIEM, CM 1974/F** : 33 p

MARSHALL (N.) - 1980 - Fishery yields of coral reefs and adjacent shallow-water environments. *In* : Stock assessment for tropical fisheries, ROEDEL (P.) & SAILA (S.B.) eds, **Proc. Int. Work. held in Kingston (P.M.)** : 103-109

MORIZE (E.) - 1984 - Contribution à l'étude d'une pêcherie artisanale et de la dynamique des populations des principales espèces exploitées. *In* : L'atoll de Tikehau (Archipel des Tuamotu, Polynésie Française), premiers résultats. **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 22 : 35-80

MORIZE (E.) - 1985 - Etude d'une pêcherie artisanale de l'atoll de Tikehau (Archipel des Tuamotu, Polynésie Française). **Proceeding of the Fifth International Coral Reef Congress, Tahiti, 1985,** 5 : 501-506

MORIZE (E.), CAILLART (B.) - 1987 - Modélisation de la croissance de *Epinephelus microdon* (Bleeker) obtenue à partir de marquage. *In* : Contribution à l'étude de l'atoll de Tikehau : IV. **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 35 : 101-114

MORIZE (E.), GALZIN (R.), HARMELIN-VIVIEN (M.L.), ARNAUDIN (H.) - 1990 - Organisation spatiale du peuplement ichtyologique dans le lagon de l'atoll de Tikehau (Polynésie française). **ORSTOM Tahiti, Notes et Doc. Océanogr.,** 40 : 1-44

MUNRO (J.L.), WILLIAMS (D.McB.) - 1985 - Assessment and management of coral reef fisheries. **Proceeding of the Fifth International Coral Reef Congress, Tahiti, 1985,** 4 : 543-581

PANNELLA (G.) - 1971 - Fish otoliths : daily growth layers and periodical patterns. **Science,** 173 : 1124-1127

PAULY (D.) - 1980 - On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. **J. cons. Cons. Int. Explor. Mer,** 39 : 175-192

RICHARDS (W.J.), LINDEMAN (K.C.) - 1987 - Recruitment dynamics of reef fishes : planktonic processes, settlement and demersal ecologies, and fishery analysis. **Bull. Mar. Sci.,** 41 (2) : 392-410

RICKER (W.E.) - 1980 - Calcul et interprétation des statistiques biologiques des populations de poissons. **Bull. Res. Bd. Can.,** 191 F : 409 p

ST. JOHN (J.), RUSS (G.R.), GLADSTONE (W.) - 1990 - Accuracy and bias of visual estimates of numbers, size structure and biomass of a coral reef fish. **Mar. Ecol. Prog. Ser.,** 64 : 253 - 262

STEVENSON (D.K.), MARSHALL (N.) - 1974 - Generalisation on the fisheries potential of coral reefs and adjacent shallow water environments. **Proceeding of the Second International Coral Reef Symposium, Manilla,** 1 : 147-156

Appendix 1 : Check-list of the fishes of Tikehau atoll (L : lagoon, P : pass, O : ocean)

CARCHARHINIDAE			
Carcharhinus melanopterus (Quoy et Gaimard, 1824)	L		
ALBULIDAE			
Albula vulpes (Linné, 1758)		P	
CHANIDAE			
Chanos chanos (Forsskäl, 1775)		P	
MURAENIDAE			
Echidna polyzona (Richardson, 1844)	L		
Gymnothorax buroensis (Bleeker, 1857)	L		
Gymnothorax fimbriatus (Bennett, 1831)	L		
Gymnothorax javanicus (Bleeker, 1859)	L		O
Gymnothorax margaritophorus Bleeker, 1864	L		
Gymnothorax zonipectis Seale, 1906	L		
*Gymnothorax sp.*3	L		
Gymnothorax sp. 16	L		
Gymnothorax sp. 18	L		
Uropterygius xanthopterus Bleeker, 1859	L		
CONGRIDAE			
Conger cinereus Rüppell, 1828	L		
OPHICHTHIDAE			
Leiuranus semicinctus (Lay and Bennet, 1839)	L		
Muraenichthys macropterus Bleeker, 1857	L		
ATHERINIDAE			
Atherinidae sp.	L		
SYNODONTIDAE			
Saurida gracilis (Quoy et Gaimard, 1824)	L		
Synodus variegatus (Lacepède, 1803)	L		
ANTENNARIIDAE			
Antennarius sp. (juv.)	L		
OPHIDIIDAE			
Brotula multibarbata Temminck and Schlegel, 1846	L		
HEMIRAMPHIDAE			
Hyporhamphus acutus (Günther, 1871)			O
HOLOCENTRIDAE			
Myripristis kuntee Valenciennes, 1831	L		O
Myripristis murdjan Forsskäl, 1775	L		O
Myripristis pralinia Cuvier, 1829			O
Myripristis violacea Bleeker, 1851	L		
Myripristis sp.	L	P	O
Neoniphon argenteus (Valenciennes, 1831)	L		
Neoniphon opercularis (Valenciennes, 1831)	L		O
Neoniphon sammara (Forsskäl, 1775)	L		O
Sargocentron caudimaculatum (Rüppell, 1838)			O
Sargocentron diadema (Lacepède, 1802)	L		
Sargocentron microstoma (Günther, 1859)	L		O
Sargocentron spiniferum (Forsskäl, 1775)	L	P	O
AULOSTOMIDAE			
Aulostomus chinensis (Linné, 1766)			O
FISTULARIIDAE			
Fistularia commersonii (Rüppell, 1838)	L		O
SYNGNATHIDAE			
Corythoichthys flavofasciatus Rüppel, 1838	L		
SCORPAENIDAE			
Scorpaenodes parvipinnis (Garrett, 1863)	L		
SERRANIDAE			
Anthias lori Randall and Lubbock, 1976			O
Anthias olivaceus Randall and Mc Cosker, 1892			O
Anthias pascalus (Jordan and Tanaka, 1927)			O
Anthias squamipinnis Peters, 1855			O
Cephalopholis argus (Bloch and Schneider, 1801)	L		O
Cephalopholis urodelus (Bloch and Schneider, 1801)			O
Epinephelus fasciatus (Forsskäl, 1775)			O
Epinephelus hexagonatus (Bloch and Schneider, 1801)	L		O
Epinephelus merra Bloch, 1793	L	P	O
Epinephelus microdon (Bleeker, 1856)	L	P	O
Epinephelus socialis (Günther, 1873)			O
Epinephelus sp.			O

Appendix 1 (cont'd)

Gracila albomarginata (Fowler and Bean, 1930)			O
Grammistes sexlineatus (Thunberg, 1792)	L		
Pseudogramma bilinearis (Schultz, 1943)	L		
Pseudogramma polyacantha (Bleeker, 1856)	L		
Variola louti (Forsskäl, 1775)			O
KUHLIIDAE			
Kuhlia marginata (Cuvier, 1829)	L		
PRIACANTHIDAE			
Priacanthus cruentatus (Lacepède, 1801)		P	O
CIRRHITIDAE			
Paracirrhites arcatus (Cuvier, 1829)			O
Paracirrhites forsteri (Bloch and Schneider, 1801)			O
Paracirrhites hemistictus (Günther, 1874)			O
APOGONIDAE			
Apogon angustatus (Smith and Radcliffe, 1911)	L		
Apogon coccineus Rüppell, 1838	L		
Apogon fraenatus Valenciennes, 1832	L		
Apogonichthys ocellatus (Weber, 1913)	L		
Cheilodipterus quinquelineatus Cuvier, 1828	L		
Fowleria aurita (Valenciennes, 1831)	L		
Fowleria marmorata (Alleyne and Macleay, 1876)	L		
Ostorhynchus savayensis (Günther, 1871)	L		
Pristiapogon snyderi Smith, 1961	L		
Pseudamia gelatinosa Smith, 1955	L		
MUGILIDAE			
Liza vaigiensis (Quoy et Gaimard, 1825)		P	
Mugil cephalus (Linné, 1758)		P	
SPHYRAENIDAE			
Sphyraena forsteri Cuvier, 1829		P	
ECHENEIDIDAE			
Echeneis naucrates Linné, 1758	L		
CARANGIDAE			
Alectis indicus (Rüppel, 1830)		P	
Carangoides orthogrammus (Jordan and Gilbert, 1881)	L	P	
Caranx ignobilis (Forsskäl, 1775)		P	O
Caranx lugubris Poey, 1860			O
Caranx melampygus (Cuvier, 1833)	L	P	O
Caranx sp.		P	
Decapterus macarellus (Valenciennes, 1833)		P	
Elagatis bipinnulata (Quoy et Gaimard, 1825)	L		O
Scomberoides lysan (Forsskäl, 1775)			
Selar crumenophthalmus (Bloch, 1793)			
LUTJANIDAE			
Aphareus furca (Lacepède, 1801)			O
Aprion virescens Valenciennes, 1830			O
Lutjanus bohar (Forsskäl, 1775)			O
Lutjanus fulvus (Bloch and Schneider, 1801)	L	P	O
Lutjanus gibbus (Forsskäl, 1775)	L	P	O
Lutjanus kasmira (Forsskäl, 1775)			O
Lutjanus monostigmus (Cuvier, 1828)	L		O
LETHRINIDAE			
Gnathodentex aureolineatus (Lacepède, 1802)	L		O
Lethrinus elongatus Valenciennes, 1830			O
Lethrinus mahsena (Forsskäl, 1775)		P	
Lethrinus miniatus Smith, 1959	L	P	O
Lethrinus variegatus Ehrenberg, 1830		P	
Lethrinus xanthochilus Klunzinger, 1870			O
Monotaxis grandoculis (Forsskäl, 1775)	L	P	O
MULLIDAE			
Mulloides flavolineatus (Lacepède, 1801)	L	P	
Mulloides vanicolensis (Valenciennes, 1831)	L	P	O
Parupeneus barberinus (Lacepède, 1801)	L	P	
Parupeneus bifasciatus (Lacepède, 1801)	L		O
Parupeneus ciliatus (Lacepède, 1801)			O
Parupeneus multifasciatus (Quoy et Gaimard, 1825)	L		O
Parupeneus porphyreus (Jenkins, 1900)	L		O
Upeneus vittatus (Forskäll, 1775)		P	

Appendix 1 (cont'd)

PEMPHERIDAE			
Pempheris oualensis Cuvier, 1831			O
KYPHOSIDAE			
Kyphosus cinerascens (Forsskäl, 1775)		P	
CHAETODONTIDAE			
Chaetodon auriga Forsskäl, 1775	L	P	O
Chaetodon bennetti Cuvier, 1831			O
Chaetodon citrinellus Cuvier, 1831	L		
Chaetodon ephippium Cuvier, 1831	L		O
Chaetodon lunula (Lacepède, 1802)	L		O
Chaetodon ornatissimus Cuvier, 1831			O
Chaetodon pelewensis Kner, 1868			O
Chaetodon quadrimaculatus Gray, 1831			O
Chaetodon reticulatus Cuvier, 1831			O
Chaetodon trifasciatus Mungo Park, 1797	L		O
Chaetodon ulietensis Cuvier, 1831	L		O
Chaetodon unimaculatus Bloch, 1787			O
Forcipiger flavissimus Jordan and Mc Gregor, 1898			O
Forcipiger longirostris (Broussonet, 1782)			O
Hemitaurichthys polylepis (Bleeker, 1857)			O
Hemitaurichthys zoster (Bennett, 1831)			O
Heniochus acuminatus (Linné, 1758)			O
Heniochus chrysostomus Cuvier, 1831			O
Heniochus monoceros Cuvier, 1831	L		O
POMACANTHIDAE			
Centropyge flavissimus (Cuvier, 1831)	L		O
Centropyge loriculus (Günther, 1874)			O
Pomacanthus imperator (Bloch, 1787)			O
Pygoplites diacanthus (Boddaert, 1772)	L		O
POMACENTRIDAE			
Abudefduf sexfasciatus (Lacepède, 1801)	L		
Abudefduf sordidus (Forsskäl, 1775)	L		
Amphiprion chrysopterus Cuvier, 1830			O
Chromis iomelas Jordan and Seale, 1906			O
Chromis margaritifer Fowler, 1946			O
Chromis vanderbilti (Fowler, 1941)			O
Chromis viridis (Cuvier, 1830)	L		
Chromis xanthura (Bleeker, 1854)			O
Chrysiptera glauca (Cuvier, 1830)	L		
Chrysiptera leucopoma (Lesson, 1830)	L		
Dascyllus aruanus (Linné, 1758)	L		
Dascyllus flavicaudus Randall et Allen, 1977			O
Dascyllus trimaculatus (Rüppell, 1828)			O
Plectroglyphidodon dickii (Liénard, 1839)			O
Plectroglyphidodon johnstonianus Fowler and Ball, 1924			O
Pomacentrus fuscidorsalis Allen and Randall, 1974			O
Pomacentrus pavo (Bloch, 1787)	L		
Stegastes albofasciatus (Schlegel and Müller, 1839-44)	L		
Stegastes aureus (Fowler, 1927)			O
Stegastes nigricans (Lacepède, 1803)	L		
LABRIDAE			
Anampses caeruleopunctatus Rüppel, 1828			O
Bodianus axillaris (Bennett, 1831)			O
Bodianus loxozonus (Snyder, 1908)			O
Cheilinus chlorourus (Bloch, 1791)	L		O
Cheilinus trilobatus (Lacepède, 1801)	L		O
Cheilinus undulatus Rüppel, 1835	L		O
Cirrhilabrus exquisitus Smith, 1957	L		
Cirrhilabrus scottorum Randall and Pyle, 1856			O
Coris aygula Lacepède, 1801			O
Coris gaimard (Quoy et Gaimard, 1824)	L		O
Cymolutes praetextatus (Quoy et Gaimard, 1824)	L		
Epibulus insidiator (Pallas, 1770)	L		
Gomphosus varius Lacepède, 1801	L		O
Halichoeres hortulanus (Lacepède, 1801)	L		O

Appendix 1 (cont'd)

Halichoeres melasmapomus Randall, 1980			O
Halichoeres trimaculatus (Quoy et Gaimard, 1834)	L		O
Hemigymnus fasciatus (Bloch, 1792)			O
Labridae sp. (juv.)	L		
Labridae sp. 8 (juv.)	L		
Labroides bicolor Fowler and Bean, 1928			O
Labroides dimidiatus (Valenciennes, 1839)	L		O
Novaculichthys taeniourus (Lacepède, 1801)	L		O
Pseudocheilinus hexataenia (Bleeker, 1857)			O
Pseudocheilinus octotaenia Jenkins, 1900	L		O
Stethojulis bandanensis (Bleeker, 1851)	L		O
Stethojulis strigiventer Bennett, 1832	L		
Thalassoma amblycephalum (Bleeker, 1856)	L		O
Thalassoma hardwicke (Bennett, 1830)	L		
Thalassoma purpureum (Forsskäl, 1775)			O
Thalassoma quinquevittatum (Lay and Bennett, 1839)	L		O
Thalassoma trilobatum (Lacepède, 1801)			O
Wetmorella ocellata Schultz and Marshall, 1954	L		
SCARIDAE			
Calotomus carolinus (Valenciennes, 1839)			O
Cetoscarus bicolor (Rüppell, 1829)	L		O
Hipposcarus harid (Forsskäl, 1775)		P	
Hipposcarus longiceps (Valenciennes, 1839)	L		O
Leptoscarus vaigiensis (Quoy et Gaimard, 1824)			O
Scarus altipinnis Steindachner, 1879	L		O
Scarus brevifilis (Günther, 1909)			O
Scarus festivus , Valenciennes, 1840			O
Scarus forsteri (Bleeker, 1861)	L		O
Scarus frenatus Lacepède, 1802	L		O
Scarus frontalis Valenciennes, 1839			O
Scarus ghobban Forsskäl, 1775	L		O
Scarus gibbus Rüppell, 1828	L	P	O
Scarus globiceps Valenciennes, 1840	L		O
Scarus niger Forsskäl, 1775	L		O
Scarus oviceps Valenciennes, 1839	L		O
Scarus psittacus Forsskäl, 1775	L		O
Scarus rubroviolaceus Bleeker, 1849	L		O
Scarus schlegeli Bleeker, 1861	L		O
Scarus sordidus Forsskäl, 1775	L		O
Scarus sp. rayé (juv.)	L		O
Scarus sp. gris (juv.)	L		O
Scarus sp. marron (juv.)	L		O
Scarus sp. parc		P	
Scarus sp. vert (juv.)			O
BLENNIIDAE			
Enchelyurus ater (Günther, 1877)	L		
Istiblennius periophthalmus (Valenciennes, 1836)	L		
Plagiotremus tapeinosoma (Bleeker, 1857)	L		
CALLIONYMIDAE			
Callionymus simplicicornis Valenciennes, 1837	L		
GOBIIDAE			
Amblygobius phalaena (Valenciennes, 1837)	L		
Asterropteryx ensiferus (Bleeker, 1874)	L		
Asterropteryx semipunctatus (Rüppell, 1830)	L		
Callogobius sclateri (Steindachner, 1880)	L		
Eviota afelei Jordan and Seale, 1906	L		
Eviota sp.	L		
Fusigobius neophytus (Günther, 1877)			O
Gnatholepis cauerensis (Bleeker, 1853)	L		
Gobiidae sp. 5	L		
Nemateleotris magnifica Fowler, 1938			O
Ptereleotris evides (Jordan and Hubbs, 1925)	L		
Quisquilius eugenius (Valenciennes, 1836)	L		
ISTIOPHORIDAE			
Istiophorus platypterus (Shaw and Nodder, 1792)			O
ZANCLIDAE			
Zanclus cornutus (Linné, 1758)	L		O

Appendix 1 (cont'd)

ACANTHURIDAE			
Acanthurus achilles Shaw, 1803	L		O
Acanthurus bleekeri Günther, 1861			O
Acanthurus glaucopareius Cuvier, 1829	L		O
Acanthurus guttatus Bloch and Schneider, 1801	L		O
Acanthurus leucopareius (Jenkins, 1903)			O
Acanthurus lineatus (Linné, 1758)	L		O
Acanthurus mata (Cuvier, 1829)	L		O
Acanthurus nigricauda Duncker and Mohr, 1929	L		O
Acanthurus nigrofuscus (Forsskäl, 1775)	L		O
Acanthurus nigroris (Valenciennes, 1835)	L		O
Acanthurus nubilus (Fowler and Bean, 1929)			O
Acanthurus olivaceus Bloch and Schneider, 1801			O
Acanthurus pyroferus Kittlitz, 1834			O
Acanthurus thompsoni (Fowler, 1923)			O
Acanthurus triostegus (Linné, 1758)	L		O
Acanthurus xanthopterus (Valenciennes, 1835)	L	P	O
Acanthurus sp. (Juv.) jaune	L		O
Ctenochaetus striatus (Quoy et Gaimard, 1825)	L	P	O
Ctenochaetus strigosus (Bennett, 1828)			O
Naso annulatus (Quoy et Gaimard, 1825)	L		O
Naso brachycentron (Quoy et Gaimard, 1825)			O
Naso brevirostris (Valenciennes, 1835)	L	P	O
Naso hexacanthus (Bleeker, 1855)	L		O
Naso lituratus (Bloch and Schneider, 1801)	L	P	O
Naso unicornis (Forsskäl, 1775)	L	P	O
Naso vlamingii (Valenciennes, 1835)	L	P	O
Zebrasoma rostratum (Günther, 1873)			O
Zebrasoma scopas (Cuvier, 1829)	L		O
Zebrasoma veliferum (Bloch, 1795)	L		O
SIGANIDAE			
Siganus argenteus (Quoy et Gaimard, 1825)		P	O
BOTHIDAE			
Bothus mancus (Broussonet, 1782)	L		
BALISTIDAE			
Balistapus undulatus (Mungo Park, 1797)	L		O
Balistoides viridescens (Bloch and Schneider, 1801)	L	P	O
Melichthys niger (Bloch, 1786)			O
Melichthys vidua (Solander, 1844)			O
Odonus niger (Rüppell, 1837)			O
Rhinecanthus aculeatus (Linné, 1758)	L		O
Rhinecanthus rectangulus (Bloch and Schneider, 1801)	L		O
Sufflamen bursa (Bloch and Schneider, 1801)			O
Sufflamen fraenatus (Latreille, 1804)			O
Xanthichthys caeruleolineatus (Randall, Matsuura, Zama, 1978)			O
MONACANTHIDAE			
Aluterus scriptus (Osbeck, 1765)			O
Amanses scopas (Cuvier, 1829)			O
Cantherhines dumerilii (Hollard, 1854)			O
OSTRACIIDAE			
Ostracion cubicus Linné, 1758	L		
Ostracion meleagris Shaw, 1796	L		O
TETRAODONTIDAE			
Arothron hispidus (Linné, 1758)	L		
Canthigaster bennetti (Bleeker, 1854)	L		
Canthigaster solandri (Richardson, 1844)	L		
Canthigaster valentini (Bleeker, 1853)	L		

Plate 1 : Most of the fish traps are located around Tuheiava pass. (Photo Morize)

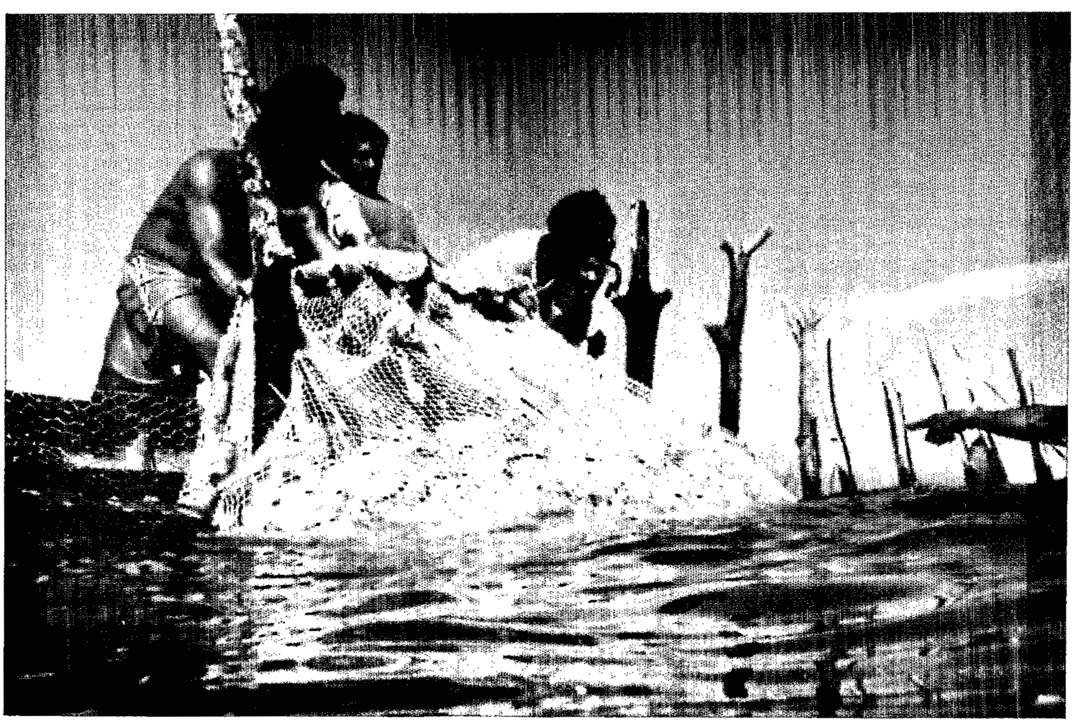

Plate 2 : The fishes held in the traps are collected about once a week. (Photo Intes)

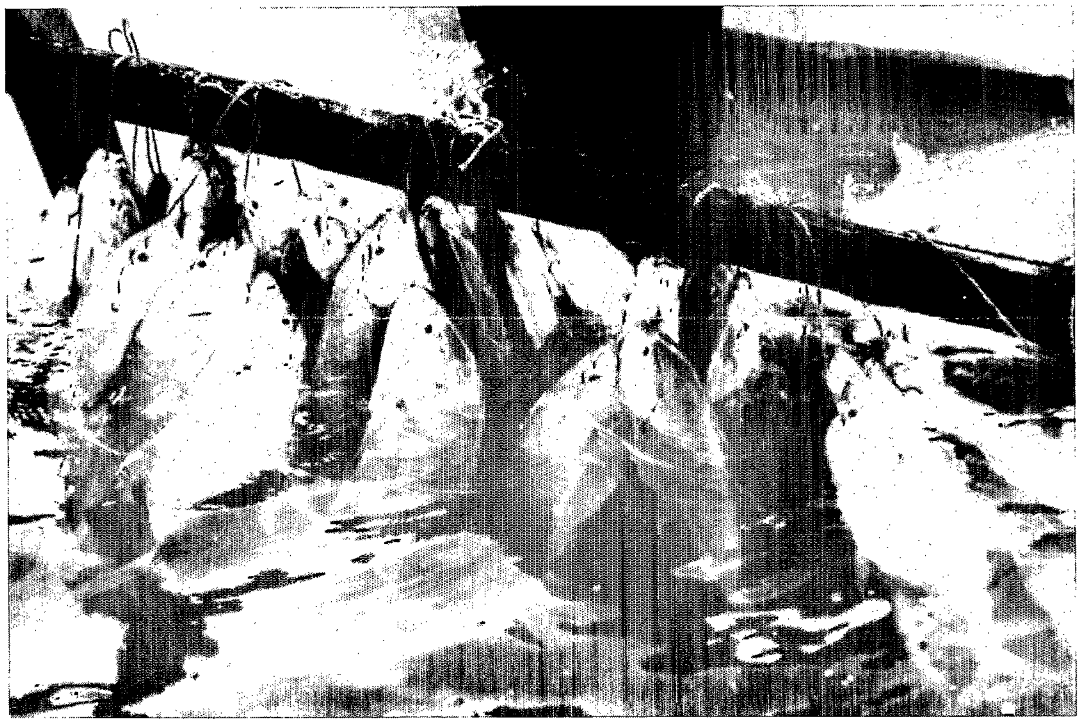

Plate 3 : The fish are tighed by about 3 kg bundles before loading on the transport ship. (Photo Intes)

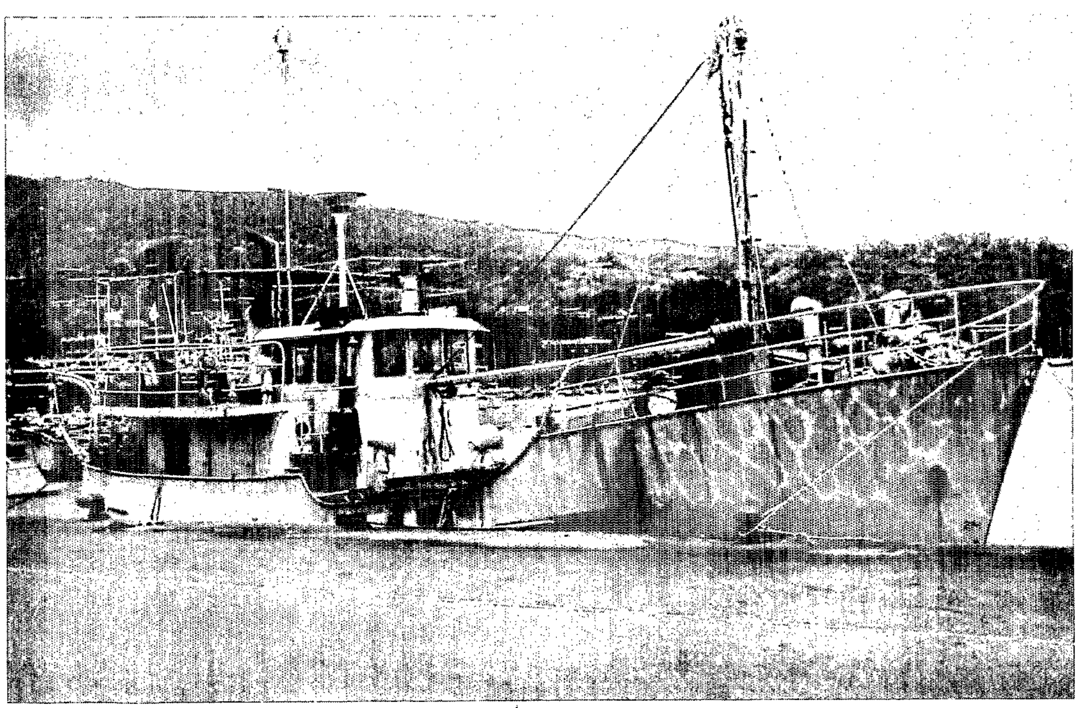

Plate 4 : A "goelette" weekly brings the fishes caught in Tikehau to the Papeete market. (Photo Morize)

ATOLL RESEARCH BULLETIN

NO. 415

TIKEHAU

AN ATOLL OF THE TUAMOTU ARCHIPELAGO (FRENCH POLYNESIA)

PART I. ENVIRONMENT AND BIOTA OF THE TIKEHAU (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)
BY A. INTES AND B. CAILLART

PART II. NUTRIENTS, PARTICULATE ORGANIC MATTER, AND PLANKTONIC AND BENTHIC PRODUCTION OF THE TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)
BY C.J. CHARPY ROUBAUD AND L. CHARPY

PART III. REEF FISH COMMUNITIES AND FISHERY YIELDS OF TIKEHAU ATOLL (TUAMOTU ARCHIPELAGO, FRENCH POLYNESIA)
BY B. CAILLART, M.L. HARMELIN-VIVIEN, R. GALZIN, AND E. MORIZE

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