

Fish stock assessment of the northern New Caledonian lagoons: 2 – Stocks of lagoon bottom and reef-associated fishes

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Abstract — Fish stocks found on lagoon bottoms and near reefs are characterized by a high diversity and heterogeneous habitat which make stock estimation difficult. In particular, it is necessary to combine several methods in order to evaluate the major components of these stocks. The present study aimed at estimating reef fish stocks in the Northern Province of New Caledonia, a region where they represent a major target for the local fishermen. These estimates were based on experimental fishing with handlines and bottom longlines. Handlines were used to assess the stocks near reefs, and longlines for those in areas away from reefs and on lagoon soft bottoms. Handline stations (363) were sampled in three different regions (west, north and east lagoons) and three biotopes (nearshore, middle lagoon and barrier reef). A total of 104 species were caught, the major families being Lethrinidae, Lutjanidae and Serranidae. Species composition and catch per unit of effort (CPUE) varied among regions and biotopes. In particular, the north zone showed characteristics of an unexploited area with very high yields. An increase in CPUE and fish size from the coast towards the barrier reef and with increasing depth was observed in all regions. Correlations between CPUE from handlines and the numerical density and biomass estimates from underwater visual censuses (UVC) performed on nearby reefs were significant. A total of 206 longline stations were sampled in the west and east regions. A total of 80 species were caught, the major families being the same as those caught in stations with handlines with the addition of Carangidae. The CPUE of longlines was significantly correlated with numerical density and biomass estimates made by UVC along the longlines. Stock estimates based on the correlations between CPUE from handlines or longlines and UVC estimates indicate that 90 % of the lagoon stock were found on soft bottoms and near reefs. Reefs, despite biomasses that were five times larger than soft-bottom and near-reef areas, made only a small contribution to total stock. The ratio between density and CPUE was highest for the lowest densities, thus indicating that fishing efficiency increased with density. Comparison of handline catch performed around reefs and UVC data from nearby reefs suggests that there were strong relationships between the fish assemblages of these two biotopes. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Demersal fish / stock assessment / handline / longline / soft bottoms / reefs / SW New Caledonia / Pacific Ocean

Résumé — Estimation des stocks de poissons des lagons de Nouvelle-Calédonie : 2 – Stocks des poissons de fond et des poissons associés aux récifs coralliens. Les stocks de poissons des fonds de lagon et vivant à proximité des récifs se caractérisent par une forte diversité et un habitat hétérogène, ce qui rend les estimations de stocks difficiles. En particulier, il est nécessaire de combiner plusieurs méthodes pour évaluer les principales composantes de ces stocks. La présente étude avait pour objectif d'estimer de tels stocks dans la Province Nord de Nouvelle-Calédonie, une région où ils représentent une des cibles privilégiées des pêcheurs locaux. Ces estimations se sont basées sur des pêches expérimentales avec des palangres (206 stations) et des lignes à main « palangrottes » (363 stations). Les « palangrottes » ont été utilisées pour estimer les stocks près des récifs, et les palangres pour les zones éloignées des récifs et les fonds de lagon. Les stations de « palangrotte » ont été effectuées dans trois régions différentes (lagons ouest, est et nord) et sur trois biotopes (côtier, milieu de lagon et à proximité de la barrière récifale). Au total, 104 espèces ont été capturées, les principales familles étant les Lethrinidés, Lutjanidés et Serranidés. L'analyse des captures montre des différences inter-région et inter-biotope dans la composition spécifique et en prises par unité d'effort (PUE). En particulier, le lagon nord présente des caractéristiques d'une région inexploitée avec des PUE très élevées. Les PUE et taille des prises augmentent de la côte vers le large ainsi qu'avec la profondeur. Les PUE des « palangrottes » étaient significativement corrélées avec les estimations de densité et de biomasse obtenues par comptage en plongée (UVC) pratiqué à proximité des récifs. Les stations de palangre ont été réalisées sur les lagons ouest et est. Un total de 80 espèces a été capturé, les familles principales étant identiques à celles des « palangrottes » avec en plus les Carangidés. Les PUE globales des palangres étaient corrélées significativement aux densités et biomasses estimées en plongée le long des palangres. Les estimations de stocks basées sur ces corrélations montrent que 90 % des stocks lagonaires se

situent sur les fonds de lagon et à proximité des récifs. Les récifs, malgré des biomasses cinq fois plus importantes ne constituent qu'une petite proportion du stock total des poissons de ligne. Le rapport entre densité et PUE était le plus élevé pour les densités les plus basses, montrant ainsi que l'efficacité des engins augmente avec la densité. La comparaison entre les PUE des « palangrottes » et les densités obtenues par UVC sur les récifs avoisinants suggère de fortes relations entre les communautés de poissons des récifs et celles des fonds avoisinants. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Poissons démersaux / évaluation de stocks / palangrottes / lignes à main / fonds meubles / récifs / Nouvelle-Calédonie / océan Pacifique

1. INTRODUCTION

Near-reef and soft-bottom fish stocks are seldom assessed in the Indo-Pacific region despite their importance in total catch [8, 9, 27]. The major reason for this is essentially technical. Indeed, these fish can be assessed in two ways. First, catch and fishing effort can be analysed. This kind of data is very difficult to collect for fish in these habitats, because the effort is highly dispersed in time and space, and the gear used and the species caught very diverse [32]. The second way is to perform experimental fishing. Due to the nature of the bottom, four main types of fishing gear can be used, namely handlines, longlines, traps and gillnets. All these methods have strong biases and in many cases the relationship between catch and actual stock is unknown (for a review, see [7]). Therefore, these methods tend to yield relative values which allow classification of areas or time periods in regard to one another, and do not give absolute values of stock. Another important problem when studying such stocks is to relate soft-bottom and near-reef fish to those living on reefs. Many species, in particular Lethrinidae, Lutjanidae and Carangidae are found both on reefs and in adjacent biotopes, and exchanges probably occur between them [17]. In particular, soft-bottom and near-reef areas could constitute reservoirs for reef fishes [39]. This could be particularly important given that in many places most fish are caught on reefs or close to them. If adjacent soft bottoms constitute reservoirs, a certain lag between the start of an over-fishing event on reefs and the onset of its effects on the fishery as a whole is expected because of this potential migration from nearby unfished (or little fished) areas.

Species composition of soft-bottom fish assemblages is known to vary with a number of environmental factors [39]. In the management of local fisheries, it may be very important to know which factors affect species distribution, fish size or density. In particular, an increase in fish size, with the distance to the coast has already been documented in this area [22], with young (small) fish being usually found nearshore.

The purpose of the present study is to investigate ways of estimating fish stocks from soft-bottom and near-reef areas. In particular, we consider the possibility of obtaining absolute values of stocks by calibrating fishing methods with UVCs (under-water visual

census). Once these stocks have been estimated, we try to answer the following questions: a) how do these stocks compare to those found on nearby reefs for the same species? [23]; b) do these stocks present major geographical variations in their composition?; and c) what are the major environmental factors which may act on the distribution of these stocks?

2. MATERIALS AND METHODS

2.1. Study zone

The area studied was divided into three regions, north, west and east (*figure 1*). In each region, several subregions were defined, near fringing reefs, near intermediate reefs, near barrier reefs and lagoon bottoms. Unless stated otherwise, sub-regions will be defined by the nearby reef type in the remainder of this article.

2.2. Handlines

Handlines were used to assess stocks near reefs in the three regions. This method was used in shallow waters (less than 20 m deep), and in areas where the bottom was too rugged to be sampled with longlines. Handline stations were approximately 1 nautical mile apart along continuous reefs (fringing and barrier reefs). These stations were located on leeward and windward sides of intermediate reefs. At each station the following procedure was observed. Fishing was performed with the gear depicted by Kulbicki et al. [17]. Two fishermen on a canoe started fishing half an hour after legal sun set time. Each station had four substations located 100 m apart. The fishermen spent half an hour on each of these substations. Bait was frozen squid, *Loligo* sp. All fish captured were later identified, counted, measured and weighed. A total of 363 handline stations were sampled (*figure 1*) and when possible they were set near underwater visual census (UVC) stations, but handline and UVC stations rarely coincided.

2.3. Longlines

The northern lagoon bottoms had previously been sampled by trawling [40]. Twenty-two handline stations were sampled in areas where trawling had taken place. A comparison between the density estimates

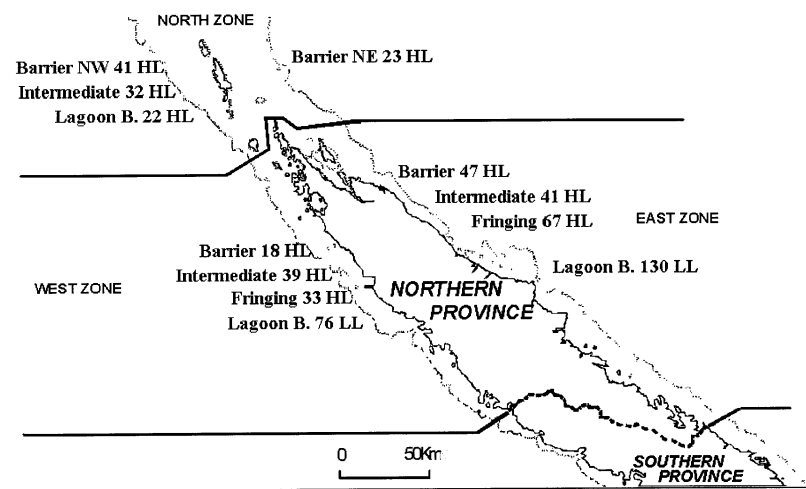


Figure 1. Sampling effort (number of handline stations or longline sets) among the three zones and the four biotopes. HL: hand line; LL: long line; Barrier: near barrier reef areas; Intermediate: near intermediate reefs areas; Fringing: near fringing reefs areas; Lagoon B.: lagoon soft-bottoms.

obtained from handlines and trawling indicated that there was no statistical difference (t -test, $P = 0.7$). As a result no additional sampling was performed over these areas during this experiment. The use of trawls in the western and eastern lagoons was, however, impossible because of the presence of numerous coral heads. For these two areas, longlines represented the best alternative as indicated by previous work in the south-west lagoon of New Caledonia [15]. Longlines were then used in the deeper areas and in places more than 2 miles from the reefs. Stations were placed according to a 3-nautical mile grid. The description of the gear used is given by Kulbicki [15]. Two longlines of 100 hooks each were laid per station. The bait used was the same as for handlines. Soaking time was 90 min and all fishing activities took place during daytime. All fish caught were identified, counted, measured and weighed.

UVCs were performed on 18 longlines. Two divers started to count as soon as the line was laid according to the method indicated elsewhere [23]. Only species that could be caught on longlines were counted. Diversity (number of species per transect), density (fish·m⁻²) and biomass (g·m⁻²) of these fishes were estimated according to the methods indicated elsewhere [23]. Correlations between longline catch and UVC estimates were later calculated in order to estimate densities and biomass of fish from longline CPUE. A total of 206 stations were sampled (*figure 1*). This relationship was later improved by adding data from a similar experiment which took place in the SW lagoon of New Caledonia [15].

2.4. Stock estimates

In order to make stock estimates, the relationships between catch weight and biomass estimates by underwater visual census (UVC) were used.

For handlines, the relationship used was from a similar study previously conducted on Ouvéa

atoll [17]. Indeed, during that study the same fishing procedure was used as in the present investigation but in addition UVC and fishing stations overlapped, which was not the case in the present survey. From the work in Ouvéa the equation relating CPUE by weight with UVC biomass were related as follows:

$$\text{Log}_{10}(\text{biomass}) = 0.455 \log_{10}(\text{CPUE}) + 0.857 \quad (1)$$

$r = 0.70$; $P = 0.015$; the confidence intervals ($P = 0.05$) for the slope is (± 0.132) and for the intercept (± 0.158).

Based on the CPUE and the area sampled, it was thus possible to estimate biomass and then, knowing the area of the near-reef biotope, standing stock could be calculated. Conservative confidence intervals for these stock estimates were obtained using the Bonferroni method [28].

2.5. Data analysis

Variations among regions and among biotopes were compared by ANOVA. For handlines, only two biotopes were sampled in all three regions and therefore could be analysed by complete design ANOVA. For the other biotopes, only two regions were available, therefore incomplete design ANOVA were used. Biotopes were considered nested within regions, this prevented the use of post hoc comparison tests for biotopes. A posteriori differences among regions were tested by Scheffé tests. All variables tested by ANOVAs were first tested for normality (Kolgomorov-Smirnoff). To analyse the effects of depth (a continuous variable) on catch, covariance analyses were performed in order to test differences in slope between regions or between biotopes (using the Sheffé multiple comparison procedure). The differences among regions or biotopes in the proportions of the main families in the catch were tested by a χ^2 test.

Table I. Composition of the catch for handlines by region. Only the major families and species are indicated.

Regions (no. stations)	West (n = 90)			North (n = 118)			East (n = 155)			Total (n = 363)		
	Sp.	Nb	W	Sp.	Nb	W	Sp.	Nb	W	Sp.	Nb	W
Carcharhinidae	4	0.08	0.19	4	0.24	0.76	5	0.15	0.43	7	0.16	0.48
Serranidae	18	1.06	0.83	16	3.25	5.94	16	1.01	0.94	20	1.75	2.54
<i>Epinephelus cyanopodus</i>		0.09	0.12		0.29	0.78		0.04	0.03		0.13	0.29
<i>E. malabaricus</i>		0.06	0.23		0.20	2.07					0.08	0.73
<i>E. merra</i>		0.14	0.02		0.31	0.04		0.49	0.05		0.29	0.03
<i>E. polyphekadion</i>		0.39	0.33		1.13	1.30		0.48	0.68		0.61	0.72
Carangidae	5	0.09	0.28	5	0.18	0.81	6	0.06	0.25	10	0.11	0.44
Lutjanidae	11	2.54	1.01	17	7.91	8.02	16	3.74	1.39	17	4.80	3.45
<i>Lutjanus adetti</i>					0.81	0.43					0.26	0.14
<i>L. bohar</i>		0.17	0.22		1.97	5.02		0.51	0.45		0.85	1.83
<i>L. fulviflamma</i>		1.14	0.28		1.05	0.27		0.90	0.22		0.91	0.23
<i>L. gibbus</i>		0.16	0.08		0.91	0.60		0.45	0.21		0.48	0.28
<i>L. quinquelineatus</i>		0.40	0.04		1.08	0.14		1.36	0.17		0.88	0.11
<i>L. vitta</i>		0.49	0.10		1.40	0.41		1.02	0.28		0.90	0.25
Haemulidae	2	0.20	0.23	1	0.18	0.37	3	0.23	0.26	3	0.21	0.29
Lethrinidae	12	4.42	2.84	17	9.25	10.8	14	4.26	3.17	19	5.92	5.57
<i>Gymnocranius</i> sp.		0.04	0.03		0.22	0.34		0.12	0.13		0.11	0.16
<i>Lethrinus atkinsoni</i>		1.30	0.70		4.40	3.68		2.63	1.96		2.58	1.99
<i>L. lentjan</i>		1.20	0.46		0.67	0.32		0.60	0.24		0.71	0.29
<i>L. nebulosus</i>		1.67	1.56		3.07	5.77		1.27	1.55		1.81	2.75
<i>L. obsoletus</i>		0.02	0.02		0.38	0.13		0.26	0.09		0.21	0.08
<i>L. rubrioperculatus</i>		0.02	0.01		0.10	0.04		0.42	0.19		0.17	0.08
Nemipteridae	1	0.02	0.00	1	0.74	0.10	1	0.12	0.02	1	0.30	0.04
Sphyrnidae	2	0.23	0.29	2	0.14	0.14	2	0.17	0.19	2	0.18	0.20
Totals												
Fringing reefs		8.8	5.2					5.6	4.0		6.8	4.4
Intermediate reefs		10.0	7.6		23.2	17.6		12.8	8.8		14.8	10.8
Barrier reefs		6.8	5.6		27.2	39.2		14.8	10.0		20.0	23.6
Lagoon bottoms					7.2	8.0					7.2	8.0
All biotopes	69	8.97	6.20	76	22.5	27.2	80	10.2	6.98	104	13.9	13.4

W: CPUE by weight (kg per station); Nb: CPUE by number (fish per station); Sp.: total number of species caught.

3. RESULTS

3.1. Handlines

The catch comprised 104 species distributed among 23 families (table I). However, three families, namely Lethrinidae, Lutjanidae and Serranidae, dominated the catch in species richness, CPUE by number and CPUE by weight (table I). The mean catch was 13.5 kg per station (equivalent to $3.37 \text{ kg} \cdot \text{fisherman}^{-1} \cdot \text{h}^{-1}$), with the three major families constituting 86 % of the catch. The average individual weight of the fish caught was 0.96 kg. There were significant differences between regions, the north region having mean species richness and CPUE more than twice those of the west or east, both of these having approximately the same yields (table II). The mean weight of fish was much larger in the north (1.21 kg) than in the west or east (0.69 kg in each case). This dominance in CPUE and mean weight of the north region was also visible at the family and species level (table I), with only a few exceptions such as *Lutjanus fulviflamma*, *Lethrinus lentjan* and Sphyrnidae being more important in the west region,

and *Lutjanus quinquelineatus*, *Lethrinus rubrioperculatus* in the east region.

The catch also varied according to the biotope (table III). In particular, there was an increase in CPUE from the coast towards the barrier reef for most species and families. This was especially true for CPUE by weight which increased more than five-fold between the fringing reefs and the barrier reefs (table III). This implies that fish were not only more numerous in the catch (three-fold increase), but also that the average size of fish increased (from 0.63 to 1.2 kg) from the coast to the barrier reef. There was, however, a confounding effect of region and biotope (table II). This effect could not be tested in a complete ANOVA design, thus two separate ANOVA had to be performed, the first one on all regions with only barrier and intermediate reefs tested as biotopes, the second one with only the west and east regions but with all three biotopes tested (table II). The fact that biotopes were nested within regions prevented post hoc comparisons between biotopes. The first ANOVA showed that all the variables tested (species per station, CPUEs

Table II. Statistical analysis of the differences between regions and biotopes for handline results. In each case, the first line represents the result of the ANOVA and the second the post hoc planned comparisons (Sheffé tests). The level of significance of the Sheffé tests are not indicated, but are at least $P < 0.05$ (NS: not significant). For region \times biotope, biotopes are considered to be nested within regions.

	Species per station	CPUE Nb	CPUE W	Average weight
Region effect	$P < 0.0001$ N > W = E	$P < 0.0001$ N > W = E	$P < 0.0001$ N > W = E	$P < 0.0001$ N > W = E
Biotope effect	$P < 0.0001$ (Ba = Int) > (Fr = LB)	$P < 0.0001$ Ba > Int > Fr = LB	$P < 0.0001$ Ba > Int > Fr = LB	$P < 0.0001$ Ba > Int; Ba > Fr
Region \times Biotope	1 – region $P < 0.0001$	1 – region $P < 0.0001$	1 – region $P < 0.0001$	1 – region $P < 0.0001$
1 – all regions \times (Ba; Int)	N > E > W no biotope effect	N > E > W no biotope effect	N > E > W biotope $P < 0.001$ no Sheffé (nested)	N > E = W biotope $P < 0.0001$ no Sheffé (nested)
2 – all Biotopes \times (W; E)	2 – region $P = 0.02$ E > W biotope $P < 0.0001$ no Sheffé (nested)	2 – region NS biotope $P < 0.0001$ no Sheffé (nested)	2 – region NS biotope $P < 0.0001$ no Sheffé (nested)	2 – region NS biotope NS

Ba: barrier reef; Int: intermediate reef; Fr: fringing reef; LB: lagoon bottom.

and average weight) had higher values in the northern region and that there was a biotope effect for CPUE by weight and for mean individual weight. The second ANOVA indicated that differences between biotopes were greater than differences between east and west regions except for mean individual weight.

The effect of depth was tested according to region and biotope by covariance analyses. The slope of the

species richness and CPUE with depth (in the 0–20-m range) was greater for the north than for east or west (F test, $P < 0.001$). In fact, mean species richness and CPUE increased with depth in the west and east for all depths sampled, whereas in the north they increased with depth down to approximately 10–15 m, and then decreased (figure 2). No biotope effect could be demonstrated.

Table III. Composition of the catch for handlines by biotope. Only the major families and species are indicated.

Biotopes (no. stations)	Fringing ($n = 120$)			Intermediate ($n = 92$)			Barrier ($n = 129$)			Lagoon bottom ($n = 22$)		
	Sp.	Nb	W	Sp.	Nb	W	Sp.	Nb	W	Sp.	Nb	W
Carcharhinidae	0.08	0.05	0.12	0.07	0.09	0.22	0.22	0.31	1.03	0.23	0.19	0.29
Serranidae	0.54	0.63	0.73	1.21	2.04	1.72	1.43	2.62	5.09	0.18	0.27	0.53
<i>Epinephelus cyanopodus</i>	0.04	0.04	0.05	0.13	0.15	0.20	0.15	0.19	0.57			
<i>E. malabaricus</i>	0.01	0.01	0.04	0.06	0.09	0.51	0.09	0.14	1.58			
<i>E. merra</i>	0.07	0.08	0.01	0.21	0.38	0.05	0.25	0.43	0.05			
<i>E. polyphkadion</i>	0.15	0.21	0.20	0.29	0.53	0.51	0.46	1.11	1.42			
Carangidae	0.12	0.1	0.32	0.15	0.15	0.47	0.07	0.07	0.46	0.18	0.18	0.67
Lutjanidae	1.04	2.2	0.73	2.10	4.93	2.02	2.56	7.37	7.31	0.27	0.91	0.51
<i>Lutjanus adetii</i>							0.06	0.41	0.22			
<i>L. bohar</i>	0.04	0.02	0.23	0.18	0.29	0.26	0.53	2.10	4.91			
<i>L. fulviflamma</i>	0.28	0.83	0.19	0.43	0.97	0.25	0.49	1.05	0.27			
<i>L. gibbus</i>	0.06	0.12	0.05	0.21	0.34	0.19	0.31	0.94	0.56	0.05	0.09	0.25
<i>L. quinquelineatus</i>	0.29	0.56	0.06	0.45	1.03	0.13	0.51	1.15	0.15			
<i>L. vitta</i>	0.15	0.42	0.08	0.29	1.40	0.38	0.12	0.88	0.28			
Lethrinidae	1.02	2.78	1.58	1.79	6.01	4.88	1.90	8.91	9.24	0.64	2.14	5.45
<i>Gymnocranius</i> sp.		0.03	0.03	0.05	0.06	0.06	0.18	0.28	0.37			
<i>Lethrinus atkinsoni</i>	0.19	0.67	0.34	0.48	1.68	1.05	0.71	5.29	4.42			
<i>L. lentjan</i>	0.41	1.06	0.40	0.39	1.17	0.52	0.04	0.13	0.06			
<i>L. nebulosus</i>	0.27	0.85	0.77	0.43	2.51	3.00	0.36	2.02	3.65	1.45	0.23	5.19
<i>L. obsoletus</i>	0.01	0.01	0.01	0.13	0.15	0.06	0.26	0.46	0.16	0.09	0.05	0.04
<i>L. rubrioperculatus</i>	0.01	0.01	0.00	0.02	0.02	0.01	0.15	0.46	0.20			
Nemipteridae	0.07	0.13	0.02	0.10	0.35	0.05	0.02	0.02	0.002	0.05	0.05	0.07
Sphraenidae	0.11	0.18	0.18	0.15	0.23	0.32	0.10	0.14	0.13	0.05	0.09	0.03
Total	3.43	6.67	4.21	6.00	14.7	10.86	6.63	19.9	23.6	2.72	7.3	7.87

W: CPUE by weight (kg/station); Nb: CPUE by number (fish /station); Sp.: number of species caught per station.

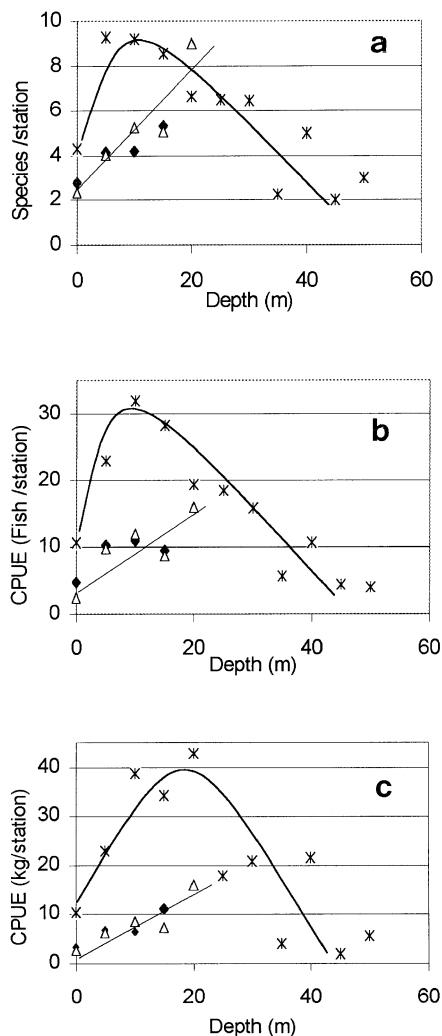


Figure 2. Variation of species richness (a), CPUE by number (b) and CPUE by weight (c) with depth for the three zones. Each point represents the mean of all observations within a 5-m depth class. Δ : east, \blacklozenge : west, $*$: north.

3.2. Longlines

The catch comprised 80 species distributed among 19 families. The major families were Lethrinidae, Carangidae, Serranidae and Lutjanidae. Twenty one of the species captured by longlines were not collected with handlines, and 34 species caught by handlines were absent from longline catches. A χ^2 test on the proportion of the four major families (Serranidae, Lutjanidae, Lethrinidae, Carangidae) indicates that the two methods yielded different proportions (CPUE weight) for these families ($P < 0.0001$ for the east and $P < 0.004$ for the west). The major differences were for Carangidae, which represented 26 % of the CPUE by weight for longlines but only 3 % for handlines (table IV). In contrast, Lutjanidae represented only 7 %

of the CPUE by weight for longlines, whereas they constituted 25 % for handlines. Within a given family there were also major differences between the two methods. For example, for Serranidae most of the longline catch was from *Epinephelus areolatus* and *E. maculatus*, whereas for handlines these species were represented by only a few specimens. It was not possible to separate differences due to the gear and differences due to habitat since both methods were not used in the same biotopes. However, for similar depths, both methods caught fish of similar size as illustrated by the example of *Lethrinus nebulosus* (figure 3), for which a covariance analysis (Scheffé multiple comparison) indicates no difference in slope between methods.

On average, the catch on longlines was 9.45 kg per 100 hooks of which the dominant families made up 77 %. The number of species per set and the CPUE by numbers were higher in the east ($P < 0.002$) than in the west; however, there was no difference in CPUE by weight or mean individual weight. There were also important regional differences at the family level in the distribution of the catch; in particular Carangidae made up 10 % of the catch in the west but 28 % in the east, and conversely Lethrinidae made up 45 % of the catch in the west but only 25 % in the east. At the species level the differences between coasts were often striking. For instance, *Caranx fulvoguttatus* and *C. papuensis* dominated the catch in the west but were rare in the east, whereas the opposite was true for *C. chrysophrys* and *C. gymnothetus* (table IV). Individual mean weights were higher on the east coast for Serranidae and Carangidae. Catches were not significantly correlated to depth on either coast ($P \geq 0.05$).

3.3. Correlations with UVC

The catch from the fishing experiments alone did not allow us to estimate densities (fish·m⁻²) or biomass (g·m⁻²) of fish in the near-reef areas. A correlation with another method yielding density or biomass estimates would have been necessary. During the present experiment a number of handline stations were sampled in the vicinity of UVC stations on reefs [23] without however overlapping. Therefore, it would not be possible to make inferences on densities or biomass on handline stations from such relationships, but this indicates whether densities and biomass found on nearby reefs influence the catch from handlines. The data show that there were significant (z-test [28]) correlations (table V), especially when all regions were considered. The weakest relationship was between density from UVC and CPUE by numbers from handlines. This could be due to either the fact that there was a saturation of the gear at high densities, or to differences in fish size between reefs and nearby handline stations. Analysis at the family level for Lutjanidae, Lethrinidae and Serranidae (table V) shows that the correlation for Serranidae was much better than that for the other two families, probably

Table IV. Catch of the major families and species by bottom longlines.

	West			East			Total		
	CPUE Nb	CPUE W	Weight	CPUE Nb	CPUE W	Weight	CPUE Nb	CPUE W	Weight
Total	4.24	8.85		6.09	9.79		5.41	9.45	
Serranidae	0.74	0.88		0.84	1.25		0.80	1.17	
<i>Epinephelus areolatus</i>	0.17	0.62	0.36	0.09	0.54	0.82	0.12	0.57	0.55
<i>E. maculatus</i>	0.26	0.26	0.94	0.15	0.28	2.20	0.19	0.27	1.80
Carangidae	0.92	0.90		1.12	2.70		1.05	2.42	
<i>Caranx fulvoguttatus</i>	0.14	0.17	3.22	0.02	0.03	5.00	0.07	0.08	3.60
<i>C. papuensis</i>	0.45	0.68	1.90	0.08	0.22	2.80	0.21	0.39	2.24
<i>C. chrysophrys</i>	0.04	0.04	0.96	0.26	0.50	1.95	0.18	0.34	1.87
<i>C. gymnothetus</i>				0.12	0.69	5.57	0.08	0.43	5.57
Lutjanidae	0.16	0.40		0.27	0.80		0.23	0.68	
Lethrinidae	1.61	4.00		1.85	2.40		1.76	2.98	
<i>Gymnocranius grandoculis</i>	0.26	0.77	2.76	0.12	0.28	2.40	0.17	0.46	2.58
<i>Lethrinus atkinsoni</i>	0.11	0.07	0.73	0.56	0.48	0.83	0.39	0.33	0.82
<i>L. nebulosus</i>	0.84	2.00	2.46	0.30	0.77	2.67	0.50	1.23	2.55
<i>L. olivaceus</i>	0.21	1.00	4.85	0.07	0.25	3.40	0.12	0.53	4.19

CPUE Nb: CPUE by numbers of fish per 100 hooks; CPUE W: CPUE by weight (kg) per 100 hooks; Weight: average weight in kg.

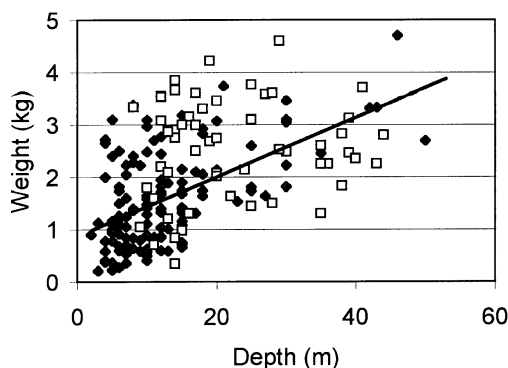


Figure 3. Distribution of the weight (in kg) of *Lethrinus nebulosus* according to depth and fishing gear. □: longlines, ◆: handlines.

because Serranidae are solitary fishes and do not move much and are thus easier to census.

The relationship between the CPUE by weight and the UVC biomass observed on nearby reefs did not vary significantly among regions (table V and figure 4) as indicated by the absence of difference of the slopes or intercepts (covariance analysis – Scheffé multiple comparisons). This suggests that visual censuses on those reefs are a good indicator of the fishing potential in the vicinity, even though fishing pressure [21] and species composition [23] may be quite different from one region to the next.

3.4. Stock estimates

Biomass estimates from handline catches were first obtained (table VI) using equation (1), then knowing

the area of near-reef biotopes it was possible to calculate stocks (table VII) and confidence intervals for these stocks.

The longline data allowed estimates of biomass (table VI) and consequently of stocks (table VII) to be made. The correlation between CPUE by numbers and UVC density (figure 5) was better ($P < 0.0001$) than the correlation between CPUE by weight and biomass ($P < 0.005$) (figure 6). For the latter, in order to improve the confidence intervals, results were first compared, then combined with data obtained using the same experimental design during a similar survey [22] in the SW lagoon of New Caledonia. The comparison (covariance analysis) between present data and data from the SW lagoon indicates that the fish response to the gear was similar in both studies (figure 6). Such a similarity allows us to pool the two data sets, which in turn improves the significance of the correlation from

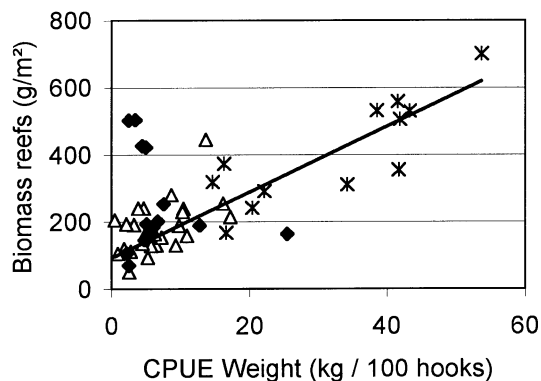


Figure 4. Relationship between CPUE from handlines and the estimated biomass from UVC on nearby reefs. Δ: east, ◆: west, *: north.

Table V. Correlation coefficients between CPUE from handlines and density, biomass or species richness from underwater visual censuses on nearby reefs.

	Density × CPUE Nb	Biomass × CPUE W	Mean individual weight	Species richness
West (<i>N</i> = 13)				
All species	-0.51	-0.19	0.70**	0.27
Serranidae	0.48	0.49	-0.14	0.44
Lutjanidae	-0.36	-0.44	0.40	-0.47
Lethrinidae	-0.14	-0.28	0.27	-0.22
North (<i>N</i> = 12)				
All species	-0.23	0.64*	0.50	-0.25
Serranidae	-0.53	0.69*	0.78**	-0.42
Lutjanidae	0.44	0.30	0.65*	-0.11
Lethrinidae	0.11	-0.28	0.44	0.04
East (<i>N</i> = 25)				
All species	0.55**	0.56**	-0.14	0.64**
Serranidae	0.62**	-0.04	0.05	0.69**
Lutjanidae	0.16	-0.06	-0.16	-0.26
Lethrinidae	0.12	0.13	0.29	0.04
All regions (<i>N</i> = 50)				
All species	0.19	0.68**	0.48**	0.53**
Serranidae	0.25	0.74**	0.14	0.45**
Lutjanidae	-0.10	0.14	0.40**	-0.10
Lethrinidae	-0.03	0.22	0.47**	0.06

CPUE Nb: CPUE by numbers; CPUE W: CPUE by weight.

* Significant at $P < 0.05$; ** significant at $P < 0.01$.

$P < 0.005$ to $P \ll 10^{-5}$. Narrowing the confidence interval on the slope of the relationship between catch and biomass thus allows smaller confidence intervals on stock estimates as well.

At the family level, only the CPUE for Lethrinidae was significantly (z-test [28]) correlated with UVC estimates (table VIII). Therefore, no attempt was made to separate stock estimates from CPUE data at the family level.

The stock estimates from longline results (figure 6) were based on the equation:

$$\text{Biomass (g}\cdot\text{m}^{-2}) = 0.95 \text{ CPUE} \\ (\text{kg per 100 hooks})$$

the confidence interval at $P = 0.05$ for the slope of the line is (± 0.097).

Stocks from lagoon bottoms (43 600 tonnes) were much greater than those from near-reef biotopes (14 100 tonnes) (table VII), due to the fact that lagoon bottoms represent very large areas (5 400 km²) com-

pared to near reef biotopes (1 560 km²). The differences in biomass between reef types or between regions were usually not significant (from confidence intervals in table VI). The few exceptions were fringing reefs in the east and near-barrier reefs on the west coast, which were significantly lower than lagoon bottoms of either the east or west coast. These stock estimates were for carnivorous species only.

4. DISCUSSION

4.1. Stock estimates

4.1.1. Handlines

Stock estimates from handlines were based on several assumptions. The major one was that there was proportionality between the catch and observations made by UVC on the same stations. The equation used to estimate biomass from CPUE, based on the work from Ouvéa atoll [17], presents several problems.

Table VI. Biomass (g·m⁻²) per biotope and region. Estimates from longlines are in italics, those from handlines are in normal characters. The numbers between brackets are lower and upper limits of the confidence intervals at $P = 0.05$.

	West	North	East
Fringing reefs	4.99 (3.43–7.15)		4.30 (3.09–5.91)
Intermediate reefs	5.87 (3.85–8.82)	8.69 (5.08–14.6)	6.35 (4.07–9.76)
Barrier reefs	5.07 (3.47–7.31)	12.39 (6.54–23.1)	6.69 (4.22–10.4)
Lagoon bottoms	8.41 (7.55–9.27)	5.93 (3.87–8.93)	9.28 (8.33–10.2)

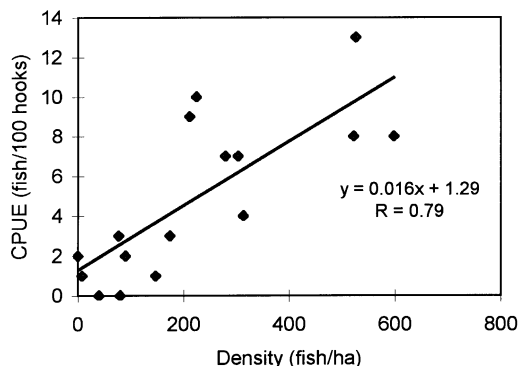


Figure 5. Relationship between UVC density (fish-ha⁻¹) estimates and CPUE by numbers for longlines.

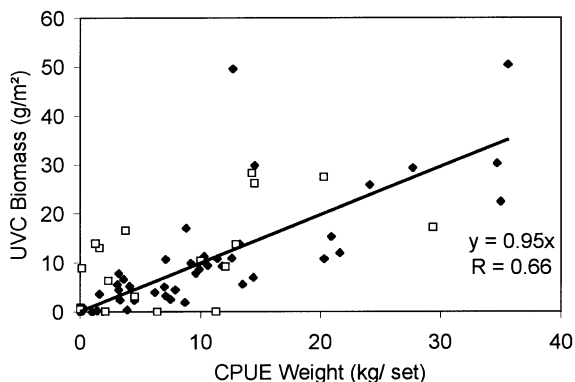


Figure 6. Relationship between CPUE by weight from longlines and UVC biomass estimates.

◆: data from the SW lagoon [25], □: present study.

First, there was only a slow increase in biomass as catch increased. For instance, a CPUE of 3.8 kg-fisherman⁻¹.h⁻¹ yielded a biomass estimate of 4.3 g.m⁻², whereas a CPUE of 38 kg-fisherman⁻¹.h⁻¹ generated a biomass estimate of 12.4 g.m⁻² (tables I and VI). In other words, a ten-fold difference in CPUE yielded only a four-fold difference in biomass. There are several possible reasons for this. Most of the species caught live in schools, and there may be an increase in the efficiency of the handlines at higher densities. High catches were also sometimes the re-

Table VIII. Correlation coefficients between catch by longlines and UVC performed along longlines.

	Density UVC versus CPUE Nb	Biomass UVC versus CPUE W
Serranidae	0.56	0.18
Lutjanidae	0.82	0.22
Lethrinidae	0.52*	0.46*
All species	0.79**	0.46*

CPUE Nb: CPUE by numbers; CPUE W: CPUE by weight.

* Significant at P < 0.05; ** significant at P < 0.01.

sults of feeding frenzies (the fish would bite even on bare hooks) which probably occur at higher densities. It is also possible that on average the higher biomass corresponded to places where fishing pressure was low and therefore the fish were less ‘educated’ and consequently more vulnerable to the gear, as demonstrated on the Great Barrier Reef [6] or for breams [43]. One of the major consequences is that handlines may not be a good tool to differentiate areas with different biomass or to look at variations of biomass through time [7].

The second problem is that equation (1) was correct when all species were pooled, but it could not be used at the family or species level. In order to obtain estimates at these levels, some indication of the proportion of the various families or species from UVC work is necessary. The major concern when considering our UVC values for some of the schooling species, in particular the Lethrinidae, is that there was a very high variance on the observations, and not enough UVC stations were sampled. Therefore, the confidence on the stock estimates became such that the values were no longer of use.

Despite these drawbacks, the present work is original because it was possible to evaluate the stocks from a method that is not usually used for such a purpose. It should be noted that in an area of the north lagoon, handlines were used in a zone that had previously been surveyed by trawling [40]. The estimates from trawling (15 stations) indicated a biomass of 5.0 g.m⁻², whereas in the same area results from handlines (22 stations) suggest biomass of 4.2 g.m⁻². These data were not statistically different and tend to confirm that handlines may yield usable estimates of biomass. This

Table VII. Stock estimates (tonnes) from handline experiments and longline experiments (italics). The numbers between brackets indicate lower and upper limits of the confidence intervals at P = 0.05.

	West	North	East	Total
Fringing	245 (170–350)		165 (120– 230)	410 (290–580)
Middle	500 (330–750)	1 560 (910–2 630)	290 (180–440)	2 350 (1 420–3 820)
Barrier	1 770 (1 200– 2 550)	8 730 (4 600–16 300)	835 (530–1 300)	11 335 (6 330–20 150)
Bottom	11 250 (10 100–12 400)	9 780 (6 400–14 700)	22 600 (20 300–24 900)	43 630 (36 800–52 000)
Total	13 765 (11 800–16 050)	20 070 (11 900 – 33 700)	23 890 (21 130–26 870)	57 725 (44 840–76 550)

is very important because very few methods allow stock estimates in these biotopes. The use of traps or hooks on a longline can generate information which may lead to biomass estimates [7, 10]; however, this requires extensive sampling for such large areas and in addition, the bottom is usually too rugged for the use of longlines in these biotopes. Another alternative is to use towed videos [7]. There are a number of problems linked to this methodology. In particular, it is often difficult to identify the species in areas where the diversity is high, as in New Caledonia. In addition, on a rugged bottom it is necessary to tow the video off the bottom, which decreases the detectability of most fishes that lie on the bottom. Furthermore, many fish are scared by the sled on which the video is mounted.

4.1.2. Longlines

Longlines were usually used in areas that were too deep or too far from shelter for handlines. Probably the most interesting result was that the yields versus UVC relationships found in the present study followed trends similar to those from the study in the south-west lagoon of New Caledonia [15]. This suggests that bottom longlines could be used over all New Caledonia as a method to estimate stocks from lagoon bottoms which are not accessible by other gears. However, one should be very cautious in extending the use of the equations adopted in the present work to other regions of the Indo-Pacific, as carried out for instance in the Maldives [2]. It will probably yield indicative values for the stocks, but as the behaviour of commercial species towards a given type of gear may drastically change from one region to the next [7], the best method is still to perform a minimum number of checks of the relationship between CPUE and UVC. Calibration between reef fishing and visual surveys (either by diver, submersible or video) has been attempted for a number of gears. Besides the present study, one may cite comparisons between UVC by divers with handline catches [34], or the use of a submersible for the same task [33, 35], the comparison of longline catches with UVCs from a submersible [25] or between shrimp trawl catches with UVCs by divers [19]. Generally the proportionality between CPUE and UVC estimates is not very good. In particular, as found for handlines in the present study, the relationship is not linear. It also varies considerably between species, the best correlation usually being found when all species are pooled, as in the present survey.

One of the drawbacks with handlines is also observed for longlines, namely the fact that it is not possible to extrapolate stock estimates at the family or species level in most instances. Indeed, a poor correlation between the catch (from an artisanal fishery) of some families (Lethrinidae and Lutjanidae in particular) and the estimates from UVC in the same zone was found in Fiji [13, 14].

Correlations between UVC and CPUE were on average rather good for longlines compared to the

results from handlines. The major reason for this is probably that the UVC work can be performed at the same time as the longline is set in the water. Therefore, fish movements are probably minimal. In contrast, the correlation used in the present study between UVC and CPUE of handlines (Ouvéa data) was based on data collected at different times of the day. This was because the handline operations were performed after sunset and the UVC during daylight hours. From observations (mainly stomach content analysis) made at Ouvéa, it was assumed that fish such as Lethrinidae and Lutjanidae probably swim some distance before starting to feed at night [17]. This distance has not been determined, but is likely to range from a hundred meters up to a few kilometers, with the largest fish covering the largest distances [11]. In such a case, the diurnal and nocturnal assemblages on near-reef bottoms may change substantially and thus explain the poor correlations found between handline CPUE and UVC estimates.

The use of handlines or longlines to estimate the characteristics of this type of stock is uncommon to date. In a review on models and methods in reef fishery assessment, the possible use of such gears for this purpose was not even mentioned [5], but the method has in fact been used on a number of occasions. Besides the work in the Maldives and the south-west lagoon of New Caledonia [2, 15] already cited, one should note the work in Hawaii [30] which has generated many applications to estimate deep water reef fish stocks in the Pacific [31]. One of the major advantages is that it becomes possible to use the yields of commercial or artisanal operations to have some idea of the stocks. However, one should be cautious in doing so. Indeed, commercial operations will choose the best spots and the best time for fishing, thus obtaining yields that may be much higher than those from an area as a whole determined by a comprehensive sampling design.

4.2. Comparison with other fisheries

4.2.1. Yields

The general yields for handlines in the north zone are in the upper limits of what is usually observed in shallow lagoonal areas (*table IX*). The three highest yields [12, 24, 36] (*table IX*) did not originate from experimental data designed to assess mean yields and were therefore probably upper limit values. All values above 5 kg·fisherman⁻¹·h⁻¹ came from places where fishing was very light or unexploited. In most of the exploited areas yields were 1–2 kg·fisherman⁻¹·h⁻¹ as found in the west and east zones of the present study. Such a difference between exploited and unexploited areas was also observed in the SW lagoon of New Caledonia when comparing the results from remote reefs [24] with those, 10 years later, from nearby exploited reefs [18]. Fishing pressure may have significantly reduced the number of fish available, but this may not be the only nor even the major cause. In

Table IX. Catch rates for handlines from various Indo-Pacific tropical shallow water reefs. All results are expressed as kg-fisherman⁻¹·h⁻¹. Results from places out of New Caledonia are ordered by decreasing yields.

Country	CPUE	Reference
Present study – West	1.6	this paper
Present study – North	6.8	this paper
Present study – East	1.8	this paper
New Caledonia –Ouvéa	6.9	[17]
New Caledonia – SW lagoon	10.0	[24]
New Caledonia – SW lagoon	2.6	[18]
Australia NW shelf	15.6	[36]
Norfolk	13.1	[12]
Nauru	5.8	Dalzell (unpubl.)
Fiji	2.3	Anderson in [8]
Micronesia – Chuuk Outer Banks	2.3	Diplock and Dalzell in [8]
Truck	2.3	Diplock and Dalzell in [8]
Maldives	1.8 ; 2.4	[2, 38]
Wallis	1.3	[37]
Philippines	0.6	[1]
Tonga	0.4	Munro in [8]

particular, it is known that fish may adapt quickly to a gear. During an experiment on the Great Barrier Reef, it was found that the target species, *Plectropomus leopardus*, would rapidly decrease in the catch around a reef newly opened to fishing [6]. UVC survey indicated, however, that the density of this target species did not decrease significantly, thus indicating that the fish were just no longer susceptible to the handlines. Therefore, it is possible that even light fishing pressure, such as found on the west or east zones of the present study [21] may be sufficient to result in a noticeable decline in the catch but not necessarily an equivalent decrease in stocks. However, work in Fiji [14] indicated that there may be a rapid decrease in UVC biomass at low levels of fishing effort, which suggests that these fish stocks may be very sensitive to exploitation.

Bottom longlines are not very often used in shallow waters in the tropical Indo-Pacific (*table X*). The yields of the present experiment are within the range of other studies. The ratios between longline and handline catches in the present survey, which were 5.4–5.6, were similar to those observed in the Maldives, with values of 5.7–7.0 [2, 38], but larger than that for the SW lagoon of New Caledonia of 3.2 [15, 18]. This suggests that gears have efficiencies that may vary between regions, as fishing pressure does not follow the same trends (highest in the Maldives and lowest in the Northern Province).

The findings of the present study (*table IV*) are in agreement with results from the south-west lagoon of New Caledonia [18] which indicated that there was a significant correlation between bottom longline CPUE by weight or number and the distance from the coast. This is a rather common result for reef fish, density (fish·m⁻²) or biomass (g·m⁻²) usually being well cor-

Table X. Catch rates of bottom longlines in the Indo-Pacific.

Country	CPUE (kg per100 hooks)	Reference
Present study – West	8.9	this paper
Present study – East	9.8	this paper
New Caledonia – SW lagoon	8.2	[15]
Maldives	10.3	[38]
Maldives	16.8	[2]
Sri Lanka	6.4	[4]
Indonesia	9.0	[20]

related to distance offshore [16, 22, 41] and therefore our results suggest that this may also be true for near-reef fishes. The present study indicates that CPUE and depth were correlated down to 15 m for the north and 25 m for west or east. Past these depths, correlations were either negative (handlines north) or did not exist (west and east longlines). In the SW lagoon [18] or in Ouvéa [17], highly significant increases of CPUE with depth were observed. Absence of correlation beyond a certain depth could be due to a change in substratum composition, in particular because there is more silt and less hard bottom.

4.2.2. Families, species

The catch composition observed in the present work is typical of handline and longline operations in the Indo-Pacific (*table XI*) and also see [9] for a review) where the four major families are also Lutjanidae, Lethrinidae, Serranidae and Carangidae. There is nevertheless some specificity to the present study. First, Lethrinidae dominated the catch, whereas in all other studies, Ouvéa and New Caledonia SW lagoon excepted, Lutjanidae was the dominant family. This indicates that New Caledonia may have higher levels of Lethrinidae than elsewhere as already suggested by earlier observations [24]. There are also differences in the composition between handline and longline (*table XI*), with longlines catching less Lutjanidae and more Carangidae in New Caledonia.

For all the areas surveyed in New Caledonia, *Lethrinus nebulosus* was the most common species captured by both handline and longline. The dominance of a single species over such a large area is unusual in the tropical Pacific. Other species with a wide distribution within New Caledonia are *Lethrinus atkinsoni*, *Lutjanus bohar*, *Diagramma pictum* and *Epinephelus cyanopodus*. However, species composition of the catch shows important regional differences within New Caledonia, thus reflecting changes in the ecology of these species. In particular, in the SW lagoon, among the five major species, are found *Bodianus perditio*, *Epinephelus maculatus* and *Gymnocranius euanus*, which do not figure in the five major species in the other surveys in New Caledonia. Similarly, *Epinephelus polyphkadion* was typical of the Northern Province; it was a major component of the catch in all three zones, whereas this species was

Table XI. Percentage of the catch (CPUE weight) for hook and line experiments in the Indo-Pacific.

Country	Gear	Serranidae	Carangidae	Lutjanidae	Lethrinidae	Reference
Present study North (NC)	HL	22	3	29	40	–
Present study West (NC)	HL	13	5	16	46	–
Present study West (NC)	LL	10	10	5	45	–
Present study East (NC)	HL	13	4	20	45	–
Present study East (NC)	LL	13	28	8	25	–
Ouvéa (NC)	HL	13	0.2	16	63	[17]
SW lagoon (NC)	LL	19	2	10	34	[15]
Maldives	LL	5	5	56	7	[2]
Maldives	HL	16	16	39	9	[2]
Kenya	HL	17		44	24	[3]
Sri Lanka	LL	9	26	27	26	[4]
Papua New Guinea	HL	10	14	26	14	[42]

HL: handlines; LL: longlines.

seldom caught at Ouvéa or in the SW lagoon [17, 18]. One should note that *E. polyphekadion* is a major species in the catch of reef fisheries closer to the equator, such as in the Tuamotu [26].

Most of the fish caught during these experiments were of large size. There are, however, important differences for a given species between regions in New Caledonia. In particular, *Diagramma pictum*, *Epinephelus cyanopodus* and *Lutjanus bohar* had the smallest average sizes in the west or east zones, whereas *Lethrinus nebulosus* and *L. atkinsoni* tended to be smaller on Ouvéa [17]. Differences in fishing pressure are unlikely to cause these variations, since these fish size variations differ depending on species and region considered. It is difficult to know if such differences are due to the environment or are linked to different stocks. Indeed, genetic differences have been observed for three species between the SW lagoon and the Northern Province [29]. The analysis of biological data for *L. nebulosus* indicated also that they mature in Ouvéa at half the weight as in the SW lagoon [11]. Similar findings are documented for Lutjanidae in Australia (Williams, pers. comm.). In some cases, differences may be due to fishing depth, because the size of many species increases with depth [17, 18]. It is probable that migration to deeper waters occurs with age, but there may also be diurnal movements of larger fish from shallow to deeper areas for feeding as suggested for *L. nebulosus* [11].

4.3. Comparison with coral reefs and among biotopes

The UVC biomass estimates of line fishes on adjacent coral reefs [23] were on average between five and ten times larger than on the soft bottoms surrounding these reefs. However, despite this relatively high biomass, reefs did not contribute more than 16 % of the total line fish stock. This was due to the small area covered by reefs (less than 4 % of total area). Most of the line fish stock was found on the lagoon bottoms,

but the lower biomass in this biotope makes it a more difficult fishing zone than reefs. The importance of soft bottoms for reef fish in this zone has already been demonstrated from trawl surveys [39]. The two major consequences are, first, that most of the fishing effort will take place on reefs or very near reefs, and second, that soft bottoms may be a major reservoir for line reef fish. This implies that a depletion of these reef stocks may not be easy to detect, as fish from nearby areas may come in to replace departures due to fishing mortality, unless the soft-bottom habitat is only of very limited extent.

The correlation between CPUE from handlines and the UVC estimates from nearby reefs indicates that there are links between the communities found on reefs and those on the nearby soft bottoms, as found on Ouvéa [17]. More importantly, there are probably feeding migrations occurring between these adjacent biotopes. With the present data, it is not possible to assess the nature or the importance of these migrations. It has been suggested [11] that *Lethrinus nebulosus* in Ouvéa lagoon probably rests during the day near reefs and that it swims away from the reefs at night to feed at distances that are proportional to the size of the fish. Similar migrations could occur in the present case, the largest individuals being found at the greatest depths. In our study there was also an increase in size for most species between fringing and barrier reefs. Several hypotheses may explain this difference in size [22]; in particular, it could be due to either differences in growth rates, offshore migration with age or both.

Line fish are the most targeted species in New Caledonia by subsistence fishing [21] and one of the most important groups in the commercial fisheries. Their uneven spatial distribution (biomass higher on reefs than on the other biotopes but stocks higher in the latter) and their ability to migrate make it difficult to assess the effects of fishing on this resource.

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