Synopsis of the biology and ecology of *Pomadasys argenteus* (Haemulidae) in New Caledonia

by

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ABSTRACT. - *Pomadasys argenteus* (Forsskål, 1775) is a major commercial and subsistence species of shore fish in most of its range (East Africa to Fiji) but little information is available on its biology and ecology. The present study investigates the major biological and ecological traits of this species in New Caledonia, on the eastern border of its range. This species was mainly found in mangroves and to a lesser extent on nearby soft bottoms. Most of the fish were found in shallow waters (< 5 m), the deepest record being 28 m. Abundance varied within habitats through the year, with fish becoming more abundant on soft bottoms during the reproductive season, which occurs between July and December. The largest specimen was 42 cm FL and 1150 g. Females were more abundant (73% of the sexed population) and larger than males, the latter never exceeding 34 cm FL. Both sexes matured at the same size (16-18 cm). A higher proportion of females was found in the mangroves than on soft bottoms. However, the proportion of males and females ready to reproduce was similar in both habitats. Diet showed little diversity and was mainly composed of crabs and to a lesser extent shrimps, bivalves and annelids. Length-weight relationships varied between sexes, with males being slightly heavier than females of the same size. Growth was estimated by analyzing daily and seasonal otolith increments which were validated by a combination of methods. An asymptotic growth formula was fitted to the data: Length (mm FL) = $420*(1 – e^{-0.346*(age-0.161)})$, where age is given in years. Growth was found to be slower than in most other studies, except in Kuwait waters. There was no significant difference in growth between sexes.

RÉSUMÉ. - Synopsis sur la biologie et l'écologie de *Pomadasys argenteus* (Haemulidae) en Nouvelle-Calédonie.

Pomadasys argenteus (Forsskål, 1775) est une espèce d'intérêt majeur pour la pêche commerciale et de subsistance sur l'ensemble de son aire de répartition (Afrique de l'Est à Fidji), mais peu d'information est disponible actuellement sur sa biologie et écologie. Notre étude porte sur les principaux traits biologiques et écologiques de cette espèce en Nouvelle Calédonie, sur la marge est de son aire de répartition. Cette espèce a été observée surtout en mangrove et à moindre degré sur les fonds meubles adjacents. La plupart des poissons ont été trouvés dans peu d'eau (< 5 m), la capture la plus profonde ayant eu lieu par 28m. L'abondance a varié au sein des habitats au cours de l'année, les poissons devenant plus abondants sur les fonds meubles durant la reproduction entre Juillet et Décembre. Le plus grand poisson mesurait 42 cm (LF) et pesait 1150 g. Les femelles étaient plus abondantes (73% des échantillons sexés) et plus grandes que les mâles, ces derniers n'excédant pas 34 cm LF. Les deux sexes deviennent mâtures à la même taille (16-18 cm). Une proportion plus importante de femelles a été observée dans les mangroves comparées aux fonds meubles. La proportion de mâles et de femelles mâtures était cependant similaire dans les deux habitats. Les aliments étaient peu diversifiés, se composant surtout de crabes et de façon moindre de crevettes, bivalves et annélides. Les relations longueur-poids varient en fonction du sexe, les mâles étant plus lourds que les femelles à taille égale. La croissance a été estimée en analysant les accroissements journaliers et saisonniers des otolithes. Ces méthodes ont été validées par un ensemble de méthodes. Une courbe de croissance asymptotique a été ajustée aux données : Taille (mm LF) = $420*(1 – e^{-0.346*(âge-0.161)})$, où l'âge est donné en années. La croissance est plus lente que dans la plupart des autres études disponibles, sauf au Koweit. Aucune différence de croissance entre les sexes n'a pu être décelée.

Key words. - Haemulidae - *Pomadasys argenteus* - PSE - New Caledonia - Growth - Reproduction - Diet.

Haemulidae represent an important family of tropical fishes and are often of high economic importance (McKay, 1998). Within this family the Pomadasynae are found mainly in inshore waters, particularly in mangroves and soft-bottom habitats. Some species within this sub-family are highly priced food fishes in most of their geographical range. They also often represent one of the major components of the fish biomass in the tropical coastal waters of continental shores in the Indo-Pacific (Thollot, 1996). Despite this economic and ecological importance there is still a lack of detailed information on the biology and ecology of many of these species. *Pomadasys argenteus* (Forsskål, 1775) is one of the larger species within this sub-family, reaching 60 cm SL (McKay, 1998). It has a wide geographic range, found from the Red Sea to Fiji. It usually lives in coastal waters, and is caught mainly in mangroves and soft-bottoms by gill-net, hook, trap or spear (McKay, 1998). It is a major food fish in most of its range, with over 1500 tonnes annual catch being reported by FAO, mainly from Malaysia and the Persian Gulf, but it is also a major target in both commercial and rec-

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reational fishing in Australia (Ley *et al.*, 2002). It is known to feed mainly on benthic invertebrates such as bivalves, shrimps and polychaetes (Sheaves and Molony, 2000) in Australia and crabs in New Caledonia (Kulbicki *et al.*, 2005). Several growth studies show that this species has a relatively rapid growth (Nammalwar, 1974; Dwiponggo, 1986; Brothers and Mattews, 1987; Mathews and Samuel, 1991; Khan *et al.*, 1997). Little is known about the reproduction of this species (Abu-Hakima, 1984) or of its movements within coastal waters. The data available at present on the biology and ecology of this species show some geographic variations.

The aim of this article is to provide basic information on the growth, diet, reproduction and relative abundance of this species within the coastal waters of New Caledonia where this species is an inshore fishery target (Thollot, 1996). It is the only representative of the Pomadasynae in New Caledonia (Fricke and Kulbicki, 2006). It should be however noticed that the data presented here is the result from a large number of surveys which were not specifically designed to collect *Pomadasys argenteus*. This species happened to be numerous in several types of sampling methods and biotopes and we therefore felt that condensing this information could be useful for the management of this poorly known species in New Caledonia and other countries of its wide geographical range.

MATERIALS AND METHODS

Sampling area

New Caledonia is a tropical island located approximately 2000 km north of New Zealand and 1800 km east of Australia. This 400 km long island harbours a wide range of marine habitats, in particular estuaries, mangroves, soft bottoms, sea grass beds, algae beds and reefs. There is an extensive lagoon surrounding the main island (Grande Terre) with a barrier reef over 1600 km long, which makes it one of the largest in the world.

Abundance

IRD ("Institut de Recherche pour le Développement") has conducted numerous experimental fishing trials (Tab. I; Fig. 1) in New Caledonia (Kulbicki, 2006) using trawls (Wantiez, 1992), gill nets, fyke nets (Thollot, 1996), rotenone, hand lines and bottom long lines (Kulbicki, 1995, 1997; Kulbicki *et al.*, 2000). All the experimental fishing methods were conducted according to preset protocols (Kulbicki, 2006). Numerous underwater visual surveys (UVC) have also been conducted (Tab. I; Fig. 1) mainly on reefs, sea grass beds and algae beds (see Labrosse *et al.*, 2001 for the UVC protocol).

Table I. - Methods used to census fish assemblages in New Caledonia (number of stations). UVC: Underwater Visual Census, expressed as number of transects (50 m x 10 m). Rotenone: fish collected with rotenone in 300 m² areas surrounded by a fine mesh net. Set nets: gill nets (100 m long x 3 m high) and fyke nets (50 m long leading net). Trawl: shrimp trawl (30 min haul) and fish trawl (23 min haul). LongLine: bottom longline (100 hooks). HandLine (2 hours x 2 fishermen) [*Méthodes utilisées pour échantillonner les peuplements de poissons en Nouvelle-Calédonie (nombre de stations). UVC : comptages visuels en plongée, exprimés en nombre de transects (50 m x 10 m). Roténone : poissons collectés par roténone sur des stations de 300 m² entourées de filets à maille fine. Filets fixes : filets maillants (100 m x 3 m) et capéchades (50 m de filet barrage). Chaluts : à crevette (traits de 30 min.) et à poisson (traits de 23 min.). Palangre : palangre de fond (100 hameçons). Lignes à main (2 heures x 2 pêcheurs).*]

	UVC	Rotenone	Set Nets	Trawl	LongLine	HandLine
Reef	2520	64	-	-	-	130
Seagrass & Algae	190	8	-	-	55	120
Soft Bottom	145	-	-	446	911	260
Mangrove	15	10	298	-	-	-

Amongst the fish caught during these fishing trials a restricted number of specimens were analysed for their biology (stomach content, gonads, length, weight). Otoliths were extracted for a restricted number of species and only if there were sufficient numbers. This work spanned from 1984 to 2001. *Pomadasys argenteus* is one of the species for which the number of available specimens is the highest (881 fish examined; 895 fish caught or observed underwater). When it was necessary to compare the number of fish caught by the various methods, catch was first reported per sampling unit (CPUE), then for each category considered (depth, month, time of day), the CPUE were divided by the mean CPUE for the gear and category.

Stomach content

Each prey item was identified in the field and allocated to one of the following broad taxonomic groups, hereafter referred to as prey types: crustaceans (crabs, shrimps, others), molluscs (gastropods, bivalves, others), echinoderms (mainly urchins), annelids, fish. The percentage of the volumetric contribution (%V) made by each prey type to the total volume of the stomach contents was estimated for each individual (volumes were used as indicated by Hyslop, 1980). Only the four most important prey types (in %V) in a stomach were noted, as in most cases, this accounted for the entire stomach content. Only fishes > 130 mm FL were examined for diet because identifying in the field prey items on smaller fishes is not reliable.

Gonads

Gonads were examined visually. Fish were sexed and gonads were classified into the following classes: I: immature; II: early level; III: developing; IV: Late developing; V: Ripe/running; VI: spent.

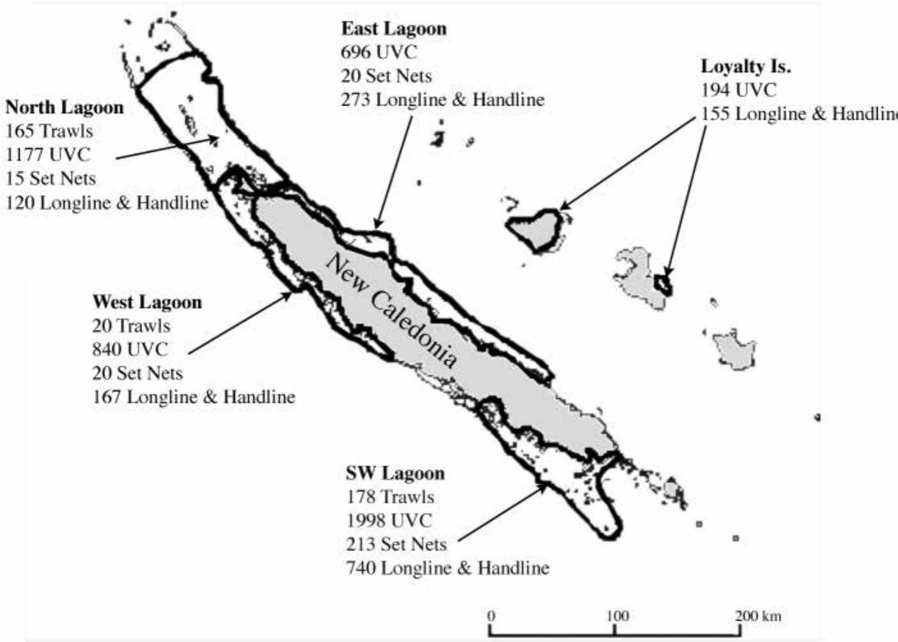

Figure 1. - Spatial distribution of the sampling effort for coastal fishes in New Caledonia. Rotenone stations all occurred in the SW lagoon. *[Distribution spatiale de l'effort d'échantillonnage des poissons côtiers en Nouvelle-Calédonie. Les stations de roténone ont toutes eu lieu dans le lagon S.O.]*

Otoliths

A total of 169 pairs of otoliths (sagittae) were analysed with 55 pairs from fish smaller than 23.5 cm FL, this size corresponding roughly to the first year of age (Nammalwar, 1974; Dwiponggo *et al.*, 1986; Mustaffa, 1999). Sagittae were embedded in Epoxy resin. A thin transverse section containing the core was then cut out with a low-speed diamond saw. The embedded section of the otolith was glued with thermal glue to a 1 x 1 cm piece of glass fixed on a microscope slide (Secor *et al.*, 1992). The side of the block containing the sectioned sagitta was ground rapidly with wet sandpaper of 1200 µm grit size and then polished up to the otolith core using successively an aluminium oxide slurry of 3, 1 and 0.3 µm on polishing cloths. When the core was reached the preparation was cleaned, dried, turned and prepared the same way on the other side. Finished preparations were 50-100 µm thick.

Sagittae preparations were observed at x1000 magnification with a light microscope equipped with a colour video camera. Daily increments were counted manually on a video monitor. The dorsal axis of the otolith appeared most appropriate for counting the number of increments in transverse preparations. On each preparation, the same reader performed a minimum of two complete counts: one count starting at the first increment after the core and towards the otolith edge, the second starting from the otolith edge towards the core. The average of the two counts was retained.

Seasonal rings were counted along the sulcus on whole otoliths for fishes larger than 23.5 cm FL using a binocular microscope (x 40 magnification). For the smaller fishes seasonal rings were counted on the otolith slices before they were polished (approx. 300 microns thickness) using a binocular microscope (x 100 magnification).

Validating the seasonality of the rings was performed with three methods. The first one considered the Relative Marginal Distance (RMD) on the smaller fishes (< 23.5 cm FL). RMD is the ratio of the distance to the edge of the last dark ring to the distance separating the last two rings (Panfili *et al.*, 2002). Distances were estimated using the TNPC software (LASAA-IFREMER Brest-France). Measurements were performed under a x 100 magnification. This method has been widely used in the analysis of cyclical macrostructures (Machias *et al.*, 2002; Santana da Sylva *et al.*, 2006). This method yields good results when distances can be accurately estimated and when the rings show up at the same time on all fishes. The second method looked at the edge of the otolith, calculating for each month the proportion of dark rings compared to all rings (Yosef and Casselman, 1995; Panfili *et al.*, 2002; Santana da Sylva *et al.*, 2006). The evolution of this percentage through time is theoretically cyclical, with usually one maximum per year. In some cases two peaks can be observed, thus indicating the formation of two rings/year. The last validating method compared the number of daily increments and of seasonal rings on the smallest fishes (< 23.5 cm FL). A regression allows then to estimate how many daily increments are needed on average to separate two dark rings.

Growth

Growth was estimated by correlating the estimated age (as number of days estimated either from the number of daily increments (fishes less than 23.5 cm FL) or from validated darks rings (fishes > 23.5 cm) with the observed length.

A von Bertalanffy model [1], the most common model used in fisheries research, was fit to the data with the L_{inf} fixed at 420 mm as 95% of the maximum length in the whole sample. The Levenberg-Marquardt routines of the Statistica 7 package were used.

$$L_t = L_{inf}*(1-\exp(-K(t-t_0))) \quad [1]$$

with L_t: fish at time t; L_{inf}: the maximum length the species can reach in the region; K: growth coefficient; t_0: theoretical age when fish length equals 0.

RESULTS

Habitat

Pomadasys argenteus was most frequently observed or caught in mangroves when using set nets (gill or fyke nets), where it represented 6.2% of the catch in weight (Tab. II). It was also caught on soft bottom by trawls, handlines and longlines, although the species only represented between 0.11 and 0.19% of the catch in weight (Tab. II). This species was never observed on reefs despite a large sampling effort in this habitat (> 2 million fishes observed) and only once on a seagrass bed along the coast (> 100,000 fishes observed). Fish were caught in shallow waters (< 5 m) by set nets, beyond that depth the CPUE was maximal for trawls and lines between 5 and 10 m with a second spike in CPUE at 15-20 m (Tab. III). It should be noted that no fish were caught deeper than 28 m despite intense sampling effort beyond that depth (193 trawl and 318 line stations). The catch in the mangroves was maximum early in the year, then declined in the winter (July-September), whereas the catch on soft bottoms was minimal in April-June and maximum in October-December (Fig. 2; Tab. III). There is no major trend in the catch during the day for soft-bottoms, whereas in the mangroves the catch is maximum between 0-4 am an decreases all day until 20-24 pm when catch is minimal (Tab. III).

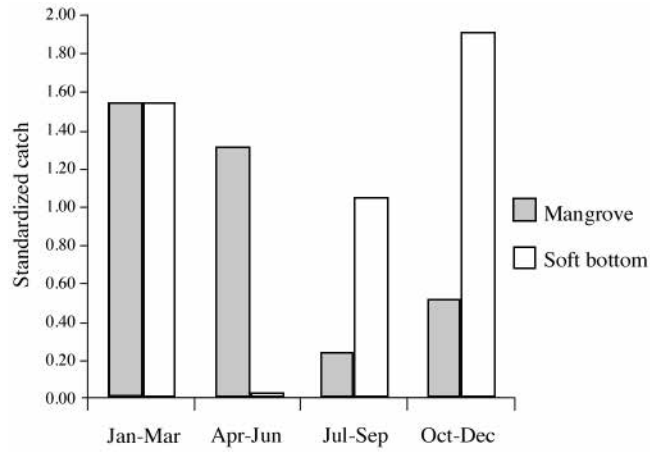

Figure 2. - Habitat distribution of *Pomadasys argenteus* according to season in New Caledonia. Catch was standardized for each fishing method (see material and method section). *[Habitat de* P. argenteus *selon les saisons en Nouvelle-Calédonie. Les captures sont standardisées pour chaque méthode de pêche (voir matériel et méthodes).]*

Table II. - *Pomadasys argenteus* observed (UVC) or caught in New Caledonia during experimental observations and fishing experiments. The first number represents the number of individuals, the second number represents the contribution (%) of *P. argenteus* to total weight or biomass. [Pomadasys argenteus *observés sous l'eau ou capturés en Nouvelle-Calédonie. Le premier chiffre correspond au nombre d'individus, le second représente la contribution (%) de* P. argenteus *au poids total ou à la biomasse.]*

	UVC	Rotenone	Set Nets	Trawl	LongLine	HandLine
Reef	0; 0	0; 0	-	-	-	0; 0
SeaGrass & Algae	1; $<10^{-6}$	0; 0	-	-	0; 0	0; 0
Soft Bottom	-	-	-	212; 0.19	32; 0.17	24; 0.11
Mangrove	2; $<10^{-3}$	5; 0.03	619; 6.2	-	-	-

Table III. - Fishing effort (number of stations) and catch per unit effort in mangroves and soft bottoms according to depth, season and time of day. [*Effort de pêche (nombre de stations) et capture par unité d'effort dans les mangroves et sur les fonds meubles en fonction de la profondeur, saison et heure du jour.]*

DEPTH	0-5 m	5-10 m	10-15 m	15-20 m	> 20 m	-
Trawls	2; 0	50; 1.68	84; 0.67	47; 1.02	241; 0	-
Lines	4; 0	169; 0.10	294; 0.010	284; 0.11	699; 0.009	-
Set Nets	298; 2.08	-	-	-	-	-
SEASON	Jan.-March	April-June	July-Sept.	Oct. - Dec.	-	-
Trawls	24; 1.17	136; 0.01	156; 0.21	108; 1.39	-	-
Lines	261; 0.092	328; 0	372; 0	498; 0.064	-	-
Set Nets	74 ; 1.91	80 ; 3.19	44 ;0.43	70. 0.96	-	-
TIME	0:00-4:00	4:00-8:00	8:00-12:00	12:00-16:00	16:00-20:00	20:00-24:00
Trawls	-	41 ; 0.59	145 ; 0.41	141 ; 0.52	84 ; 0.45	13 ; 1.23
Lines	-	186; 0.002	384; 0	344; 0.084	537; 0.052	-
Set Nets	17 ; 2.6	52 ; 2.7	104 ; 1.9	30 ; 1.5	37 ; 1.0	28 ; 0.69

Size distribution

The largest fish observed was 430 mm FL with a weight of 1080 g and the smallest was 40 mm FL with a weight of 1 g. The size distribution was significantly different between habitats (Kolmogorov-Smirnov test, p < 0.001) (Fig. 3). Fish less than 120 mm were only observed in mangroves. It should be noted that the mesh of the cod-ends of the trawls was very fine and therefore that small individuals from many other species were caught by trawls. Two modes were observed in mangroves (80 mm and 240 mm FL) whereas on soft bottoms only one mode was observed at 160 mm FL with a tailing distribution up to 430 mm. An analysis per depth classes shows similar

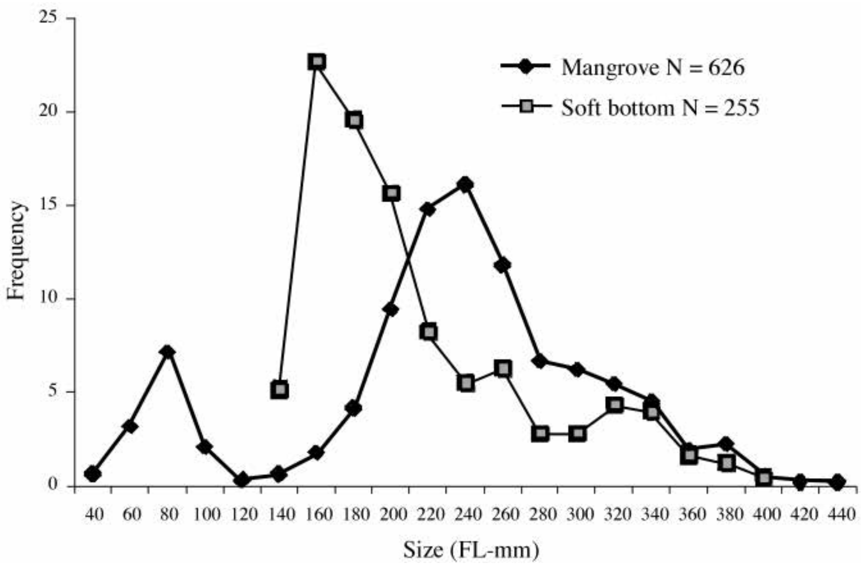

Figure 3. - Size distribution according to habitat of *Pomadasys argenteus* in New Caledonia. *[Fréquences de taille selon l'habitat de* P. argenteus *en Nouvelle-Calédonie.]*

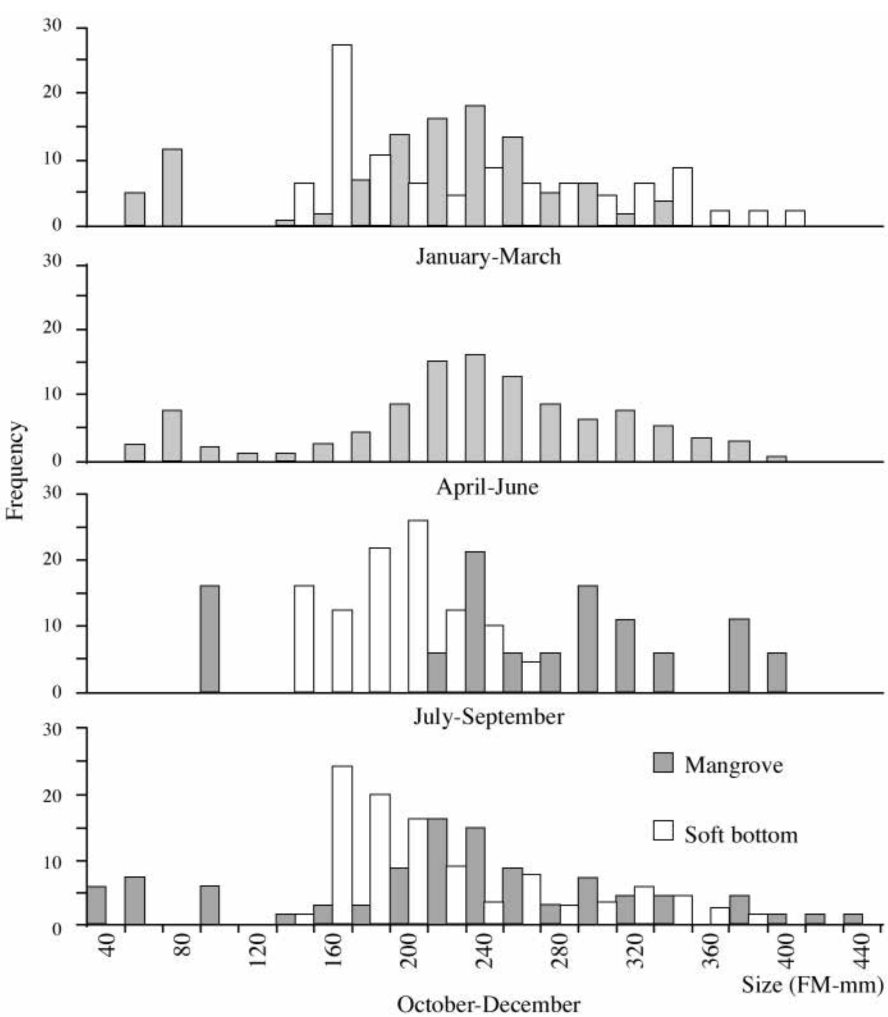

Figure 4. - Size distribution of *Pomadasys argenteus* according to season and biotope. *[Distribution des tailles de* P. argenteus *selon la saison et le biotope.]*

results with two modes at 80 and 240 mm FL for waters shallower than 5 m, one mode between 160 and 180 mm FL for all other depth classes and a second mode at 330 mm FL for waters deeper than 15 m. There were significant changes in the size distribution according to seasons (Fig. 4). In particular smaller fishes are observed between October and June, but these fishes are not recorded between July and September. This corresponds to the low catch of these fishes in the mangroves. From January to September there is a mode at 240 mm while a strong peak at 180 mm appears between October and December.

Table IV. - Equations of the length-weight relationships. Length are in cm and weight in g. Weight (g) = A Length (cm)^B; *: estimated weight (g) for a 50 cm FL fish. *[Équation longueur-poids. Longueur en cm et poids en g. Poids (g) = A taille (cm)^B ; * : poids estimé (g) pour un poisson de 50 cm LF.]*

	A	B	N	r^2	Weight at 50 cm*	Country	Reference
Unsexed	0.0229	2.9371	869	0.994	2243	New Caledonia	Present Study
Male	0.0408	2.8258	195	0.978	2578	New Caledonia	Present Study
Female	0.0307	2.8866	534	0.978	2460	New Caledonia	Present Study
Unsexed	0.0424	2.66			1402	South Africa	Torres, 1991
Unsexed	0.0566	2.762	190		2789	Kuwait	Hussain and Abdullah, 1977
Unsexed	0.0520	2.769			2633	Bangladesh	Mustaffa, 1999
Unsexed	0.0267	2.855			1893	Indonesia	Pauly *et al.*, 1996
Female	0.0150	2.999	200		1868	Yemen	Al Sakaff and Esseen, 1999
Male	0.0090	3.138	214		1930	Yemen	Al Sakaff and Esseen, 1999

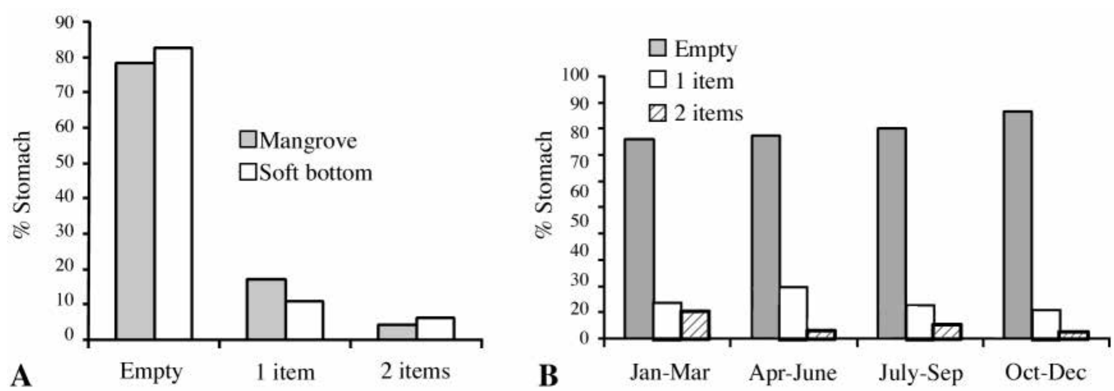

Figure 5. - Proportion of empty stomachs and of stomachs with either one or two food items according to habitat (**A**) or season (**B**). N = 795 fishes. [*Proportion d'estomacs vides et d'estomacs avec un ou deux aliments, selon l'habitat (**A**) ou la saison (**B**). N= 795 poissons.]*

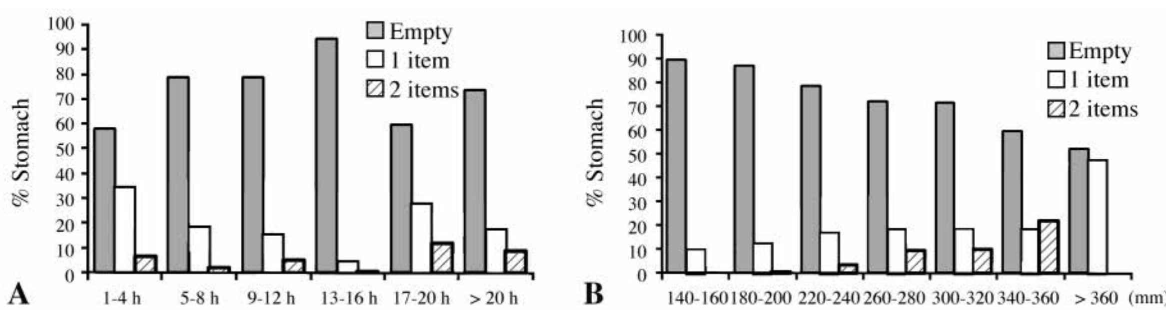

Figure 6. - Proportion of empty stomachs and stomachs with either one or two food items according to time of day (**A**) or fish size (**B**). Sizes as FL. N = 795 fishes. *[Proportion d'estomacs vides et d'estomacs avec un ou deux aliments, selon l'heure du jour (**A**) ou la taille des poissons (**B**). Taille LF. N= 795 poissons.]*

Length-weight relationship

Length-weight relationships were estimated for all fishes and also separately for males and females (Tab. IV). Males were significantly larger than females (covariance analysis, $p < 0.001$), males being 5.4% heavier than females on average.

Diet

Only 17.5% of the fish (139 specimens/795 fish examined) had food in their stomachs. The proportion of full stomachs varied according to habitat, season, time of day and size. The proportions of food items in the stomachs varied with habitats (χ^2 test, $p = 0.04$; Fig. 5A). The proportion of full stomachs was slightly higher in the mangroves (21.6%) than on soft bottoms (17.3%), however the difference was not significant (χ^2 test, $p > 0.05$) (Fig. 5A) fish feeding on soft bottoms more frequently had two food items (probably because on average fish were larger on soft bottoms). The proportion of empty stomachs increased significantly from January to December (χ^2 test, $p < 0.001$)

(Fig. 5B), the number of stomachs with one item was the highest in the January-March period (χ^2 test, $p < 0.001$) (Fig. 5B). The proportion of empty stomach changed significantly during the day (χ^2 test, $p < 0.001$) (Fig. 6A), with the proportion of full stomachs higher at night between 17 and 20 h and 0 and 4 h. The proportion of full stomachs increased significantly with fish size (χ^2 test, $p < 0.001$) (Fig. 6B).

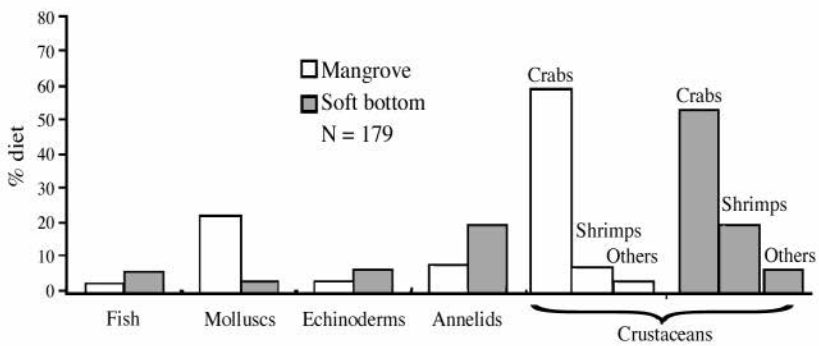

Figure 7. - Food items according to habitat for *Pomadasys argenteus* in New Caledonia. *[Proies selon l'habitat de* P. argenteus *en Nouvelle-Calédonie.]*

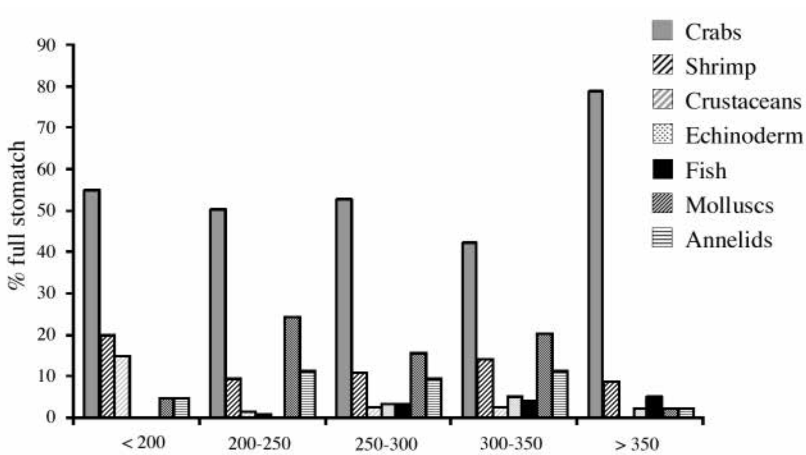

Figure 8. - Food items according to size class (FL in mm) for *Pomadasys argenteus* in New Caledonia. *[Proies selon la classe de taille (mm LF) pour* P. argenteus *en Nouvelle-Calédonie.]*

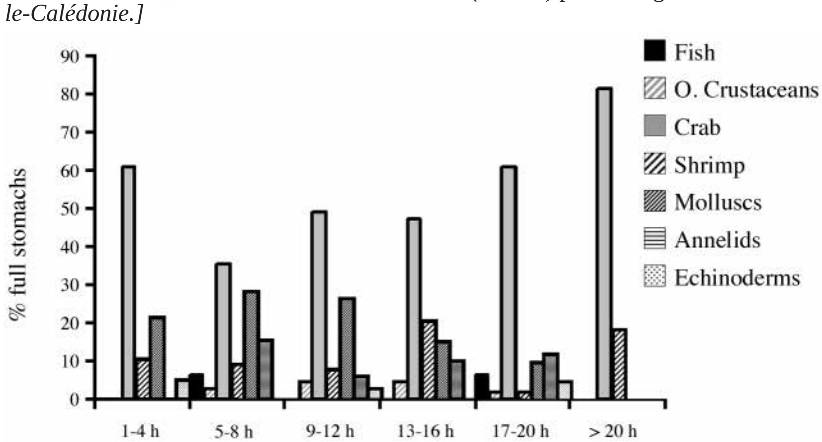

Figure 9. - Food items according to time of day for *Pomadasys argenteus* in New Caledonia. *[Aliments selon l'heure du jour pour* P. argenteus *en Nouvelle-Calédonie.]*

A total of 15 prey items were found, but only four items were frequent and abundant: crabs (53% by volume), bivalves (16%), shrimps (12%) and annelids (9%). Diet was not diversified as 75.5% of the stomachs contained only one prey item, 24% two prey items and 0.5% 3 prey items. The diversity of the prey items was higher at the beginning of the night. The proportion of stomachs with 2 prey items increased significantly with fish size (χ^2 test, $p < 0.001$) except for the largest fishes (> 360 mm) which had only one item in the stomach. The food items were less diversified at night than during the day.

Prey items varied according to habitat, size, time of day and season. There were significantly more molluscs and crustaceans in the stomachs of fishes caught in mangroves than soft bottoms (χ^2 test, $p < 0.001$) (Fig. 7). On the other hand, there were significantly more annelids in the stomachs of fish caught on soft bottoms (χ^2 test, $p = 0.02$). Shrimps made a significantly higher proportion of the crustaceans on soft bottoms than in mangroves (χ^2 test, $p < 0.001$). Variations in diet according to size were less pronounced (Fig. 8). However, no molluscs were found in the diets of fish < 200 mm and no fish were found in the diets of fish < 250 mm. Crabs made a higher proportion of prey for the largest fishes (> 350 mm) (χ^2 test, $p < 0.001$). The proportion of crabs in the diet changed significantly during the day (χ^2 test, $p < 0.001$), being highest in the early night (20-24 h) (Fig. 9). Fish were only eaten at dawn and dusk (5-8 h and 17-20 h). There were important seasonal differences in prey items (Fig. 10). In particular, crabs were significantly more important in April-June (χ^2 test, $p < 0.001$), whilst molluscs dominated the July-September period (but not significantly) (Fig. 10).

Reproduction

Males were only 27% of the sexed fishes. There was a significant difference in the size distribution of males and females (Kolmogorov-Smirnov test, $p < 0.001$). Males never exceeded 340 mm FL whereas females reached 430 mm (Fig. 11A). The difference in weight was even greater, with males weighing at most 650 g and females reaching 1150 g. As a conse-

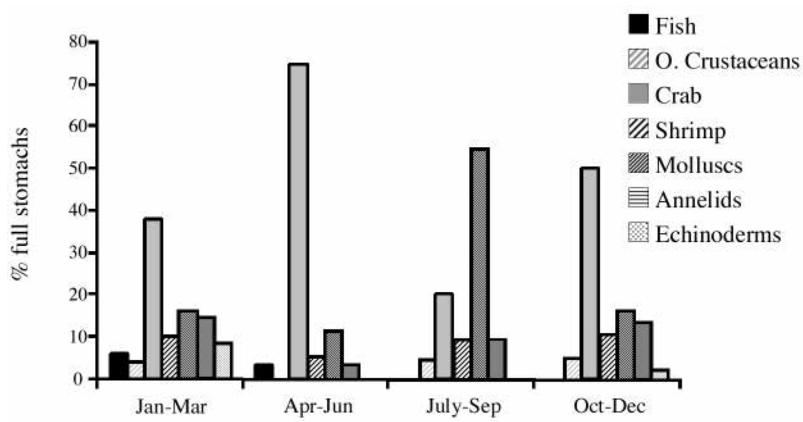

Figure 10. - Food items according to season for *Pomadasys argenteus* in New Caledonia. *[Aliments selon la saison pour* P. argenteus *en Nouvelle-Calédonie.]*

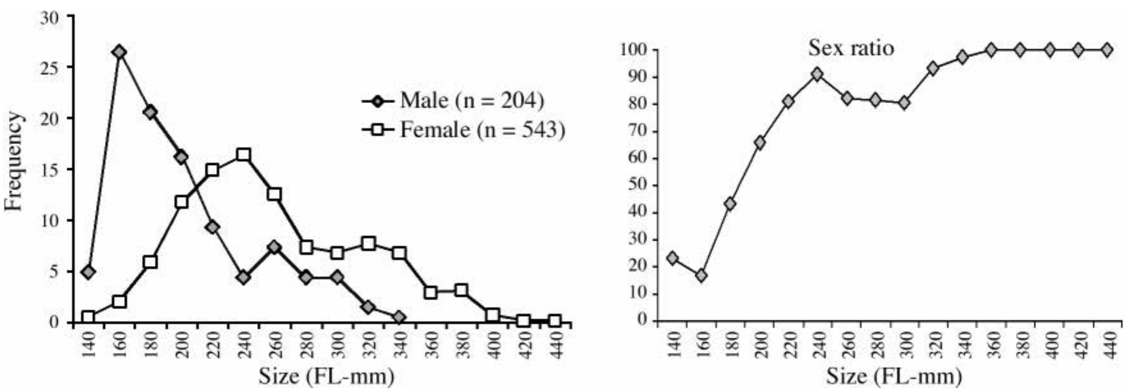

Figure 11. - Size distribution according to sex (left graph) and sex ratio according to size (right graph) for *Pomadasys argenteus* in New Caledonia. *[Fréquence de taille selon le sexe (graphe de gauche) et le sex-ratio selon la taille (graphe de droite) pour* P. argenteus *en Nouvelle-Calédonie.]*

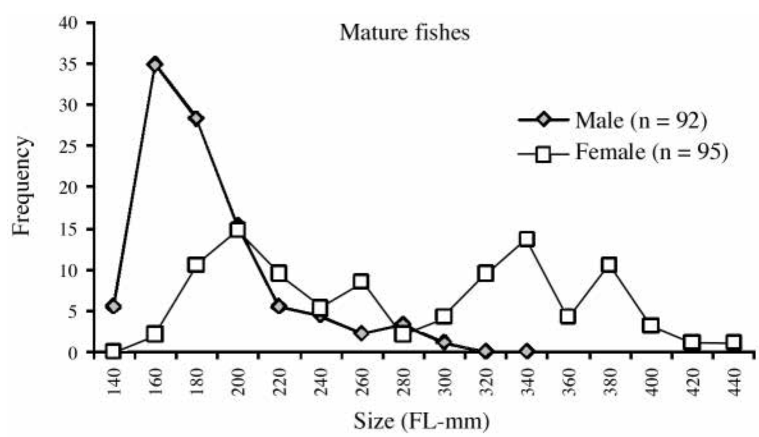

Figure 12. - Number of mature fishes according to size for *Pomadasys argenteus* in New Caledonia. Mature fishes were defined as fish with a gonadic index above 4. *[Nombre de poissons matures selon la taille de* P. argenteus *en Nouvelle-Calédonie. Les poissons matures sont définis comme ceux ayant un index gonadique supérieur à 4.]*

quence, the proportion of females increased as size increased (Fig. 11B). Both sexes were first mature between 140 and 160 mm FL (Fig. 12), the size distribution of mature males being characterized by a log-normal pattern, whereas for mature females there were several modes. Gonads were mature between July and December (Fig. 13) for over 60% of fish throughout the reproductive season. Females were mature slightly earlier than males. Males and females were found in significantly different proportions between depths (χ^2 test, $p < 0.001$) (Fig. 14). Females were mainly found inshore in mangroves, whereas males were more frequent in the catch on soft bottoms (χ^2 test, $p < 0.001$) (Fig. 15A). Juveniles were found either in mangroves or in the deepest waters (> 15 m) (χ^2 test, $p < 0.001$). The proportion of mature males and females was similar for both mangroves and soft bottoms (χ^2 test, $p > 0.05$) (Fig. 15B).

Growth

Otolith samples were taken from fishes between 40 and 380 mm. There was no indication of a modal progression according to season (Fig. 4). Microstructures ("daily" increments) were clearly distinguished on otolith slices for fish < 23.5 cm. For larger fishes these microstructures became increasingly difficult to count near the margins. Macrostructures ("seasonal" increments) were always easy to identify, especially along the sulcus, either on 300 micron sections (fishes < 23.5 cm) or on the whole otoliths.

Increment validation

The value of RMD was larger than 0.5 throughout the year and this index showed no clear seasonal variation. Clear and dark rings were certainly easy to identify, but along the margin the limit between clear and dark rings was often difficult to position because of diffraction. In addition, on large fish these rings were so narrow that measurements became less precise and relative errors increased. The strong variation of results with season suggested that the formation of these rings was probably spread through time and not synchronous amongst all fishes. Analysing the otolith margin indicated two peaks (Fig. 16) in the ratio of dark margins, one in summer (February) and one during the cold season (July-October), suggesting the formation of two dark rings per year. However this ratio never fell to zero thus indicating that year round there were at least some fishes forming dark rings.

A regression (Fig. 17) between the number of microstructures ("daily" rings) with macrostructures ("seasonal" rings) indicated a slope of 0.00523, which was not significantly different ($p < 0.0001$) than 0.00548, the value that corresponded to 2 seasonal rings/year. This slope tends therefore to confirm the previous result on margin analysis which suggested also two seasonal rings /year.

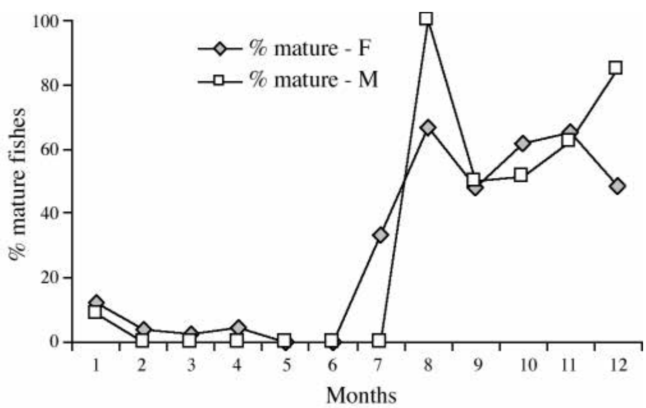

Figure 13. - Proportion of mature fishes along the year. Number of mature Males (M): 92; Number of mature Females (F): 95. *[Nombre de poissons matures le long de l'année. Nombre de mâles matures (M) = 92 ; nombre de femelles matures (F) = 95.]*

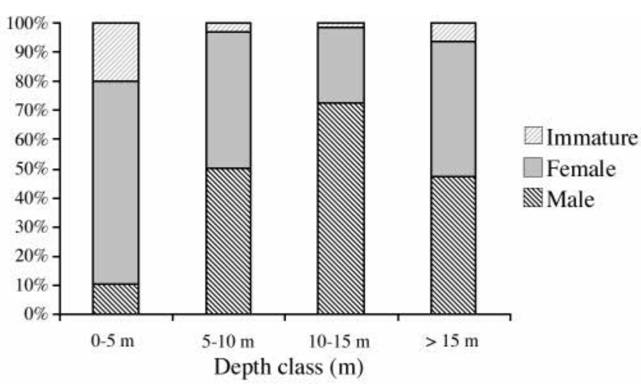

Figure 14. - Sexual distribution of fish with depth. [*Distribution des sexes en fonction de la profondeur.]*

Growth curve

To estimate length at age the number of microstructures ('daily' rings) were used for fish < 23.5 cm and macrostructures ('seasonal' rings) for fishes > 23.5 cm. It was assumed that microstructures were deposited daily and that two macrostructures were deposited each year. This resulted with the following growth curve equation:

Length (mm FL) = $420*[1 - \exp^{(-0.346*(age-0.161))}]$ where age is given in years. There was no difference in growth according to sex (Fig. 18).

DISCUSSION

Pomadasys argenteus was initially reported from New Caledonia as *P. hasta* (Fourmanoir and Laboute, 1976). In this country, this species is caught mainly with gill nets within or near the mangroves, with a few specimens caught by hook and line. It is an important food fish but it is seldom

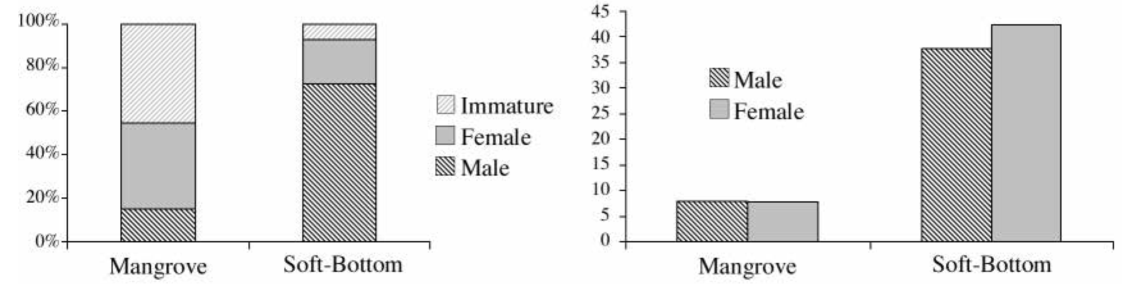

Figure 15. - Sexual distribution of fish according to habitat for all fish (left graph) and mature fishes only (right graph). *[Distribution des sexes des poissons selon l'habitat pour tous les poissons (graphe de gauche) et les poissons matures (graphe de droite).]*

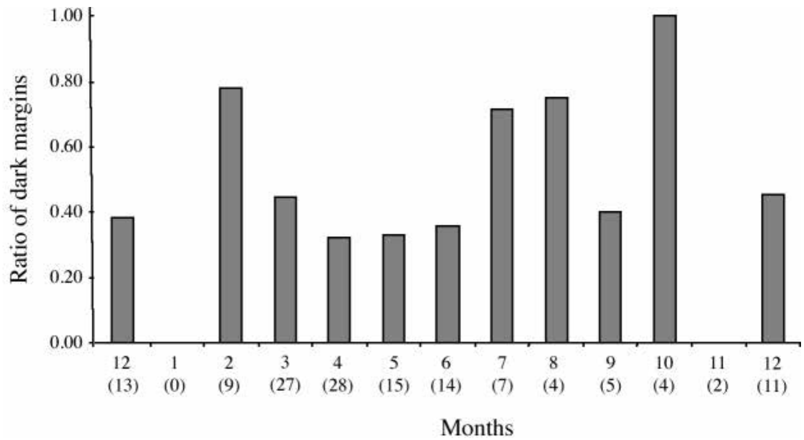

Figure 16. - Relationship between macrostructures ('seasonal' rings) and microstructures ('daily' rings). R = 0.86; N = 35; Y = 0.823 + 0.00523X. *[Relation entre macrostructures (marques saisonnières) et microstructures (marques journalières).]*

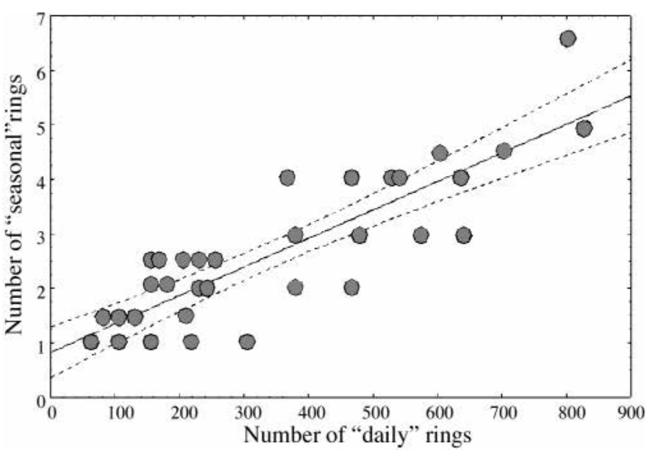

Figure 17. - Proportion of margins with a dark "seasonal" ring. Numbers between brackets indicate how many otoliths were analysed. *[Proportion des marges avec un anneau saisonnier foncé. Les nombres entre crochets indiquent combien d'otolithes ont été analysés.]*

found on the major markets. The largest size caught during our surveys (43 cm FL) corresponds with the largest specimens observed on markets but is smaller than the 50 cm reported by Fourmanoir and Laboute (1976) for this species in New Caledonia or the 57.5 cm reported in Iran (Anon, 1983) and the 66 cm (total length) reported in Kuwait (Mathews and Samuel, 1991). A comparison with the sizes observed nearby in Queensland (Australia) (Ley *et al.*, 2002) indicates that fish are smaller in New Caledonia. Ley *et al.* (2002) demonstrated that in Queensland *P. argenteus* caught in estuaries protected from fishing were larger than in those opened to fishing. The absence of large fish in our catch or on the Nouméa market could be attributed to a high fishing pressure on this species as mangroves are not very developed in New Caledonia (approx. 250 km^2 of mangroves) and represent a major zone for subsistence fishing.

Our results suggest that this species lives mainly near shore in mangroves and on associated soft bottoms. In particular despite an intense sampling effort on reefs, seagrass beds and algae beds, this species was never observed in these habitats, even as juveniles (except for one fish observed on a seagrass bed). Elsewhere this species is also mainly found in mangroves and soft bottoms. It is reported to enter as juveniles the lower reaches of freshwater systems in New Caledonia (Marquet *et al.*, 1997), Australia (Blaber, 1980; Sheaves, 1998), the Philippines (Pauly *et al.*, 1990) and East Africa (Roux, 1986). The deepest record of this species in

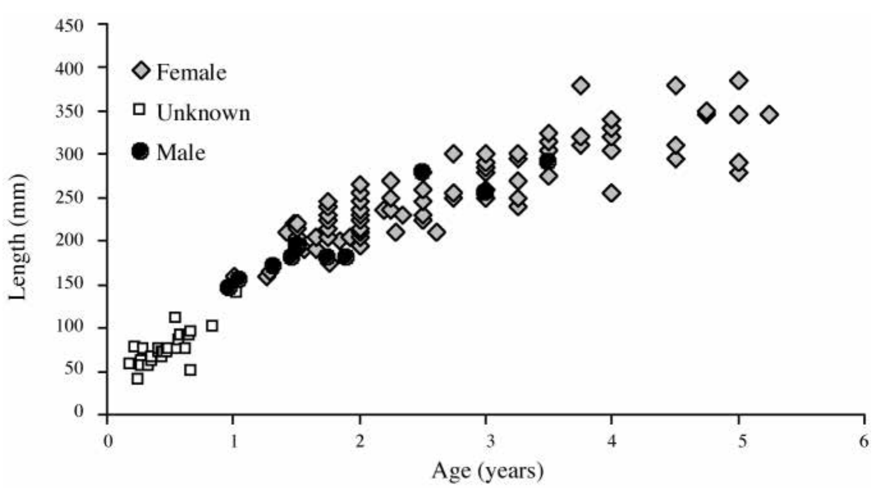

Figure 18. - Growth curve for *Pomadasys argenteus* in New Caledonia. No difference between sexes could be found. *[Courbe de croissance de* P. argenteus *en Nouvelle-Calédonie. Aucune différence entre les sexes n'est observée.]*

our catch was 28 m but it is reported from deeper waters elsewhere (> 50 m in the Gulf of Carpentaria by Gloerfelt-Tarp and Kailola, 1984; 74 m in Iran by Anon, 1983; 115 m in Indonesia by Pauly *et al.,* 1996). It is likely that there is no suitable habitat for this species in New Caledonia beyond 30 m as our fishing effort was significant beyond that depth.

Our data suggest seasonal migrations of this species between mangroves and nearby soft-bottoms. To our knowledge such migrations are not reported for this species in the literature, but most likely occur as juveniles are reported from inshore waters (e.g. Little *et al.*, 1988; Tzeng and Wang, 1992) and large specimens from deeper waters (e.g. Anon, 1983). The reasons for these migrations are not identified but it is likely that *P. argenteus* migrates offshore to reproduce and later comes back inshore to feed, with juveniles seeking protection in the mangroves. This is suggested by the absence of small individuals beyond 5 m depth and by the correspondence between the presence of large fish offshore with mature gonads.

There is little information on the diet of this species, with the exception of the studies by Sheaves and Molony (2000) and Kulbicki *et al.* (2005). However, information given for *P. hasta* by Blaber (1980) for Queensland is very likely related to *P. argenteus*, as *P.hasta* was a common misidentification at that time for *P. argenteus* in Queensland. Sheaves and Molony (2000) as well as Blaber (1980) indicate that Penaeid shrimps were a major part of the diet of this species. Sheaves and Molony (2000) also found bivalves and to a lesser extent polychaetes, but their sample size was very small (16 fishes). The major diet components in New Caledonia were crabs (49% by volume), bivalves (17%) and annelids (10%). In particular crabs are the major component of the diet at any size, time of day and habitat, thus showing that this species has a preference for this prey item. The proportion of crabs in the diet increases slightly amongst larger fishes and during the night. This is probably due to the increased activity of crabs during the night and to the capacity of larger fishes to catch crabs (larger mouth and faster swimming speed). Molluscs, the second prey item by importance, are taken during the day in mangroves by medium size fish and mostly between July and September. Most (93%) of these molluscs are bivalves which is similar to the findings of Sheaves and Molony (2000). Annelids, the third major diet item, are eaten mainly during the day on soft bottoms by average size fishes. In New Caledonia the importance of annelids in the carnivorous fish diet decreases as fish size increases (Kulbicki *et al.,* 2005). This trend is not observed for *P. argenteus* probably because annelids are eaten on soft bottoms where small *P. argenteus* are seldom found.

The proportion of full stomachs is nearly the same according to habitat, but increases as fish size increases. The proportion of empty stomachs is highest during the reproductive season and during the day. As fish grow their capacity to catch prey will likely increase as their swimming speed and mouth size increase. A lower proportion of full stomachs during reproduction is a frequent observation as many species stop feeding during reproductive periods. *P. argenteus* seems more active during the night. This is a common trait to most Haemulidae in the South Pacific (Randall *et al.*, 1990).

There is little information regarding the reproductive traits of *P. argenteus* in the literature besides the study by Abu-Hakima (1984) in Kuwait. In our study the sex ratio is highly skewed in favour of females (73%). The data of Abu-Hakima (1984) also suggest more females than males (57%). In New Caledonia this proportion increases with fish size, with no males observed greater than 340 mm and the proportion of females was at least 80% for fish over 220 mm. For *Pomadasys incisus* (an Atlantic species) the ratio of females to males is 1:1 and there was no difference in the size distribution between sexes (Pajuelo *et al.,* 2003). Several hypotheses may explain our pattern. *P. argenteus* could be protandrous, changing from male to female with age. In the absence of histological work, the very low proportion of small mature females opposite to the high proportion of small mature males (Figs 11-12) tends to support this view. However, Abu-Hakima (1984) does not report any sign of sex-changing for this species in his histological work. Males could also live in a habitat which was not sampled or not well sampled. In the present study most males were found on soft bottoms with a very low proportion found in mangroves, which suggests that males could indeed have a different habitat than females. Our sampling covered all major marine habitats in New Caledonia with the exception of the upper reaches of estuaries. As mentioned earlier, *P. argenteus* is known to be found in estuaries all the way up to fresh water. In estuaries there is often a decrease of size for marine fish upstream (e.g. Reid and Hoese, 1958; Miglarese *et al.,* 1982; Able *et al.,* 2001). Therefore one possibility would be for male *P. argenteus*, which are much smaller than females, to frequent the boundary between salt and fresh water in the mangrove system. The combination of the two hypotheses could well explain most of our observations: immature fish (< 1 year of age) are found essentially in mangroves, then most fish become males (starting at 140 mm, i.e. between 1 and 2 years of age) and soon after migrate to soft bottoms to spawn. However not all fish would become male as small females (160 mm) were observed. After the first reproduction (> 2 years of age) the proportion of males (fishes > 240 mm) decreases drastically. This would explain why females dominate the catch in mangroves and why the proportion of males increases on soft bottom. This hypothesis would mean also nearly equal numbers of males and females on the reproductive grounds and simultaneous spawning. Spawning is most likely to occur on soft bottoms as there is a much higher proportion of mature fish of both sexes in that habitat. It should

Table V. - Comparative growth values for *Pomadasys argenteus* according to several studies. *[Comparaison de la croissance de* P. argenteus *de différentes études.]*

Method	Otolith	Otolith	Otolith	Otolith	Elefan	Elefan	Unknown
Region	N. Caledonia	Persian Gulf	India	Koweit	Bengal	Indonesia	Bangladesh
Reference	Present study	Brothers and Mathews, 1987	Nammalwar, 1974	Mathews and Samuel, 1991	Mustaffa, 1999	Dwiponggo *et al.*, 1986	Khan *et al.*, 1997
0.5 year	46	55	137	88	135	119	98
1 year	106	104	243	165	238	213	180
1.5 year	156	149	326	231	318	284	247
2 year	198	189	391	289	380	341	303
2.5 year	233	225	442	339	427	385	349
3 year	263	257	481	382	464	419	387
3.5 year	288	287	512	420	493	446	419
4 year	309	313	536	453	514	466	445
4.5 year	326	336	555	482	531	483	466
5 year	341	358	570	506	544	495	484

be noted, however, that the Haemulidae are reported to display dioecism (Breder and Rosen, 1966). To our knowledge there is no indication in the literature of major size differences between sexes in this genus. For *Pomadasys stridens* females mature before males and females outnumber males by a 2.5/1 ratio (Al-Ghais, 1995). Spawning migrations are known for *P*. *corvinaeformis* in Brazil (Chabes and Correâ, 2000), as this species leaves estuaries when salinity drops to go to sea for reproduction. This is a trend opposite to the present study where *P. argenteus* leaves estuaries when salinity is at its highest.

Our finding of a single reproductive season for *P. argenteus* is a little different from the data presented by Abu-Hakima (1984) who observed a major spawning season in Kuwait during the spring and early summer as in our study, but this author noted a second and much smaller spawning peak during fall.

Length-weight relationships are available for *P. argenteus* from several sources (Tab. IV). The equations obtained for New Caledonia yield similar results as Kuwait and Bangladesh, but yield higher values than in Yemen, Indonesia or South Africa. In Yemen as in our study males are slightly heavier than females.

There have been several studies on the growth of *P. argenteus*, but this is the first to combine daily increments and seasonal rings. The hypothesis that otolith microstructures are deposited daily in young fishes has been confirmed numerous times (e.g. Quinonez-Velazquez, 1999; Powell *et al.*, 2000; Wexler *et al.*, 2001; Bundy and Bestgen, 2001; Cermeno *et al.*, 2003). For instance, Al-Husaini *et al.* (2001) found that for *Pomadasys kaakan*, a species closely related to *P. argenteus*, these microstructures were deposited daily for 70-110 mm fishes by marking otoliths with alizarine. Daily deposition is not proved in the present study but is most likely as no stress mark could be observed on the otoliths of fish < 240 mm and there is no change in the slope of the growth curve before (microstructures) and after (macrostructures) that size.

Relative Marginal Distance (RMD) has already been used to analyze the periodicity of otolith macrostructures for *P. kaakan* (Al-Husaini *et al.*, 2001). RMD suggested a yearly deposition of macrostructures, whereas the analysis of microstructures between two macrostructures suggested a faster deposition rate. When macrostructures are not well isolated or when they are too close to one another, the RMD method may not yield clear results as in the present study. Analyzing the otolith margins suggested that two macrostructures are deposited each year, but the number of otoliths available for this analysis is too low to confidentially make a decision. However, counting microstructures between two macrostructures confirms this trend. It is not usual to find two macrostructures per year, although Samuel *et al.* (1987) found that seasonal marks were not necessarily annual marks and Yosef and Casselman (1995) found the same result on tropical fish. In the present case there is little information on why two seasonal rings would be deposited each year. As dark rings correspond to a decrease in growth rate, one hypothesis would be that one of the ring corresponds to the spawning season, during which this species feeds less (July-October), and the second ring could correspond to the wet season (December-March) during which mangroves are flooded by freshwater and fish could be stressed (salinity change, decrease in food abundance and quality). Samuel *et al.* (1987) reported that for *P. argenteus* seasonal rings were not necessarily formed on a yearly basis, but in some cases with a shorter periodicity, thus converging with our findings and those of Al-Husaini *et al.* (2001) for *P. kaakan*.

There are several growth studies for *P.argenteus* (Tab. V). Our results show the slowest growth, with results closest to those of Brothers and Mathews (1987) for this species in the Persian Gulf. In Kuwait, India and Bangladesh the reported growth is much faster. The origin of such differences is difficult to identify. However, in New Caledonia the terrigenous inputs bring little nutrients to the system because of the unique geologic structure of this island. This could induce a low availability of food in the mangroves and adjacent soft bottoms. On the other hand the studies reporting a fast growth for *P. argenteus* are all located in areas with very high productivity due to huge delta systems. It should also be noted that results obtained by cohort analysis, such as those using the Elefan software (Pauly and David, 1981), are questionable for tropical species as there may be numerous cohort overlaps which are not detectable. In addition if this species displays strong differences in size distribution with sex this could disturb even more the interpretation of a cohort analysis.

In conclusion, in New Caledonia *P. argenteus* is a medium size (max. 42 cm; 1200 g) species found mainly inshore, especially in mangroves, with a likely seasonal migration to deeper waters for reproduction on nearby soft bottoms. Reproduction is spread over several months during the cold season, which corresponds to findings elsewhere. Both sexes mature at the same size, but females become larger and are more numerous than males. The latter are slightly heavier than females for a given size, but no difference in growth could be evidenced between sexes. Growth is slower than what is reported in the literature from other localities of this widespread species. Feeding occurs at all times of day, but nocturnal feeding is more important. Fish feeds more often earlier in the year and large fish have more diversified diets than small fish. Crabs dominate the diet, the proportion of this prey item increasing with size.

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