Life history of *Pomadasys incisus* (Osteichthyes: Haemulidae) in the Canarian Archipelago*

JOSÉ G. PAJUELO, JOSÉ M. LORENZO, MURIEL GREGOIRE and ROSA DOMÍNGUEZ-SEOANE

Departamento de Biología, Universidad de Las Palmas de Gran Canaria, Campus de Tafira, 35017 Las Palmas de Gran Canaria, Spain. E-mail: Pajuelo@ccbb.ulpgc.es.

SUMMARY: *Pomadasys incisus* is one of the most abundant coastal demersal species around the Canary Islands. It is a gonochoric species with similar biological characteristic in males and females. The adult sex ratio is not significantly different from 1:1, and the mean size of males and females is similar. It reaches first maturity at the end of the second year of life (183 mm). Spawning takes place throughout the year. Growth analysis reveals that the species is fast-growing and relatively short-lived (7 years). Length at age is well described by the von Bertalanffy growth model. Individuals grow quickly in their immature first year, attaining approximately 45% of their maximum length. After one year, the annual growth rate drops rapidly. The direct effects of fishing result in changes in abundance, with an 80% reduction from the unexploited equilibrium level. Recruitment into the commercial fisheries occurs before size at sexual maturity, resulting in all spawners being accessible using the current fishing pattern. The length at first capture (168 mm) is less than the length at maturity; 45% of the total catch are smaller than this, indicating a danger of recruitment-overfishing.

Key words: Pomadasys incisus, growth, reproduction, mortality, impact, discard, Canary Islands.

RESUMEN: PARÁMETROS BIOLÓGICOS DEL *POMADASYS INCISUS* (OSTEICHTHYES: HAEMULIDAE) EN EL ARCHIPIÉLAGO CANARIO. – *Pomadasys incisus* es una de las especies demersales costeras más abundantes en las aguas de las Islas Canarias. Es una especie gonocórica con características que presenta características similares para los machos y hembras. La proporción de sexos no difiere de la relación 1:1. Las tallas medias son similares para los machos y las hembras. Las individuos de esta especie alcanzan la madurez sexual al final del segundo año de vida (183 mm). La puesta tiene lugar durante todo el año. El análisis de su crecimiento muestra que la especie es de crecimiento rápido y de longevidad reducida (7 años). La relación entre la talla y la edad es descrita de forma adecuada por el modelo de von Bertalanffy. Los individuos inmaduros crecen de forma rápida durante sus primeros años, alcanzando, aproximadamente, el 45 % de su talla máxima. Después del primer año de vida, la tasa de crecimiento se reduce considerablemente. El efecto directo causado por la pesca es una reducción del 80 % de su biomasa con respecto al nivel de equilibrio previo a la explotación. El reclutamiento ocurre antes de alcanzar la talla de madurez sexual y como consecuencia de ello todo el stock reproductor esta sometido a presión pesquera según el patrón de explotación actual. La talla de primera captura (168 mm) es menor que la talla de madurez sexual, con un 45 % del total de individuos capturados por debajo de dicha talla de madurez, lo que apunta hacia una sobrepesca en reclutamiento.

Palabras clave: Pomadasys incisus, crecimiento, reproducción, mortalidad, impacto, descartes, Islas Canarias.

INTRODUCTION

In the multispecies and multigear Canarian demersal fishery more than ninety species are caught. Of

*Received April 18, 2002. Accepted October 15, 2002.

the total fish species caught, approximately twentyfive are impacted by the fishing activity and discarded as a consequence of their low commercial value (Pajuelo, 1997). The discarded fish species represent approximately five percent of the total biomass demersal fish catches. Of the discarded fish species, the bastard grunt *Pomadasys incisus* (Bowdich, 1825) is the most abundant species in the catches. It is observed in relatively high-density schools in the coastal waters of the Canarian Archipelago and is considered to be among the twenty most abundant demersal species in the area, all of them with commercial interest except *P. incisus*. The bastard grunt is caught by the demersal trap fishery of the Canary Islands jointly with the sparids that are the main demersal fish target species (Pajuelo, 1997).

Discarding fish has for some time been accepted as an inevitable component of harvest fisheries, althought it can be illegal. Recent estimates suggest that more than one quarter of all fish caught annually are wasted throught discarding (Alverson *et al.*, 1994). Such estimates help to show the magnitude of the phenomenon and discarding is gradually becoming a major management issue (Alverson and Hughes, 1996).

In the Canarian Archipelago the main target species of the demersal fishery are heavily overexploited and information on their biology and life cycle is known. However, the total catches of the non-target species such as the bastard grunt are unknown because they are not monitored. Accordingly, the exploitation status of the populations is unknown. Furthermore, information on the biology of *Pomadasys* species is very scarce anywhere in the world and no information was found in the literature on any biological aspects of *P. incisus*.

The need for an ecologically based discard management strategy and the paucity of available data on the biology of this species prompted an investigation into aspects of its life history including population structure, sexuality, spawning cycle, maturity, age and growth, and mortality (especially the incidental fishing mortality on this discarded species).

MATERIALS AND METHODS

Pomadasys incisus specimens caught with traps by the artisanal demeral fishery were sampled fortnightly from October 2000 to September 2001. Fish were caught at depths of 5-70 m off south-west Gran Canaria, Canary Islands. A total of 9651 discarded individuals were measured (total length, nearest mm). A subsample of 878 specimens was taken from the whole sample by a random length stratified method for biological analysis. Each of these individuals was measured to the nearest mm for total length (L_t), and weighed to the nearest 0.1 g for total body weight (W_t). The gonads were removed and weighed (W_g) to the nearest 0.001 g and the eviscerated weight (W_e) was recorded to the nearest 0.1 g. Furthermore, the sex and the stage of maturity were assessed visually. Stages of maturity were classified as follows: I, immature; II, resting; III, ripe; IV, ripe and running; and V, spent.

Sagittal otoliths were removed, cleaned with seawater, and stored dry for later age determination.

The overall sex ratio (males:females) was determined as well as the sex ratio by size classes. The spawning season was ascertained using two methods: a gonadosomatic index calculated by expressing gonad mass as a percentage of eviscerated body mass (Anderson and Gutreuter, 1983), and by calculating the proportions of different maturity stages. The length at maturity was calculated by determining the proportion of reproductively active fish in each sizeclass (stages III, IV and V). Length at maturity was estimated by fitting the logistic function:

$$P = \frac{100}{1 + e^{-v \cdot (L_t - L_{50})}}$$

where: P is the percentage of fish mature at length L_t , L_{50} is the length at 50% maturity, and v is the parameter which determines the width of length specific maturity function. The parameters were estimated by means of Marquardt's algorithm for non-linear least-squares parameter estimation (Saila *et al.*, 1988).

Age was determined by interpreting growth rings on the otoliths. The pairs of whole otoliths were placed in water and examined under a compound microscope $(10\times)$ with reflected light against a dark background. Counts of the growth bands were made by two readers without knowledge of size, sex or each other's results. Counts were made for otoliths of each fish on two separate occasions, and only coincident readings were accepted. The same approach was used to determine the final number of bands in each specimen, with a unanimity reached between the final counts of each reader. The index of average percentage error (IAPE) was calculated for the band counts of each reader using the formula described by Beamish and Fournier (1981). Periodicity of band formation was evaluated by noting the visual appearance of the otolith margin and expressing it as a percentage of the monthly sample. Once the periodicity and the timing of ring formation were verified, the age of each fish was determined by enumerating the marks, and then assigning it to an ageclass. 1 January was considered as the birthdate for assigning the ages to age-classes. Length at age was described by the von Bertalanffy growth model (Ricker, 1975). The model was fitted by means of Marquardt's algorithm for non-linear least-squares parameter estimation (Saila *et al.*, 1988).

Estimates of the total instantaneous rate of mortality were obtained by catch-curve analyses (Pauly, 1983). An estimate of the instantaneous rate of total mortality was obtained from the negative of the slope of the straight line fitted to points greater than the age at full recruitment using the FiSAT program (Gayanilo et al., 1996). Z was also obtained from Beverton and Holt's mean length in the catches (Beverton and Holt, 1956) and the Ault and Ehrhardt (1991) method. The instantaneous rate of natural mortality (M) was estimated by a variety of methods (Beverton and Holt, 1959; Tanaka, 1960; Taylor, 1960; Rikhter and Efanov, 1976; Pauly, 1980; Hoenig, 1983). To delimit a range of values of this rate that includes its real value, the longevity for each value of M was estimated using the method of Alagaraja (1984). The instantaneous rate of fishing mortality (F) was estimated from the difference between Z and M. The exploitation ratio (E) was estimated by dividing F by Z (Gulland, 1971). Length at first capture was determined from the selection ogive generated from the catch curve (Pauly, 1983).

Spawning biomass per recruit (SBR) as a function of fishing mortality F was determined as:

$$\mathbf{SBR}_{\mathrm{F}} = \sum_{i=0}^{7} \mathbf{B}_{i} \mathbf{w}_{i} \mathbf{N}_{i} \Delta_{i}$$

where: N_i is the relative proportion of fish at age i, w_i is the weight of fish at age i, and B_i the proportion of mature fish at age i (Butterworth *et al.*, 1989). Two biological reference points, expressed in terms of F, were estimated from the SBR curves. These included F_{SB40} and F_{SB50} , which are the values of F at which the spawning biomass is reduced to below 40 and 50% respectively of its unexploited equilibrium level (Booth and Punt, 1998). According to Buxton (1992) and Booth and Buxton (1997), the F_{SB50} strategy is the most suitable and is sufficient to protect the spawner stock.

RESULTS

Sex and spawning

The gonad was present as a single testis in the male and as a single ovary in the female. In both sexes it was suspended by the dorsal mesentery in the posterior region of the visceral cavity with both gonadal lobes equally developed. Of the 878 fish examined, 377 (41.2%) were male and 412 (45.8%) were female. The sex of the remaining 89 (13.0%) fish could not be identified macroscopically and they were considered to be immature as they had very thin and traslucent gonads. The overall ratio of



FIG. 1. – Size distributions of male, female and immature *P. incisus* off the Canary Islands.



FIG. 2. – Mean monthly evolution (top) of the gonadosomatic index (GSI) and (bottom) maturity stages for all *P. incisus* collected off the Canary Islands.

males to females (1:1.09) was not significantly different from a 1:1 ratio (Chi-square, $\chi^2 = 1.5 < \chi^2_{t,1,0,05} = 3.84$).

Males and females showed the same size range (Fig. 1). Males ranged in size from 143 to 298 mm total length and females from 134 to 304 mm. The length range of immature fish was 103 to 186 mm. Sex ratios for males and females grouped into 10-mm length classes showed no significant departures from the 1:1 ratio ($\chi^2 < \chi^2_{t 0.05,1}$ =3.84).

No significant difference in length at sexual maturity was found between males and females (t-test, t= $0.67 < t_{0.05,787} = 1.96$), so the results were pooled. The length at which 50% of fish had become mature (L₅₀) was 183 mm and v was 0.082.

All macroscopic stages of gonadal development were easily discernible. The same evolution was observed for both sexes in the pattern of the gonadosomatic index. The monthly mean values of GSI were high throughout the year (Fig. 2), but peaked in late autumn and winter (November-January) and summer (June-July). A similar trend was evident using the maturity stages (Fig. 2). Ripe and ripeand-running gonads (stages III and IV) were evident throughout the year. Spent gonads (stage V) were rare throughout the year.

Age and growth

Otolith alternated opaque and hyaline zones were clearly visible (Fig. 3). For each fish, the number of bands counted for each individual by the two readers was similar. The number of specimens for which consensus could be reached was high. The IAPE of



FIG. 3. - Saggital otoliths of P. incisus off the Canary Islands. (A), a three years old (202 mm), (B) five years old (265 mm).



FIG. 4. – Mean monthly evolution of the marginal edge of the otoliths for all *P. incisus* collected off the Canary Islands, and the associated sea surface temperature.

bands counts for each reader did not differ greatly, being slightly lower for the first author (2.47) than the second (2.97). In total, 812 otoliths (92.4%) were readable and used for the study of age and growth.

Marginal zone analysis showed that the opaque and translucent zones were deposited throughout the year, but with different frequency. The highest percentages of otoliths with opaque edges were observed between June and November (Fig. 4); otoliths with translucent edges were observed mainly between December and May. Therefore, it was assumed that each translucent zone represented an

 TABLE 1. – Age-length key for all P. incisus collected off the Canary Islands.

Size (1	mm) 0	Ι	II	A III	ige (yea IV	urs) V	VI	VII
100 110 120 130 140 150 160 170 180 190 200 210 230 240 250 260 270 280 290 300	2 1 1	3 10 17 19 15 4	6 19 33 47 69 52 25 14 5	2 29 61 96 89 57 14 2 1	1 6 23 38 17 9 2 1	1 4 6 1 1	1 2 2 1 1	1
x n sd	107 4 5.8	125 68 12.6	176 270 17.3	212 351 18.1	236 97 12.4	261 13 11.4	275 7 11.4	295 2 14.1

annulus, with a year's growth represented by an opaque and its adjacent hyaline zone.

The sampled population consisted of 8 age-classes (0-7). More than 45% of the maximum length was achieved by the first year (Table 1); by the second year, fish had attained 60%. Length at age was adequately described by the von Bertalanffy growth model. There were no significant differences between mean lengths at age of males and females (t-test, t= $0.52 < t_{0.05,787} = 1.96$) or between the von Bertalanffy growth curves using (Hotelling's T² test, $T^2=4.73 < T_0^2 T_{0,0,05,3,784} = 7.89$). Data were pooled as a single-growth model. The relationship between age and length, derived from the assumed annual periodicity of the growth rings, was described by the growth parameters: L_∞=3325 mm, k=0.271 years⁻¹, and t_0 =-0.710 years. In fitting the growth curve to the age/length data, age 0 was disregarded because this age class was not well represented.

Mortality

Age frequencies derived from transformed length frequency data provided estimates of total mortality (Fig. 5). The values of Z obtained from Pauly's length converted catch curve (Z=1.37 year⁻¹), the Beverton and Holt method (Z=1.32 year⁻¹), and the Ault and Ehrhardt method (Z=1.31 year⁻¹) were similar. The values of the instantaneous rate of natural mortality obtained using different methods ranged between 0.76 and 0.32 year⁻¹ and the corresponding values of longevity were comprised between 5.9 and 14.2 years (Table 2). Some of the values of M are unreal because the lifespawn expected using only these data are lower than the maximum age observed for the population under a natural and fishing mortalities. This is the case of the methods of Beverton



FIG. 5. – Length-converted catch curve for all *P. incisus* collected off the Canary Islands. ● Data point used; ◆ not used.

TABLE 2. – Values of instantaneous rate of natural mortality (M) and longevity for all *P. incisus* off the Canary Islands.

Calculationm method	M (years-1)	Longevity (years)		
Tanaka	0.429	10.74		
Taylor	0.451	10.22		
Pauly	0.324	14.21		
Hoenig	0.606	7.59		
Beverton and Holt	0.714	6.44		
Rikhter and Efanov	0.768	5.99		

and Holt (M=0.71 years⁻¹) and Rikhter and Efanov (M=0.76 years⁻¹) who reported values of longevity of 6.5 and 5.9 years respectively, lower than the age of the individual of 7 years sampled. The remaining values of M are higher than of the age of the old fish sampled. However, the expected lifespan of the individuals of the population studied under natural mortality must only be higher than 7 years. For this reason the values of M obtained using the Hoenig methods (near to the maximum age obtained in a population under a fishing and natural mortality) underestimated the real value of M. The real value of the instantaneous rate of natural mortality must be comprised between 0.32 (as the lower limit) and 0.61 year⁻¹ (as the upper limit). The values of the instantaneous rate of fishing mortality and exploitation ratio were estimated using a mean value of the instantaneous rate of natural mortality of 0.46 year¹ and the limits of M estimated. The mean value of the instantaneous rate of fishing mortality was F=0.88 year⁻¹, and the exploitation ratio was E=0.65. The length at first capture (S_{50}) was estimated at 168 mm (1.8 years). The mean length of fish caught was 199 mm total length. There was no significant difference in mean length between males (193 mm) and



FIG. 6. – Spawning biomass per recruit for all *P. incisus* collected off the Canary Islands.

females (202 mm) (t-test, t= $0.29 < t_{0.05,787} = 1.96$). The SBR curve declined quickly with increasing values of F. At the current level of exploitation, the spawner biomass is less than half of the unexploited level (Fig. 6).

DISCUSSION

P. incisus off the Canarian Archipelago is a gonochoric species with no evidence of sexual dimorphism, as for all species of the genus *Pomadasys*.

P. incisus in the Canarian Archipelago spawn throughout the year. A prolonged breeding season is generally characteristic of repeat spawners (Nikolskii, 1963) and fish living in variable and unstable and/or highly productive environments (Tomasini *et al.*, 1996). Non-seasonal spawning with an increase in activity over different periods of the year is common in populations inhabiting areas with low amplitude oceanographic cycles (Grimes, 1987). Protracted spawning has also been described for *P. kaakan* and for *P. olivaceus* and appears to be a feature of the biology of *Pomadasys* species (Joubert, 1981; Lee *et al.*, 1990; Al-Husaini *et al.*, 2001).

Age at sexual maturity does not differ between male and female *P. incisus*, corresponding to 2 years of age. Wallace and Schleyer (1979), Joubert (1981), Mathews *et al.* (1989), and Diouf (1996) respectively found that male and female *P. commersonnii*, *P. olivaceus*, *P. kaakan* and *P. perotaei* attain sexual maturity at a similar length or age. Maturity at a relatively early age seems to be a characteristic of *Pomadasys*.

Otoliths of P. incisus from the Canaries show a ring pattern common to teleost fish. One calcified opaque zone and one less calcified translucent zone are laid down each year, allowing age determination with relative ease. These rings are deposited during periods of fast and slow growth respectively (Williams and Bedford, 1974). Seasonal growth cycles might be related to physiological changes produced by the influence of temperature, feeding regime and reproductive cycle (Morales-Nin and Ralston, 1990). Related to this, the formation of the daily growth increments depends on the infradian rhythms which are synchronised with the photoperiod or other external daily factors (Campana and Neilson, 1985). Opaque rings are formed during spring/summer, when the sea temperature is highest, and hyaline rings during winter, when the temperature is lowest. The water column is well mixed during winter and an isotherm is formed during the summer. The average sea surface temperature of the Canary Islands is 18°C in February, rising to 24°C in August and September. This rise in water temperature could introduce a change in the metabolic activity of the individuals during spring and summer and be the main factor responsible for opaque zone deposition. Al-Husaini *et al.* (2001) also found that the translucent zone formation in the otoliths of *P. kaakan* takes place during the slow-growth season. The evidence currently available suggests that a seasonal temperature difference of 6°C might be sufficient to cause ring formation (Morales-Nin and Ralston, 1990).

The increase in sea surface temperature affects the physiology of otolith growth and results in the formation of the annulus. Data in this study show that the first annulus is deposited irrespective of gonad maturation. The minimum total length of mature fish is 156 mm, but juvenile fish also show a first annulus.

As a whole, growth of *P. incisus* is fast, males and females growing at the same rate. The theoretical maximal length value is higher than the size of the largest fish sampled and the growth coefficient indicates a relatively fast attainment of maximum size, a characteristic of short-lived species. *P. incisus* grows quickly when immature, attaining approximately 45% of its maximum length after the first year, with the annual growth rate dropping rapidly thereafter. The change in growth rate is probably the result of the available energy being used for reproduction rather than somatic growth.

The value of the exploitation rate (>0.50) suggests, according to Gulland (1971), that the bastard grunt is heavily exploited in the Canarian Archipelago, so it may be necessary to advise a change in fishing pattern. The length at first capture is less than the length at first maturity, 45% of the total catch being below this length and thus indicating a danger of recruitment-overfishing.

The average estimate of fishing mortality is high, suggesting that *P. incisus* is heavily impacted by fishing, even though it is not a target species. The direct effects of fishing will result in changes its abundance, with a reduction of 80% regardless of the unexploited equilibrium level, and in the size structure, with fewer fish growing to large size. Pope *et al.* (1988) point out that exploitation tends to remove larger fish from ecosystems and, consequently, the abundance of smaller fish and species of smaller size increases.

A specialist species has a life history strategy that tends towards low productivity. Typical life history characteristics include large body size, delayed age at sexual maturity, a long life and a low natural mortality (Booth, 1997). In contrast, a generalist has a life history strategy that tends towards the oportunistic use of the resources. Therefore, generalists exhibit early maturity, fast growth rate, small body size, and high natural mortality (Booth, 1997). To understand where P. incisus fits into this life history classification continuum, various life history parameters such as maximum length, maximum age, growth rate, size and age at maturity must be analysed together. In this context, the life history parameters of the bastard grunt suggest that the species has a generalist life history style. Fisheries based on r-selected species are less susceptible to growth-overfishing and population depletion (Buxton and Clarke, 1991; Booth and Buxton, 1997). Bastard grunt have large ovaries in large ripe-and-running individuals, suggesting that they are moderately fecund and that a moderate number of eggs is released during the spawning. As a result, they may be less sensitive to heavy fishing than species exhibiting a lower reproductive output (Smale, 1988).

The large number and relatively high biomass of bastard grunt in the Canary Islands suggest that the species plays an important role as an epibenthic predator. However, the high fishing pressure could result in a large reduction in numbers, impacting the epibenthic fauna. Unfortunately, its recruitment into the commercial fishery occurs before sexual maturity and consequently the whole spawner biomass is accessible at the current fishing pattern.

A possible option which may improve the situation for such fish species of the benthic community would be to protect part of the spawning stock and their recruits in marine reserves that encompass the coastal inshore areas of seagrass beds, and to establish a minimum fishing depth of 30 m to protect the nursery areas located in shallow waters (Planes *et al.*, 1999). In addition, it would be advisable to assess the impact of various management options for the multispecies fisheries.

ACKNOWLEDGEMENTS

The authors are grateful to Dr. A.I.L. Payne (CEFAS, UK) and to one anonymous reviewer for their critical and useful comments on the manuscript. This study was funded by the Universidad de Las Palmas de Gran Canaria (ULPGC).

REFERENCES

- Alagaraja, K. 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. *Indian J. Fish.*, 31: 177-208.
- Al-Husaini, M., S. Al-Ayoub and J. Dashti. 2001. Age validationof nagroor, *Pomadasys kaakan* (Cuvier, 1830) (Family: Haemulidae) in Kuwaiti waters. *Fish. Res.*, 53: 71-81.
- Alverson, D.L. and S.E. Hughes. 1996. Bycatch: from emotion to effective management. *Rev. Fish. Biol. Fish.*, 6: 443-462.
- Alverson, D.L., M.H. Freeberg, S.A. Murawski and J.G. Pope. 1994. A global assessment of fisheries bycatch and discards. FAO Fish. Tech. Pap., 339: 233 pp.
- Anderson, R.O. and S.J. Gutreuter. 1983. Length, weight, and associated structural indices. In: L.A. Nielsen and D.L. Johnson (eds.), *Fisheries Techniques*, pp. 283-300. American Fisheries Society, Bethesda.
- Ault, J.S. and N.M. Ehrhardt. 1991. Correction to the Beverton and Holt Z-estimator for truncated catch length-frequency distributions. *Fishbyte*, 9: 37-39.
- Beamish, R.J. and D.A. Fournier. 1981. A method for comparing the precision of a set of age determinations. *Can. J. Fish Aquat. Sci.*, 38: 982-983.
- Beverton, R.J.H. and S.J. Holt. 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *Rapp. P.v Réun. CIEM*, 140: 67-83.
- Beverton, R.J.H. and S.J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: G.E.W. Woilstenholme and M. O'Connor (eds.), *Ciba Fundation, Colloquia on Ageing*, pp. 142-180. Churchill, London.
- Booth, A.J. 1997. On the life history of the lesser gurnard (Scorpaeniformes: Triglidae) inhabiting the Agulhas Bank, South Africa. J. Fish. Biol., 51: 1155-1173.
- Booth, A.J. and C.D. Buxton. 1997. Management of the panga *Pterogymnus laniarius* (Pisces: Sparidae), on the Agulhas Bank, South Africa using per-recruit models. *Fish. Res.*, 32: 1-11.
 Booth, A.J. and A.E. Punt. 1998. Evidence for rebuilding in the
- Booth, A.J. and A.E. Punt. 1998. Evidence for rebuilding in the panga stock on the Agulhas Bank, South Africa. *Fish. Res.*, 34: 103-121.
- Butterworth, D.S., A.E. Punt, D.L. Borchers and G.S. Hughes. 1989. A manual of mathematical techniques for linefish assessment. South African National Scientific Programmes Report, 160: 1-89.
- Buxton, C.D. 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. *Fish. Res.*, 15: 1-16.
- Buxton, C.D. and J.R. Clarke. 1991. The biology of the white musselcracker Sparadon durbanensis (Pisces: Sparidae) on the Eastern Cape Coast South Africa. S. Afr. J. mar. Sci. 10: 285-296
- ern Cape Coast, South Africa. S. Afr. J. mar. Sci., 10: 285-296. Campana, S.E. and J.D. Neilson. – 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci., 42: 1014-1032.
- Diouf, P.S. 1996. Les peuplements de poissons des milieux estuarines de l'Afrique de l'Ouest: L'Example de l'estuaire hyperhalin du Sine-Saloum. Doctoral Thesis. Université de Montpellier.
- Gayanilo, F.C., P. Sparre and D. Pauly. 1996. FAO-ICLARM stock assessment tools (FiSAT) User's Guide. FAO, Comp. Inf. Ser. (Fisheries), 8: 126 pp.
- Grimes, C.B. 1987. Reproductive biology of the Lutjanidae: A review. In: J.J. Polovina and S. Ralston (eds.), *Tropical Snnapers and Groupers: Biology and Fisheries Management*, pp. 239-294. Westview Press, London.
- Gulland, J.A. 1971. The Fish Resources of the Oceans. Fishing News Books Ltd, West Byfleet.

- Hoenig, J. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.*, 82: 898-903.
- Joubert, C.S.W.- 1981. Aspects of the biology of five species of inshore reef fishes on the Natal Coast, South Africa. *Invest. Rep. Oceanogr. Res. Inst.*, 51: 1-16.
- Lee, J.U., M. Samuel, F.Y. Al-Yamani and P.S. Joseph. 1990. Fin fisheries management project, phase IV. Final Report of the Kuwait Institute for Scientific Research, 384.
- Mathews, C.P., J.U. Lee, M. Samuel and P.S. Joseph. 1989. Fin fisheries management projet phase III. Final Report of the Kuwait Institute for Scintific Research, 243.
- Morales-Nin, B. and S. Ralston. 1990. Age and growth of Lutjanus kasmira (Forskal) in Hawaiian waters. J. Fish Biol., 36: 191-203.
- Nikolskii, G.V. 1963. *The ecology of the fishes*. Academic Press, London.
- Pajuelo, J.G. 1997. La pesquería artesanal canaria de especies demersales: análisis y ensayo de dos modelos de evaluación. PhD Thesis, University of Las Palmas de Gran Canaria.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. int. Explor. Mer, 39: 175-195.
- Pauly, D. 1983. Some simple methods for the assessment of tropical fish stock. *FAO Fish. Tech. Pap.*, 234: 1-52.
 Planes, S., E. Macpherson, F. Biagi, A. García-Rubies, J. Harmelin,
- Planes, S., E. Macpherson, F. Biagi, A. García-Rubies, J. Harmelin, M. Harmelin-Vivien, J.Y. Jouvenel, L. Tunesi, L. Vigliola and R. Galzin. – 1999. Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. J. Mar. Biol. Ass. U.K., 79: 137-143.
 Pope, J.G., T.K. Stokes, S.A. Murawski and S.I. Idoine. – 1988. A
- Pope, J.G., T.K. Stokes, S.A. Murawski and S.I. Idoine. 1988. A comparison of fish size composition in the North Sea and on George bank. In: W. Wolff, C.J. Soeder and F.R. Drepper (eds.), *Ecodynamics, Contributions to Theoretical Ecology*, pp. 146-152. Spring Verlarg, Berlin.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, 191: 382 pp.
 Rikhter, V.A. and V.N. Efanov. 1976. On one of the approaches
- Rikhter, V.A. and V.N. Efanov. 1976. On one of the approaches to estimation of natural mortality of fish populations. *ICNAF Res. Doc.*, 76: 1-12.
- Saila, S.B., C.W. Recksiek and M.H. Prager. 1988. Basic fishery science programs. A compendium of microcomputer programs and manual of operation. *Developments in Aquaculture and Fisheries Science*, 18: 1-230.
- Smale, M.J. 1988. Distribution and reproduction of the reef fish *Petrus rupestris* (Pisces: Sparidae) off the coast of South Africa. S. Afr. J. Zool., 23: 272-287.
- Tanaka, S. 1960. Studies on the dynamics and the management of fish populations. Bull. Tokai Reg. Fish. Res. Lab., 28: 1-200.
- Taylor, C.C. 1960. Natural mortality rate of Georges Bank haddock. U.S. Fish Wild. Serv., Fish. Bull., 58: 1-7.
- Tomasini, J.A., D. Collart and J.P. Quignard. 1996. Female reproductive biology of the sand smelt in brackish lagoons of southern France. J. Fish Biol., 49: 594-612.
- Wallace, J.H. and M.H. Schleyer. 1979. Age determination in two important species of South Africa angling fishes, the knob (Argyrosomus hololepidotus Lacep) and the spotted grunter (Pomadasys commersonnii Lacep). Trans. R. Soc. S. Afr., 44: 15-26.
- Williams, T. and B.C. Bedford. 1974. The use of otoliths for age determination. In: T.B. Bagenal (ed.), *The Ageing of Fish*, pp. 114-123. Unwin Brothers, Surrey.
- Scient. ed.: B. Morales-Nin