IOTC-2011-WPNT01-22



Available online at www.sciencedirect.com



Fisheries Research 76 (2005) 277-290



www.elsevier.com/locate/fishres

# Preliminary assessment of the biology and fishery for the narrow-barred Spanish mackerel, *Scomberomorus commerson* (Lacépède, 1800), in the southern Arabian Gulf

E.M. Grandcourt\*, T.Z. Al Abdessalaam, F. Francis, A.T. Al Shamsi

Marine Environmental Research Centre, Environmental Research and Wildlife Development Agency, P.O. Box 45553, Abu Dhabi, United Arab Emirates

Received 9 March 2005; received in revised form 27 June 2005; accepted 8 July 2005

#### Abstract

The population biology and fishery for Scomberomorus commerson in the southern Arabian Gulf were investigated using a combination of size frequency, biological and size-at-age data. Transverse sections of sagittal otoliths showed structural increments consisting of alternating translucent and opaque bands, which were used to estimate age. Edge analysis revealed an annual periodicity of formation with opaque zones being deposited between May and July in association with increasing seawater temperatures. The maximum absolute age estimates were 16.2 years (males) and 15.3 years (females). Initial growth was rapid with fish reaching more than half the asymptotic size by their second year and there were no significant differences in growth characteristics between sexes. Parameter values of the von Bertalanffy growth function fit to size-at-age data (males and females combined) were: k = 0.21,  $L_{\infty} = 138.6$  cm ( $L_{\rm F}$ ) and  $t_0 = -1.9$  years. Spawning occurred between April and August, the mean sizes and ages at first sexual maturity were 72.8 cm  $L_{\rm F}$  (1.9 years) for males and 86.3 cm  $L_{\rm F}$  (2.1 years) for females. The size at which fish were fully recruited to the fishery ( $62.6 \text{ cm } L_{\rm F}$ ) was considerably smaller than both the mean size at first sexual maturity for females and the size at which yield per recruit would be maximised (95.6 cm  $L_{\rm F}$ ). Furthermore, the annual instantaneous fishing mortality rate of 0.62 year<sup>-1</sup> (0.46–0.79 year<sup>-1</sup> 95% CI) was by far in excess of the precautionary target ( $F_{opt} = 0.13$  year<sup>-1</sup>) and limit ( $F_{\text{limit}} = 0.17 \text{ year}^{-1}$ ) biological reference points, indicating that the resource is heavily over-exploited. The results suggest that an increase in mesh size regulations for gillnets in combination with a substantial reduction in fishing effort will be required if resource conservation and stock rebuilding objectives are to be achieved. The study also highlights the need for a strategic regional approach to the assessment and management of this highly migratory species. © 2005 Elsevier B.V. All rights reserved.

Keywords: Demography; Spanish mackerel; Fisheries; Stock assessment

1. Introduction

\* Corresponding author. Tel.: +971 2 681 7171; fax: +971 2 681 0008.

E-mail address: egrandcourt@erwda.gov.ae (E.M. Grandcourt).

The narrow-barred Spanish mackerel, *Scombero*morus commerson (Lacepède, 1800) is a member of

 $<sup>0165\</sup>text{-}7836/\$$  – see front matter © 2005 Elsevier B.V. All rights reserved. doi:10.1016/j.fishres.2005.07.001

the family Scombridae (Mackerels, tunas, bonitos), subfamily: Scombrinae. It is distributed in the Indo-Pacific from the Red Sea and South Africa to southeast Asia, north to China and Japan and south to Australia (Randall, 1995), being an immigrant to the eastern Mediterranean Sea by way of the Suez Canal (Ben-Tuvia, 1978).

*S. commerson* occurs from the edge of the continental shelf to shallow coastal waters where it is found along drop-offs, gently sloping reefs and lagoon waters from depths of 10–70 m. (McPherson, 1985; Myers, 1991). In north Queensland Australia, small juveniles up to 10 cm fork length live in creeks, estuaries and sheltered mud flats during the early wet season (McPherson, 1981). Large adults may be solitary, whereas juveniles and young fish occur in small schools (Collette, 2001). The diet mainly consists of small fishes like anchovies, clupeids and carangids, though squids and shrimps are also consumed (Blaber et al., 1990). It reaches a maximum size of 240 cm fork length and maximum weight of 70.0 kg (McPherson, 1992).

Whilst *S. commerson* is an inshore pelagic species, it is known to undertake lengthy long-shore migrations (Randall, 1995). In Australia, migrations extend along the entire east coast of Queensland, however, permanently resident populations also seem to exist. The resident fish disperse from reefs after spawning, whilst migrating fish move up to 1000 nautical miles to the south (McPherson, 1989). In the waters off the United Arab Emirates in the southern Arabian Gulf it is most abundant between September and May, with fish generally moving in an east to west direction during this period. The migration coincides with reduced water temperatures and an increase in the abundance of small pelagic species.

*S. commerson* is caught with a variety of gears including nets, bamboo stake traps, mid-water trawls and trolling lines in coastal waters throughout its range (Collette, 2001). In terms of consumption, it is the most important highly migratory species occurring in the Arabian Gulf (Hoolihan, 2004). In the southern Arabian Gulf, it is mainly caught using encircling gillnets set around schools from outboard powered fibreglass dories and traditional wooden dhows, trolling lines are also used and it is targeted by the recreational fishery.

Many fish populations in the Arabian Gulf have been heavily exploited and fishing effort may be above optimum levels for some species (Samuel et al., 1987; Siddeek et al., 1999). The threat of growth over-fishing and potential of recruitment failure associated with the intensive harvest of immature fish has been of particular concern for *S. commerson* in this region (Dudley et al., 1992; Kingfish Task Force, 1996). In the neighbouring Gulf of Oman, there has been a progressive 10-fold decrease in yields during recent years (Al-Oufi et al., 2002). The fishery status of *S. commerson* in the Arabian Gulf has not been ascertained to date, although it has been an issue for some time (Shotton, 1997). The expansion of the fishing fleet of the United Arab Emirates and lack of appropriate data on most stocks underscores the need to assess this important fisheries resource.

In this context, the goal of this study was to evaluate the fishery of *S. commerson* and provide biological reference points and other pertinent information required for management. Specific objectives included establishing key demographic parameters using validated age estimates and identifying characteristics of the reproductive biology of *S. commerson* in these waters.

## 2. Materials and methods

# 2.1. Study site and sampling protocol

Size frequency data were collected from commercial catches of *S. commerson* made off the coast of the Emirate of Abu Dhabi in the United Arab Emirates (Fig. 1) between October 2003 and September 2004. Fish were selected at random from landings, lengths were taken using a measuring board and recorded to the nearest cm fork length ( $L_F$ ). The monthly target sample size was 250 fish.

Biological data were collected from specimens purchased from commercial catches between October 2003 and September 2004. Samples were obtained from 30 fish from a representative size range during the first week of each month. Standard length  $(L_s)$ , fork length  $(L_F)$  and total length  $(L_T)$  were obtained using a measuring board and recorded to the nearest millimeter. Whole wet weight was taken with an electronic balance and recorded to the nearest gram. Fish were sexed by macroscopic examination of the gonad which was dissected out and subsequently



Fig. 1. Study site showing the location of the Emirate of Abu Dhabi in the southern Arabian Gulf and designated fishing areas for *S. commerson* (F).

weighed to 0.1 g using an electronic balance. The maturity development stage was assessed according to the criteria given in Table 1. Sagittal otoliths were extracted, cleaned in water, dried and stored in seed envelopes.

## 2.2. Age and growth

In order to evaluate the most suitable ageing technique, four methods were tested using 240 otoliths collected during the first 4 months of sampling. Whole

Table 1	
Maturity stage classification for S. commerson	

Development stage	Category	Description				
Male						
Ι	Juvenile or resting	Gonad with no development, thin and threadlike				
II	Maturing	Gonad with signs of development, white in colour but no milt when cut				
III	Mature	Gonad with milt when cut but milt not free running				
IV	Ripe	Milt freely flowing when cut				
V Spent		Gonad has a dark brown bruised appearance. A very small amount of residua milt may be present				
Female						
Ι	Juvenile or resting	Gonad with no development, translucent or glassy in appearance				
II	Maturing	Gonads with signs of development, small cream coloured eggs visible				
III	Mature	Gonads with hyaline (clear) eggs, hyaline eggs not free running				
IV	Ripe	Hyaline eggs free running, expressed when pressed				
V	Spent	Gonad dark in colour. Few residual eggs may be present				

otoliths immersed in water were examined in both unburnt and burnt conditions under low power magnification and reflected light. Burning was achieved by placing the otolith on a hotplate until it changed to a dark brown colour.

Otoliths were embedded in epoxy resin and transverse sections through the nucleus of approximately 200-300 µm thick were obtained using a twin blade saw. Sections of both the burnt and unburnt otoliths were mounted on glass slides and examined under low power magnification and reflected light. For each type of preparation, three independent readings were made with a minimum period of 2 weeks between each reading. The precision of each method was established using the index of average percent error (APE) given by Beamish and Fournier (1981). The method with the lowest APE value, which corresponded to the highest precision or reproducibility of the age readings, was selected for all otoliths. Data were only included in the subsequent analyses if two or more readings were in agreement. The reproducibility of otolith readings was also assessed for the whole sample using the index of average percent error.

In addition to the number of opaque bands observed in transverse sections, the optical characteristic of the outer margin (opaque or translucent) was recorded. The proportion of samples with opaque/translucent margins was calculated for each month and used to infer the timing and periodicity of increment formation. The age at which the first opaque band formed was calculated as the time between the mean birth date, derived from reproductive indices, and the time of formation of opaque bands. The absolute age was calculated as the age at formation of the first band plus the number of opaque bands outside the first plus the time between the formation of the last band and capture. In order to establish the relationship of the timing of opaque zone formation with trends in seawater temperature, time series data were converted using the scaling process given in Newman and Dunk (2003).

Growth was investigated by fitting the von Bertalanffy growth function (von Bertalanffy, 1938) to size-at-age data using standard nonlinear optimization methods. The model was fitted to pooled data and that for each sex separately. The von Bertalanffy growth function is defined as follows:

$$L_t = L_{\infty}(1 - e^{-k(t-t_0)})$$

Where  $L_t$  is length at time t,  $L_{\infty}$  the asymptotic length, k the growth coefficient and  $t_0$  is the hypothetical time at which length is equal to 0. Growth parameters were compared between sexes by plotting the ellipsoidal 95% confidence regions around the estimates of k and  $L_{\infty}$  following the method of Kimura (1980). The rate of increase in size with age between sexes was compared using a modified *t*-test (Sokal and Rohlf, 1995). Differences in the mean size at age between sexes were determined using analysis of covariance (ANCOVA) with Log<sub>e</sub> age as the covariate, Log<sub>e</sub> size the dependent variable and sex as the fixed factor.

Parameters of the length weight relationship were obtained by fitting the power function  $W = aL_F^b$  to length and weight data, where W is the total wet weight, *a* a constant determined empirically,  $L_F$  the fork length and *b* is close to 3.0 for species with isometric growth.

## 2.3. Reproduction

The mean size at first sexual maturity  $(L_m)$  was estimated for both sexes by fitting the logistic function to the proportion of mature fish in  $10 \text{ cm} (L_F)$  size categories. The mean size at first sexual maturity was taken as the size at which 50% of individuals were mature. The same procedure was used to estimate the mean age at first sexual maturity  $(A_m)$  using the proportion of mature fish in each year class. Mean monthly gonadosomatic indices (GSI) were calculated for each sex by expressing the gonad weight as a proportion of the total body weight. The timing and frequency of spawning were established by plotting the proportion of fish by maturity stage and gonado-somatic indices against the sample period. The mean birth date was estimated from the period when the highest proportion of fish were observed in spawning condition.

The population sexual structure was examined using  $\chi^2$  goodness of fit tests. Independent tests were conducted to determine whether sex ratios differed significantly from unity for the whole sample and age categories within the sample. The probability level was set at .05 ( $\propto$ .05) and Yates's correction factor was used on account of there being only 1 degree of freedom for each comparison.

#### 2.4. Mortality

An age length key was developed with size-atage data following the method of Ricker (1975), this was used to convert aggregated length frequency data into an age frequency distribution. The annual instantaneous rate of total mortality (*Z*) was subsequently determined using the age-based catch curve method (Beverton and Holt, 1957). The natural logarithm of the number of fish in each age class was plotted against the corresponding age and *Z* ( $\pm$ 95% CI) was estimated from the descending slope of the best fit line using least-squares linear regression. Initial ascending points representing fish that were not fully recruited to the fishery were excluded from the analysis.

The annual instantaneous rate of natural mortality (*M*) was estimated using the empirical equation derived by Hoenig (1983). The annual instantaneous rate of fishing mortality (*F*) was calculated by subtracting the natural mortality rate (*M*) from the total mortality rate (*Z*) derived from the age-based catch curve (F = Z - M). The calculation was also made for the upper and lower 95% confidence intervals for *Z* in order to derive a range of fishing mortality rate estimates. The exploitation rate (*E*) was calculated as the proportion of fishing mortality relative to total mortality (E = F/Z).

## 2.5. Fishery assessment

Pooled length frequency samples were converted into a relative age frequency distribution using parameters of the von Bertalanffy growth function following the method of Pauly (1983). The natural logarithm of the number of fish in each relative age group divided by the change in relative age was plotted against the relative age. Backwards extrapolation of the descending limb was used to estimate probability of capture data. A selectivity curve was generated by fitting the logistic function to probability of capture and size data which was used to derive values of the sizes at capture at probabilities of 0.5 ( $L_{50}$ ), 0.75 ( $L_{75}$ ), and the size at which fish were fully recruited to the fishery ( $L_{100}$ ).

The Beverton and Holt (1966) yield per recruit model modified by Pauly and Soriano (1986) was used to determine the size at which yield per recruit would be maximised ( $L_{max}$ ). The girth at (i) the mean size at first sexual maturity for females and (ii) the size at which yield per recruit would be maximised, was calculated from the equation: 0.5girth =  $0.217L_F - 1.60$ , in order to provide a basis for mesh size regulations as half girth is comparable to the maximum stretched mesh that would retain the fish at this size. Resource status was evaluated by comparing estimates of the fishing mortality rate with target ( $F_{opt}$ ) and limit ( $F_{limit}$ ) biological reference points (BRP's) which were defined as:  $F_{opt} = 0.5M$  and  $F_{limit} = 2/3M$ , following Patterson (1992). Juvenile retention was calculated as the proportion of fish in aggregated size frequency samples below the mean size at first sexual maturity.

# 3. Results

A total of 360 biological samples were collected, ranging in size from 46.2 to 132.9 cm  $L_F$  (males) and 44.1 to 155.2 cm  $L_F$  (females). A total of 3149 length frequency samples were collected ranging in size from 21.0 to 135.0 cm  $L_F$ .

## 3.1. Age and growth

Alternating translucent and opaque bands were observed in whole otoliths and transverse sections in both burnt and unburnt states. Of the four methods evaluated using the otolith sub sample, sectioned and unburnt otoliths had the lowest average percent error (APE) of 14.4%. Values of APE for sectioned burnt otoliths, whole unburnt and whole burnt otoliths were 15.3, 15.9 and 26.1%, respectively. Ages were underestimated for both of the whole reading methods, in particular those for the older and larger fish. All subsequent otoliths were prepared using the unburnt and sectioned method (see Fig. 2). Of the 360 otoliths that were processed, 42 could not be read and data from 41 were excluded from the age-associated analyses due to a lack of agreement between readings. The APE for the whole sample of sectioned and unburnt otoliths was 9.4%.

One growth increment consisting of a broad opaque and narrow translucent zone was formed on an annual basis with the opaque band being deposited between May and July (Fig. 3). The first opaque band was estimated to form at 1 year of age. There was an apparent time lag of 2 months from the start of the increase in seawater temperature and the commencement of formation of the opaque band. The formation of the translucent zone, however, coincided with the decrease in seawater temperature. Absolute age estimates ranged from 0.4 to 16.2 years (males) and 0.2 to 15.3 years (females).



Fig. 2. Photomicrograph of a transverse section through the sagittal otolith of *S. commerson* (128.7 cm  $L_F$ ). Numbers show the position of opaque bands (scale bar = 1 mm).

The size-at-age relationships were asymptotic in form with the majority of growth occurring during the first 6 years of life and there was a high degree of individual variability in size at age (Fig. 4). Initial growth was rapid with fish reaching more than half the asymptotic size (82.8 cm  $L_F \pm 12.7$  cm S.D.) by the second year. There was an overlap of the 95% confidence ellipses around the growth parameter (*k* and  $L_{\infty}$ ) estimates suggesting that there were no differential growth characteristics between sexes (Fig. 5). The results of the modified *t*-test revealed that there was no significant difference in the rate of increase in size with age between sexes (P = 0.51, t = 0.65, 273 d.f.)



Fig. 3. The proportion of otoliths with opaque outer margins for *S. commerson* and monthly sea temperatures off the Emirate of Abu Dhabi. Note that the values have been converted to a standardised scale to enable a comparison of the trends.

whilst the ANCOVA indicated that there was no significant difference in the mean size at age between sexes (P = 0.21, F = 1.55, 1 d.f.). Parameters of the von Bertalanffy growth function for each sex and pooled size-at-age data are presented in Table 2 and the age length key is given in Table 3. The length weight relationship ( $y = 9^{-6}x^{2.96}$ ) provided a good fit to length and weight data ( $r^2 = 0.99$ ).

## 3.2. Reproduction

The mean size at first sexual maturity  $(L_m)$  was 72.8 cm  $L_F$  (82.5 cm  $T_L$ ) for males and 86.3 cm  $L_F$ 



Fig. 4. The von Bertalanffy growth function fit to size at age relationships for *S. commerson* for males (n = 110) and females (n = 167).



Fig. 5. Confidence regions (95%) for growth parameter estimates (k and  $L_{\infty}$ ) for male (n = 110) and female (n = 167) *S. commerson*.

(97.8 cm  $T_{\rm L}$ ) for females. The mean age at first sexual maturity ( $A_{\rm m}$ ) was 1.9 years for males and 2.1 years for females.

The gonado-somatic index for both males and females increased rapidly between February and April with spawning occurring between April and August (Fig. 6). Patterns in the proportion of fish by maturity development stage also suggested that spawning took place between April and August with fish in spawning condition only being observed during this period (Fig. 7). The mean birth date was estimated as the 1st June. There was a significant (P < 0.05) female bias in the overall male to female sex ratio of 1:1.5 though the female bias was only significant in the youngest age category (Table 4).

#### 3.3. Mortality

The annual instantaneous rate of total mortality (Z) derived from the age-based catch curve was

Table 2 Parameters of the von Bertalanffy growth function, coefficients of determination  $(r^2)$  and sample sizes (*n*) by sex for *S. commerson* 

Parameter	All	Males	Females
k	0.21	0.22	0.24
$L_{\infty} \operatorname{cm} (L_{\mathrm{F}})$	138.6	125.6	136.1
$t_0$ (years) $r^2$	-1.9	-2.3	-1.7
$r^2$	0.68	0.71	0.71
n	277	110	167



Fig. 6. Mean monthly gonado-somatic indices for male (n = 144) and female  $(n = 216 \pm S.E.)$  *S. commerson* in the southern Arabian Gulf.

0.88 year<sup>-1</sup> (0.72–1.05 year<sup>-1</sup> 95% CI). The annual instantaneous rate of natural mortality (*M*) derived from the Hoenig (1983) equation was estimated at 0.26 year<sup>-1</sup> using the maximum absolute age of 16.2 years. The annual instantaneous rate of fishing mortality (*F*) was 0.62 year<sup>-1</sup> (0.46–0.79 year<sup>-1</sup> 95% CI) and the exploitation rate (*E*) was 0.7.

#### 3.4. Fishery assessment

The mean size at first capture ( $L_c$ ) was 29.7 cm  $L_F$ and the size at capture at a probability of 0.75 ( $L_{75}$ ) was 46.2 cm  $L_F$ . Fish were fully recruited to the fishery at a size that was considerably smaller ( $L_{100} = 62.6$  cm  $L_F$ ) than the mean size at first sexual maturity for females (86.3 cm  $L_F$ ).

The size at which yield per recruit would be maximised ( $L_{max}$ ) was 95.6 cm  $L_F$ . The girth at the mean size of first sexual maturity was 28.4 and 34.2 cm for males and females, respectively. The stretched mesh size that would retain females at the mean size at first sexual maturity was 17.1 cm. The girth and associated stretched mesh size at the size at which yield per recruit would be maximised ( $L_{max}$ ) were 38.2 and 19.1 cm, respectively.

The annual instantaneous rate of fishing mortality  $(F = 0.62 \text{ year}^{-1}) (0.46 - 0.79 \text{ year}^{-1} 95\% \text{ CI})$  was considerably greater than the target  $(F_{\text{opt}} = 0.13)$  and limit  $(F_{\text{limit}} = 0.17)$  biological reference points, suggesting

$L_{\rm F}$ (cm)	Age	class																Total
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
45	3	2																5
50	7	5	1															13
55	6	11	1															18
60	8	8	2	1														19
65	4	22		1														27
70	2	7		2														11
75		4	11		1													16
80	6	5	10	6														27
85	1	4	13	3	1													22
90		3	4	3	1	1	1	1										14
95			1	3	1	1												6
100	1	1	2	7	5		1	2										19
105		1	3	7	4	2	2	2		1								22
110			1	2	3	1		2										9
115			1	2	1	5			1	2		1						13
120				5	2	3	5					1		2	1			19
125					1	2				1				1		1	1	7
130				2		1			1	1	1				1			7
135													2					2
140												1						1
n	38	73	50	44	20	16	9	7	2	5	1	3	2	3	2	1	1	277
Mean	63.1	66.3	82.8	97.7	103.3	114.2	110.9	102.6	123.4	118.0	132.5	124.6	134.4	121.6	123.9	126.8	124.4	
S.D.	14.2	11.6	12.7	17.1	11.9	10.5	11.8	7.6	11.9	10.0	-	13.8	2.1	3.5	7.2	-	-	

 Table 3

 Age length key for S. commerson in the southern Arabian Gulf



Fig. 7. The proportion of fish by maturity stage and month for S. commerson in the southern Arabian Gulf (males and females combined).

Age category	Males		Females		Total	Chi-squar	e		Р
	Obs.	Exp.	Obs.	Exp.		Males	Females	Total	
0-2	38	55.5	73	56	111	5.84	5.21	11.05	< 0.01
3–5	48	57	66	57	114	1.58	1.27	2.85	0.09
6–16	24	26.5	29	27	53	0.34	0.15	0.49	0.48
Total	110		168		278				

Table 4 Results of chi-square goodness of fit tests on sex ratios within age categories for *S. commerse* 



Fig. 8. Aggregated length frequency distribution for *S. commerson* showing the mean size at first capture ( $L_{50}$ ), the size at which fish are fully recruited ( $L_{100}$ ), the mean size at first sexual maturity ( $L_m$ ) and the size at maximum yield per recruit ( $L_{max}$ ) (n = 3149).

that the stock is heavily over-exploited. The proportion of fish in aggregated size frequency samples that were below the mean size at first sexual maturity for females (juvenile retention rate) was 94.7% (see Fig. 8).

# 4. Discussion

#### 4.1. Age and growth

As a result of the importance of *S. commerson* to fisheries throughout its range, there have been a number of studies relating to the age and growth of this species. These have confirmed the utility of seasonally deposited increments in sagittal otoliths for demographic investigations. Age structures, growth rates, longevity and other population characteristics have

subsequently been established over a broad geographical range extending from South Africa (Govender, 1994), the Gulf of Oman/Arabian Sea (Dudley et al., 1992; McIlwain et al., 2005) and the Gulf of Mannar (Devaraj, 1983) to Australia (McPherson, 1992). This study supports these findings and demonstrates that growth zones in the sagittal otoliths of *S. commerson* from the Arabian Gulf are suitable for age estimation. The structural increments are consistent with the observations of Brothers and Mathews (1987) for this species in the waters off Kuwait and it is probable that the samples examined here are taken from the same stock given its highly migratory nature.

The southern Arabian Gulf exhibits marked seasonal variability in oceanographic characteristics with seawater temperatures exceeding 34 °C in summer and falling to 21 °C in the winter (Sheppard et al., 1992). It is plausible that this extreme temperature fluctuation and variables, such as productivity and subsequent food availability, are associated with seasonal growth rate changes and the deposition of translucent and opaque bands observed in the otoliths of S. commerson. Whilst the mechanisms of growth increment formation are poorly understood, the deposition of the opaque zone in tropical species generally occurs in the spring and summer months during periods of accelerated growth, whereas the translucent zone is formed when there is reduced metabolic activity (Beckman and Wilson, 1995). The formation of opaque and translucent zones in the sagittal otoliths of S. commerson determined here follows this generalised pattern and appears to be associated with seawater temperature.

The peak in the proportion of otoliths with opaque outer margins coincided with the peak in spawning activity, an observation that has also been made for *S. commerson* off the east coast of Australia (Tobin and Mapleston, 2004). Validation using counts of daily rings between presumed annuli (Dudley et al., 1992) and edge analysis (McIlwain et al., 2005) demonstrated that annually deposited growth zones were formed in the otoliths of *S. commerson* in the waters off Oman. The annual periodicity of growth increment formation established here substantiates these findings and reinforces the utility of the method for conducting age-based assessments for this species around the Arabian Peninsular.

Whilst structural increments in sagittal otoliths were suitable for ageing S. commerson off the southern coast of India, two growth zones (each consisting of an opaque and hyaline band) were found to be deposited annually Devaraj (1981). The same pattern was also observed for this species in South Africa by Govender (1994). The disparity of these findings by comparison with our results could be attributed to differences in environmental regimes between regions and/or methodological differences in otolith processing techniques and interpretation. McPherson (1992) validated the annual periodicity of opaque bands in 1-3-yearold S. commerson in Australia but also observed secondary opaque zones. These secondary bands may have been what led Devaraj (1981) and Govender (1994) to conclude that two growth zones are formed annually. This is a tenable explanation given the similarity in growth characteristics obtained by these investigators with those where annual periodicity was determined (this study; Dudley et al., 1992; McPherson, 1992).

The growth of S. commerson in the Gulf of Oman was characterised by a very rapid initial increase in size with fish achieving between 100 and 110 cm during the first 2 years of life (Dudley et al., 1992; McIlwain et al., 2005). Whilst initial growth reported here was not quite as pronounced as that observed in neighbouring waters, it was nevertheless very rapid with 2-year-old fish reaching a mean size of  $82.8 \text{ cm } L_{\text{F}}$  $(\pm 12.7 \text{ cm S.D.})$ . This pattern has also been described for young S. commerson from Australia (McPherson, 1992) Kuwait (Brothers and Mathews, 1987) and South Africa (Govender, 1994). Our results also appear to be of the right order by comparison with a range of published estimates of von Bertalanffy growth function parameters derived from size-at-age data (Table 5), though improvements could be made by the addition of larger specimens closer to the maximum reported size and juvenile fish less than  $45 \text{ cm } L_{\text{F}}$ .

The maximum absolute age estimate for S. commerson (16.2 years) was greater than the maximum

Table 5

Parameters of the von Bertalanffy growth function (k and $L_{\infty}$ ) for S.
commerson derived from size-at-age data

VBGF	parameter	Sex	Source
k	$L_{\infty} \operatorname{cm}(L_{\mathrm{F}})$		
0.24	136.1	Females	This study
0.22	125.6	Males	This study
0.21	138.6	Combined	This study
0.18	187.1	Combined	Devaraj (1981)
0.36	138.3	Combined	Dudley et al. (1992)
0.29	134.3	Combined	Govender (1994)
0.31	140.4	Females	McIlwain et al. (2005)
0.60	118.8	Males	McIlwain et al. (2005)
0.17	155.0	Females	McPherson (1992)
0.25	127.5	Males	McPherson (1992)

age of 12.7 years estimated by Dudley et al. (1992) and that of McPherson (1992) who estimated the oldest fish to be 14 years from samples taken off the north eastern coast of Queensland, Australia. It is noteworthy that the maximum sizes of males (132.9 cm  $L_F$ ) and females (155.2 cm  $L_F$ ) sampled for otoliths and biological data here correspond to those sampled by McPherson (1992) (132 and 155 cm  $L_F$ , respectively). Our maximum age estimate was in agreement with that of 17 years for this species in Queensland (Tobin and Mapleston, 2004). As a maximum age of 20 years has been reported by McIlwain et al. (2005) from the Gulf of Oman, the maximum age observed here may have under estimated longevity due to the limited number of samples that were close to the maximum reported size.

Our study showed that whilst females approached their asymptotic size at a faster rate than males, as well as growing to a greater mean length at age, the differences observed were not significant. Still, larger sample sizes, in particular for specimens closer to the maximum reported size and juvenile fish less than 45 cm  $L_{\rm F}$ , would have improved the integrity of the results derived from the comparison of growth characteristics between sexes. Devaraj (1981) found that there were no differential growth characteristics between sexes for S. commerson from India. However, in north eastern Queensland, females have been found to grow to larger asymptotic sizes and live longer than males (McPherson, 1992). In the Gulf of Oman and Arabian Sea, female kingfish have been shown to grow at a slower rate but reach a greater asymptotic length than males (McIlwain et al., 2005).

#### E.M. Grandcourt et al. / Fisheries Research 76 (2005) 277-290

## 4.2. Reproduction

The mean sizes at first sexual maturity for males and females, respectively (72.8 and 86.3 cm  $L_F$ ), compare to the estimated size at spawning of 75–80 cm  $L_F$  given by Dudley et al. (1992) for males and females combined off Oman. Claereboudt et al. (2004) later estimated the size at first sexual maturity (also off Oman) at 84.7 cm  $L_F$  for males and 80.4 cm  $L_F$  for females. *S. commerson* has been found to mature between 70–80 cm  $L_F$ off Madagascar, Papua New Guinea and Fiji (Collette and Russo, 1984), and in the northern Indian Ocean the mean size at first sexual maturity was estimated at 75 cm  $L_F$  by Devaraj (1983). Whilst our values compare well with those from other regions, histological diagnosis of the maturity development stage would have improved the estimates.

The period during which there was a decline in the gonado-somatic indices and when fish in spawning condition were observed in our samples suggests a single spawning period from April to August. The results of Claereboudt et al. (2004, 2005) also revealed a single though earlier spawning season in May and June for kingfish off Oman. The reproductive activity of S. commerson in waters off the east coast of Australia also peaked in the spring and summer months (McPherson, 1993). In contrast to the defined single seasonal spawning pattern for this species, Devaraj (1983) established three distinct spawning periods between January and September in the waters off the southern coast of India. Whilst seasonal fishery closures have often been dismissed as a management tool for tropical species because of the assumption that spawning is protracted, the existing ban on the use of gillnets to target S. commerson between the end of April and the beginning of October is appropriate in relation to the reproductive cycle of this species.

Whilst there was a significant female bias in the overall sex ratio, the analyses of sex ratios in age categories indicated that only the youngest age category (0-2 years) had a sex ratio that was significantly different from unity. As many of these fish would have been immature, males could have been falsely diagnosed as females during macroscopic sex determination and histological diagnosis would have provided more conclusive results. Still, Claereboudt et al. (2004, 2005) found that significantly more females were caught in two regions along the coast of Oman and suggested this

to be a result of the methods used by traditional fishermen. Furthermore, there is evidence that males and females migrate separately (Lester et al., 2001) off the west coast of Australia. If this occurs in the southern Arabian Gulf, females may have been differentially targeted by the fishery, which would explain the observed bias.

# 4.3. Mortality

Total mortality values of 0.61 and 0.66 year<sup>-1</sup> were obtained by Govender (1995) for *S. commerson* in South Africa. Tobin and Mapleston (2004) estimated total mortality as 0.40 and 0.35 year<sup>-1</sup> for the commercial and recreational fisheries, respectively, in eastern Australia, and Edwards et al. (1985) established a total mortality rate of 0.44 year<sup>-1</sup> for *S. commerson* in the Gulf of Aden. The high total mortality rate (Z=0.88 year<sup>-1</sup>) derived from the age-based catch curve here compares well to the estimates of 0.90 and 0.89 year<sup>-1</sup> for females and males, respectively, in the waters off Oman (McIlwain et al., 2005) which is potentially the same stock as that occurring in the Arabian Gulf.

Nevertheless, the total mortality and consequently fishing mortality rates estimated here may have been biased upwards due to the differential targeting of younger schooling fish. Estimates of Z and the size/age compositions may also have been biased by ontogenetic and/or seasonal migrations. McPherson and Williams (2002) considered that certain gear types resulted in the larger older fish being proportionately higher on fishing grounds than their representation in catches would suggest. Size-specific selectivity would explain the small proportion of larger and older fish in the size and age frequency distributions. However, the impact of fishing cannot be discounted, especially given the limited regulation and intensity of fisheries targeting *S. commerson* throughout the Arabian Gulf.

Our estimate of the natural mortality rate  $(M = 0.26 \text{ year}^{-1})$  was considerably lower than the estimates of Govender (1995) which ranged from 0.45 to 0.55 year<sup>-1</sup>. Dudley et al. (1992) estimated the natural mortality rate of *S. commerson* as 0.44 year<sup>-1</sup> in the Gulf of Oman and Edwards et al. (1985) estimated a rate of 0.38 year<sup>-1</sup> for this species in the Gulf of Aden. However, these were derived from the empirical equation of Pauly (1980), which has been shown

to overestimate M (Russ et al., 1998; Newman et al., 2000). Welch et al. (2002) and Hoyle (2003) used a natural mortality rate of 0.34 year<sup>-1</sup> in their assessment models for *S. commerson* in eastern Australia though this value was considered to be overestimated on the basis of total mortality rates established later on for the same stock (Tobin and Mapleston, 2004). Whilst estimates derived from the Hoenig (1983) relationship have been shown to provide a reasonable approximation of M in tropical species (Hart and Russ, 1996; Newman et al., 1996), the generalised nature of the derivation of this parameter is a potential source of error in the assessment.

#### 4.4. Fishery assessment

As the mean size at first capture  $(29.7 \text{ cm } L_F)$  and size at which fish were fully recruited to the fishery  $(L_{100} = 62.6 \text{ cm } L_F)$  were considerably smaller than the size at first sexual maturity for females  $(86.3 \text{ cm } L_T)$ and the size at which yield per recruit would be maximised (95.6 cm  $L_{\rm F}$ ), it is apparent that an increase in the minimum mesh size regulation for the gillnet fishery is required. This is particularly important given that 94.7 % of the yield consisted of fish that were below the mean size at first sexual maturity. The existing mesh size of 8.5 cm and possibility that young schooling fish are differentially targeted would explain the high level of juvenile retention. As the estimated stretched mesh size that would retain fish at the size at which yield per recruit would be maximised was 19.1 cm, a considerable increase from the existing current minimum mesh size regulation of 7.5 cm should be considered. Nevertheless, given the limited sample sizes and generic nature of the selectivity estimates, the values determined are considered initial approximations.

Dudley et al. (1992) estimated the size at first capture to be between 40 and 60 cm, corresponding to an age at first capture of 4–6 months for *S. commerson* off Oman. In addition, up to 90% of the fish captured were immature with very few reaching their third year of life (Claereboudt et al., 2004; McIlwain et al., 2005). The selectivity characteristics of the fishery for *S. commerson* off Oman are therefore remarkably similar to those obtained here.

Setting a minimum size above the mean size at first sexual maturity was predicted to be associated with short-term decreases in yield and substantial gains in spawning biomass per recruit for *S. commerson* in South Africa (Govender, 1995). In addition, simulation models used by Dudley et al. (1992) for *S. commerson* in the waters off Oman suggested that appropriate management action would be to protect the young fast growing fish as this would lead to increases in catch in the year following implementation. Such a strategy was also considered prudent in terms of enhancing reproductive capacity, predicting a 40% increase in egg production to be associated with the protection of 0–2-year-old fish.

Gulland (1970) suggested that in an optimally exploited stock, fishing mortality should be about equal to natural mortality, resulting in an exploitation rate of  $0.5 \text{ year}^{-1}$ . However, exploitation rates should be very conservative for relatively long lived species (Newman and Dunk, 2003), especially given that potential yields may be over estimated by a factor of 3–4, where F = M(Beddington and Cooke, 1983). Furthermore, the yield and spawning biomass per recruit analyses of Govender (1995) for S. commerson in South Africa predicted a virtual collapse of the fishery when the fishing mortality rate was equal to the natural mortality rate. The specified precautionary target ( $F_{opt} = 0.5M$ ) and limit  $(F_{\text{limit}} = 2/3M)$  biological reference points are therefore considered to be appropriate, particularly given existing management objectives which are aimed at resource conservation and stock re-building.

The fishing mortality rate of  $0.62 \text{ year}^{-1}$  (0.46– 0.79 year<sup>-1</sup> 95% CI) was substantially greater than both the target ( $F_{\text{opt}} = 0.13 \text{ year}^{-1}$ ) and limit ( $F_{\text{limit}} =$ 0.17 year<sup>-1</sup>) biological reference points. These results are important to fisheries management authorities as they suggest that the resource is heavily over-exploited and in addition to a revision of mesh size regulations, a substantial reduction in fishing effort would also be required if management objectives are to be achieved. The findings also substantiate the concerns of Dudley et al. (1992) that *S. commerson* is threatened by overfishing and the potential of recruitment failure associated with the intensive harvest of immature fish.

In the absence of any previous assessments, the Government of the Emirate of Abu Dhabi in the United Arab Emirates has taken a precautionary approach to the regulation of the fishery for *S. commerson* in the southern Arabian Gulf. Both drift and set gillnets have been banned as is the use of monofilament. Fishing operations are restricted to four zones (see Fig. 1) and there is a seasonal fishery closure between the 30th of April and the 1st of October, which coincides with the spawning season. Input controls constrain the total length of gillnets to 700 m, fishers may use a maximum of two nets per licensed vessel and there is limited entry to the fishery with 383 permits being issued in 2003. However, the fisheries for S. commerson in other locations throughout its range are largely unregulated and drift nets are still used (Claereboudt et al., 2005; Hoolihan, 2004). Given the highly migratory nature of this species, and that the stock is probably homogenous throughout the Arabian Gulf and Arabian Sea (Hoolihan, personal communication), it is unlikely that the initiatives of any one of the littoral states alone would be sufficient to achieve resource management objectives. Clearly, a strategic regional approach to the assessment and management of S. commerson is imperative in this context.

#### Acknowledgements

We are very grateful to Sultan Al Ali, Khaled Al Ali and Ahmed Al Suwaidi for their assistance with data collection. The Abu Dhabi Fishermens Cooperative Society facilitated size frequency sampling. This study was funded by the Government of the United Arab Emirates through the Environmental Research and Wildlife Development Agency.

#### References

- Al-Oufi, H.S., McLean, E., Goddard, J.S., Claereboudt, M.R.G., Al-Akhzami, Y.K., 2002. The kingfish, *Scomberomorus commerson* (Lacepède 1800) in Oman: reproduction, feeding and stock identification. In: McLean, E., Al-Oufi, H.S., Al-Akhzami, Y.K., Najamuddins (Eds.), Contemporary Issues in Marine Science and Fisheries. Hasanuddin University Press, Makassar, pp. 1–17.
- Beamish, R.J., Fournier, D.A., 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38, 982–983.
- Beckman, D.W., Wilson, C.A., 1995. Seasonal timing of opaque zone formation in fish otoliths. In: Secor, D.H., Dean, J.M., Campana, S.E. (Eds.), Recent Developments in Fish Otolith Research. University of South Carolina Press, Colombia, SC, pp. 27–43.
- Beddington, J.R., Cooke, J.G., 1983. The potential yield of fish stocks. Food and Agricultural Organisation, Fisheries Technical Paper No. 242. Food and Agricultural Organisation, Rome, 47 pp.
- Ben-Tuvia, A., 1978. Immigration of fishes through the Suez Canal. Fish. Bull. 76 (1), 249–255.

- Beverton, R.J.H., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations. Chapman and Hall, London, 533 pp.
- Beverton, R.J.H., Holt, S.J., 1966. Manual of methods for fish stock assessment. Part II. Tables of yield function. Food and Agricultural Organisation, Fisheries Biology Technical Paper No. 38, 67 pp.
- Blaber, S.J.M., Milton, D.A., Rawlinson, N.J.F., Tiroba, G., Nichols, P.V., 1990. Diets of lagoon fishes of the Solomon Islands: predators of tuna baitfish and trophic effects of baitfishing on the subsistence fishery. Fish. Res. 8, 263–286.
- Brothers, E.B., Mathews, C.P., 1987. Application of otolith microstructural studies to age determination of some commercially valuable fish of the Arabian Gulf. Kuw. Bull. Mar. Sci. 9, 127–157.
- Claereboudt, M.R.G., Al-Oufi, H.S., McIlwain, J., Goddard, J.S., 2004. Relationships between fishing gear, size frequency and reproductive patterns for the kingfish (*Scomberomorus commerson* Lacepède) fishery in the Gulf of Oman. In: Payne, A.I.L., O'Brien, C.M., Rogers, S.I. (Eds.), Management of Shared Fish Stocks. Blackwell Publishing, Oxforshire, pp. 56–67.
- Claereboudt, M.R., McIlwain, J.L., Al-Oufi, H.S., Ambu-Ali, A.A., 2005. Patterns of reproduction and spawning of the kingfish (*Scomberomorus commerson* Lacépède) in the coastal waters of the Sultanate of Oman. Fish. Res. 73, 273–282.
- Collette, B.B., 2001. Scombridae. Tunas (also, albacore, bonitos, mackerels, seerfishes, and Wahoo). In: Carpenter, K.E., Niem, V. (Eds.), FAO Species Identification Guide for Fishery Purposes. The Living Marine Resources of the Western Central Pacific, vol. 6. Bony Fishes Part 4 (Labridae to Latimeriidae). Food and Agricultural Organization, Rome, pp. 3721–3756.
- Collette, B.B., Russo, J.L., 1984. Morphology, systematics, and biology of the Spanish Mackerels (Scomberomorus, Scombridae). Fish. Bull. 82 (4), 545–689.
- Devaraj, M., 1981. Age and growth of three species of Seerfishes Scomberomorus commerson, S. guttatus and S. Lineolatus. Ind. J. Fish. 28 (1–2), 104–127.
- Devaraj, M., 1983. Maturity, spawning and fecundity of the king seer, Scomberomorus commerson (Lacepède), in the seas around the Indian Peninsula. Ind. J. Fish. 30, 203–230.
- Dudley, R.G., Prabhakar, A., Brothers, E., 1992. Management of the Indo-Pacific Spanish mackerel (*Scomberomorus commerson*) in Oman. Fish. Res. 15, 17–43.
- Edwards, R.R.C., Bakhader, A., Shaher, S., 1985. Growth, mortality, age composition and fishery yields of fish from the Gulf of Aden. J. Fish. Biol. 27, 13–21.
- Govender, A., 1994. Growth of the king Mackerel (*Scomberomorus commerson*) off the coast of Natal, South Africa—from length and age data. Fish. Res. 20, 63–79.
- Govender, A., 1995. Mortality and biological reference points for the king mackerel (*Scomberomorus commerson*) fishery off Natal, South Africa (based on per-recruit assessment). Fish. Res. 23, 195–208.
- Gulland, J.A., 1970. The fish resources of the ocean. FAO Fisheries Technical Paper No. 97. Food and Agricultural Organisation, Rome.
- Hart, A.M., Russ, G.R., 1996. Response of herbivorous fish to crown of thorns starfish Acanthaster planci outbreaks. III. Age, growth,

mortality and maturity indices of *Acanthurus nigrofuscus*. Mar. Ecol. Prog. Ser. 136, 25–35.

- Hoenig, J.M., 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82, 898–902.
- Hoolihan, J., 2004. Managing Arabian Gulf sailfish—issues of transboundary migration. In: Payne, A.I.L., O'Brien, C.M., Rogers, S.I. (Eds.), Management of Shared Fish Stocks. Blackwell Publishing, Oxforshire, pp. 339–347.
- Hoyle, S., 2003. Management Strategy Evaluation for the Queensland East Coast Spanish Mackerel Fishery. Brisbane Department of Primary Industries, Queensland, 56 pp.
- Kimura, D.K., 1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77, 765–776.
- Kingfish Task Force, 1996. Kingfish Resource and Fisheries in the Sultanate of Oman. Indo-Pacific Tuna Development and Management Programme (IPTP/96/WP/27), Colombo, 55 pp.
- Lester, R.J.G., Thompson, C., Moss, H., Barker, S.C., 2001. Movement and stock structure of narrow-barred Spanish mackerel as indicated by parasites. J. Fish. Biol. 59, 833–842.
- McIlwain, J.L., Claereboudt, M.R., Al-Oufi, H.S., Zaki, S., Goddard, J.S., 2005. Spatial variation in age and growth of the kingfish (*Scomberomorus commerson*) in the coastal waters of the Sultanate of Oman. Fish. Res. 73, 283–298.
- McPherson, G.R., 1981. Preliminary report: investigations of Spanish mackerel, *Scomberomorus commerson* in Queensland waters. In: Grant, C.J., Walter, D.G. (Eds.), Northern Pelagic Fish Seminar. Darwin, Northern Territory, 20–21 January. Australian Government Publishing Service, Canberra, pp. 51–58.
- McPherson, G.R., 1985. Northern line fishery for mackerels still important. Aust. Fish. 44 (8), 12–14.
- McPherson, G.R., 1989. North-eastern Australian mackerel (*Scomberomorus*) fishery. In: Chavez, E.A. (Ed.), Proceedings of the Workshop Australia–Mexico on Marine Sciences. Quintana Roo, Mexico, 6–17 July. Quintana Roo, Mexico, pp. 341–348.
- McPherson, G.R., 1992. Age and growth of the narrow-barred Spanish mackerel (*Scomberomorus commerson* Lacepède 1800) in north-eastern Queensland waters. Aust. J. Mar. Freshwater Res. 43 (5), 1269–1282.
- McPherson, G.R., 1993. Reproductive Biology of the Narrow Barred Spanish Mackerel (*Scomberomorus commerson* Lacepède, 1800) in Queensland waters. Asian Fish. Sci. 6, 169–182.
- McPherson, G.R., Williams, L.E., 2002. Narrow-barred Spanish mackerel. In: Williams, L.E. (Ed.), Queenslands Fisheries Resources: Current Condition and Recent Trends 1988–2000. Department of Primary Industries Brisbane, Queensland, pp. 88–93.
- Myers, R.F., 1991. Micronesian Reef Fishe, second ed. Coral Graphics, Barrigada, Guam, 298 pp.
- Newman, S.J., Cappo, M., Williams D., McB., 2000. Age, growth and mortality of the stripey, *Lutjanus carponotatus* (Richardson) and the brown-stripe snapper, L. vitta (Quoy and Gaimard) from the central Great Barrier Reef, Australia. Fish. Res. 48, 263– 275.
- Newman, S.J., Dunk, I.J., 2003. Age validation, growth, mortality, and additional population parameters of the goldband snapper

(*Pristipomoides multidens*) off the Kimberley coast of northwestern Australia. Fish. Bull. 101 (1), 116–128.

- Newman, S.J., Williams D, McB., Russ, G.R., 1996. Age validation, growth and mortality rates of the tropical snappers (Pices: Lutjanidae) *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the Central Great Barrier Reef, Australia. Aust. J. Mar. Freshwater Res. 47, 575–584.
- Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management targets. Rev. Fish. Biol. Fish 2, 321–338.
- 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, 175–199.
- Pauly, D., 1983. Length-converted catch curves: a powerful tool for fisheries research in the tropics (part 1). Fishbyte 1 (2), 9–13.
- Pauly, D., Soriano, M.L., 1986. Some practical extensions to Beverton and Holt's relative-yield-per-recruit model. In: Maclean, J.L., Dizon, L.B., Hosillo, L.V. (Eds.), The First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines, pp. 491–496.
- Randall, J.E., 1995. Coastal Fishes of Oman. University of Hawaii Press, Honolulu Hawaii, 439 pp.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Bd. Can. 191, 382.
- Russ, G.R., Lou, D.C., Higgs, J.B., Ferreira, B.P., 1998. Mortality rate of a cohort of the coral trout, *Plectropomus leopardus*, in zones of the Great Barrier Reef Marine Park closed to fishing. Aust. J. Mar. Freshwater Res. 49, 505–511.
- Samuel, M., Mathews, C.P., Bawazeer, A.S., 1987. Age and validation of age from otoliths for warm water fishes from the Arabian Gulf. In: Summerfelt, R.C., Hall, G.E. (Eds.), Age and Growth of Fish. Iowa State University Press, pp. 253–265.
- Sheppard, C., Price, A., Roberts, C., 1992. Marine Ecology of the Arabian Region. Patterns and Processes in Extreme Tropical Environments. Academic Press, London.
- Shotton, R., 1997. Western Indian Ocean. In: Review of the State of World Fishery Resources: Marine Fisheries. Food and Agricultural Organisation Fisheries Circular No. 920 FIRM/C920. Food and Agricultural Organisation of the United Nations, Rome.
- Siddeek, M.S.M., Fouda, M.M., Hermosa Jr., G.V., 1999. Demersal fisheries of the Arabian Sea, the Gulf of Oman and the Arabian Gulf. Est. Coast. Shelf Sci. 49, 87–97.
- Sokal, R.R., Rohlf, F.J., 1995. Biometry. The Principles and Practice of Statistics in Biological Research, third ed. W.H. Freeman and Co., New York, pp. 887.
- Tobin, A., Mapleston, A., 2004. Exploitation dynamics and biological characteristics of the Queensland east coast Spanish mackerel (*Scomberomorus commerson*) fishery. CRC Reef Research Centre Technical Report No. 51. CRC Reef Research Centre, Townsville, 61 pp.
- von Bertalanffy, L., 1938. A quantitative theory of organic growth. Hum. Biol. 10, 181–213.
- Welch, D., Hoyle, S., Gribble, N., McPherson, G., 2002. Preliminary Assessment of the East Coast Spanish Mackerel Fishery in Queensland. Department of Primary Industries, Brisbane, 34 pp.

290