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ASPECTS OF THE BIOLOGY AND LIFE HISTORY OF WHITE STEENBRAS *LITHOGNATHUS LITHOGNATHUS* IN SOUTHERN AFRICA

*B. A. BENNETT**

Data on the seasonal abundance, size composition, reproduction, growth and diet of *Lithognathus lithognathus* are presented to outline the life history of the species. Spawning appears to be localized on the Transkei and Eastern Cape coasts during a short period in late winter. Small juveniles (<50 mm) enter estuarine nursery grounds along the Cape coast between September and November, remaining there for at least their first year of life before re-entering the marine environment. The post-estuarine juveniles (>150 mm) are semi-resident in the surf zone of sandy and mixed shores for about five years until maturing at a length of 650 mm, when they commence annual migrations. During autumn and early winter these mature fish migrate eastwards to near the north-eastern limit of their distributional range, to spawn during late winter. The return migration takes place during spring and large numbers of mature fish arrive in the South-Western Cape during summer. The high degree of estuarine dependence, the confinement of juveniles and subadults to the surf-zone, the large size at maturation and the predictable aggregations of mature individuals in particular areas are considered to render *L. lithognathus* particularly vulnerable to estuarine degradation and exploitation by fishermen.

Gegewens oor seisoensgewyse talrykheid, groottesamestelling, voortplanting, groei en dieet van *Lithognathus lithognathus* word aangebied om die lewensloop van die spesie te skets. Kuitskiet is blykbaar tot die Oos-Kaapse en Transkeise kus gedurende 'n kort tydperk laat in die winter beperk. Klein jongvis (<50 mm) gaan estuariene grootwordgronde langs die Kaapse kus tussen September en November binne en bly vir ten minste hul eerste lewensjaar daar voor hul weer die mariene omgewing betree. Die post-estuariene jongvis (>150 mm) bly so te sê pal in die brandersone van sand- en gemengde strande vir sowat vyf jaar tot hul op 'n lengte van 650 mm geslagsryp word en dan jaarliks begin migreer. Gedurende die herfs en en vroeë winter trek hierdie geslagsrypes ooswaarts tot na aan die noordoostelike grens van hul verspreidingsgebied om laat in die winter kuit te skiet. Die trek terug vind in die lente plaas, en groot getalle geslagsryp vis kom in die Suidwes-Kaap in die somer aan. Daar word gemeen dat die groot afhanklikheid van getymondings, die beperking van jongvis en grotere onrypes tot die brandersone, die aansienlike grootte by geslagsryping en die voorspelbare samedromming van geslagsrypes in bepaalde gebiede *L. lithognathus* veral kwesbaar maak ten opsigte van ontaarding van getymondings en ontginning deur vissermanne.

White steenbras *Lithognathus lithognathus* are endemic to southern Africa, occurring between the mouth of the Orange River and Natal (Smith and Smith 1986). They are highly sought-after by shore-anglers (Biden 1930, Schoeman and Schoeman 1990) and have provided a substantial proportion of their historical catch (Bennett 1991). Prior to 1983 they were also an important component of commercial beach-seine catches (Penney 1991). Both recreational and commercial catches have, however, declined markedly over the past decade (Bennett 1991, Penney 1991) and effective management measures are urgently required to halt these declines.

Some published information on the biology of this species is available, especially concerning juveniles in estuaries. Occurrence, size composition and relative abundance in a number of estuaries have been reported by Millard and Scott (1954), Talbot (1955), Mehl (1973), Blaber (1974), Beckley (1984), Bennett (1989a) and Whitfield and Kok (1992), diets have been described by Mehl (1973), Whitfield (1985) and Bennett (1989b), and growth rates have been reported by Mehl (1973), Blaber (1974), Beckley (1984), Bennett (1989a) and Whitfield and Kok (1992). Therefore, the juvenile estuarine phase of the life cycle is reasonably well understood; they are considered to be entirely dependent on estuarine habitats for their first year of life (Wallace *et al.* 1984a).

Considerably less is known about *L. lithognathus* in the marine environment. Mehl (1973) and Lasiak (1984) provided some data on diet, growth and reproduction, but their samples were small, lacking in mature individuals and geographically limited. As a result, insufficient information is available on which to base management decisions concerning this species.

This study was initiated to provide comprehensive data on the occurrence, seasonality, size composition, diet, growth rate and reproductive biology of *L. lithog-*

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Table I: Origins of the information concerning *Lithognathus lithognathus* in the marine environment on which the present study is based. Included are the data sources, the time periods, the areas they represent, the sample sizes and the different types of data provided

Source	Period	Area	Sample	Data
		Marine beach-seining		
Commercial catch returns Gilchrist (1897, 1899–1904, 1906, 1907)	1897–1906	Entire Cape	230 611	Seasonal abundance
Private commercial catch records	1951–1968	Northern coast of False Bay	23 881	Seasonal abundance
Private commercial catch records	1977–1987	Northern coast of False Bay	31 922	Seasonal abundance
Commercial catch returns (Sea Fisheries Research Institute unpublished data)	1983–1991	Entire Cape	28 188	Seasonal abundance
Lasiak (1984)	1978–1980	Eastern Cape	86	Seasonal abundance, size composition, diets
This study	1989–1991	Simon's Bay	1 278	Seasonal abundance, size composition, biological material
This study	1989–1991	Northern coast of False Bay	1 033	Seasonal abundance, size composition, biological material
		Marine shore-angling		
Club records	1938–1991	False Bay	4 615	Seasonal abundance, size composition
Mehl (1973)	1971–1972	False Bay	68	Seasonal abundance, size composition, biological material
Catch cards (Coetzee *et al.* 1989)	1959–1982	Eastern Cape	788	Seasonal abundance, mean size
Catch cards (Guastella 1991)	1976–1984	Eastern Cape	122	Seasonal abundance, size composition
Research angling (BAB unpublished)	1984–1991	De Hoop Marine Reserve, Southern Cape	469	Seasonal abundance, size composition, biological material
This study	1990–1991	Bashee River mouth, Transkei	87	Size composition biological material
Catch records (The Haven Hotel)	1990–1991	Bashee River mouth, Transkei	78	Seasonal abundance, size composition

nathus in the marine environment throughout their distributional range. Such information is necessary for the management of the resource.

MATERIAL AND METHODS

Data on the seasonal abundance, size composition and biology of *L. lithognathus* in commercial and recreational catches around the Cape coast were collected from as wide a variety of sources and covering as long a time period as possible (Table I). Seasonal abundance and size data were available for various time periods since 1896, but biological material was collected primarily from 1989. Biological sampling involved obtaining total lengths (*TL*) and masses and extracting gonads, otoliths and stomachs from fish in a variety of habitats throughout the Cape.

Gonads were examined macroscopically and indi-

Table II: Gonad maturity stages and the criteria used to allocate gonads to the various stages (%*H* = % hermaphrodites, *GL* = gonad length, *GW* = gonad width, *TL* = total fish length, *GM* = gonad mass, *OM* = ovary mass, *TM* = testis mass, *BM* = fish body mass)

Stage	State	%H	Males	Females
1	Immature	>80	Testicular portion of testis thin and thread-like, usually off-white or greyish. *TM* = 65–75% *GM*, *GM* = <0,5% *BM*, *GL* = 7–12% *TL*, *GW* = <2% *TL*	Ovarian portion of gonad clear, pinkish, elongate and slightly rounded. *OM* = 65–75% *GM*, *GM* = <1% *BM*, *GL* = 8–14% *TL*, *GW* = 1–3% *TL*
2	Early development or recovery	7	*GM* = <0,75% *BM*, *GL* = 7–14% *TL*. Developing testis elongate, flattened and whitish. *TM* = 65–75% *GM*, *GW* = 1–4% *TL*. Recovering testis flattened and brownish. *TM* = >90% *GM*, *GW* = 2,5–5,5% *TL*	Developing ovary translucent, pale orange or yellow and rounded in cross-section. *OM* = 65–75% *GM*, *GM* = <1% *BM*, *GL* = 8–16% *TL*, *GW* = 2–5% *TL*. Recovering ovary translucent, orange or pinkish, slightly flaccid, but rounded in cross-section. *OM* = >90% *GM*, *GM* = 0,7–2% *BM*, *GL* = 10–20% *TL*, *GW* = 3–7% *TL*
3	Late development or recovery	2	Gonads more rounded in cross-section. Some milt may be present in vas deferens. *GM* = 0,6–1,25% *BM*, *GL* = 10–17% *TL*. Developing testis whitish or cream. *TM* = 70–80% *GM*, *GW* = 3–5,5% *TL*. Recovering testis pale brown or cream. *TM* = >90% *GM*, *GW* = 5–7% *TL*	Ovaries opaque and yellow, eggs very small, hardly visible to the naked eye. *OM* = >80% *GM*, *GM* = 1–2,5% *BM*, *GL* = 10–22% *TL*, *GW* = 3–8% *TL*
4	Ripe	0	Testis cream or white and rounded in cross-section, varying quantities of milt present in vas deferens. *GM* = 1,25–3% *BM*, *GL* = 15–20% *TL*, *TM* = >85% *GM*, *GW* = 5–8% *TL*	Ovaries yellow and turgid, eggs visible, but not easily teased from the matrix. *OM* = >85% *GM*, *GM* = 1–4% *BM*, *GL* = 14–22% *TL*, *GW* = 4–8% *TL*
5	Prespawning or ripe-and-running	0	Testis turgid and white, milt may be extruded from cloaca under slight pressure or may flow freely when fish is handled. *GM* = 2–8% *BM*, *GL* = 15–28% *TL*, *GW* = 4,5–11% *TL*, *TM* = >90% *GM*	Ovaries similar in appearance to Stage 4, but larger, and eggs may be squeezed from the cloaca or may flow freely. Hydrated eggs occasionally present. *OM* = >90% *GM*, *GM* = 2,5–6,5% *BM*, *GL* = 19–28% *TL*, *GW* = 5,5–11% *TL*
6	Partially spawned	0	As above, but white colour replaced by obvious signs of varying degrees of haemorrhaging	Gonad size and proportions similar to Stage 5, but fairly extensive haemorrhaging is evident. Hydrated eggs frequently present
7	Spent	0	Testis flaccid and reddish due to extensive haemorrhaging. *GM* = 1–3,5% *BM*, *GL* = 15–26% *TL*, *GW* = 3–10% *TL*, *TM* = >90% *GM*	Ovaries flaccid and bloodshot. Eggs occasionally visible. *OM* = >90% *GM*, *GM* = 1–3,5% *BM*, *GL* = 16–26% *TL*, *GW* = 3–10% *TL*

viduals were allocated to one of seven maturity stages according to the criteria set out in Table II. *L. lithognathus* are rudimentary hermaphrodites and individuals were considered to be either male or female if the dominant portion of the ovotestis comprised more than two-thirds of the mass of the gonad. This approach was validated by Mehl (1973), who showed that genetic sex, established according to the percentage of liver cell nuclei containing sex chromatin, corresponded to the actual dominant sex established macroscopically. For the purposes of this study, fish with gonads in which ovarian and testicular development was approximately equal, were called hermaphrodites.

Sagittal otoliths were removed and stored dry. Preparation of the otoliths for age determination involved cutting thin sections with a parallel-bladed saw. These were lightly burned before being mounted on glass slides, as detailed by Buxton and Clarke (1989). Alternating opaque hyaline zones were visible when the sections were viewed under low magnification. The zones were counted by three separate persons and, if all three counts corresponded, the otolith was accepted. If two of the three readings corresponded, the otolith was re-read and accepted if five of the six readings corresponded. Otoliths failing to meet these criteria were rejected, as were unreadable otoliths.

Length-at-age data were fitted to Schnute's generalized growth equation (Schnute 1981), using the absolute error model according to the procedures recommended by Punt and Hughes (1989). This equation was selected over the Von Bertalanffy model because it provided a statistically superior fit to the data.

Stomachs for analysis were selected so as to be representative of the whole study area, all seasons and the full size-range of fish sampled. Only stomachs containing a substantial quantity of food (usually >3 g) were considered, because those containing well digested food might bias the results in favour of hard, less digestible foods. The relative contribution of the different prey species to the diet was assessed by frequency of occurrence (*%F*) and gravimetric methods (*%M*), as described by Berg (1979).

RESULTS AND DISCUSSION

Distribution, abundance and size composition

Samples from estuaries in the Eastern, Southern and Western Cape show that the majority of *L. lithognathus* in these habitats are <250 mm long, i.e. less than two years old (Mehl 1973, Blaber 1974, Beckley 1984, Bennett 1989a, Whitfield and Kok 1992). The majority of these juveniles enter estuaries during spring and summer when less than 50 mm long. Recruitment shows a temporal trend, commencing in the Eastern Cape in August/September (Beckley 1984), in the Southern Cape in September/October (Whitfield and Kok 1992) and in the Western Cape in October/November (Bennett 1989a). There is also a trend in the size at which recruitment takes place, recruits being smaller in the Eastern than in the Western Cape. Juveniles remain in the estuaries at least until the following winter before vacating them. It should be noted, however, that larger fish do occur in estuaries (Ratte 1978, Marais 1983, Bennett *et al.* 1985), because some one-year-old fish may remain for another year or more and larger fish may re-enter estuaries if the mouth is sufficiently open. The species also survives in estuaries that are isolated from the sea for considerable periods, and they have been reported in salinities of 1×10^{-3} (Whitfield *et al.* 1981, Marais 1982), although there may be mass mortalities if salinities remain less than 3×10^{-3} for prolonged periods (Bennett 1985).

Seining with small-mesh nets in the surf zone of sandy beaches indicates that *L. lithognathus* of <10 cm do not occur in that habitat (Lasiak 1984, Bennett 1989c, this study). Fish longer than 15 cm, however, are common in commercial beach-seine catches along the northern shore of False Bay (Fig. 1). One-year-olds

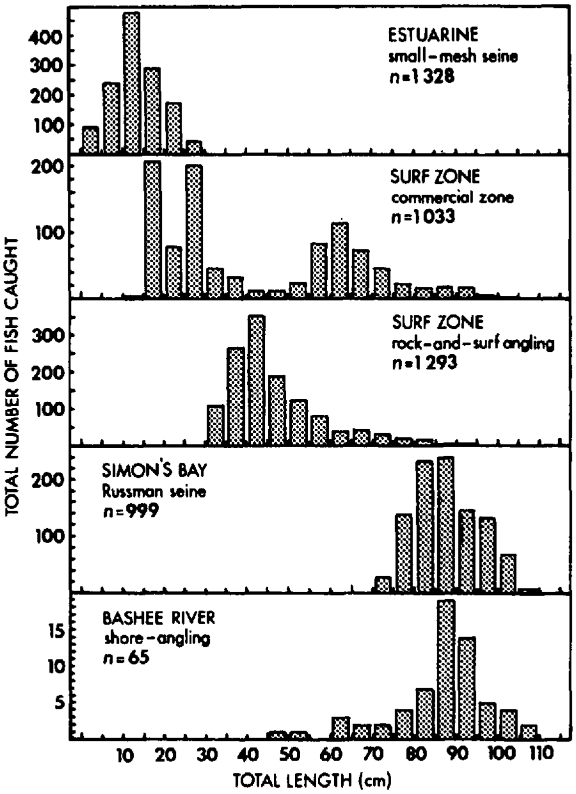

Fig. 1: The size composition of *Lithognathus lithognathus* taken by a variety of methods in different areas throughout its distributional range for this study

(15–20 cm) and two-year-olds (25–30 cm) dominate these catches, occurring frequently in small numbers, primarily between late winter and the end of the year. Larger fish are caught infrequently and in small numbers mainly during late summer. An important feature of the catches in this habitat is the infrequent, but often very large, catches of fish in the 50–85 cm size range.

The size distribution of catches made by shore-anglers (Fig. 1) is strongly influenced by selectivity effects. Self-imposed size limits and the current legal minimum size of 40 cm ensure that most fish smaller than this are not recorded. Hook selectivity also ensures that few fish of less than 30 cm are landed. Despite the possibility of these data being positively skewed, it is likely that angling results in a relatively random sample of larger fish in the surf zone.

Recreational data show marked seasonal variation in *L. lithognathus* catches. In the South-Western Cape, catch per unit effort (*cpue*) was lowest in December,

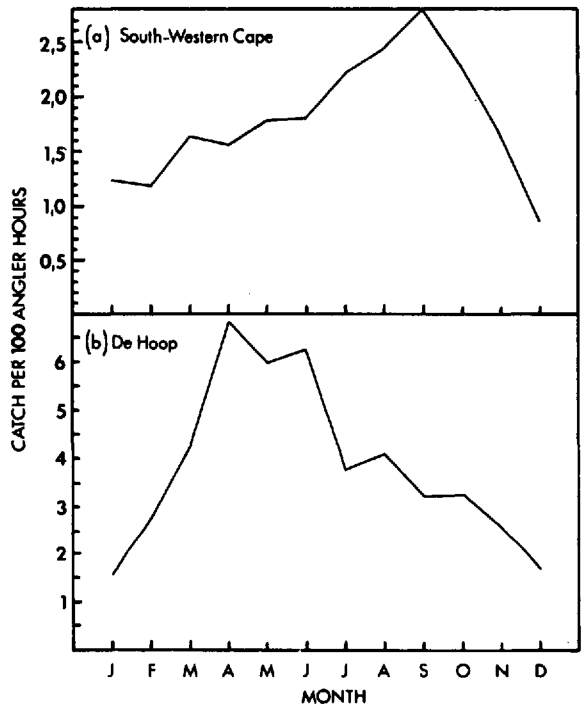

Fig. 2: Monthly catches of *Lithognathus lithognathus* per unit of effort expended by shore-anglers in (a) the South-Western Cape and (b) the De Hoop marine reserve on the Southern Cape coast

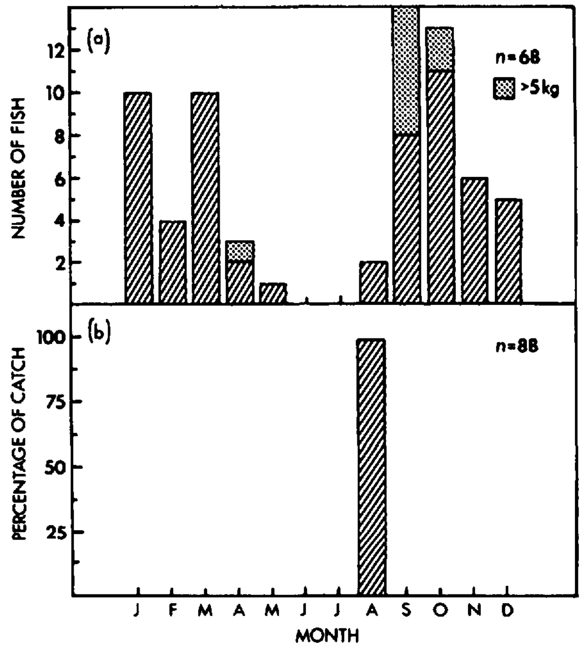

Fig. 3: Seasonal occurrence of *Lithognathus lithognathus* in the catches of shore-anglers on the Eastern Cape and Transkei coasts — (a) number of fish recorded on the Marine Linefish Database (Guastella 1991); (b) percentage of the total catch of *L. lithognathus* recorded each month by guests at The Haven Hotel, Transkei, during 1990 and 1991

but increased steadily to a peak in September before decreasing sharply (Fig. 2a). In the De Hoop marine reserve, on the Southern Cape coast, *cpue* was also at a minimum during midsummer, but it increased rapidly to peak in April before declining gradually (Fig. 2b). No monthly *cpue* data for the Eastern Cape coast were obtained, but catch records from the Marine Linefish Database (Guastella 1991) indicate that most *L. lithognathus* are caught between September and March (Fig. 3a). These data should, however, be treated with caution, because very few returns for any species in this area were recorded for June and July. Records of catches made near the Bashee River mouth, Transkei, show that almost all *L. lithognathus* were caught in August (Fig. 3b).

Gilchrist's (1897, 1899–1904, 1906, 1907) data similarly show that mean monthly catches in five of the six regions of the Cape coast varied seasonally (Fig. 4). This variation was most marked off the West Coast, where catches showed well-defined peaks between October and December north of Cape Columbine and between September and November between Cape Columbine and Cape Point. During the remainder of the year, catches in these two regions were very low. The peak in monthly catches in False Bay was less well defined and of longer duration than off the West Coast. On the western coast of False Bay, the best catches were made between September and March, whereas along the northern shore, the poorest catches were made between January and March. Between Cape Hangklip and Cape Agulhas, catches were very low between August and November and highest during April and May. East of Cape Agulhas, there was very little variation in catches throughout the year.

Data on which to base an assessment of seasonality during the period 1983–1991 are more limited because sample sizes were much smaller, a consequence of a closed season being effective from 1988 onwards, and because it was illegal to net white steenbras in most areas after 1983. Nevertheless, data for the period 1983–1987 can be used (Fig. 5), and they show similar trends to those for the period 1897–1906. Differences are that the peaks and troughs of the seasonal cycles are not as pronounced and, in four of the areas (the two

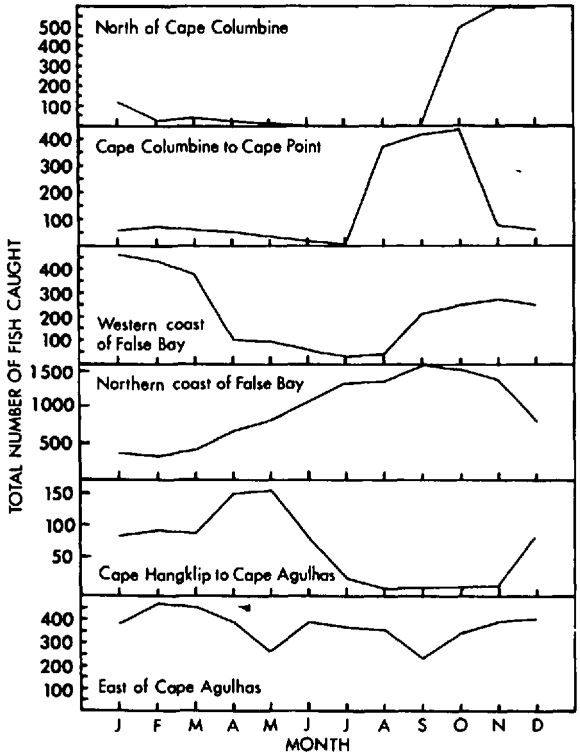

Fig. 4: Seasonal occurrence of *Lithognathus lithognathus* in catches recorded from six areas off the Cape coast between 1897 and 1906 (data from Gilchrist 1897, 1899–1904, 1906, 1907)

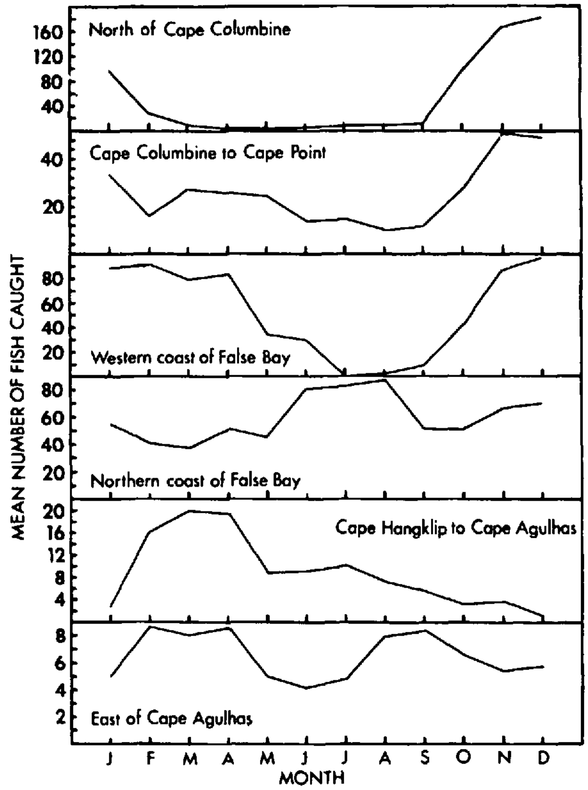

Fig. 5: Seasonal occurrence of *Lithognathus lithognathus* in catches recorded from six areas off the Cape coast between 1983 and 1991 (unpublished data from the Sea Fisheries Research Institute)

areas north of Cape Point, the western coast of False Bay and between Cape Hangklip and Cape Agulhas), the cycles are delayed by approximately one month when compared with the 1897–1906 data. The highest mean monthly catches along the northern coast of False Bay were therefore in June, July and August, whereas in the earlier data set, they were between June and November.

The two other data sets, from the northern coast of False Bay for the periods 1951–1968 and 1977–1987, do not indicate any trends in either mean monthly catch or *cpue* (Fig. 6a, b). Monthly *cpue* was highly variable throughout the year during both periods.

Catches in Simon's Bay with the "Russman" net, a sinking net which is laid up to 1 km offshore at a depth of approximately 15 m, consisted entirely of large fish. The smallest *L. lithognathus* caught in this habitat was 68 cm long, even though considerably smaller individuals of other species were frequently taken. The size distribution of anglers' catches in the vicinity of the Bashee River mouth, Transkei, during August is similar to the catches made in Simon's Bay during summer (Fig. 1).

The information presented above, although it does not include a complete geographical coverage of all habitats, provides a reasonable appraisal of the distribution and size structure of the Cape *L. lithognathus* population. These data confirm the view of Wallace *et al.* (1984a) that juveniles of the species are entirely dependent on estuaries for their first year of life (i.e. <15 cm). These juveniles utilize estuaries only between approximately the Kei River in the east and the Berg River in the west. They have not been recorded in northern Transkei and Natal estuaries, nor north of the Olifants River mouth on the West Coast (Day *et al.* 1981). Although many individuals may either remain in or re-enter estuaries, the bulk of the population one year old or older (i.e. >15 cm), is marine in habitat. Fish 15–60 cm long appear to be confined almost entirely to the surf zone, because none of this size range was taken in the deeper (approx. 10–20 m)

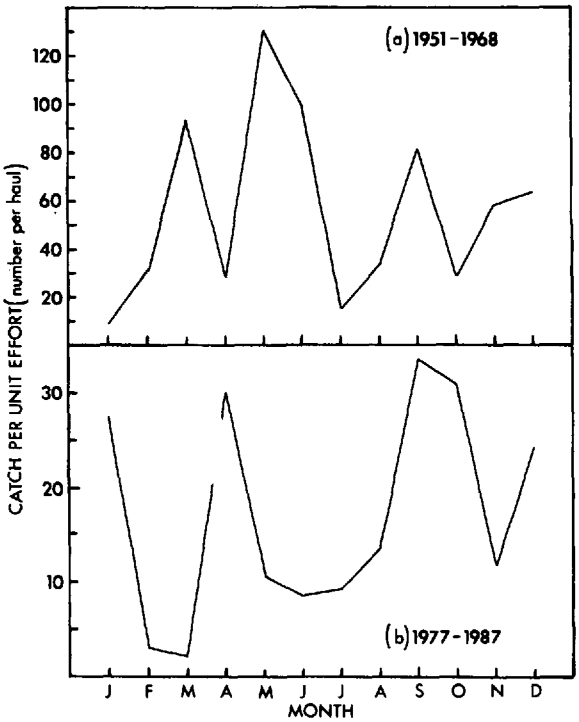

Fig. 6: Seasonal occurrence of *Lithognathus lithognathus* in catches from the northern coast of False Bay recorded by beach-seine permit holders (a) 1951–1968 and (b) 1977–1987

waters of False Bay, either by beach- or purse-seining. Moreover, none was taken in a comprehensive inshore (10–50 m depth), small-mesh trawl survey off the Southern and South-Eastern Cape coasts (Wallace *et al.* 1984b). Furthermore, only five specimens, the smallest of which was 59 cm long, were taken in over 800 hours of trawling at depths greater than 40 m during demersal trawl surveys, undertaken by the Sea Fisheries Research Institute, in the area east of Cape Point. These observations suggest that *L. lithognathus* is largely confined to shallow water.

Reproductive biology

Mehl (1973) undertook an extensive micro- and macroscopic study of the reproductive biology of *L. lithognathus*. Unfortunately, the collection he used consisted almost entirely of small, immature specimens (less than approximately 35 cm long) that were obtained from the Heuningnes Estuary. He was only able to examine 68 marine individuals from False Bay, the majority of which were <65 cm long. This limited sample precluded examination of any reproductively active individuals. Nevertheless, Mehl did establish that *L. lithognathus* are rudimentary hermaphrodites with genetically determined sexes and, although some mature fish have approximately equal ovarian and testicular development in the gonads, individuals function only as males or females.

In the present study, 601 gonads from fish 33–109 cm long were examined. Most were collected in the South-Western and Southern Cape, but a sample of 70 large fish was also obtained from Transkei. The sex ratio of the whole sample was 199 males : 249 females : 153 hermaphrodites. For mature fish (Stages 2–7), it was 172 : 233 : 20 and, for reproductively active fish (Stages 5–7), 42 : 41 : 0. These differences in ratio reflect the size composition of the sample and the stage of development of the fish. If more immature fish, especially from estuaries, were included, the proportion of hermaphrodites would have been greater and, because the female portion of the ovotestis is larger during the earlier stages of development (Stages 2–3), genetic males may have been misidentified as females on macroscopic examination. For these reasons, large and reproductively active fish provide the best indicator of the true genetic sex ratio of the population.

Lengths at maturity were established from the relative frequencies of immature (Stage 1) and mature (Stages 2–7) fish in different size-classes (Fig. 7). For the purpose of this exercise, the sex ratio of hermaphrodites was assumed to be 1 : 1. The smallest reproductively active male and female observed were 49 and 50 cm respectively. The proportion of mature fish increased to 90 cm; thereafter all fish were mature. The level of 50% maturity was at approximately 65 cm in both sexes.

Annual variation in the gonad stages of fish greater than the length at 50% maturity is shown in Figure 8. This Figure represents only fish sampled in the South-Western and Southern Cape (n = 270 for Stage 2 and 69 for Stages 3–4), because no year-round samples were obtained from other regions. It is apparent from the Figure that the gonads of most mature fish were in the early recovery stage (Stage 2) between September and March. By April signs of gonad development were evident, with 40–50% of gonads being classed as Stages 3 or 4. These levels of development were sustained until July, whereafter early recovery stages again dominated the sample. No reproductively active fish were sampled in this region. In contrast, a sample of 70 mature fish obtained in Transkei during August of 1990 and 1991 were all ripe-and-running, partially spawned or spent, indicating that this was an important spawning area for *L. lithognathus*.

The lack of size information in the large, historical, commercial data sets, which cover the whole coast,

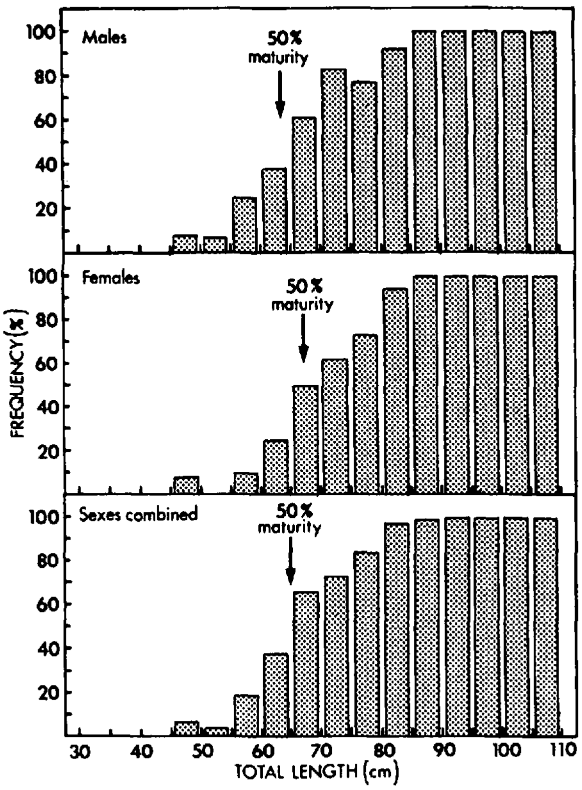

Fig. 7: Frequency of mature (Stages 2–7) *Lithognathus lithognathus* in different length-classes

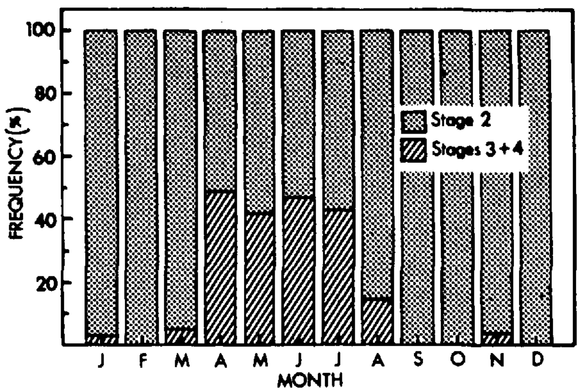

Fig. 8: Seasonal gonad condition of mature *Lithognathus lithognathus* in the South-Western and Southern Cape

makes it difficult to establish clearly whether or not a spawning migration takes place. There are, however, some data which suggest that such migrations do occur. Figure 9 shows that the percentage of mature fish (>65 cm) is greatest in beach-seine catches along the north coast of False Bay during summer and least during winter. Moreover, catches along the western coast of False Bay, which are known to be dominated by large fish (Fig. 1), are almost non-existent during winter (Figs 4, 5). These data suggest that the majority of mature *L. lithognathus* vacate False Bay during winter.

No data concerning the seasonal occurrence of mature white steenbras farther east were available, but anecdotal evidence from experienced fishermen suggests that the best catches in the Southern Cape are made between April and June, in the South-Eastern Cape between May and July and in the Eastern Cape between June and October. Limited data from Transkei support the view of fishermen that this species has a very restricted season there, being caught only in late July and August (Fig. 3b).

Whether or not a return migration takes place is even more difficult to establish, because no fishermen have identified periods in the latter half of the year as being productive as regards catches of large fish in the South-Eastern or Southern Cape. There is some evidence to suggest that this may be because these fish are not feeding actively during this period. Partially spawned and spent fish in Transkei are in poor condition, 100-cm fish weighing an average of approximately 10,11 kg. When these fish first reappear in catches in False Bay in November, their mean mass is more or less unchanged (10,24 kg), but two months later their average mass is 11,19 kg and, by the time they become scarce in that area in May, average mass at 100 cm is 12,68 kg.

Age and growth

White steenbras have a restricted spawning period, and a birthrate in mid August may be assumed for all individuals. Modal progressions in monthly samples of juveniles from the Kleinmond and Palmiet estuaries (Bennett 1989a) indicate growth rates of approximately 13 mm · month^{-1} with total lengths of 160 and 230 mm being attained after 12 and 18 months respectively. These juvenile growth rates are similar to those observed by Whitfield and Kok (1992) in the Swartvlei and Knysna estuaries and by Beckley (1984) in the Sundays Estuary, but they are faster than the rates reported by Mehl (1973) and Blaber (1974).

Examination of the otoliths of these juveniles indicated that a "false" or "juvenile" opaque ring was laid down at about six months and a second (the first annual) ring was laid down the following winter. Otoliths from individuals of the same size (140–170 mm) obtained in the marine environment exhibited the same pattern.

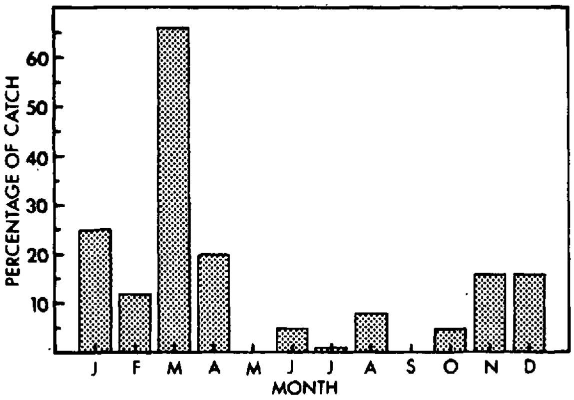

Fig. 9: Monthly percentage of the total *Lithognathus lithognathus* catch made by beach-seining along the northern coast of False Bay that exceeded 65 cm *TL*

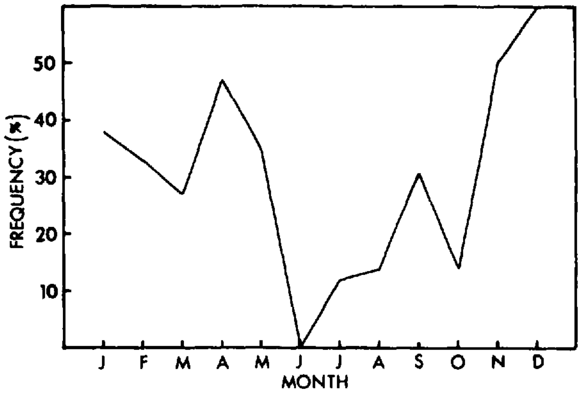

Fig. 10: Monthly frequency of hyaline edges on the otoliths of *Lithognathus lithognathus*

A total of 496 otoliths from fish of between 45 and 1 090 mm long, collected in both marine and estuarine environments, was examined. Of these otoliths, 134 were discarded after initial examination because they were not sectioned, burned or mounted correctly, and a further 51 were discarded because replicate counts of the opaque zones did not correspond. The results presented are therefore based on 311 fish, 116 females, 104 males and 91 hermaphrodites.

Seasonal trends in the frequency of opaque and hyaline edges were evident for most 150–850 mm fish (1–9 years old), and it is evident that hyaline zones are laid down during summer and opaque zones in winter (Fig. 10). Interpretation of otolith margins in larger fish was difficult because the zones were very narrow. It was assumed, however, that one hyaline and one opaque zone represented one year of growth, and the age of the fish was taken to correspond to the number of opaque zones, excluding the nucleus and the "juvenile" ring which, in most otoliths, were incorporated into the nucleus after 3–4 years.

The length-age relationship of *L. lithognathus*, based on otolith ring counts, is shown in Figure 11 and is described by the equation

$$L_t = \left[205{,}7^{-1{,}297} + (997{,}8^{-1{,}297} - 205{,}7^{-1{,}297})\frac{1-e^{-0{,}441(t-t_1)}}{1-e^{-0{,}441(t_2-t_1)}}\right]^{1/-1{,}297}.$$

There were no apparent differences in the lengths at age of males and females, or of estuarine and marine individuals of equivalent age.

Diets

The diets of *L. lithognathus* in various estuaries in the Southern and South-Western Cape have been described by Mehl (1973), Whitfield (1985) and Bennett (1989b). It is evident from these studies that small juveniles (<30 mm *TL*) consume mainly copepods, ostracods and amphipods. Larger individuals (30–100 mm) had more diverse diets, adding polychaetes, insect larvae and decapods to the list of taxa consumed. The largest size-class (>100 mm) examined in estuaries was found by Bennett (1989b) to consume a wide variety of invertebrates and appreciable quantities of weed. That author therefore suggested that the species is omnivorous in estuaries, possibly because of the short supply of larger invertebrates in that environment.

The diet of *L. lithognathus* in the marine environment has previously been described by Lasiak (1984) from 60 stomachs of fish primarily 150–400 mm long collected in Algoa Bay. The predominant food items were the macruran *Macropetasma africanus*, the sand-dwelling bivalves *Donax* spp. and a number of polychaetes.

In the present study an attempt was made to collect stomach contents from the full size range of *L. lithognathus* in all marine habitats throughout its distributional range and throughout the year. However, this was not possible because of size-related habitat segregation and seasonal variations in the distribution and abundance of white steenbras. A total of 218 stomachs containing significant amounts of food was nevertheless analysed, 89 from False Bay in the South-Western Cape, 106 from De Hoop on the Southern Cape coast and 23 from Transkei at the eastern limit of the distributional range. All fish from False Bay were collected in seine-nets over sandy substrata. All the small fish (<800 mm) were collected throughout the year in the surf zone along the northern shores of the Bay, whereas most larger fish were caught in deeper water in Simon's Bay during summer. The Southern and Eastern Cape

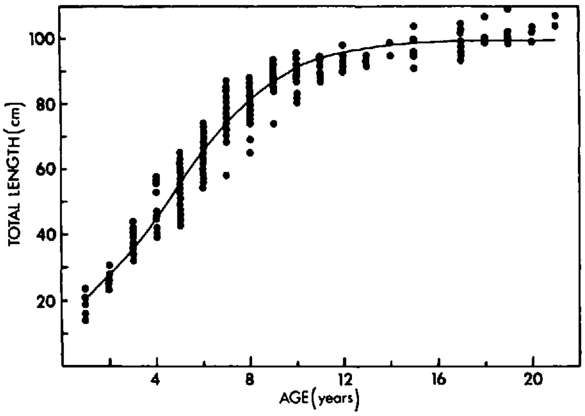

Fig. 11: Age-length relationship and growth curve of *Lithognathus lithognathus* in the marine environment

samples were collected by angling from the shore. Those from the vicinity of the Bashee River mouth were also taken over sandy substrata, but all the fish were collected in August. The De Hoop samples were fish taken throughout the year, but, in contrast to the two aforementioned samples, these fish were all caught in areas of mixed rock and sand.

Data presented in Table III indicate that, in the marine environment, *L. lithognathus* are exclusively carnivorous, polychaetes, crustaceans and molluscs being the most important prey taxa. There were, however, some substantial differences in diet between different areas and size-classes. In False Bay, almost the entire diet consisted of infaunal and epibenthic species. Small fish (<400 mm) consumed primarily epibenthic crustaceans such as amphipods, mysids and macrurans, as well as shallow-burrowing species such as the polychaete *Orbinia* sp. Sand-dwelling bivalves were the most important prey of the intermediate size-class (400–800 mm), but for this size range, the bloodworm *Arenicola loveni* and the sand prawn *Callianassa kraussi* were also important, indicating the predator's ability to obtain prey which is usually found at least 250 mm under the surface of the sand. The diet of large fish (>800 mm) consisted almost entirely of the burrowing mud prawn *Upogebia* spp. The diets of fish sampled over mixed rock and sand substrata at De Hoop were similar to those observed in False Bay, the majority of smaller fish (<400 mm) feeding over sandy substrata and consuming primarily *Orbinia* sp., *Gastrosaccus psammodytes* and *Macropetasma africanus*. The stomach contents of larger fish, however, differed substantially from those in False Bay, black mussels being the most important dietary component. Other rock-dwelling species, such as the small abalone *Haliotis spadicea*, the crab *Plagusia chabrus* and the urchin *Parechinus angulosus*, were also consumed. At De Hoop, rock-associated prey species accounted for over 90% of all food consumed by fish >400 mm long. Large fish (>800 mm) collected near the Bashee River mouth had diets that differed substantially from the other samples, the epibenthic crab *Ovalipes punctatus* dominating the stomach contents.

The life cycle of *L. lithognathus*

Based on the information presented above, the life cycle of *L. lithognathus* can be summarized as follows:

(i) spawning takes place along the Eastern Cape and Transkei coasts primarily during August;
(ii) eggs and larvae drift southwards along the coast and, after metamorphosis, enter estuaries along the South-Eastern, Southern and South-Western Cape coasts, mainly between September and November;
(iii) 0+ juveniles are dependent on estuaries, where they remain for at least their first year of life;
(iv) on vacating estuaries, the juveniles (<65 mm) occupy the surf zone of sandy or mixed rock and sand shores, where they remain semi-resident in shoals until maturity;
(v) on maturing, at an age of at least five years, the larger fish extend their distributional range into deeper water (<25 m) and commence annual spawning migrations;
(iv) in autumn the mature fish commence a migration that takes them eastwards and northwards to the Eastern Cape and Transkei coasts in time for late winter spawning;
(vii) after spawning, they return southwards and westwards and, by late summer, a large proportion of the mature population may have congregated off the South-Western Cape.

The high degree of reliance on estuarine "nursery grounds" is well documented for a large number of fish species worldwide (Oviatt and Nixon 1973, Whitfield 1980, Beckley 1984, Claridge *et al.* 1986). It is considered to occur because estuaries, being highly productive, calm, shallow and turbid, provide superior conditions for growth and lower rates of predation relative to adjacent marine habitats (Blaber and Blaber 1980, Lenanton 1982, Boesch and Turner 1984). The advantages of estuaries are considered to be sufficiently important for a number of species, *L. lithognathus* included, for them to become dependent on estuaries and possibly prone to extinction if excluded from such habitats (Wallace *et al.* 1984a). This high degree of

Table III: Percentage occurrence (%*O*) and mass (%*M*) of different prey categories in the diets of three size-classes of *Lithognathus lithognathus* sampled from three localities around the Cape coast. Totals represent the number of guts examined and the quantity (g) of food present

Prey	False Bay						De Hoop						Bashee	
	<400 mm		400–800 mm		>800 mm		<400 mm		400–800 mm		>800 mm		>800 mm	
	%*O*	%*M*	%*O*	%*M*	%*O*	%*M*	%*O*	%*M*	%*O*	%*M*	%*O*	%*M*	%*O*	%*M*
Polychaeta	96	53	94	38	37	3	85	72	61	10	56	3	22	6
Arenicola loveni	17	11	38	29	8	2	0	0	0	0	0	0	0	0
Orbinia sp.	88	39	59	7	4	0	69	54	32	4	11	1	0	0
Crustacea	83	43	75	23	98	92	77	23	34	5	22	2	91	94
Isopoda	13	1	6	8	2	0	12	1	3	0	0	0	0	0
Amphipoda	50	27	19	0	0	0	31	1	13	0	6	0	0	0
Mysidacea	21	2	13	0	0	0	35	9	15	1	0	0	0	0
Gastrosaccus psammodytes	17	2	13	0	0	0	27	7	11	1	0	0	0	0
Macrura	38	13	19	2	0	0	27	6	8	1	0	0	0	0
Macropetasma africanus	33	13	19	2	0	0	19	6	8	1	0	0	0	0
Anomura	0	0	6	10	98	92	0	0	0	0	0	0	0	0
Callianassa kraussi	0	0	6	10	0	0	0	0	0	0	0	0	0	0
Upogebia spp.	0	0	0	0	98	92	0	0	0	0	0	0	0	0
Brachyura	0	0	6	3	0	0	8	3	11	3	17	2	91	94
Ovalipes punctatus	0	0	6	3	0	0	0	0	0	0	0	0	74	87
Mollusca	13	4	69	38	14	4	8	3	66	82	89	91	0	0
Pelecypoda	13	4	69	38	14	4	4	1	66	82	72	84	0	0
Sand-dwelling spp.	13	4	69	38	14	4	4	1	13	1	0	0	0	0
Rock-attached spp.	0	0	0	0	0	0	0	0	58	81	72	84	0	0
Gastropoda	0	0	0	0	0	0	4	3	0	0	11	6	0	0
Haliotis spadicea	0	0	0	0	0	0	0	0	0	0	11	6	0	0
Totals	24	86	16	145	49	2 544	26	95	62	950	18	468	23	943

estuarine dependence offers a plausible explanation for some aspects of the life cycle of *L. lithognathus*, because it may be suggested that the life cycle evolved to facilitate the optimum use of Cape estuarine habitats.

The migration which results in the localization of spawning near the eastern limit of the distributional range of *L. lithognathus* is probably the result of a combination of the following factors: first, higher winter water temperatures in the east enhance growth rates of eggs and larvae; second, predation of the early life history stages is lower in the region because the biomass of predators such as clupeoids is considerably less than it is on the Agulhas Bank and areas farther west; third, the number of estuaries per unit of coastline declines westwards.

The restricted winter spawning period provides small juveniles with the best chance of entering estuaries. In the South-Western Cape, rainfall is strongly seasonal, increasing during winter. Towards the east, seasonality becomes less pronounced and the highest rainfall occurs during spring and autumn in the Southern and South-Eastern Cape. This pattern indicates that Cape estuaries are most likely to be open between August and November. The South-Eastern, Southern and South-Western Cape coasts experience arid conditions during mid and late summer, and estuaries are most likely to be closed at that time (Heydorn and Tinley 1980). Therefore, in order to benefit from estuarine conditions, *L. lithognathus* spawn during late winter.

One of the most important reasons why juveniles vacate estuaries before attaining maturity is probably because suitable food is in short supply in the 150–400 mm length range. Although this statement is not consistent with the findings of Bennett and Branch (1990) and others, who show that estuarine production greatly exceeds consumption by predators, dietary analysis indicates that a large proportion of this production is not available to *L. lithognathus* in the 150–400 mm size range. Much of the invertebrate production is provided by very small crustaceans, insect larvae and polychaetes, which are well below the optimal prey size of the >150 mm size-class fish. A substantial proportion of the production, however, is also provided by larger prey species such as *Callianassa kraussi* and *Upogebia* spp., which are seldom found in the stomach contents of estuarine fish of <400 mm, even though they are abundant in the environment. The scarcity in the stomachs of these potential prey species, which usually live well below the sediment surface, is probably because 150–400 mm fish are incapable of capturing them efficiently. This view is substantiated by the absence of deeper-living prey from the diets of marine *L. lithognathus* of <400 mm, despite their importance in the diets of larger fish.

The data presented in the present paper provide a clear indication that juveniles are restricted almost entirely to the surf zone between the time that they vacate the estuaries and the time that they mature at a length of approximately 650 mm. There is no indication that these fish undertake seasonal migrations, because they are caught throughout their distributional range at all times of the year. There is also some evidence that they may be resident in fairly restricted areas for prolonged periods. Therefore, of approximately 200 individuals tagged in the De Hoop marine reserve since 1986, 11 specimens between 320 and 750 mm were recaptured 11–601 days after release. All but one of these fish were recaptured within 5 km of their point of release, indicating a high degree of residency. The one fish that moved farthest was the largest individual recaptured (720 mm, greater than the length at 50% maturity). It was recaught 18 km east of where it was tagged after 11 days.

Data from False Bay suggest an increase in the depth distribution of mature *L. lithognathus*. All size-classes are caught in shallow water (<3 m) by angling and with seine-nets, but in deeper water (3–25 m), only mature fish are caught either by "Russman" seine, purse-seine or angling. Observations by divers confirm this pattern.

Evidence to support the existence of a spawning migration is largely circumstantial, because no fish tagged on the Southern or South-Western Cape coasts have been recaptured on the East Coast during the breeding season. This is probably a consequence of so few mature fish having been tagged. There are also no comprehensive data concerning the seasonal occurrence and size composition of *L. lithognathus* in the South-Eastern Cape. Despite these shortcomings, the catch data suggest that mature fish vacate the South-Western Cape during autumn and return during early summer, and that these fish occur near the eastern limit of the species' distributional range only during late winter. These observations, together with the data which show that fish in spawning condition are found only in the eastern areas, suggests that a spawning migration does indeed take place.

CONCLUSIONS

A number of aspects of the biology of *Lithognathus lithognathus* make it vulnerable to decline as a result of human activities. One of particular concern is the high degree of estuarine dependency exhibited by juveniles. There is no doubt that the Cape estuarine habitat as a whole has been progressively degraded over the years. Instances of severe siltation as a result of erosion in catchment areas and reduced freshwater inputs to estuaries are common, as are other disruptions caused by constructions, recreational utilization and urban and industrial pollution (Heydorn and Tinley 1980). While the effects of this degradation on the carrying capacity of the estuaries and the survivorship of juvenile fish in them has not been quantified, it is almost certainly substantial and negative for the fish fauna.

Another reason for concern is that post-estuarine juveniles and subadults are confined almost entirely to the surf-zone of sandy and mixed shores. In these habitats they are accessible to, and highly prized by, anglers who exploit them, as do commercial beach-seiners in False Bay. When one considers that there are already approximately 500 000 anglers operating along the South African coastline, and that this number is doubling every 12 years (Van der Elst 1989, Bennett 1992), the inevitable conclusion is that the species is under heavy and increasing pressure.

A rapid growth rate ensures that this species reaches what many fishermen consider "pan" size (30 cm) when only two years old. There is, however, a legal minimum size limit of 40 cm, which is attained in the third year. This legal minimum size limits catches to some extent, but it will not provide protection at very high levels of effort, because it is well below the size at which the species matures. Half the fish are mature at a length of 65 cm, so the majority of individuals are subject to exploitation for at least three years before they mature. In order to provide *L. lithognathus* with some measure of reproductive security in the face of exponentially increasing effort, a minimum size would need to be set at approximately 65–70 cm to allow the majority of individuals the opportunity to spawn at least once before capture.

Predictable aggregations by mature *L. lithognathus* also make them more vulnerable to exploitation. One such aggregation occurs during late winter in the vicinity of the Bashee River mouth, Transkei, and the other during late summer in False Bay. Both aggregations attract considerable fishing effort and, in some years, very large catches are made. A major shortcoming of the present study is the lack of knowledge concerning the proportion of the entire mature stock present in these aggregations at the limits of their eastward and westward migrations. Nevertheless, if there was evidence to suggest that *L. lithognathus* was being seriously overexploited, appropriately timed closed seasons in these two areas would effectively reduce catches.

The details of the biology and life history of *L. lithognathus* presented in this paper clearly show that the species is vulnerable to the activities of man. This knowledge has been used to indicate ways in which some of these pressures could be reduced. However, there is no direct evidence to suggest that the species is currently overexploited and in need of immediate management attention. An assessment of the fishery for this species and the state of the stock is currently in progress. When this additional information becomes available, it will be possible to tailor a management package that will ensure the future of the commercial and recreational fisheries for *L. lithognathus*.

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