

**POPULATION DYNAMICS AND SPAWNING OF THE FLATFISH
SOLEA BLEEKERI AND *PSEUDORHOMBUS ARSIUS* IN THE
INTERTIDAL AREA OF INHACA ISLAND, MOÇAMBIQUE**

A. M. P. VAN SCHIE* and W. F. DE BOER†

The population dynamics of flatfish *Solea bleekeri* and *Pseudorhombus arsius* within the intertidal area of Inhaca Island, Moçambique, was investigated using bottom trawl data collected during summer (December 1996–March 1997) and winter (June 1997–August 1997). The endemic *S. bleekeri* is a small, relatively slow-growing species with low rates of natural mortality. Densities of juveniles were significantly greater in winter (24.7 fish 1 000 m⁻²) than in summer (10.8 fish 1 000 m⁻²), probably because of intensive spawning during summer. Greater catches of *S. bleekeri* were taken by night than by day. Densities of *P. arsius* did not differ significantly between day and night or among seasons. Mean density of *P. arsius* was 53 fish 1 000 m⁻² for the survey. Both species preferred the same substrata, significantly greater densities being found on the mudflats and in the tidal channels. Both seem to complete two life cycles within a year.

Key words: density, flatfish, growth rate, Inhaca Island, juveniles, maturation, Moçambique, spawning

The blackhand sole *Solea bleekeri* is a flatfish species endemic to southern African, extending from False Bay on the south-west coast of South Africa to the Murrumbidgee Estuary in Moçambique (Day 1974, Smith and Heemstra 1986). The species generally prefers muddy substratum and regions of high turbidity (Cyrus and Blaber 1987), but adults and juveniles also inhabit beds of seagrass *Zostera capensis* (Cyrus and Martin 1991). *S. bleekeri* is part of a group of fish that are able to complete their entire life cycle in estuaries, where they spawn during late spring and summer (Cyrus and Martin 1991).

The largemouth flounder *Pseudorhombus arsius* occurs in the Indo-West Pacific and extends to South Africa's Southern Cape (Smith and Heemstra 1986). The species prefers muddy, sandy or gravel seabed (Smith and Heemstra 1986), but juveniles can also inhabit mangrove swamps. *P. arsius* is an euryhaline marine species and spawns exclusively at sea, but juveniles can make extensive use of estuaries (Cyrus and Martin 1991).

Within the intertidal area of Inhaca Island, Moçambique, juvenile and adult *S. bleekeri* and *P. arsius* are found on muddy and sandy substrata and near mangroves and seagrass beds (De Boer *et al.* 2001). The island's geographical location is subtropical, but biogeographically its surrounding waters may be considered tropical, because the majority of marine organisms there are of Indo-West Pacific origin (Kalk

1959, de Boer and Longamane 1996). The waters surrounding the island are brackish, because of the mixing of freshwater from the three rivers in Maputo Bay and drainage water from freshwater swamps with the Indian Ocean (Kalk 1995).

The aim of this study is to describe the life cycles of *S. bleekeri* and *P. arsius* at Inhaca Island and to compare them with those reported by Cyrus and Martin (1991) for the same species on the southern coast of South Africa.

MATERIAL AND METHODS

Inhaca Island (26°S, 33°E) is 35 km east of Maputo in southern Moçambique. It is surrounded by the Indian Ocean to the east and Maputo Bay to the west. The island is 12.5 km long and 7 km wide, and is indented by bays fringed by mangroves and colonized by seagrass (e.g. *Zostera capensis*; Kalk 1995). Mean annual rainfall (mainly in summer) is 884 mm. Water temperatures range from 18 to 32°C, averaging 28°C in summer and 21°C in winter (de Boer *et al.* 2000.).

A demersal fishing programme was carried out within the intertidal area of the southern bay (Fig. 1). Two sites, Saco and Banco, were sampled, Saco, in the northern part of the bay, covering an area of 63 ha, is completely fringed by mangroves and almost totally

* Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands

† Departamento de Ciências Biológicas, Universidade Eduardo Mondlane, C.P. 257, Maputo, Moçambique and Tropical Nature Conservation and Vertebrate Ecology Group, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands (correspondence address). E-mail: fred.deboer@wur.nl

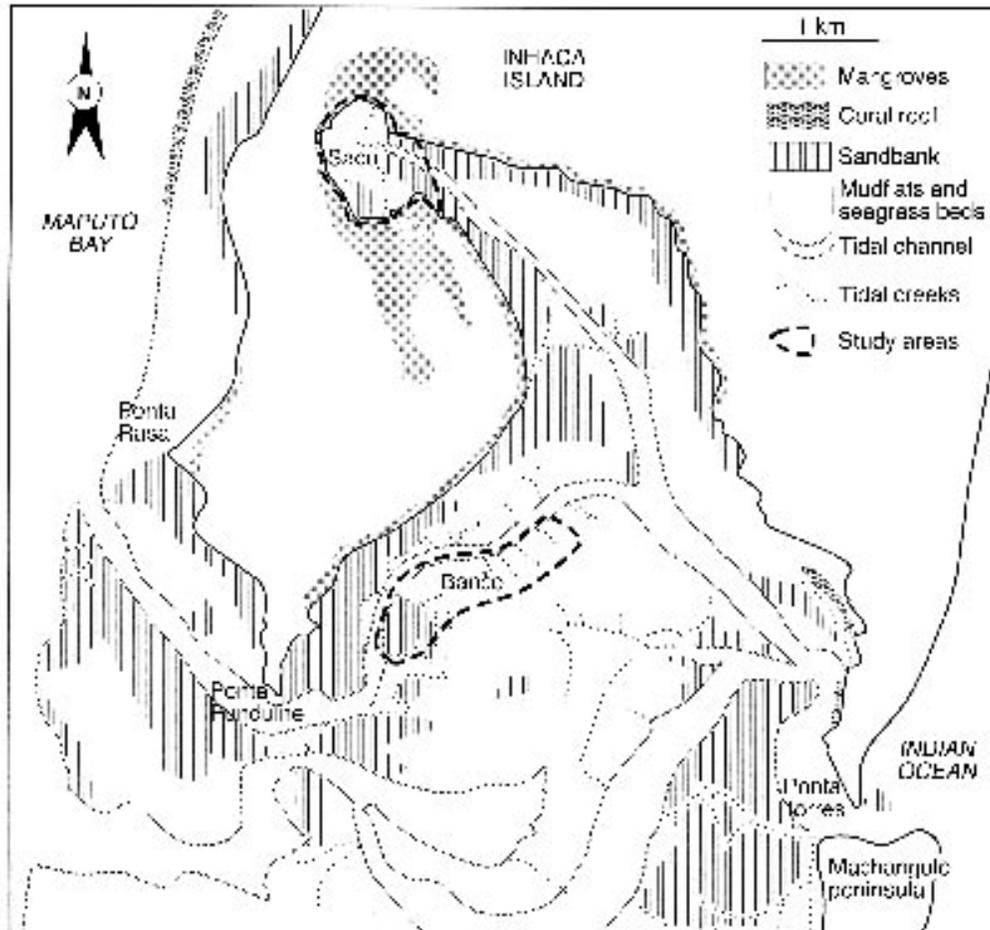


Fig. 1: Location of the Saco and Banco sampling sites within the southern bay of Inhaca Island, and the different substrata

exposed at low tide, and Banco in the southern part of the bay, with an area of 83 ha. There are mudflats in the lower lying areas, which are totally inundated during low water neap tides (LWNT). Sandbanks typify the higher lying areas and consist of coarser sand, some parts of which are exposed during high water neap tides (HWNT). Sandflats are intermediate in depth, consisting of finer sands than the sandbanks, and cover extensive areas. Tidal channels, the beds of which are exposed only during LWNT, border both areas. The seabed of the channel in Saco is covered by old coral debris and rocks, with small patches of seagrass *Halodule wrightii*. In Banco, the channel is mainly coarse sand

with a sparse growth of seagrass *Cymodocea serrulata*. Other substrata types are the mangrove fringes in Saco and the extensive *Zostera capensis* seagrass beds in Banco.

In all, 280 trawls were made between December 1996 and March 1997 (summer) and between June and August 1997 (winter), equally divided over five substrata within either Saco or Banco. Fish were caught with a 2-m beam-trawl with a mesh size of 5×5 mm, with one tickler chain in front of the net (Kuipers 1975, Kuipers *et al.* 1992). In all, 180 and 100 trawls were made at night and by day respectively, using a boat equipped with a 25 hp outboard motor. All sub-

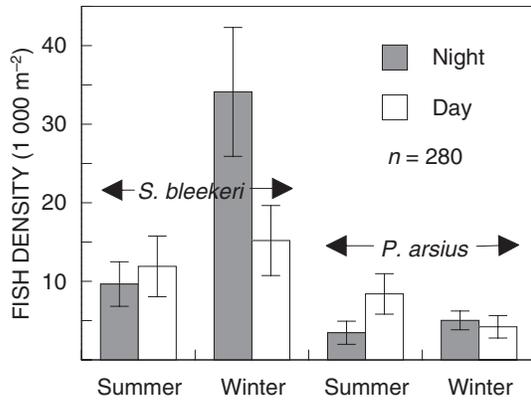


Fig. 2: Mean fish densities of *S. bleekeri* and *P. arsius* from day and night trawls in summer and winter. Error bars denote \pm SE

strata within each area were sampled within the one hour before and one hour after high tide. Haul duration was standardized to five minutes, in which an average distance of 150 m was covered (towing speed aver-

aged 0.5 m s⁻¹). After each haul, fish catches were either stored temporarily in plastic buckets and sorted at the biological station the same day (day trawls) or stored in a 4% formalin seawater solution and sorted the next day (night trawls).

Fish were measured (standard length, *SL*, in mm) and weighed (fresh weight to 0.1 g). Day and night catches were converted into catches per 1 000 m² (without correction for net efficiency). Non-parametric Mann-Whitney U-tests were used to detect seasonal or time-of-day differences in fish density. Differences in fish densities among substrata were tested with a Kruskal-Wallis test. Daily instantaneous mortality (*Z*) and settlement rates were calculated according to the formula

$$Z = \frac{1}{t \ln(N_t/N_0)}$$

where *N*₀ is the density of fish at day 0 and *N*_{*t*} the density of fish after *t* days. Sagittal otoliths were removed for age determination. Adults caught in summer (19 female *S. bleekeri* and 2 female and 5 male *P. arsius*) were weighed, sexed and their maturity stage assessed following Cyrus (1991a) and Rijnsdorp

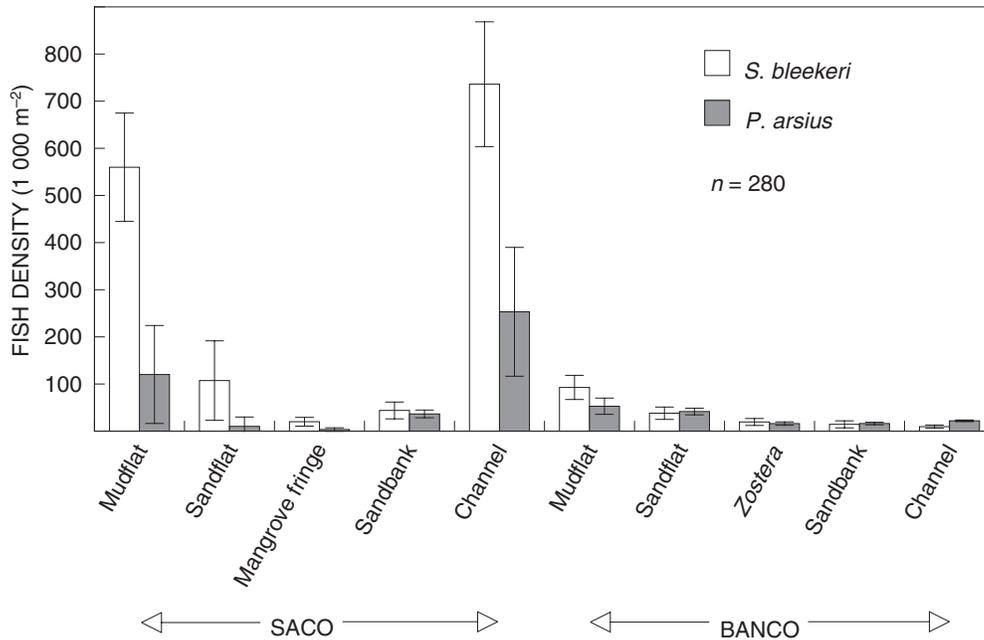


Fig. 3: Mean fish densities of *S. bleekeri* and *P. arsius* over 10 different substrata at Saco and Banco. Error bars denote \pm SE

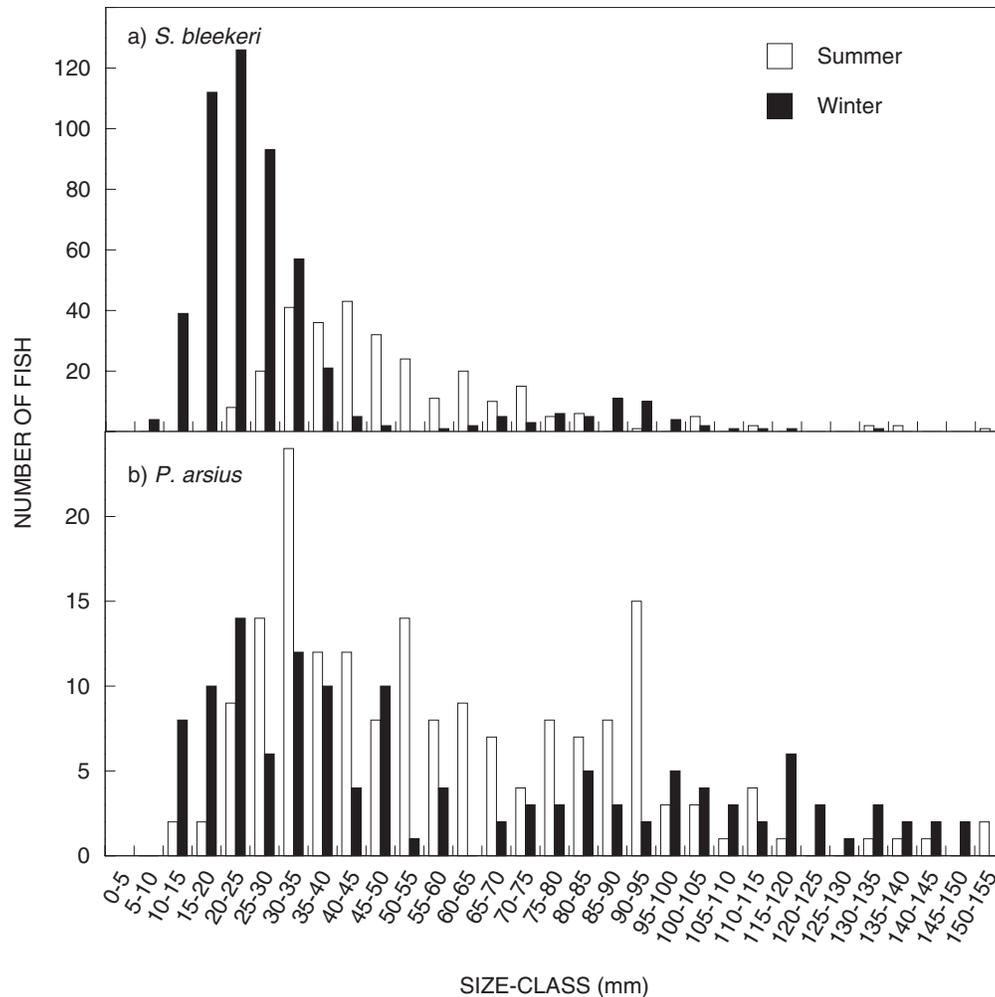


Fig. 4: Length frequency distributions of (a) *S. bleekeri* and (b) *P. arsius* during summer and winter

(1992). Gonads of mature adults were dissected and weighed to calculate the relationship between total fish weight and gonad weight. The condition factor K was determined using Berger and Connolly (1989).

RESULTS

Abundance

In all, 285 *S. bleekeri* were caught in summer and 517

in winter. For *P. arsius*, the totals were 185 and 132 respectively. Figure 2 shows that the density of *S. bleekeri* was higher in summer than in winter (24.7 v. 10.8 fish 1 000 m⁻²; $p < 0.02$). This difference was mainly caused by significantly more fish being caught at night ($p < 0.001$). Densities of *P. arsius* were generally lower than *S. bleekeri*, with a daytime maximum of 8.4 fish 1 000m⁻² in summer and a mean overall density of 5.3 fish 1 000 m⁻². Densities of *S. bleekeri* did not differ between day and night or season ($p > 0.05$).

Both fish species were more abundant at Saco than at Banco (Fig. 3). Mean abundances differed signifi-

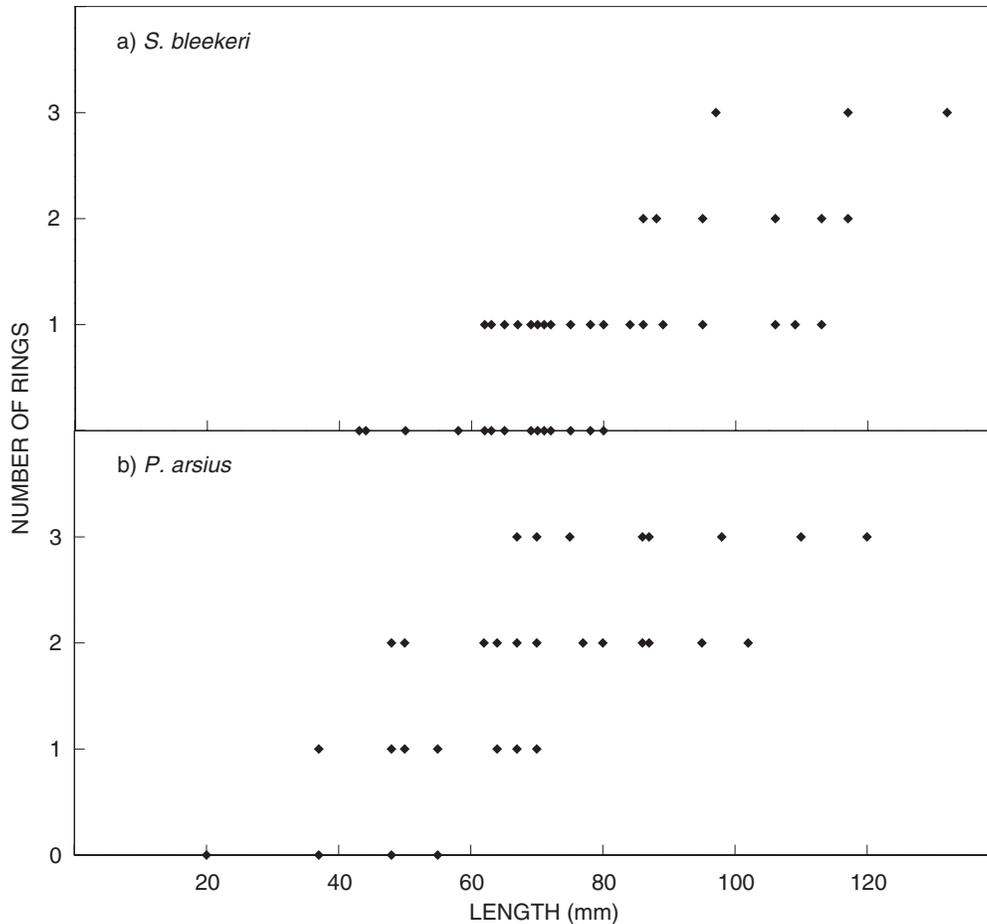


Fig. 5: Relationship between the number of otolith rings and the length of (a) *S. bleekeri* and (b) *P. arsius*

cantly between the 10 different substrata ($p < 0.001$) for both species, and the mudflats and the channel in Saco were preferred by both species. Mean densities of the two species were positively correlated ($p < 0.0001$, $r^2 = 0.88$).

Population structure

The length frequency distribution of *S. bleekeri* (Fig. 4a) shows that the winter population consisted mainly of fish of 10–30 mm, whereas fish 20–80 mm were more abundant in summer. The periodic ring in the sagittal otoliths was found in fish 60–110 mm (Fig. 5a).

The second and third rings appeared in fish 90 and 100 mm long respectively. *P. arsius* had a multimodal population structure (Fig. 4b). In summer, peaks were found at 30–35 and 90–95 mm; peaks were less pronounced in winter. Fish were smaller (10–25 mm) in winter than in summer. The first ring was found in fish 35–70 mm, two rings appeared from 50 to 100 mm and three rings from 65 to 120 mm (Fig. 5b).

Mortality and settlement

Densities of *S. bleekeri* were highest at the beginning of summer and midway through winter (Fig. 6a). The

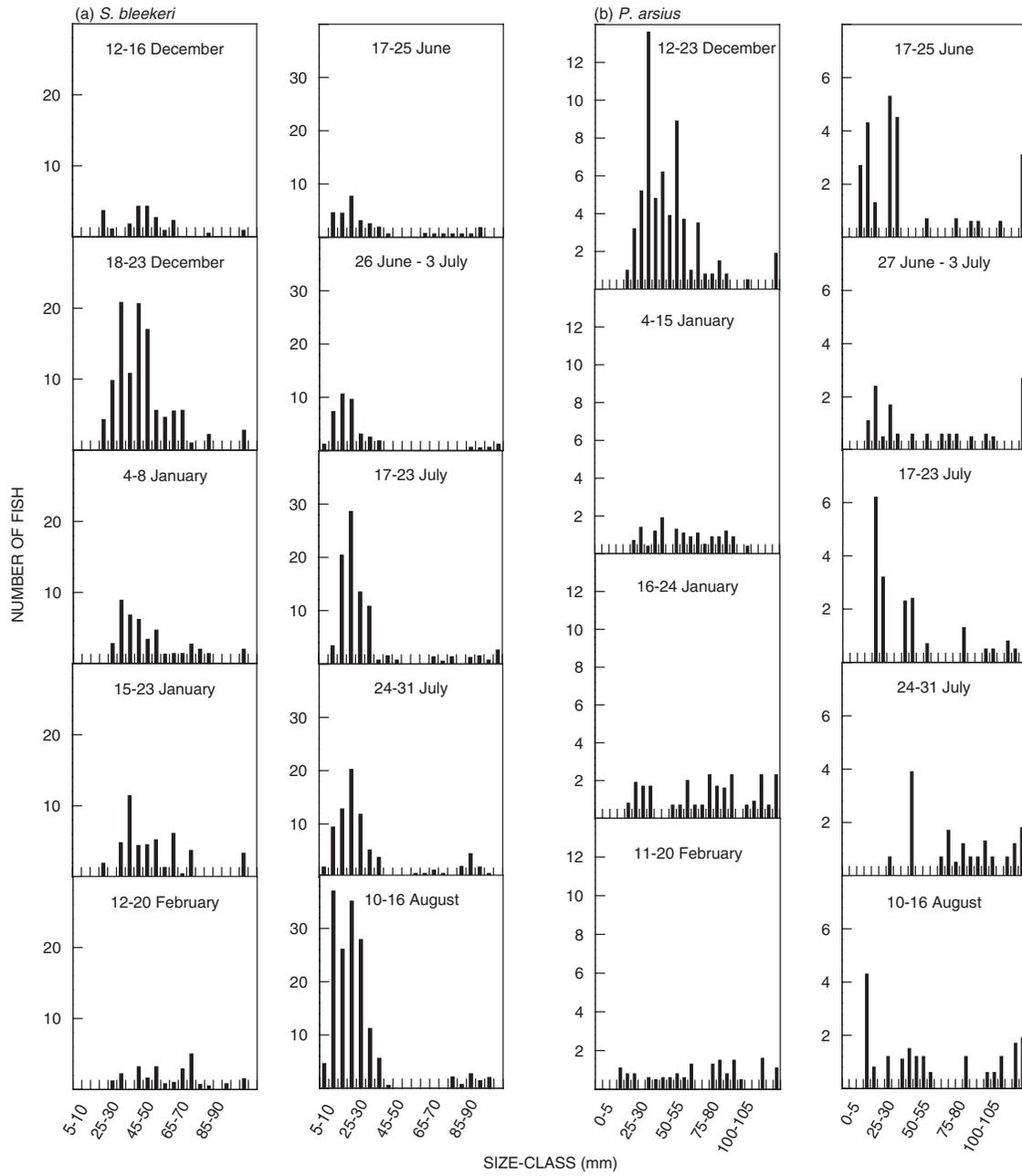


Fig. 6: Weekly length frequency distributions of day and night catches combined for (a) *S. bleekeri* and (b) *P. arsius*

Table I: Length, weight, maturity stage and condition factor K of female *S. bleekeri* and *P. arsius*. Maturity stages for *S. bleekeri* are defined according to Cyrus (1991a) and *P. arsius* as defined by Rijnsdorp (1992)

Date	Length (cm)	Weight (g)	Maturity stage		Condition factor
<i>Solea bleekeri</i>					
17 June	8.8	12.3	IV–V	Mature–ripe	1.81
20 June	7.8	7.5	V	Ripe	1.59
26 June	8.7	9.0	IV	Mature	1.37
2 July	9.5	10.9	V	Ripe	1.27
2 July	13.2	28.4	VI	Ripe running	1.24
2 July	8.5	9.8	V	Ripe	1.59
21 July	7.8	7.5	IV	Mature	1.59
21 July	8.6	9.4	IV	Mature	1.48
21 July	7.8	7.0	III	Developing	1.48
22 July	8.7	11.2	IV	Mature	1.71
24 July	8.7	9.5	III	Developing	1.44
24 July	9.3	12.0	IV	Mature	1.49
24 July	8.5	10.5	II	Inactive	1.17
25 July	9.6	14.5	III–IV	Developing–mature	1.64
10 August	9.7	15.8	VI	Ripe running	1.73
11 August	9.7	12.3	VI	Ripe running	1.35
11 August	8.7	10.6	V	Ripe	1.61
12 August	9.0	9.6	VI	Ripe running	1.31
12 August	7.6	6.0	IV	Mature	1.37
<i>Pseudorhombus arsius</i>					
17 June	12.4	35.8	6(F)	Nearly spent	1.88
17 June	14.7	56.0	7(F)	Spent	1.76
26 June	13.3	42.4	7(M)	Shrunk	1.80
28 June	14.2	50.0	6(M)	Spent	1.75
12 August	10.2	18.0	4(M)	Spawning	1.69
12 August	10.9	21.1	5(M)	Nearly spent	1.63
15 August	14.4	52.6	6(M)	Spent	1.76

first cohort of fish, ranging in length from 20 to 75 mm, could be followed in time until the end of January. During that period of 58 days, the cohort was reduced in numbers from 105.6 to 19.7 fish 1 000 m⁻², which corresponds to an instantaneous rate of mortality of 0.0289 day⁻¹. However, this value is an over-estimation of mortality, because during that period there was new settlement of small fish. In winter, the settlement of 0-group fish (5–50 mm) prevailed. From 17 to 25 June, 24.9 fish 1 000 m⁻² were caught compare to 148.0 fish 1 000 m⁻² caught from 10 to 16 August. This corresponds to an instantaneous settlement rate of 0.0320 day⁻¹.

P. arsius were abundant at the beginning of summer (12–23 December), and of the fish caught then, 54 belonged to a cohort ranging from 20 to 70 mm (Fig. 6b). This cohort was reduced to 10 fish by the next sampling period (4–15 January), which corresponds to an (overestimated) instantaneous mortality rate of 0.0733 day⁻¹. Repetitive settlement of 0-group fish (<55 mm) was observed halfway through summer (11–20 February) and throughout the winter. No attempt was made to calculate settlement rates because length-classes were not continuous.

Spawning condition

From mid-June to mid-August, 34 adult *S. bleekeri* and 50 *P. arsius* were sexed and their gonad activity assessed. The majority of *S. bleekeri* specimens were female ($n = 29$), of which 66% were reproductively active (Table I). *P. arsius* were mostly males (90%), and five were reproductively active (Table I). Only two females were reproductively active.

Maturity stages were related to SL for both species (Fig. 7a). The relationship between length (mm) and fresh weight (g) for these mature adults are given by the equations: $W = 0.166L^{2.948}$ for *S. bleekeri* ($n = 19$, $r = 0.96$) and $W = 0.0117L^{3.158}$ for *P. arsius* ($n = 7$, $r = 0.99$). The exponents of 2.948 and 3.158 respectively were not significantly different from 3.0 and the condition factor K (equal to $100W L^{-3}$) could therefore be estimated. Condition values of *S. bleekeri* varied from 1.17 for an inactive female in July to 1.81 for a mature/ripe female in June. The value for a nearly spent *P. arsius* female in June (1.88) was higher than a nearly spent male in August (1.63). The condition factors of the reproductively active adults were significantly linearly correlated to maturity stages (Fig. 7b,

$F = 4.463$, $df = 24$, $p < 0.05$), but the percentage of explained variance was low (adjusted $r^2 = 0.13$). Gonad weights ranged from 1.3 to 7.7% of the total weights for *S. bleekeri* and from 3.6 to 6.2% for *P. arsius*.

DISCUSSION

Abundance

Mean densities of *S. bleekeri* and *P. arsius* off Inhaca Island were comparable to flatfish densities in other shallow subtropical waters using similar trawling methods, e.g. off the coasts of Puerto Rico (0–30 fish 1 000 m⁻²; Reichert and Van Der Veer 1991), Guinea-Bissau (0–50 fish 1 000 m⁻²; Van Der Veer *et al.* 1995) and around Netherlands Antilles or Curacao (2 fish 1 000 m⁻²; Van Der Geest and Langevoord 1995). The higher densities of *S. bleekeri* during the night at Inhaca Island may be associated with their inshore migration, as has been documented for other flatfish species (Gibson 1997). Differences in maximum densities of *S. bleekeri* in winter and of *P. arsius* during the day in summer for could be attributable to their different life-cycle strategies (see below).

Both species preferred similar habitats, and densities were highest at Saco, which is fringed by large mangrove forests. They favoured the relatively deeper substrata that remain flooded during LWNT and are only partly exposed during LWST. The species preferred the more turbid waters above the mudflats, which could be a means of decreasing predation pressure (Cyrus 1991b).

Population structure

Length ranges of *S. bleekeri* at Inhaca (8–154 mm) were larger than for the same species along the south and east coasts of South Africa (77–141 mm; Wallace *et al.* 1984), the Sundays Estuary (11–133 mm; Beckley 1984), Lake St Lucia (15–125 mm; Cyrus 1991b) and some estuaries in KwaZulu-Natal (30–140 mm; Wallace 1975, Wallace and Van Der Elst 1975).

Length and growth of *P. arsius* at Inhaca differed from the literature for Kuwait, where lengths ranged from 80 to 380 mm (Bawazeer 1987). There, the smallest fish of 80–150 mm had no otolith ring and were assumed to represent the young-of-the-year. Mature fish from 210–270 mm were most abundant and represented several year-classes. The largest fish (380 mm) was estimated to be seven years old. The

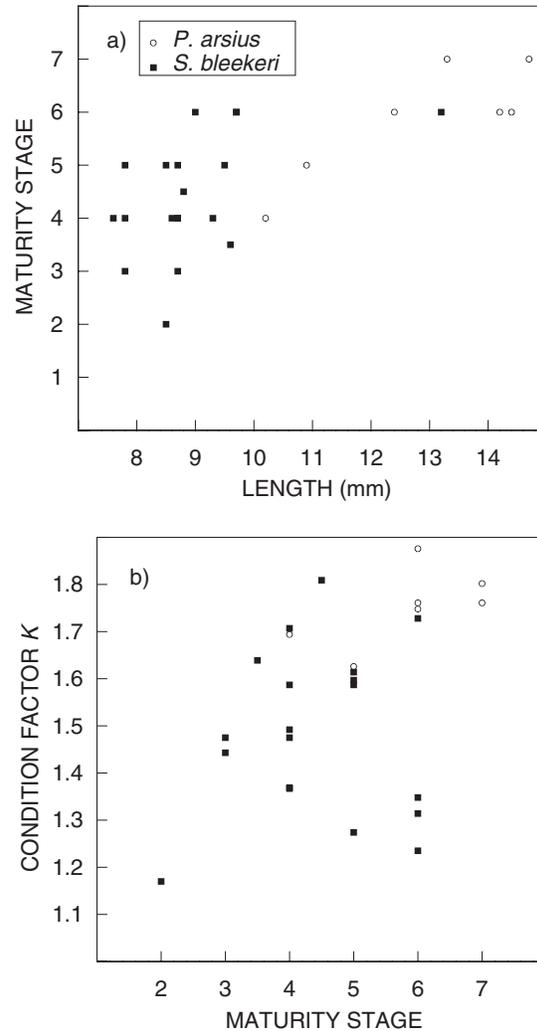


Fig. 7: Maturity stage in relation to (a) length and (b) condition factor of *S. bleekeri* and *P. arsius*

length (L) – weight (W) relationship for the species off Kuwait was $W = 0.0298 L^{3.418}$. Off India and Australia, length exponents > 3.0 were estimated for *P. arsius* (Bawazeer 1987), indicating that the species exhibits allometric growth. The present study showed that the *P. arsius* were smaller overall, adult fish were fewer and spawning adults smaller than the same species off Kuwait.

Mortality and settlement

The instantaneous rate of mortality for *S. bleekeri* (0.0289 day^{-1}) at Inhaca is similar to that estimated for other subtropical flatfish species elsewhere, e.g. Georgia, USA, and Guinea-Bissau (Reichert and Van Der Veer 1991, Van Der Veer *et al.* 1995). The calculated settlement rate of 0.0320 day^{-1} is 10% higher than the mortality rate.

In Kuwait waters, the total annual mortality for *P. arsius* was estimated at 83% (Bawazeer 1987). This value is similar to the instant mortality of 81.5% estimated here for juveniles at the onset of summer. It should be noted, however, that these calculations are based on the assumptions that there was no migration and no size-selective net efficiency. The relatively small fish at Inhaca are assumed to complete their juvenile phases within the estuaries (Whitfield 1990, Cyrus 1991b). Net efficiency is close to 100% for juvenile flatfish but, because of the negative correlation between fish size and net efficiency (Kuipers 1975, Kuipers *et al.* 1992), the natural mortality rates are probably slightly lower than those estimated here.

Spawning

Data on the spawning cycle of *S. bleekeri* are available from estuaries in South Africa (Wallace 1975, Melville-Smith and Baird 1980, Beckley 1983, 1984, 1986, Cyrus 1988, 1991b). Spawning adults within Lake St Lucia range from 55 to 122 mm (Cyrus 1991b), and Van Der Elst (1981) reports first sexual maturity of *S. bleekeri* at between 90 and 100 mm. For the smaller estuaries of KwaZulu-Natal, first sexual maturity was recorded at 75–145 mm (Wallace 1975), a size range similar to that found for mature females at Inhaca (75–132 mm).

Spawning took place in Lake St Lucia from September to December, following a 4–5 month period of gonad maturation (Cyrus 1991a), and the reproductive cycle there was similar to that in the Swartkops Estuary (Melville-Smith and Baird 1980). There, pelagic *S. bleekeri* larvae (4–6 mm) first appeared in October/November and larval abundance peaked until February. Wallace (1975) recorded ripe-running *S. bleekeri* from June to August in the smaller estuaries of KwaZulu-Natal. However, those fish were probably not breeding within the estuaries, but rather migrated to sea to spawn. Off St Lucia, Cyrus (1991b) recorded post-larvae of *S. bleekeri* (<30 mm) as early as September at sea, when adult females had become ripe/running within the estuary. Spawning adults had first moved into the surf zone, while juve-

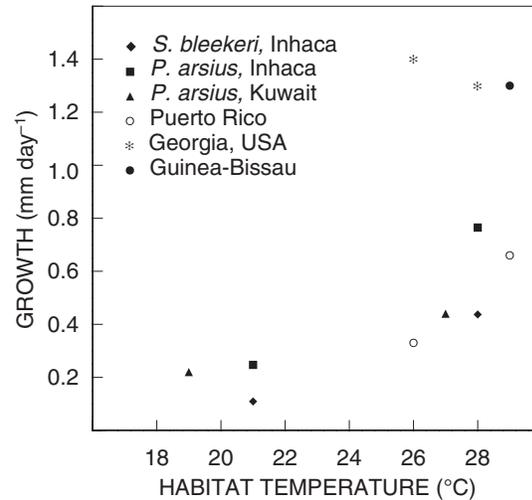


Fig. 8: Daily growth rates of subtropical flatfish species in relation to habitat temperature

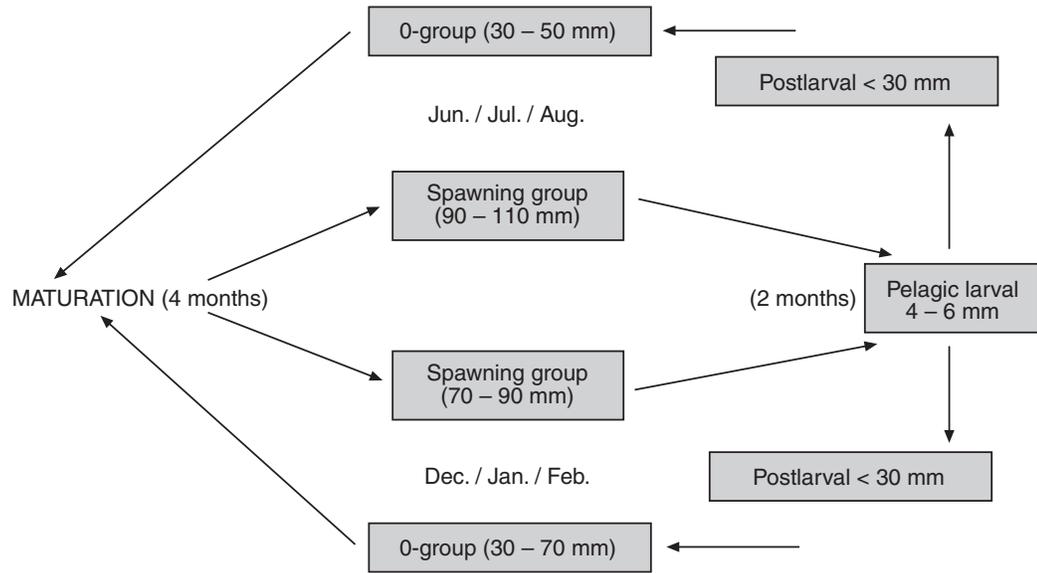
niles were migrating back into the estuarine system.

Besides the estuarine environment, the surf zone plays an important role as a nursery for estuary-associated marine fish (Lasiak 1981). The use of the surf zone by *S. bleekeri*, especially during summer, has been documented by Whitfield (1989) for the coast around Swartvlei in South Africa. In the surf zones within Algoa Bay, larval abundance of *S. bleekeri* (1.7–5.3 mm) was also highest during summer (Beckley 1986).

Pelagic stages of *S. bleekeri* in estuaries and bays are either the result of residing stock spawning within estuaries in summer or offshore stock migrating in winter (Cyrus and Martin 1991). In the intertidal areas of Inhaca, both spawning strategies were observed, which resulted in two different settlement periods. However, more research is needed to confirm the different origins of these two 0-groups.

Spawning cycles of *P. arsius* are only reported for Kuwait (Bawazeer 1987) and the coast of India (Ramanathan and Natarajan 1980), both in the northern hemisphere. The spawning season in Kuwait extends from February to May, with the highest proportion of fully mature females being found in March. The minimum size at maturity for *P. arsius* in those studies was 190 mm for both females and males, corresponding to between 1 and 2 years of age. In the intertidal area of Inhaca, spent or nearly spent fish of both sex were caught in June and August respectively.

(a) *S. bleekeri*



(b) *P. arsius*

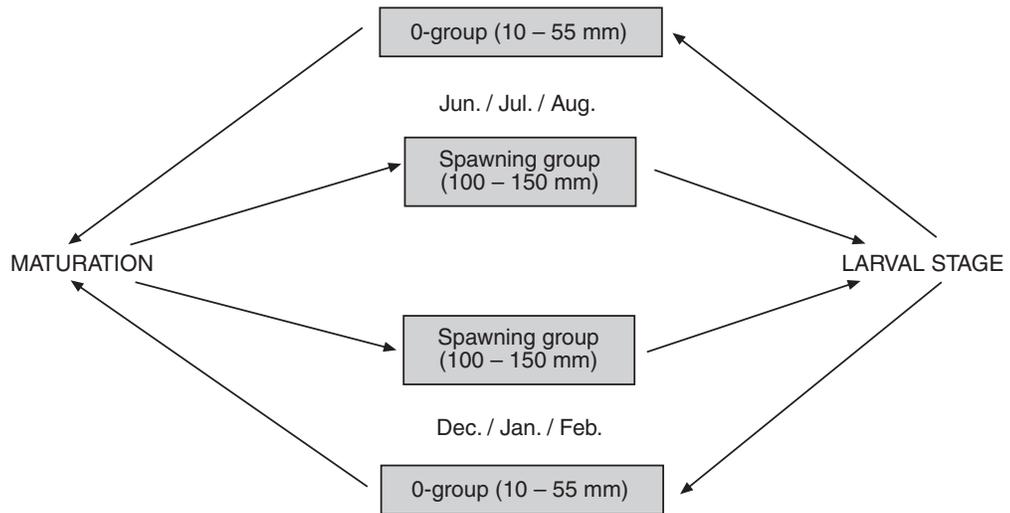


Fig. 9: Possible life-cycle strategies for (a) *S. bleekeri* and (b) *P. arsius* in the intertidal area of Inhaca

Therefore, it must be concluded that *P. arsius* attains sexual maturity at Inhaca at a smaller size than off Kuwait.

Growth

The maximum and minimum growth rates for *S. bleekeri* in Inhaca waters (Fig. 8) was estimated at 0.044 mm day⁻¹ (increasing from 30 to 110 mm between January and July) and 0.11 mm day⁻¹ (50–70 mm from July to January) respectively. For *P. arsius*, the maximum and minimum growth in summer and winter was estimated at 0.77 mm and 0.25 mm day⁻¹ respectively. The estimated annual growth rates of juveniles in Kuwait waters was between 0.22 and 0.44 mm day⁻¹ at water temperatures of between 19 and 27°C (Bawazeer 1987). Comparison of these growth rates with those of other flatfish species (Fig. 8; Reichert and Van Der Veer 1991, Van Der Veer *et al.* 1994, 1995) show that flatfish in Puerto Rico attained growth rates of 0.33–0.66 mm day⁻¹ at temperatures of 26–29°C, whereas subtropical flatfish species in Georgia and Guinea Bissau grew faster at between 1.3 and 1.4 mm day⁻¹ at similar temperatures (Fig. 8). The relation between water temperature and growth of flatfish species from different subtropical locations follows an exponential curve; $y = 0.0006 x^{4.2364}$ (where $y =$ mm growth day⁻¹ and $x =$ water temperature in °C; $n = 11$, $r = 0.77$).

Life cycles

Possible life-cycle strategies for *S. bleekeri* and *P. arsius* are shown in Figure 9. For *S. bleekeri*, relatively large fish (90–110 mm) probably spawn and undertake winter migration, whereas smaller fish (70–90 mm) likely spawn in the bay in summer. Seasonal differences in the size of spawning adults could be attributable to the lesser ability of smaller fish to undertake migration to and from the sea in comparison with larger fish (Whitfield 1990). This could explain the smaller sizes at first sexual maturity in Lake St Lucia (summer spawning) and the larger size in the other estuaries of KwaZulu-Natal (winter spawning; Wallace 1975, Wallace and Van der Elst 1975, Cyrus 1991b).

After a 2-month period in which hatching and metamorphosis takes place, pelagic larvae (4–6 mm) grow into post-larvae (<30 mm), which were present in most of the samples. Post-larvae pass through a 4-month maturation period and thereafter become the spawning group after one year. During these states of

transition, there is an overlap of fish of between 60 and 90 mm, which either have no or just one ring. This overlap might contain a mixture of rapidly growing fish (no rings) from summer and slow-growing fish (one ring) from winter. The same phenomenon was found in the Sundays Estuary, South Africa, where a bimodal distribution pattern was found for *S. bleekeri*, with peaks at 30–40 mm and 70–80 mm. The species bred inside that estuary as well as at sea (Beckley 1984).

A possible life-cycle strategy for *P. arsius* at Inhaca (Fig. 9b) is that the spawning group consists of mature adults, which have a minimum of four rings. Juveniles with no rings appeared in all samples in both winter and summer. They mature and become the spawning group about one year after hatching. This seasonal spawning pattern might explain the multimodal population structure of *P. arsius*. Young of the year settle both in winter and summer at average lengths of 30–35 mm (first peak), and grow another 60 mm in their first year of life (second peak).

ACKNOWLEDGEMENTS

We thank the staff of the Marine Biological Station at Inhaca Island and Dr D. Gove of the Universidade Eduardo Mondlane for their hospitality and help. Mr D. Jocene and several other students of the Department of Biological Sciences of that university assisted with the fieldwork. We also thank Prof. P. C. Heemstra of the J. L. B. Smith Institute for Ichthyology, Grahamstown, for checking fish identifications. Second opinions on analyses of the otoliths were given by Mr H. Witte (Netherlands Institute for Sea Research) and Messrs M. Reichert (Belle W. Baruch Institute for Marine Biology and Coastal Research). The manuscript was improved by the inputs of Drs H. Van Der Veer (Royal Netherlands Institute for Sea Research), P. Walker and J. van Gils (both of the Netherlands Institute for Coast and Sea) and two anonymous referees. The research was made possible with the financial support of the Treub Maatschappij and the Beyerinck-Poppingfonds, and was carried out within the framework of the Desenvolvimento de Ensino e de Investigação na area de Biologia project.

LITERATURE CITED

- BAWAZEER, A. S. 1987 — Stock assessment of the largemouthed flounder (Khoffah, *Pseudorhombus arsius*) in Kuwait waters. *Kuwait Bull. mar. Sci.* 9: 207–214.

- BECKLEY, L. E. 1983 — The ichthyofauna associated with *Zostera capensis* Setchell in the Swartkops Estuary, South Africa. *S. Afr. J. Zool.* **18**(1): 15–24.
- BECKLEY, L. E. 1984 — The ichthyofauna of the Sundays Estuary, South Africa, with particular reference to the juvenile marine component. *Estuaries* **7**(3): 248–258.
- BECKLEY, L. E. 1986 — The ichthyoplankton assemblage of the Algoa Bay nearshore region in relation to coastal zone utilization by juvenile fish. *S. Afr. J. Zool.* **21**(3): 244–252.
- BOLGER, T. and P. L. CONNOLLY 1989 — The selection of suitable indices for the measurement and analysis of fish condition. *J. Fish Biol.* **34**: 171–182.
- CYRUS, D. P. 1988 — Episodic events and estuaries: effects of cyclonic flushing on the benthic fauna and diet of *Solea bleekeri* (Teleostei) in Lake St Lucia on the south-eastern coast of Africa. *J. Fish Biol.* **33**(Suppl. A): 1–7.
- CYRUS, D. P. 1991a — The reproductive biology of *Solea bleekeri* (Teleostei) in Lake St Lucia on the south-east coast of Africa. *S. Afr. J. mar. Sci.* **10**: 45–51.
- CYRUS, D. P. 1991b — The biology of *Solea bleekeri* (Teleostei) in Lake St Lucia on the southeast coast of Africa. *Neth. J. Sea Res.* **27**(3/4): 209–216.
- CYRUS, D. P. and S. J. M. BLABER 1987 — The influence of turbidity on juvenile marine fishes in estuaries. 1. Field studies at Lake St Lucia on the southeastern coast of Africa. *J. expl mar. Biol. Ecol.* **109**: 53–70.
- CYRUS, D. P. and T. J. MARTIN 1991 — The importance of estuaries in life histories of flatfish species on the southern coast of Africa. *Neth. J. Sea Res.* **27**(3/4): 255–260.
- DAY, J. H. 1974 — The ecology of Morrumbene Estuary, Moçambique. *Trans. R. Soc. S. Afr.* **41**(1): 43–97.
- DE BOER, W. F. and F. A. LONGAMANE 1996 — The exploitation of intertidal food resources in Inhaca Bay, Mozambique, by shorebirds and humans. *Biol. Conserv.* **78**: 295–303.
- DE BOER, W. F., VAN SCHIE, A. M. P., JOCENE, D. F., MABOTE, A. B. P. and A. GUISSAMULO 2001 — The impact of artisanal fishery on a tropical intertidal benthic fish community. *Environ. Biol. Fishes* **61**: 213–229.
- DE BOER, W. F., RYDBERG, L. and V. SAIDE 2000 — The influence of tidal currents on an intertidal ecosystem at Inhaca Island, Mozambique. *Hydrobiologia* **428**: 187–196.
- GIBSON, R. N. 1997 — Behaviour and distribution of flatfishes. *J. Sea Res.* **37**: 241–256.
- KALK, M. 1959 — The zoogeographical composition of the intertidal fauna at Inhaca Island, Mocambique. *S. Afr. J. Sci.* **55**(7): 178–180.
- KALK, M. 1995 — *A Natural History of Inhaca Island, Mozambique*. Johannesburg: Witwatersrand University Press: 395 pp.
- KUIPERS, B. 1975 — On the efficiency of a two-metre beam trawl for juvenile plaice (*Pleuronectes platessa*). *Neth. J. Sea Res.* **9**(1): 69–85.
- KUIPERS, B. R., MACCURREN, B., MILLER, J. M., VAN DER VEER, H. W. and J. I. J. WITTE 1992 — Small trawls in juvenile flatfish research: their development and efficiency. *Neth. J. Sea Res.* **29**(1–3): 109–117.
- LASIAK, T. A. 1981 — Nursery grounds of juvenile teleosts: evidence from the surf zone of King's Beach, Port Elizabeth. *S. Afr. J. Sci.* **77**(9): 388–390.
- MELVILLE-SMITH, R. and D. BAIRD 1980 — Abundance, distribution and species composition of fish larvae in the Swartkops Estuary. *S. Afr. J. Zool.* **15**(2): 72–78.
- RAMANATHAN, N. and R. NATARAJAN 1980 — Food and feeding habits of *Psettodes erumei* (Bloch and Schn.) and *Pseudorhombus arsius* (Ham. Buch.). *Matsya* **6**: 30–42.
- REICHERT, M. J. M. and H. W. VAN DER VEER 1991 — Settlement, abundance, growth and mortality of juvenile flatfish in a subtropical tidal estuary (Georgia, U.S.A.). *Neth. J. Sea Res.* **27**: 375–391.
- RIJNSDORP, A. D. 1992 — Long-term effects of fishing in North Sea plaice. Ph.D. thesis, University of Amsterdam: 200 pp.
- SMITH, M. M. and P. C. HEEMSTRA (Eds) 1986 — *Smith's Sea Fishes*. Johannesburg: Macmillan: xx + 1047 pp.
- VAN DER ELST, R. P. 1981 — *A Guide to the Common Sea Fishes of Southern Africa*. Cape Town: Struik: 367 pp.
- VAN DER GEEST, H. G. and M. LANGEVOORD 1995 — *Ecological Observations on Flatfish on the Reefs and in the Inner Bays around Curacao, Netherlands Antilles*. NIOZ-Rapport 1995–9. Texel, Netherlands: NIOZ: 59 pp.
- VAN DER VEER, H. W., ALIAUME, C., MILLER, J. M., ADRIAANS, E. J., WITTE, J. I. J. and A. ZERBI 1994 — Ecological observations on juvenile flatfish in a tropical coastal system, Puerto Rico. *Neth. J. Sea Res.* **32**: 453–460.
- VAN DER VEER, H. W., ADRIAANS, E. J., BOLLE, L. J., DANKERS, N., MALABA DE FONSECA, L., WALKER, P. A. and J. I. J. WITTE 1995 — Ecological observations on juvenile flatfish in a tropical estuary: Arquipelago dos Bijagos, Guinea-Bissau. *Neth. J. Sea Res.* **34**: 221–228.
- WALLACE, J. H. 1975 — The estuarine fishes of the east coast of South Africa. 1. Species composition and length distribution in the estuarine and marine environments. 2. Seasonal abundance and migrations. *Investl Rep. oceanogr. Res. Inst. S. Afr.* **40**: 72 pp.
- WALLACE, J. H., KOK, H. M., BECKLEY, L. E., BENNETT, B. A., BLABER, S. J. M. and A. K. WHITFIELD 1984 — South African estuaries and their importance to fishes. *S. Afr. J. Sci.* **80**(5): 203–207.
- WALLACE, J. H. and R. P. VAN DER ELST 1975 — The estuarine fishes of the east coast of South Africa. 4. Occurrence of juveniles in estuaries. 5. Ecology, estuarine dependence and status. *Investl Rep. oceanogr. Res. Inst. S. Afr.* **42**: 63 pp.
- WHITFIELD, A. K. 1980 — Distribution of fishes in the Mhlanga Estuary in relation to food resources. *S. Afr. J. Zool.* **15**(3): 159–165.
- WHITFIELD, A. K. 1989 — Ichthyoplankton in a southern African surf zone: nursery area for the postlarvae of estuarine associated fish species? *Estuar. coast. Shelf Sci.* **29**(6): 533–547.
- WHITFIELD, A. K. 1990 — Life history styles of fishes in South African estuaries. *Environ. Biol. Fishes* **28**: 295–308.