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Comparisons between the biology of two co-occurring species of whiting (Sillaginidae) in a large marine embayment

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Synopsis

We compare the biology of the tropical species *Sillago analis* and the temperate species *Sillago schomburgkii* in Shark Bay, a large subtropical marine embayment on the west coast of Australia. This environment constitutes the approximate southernmost and northernmost limits of the distributions of these two species, respectively. The annuli visible in sectioned otoliths of *S. analis* and *S. schomburgkii* were shown to be formed annually. Their numbers were thus used to age the individuals of these two species, which are morphologically very similar and live in the same habitats. Although the growth rates of *S. analis* and *S. schomburgkii* are very similar until maturity is attained, they subsequently diverge, with *S. schomburgkii* investing relatively more energy into somatic growth. The maximum total lengths and ages of both the females (320 mm, 6 years) and males (283 mm, 8 years) of *S. analis* were not as great as those of the females (383 mm, 9 years) and males (302 mm, 9 years) of *S. schomburgkii*. In Shark Bay, *S. schomburgkii* spawns earlier and longer than *S. analis*, i.e. August to December vs January to March, which would result in the juveniles of these two species recruiting into nursery areas at different times. In addition, *S. schomburgkii* spawns earlier and for longer in Shark Bay than in temperate marine waters ~ 800 km further south, presumably reflecting an earlier attainment in that subtropical embayment of the range of water temperatures over which this species typically spawns. However, although environmental conditions in Shark Bay and those temperate marine waters differ markedly, the growth of the corresponding sexes of *S. schomburgkii* in these two water bodies is similar.

Introduction

The members of the Sillaginidae (whiting) are found in coastal marine and estuarine waters throughout the Indo-West Pacific region, where they often make an important contribution to the commercial and recreational fisheries (McKay 1992, Kailola et al. 1993). One of the largest commercial fisheries for sillaginids in Western Australia is located in Shark Bay, in which fishers target the yellowfin whiting *Sillago schomburgkii* and the golden lined whiting *Sillago analis* (Anon. 2002). The former species attains a greater size than the latter species in Shark Bay (Lenanton 1970).

Shark Bay, which is one of only 14 World Heritage areas in Australia (Anon. 2002), is a large marine embayment located at 26ºS in a transitional zone between tropical and temperate biotic regions on the west coast of Australia (Hutchins 1990, Walker 1990). This location accounts for Shark Bay representing the southern end of the distribution of the largely tropical species *S. analis* and the northern end of the distribution of the essentially temperate species *S. schomburgkii* (Hutchins & Swainston 1986, McKay 1992).

Data on the age compositions, growth rates, age at first maturity and reproductive biology of *S. analis* and *S. schomburgkii* in Shark Bay were provided by Lenanton (1970). However, the ages recorded for individual fish in that study were derived from counts of circuli in scales, a method that often yields underestimates of age and is typically less reliable than using the counts of annuli in otoliths (Beamish & McFarlane 1987, Casselman 1990). Furthermore, no attempt was made to validate that the circuli on the scales of either of these sillaginid species are formed annually, a procedure now considered mandatory prior to using the number of growth zones in hard structures to age the individuals of a fish species (Campana 2001). On the basis of the macroscopic appearance of their gonads, Lenanton (1970) concluded that, in Shark Bay, *S. analis* and *S. schomburgkii* spawn from November to March and from September to March, respectively. Although there are data on the biology of *S. schomburgkii* that were based on validated ages of fish, these were

obtained for a population on the lower west coast of Australia at 32ºS and thus over 800 km to the south of Shark Bay, where the environment is very different (Hyndes & Potter 1997).

The vast majority of the studies that have compared the onset and duration of spawning of populations of conspecific species at very different latitudes, e.g. tropical vs temperate regions, have been conducted in the northern hemisphere (e.g. Vouglitois et al. 1987, Conover 1992, Barbieri et al. 1994, McBride et al. 2002). From his review of the literature, Conover (1992) concluded that, in general, the spawning season of widely-distributed fish species in the northern hemisphere commences earlier and lasts longer in populations at lower latitudes. He proposed that the spread of spawning over a longer period at lower latitudes is related to the presence of a longer growing season and a shorter winter. Furthermore, McBride et al. (2002) have found that, for each of two congeneric triglid species on the eastern coast of North America, the individuals occurring at the higher latitude grew faster and attained a larger size.

The first aim of the present study was to validate that a single opaque zone is formed annually in the otoliths of *S. analis* and *S. schomburgkii* in Shark Bay and that the number of such zones (annuli) could therefore be used to age these two species. The second aim was to determine whether differences in the size attained by these two co-occurring and morphologically very similar species are reflected in differences in their age compositions and growth rates. The third aim was to test the hypothesis that the duration of the spawning period of *S. analis* will be relatively short in Shark Bay because the temperatures suitable for spawning are likely to be more restricted than in the main part of the distribution of this tropical species. The fourth aim was to test the hypothesis that, as Shark Bay is located at a lower latitude (26ºS) than temperate waters much further south (32ºS) and yet has higher water temperatures for much of the year, *S. schomburgkii* will

grow more slowly but spawn earlier and over a longer period in that more northern environment.

Materials and Methods

We sampled *Sillago analis* and *Sillago schomburgkii* at sites in Shark Bay (Figure 1), where these species are abundant (e.g. Lenanton 1970, Travers & Potter 2002). We sampled mangrove areas at Herald Bight and Dubaut Inlet bimonthly by seine netting and rod and line fishing between December 2001 and November 2003 and at Oyster Creek by seine netting between September 2002 and September 2003. We also regularly obtained samples by rod and line angling from unvegetated sites near Cape Peron on the eastern side of the Peron Peninsula (Figure 1). In addition, we regularly purchased from fish markets both *S. analis* and *S. schomburgkii*, which had been caught by commercial fishers in Shark Bay. We recorded to the nearest 1 mm and 1 g, respectively, the total length and total weight of each *S. analis* and *S. schomburgkii* that we caught or purchased.

The seine net, which was 21.5 m long, comprised two 10 m long wings, each consisting of 6 m of 9 mm mesh and 4 m of 3 mm mesh, and a 1.5 m long pocket of 3 mm mesh. On each occasion that we sampled at Herald Bight, Dubaut Inlet and Oyster Creek, we recorded the water temperature and salinity to the nearest 0.1ºC and 0.1‰, respectively, using a Yellow Springs Instruments Salinity, Conductivity and Temperature Meter, Model YSI 30.

Ageing techniques and age validation

Initially, we removed both of the sagittal otoliths and five scales from behind the pectoral fins of 85 *S. analis* and 85 *S. schomburgkii* that were obtained from several sites and which covered the full size range of each species. The otoliths were placed in a black dish, covered with methyl salicylate and examined under reflected light using a dissecting

microscope. Scales were placed between two glass microscope slides and viewed on a black surface in the same way as whole otoliths. The number of circuli on each scale and the number of opaque zones in each otolith were recorded. The same otoliths were then mounted in clear epoxy resin and cut transversely through their primordia into 0.3 mm sections using an Isomet Buehler low-speed diamond saw. The sections were ground with wet and dry carborundum paper (Grade 1200) and mounted on glass microscope slides with DePX mounting adhesive and a cover slip. The sectioned otoliths were viewed in the same manner as whole otoliths and the number of opaque zones recorded. Since the opaque zones were usually more clearly visible in the otoliths of both *Sillago* species after they had been sectioned, the number of circuli on scales were compared with the number of opaque zones in sectioned otoliths rather than with those visible in whole otoliths.

The opaque zones visible in 100 sectioned otoliths from a wide size range of both *S. analis* and *S. schomburgkii* were counted independently by two of the authors (P.G. Coulson and S.A. Hesp). The counts made on the otoliths of *S. analis* and *S. schomburgkii* were the same in 90 and 92% of cases, respectively. In the few cases where there were discrepancies, the counts of the two readers never differed by more than one. After re-examining and discussing the location of the zones in those otoliths, it was agreed that the discrepancy was due to difficulties in detecting the first of those zones. Consequently, throughout the study, P.G. Coulson consulted with S.A. Hesp on those occasions when the location of the first opaque zone in an otolith was not well defined.

In the case of all fish examined during the study, the marginal increment on one of their sectioned otoliths, i.e. the distance between the outer edge of the single or outermost opaque zone and the periphery of that otolith, was expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present. All

measurements were made along the same axis, i.e. perpendicular to the opaque zone(s), and were recorded to the nearest 0.1 mm using a dissecting microscope with an eyepiece graticule and reflected light.

Growth

We fitted von Bertalanffy growth curves to the lengths of individuals of both sexes at their estimated ages at time of capture using SPSS (SPSS Inc. 2001). The lengths at age of juvenile fish of both *Sillago* species < 80 mm in length, at which lengths the fish could not be sexed macroscopically, were allocated randomly, but equally, to the female and male data sets used for calculating the von Bertalanffy growth curves. The von Bertalanffy growth equation is $L_t = L_\infty[1-\exp^{-k(t-t_o)}]$, where L_t is the length (mm TL) at age t (years), L_∞ is the mean asymptotic length (mm) predicted by the equation, k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have zero length.

The von Bertalanffy growth equations and parameters for the females and males of both *S. analis* and *S. schomburgkii* in Shark Bay were compared using a likelihood ratio test (Kimura 1980). The hypothesis that the data in each case could be described by a common growth curve was rejected at the $\alpha = 0.05$ level of significance if the test statistic, calculated as twice the difference between the log-likelihood obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex, exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the two approaches. The log-likelihood, λ, for each curve, ignoring constants, was calculated as $\lambda = -\frac{n}{2}\ln\left(\frac{ss}{n}\right)$, where n refers to the sample size, and ss refers to the sum of the squared residuals between the observed and expected lengths at age. If the growth curves were found to differ significantly, the likelihood ratio test was then employed to determine

whether all three of the von Bertalanffy growth parameters of these two curves differed significantly or whether it was statistically appropriate to use von Bertalanffy growth curves in which one of the parameters was common to describe the two sets of data (e.g. Kimura, 1980). The same approach was then used to compare the von Bertalanffy growth curves of the corresponding sexes of *S. analis* and *S. schomburgkii* and to test whether the growth curves of the females and males of *S. schomburgkii* in Shark Bay differed from those derived from data collected by Hyndes and Potter (1997) for the corresponding sexes of this species in temperate marine waters at 32ºS.

The length-weight relationships of the females and males of *S. analis* and *S. schomburgkii* in Shark Bay were compared using analysis of covariance (ANCOVA) and employing the natural logarithm of weight as the dependent variable, sex as the fixed factor and the natural logarithm of length as the covariate. Since the length-weight relationships of the two sexes of neither species differed significantly (both $P > 0.05$), the length-weight data for both sexes of each species were pooled. Analysis of covariance was then used to compare the length-weight relationships of the two species.

Reproductive variables

We determined macroscopically the sex of all fish > 80 mm in length. The paired gonads of each fish were weighed to the nearest 0.01 g and allocated macroscopically to one of the following stages of maturity, based on criteria adapted from Laevastu (1965): I = virgin; II = immature; III = developing; IV = maturing; V = mature; VI = spawning; VII = spent; VIII = recovering spent. The macroscopic characteristics of each gonadal stage and of the corresponding histological characteristics of each ovarian stage are given in Table 1. Mean monthly gonadosomatic indices (GSIs) were determined for females and males with lengths ≥ that at which 50% of females and 50% of males reached maturity (L_{50}) using the

equation $GSI = W1/(W2 - W1) \times 100$, where $W1$ = wet gonad weight and $W2$ = wet body weight.

The ovaries of approximately 10 large females of both *S. analis* and *S. schomburgkii* from each calendar month were placed in Bouin's fixative for 24 h, dehydrated in an ascending series of ethanol concentrations and embedded in paraffin wax. Transverse sections (6 μm) of the mid-region of each ovary were stained with Mallory's trichrome and examined using a compound microscope.

The lengths at which 50% of the females and males of both *S. analis* and *S. schomburgkii* reached maturity (L_{50}) and their 95% confidence limits were estimated by fitting a logistic regression to the proportion of those fish in each 10 mm length class which, during the spawning period, possessed gonads at stages III to VIII and were thus likely to have spawned during that period (see Results). The curves were fitted using SPSS (SPSS Inc. 2001). The form of the logistic equation used for this analysis is $P = \frac{1}{1 + \exp[-\ln(19)(L - L_{50})/(L_{95} - L_{50})]}$, where P = proportion mature, L = total length in mm, and L_{50} and L_{95} = the length in mm at which 50% and 95% of fish reach sexual maturity, respectively. The lengths at maturity of the females and males of both *S. analis* and *S. schomburgkii*, and of the same sex of these two species, were compared using a likelihood ratio test (Kimura 1980).

Results

Environmental measurements

The mean monthly water temperatures at the sampling sites declined from a maximum of 29ºC in mid-summer to 26ºC in mid-autumn and then to a minimum of 17ºC in late winter, before rising to 27ºC in late spring (Figure 2). Salinity varied considerably throughout the year, ranging from a monthly mean of 45‰ in late summer to 35‰ in early winter (Figure 2).

Validation of ageing method and growth of Sillago analis *and* Sillago schomburgkii

The mean monthly marginal increments on sectioned otoliths of *S. analis* with two opaque zones remained at 0.48 to 0.58 between July and October, before declining to a minimum of 0.19 in November and then increasing progressively to 0.57 in March and remaining at about this level in the immediately ensuing months (Figure 3). The mean monthly marginal increments for otoliths with one, three and ≥ four opaque zones followed essentially the same trend as that just described for otoliths with two opaque zones. Similar trends were exhibited by the mean monthly marginal increments on sectioned otoliths of *S. schomburgkii* (Figure 3).

The number of circuli visible in the scales of 77 of the subsample of 85 *S. analis* differed from the number of annuli visible in sectioned otoliths of those same fish. The number of circuli visible in scales was one less in all but one of these 77 cases. The number of circuli visible in the scales of 49 of the 85 *S. schomburgkii* examined was less by one or more than the number of opaque zones visible in the sectioned otoliths of the same fish. The magnitude of the discrepancies increased as the number of opaque zones in sectioned otoliths increased and in one case the difference was as great as four.

Since the trends in the reproductive data strongly indicate that *S. analis* spawns mainly between January and March and that *S. schomburgkii* spawns mainly between August and December (see later), *S. analis* and *S. schomburgkii* were assigned birth dates of 1 February and 1 October, respectively.

The von Bertalanffy growth curves provided good fits to the lengths at age of the females and males of both *S. analis* and *S. schomburgkii* (Figure 4), which was reflected in the relatively high R^2 values of 0.829 and 0.879 for female and male *S. analis*, respectively, and of 0.904 and 0.875 for female and male *S. schomburgkii*, respectively (Table 2). The females of *S. analis* and *S. schomburgkii* attained slightly greater lengths than their males

at the same ages. The maximum lengths attained by the females of *S. analis*, i.e. 320 mm, and of *S. schomburgkii*, i.e. 383 mm, were greater than those of their males, i.e. 283 and 302 mm, respectively (Figure 4). However, the maximum age of the females of *S. analis* (6 years) was less than that of its males (8 years) and the maximum ages of females and males of *S. schomburgkii* were both 9 years. These differences in maximum lengths between the males and females of both *S. analis* and *S. schomburgkii* and of differences in maximum age of the two sexes of *S. analis* are reflected in significant differences between the von Bertalanffy growth curves for the two sexes of both of these species (all $P < 0.001$). Each of the growth parameters was also found to differ significantly between the sexes of both species (all $P < 0.001$).

The growth curves and each of the growth parameters for the females of *S. analis* and *S. schomburgkii* were significantly different and the same was true for their males (all $P < 0.001$). The data in Figure 4 emphasize that the females and males of *S. schomburgkii* both attain a greater maximum size and age than those of *S. analis*.

The likelihood ratio test demonstrated that the von Bertalanffy growth curves for female and male *S. schomburgkii* in Shark Bay differ significantly from those of the corresponding sexes of this species on the lower west coast at 32ºS (all $P < 0.001$). Furthermore, for both sexes, the likelihood ratio test demonstrated that each of the three parameters of the von Bertalanffy growth curves for the two populations differed significantly ($P < 0.001$). However, the likelihood ratio test is extremely sensitive when comparisons are being made between curves derived from data sets with large numbers of observations and that much of the difference between the above curves for *S. schomburgkii*, and particularly for the males, is attributable to differences in the values for t_0. Thus, the growth curves for both the females and males in temperate waters were adjusted by shifting their ages forward so that they would have the same t_0s as those of the corresponding sexes in Shark Bay. After this adjustment, the lengths of females at ages

one, two and three years in marine temperate waters were 138, 218 and 266 mm, compared with 132, 213 and 264 mm in Shark Bay. The corresponding values for the males at the same ages were 125, 202 and 250 mm for temperate marine waters and 128, 200 and 240 mm in Shark Bay. The maximum differences between these three predicted lengths at age in the curves for the two regions, when expressed as percentages of the lowest L_∞ of the two curves, were small, i.e. 1.8% for females and 3.2% for males. Therefore, from a biological perspective, the growth of *S. schomburgkii* in Shark Bay and in marine temperate waters is very similar.

The relationships between total length (TL) in mm and total weight (W) in g are described by the following regression equations:

Sillago analis $ln\ W = 2.993(ln\ TL) - 11.664$ ($R^2 = 0.995$, $n = 1171$).

Sillago schomburgkii $ln\ W = 3.005(ln\ TL) - 11.783$ ($R^2 = 0.997$, $n = 1748$).

The subjection of the length-weight relationships for *S. analis* and *S. schomburgkii* to ANCOVA demonstrated that the intercepts were significantly different ($P < 0.001$), but that the slopes did not differ significantly ($P > 0.05$). At any given length, the weight of *S. schomburgkii* exceeds that of *S. analis* by only about 5%.

Gonadal development of Sillago analis *and* Sillago schomburgkii

The mean monthly GSIs of female *S. analis* ≥ the L_{50} of females at first maturity, i.e. 216 mm (see later), rose sharply from 0.7 in July to reach a peak of 4.2 in January, before declining to ≤ 1.0 between April and June (Figure 5). Although the mean monthly GSIs for male *S. analis* ≥ the L_{50} of males at first maturity followed essentially the same trend as those of females, they peaked a month later, i.e. February, and at a lower level. In comparison with *S. analis*, the mean monthly GSIs for female and male *S. schomburgkii* peaked earlier and were elevated for a longer period, i.e. between August and December

(Figure 5). The maximum mean monthly GSIs of the females and males of *S. schomburgkii* were far greater than those of the corresponding sexes of *S. analis*.

All of the female *S. analis* caught during July and August with lengths$\geq L_{50}$ at maturity possessed ovaries at stage I/II, i.e. immature (Figure 6). The percentage of fish with stage I/II ovaries declined progressively to very low levels in January to March. Fish with stage III ovaries first appeared in September and those with stage IV and stages V/VI ovaries were first caught in October. The prevalence of fish with stage III or IV ovaries declined after December and the occurrence of fish with stage V/VI ovaries was high between January and March (Figure 6). Stage VII ovaries were first recorded in March and, together with stage VIII ovaries, were prevalent in May and June. Similar trends were exhibited by the gonadal stages of male *S. analis*.

The monthly prevalances of gonads of *S. schomburgkii* at each stage of development followed a different trend from those of *S. analis*. Thus, in July, many female and male *S. schomburgkii* possessed gonads at stages III and IV and a few individuals possessed gonads at stages V/VI (Figure 6). Furthermore, unlike *S. analis*, the vast majority of *S. schomburgkii* caught between August and December possessed gonads at stages V/VI and most of those caught between January to March possessed gonads at either stages I/II or VII.

The trends described above for the reproductive variables throughout the year demonstrate that *S. analis* and *S. schomburgkii* spawn mainly from January to March and from August to December, respectively (see Discussion for rationale for these conclusions). From the trends shown by the prevalences of individuals with gonads at different stages of development, it then follows that those individuals of both sexes that possess stage III and IV gonads at the commencement of the spawning period will progress through to maturity by the end of the spawning period. Thus, for determining the L_{50} for females and males of the two *Sillago* species at maturity, it was appropriate to subject to

regression analysis the prevalence in successive length intervals of *S. analis* and *S. schomburgkii* with gonads at stages III to VIII in January to March and in August to December, respectively.

Length and age of Sillago analis *and* Sillago schomburgkii *at maturity*

During the spawning period of *S. analis*, virtually all females > 220 mm and all of those > 240 mm contained ovaries at stages III to VIII (Figure 7, Table 3). Just over half of the males between 180 and 199 mm and all of those > 220 mm possessed testes at stages III to VIII. The L_{50}s at which female and male *S. analis* first reached maturity were 216 and 184 mm, respectively. During the spawning period, the proportions of female and male *S. schomburgkii* in each size class with gonads at stages III to VIII, were similar to those of the females and males of *S. analis* (Fig. 7). The L_{50}s for female and male *S. schomburgkii* at first maturity were 223 and 195 mm, respectively.

The L_{50}s for female and male *S. analis* at maturity and for female and male *S. schomburgkii* at maturity were significantly different (both $P < 0.001$). However, the L_{50}s for the corresponding sexes of the two species were not significantly different ($P > 0.05$).

Very few females and males of *S. analis* and no *S. schomburgkii* had attained maturity by the end of their first year of life. Twenty percent of the females and 60% of the males of *S. analis* and 35% of the females and 70% of the males of *S. schomburgkii* had reached maturity by the end of their second year of life. By the end of their third year of life, all or virtually all of the individuals of both species had become mature.

Discussion

Lenanton (1970) based his ageing of *S. analis* and *S. schomburgkii* in Shark Bay on the number of circuli on scales. His decision to use scales rather than whole otoliths was based

on his observation that growth zones, particularly in the thicker otoliths that are found in larger fish, were often undetectable (Lenanton 1970). Although we also found it difficult to detect growth zones in whole otoliths, the clarity of those zones became greatly enhanced once the otoliths had been sectioned.

The single pronounced decline and subsequent progressive rise undergone by the mean monthly marginal increments on sectioned otoliths of *S. analis* and *S. schomburgkii*, irrespective of the number of opaque zones in those otoliths, demonstrates that a single opaque zone is formed annually in the otoliths of these species. It was thus valid to use the number of growth zones in sectioned otoliths to age these two species. However, the numbers of circuli on the scales of both *S. analis* and *S. schomburgkii* were frequently less than the numbers of opaque zones in the otoliths of the corresponding fish. The tendency for the ages of *S. analis* and *S. schomburgkii* to be underestimated when using counts of scale circuli rather than otolith annuli parallels the situation with numerous other species (e.g. Boxrucker 1986, Beamish & McFarlane 1987, Casselman 1990, Booth et al. 1995)

Inter- and intraspecific comparisons of growth

Our data showed that the corresponding sexes of *S. schomburgkii* and *S. analis* grow at essentially the same rate prior to the attainment of maturity, and that consequently their lengths and ages at maturity are very similar (Figure 8). However, the growth curves of the corresponding sexes of these two species diverge immediately after the attainment of maturity, reflecting a relatively greater investment of energy into somatic growth by *S. schomburgkii* than by *S. analis*. The greater L_∞s recorded for the females and males of *S. schomburgkii* than for those of the corresponding sexes of *S. analis* are also associated with a longer life span. The larger size attained by *S. schomburgkii* than *S. analis* would presumably enable that species to target larger prey and thereby reduce the potential for competition between the adults of these two abundant species for food resources. Although

there are no data on the dietary composition of these two *Sillago* species in Shark Bay, there are such data for *Sillago bassensis* and *Sillago robusta*, which co-occur in the deeper inner shelf waters of temperate Western Australia. These data demonstrate that *S. bassensis*, the larger of these two congeneric species, targets larger prey (Hyndes et al. 1997).

Although water temperatures during the main growth period of late spring to early autumn in Shark Bay at 26ºS are, on average, ~ 5ºC warmer than those in temperate coastal waters at 32ºS (*cf* Figure 2, Hyndes & Potter 1996), the growth rates of both the females and males of *S. schomburgkii* in these two areas are similar. This lack of a marked difference in growth rate between the populations of *S. schomburgkii* in these two distantly-located and different waters is paralleled by that recorded by Hesp et al. (2004) for the sparid *Rhabdosargus sarba*. However, these similarities between latitudinally well separated populations of *S. schomburgkii* and *S. analis* contrast with the findings of several other workers, including McBride et al. (2002) for *Prionotus carolinus* and *Prionotus evolans*, Jonassen et al. (2000) for *Hippoglossus hippoglossus* and Conover et al. (1997) for *Morone saxitilis*, all of whom found that their species grew faster at higher latitudes. The similarities in the growth rates of both *S. schomburgkii* and *R. sarba* at different latitudes imply either that the growth rates of each of these species are, to a large degree, genetically fixed, and/or that the different environmental factors that influence growth in these two waters have a similar combined effect on growth.

Spawning time and period

The presence of high mean monthly GSIs for female and male *S. analis* between January and March indicates that this species spawns mainly between mid- to late summer and early autumn. This conclusion is strongly supported by the fact that, although ovaries and testes at stages V/VI were found in fish as early as October and December, respectively,

their prevalences only became high between January and March. Furthermore, since the prevalence of fish with ovaries at stages V/VI declined dramatically between March and April, *S. analis* would essentially have ceased spawning by that latter month. Lenanton (1970) estimated that the spawning period of *S. analis* extends from November to March.

In contrast to the situation with *S. analis*, the fact that the mean monthly GSIs and proportions of ovaries and testes at stages V/VI were high for *S. schomburgkii* between August and December provides strong evidence that this species exhibits substantial spawning activity between late winter and early summer. Although some *S. schomburgkii* with stages V/VI ovaries or testes were caught in each month between January and April, the higher prevalence of stage VII or VIII gonads and the presence of very low GSIs indicate that limited spawning occurred between these months. Lenanton (1970) concluded that the full spawning period of this species in Shark Bay extended from September to January.

The main spawning period of *S. schomburgkii* occurs far sooner in Shark Bay, i.e. August to December, than in temperate marine waters at 32ºS, i.e. December to February (Hyndes & Potter 1997). Since water temperature plays a crucial role in stimulating spawning activity in fish (Lam 1983), these differences are likely to be related, at least in part, to the pronounced differences that exist between the water temperature regimes in these two widely separated areas. It is thus highly relevant that water temperatures during the middle of the spawning periods of *S. schomburgkii* on the lower west coast of Australia, i.e. 22-24ºC, are attained far earlier in Shark Bay, i.e. October/November, and that these months coincide with the middle of the spawning period of this species in this embayment. This provides strong circumstantial evidence that the range in water temperatures critical for peak spawning activity of *S. schomburgkii* is the same in subtropical and temperate waters.

The temperatures of 22-24ºC at which the spawning of *S. schomburgkii* peaks in December to February in waters at 32ºS represent the maximum temperatures attained during the year (Hyndes & Potter 1997). However these and slightly higher water temperatures are present between mid-August and December in Shark Bay, which could thus account for the longer spawning period of this species in this environment than in temperate waters, i.e. 4½ vs 3 months. The possession of a protracted spawning period by *S. schomburgkii* in Shark Bay at the northern end of its distribution is paralleled by the extended spawning period of eight months exhibited by *Sillago bassensis* in temperate waters at 32ºS, which in this case, is close to the northernmost limit of the distribution of this sillaginid (McKay 1992). In contrast, three other *Sillago* species, *S. robusta S. vittata* and *S. burrus*, which are abundant at 32ºS and whose distributions extend northwards into tropical waters (Hutchins & Swainston 1986), spawn for no longer than four months at 32ºS (Hyndes & Potter 1996, Hyndes et al. 1996).

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Figure 1. Map showing location of Shark Bay in Western Australia (box) and the main sampling sites (black circles) in that embayment.

Figure 2. Mean monthly water temperatures (closed circles) and salinities (open circles) ± 1 SE at the main sampling sites in Shark Bay. In this Figure and Figures 3 and 5, closed rectangles on the x axis refer to summer and winter months and the open rectangles to autumn and spring months.

Figure 3. Mean monthly marginal increments ± 1 SE for sectioned sagittal otoliths of *Sillago analis* and *Sillago schomburgkii* with different numbers of opaque zones.

Figure 4. von Bertalanffy growth curves fitted to the length at age of individuals of female and male *Sillago analis* and *Sillago schomburgkii*.

Figure 5. Mean monthly gonadosomatic indices ± 1 SE for female and male *Sillago analis* and *Sillago schomburgkii*.

Figure 6. Monthly percentage frequencies of occurrence of sequential stages in the gonadal development of female and male *Sillago analis* and *Sillago schomburgkii* $>L_{50}$ at maturity. Histograms for stages V/VI are highlighted in black.

Figure 7. Logistic curves (solid lines) and 95% confidence intervals (dotted lines) fitted to the percentage frequency of occurrence of fish with gonads at stages III-VIII (grey histograms) in sequential 20 mm length classes of female and male *Sillago analis* caught between January and March and female and male *Sillago schomburgkii* caught between August and December. The sample size is shown at the top of each bar.

Figure 8. von Bertalanffy growth curves for female and male *Sillago analis* (dashed line) and for female and male *Sillago schomburgkii* (dotted line) in Shark Bay. Arrows denote the length and age at which maturity is reached.

Table 1. Description of the macroscopic characteristics of gonadal development stages of female and male *Sillago analis* and *Sillago schomburgkii* and the corresponding histological characteristics of these stages for females. Macroscopic stages are adapted from Laevastu (1965), while the oocyte stages follow the terminology used by Wallace and Selman (1981).

Stage	Macroscopic stage (female and male)	Histological stage (female)
I Virgin	Ovaries and testes very small. Ovaries transparent. Testes black and strand-like.	Oogonia and chromatin nucleolar oocytes present. Oocytes neatly arranged along ovarian lamellae. Previtellogenic oocytes present in all subsequent stages.
II Immature	Ovaries light red, but still transparent. Eggs invisible to naked eye. Testes black and strand-like.	Same as for previous stage, although perinucleolar oocytes often present.
III Developing	Ovaries opaque, rose to light pink. Small white eggs visible through ovarian wall. Testes dark purple.	Cortical alveolar oocytes abundant.
IV Maturing	Ovaries yellow-orange. Capillaries visible on ovarian wall. Yellow eggs visible through ovarian wall. Testes light purple. Milt extruded when testes placed under pressure.	Cortical alveolar oocytes and yolk granule oocytes abundant.
V Mature	Ovaries and testes large, occupying ~ 2/3 of body cavity. Ovaries yellow with extensive capillaries visible on ovarian wall. Testes light purple with white edges to lobes. Milt extruded when testes placed under light pressure.	Yolk granule oocytes very abundant and tightly packed throughout ovary.
VI Spawning	No female fish at this stage were observed macroscopically (i.e. those with hydrated oocytes visible through ovarian wall). Testes white and easily ruptured.	No ovaries of spawning females (i.e. those containing migratory nucleus stage oocytes, hydrated oocytes or post-ovulatory follicles) were found in the samples prepared for histology.
VII Spent	Ovaries and testes flaccid and ~ 1/3 the size of those at stage V/VI. Ovaries deep red with a few remnant eggs visible through ovarian wall. Testes pale purple.	More than 50% of the remaining yolk granule oocytes are atretic.
VIII Recovering spent	Ovaries and testes similar in size to stage II. No oocytes visible through ovarian wall.	No cortical alveolar or yolk granule oocytes present. Ovaries contain extensive connective tissue.

Table 3. Estimates of the lengths at which 50% of *S. analis* and *S. schomburgkii* reach maturity (L_{50}) in Shark Bay and the 95% confidence limits.

		L_{50} (mm)	L_{95} (mm)
Sillago analis			
Female	**Estimate**	**215.7**	**238.2**
	Upper	219.4	245.9
	Lower	211.9	230.4
Male	**Estimate**	**183.9**	**209.8**
	Upper	187.7	218.3
	Lower	179.8	201.4
Sillago schomburgkii			
Female	**Estimate**	**223.3**	**253.7**
	Upper	228.7	268.9
	Lower	218.5	237.3
Male	**Estimate**	**195.9**	**218.9**
	Upper	200.7	225.6
	Lower	189.1	208.6

*Table 2***.** The von Bertalanffy growth parameters L_∞, k, and t_0, including upper and lower 95% confidence limits, of *Sillago analis* and *Sillago schomburgkii*, derived from the length at age of individuals caught in Shark Bay. R^2 = coefficient of determination; n = sample size. von Bertalanffy growth parameters for *S. schomburgkii* in temperate marine waters at 32ºS.

		von Bertalanffy parameters				
		L_∞ **(mm)**	k **(year^{-1})**	T_0 **(years)**	R^2	n
Sillago analis **(Shark Bay)**						
Female	**Estimate**	**279.5**	**0.715**	**0.093**	**0.829**	**753**
	Upper	285.8	0.774	0.153		
	Lower	273.2	0.656	0.033		
Male	**Estimate**	**253.9**	**0.750**	**0.119**	**0.879**	**483**
	Upper	260.0	0.815	0.175		
	Lower	247.9	0.686	0.063		
Sillago schomburgkii **(Shark Bay)**						
Female	**Estimate**	**345.9**	**0.477**	**-0.008**	**0.904**	**997**
	Upper	354.7	0.507	0.027		
	Lower	337.2	0.447	-0.044		
Male	**Estimate**	**290.4**	**0.588**	**0.012**	**0.875**	**924**
	Upper	299.4	0.633	0.048		
	Lower	281.3	0.545	-0.022		
Sillago schomburgkii **(Temperate marine waters, 32ºS)**						
Female	**Estimate**	**333.3**	**0.53**	**-0.16**	**0.95**	**662**
Male	**Estimate**	**324.7**	**0.49**	**-0.22**	**0.93**	**554**