Abstract.—The age structure, growth and reproductive biology have been determined for the recreationally and commercially important King George whiting, *Sillaginodes punctata*, off southwestern Australia. The maximum lengths and ages, asymptotic lengths (L_∞), and growth coefficients (K) were 596 mm, 14 years, 532 mm, and 0.47, respectively, for females, and 555 mm, 13 years, 500 mm and 0.53, respectively, for males. Sexual maturity is attained by 50% of female *S. punctata* by ca. 410 mm in length, and by the majority of both female and male fish at the end of their fourth year of life. The monthly trends in the proportions of mature gonads and the prevalence of different oocyte stages and postovulatory follicles indicated that, in southwestern Australia, *S. punctata* spawns from June to September. Spawning is thus initiated when water temperatures are declining from their maxima. During the spawning period, many of the ovaries of large fish contained yolk vesicle and yolk granule oocytes, as well as hydrated oocytes or postovulatory follicles (or both), indicating that *S. punctata* is a multiple spawner. Furthermore, because hydrated oocytes or postovulatory follicles were often found together with large numbers of yolk granule oocytes, *S. punctata* presumably releases eggs in batches during the spawning period. Recruitment of *S. punctata* into sheltered nearshore waters (<1.5 m) commences in late September, three months after the onset of spawning, and continues until early November. When juvenile *S. punctata* reach ca. 1.5 years of age and ca. 250 mm, the legal minimum length for capture, they move out into slightly deeper waters (2–6 m) in marine embayments and estuaries. After attaining ages of ca. 4 years and lengths of ca. 370 mm, they then migrate from these waters, where fishing pressure is greatest, into regions near or around reefs at depths of 6–50 m, where spawning occurs. In contrast to *S. punctata*, the five other whiting species in southwestern Australian waters, which all belong to the genus *Sillago*, spawn between late spring and early autumn. In the case of the three *Sillago* species that undergo an offshore migration, this movement occurs at a relatively small size and young age and leads to their occupying open sandy areas. The implications of *S. punctata* habitat and biological data for fishery management are discussed.

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Age composition, growth, reproductive biology, and recruitment of King George whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia

Glenn A. Hyndes
Margaret E. Platell
Ian C. Potter
Biological Sciences, Murdoch University
Murdoch, Western Australia, 6150, Australia
E-mail address (for G. A. Hyndes): hyndes@central.murdoch.edu.au

Rodney C. J. Lenanton
Bernard Bowen Fisheries Research Institute
Western Australian Marine Research Laboratories
P.O. Box 20, North Beach
Western Australia, 6020, Australia

The King George whiting, *Sillaginodes punctata*, which is the largest of the 31 species belonging to the Sillaginidae, occurs along the lower west and southern coasts of Australia (McKay, 1992), where it is a very important recreational and commercial species (see Kailola et al., 1993). Although a number of studies have been carried out on the biology of *S. punctata* (Scott, 1954; Thomson, 1957a; Gilmour, 1969; Robertson, 1977; Caton[1]; Cockrum and Jones[2]), these have concentrated mainly on fish caught in shallow waters, in which mature fish tend not to be found. Although Cockrum and Jones[2] obtained *S. punctata* from deeper waters, where spawning presumably occurs, data on the pattern of gonadal development, which is required to determine precisely the peak time and duration of spawning of this species, are very limited. Indeed, estimates of the timing and duration of spawning of *S. punctata* have been derived predominantly from backcalculations of daily growth increments of recently settled juveniles (Bruce, 1989; Bruce and Short, 1992; Jenkins and May, 1994; Fowler and Short, 1996). These latter studies, which were carried out off southeastern Australia, indicate that *S. punctata* spawns between early autumn and early winter. However, *S. punctata* is recruited into nearshore waters far earlier off South Australia than off southwestern Australia, which suggests that this species spawns later in the latter region (cf. Fowler and Short, 1996; Hyndes et al., 1996a).

Although age structures and growth parameters have been estimated for populations of *S. punctata* off southeastern Australia, the ages

[1] Caton, A. E. 1966. Preliminary synopsis of biological data on the Australian (spotted or King George) whiting (*Sillaginodes punctatus*) (Cuv. and Val.) 1829. CSIRO Technical Session, Department of Fisheries and Fauna Conservation Agenda Item 5, 43 p.

[2] Cockrum, K. S., and G. K. Jones. 1992. The reproductive biology and fecundity of King George whiting (*Sillaginodes punctata*) in South Australian waters, 1953–1988. South Australian Research and Development Institute Fisheries Research Paper 25, 18 p.

of fish in those studies were determined by the growth zones on scales or whole otoliths, which in neither case had been validated as being formed annually (Scott, 1954; Gilmour, 1969; Caton[1]; Jones et al.[3]). The present study demonstrates that, in the case of the populations of *S. punctata* in southwestern Australian waters, the growth zones on scales are difficult to discern and all of those on the otoliths of larger fish are only revealed after the otoliths have been sectioned. Data obtained from sectioned otoliths have thus been used to determine the age structure and growth rate of *S. punctata* on the lower west coast of Australia. Emphasis has then been placed on determining the length and age at first maturity, the location and period of spawning, and the period during which *S. punctata* is recruited into its nearshore nursery grounds. The implications of these biological data for managing this important species are then considered. Our results have been compared with those obtained for populations of *S. punctata* elsewhere in Australia. We have also compared aspects of the biology of *S. punctata* with those of the five other whiting species in the same region, all of which belong to the genus *Sillago* and, in the case of *S. schomburgkii* and *S. bassensis*, are fished both recreationally and commercially. This comparison enabled us to elucidate the extent to which age composition, growth, spawning period, and size-related shifts in habitat vary among the species comprising this abundant family.

Materials and methods

Small *S. punctata*, i.e. <300 mm, were collected from sites in nearshore marine waters (<1.5 m depth) between latitudes 32°00'S and 32°31'S on the lower west coast of Australia between June 1991 and May 1993 (see map in Hyndes et al., 1996a). Sampling was undertaken with a 21.5 m long seine net, which had a mesh size of 3 mm in the pocket. Large *S. punctata*, i.e. >300 mm, were obtained from recreational anglers, who were fishing between February 1993 and August 1996 in waters <50 m in depth between 31°55'S and 32°45'S. These anglers kindly supplied frozen carcasses, including gonads, after they had been filleted, together with a record of the date, location, and depth at which each fish had been captured.

The total length (TL) of each fish was measured to the nearest 1 mm. When a gonad could be identified as either an ovary or a testis, it was assigned to one of eight developmental stages, according to the criteria of Laevastu (1965): I = virgin; II = maturing virgin; III = developing; IV = maturing; V = mature; VI = spawning; VII = spent; and VIII = recovering or spent. However, multiple spawning by representatives of this species in each spawning season (see "Results" section) meant that it was often difficult to ascertain whether certain gonads should be recorded as stages V, VI, or VII. The data for these three stages, subsequently referred to collectively as mature gonads, were therefore pooled. It was not possible to recognize stage VIII gonads in males. Ovaries of the large female *S. punctata* collected in each month of the study were placed for 24 h in Bouin's fixative and then dehydrated in a series of ethanols. The midregion of each of these ovaries was embedded in paraffin wax, cut transversely (6 µm) and stained with Mallory's trichrome. The circumferences of 30 oocytes, where the section passed through the nucleus, were recorded to the nearest 5 µm by using the OPTIMAS (OPTIMAS Corp., 1994) computer imaging package. This enabled the diameters of these oocytes to be calculated. Because hydrated oocytes had collapsed as a result of freezing, their circumferences could not be measured. The oocyte measurements for fish in each calendar month during the three years of this study were pooled in order to provide histological data for up to 10 ovaries from each of those months. The terminology for the oocyte stages was adapted from that given in Khoo (1979).

The length at which 50% of female *S. punctata* first attained maturity (L_{50}) was calculated by fitting a logistic function to the proportion of mature fish in each 50-mm length interval in the spawning period of June to September (see "Results" section) by a nonlinear technique (Saila et al., 1988) with a nonlinear subroutine in SPSS (SPSS Inc., 1994). The logistic equation is

$$P_L = \left[1 + e^{(a+bL)}\right]^{-1}$$

where P_L = the proportion of fish with mature gonads at length interval L; and
a and b = constants.

The L_{50} was then derived from the equation

$$L_{50} = -ab^{-1}.$$

Preliminary examination of scales and sagittal otoliths collected from large *S. punctata* caught during the initial stages of the study showed that growth zones were often difficult to detect in scales, whereas at least some growth zones could be clearly discerned

[3] Jones, G. K., D. A. Hall, K. L. Hill, and A. J. Staniford. 1990. The South Australian marine scalefish fishery stock assessment; economics; management. South Australian Department of Fisheries Green Paper, January 1990, 186 p.

in whole otoliths. For this reason, sagittal otoliths were subsequently removed from each fish, cleaned, dried, stored, and used to estimate the ages of fish. In order to determine whether it was necessary to section otoliths to reveal all translucent zones, the number of translucent zones in the otoliths of 100 randomly selected *S. punctata*, in which whole otoliths displayed at least one such zone, were counted prior to and after sectioning. Of the otoliths that showed two to six translucent zones after sectioning, 19% exhibited one less zone prior to sectioning. Furthermore, in those otoliths that displayed seven or more translucent zones after sectioning, over 50% exhibited one less zone and 30% displayed between two and four fewer zones prior to sectioning. Thus, the otoliths of *S. punctata* had to be sectioned in order to discern all the translucent zones in those structures, a procedure that is also required for ageing several other fish species (e.g. Campana, 1984; Beamish and McFarlane, 1987; Casselman, 1987; Hyndes et al., 1992a). Otoliths were mounted and embedded in black epoxy resin and cut into approximately 0.8-mm transverse sections with a diamond saw. Sections were mounted on glass slides and their surface ground on sequentially finer grades of carborundum paper , with particle sizes ranging between ca. 30–10 µm. They were then coated with clear nail polish and examined microscopically under reflected light. The distance between the outer edge of the outermost translucent zone and the periphery of each otolith (marginal increment) was measured. This was expressed either as a proportion of the distance between the focus and the outer edge of the translucent zone, when only one translucent zone was present, or as a proportion of the distance between the outer edges of the two outermost translucent zones, when two or more translucent zones were present. Measurements were always made along the longest axis of each sectioned otolith and recorded to the nearest 0.05 mm. The number of translucent zones on each otolith was recorded. The birth date was designated as the midpoint of the main spawning period, based on the trends shown by gonadal and oocyte development (see "Results" section). Von Bertalanffy growth curves were fitted to the individual lengths of females and males at the estimated age at capture by a nonlinear technique (Gallucci and Quinn, 1979) with a nonlinear subroutine in SPSS (SPSS Inc., 1994). The von Bertalanffy equation is

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right],$$

where L_t = the length at age t (years);
L_∞ = the mean of the asymptote predicted by the equation;
K = the growth coefficient; and
t_0 = the hypothetical age at which fish would have zero length if growth followed that predicted by the equation.

The growth curves derived for females and males were compared by using a maximum-likelihood test (Kimura, 1980).

A fine mesh seine net, which was 5.5 m long and consisted of 1-mm mesh, was used in alternate weeks between late July and late December 1994 to collect recently settled *S. punctata* from sheltered nearshore sites in regions similar to those sampled by the 21.5-m seine net. The standard length (SL) of each of these fish on each sampling occasion was measured to the nearest 0.1 mm, except when the sample size was large, in which case measurements were made on a subsample of 100 fish.

Results

Age and growth

The mean marginal increment in sectioned otoliths with one translucent zone ranged from 0.42 to 0.54 between May and October, but then fell precipitously to 0.09 in November, before gradually increasing to 0.39 by April (Fig. 1). The marginal increments in otoliths with 2, 3, and 4–13 translucent zones also declined markedly between October and November and followed similar trends (Fig. 1). Thus, irrespective of the number of translucent zones in the otoliths, the marginal increment declined markedly and then rose progressively only once during a 12-month period, demonstrating that the translucent zones are formed annually.

In order to determine the size and age composition of *S. punctata* at different times of the year, the total lengths of fish caught in nearshore waters by seine net and in more offshore waters by anglers were pooled (Fig. 2A). Small *S. punctata* were first caught with seine nets in nearshore waters in early November, in which month their lengths ranged from 25 to 50 mm. By late December, the maximum length had increased to 68 mm (data not shown). The length range of the corresponding cohort, which comprised fish with otoliths that did not possess a translucent zone, increased to between 122 and 298 mm by August to October (Fig. 2A). Because the birth date of *S. punctata* was designated as 1 August (see below), the members of this cohort represent early 1+ fish. By November, a translucent zone had become discernible at the edge of the otoliths of these 1+ fish. The length range of this cohort ranged from 158 to

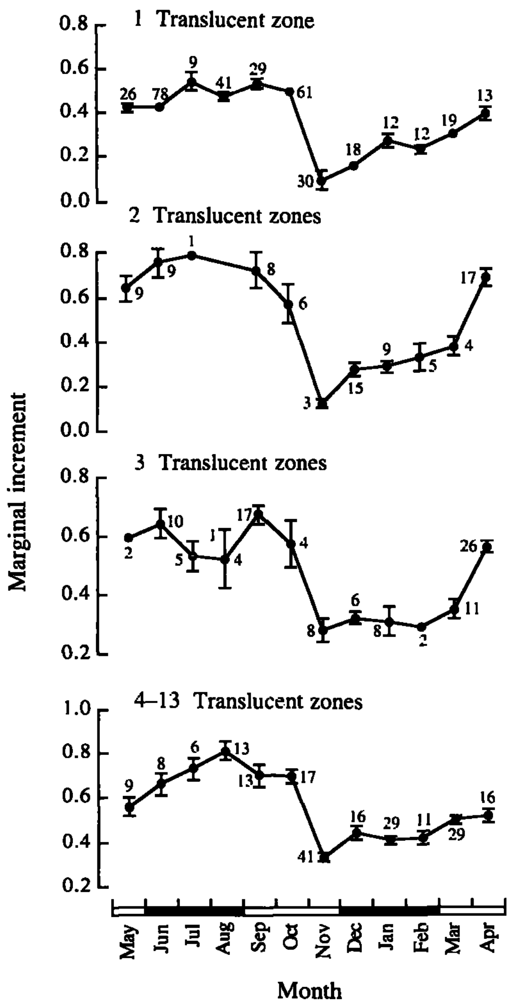

Figure 1

Mean monthly marginal increments ±1SE for sagittal otoliths of *Sillaginodes punctata*. Sample sizes are given for each month. In this Figure and Figure 5, the filled bars on the x-axis refer to winter and summer months, and the open bars to autumn and spring months.

282 mm from November to January, and from 251 to 403 mm from August to October, when this group of fish had just commenced their third year of life, and thus represents early 2+ fish (Fig. 2A). Between August and October, the lengths of 3+, 4+, and 5+ fish ranged from 340 to 425, from 403 to 480, and from 431 to 495 mm, respectively. *Sillaginodes punctata* attained maximum ages of 14+ and lengths of 596 mm in the case of females and maximum ages of 13+ and lengths of 555 mm with males.

Growth curves derived for female and male *S. punctata* (Fig. 3) differed significantly ($P<0.05$). The asymptotic length (L_∞) and growth coefficient (K) for

Table 1

Von Bertalanffy growth parameters (±95% CL) derived from length at age data for *Sillaginodes punctata* caught on the lower west coast of Australia. L_∞ is the asymptotic length, K is the growth coefficient, t_0 is the hypothetical age at which fish would have zero length, r^2 is the regression coefficient, n is the sample size.

	von Bertalanffy parameters				
	L_∞	K	t_0	r^2	n
Females	532.4 ±6.9	0.47 ±0.02	0.13 ±0.02	0.97	760
Males	500.1 ±7.7	0.53 ±0.02	0.16 ±0.02	0.96	637

females were 532 mm and 0.47, respectively, whereas for males they were 500 mm and 0.53, respectively (Table 1).

Age and length at sexual maturity

For determining the length and age at maturity of female *S. punctata*, the data for mature (stages V–VII) and recovering or spent (stage VIII) ovaries were combined (Fig. 4). During the spawning period, which was determined as occurring from June to September (see below), the proportion of female fish with mature and recovering or spent ovaries increased sharply from 4% in the 350–399 mm length class to 71% in the 400–449 mm length class, and 100% in fish >500 mm (Fig. 4A). The length at which 50% of female *S. punctata* were mature, represented by the L_{50}, was 413 mm. Maturity was first attained by females at the end of their third year of life, when ca. 15% of fish possessed mature ovaries (Fig. 4B). However, by the end of the fourth year of life, the proportion of mature females had increased markedly to 72% and in subsequent years to 100%. A similar pattern was shown by the maturity stages for male fish (data not shown).

Gonadal and oocyte development

Because the vast majority of *S. punctata* did not reach maturity until the end of their fourth year of life, the following monthly trends shown by gonadal stages were derived from fish that were ≥3.4 years old and thus these fish were expected to reach maturity in the following spawning period. Between January and May, the ovaries of all female *S. punctata* ≥3.4 years old were at either stages III or IV (Fig. 5). Mature ovaries were found in over 70% of females by June and in 90 and 100% by July and August, respectively. The proportion of mature ovaries declined markedly to 43% in September, whereas the contribution of recovering or spent ovaries (stage VIII) increased from 9 to 48% between August and September (Fig. 5). Female fish with mature ovaries were virtually absent by November, and those with stage-VIII ovaries represented only ca. 8% of the fish caught both in this month and in December. The gonadal development of males followed a similar trend to that of females (Fig. 5).

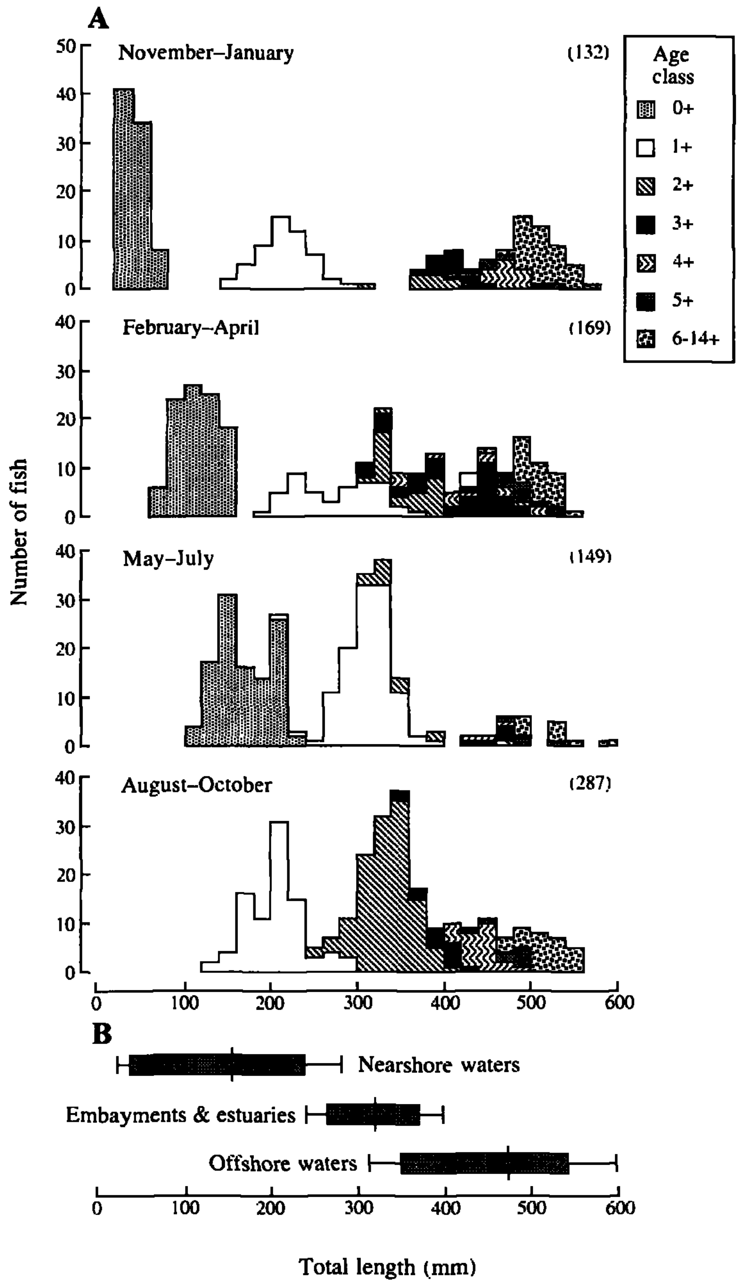

Figure 2

(**A**) Frequency histograms for total lengths of the different age classes of *Sillaginodes punctata*, from data obtained from samples collected by the 21.5-m seine net in nearshore marine waters and from anglers in deeper waters. Sample sizes are given in parentheses. (**B**) Median, 90 percentiles, and range of lengths for fish caught in shallow nearshore marine waters, deeper waters in marine embayments and estuaries, and in deeper and more offshore marine waters around reefs.

In each month, the oocyte diameters for *S. punctata* exhibited a well-defined mode between 50 and 80 µm (Fig. 6), which represents the perinuclear oocytes. Yolk vesicle and yolk granule oocytes first appeared in ovaries in April, when the diameters of these larger oocytes ranged between 255 and 430 µm. However, many other yolk vesicle and yolk granule oocytes were undergoing atresia. In the following month, the maximum oocyte diameter declined to 150 µm, reflecting the fact that no yolk vesicle or yolk granule oocytes were present. In June, the maximum diameter increased to 465 µm (Fig. 6), as a result of the development of yolk vesicle and yolk granule oocytes. These large oocytes were abundant between June and August, and many ovaries were dominated by yolk granule oocytes. The proportion of yolk vesicle and yolk granule oocytes declined in September, and the few remaining yolk vesicle and yolk granule oocytes that were present in October were at an advanced stage of atresia.

Hydrated oocytes that had collapsed during sectioning were found in large numbers in some ovaries between June and August. Because the ovaries in those months sometimes contained large numbers of postovulatory follicles, they had already discharged hydrated oocytes. Furthermore, hydrated oocytes and postovulatory follicles were occasionally found in the same ovary.

Juvenile recruitment and depth distribution

The new 0+ recruits of *S. punctata* were first caught in late September 1994. The minimum standard length of these fish remained at ca. 14 mm between 23 September and 3 November, before increasing to ca. 30 mm between mid-November and mid-December (Fig. 7). The maximum length of these new recruits increased progressively from 26 mm in late September to 64 mm by mid-December (Fig. 7).

Although the vast majority of *S. punctata* caught by anglers in embayments and estuaries at depths of 2–6 m were <370 mm in length and <4 years of age, those that were collected outside embayments and estuaries and in the vicinity of reefs at depths of 6–50 m were predominantly greater than this length and age (Fig. 8, A and B). Furthermore, *S. punctata* that contained mature (stages V–VII) or recovering or spent (stage VIII) gonads were caught predominantly in and around reefs and at the edges of seagrass beds adjacent to these areas, where water depths exceeded 6 m (Fig. 8).

Discussion

Sexual maturity and spawning period

Gonadal data indicate that, in southwestern Australia, female *S. punctata* reach maturity at the end of their fourth year of life or when they have attained a length of ca. 410 mm. This length far exceeds the 350 mm at which 50% of the members of this species reach maturity in southeastern Australian waters (see Cockrum and Jones[2]). However, the data of Cockrum and Jones[2] suggest that the length at maturity of *S. punctata* in southeastern Australia has declined since the 1950's as a result of fishing pressure, a trend that has been observed with increased fishing pressure in other species of teleosts (Wootton, 1990). Such a conclusion would be consistent with the fact that in southwestern Australia, where *S. punctata* is not at present as heavily exploited, the length at maturity (ca. 410 mm) is similar to that recorded in South Australia in the 1950's (Scott, 1954; Cockrum and Jones[2]).

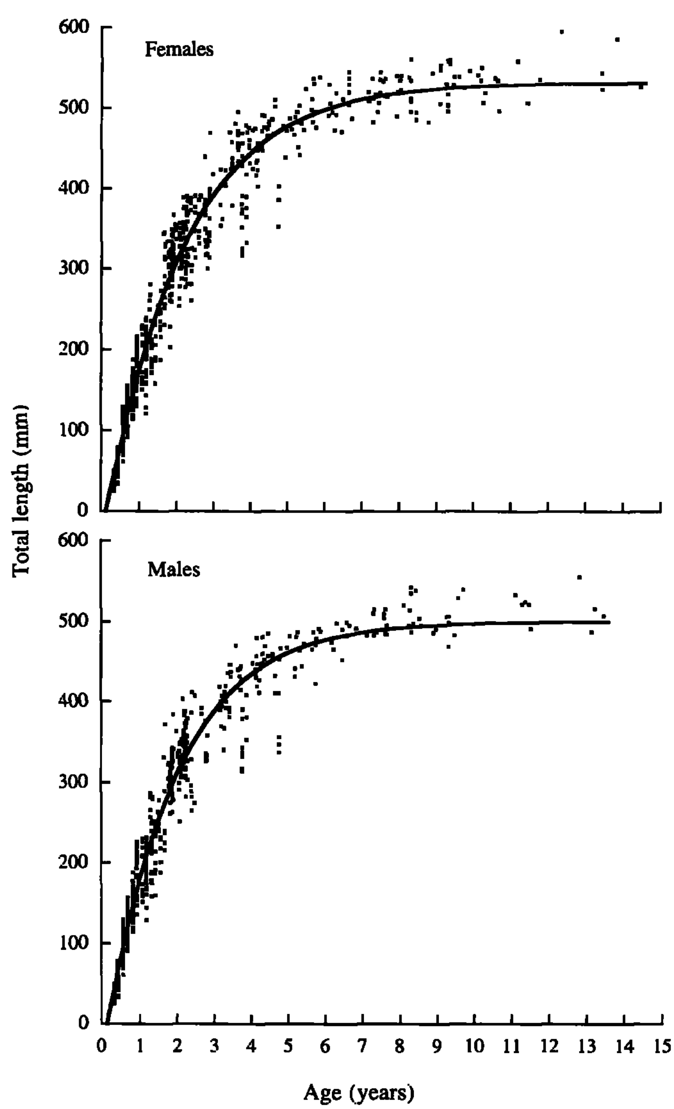

Figure 3

Von Bertalanffy growth curves fitted to total length-at-age data derived from sagittal otoliths of female and male *Sillaginodes punctata*.

Because large numbers of yolk granule and hydrated oocytes and postovulatory follicles were first found in the ovaries of large female *S. punctata* in June and were prevalent in ovaries through September, we conclude that this species spawns during this four-month period between early winter and early spring. Because the advanced oocytes present in ovaries in October and November were usually undergoing atresia, the spawning period of *S. punctata* rarely extends beyond September. The spawning of *S. punctata* during winter to early spring in southwestern Australia contrasts with the autumn and early winter spawning period found for *S. punctata* in southeastern Australia (Bruce, 1989; Jenkins and May, 1994; Fowler and Short, 1996; Cockrum and Jones[2]). Thus, although the duration of the spawning period of *S. punctata* is similar in both regions, it is initiated three months later on the lower west coast of Australia. It may thus be relevant that, in both regions, this species spawns when water temperatures are declining from their maxima and that this decline occurs more rapidly in southeastern Australia than on the lower west coast of Australia (Fig. 1 in Hyndes and Potter, 1996; Fowler[4]). The above

[4] Fowler, A. 1995. SARDI (South Australian Research and Development Institute), PO Box 120, Henley Beach, Adelaide, South Australia 5022, Australia.

spawning periods for *S. punctata* contrast with those of the majority of other temperate marine teleost species, including other whiting species, which typically breed at some period between late spring and early autumn (Morton, 1985; Vouglitois et al., 1987; Conover, 1992; Hyndes and Potter, 1996, 1997; Hyndes et al., 1996b). Because some of the estuaries of southwestern Australia often become closed from the sea by a sand bar in summer, a winter spawning period would allow the juveniles to become recruited into those estuaries (see "Nursery and spawning grounds" heading).

The presence in some ovaries of *S. punctata* of large numbers of yolk granule oocytes, together with either hydrated oocytes or postovulatory follicles, suggests that this species releases its eggs in batches. Furthermore, the presence of hydrated oocytes or postovulatory follicles, or both, in many of those ovaries which also contained advanced oocytes indicates that, although many oocytes were close to being released from those ovaries, others had recently been discharged. There is thus strong circumstantial evidence that *S. punctata* spawns on more than one occasion and possibly frequently during each breeding period. The conclusion that *S. punctata* is a multiple spawner (sensu de Vlaming, 1983) supports the conclusions of Cockrum and Jones[2] and parallels the situation recorded for several other sillaginid species (Morton, 1985; Hyndes and Potter, 1996, 1997; Hyndes et al., 1996b) and other teleosts in marine and estuarine waters in southwestern Australia (e.g. Hyndes et al., 1992b; Sarre et al., 1997).

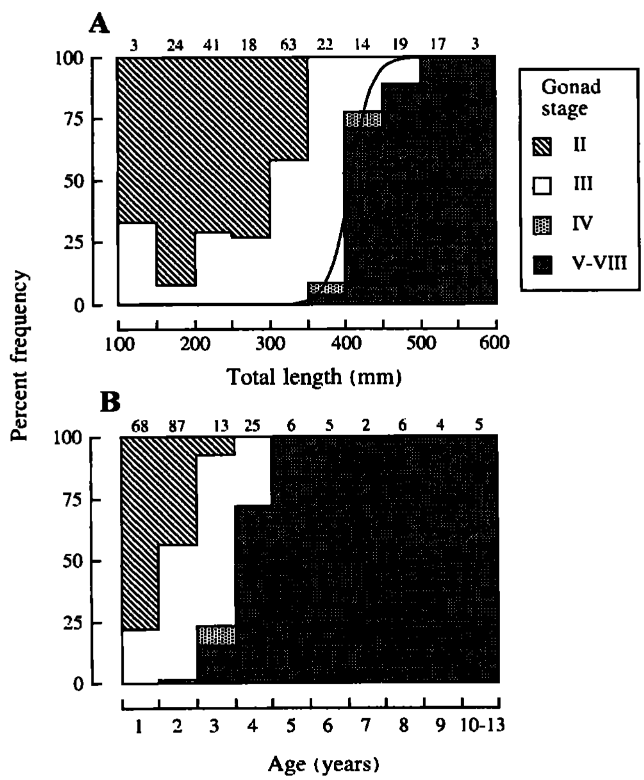

Figure 4

Percent frequency of occurrence of sequential stages in gonadal development in (**A**) each sequential 50-mm length class, and at (**B**) each age of female *Sillaginodes punctata* caught between June and September. The logistic curve, derived from the percentage of mature gonads for each length class, is also shown. Sample sizes are given above each length and age class.

Age and growth

The asymptotic lengths (L_∞) and growth coefficients (K) of female and male *S. punctata* in southwestern Australia, i.e. 532 and 0.47, and 500 mm and 0.53, respectively, lie within the range calculated for this species in southeastern Australia. However, these two parameters varied markedly in different localities within that latter region, i.e. 444 to 715 mm and 0.15 to 0.45 (Scott, 1954; Gilmour, 1969; Jones, 1980; Caton[1]; Jones et al.[3]). Such variation reflects either differences in the patterns of growth of this species in different locations or errors associated with deriving the age of fish from growth zones in scales or whole otoliths.

Sillaginodes punctata reaches a far greater size and age than the five other sillaginid species in southwestern Australia, all of which belong to the genus *Sillago* (Table 2). Furthermore, *S. punctata* does not attain maturity until it is four years old, which is far older than the age at which most of those *Sillago* species first spawn (Table 2). Because size and age at maturity are usually related to the length and age attained by teleosts (e.g. Beverton, 1992; Hyndes and Potter, 1997), this difference presumably reflects the greater size and age attained by *S. punctata*.

Nursery and spawning grounds

0+ *S. punctata* were first caught in the sheltered nearshore waters of marine embayments of southwestern Australia in late September, when their lengths ranged from 14 to 24 mm. Because this length range approximates that at which this species settles to a benthic habit (Jenkins and May, 1994; Bruce, 1995), these early juvenile fish would only recently have moved into those nearshore waters. The fact

Table 2

Asymptotic total length (mm), growth coefficient, maximum age (years), length at maturity (mm), age at maturity (years), and location of the nursery and spawning areas for *Sillaginodes punctata* and the *Sillago* species found in southwestern Australian waters. F = females; M = males.

Species	Asymptotic length (L_∞)		Growth coefficient (K)		Maximum age (T_{max})		Length at maturity (L_m)		Age at maturity (T_m)		Nursery grounds	Spawning grounds
	F	M	F	M	F	M	F	M	F	M		
Sillaginodes punctata	532	500	0.47	0.53	14	13	400	400	4	4	Sheltered nearshore	Reefs
Sillago bassensis	329	307	0.26	0.29	7	9	200	200	3	3	Exposed nearshore	Deep offshore
Sillago burrus	188	179	2.37	2.44	4	4	130	120	1	1	Sheltered nearshore	Shallow offshore
Sillago robusta	169	172	1.03	0.98	6	5	150	140	2	2	Offshore	Deep offshore
Sillago schomburgkii	333	325	0.52	0.53	7	7	200	180	2	2	Sheltered nearshore	Nearshore
Sillago vittata	331	312	0.43	0.45	7	6	140	130	1	1	Sheltered nearshore	Shallow offshore

that this size range of *S. punctata* was consistently observed in its specimens from nearshore waters between late September and early November (midspring), indicates that this species settles in its nearshore nursery grounds predominantly during this period. Thus, the first recruits of *S. punctata* enter those nearshore waters approximately three months after spawning is initiated, a time that corresponds to the time that the larvae of this species take to recruit into their nursery areas in South Australia (Bruce, 1989; Bruce and Short, 1992; Fowler and Short, 1996). Recruitment of juvenile *S. punctata* into the shallows commences far earlier in South Australian than in southwestern Australian waters, i.e. June vs. September, reflecting an earlier start to the spawning period, i.e. March vs. June (cf. Bruce, 1989; Fowler and Short, 1996). However, because the juveniles that are recruited into nursery habitats much farther east in Victoria are derived from a spawning that occurs in South Australia (Jenkins and Black, 1994; Jenkins and May, 1994), their larvae have to travel a far longer distance towards their nursery grounds than those recruited into nearshore waters of South Australia; thus recruitment commences far later in Victoria, i.e. September vs. June (Bruce, 1989; Jenkins and May, 1994; Fowler and Short, 1996).

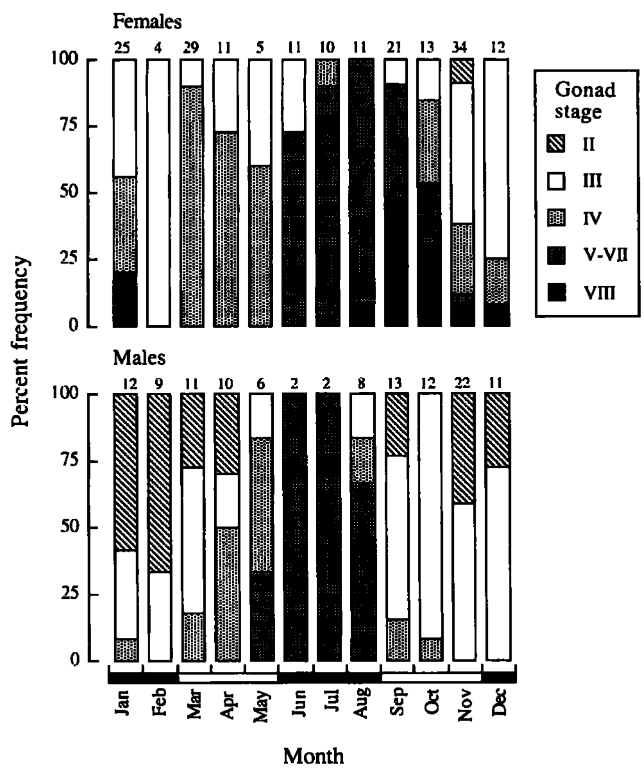

Figure 5

Monthly percent frequencies of occurrence of sequential gonadal development stages in female and male *Sillaginodes punctata* ≥3.4 years old. Numbers indicate sample sizes.

After settlement, large numbers of *S. punctata* remain in the sheltered nearshore marine waters of the lower west coast for about 1.5 years (Hyndes et al., 1996a). The fact that the densities of juveniles were far higher in these waters than in nearby exposed waters and even the shallows of estuaries (Hyndes et al., 1996a) indicates that the juveniles of this species prefer sheltered nearshore marine habitats. This conclusion is supported by the fact that juveniles of *S. punctata* are absent in nearshore waters along the southern coastline of southwestern Australia (Lenanton, 1982; Ayvazian and Hyndes, 1995), where the shoreline is more exposed to rough sea conditions (Hegge et al., 1996). The relative paucity of sheltered nearshore marine habitats on this coastline would account for the relatively high densities of juvenile *S. punctata* that are found in the relatively protected waters of estuaries in this region (Potter et al., 1993; Potter and Hyndes, 1994).

Estuaries along the southern coast of southwestern Australia, where the adjacent marine waters are exposed to wave and swell activity, may thus provide particularly important nursery habitats for *S. punctata*. Many estuaries in this region, however, become closed off from the sea during the summer and autumn, when, as a result of low freshwater discharge, a sand bar forms at their mouths (Lenanton and Hodgkin, 1985). It is thus relevant that *S. punctata* spawns during winter, because this would enable juveniles to enter those estuaries before their mouths become closed. This event parallels the situation with the mugilids *Mugil cephalus* and

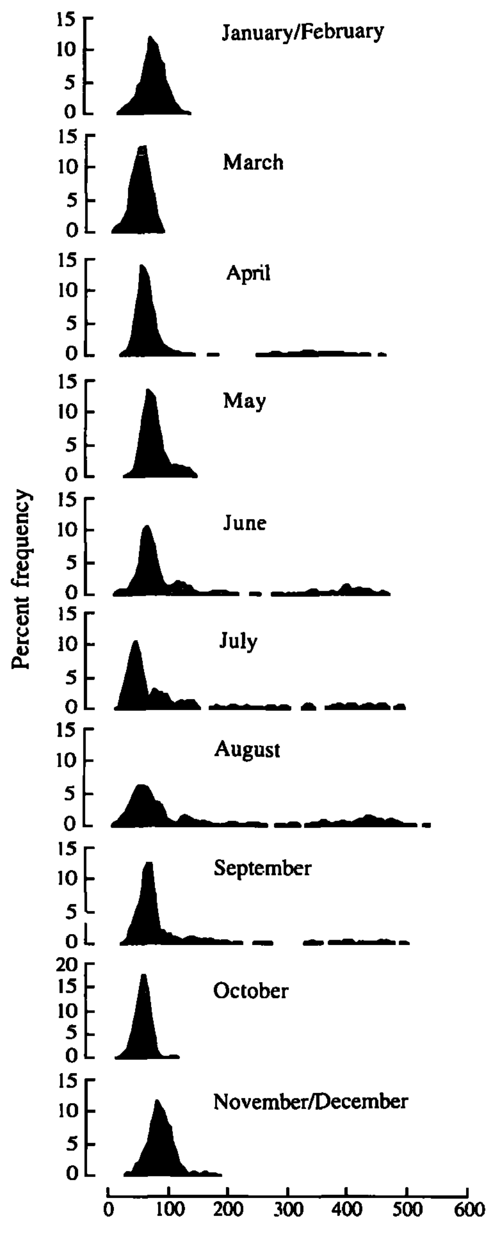

Figure 6

Monthly percent frequencies for oocyte diameters in ovaries of *Sillaginodes punctata*. Sample size in each month was 7–10 fish.

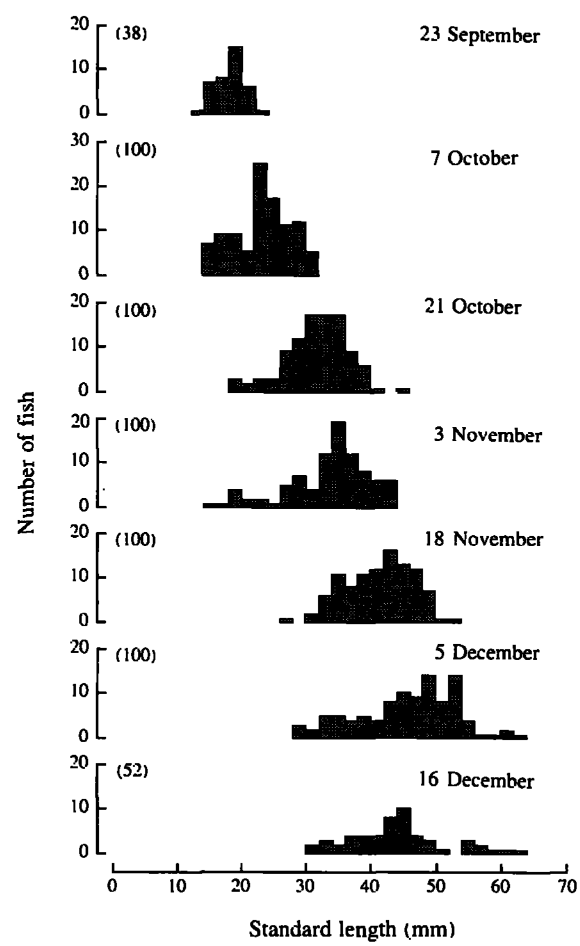

Figure 7

Frequency histograms for standard lengths of *Sillaginodes punctata* caught at two weekly intervals by the 5.5-m seine net in sheltered nearshore marine waters between September and December 1994. The numbers in parentheses represent the number of fish measured.

Aldrichetta forsteri, which also both spawn in winter in southwestern Australia and whose juveniles soon after enter estuaries in large numbers (Thomson, 1957b; Chubb et al., 1981).

Sillaginodes punctata typically remains in sheltered nearshore marine and estuarine waters until it reaches ca. 250 mm in length and ca. 1.5 years of age (Robertson, 1977; Potter et al., 1983; Loneragan et al., 1989; Potter et al., 1993; Potter and Hyndes, 1994; Hyndes et al., 1996a). Thus, unlike smaller species of whiting, such as *Sillago burrus* and *Sillago vittata*, which typically move offshore at lengths of ca. 100 mm and at ages of three to nine months (Hyndes et al., 1996a, 1996b), *S. punctata* remains in its nursery habitats for a far longer period. Because *S. burrus* and *S. vittata* reach maturity at the end of their first year of life, whereas most *S. punctata* first attain maturity at the end of their fourth year of life, this last species takes advantage of the productive waters of marine embayments or estuaries for a longer period before migrating out into spawning grounds in deeper marine waters.

Because the nursery areas of *S. punctata* are located initially in nearshore waters and subsequently in the deeper waters of marine embayments and estuaries, whereas adults occupy areas in and around reefs where water depths are generally greater, this species migrates offshore from shallow nursery grounds as it approaches the size and age at which it will become mature. A movement offshore as body size increases parallels that recorded for populations of *S. punctata* in southeastern Australia and for other whiting species (Scott, 1954; Gilmour, 1969; Robertson, 1977; Weng, 1986; Burchmore et al., 1988; Hyndes et al., 1996a; Caton[1]). Although anglers often caught *S. punctata* in deeper waters near reefs or at the edges of adjacent seagrass beds, they rarely caught them during extensive trawling over the expansive open, sandy areas of the same region where large numbers of other whiting species were caught (Hyndes et al., 1996a). The presence of mature and recovering or spent gonads in the larger members of *S. punctata* caught in areas around reefs also suggests that, unlike the three whiting species *Sillago burrus*, *S. vittata*, and *S. bassensis*, which migrate out into the more open and sandy areas of the inner shelf to spawn (Table 2; Hyndes et al., 1996b; Hyndes and Potter, 1996), *S. punctata* spawns in areas in and around reefs or at the edges of adjacent seagrass beds. Furthermore, whereas *S. burrus* and *S. vittata* move into spawning grounds ranging from 5–15 m in depth, and *S. bassensis* migrates into more offshore waters where the depth is 20–35 m deep (Hyndes et al., 1996a, 1996b; Hyndes and Potter, 1996), *S. punctata* spawns at depths that range from six to at least 50 m.

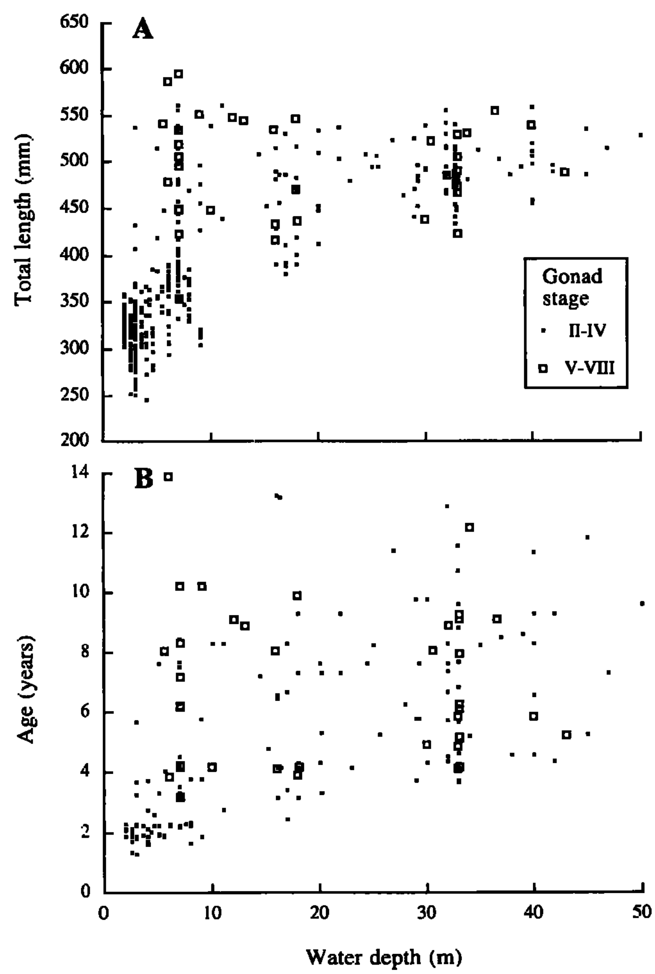

Figure 8

(A) Total lengths and (B) ages at capture, of female and male *Sillaginodes punctata* with immature (stages II–IV) and mature or recovering or spent (or both) (stages V–VIII) gonads collected at different depths by recreational fishers in the inner-shelf waters of the lower west coast of Australia.

Implications for management

Because *S. punctata* exhibits size-related offshore movements, that involve firstly a movement from nearshore nursery areas to deeper waters in marine embayments and estuaries and subsequently a movement into areas around reefs farther offshore (Fig. 2B), this species essentially occupies three different habitats during the course of its life cycle. Any management plans for *S. puncata* must therefore take into account the need both to protect these habitats and to ensure that fishing pressure in those habitats where fishing occurs does not have a deleterious effect on the stock of this species.

The postlarvae of *S. punctata* settle predominantly in very sheltered nearshore waters of marine embayments and estuaries (Jenkins and May, 1994; Fowler and Short, 1996; Hyndes et al., 1996a; Hyndes, unpubl. data). However, *S. punctata* moves out into slightly deeper waters (2–10 m) in marine embayments and estuaries at ca. 1.5 years in age and at a total length of 250 mm (Fig. 2B). Because this latter length corresponds to the legal minimum length for capture (LML) of *S. punctata* on the lower west coast and approaches the LML of 280 mm on the south coast, this species does not become commercially and recreationally exploited until it has left its very shallow nursery areas and has entered deeper waters. This species remains in these slightly deeper waters until it reaches 350–400 mm (Fig. 2B) and is thus available for capture in marine embayments and estuaries when it is predominantly between 1.5 and 2.5 years in age. Because this species is most heavily exploited when it is in the deeper waters of marine embayments and estuaries, it is fished mainly during this relatively restricted period of its life cycle. From a management point of view, it is also relevant that the fishery in marine embayments and estuaries is based on fish that have not yet reached 410 mm, the length at which they typically first become mature. Subsequently, those *S. punctata* that have run the "gauntlet" of numerous fishermen in marine embayments and estuaries move farther out into areas in and around reefs in deeper waters where they attain maturity and where the reduced number of fishermen targeting this species makes it less susceptible to capture. Furthermore, the catches of *S. punctata* in the more offshore waters are further reduced in winter, when sea conditions are far less favorable for fishing and when, according to fishermen, *S. punctata* are less likely to take bait. Thus, because *S. punctata* spawns during winter, fishing pressure on this species is relatively low during the spawning period.

Because catch and effort statistics for the commercial fishery in southwestern Australia do not suggest that the catch rate for *S. punctata* is declining, this species would not appear currently to be overexploited in this region. However, the number of sheltered nearshore areas that act as nursery areas for *S. punctata* are limited and are often located in the type of region where marinas and other developments are likely to be proposed. Furthermore, recreational fishing effort is rising markedly, and the increasing use of larger vessels and more sophisticated equipment, such as global positioning systems (GPS), means that, particularly in deeper waters, fish are now beginning to be exploited to a greater extent. The resultant advances in fishing efficiency also mean that more sophisticated measures of effort are required to obtain reliable and comparable catch-per-unit-of-effort data for *S. punctata* from the recreational sector, which is ultimately expected to become the main exploiter of this resource.

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