Life history of South African snoek, *Thyrsites atun* (Pisces: Gempylidae): a pelagic predator of the Benguela ecosystem

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Abstract—Snoek (*Thyrsites atun*) is a valuable commercial species and an important predator of small pelagic fishes in the Benguela ecosystem. The South African population attains 50% sexual maturity at a fork length of ca.73.0 cm (3 years). Spawning occurs offshore during winter–spring, along the shelf break (150–400 m) of the western Agulhas Bank and the South African west coast. Prevailing currents transport eggs and larvae to a primary nursery ground north of Cape Columbine and to a secondary nursery area to the east of Danger Point; both shallower than 150 m. Juveniles remain on the nursery grounds until maturity, growing to between 33 and 44 cm in the first year (3.25 cm/month). Onshore–offshore distribution (between 5- and 150-m isobaths) of juveniles is determined largely by prey availability and includes a seasonal inshore migration in autumn in response to clupeoid recruitment. Adults are found throughout the distribution range of the species, and although they move offshore to spawn—there is some southward dispersion as the spawning season progresses—longshore movement is apparently random and without a seasonal basis. Relative condition of both sexes declined dramatically with the onset of spawning. Mesenteric fat loss was, however, higher in females, despite a greater rate of prey consumption. Spatial differences in sex ratios and indices of prey consumption suggest that females on the west coast move inshore to feed between spawning events, but that those found farther south along the western Agulhas Bank remain on the spawning ground throughout the spawning season. This regional difference in female behavior is attributed to higher offshore abundance of clupeid prey on the western Agulhas Bank, as determined from both diet and rates of prey consumption.

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Snoek (*Thyrsites atun*) is a medium-size, pelagic predator (max. size 9 kg; Nepgen, 1979a) inhabiting the coastal waters of the temperate Southern Hemisphere; it is found from the surface to the seabed, to depths of 550 m (Kailola et al., 1993). Occurring off southern Africa, Australia, New Zealand, the east and west coasts of southern South America, Tristan da Cunha, and the islands of Amsterdam and St. Paul (Nakamura and Parin, 1993), snoek have successfully colonized environments as diverse as oceanic island, west coast upwelling, and subtropical convergence ecosystems. It is an important food fish throughout much of its distribution, supporting moderate fisheries (<1000 metric tons [t]/yr) off southern Australia, Chile, and Tristan de Chuna, and substantial fisheries (>10,000 t/yr) off New Zealand and Southern Africa (Andrew et al., 1995; FAO, 1997).

Southern African snoek have been recorded from northern Angola to Algoa Bay on the South African east coast but are mostly found between the Cunene River and Cape Agulhas, i.e. in the Benguela ecosystem. *Thyrsites atun* has been an important commercial species in this system since the early 1800s, caught initially with hand lines but also trawled after 1960 (Crawford, 1995). Total catch peaked at about 81,000 t in 1978 but dropped substantially with the exclusion of foreign trawlers from the Namibian fishing grounds in 1991 (FAO, 1978, 1981, 1990, 1997). Current annual-catch ranges between 14,437 and 22,920 t (1991–95), and 93% of it is made in South African waters (FAO, 1995). *Thyrsites atun* is far the most important species caught by the South African commercial line fishery[1] (comprising 39% of the 1986–97 catch [National Marine Linefish System[2]]); it is also targeted by recreational anglers, for which catch statistics are not available. Around 40% of the South African catch (1990–96) is made by commercial handline fishermen and 60% by trawlers (Demersal Commercial Data Base[3]). However, the commercial line-catch may be under-reported by as much as 75% (Sauer et al., 1997); therefore the total catch could be substantially larger. In addition to its fishery significance, *T. atun* is a major predator of anchovy (*Engraulis japonicus*) and sardine (*Sardinops sagax*) in the southern Benguela ecosystem (Wickens et al., 1992) and has been implicated in top down effects on both prey and consequently zooplankton populations (Verheye et al., 1998).

Life-history information is fundamental to identifying and assessing fish stocks, as well as to formulating management strategies for their sustainable use. Whereas snoek stocks off Australia (Blackburn and Gartner, 1954; Blackburn, 1957; Grant et al., 1978) and New Zealand (Mehl, 1971;

[1] The South African commercial linefishery consists of about 2500 vessels (5.5–15 m long) that operate on the continental shelf using handline or rod-and-reel.

[2] National Marine Linefish System. 2000. Unpubl. data. Linefish Section, Marine and Coastal Management, Private Bag X2 Roggebaai 8012, Cape Town, South Africa.

[3] Demersal Commercial Data Base. 2000. Unpubl. data. Demersal Section, Marine and Coastal Management, Private Bag X2 Roggebaai 8012, Cape Town, South Africa.

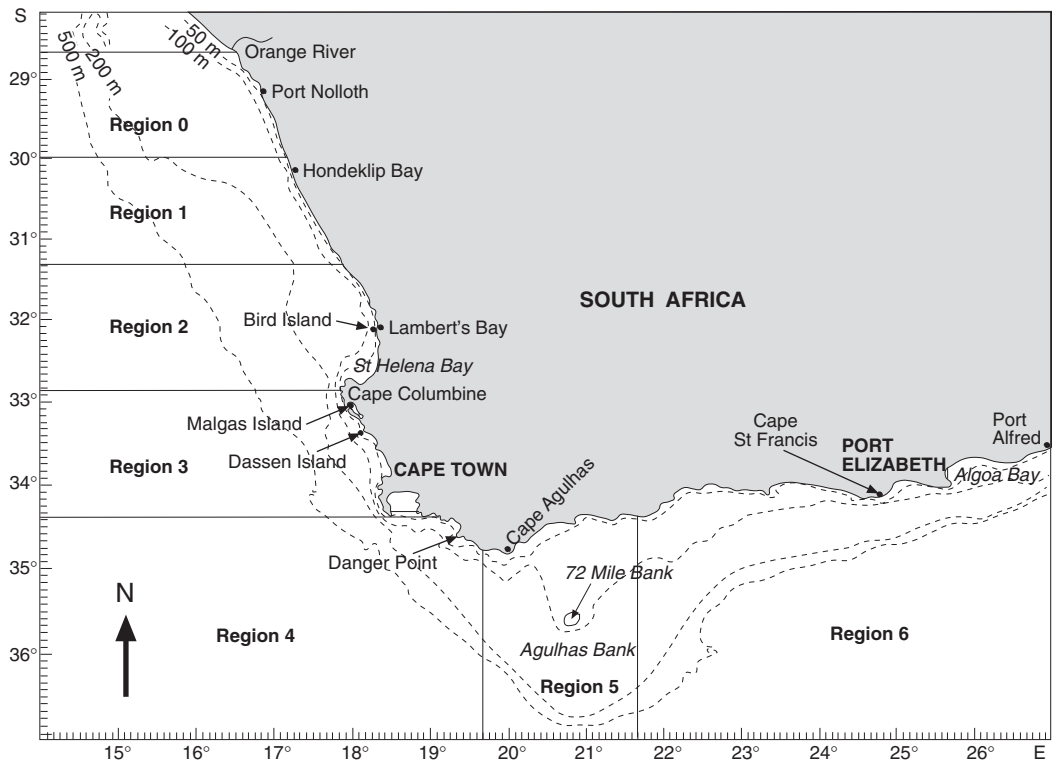

Figure 1

Map of the seven regions in which snoek (*Thyrsites atun*) were sampled, and the localities mentioned in the text. Snoek caught by hook and line were, with the exception of the 72-mile bank (region 5), taken within 15 km of the coastline, whereas those that were trawled were caught farther from the shore at water depths between 150 and 600 m.

Hurst, 1988; Hurst and Bagley, 1987; 1989) have been extensively studied, knowledge of the life history of the Benguela snoek is surprisingly fragmented, in spite of its socioeconomic and ecological importance and long history of exploitation. An extensive seasonal migration between the northern and southern regions of the Benguela system has been postulated (Davies, 1954; Crawford and De Villiers, 1985; Crawford et al., 1987); however, this migration was based largely on anecdotal reports of line catches and remains to be confirmed. Preliminary observations of gonad maturity (Davies, 1954; Nepgen, 1979a) and trends in the abundance of eggs and larvae (Olivar and Fortuño, 1991; Olivar and Shelton, 1993) suggest that spawning occurs in winter and spring, but the spawning season has not been accurately described. Three previous studies on the diet of snoek in South African waters (Nepgen, 1979b, 1982; Dudley, 1987) excluded juveniles (<75 cm fork length) because nursery grounds were not sampled, and inadequate sample sizes precluded meaningful comparisons of snoek offshore and closer to the coast, and spatial comparisons of offshore diet.

The objective of this study was to provide information on the life history of South African *T. atun*, including season and localities of spawning, condition, nursery areas, juvenile growth, size-at-maturity, diet, and patterns of juvenile and adult distribution.

Materials and methods

The South African coastline between the Orange River and Cape St Francis was divided into seven sampling regions (Fig. 1). Biological (September 1994–January 1998) and length-frequency (January 1985–December 1997) data were collected in each region from fish caught by 1) the line fishery, 2) the demersal trawl fishery, and 3) research trawl surveys of pelagic and demersal fish conducted by Marine and Coastal Management. The trawl fishery operates farther offshore than the line fishery; consequently all fish sampled deeper than 150 m were trawl caught, whereas the bulk of those from shallower depths were caught by hook and line (except for a small number caught by trawl during research cruises).

Demersal biomass surveys (DBS), based on the swept-area method, are designed to provide annual indices of biomass for the resources exploited by the South African hake-directed trawl fishery, and methods have been fully described by Badenhorst and Smale (1991). DBSs are subdivided into two areas: the Namibian border to Cape Agulhas (west coast), and Cape Agulhas to Port Alfred (south coast). In each survey, area was divided into four depth zones (0–50 m, 51–100 m, 101–200 m, and 200–500 m) which, in turn, were subdivided into blocks of 5 × 5 nautical miles. The blocks trawled each survey were

determined semirandomly according to the ratio of blocks per stratum. Bobbins were not used, so that trawling was limited to nonreef substrata. A 180-foot German trawl was used with 25-mm mesh (bar) liner attached to the bag. Trawl duration was limited to 30 minutes; results of shorter trawls (caused by technical reasons or to hitting reef) were standardized to that time. Winter and summer cruises were undertaken on the west coast between July 1985 and January 1991; and autumn and winter–spring cruises on the south coast between September 1987 and April 1996.

Pelagic biomass surveys (PBS) are hydroacoustic surveys designed to estimate annual spawner biomass and recruitment strength of small, pelagic clupeoids—*E. japonicus*, *S. sagax,* and round herring, *Etrumeus whiteheadi* (see Hampton, 1992, for details). Acoustic targets are identified by directed trawling with an Engels 308 midwater trawl fitted with a codend liner of 8-mm mesh. Small *T. atun* (<30 cm) shoal with the pelagic species while larger individuals feed on them. As a result snoek are regularly caught by trawl on PBSs, albeit in small numbers (<30 per trawl). These surveys provide qualitative data on the distribution of juvenile snoek. A total of 80 PBSs, including more than 1500 midwater trawls, were completed between 1985 and 1997. Although the survey area varied considerably, with the extremes being Lüderitz (26°39′S; 15°09′E) in southern Namibia and Cape St Lucia (28°31′S; 32°25′E) in northern KwaZulu-Natal, regions 0–5 of the present study were consistently covered.

Migration of *T. atun* was studied by using spatial and temporal variation in magnitude and size composition of catches. Owners of commercial line boats and trawlers are required to submit daily catch returns to Marine and Coastal Management (MCM). The monthly catches of snoek reported by the trawl and line fisheries in each of the seven regions (1986–97) were expressed as percentages of the respective annual totals. Mean monthly handline catch per unit of effort (kg/boat/day) and trawl CPUE (kg/hour) by 50-m depth zones were calculated for each region. Catch rates recorded during fishery-independent DBSs were mapped separately for summer and winter cruises and presented as mean numbers of snoek per 30-min trawl, per grid block.

Fish sampled for biological purposes were measured to the nearest 1 mm (fork length), weighed, to the nearest gram (fish <500 g), or the nearest 10 g (fish >500 g), cut open, and sex was determined. Gonads were removed, assigned a macroscopic index of maturity (see Table 1), and weighed to the nearest 0.1 g. Random samples (n=5–30) of each macroscopic ovarian stage were fixed in Bouins solution for 48 hours and then stored in 70% ethanol for microscopic verification. They were routinely embedded in paraffin wax, sectioned to 3–7 µm, and stained with haemotoxylin and eosin. Stomach contents were analyzed fresh, and prey items were identified to the lowest possible taxon and weighed (wet) to the nearest 0.1 g. Bait was recognized easily and discarded.

The size at 50% maturity (L_{50}) for males and females was estimated by PROBIT analysis (SPSS, 1992) of the fractions of mature fish (gonad stage 3+) per 5-cm length class (midpoint), sampled during the breeding season. Upper and lower 95% confidence limits were calculated by the software package by using maximum-likelihood estimation.

Seasonal patterns of reproduction were established by calculating gonadosomatic indices (GSIs) and the monthly percent frequency of each maturity stage, for fish >L_{50}:

$$GSI = gonad\ weight \Big/ \left(\begin{bmatrix} fish\ weight - \\ gonad\ weight + \\ stomach\ content\ weight \end{bmatrix} \right) \times 100.$$

The extent of the spawning area was determined by computing the percent frequency of each maturity stage for females (>L_{50}) that were sampled in each region during peak spawning (June–October). Snoek spawn on the trawl grounds (see below); thus spawning grounds were further delineated by mapping commercial trawl CPUE (standardized by using general linear modelling to account for vessel size) during June–October (1986–97) with a 20×20 mile grid system. Commercial trawl CPUE was also used to establish the depth distribution of snoek on the trawl grounds, and hence the depth of the spawning area. Sex ratios were tested statistically for significant deviations from equality with chi-square tests.

Nursery areas were delineated by comparing the length-frequency distributions of snoek caught in each region 1) during pelagic and demersal biomass surveys, 2) by the line fishery, and iii) by Cape gannets, *Morus capensis*. Because trawling activities during PBSs were aimed at small pelagic clupeoids, it was not possible to use CPUE data from these cruises to analyze spatial patterns in juvenile snoek abundance. However, gannets from Lambert's Bay and Malgas Island (Fig. 1) have feeding distributions that, although large, are separated at Cape Columbine and do not overlap to any large extent (Berruti, 1987). Previous studies (Crawford et al., 1992; Berruti et al., 1993; Crawford, 1998) have demonstrated that gannet diet adequately reflects temporal and spatial patterns in prey abundance. Relative abundance of early-juvenile snoek north and south of Cape Columbine was therefore estimated by comparing rates of snoek consumption by the two colonies. Stomach contents of gannets at the two colonies have been sampled on a monthly basis since 1978 (see Berruti et al., 1993, for methods). Lengths of snoek prey were obtained from undigested specimens, and snoek consumption by the two colonies was compared annually (1978–97) using the mean mass per stomach containing food and percentage frequency of occurrence (i.e. percentage of stomachs with food that contained snoek).

Dietary importance of snoek prey was assessed by percentage frequency of occurrence (%F), which provides an indication of how often a particular item is selected within a population (Hynes, 1950), and by percentage by mass (%M) (Windell and Bowen, 1978), a measure of the energy contribution of that item (Macdonald and Green, 1983). An index of relative importance (*IRI*) was calculated for each prey category i as the product of $\%M_i$ and $\%F_i$. To facilitate comparisons of prey importance between analyses (e.g. separated spatially, temporally or according to predator size), this was expressed as a percentage (Cortés, 1997):

Table 1

Description of gonad maturity stages of snoek (*Tyrsites atun*) in South African waters. Microscopic descriptions are given only for females.

Stage	Macroscopic appearance	Microscopic appearance
1 Immature and resting	Ovaries appear as clear, pinkish, or translucent orange tubes. Eggs are not visible to the naked eye. Testes thread-like and clear, to ribbon-like and pinkish white in color.	Some ovaries in this stage consist entirely of primary growth oocytes and others contain oocytes to the early cortical alveoli stage. α atresia of unyolked and β atresia of yolked oocytes are also observed.
2 Active	Eggs discernible to the naked eye as yellow granules that do not occupy all available space in ovary. There is very little increase in the diameter of the ovary. Testes are wider, triangular in cross-section, and beige or cream in color. Sperm is present if the gonad is cut and gently squeezed.	Primary growth to early yolked oocytes evident. Those at the end of the spawning season show a high degree of α atresia.
3 Ripe	Ovaries completely opaque and orange to yellow in color. They are larger in diameter and eggs occupy all available space. Testes still larger in cross-section and softer in texture. They become creamier in color due to considerable quantities of sperm.	Primary growth to late yolk-stage oocytes present. Atresia and postovulatory follicles evident in some.
4 Ripe or running	Ovaries considerably larger in diameter, amber in color with a substantial proportion of hydrated eggs. Sperm is freely extruded when pressure is applied to the abdomen of the whole fish.	All stages from primary growth to hydrated oocytes present.
5 Spent	Ovaries are reduced in size, similar in appearance to stage-1 ovaries, and have a few yolked oocytes remaining. These yolked oocytes are generally aspherical and appear to be undergoing resorption. Testes are shrivelled in appearance and mottled beige and cream in color. A little viscous semen may still ooze from the genital pore when pressure is applied to the abdomen.	Primary growth to advanced yolk-stage oocytes present, but a much lower proportion of yolked oocytes than in previous stages; major atresia of yolked oocytes also present.

$$\%IRI_i = 100IRI_i / \sum_{i=l}^{n} IRI_i,$$

where n = the total number of food categories considered at a given taxonomic level.

Numerical percentage contribution (Pillay, 1952) was excluded because *T. atun* has a diverse diet and this method would bias the results towards small crustaceans, e.g. euphausiids and amphipods, which are not individually selected. Inshore samples for dietary analysis were collected from the west coast (regions 1–3) while offshore samples were collected from both the west coast (regions 1–3) and western Agulhas Bank (regions 4 and 5).

Proportion of stomachs containing food and the mean mass of stomach contents (including fish with empty stomachs) were used as indices of the rate of prey consumption for adult (≥75 cm) snoek. Sexual and spatial differences were tested for statistical significance by using chi-square tests (2×2 contingency tables) for frequency data (i.e. numbers with and without food), and a two-way ANOVA with single observations for mean prey mass data.

Monthly relative condition (Kn) was calculated for adult snoek (≥75 cm) as follows:

$$Kn_j = \frac{\sum_{i}^{n} \frac{w_i}{aFL_i^b}}{n_j},$$

where W_I = the gonad and stomach content free weight (g) of the i^{th} individual in the j^{th} month;
FL_i = the fork length (mm) of the i^{th} individual;
a (0.000018) and b (2.80) are constants from the length-weight (gonad and stomach content free) relationship derived from data collected during the present study (all months combined); and
n_j = the number of fish sampled in the j^{th} month.

Snoek accumulate fat as three longitudinal mesenteric deposits along the outer walls of the stomach. Monthly

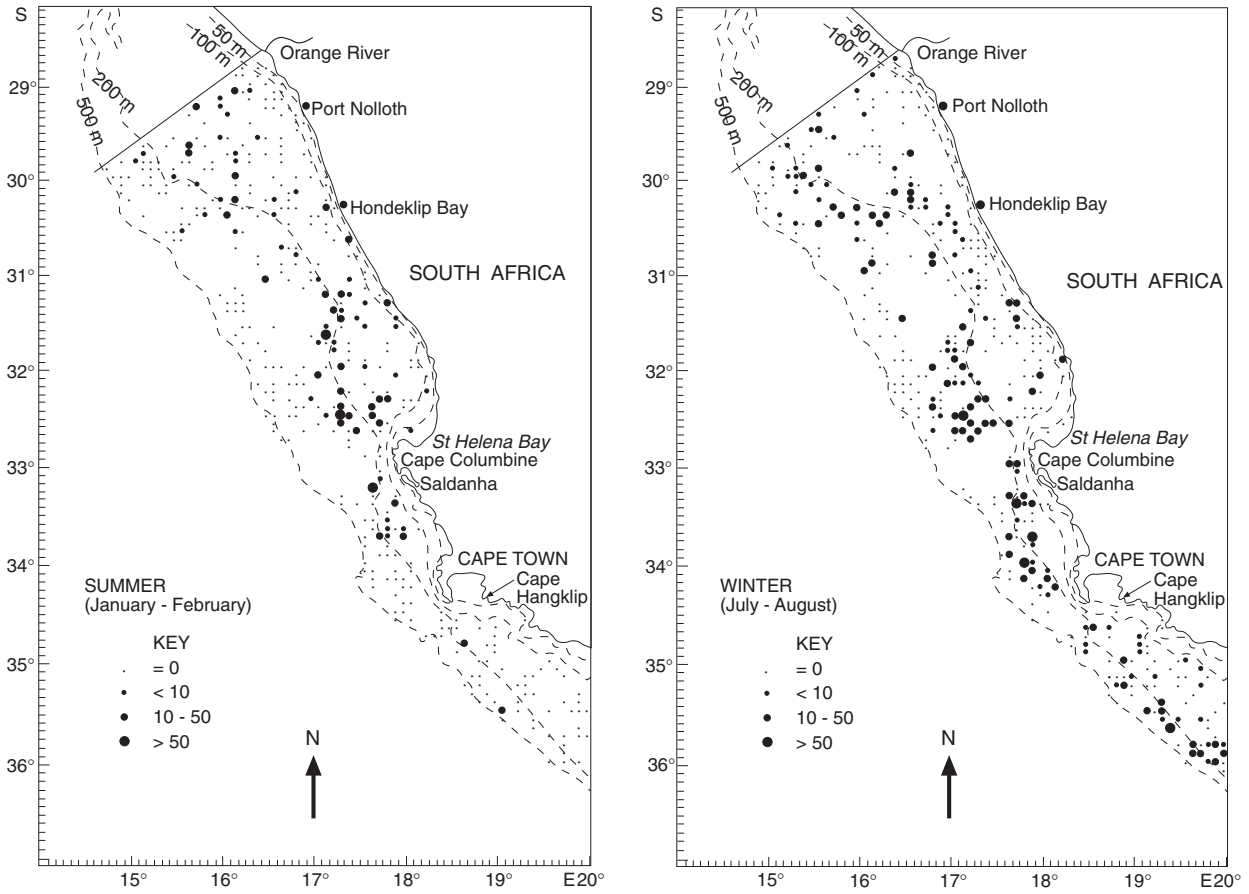

Figure 2A

Mean number of *Thyrsites atun* per trawl per grid block (5 × 5 nmi) by season for (**A**) the west coast (July 1985–Jan 1991; n=18 surveys and 1624 trawls) and (**B**) the south coast (September 1987–April 1996; n=18 surveys and 1554 trawls) demersal biomass surveys off South Africa.

proportions of stomachs with no fat were calculated separately for adult (≥75 cm) males and females.

Results

Migration

Spatial analysis of CPUE from fishery-independent DBSs indicated that *T. atun* are distributed farther offshore and farther southeast in winter and spring than in summer and autumn (Fig. 2). Fishery-dependent data support this pattern; commercial catches from the trawl grounds (i.e. >150 m) were highest from June to October, and those in the southern regions (3–6) lagged behind catches in the north (regions 0–2) by approximately one month (Fig. 3). Analysis of trawl CPUE by depth, area, and season (Fig. 4) further confirmed offshore movement during the spawning period (June–October) and furthermore revealed that *T. atun* were most abundant between bottom depths of 150 m and 350 m while on the trawl grounds. Snoek found on the trawl grounds were generally >65 cm FL (Fig. 5A).

Line-based catch and CPUE in regions 0–2 was distinctly seasonal; most of the catch was made from April to June (Fig. 3) and a slight southwards progression in peak catch and CPUE occurred within this period (Fig. 3). Line-caught snoek from regions 1 and 2 were substantially smaller (50–75 cm) and younger (1–3 years; author, unpubl. data) than those from region 3 (80–95 cm; 3–7 years) (Fig. 5B).

Line-caught snoek in region 3 were mostly >L_{50} (Fig. 5B). Monthly catch and CPUE statistics from this region depicted no trend, indicating that adult snoek are available to line fishermen throughout the year (Fig. 3). Catch rates in region 4 were highest between July and October, which is consistent with the winter–spring south–eastward dispersal of adult snoek evident from trawl data (above). Handline catch and CPUE in regions 5 and 6 were highest during the first half of the year but declined dramatically in winter.

Size at maturity

The ratio of active (stage-2) to ripe (stage-3) ovaries during the spawning season decreased with fish length

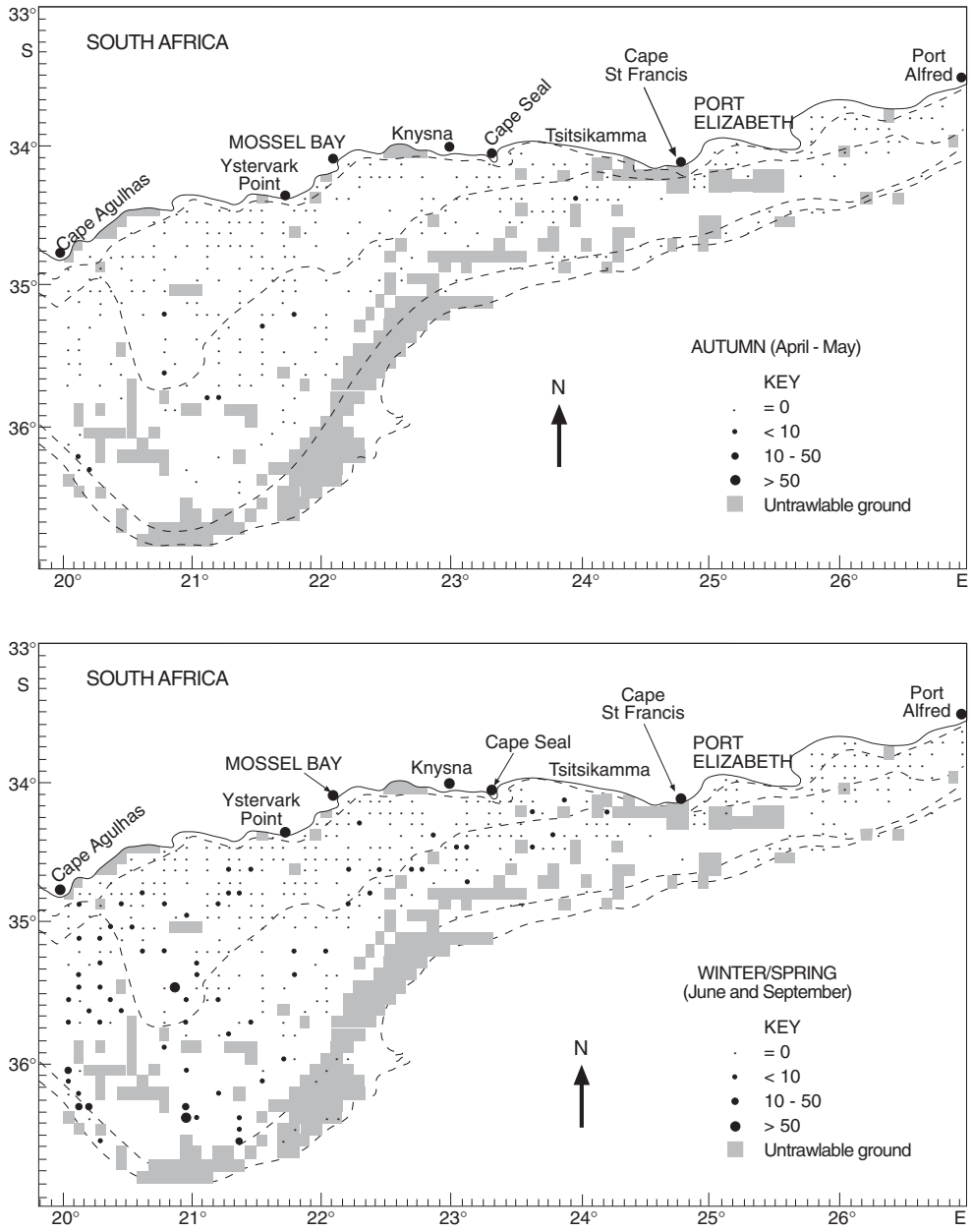

Figure 2B

(Fig. 6A), suggesting (as in other teleosts; Griffiths and Hecht, 1995) that substantial proportions of snoek in the smaller size classes undergo partial gonad development during the season prior to maturity. Because these fish are unlikely to spawn, only specimens with gonads developed to at least stage 3 (ripe) were regarded as mature. Given that snoek spawn offshore (see below) and that almost all fish on the trawl grounds (regardless of size) were mature (Fig. 6B), L_{50} maturity calculations were limited to fish sampled inshore (<150 m)[4]: 72.0 cm for males and 73.4 cm for females (Fig. 7). Upper and lower 95% confidence limits were 69.3 and 74.3 cm for males, and 71.3 and 75.4 cm for females. L_{50} for combined male and female data was 73.0 cm with 95% confidence intervals of 70.0 and 75.2 cm. In all cases the L_{50} values corresponded with an age of 3 years (author, unpubl. data).

[4] In situations where fish migrate to spawn, all fish on the spawning ground are mature. As a result, even if 10% of a particular size class (x–y cm) in the population are mature, the sampling of that 10% once it had migrated onto the spawning grounds would suggest that 100% of that size class are mature. Because mature snoek move back and forth between the spawning and feeding grounds (offshore and inshore) in regions 0–3 during the spawning season, and could readily be distinguished from immature fish, inshore samples were used to determine size at maturity.

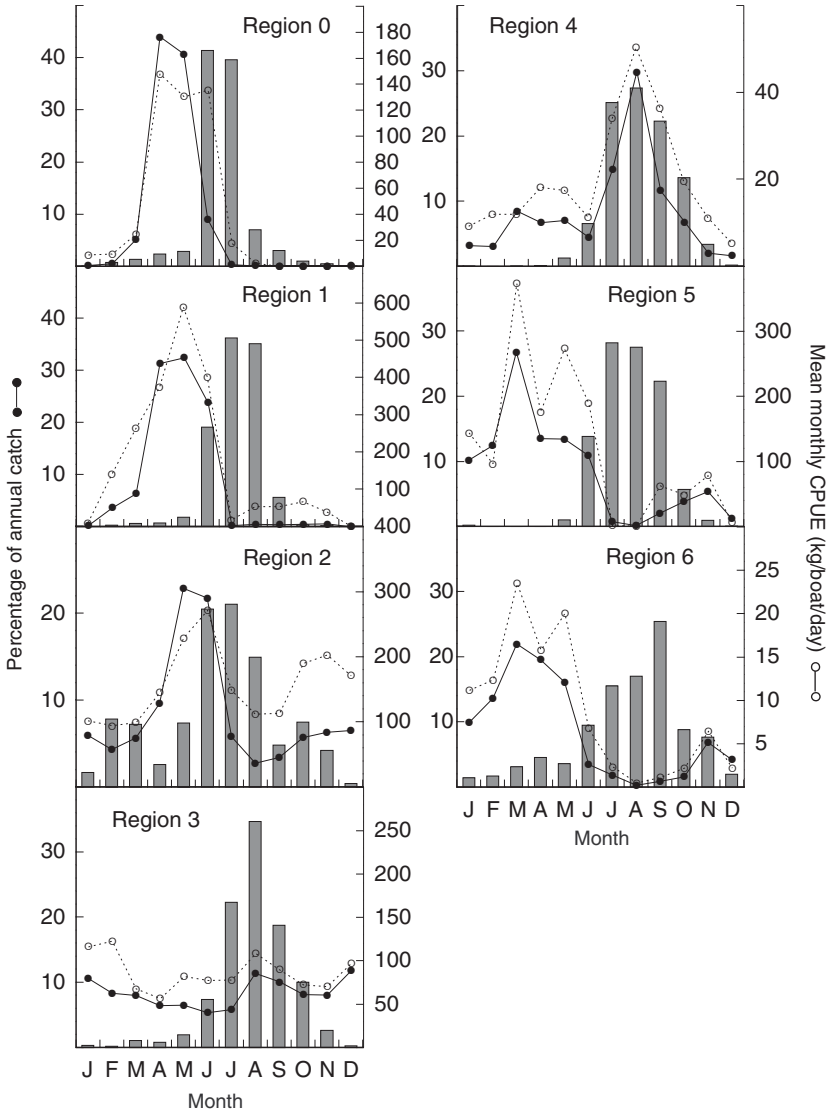

Figure 3

Catches of *Thyrsites atun* made by South African commercial trawlers (bars) and line fishermen (black circles) summed on a monthly basis in each region and expressed as percentages of the total catch for the period 1985–1997. Mean monthly catch per unit of effort (kg/boat/day) of *T. atun* caught by South African commercial line fishermen in each region (open circles) is also given (1985–97). Because the bulk (70 %) of the line catch in region 5 was made on offshore pinnacles (i.e. over a 72-mile bank), the CPUE trend for this region was based on data from this area. The offshore pinnacles (the 72-mile bank being the deepest) are, however, located well inshore of the trawl grounds in that region (see Fig. 1).

Spawning

Gonadosomatic indices (Fig. 8) and gonad maturity indices (Fig. 9) showed that South African snoek spawn from May to November and that peak spawning occurs from June to October (winter–spring). Monthly male GSIs were similar inshore and offshore, but female values were higher offshore during the spawning season. In addition, a substantial proportion (20+%) of offshore females in regions 2 to 5 had hydrated oocytes (stage 4), whereas this gonad stage was rarely observed inshore. Spatial patterns in trawl CPUE from both fishery-independent (Fig. 2) and fishery-dependent (Fig. 10) data collected during winter–spring suggest an extensive spawning ground that encom-

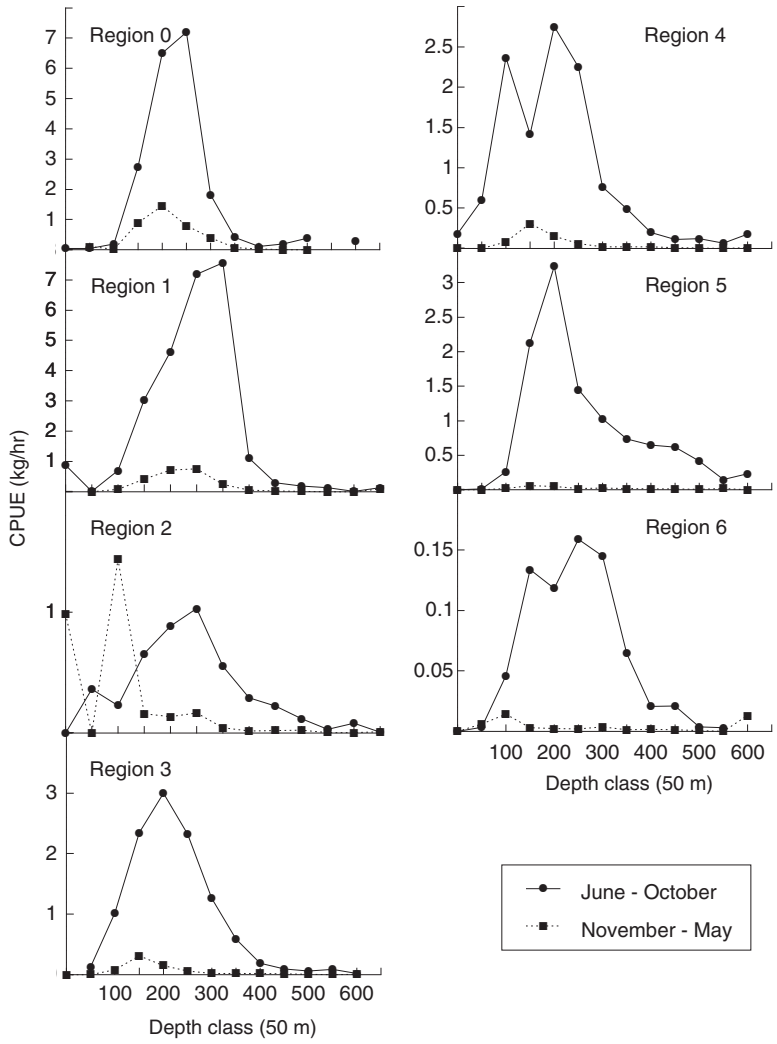

Figure 4

Catch per unit of effort (CPUE; kg/h) per 50-m depth category for *Thyrsites atun* commercially bottom trawled in each of the seven regions during winter–spring and summer–autumn, 1986–97.

passed the western edge of the Agulhas Bank and most of the South African west coast, to a point just north of Hondeklip Bay.

The predominance of ripe (stage-3) females (both inshore and offshore) throughout the protracted spawning season (Fig. 9) is indicative of multiple spawning (Griffiths, 1997). Moreover, the simultaneous occurrence of postovulatory follicles (POFs) with both primary growth and advanced yolked-stage oocytes (Fig. 11) confirmed that snoek are indeterminate, serial spawners.

Sex ratio

Sex ratios in regions 0–3 were skewed towards females inshore and males offshore (Table 2), a pattern most pronounced during the spawning season (winter–spring). Inshore, this pattern was most evident in the adult size class (≥75 cm). Adult sex ratios in regions 0–3 during the spawning season were 2.9F:1M inshore and 1F:2M offshore. Inshore and offshore sex ratios of adult snoek in regions 4 and 5 (Table 2) revealed no clear pattern; although moderately more females were sampled on the trawl grounds of these regions during the spawning season (1.6F:1M), the inshore ratio (1M:1.2F) did not deviated significantly from unity.

Nursery areas

Monthly length-frequency distributions comprised fairly discrete modes in spite of variation in collection method and sampling period and clearly depicted early juvenile growth (Fig. 12). Young-of-the-year snoek first appeared

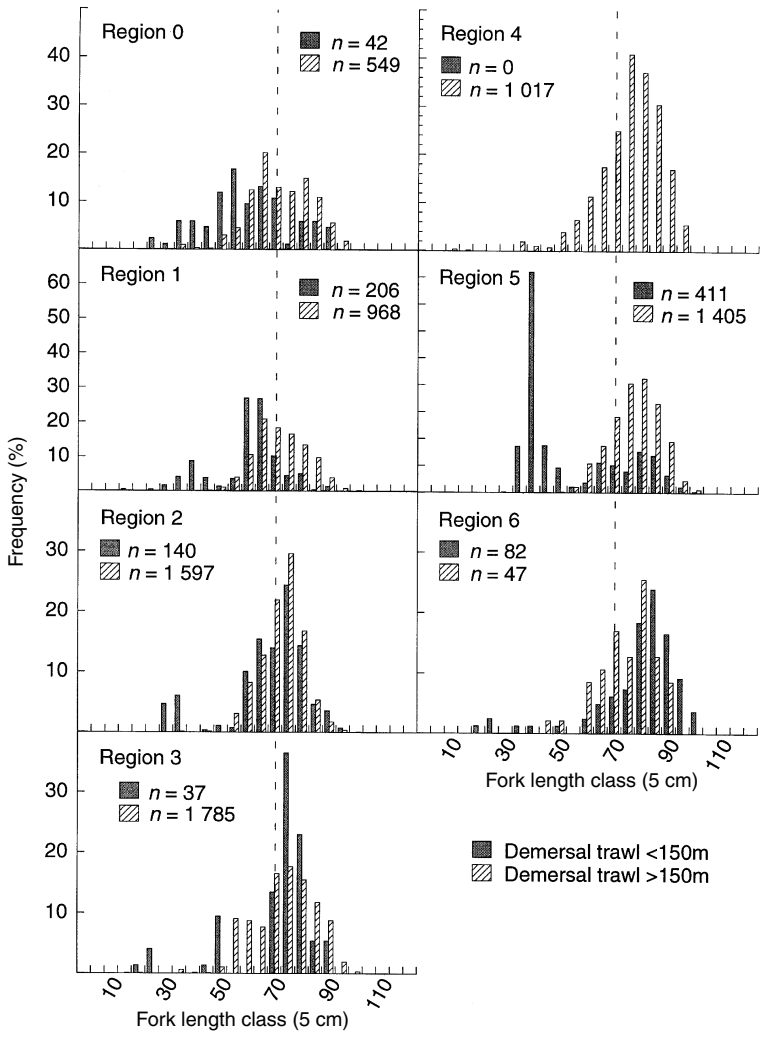

Figure 5A

Fork-length distributions of *Thyrsites atun* caught by (**A**) demersal trawl and (**B**) handline and midwater trawl in each region. Handline and midwater catches were made shorewards of the 150-m isobath and demersal catches were divided into those made deeper and shallower than this depth. The dotted line indicates length at maturity (L_{50}).

in the diets of gannets and in pelagic trawls during spring (Oct–Nov) at lengths 7–12 cm and grew rapidly to 33–44 cm by the spawning season (winter) of the following year (±3.25 cm/month). Early juveniles (<1 year old) were sampled (with fishing gear) in each of the seven regions (Fig. 5) but formed a larger proportion (by mass and frequency of occurrence) of the diet of gannets at Bird Island (Lamberts Bay) than in gannets of Malgas Island (Fig. 13). Snoek smaller than 70 cm comprised a far higher proportion of the handline and pelagic trawl catches of regions 0–2 than those from region 3 (Fig. 5B). Length frequencies of pelagic trawl, demersal trawl (<150 m), and line-caught snoek suggested that juveniles were also found in reasonable numbers to the east of Danger Point in regions 4 and 5. *Thyrsites atun* collected in demersal trawls deeper than 150 m were mostly >65 cm, whereas those from shallower bottom trawls included substantial proportions smaller than this length (Fig. 5A). Juveniles <30 cm, although present in pelagic trawls (Fig. 5B), were notably absent from demersal trawls, including those shallower than 150 m (Fig. 5A).

Diet

Snoek prey on a wide variety of demersal and pelagic organisms, including teleosts, crustaceans, and cephalopods (Tables 3 and 4) and show ontogenetic shifts. The diet of *T. atun* sampled inshore of the 150-m isobath along the west coast (regions 0–3) consisted predominantly of pelagic fishes, and crustaceans comprised a smaller but

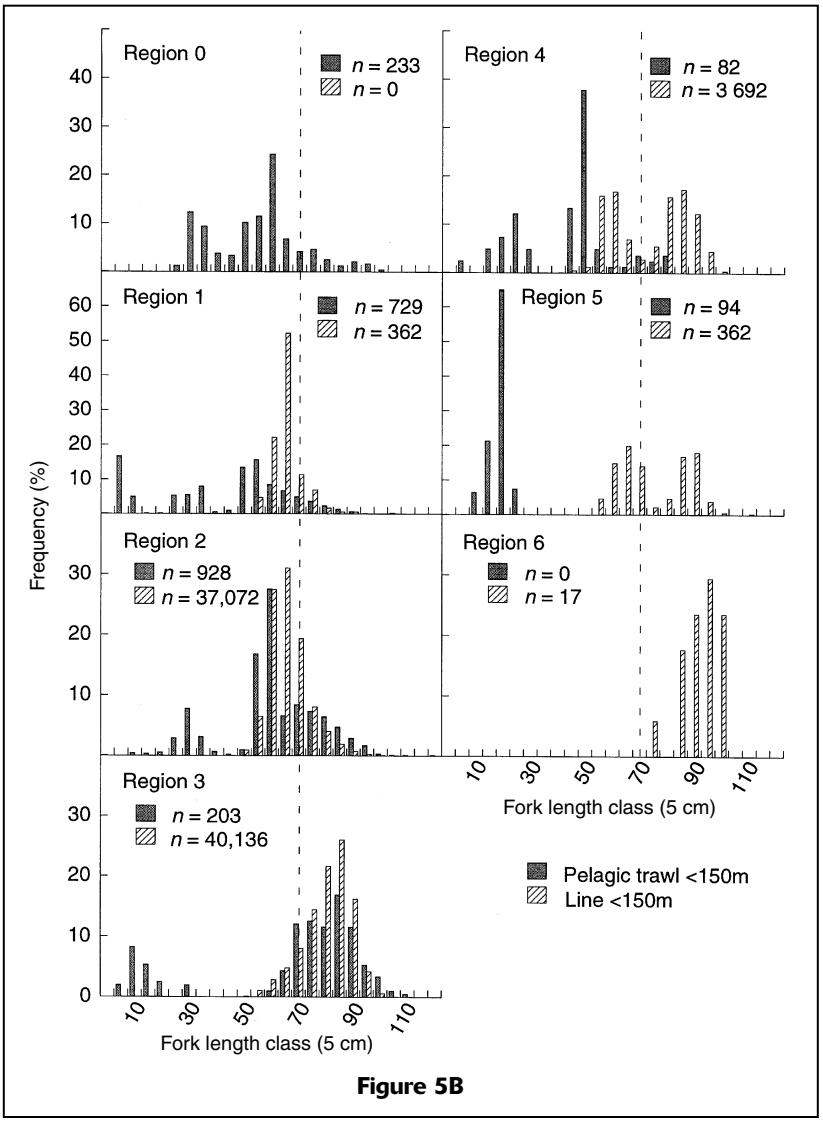

Figure 5B

Table 2

Inshore and offshore sex (M:F) ratios of *Thyrsites atun* during summer–autumn and winter–spring (spawning season) for the period 1994–97. Levels of significance—* ($P<0.05$), ** ($P<0.01$), and *** ($P<0.001$)—were determined by using a chi-square test (Yates' correction factor was applied as df =1).

	Inshore (<150 m)						Offshore (>150m)					
	Summer–Autumn			Winter–Spring			Summer–Autumn			Winter–Spring		
Fork length (cm)	M:F	*n*	χ^2	M:F	*n*	χ^2	M:F	*n*	χ^2	M:F	*n*	χ^2
Regions 0–3												
20–49	1:1	203	0.01	1:1.3	7	0						
50–74	1:1.2	647	4.5*	1:1.1	524	0.6	1.2:1	105	1.0	2.4:1	228	20.3***
>75	1:1.8	523	42.0***	1:2.9	1131	263.0***	1:1.2	134	1.3	2.0:1	704	61.3***
All sizes	1:1.4	1373	30.5***	1:2.0	1662	192.3***	1:1	241	0	2.1:1	933	82.3***
Regions 4–5												
20–49										1.3:1	7	0
50–74	1:1.1	53	0	1:1	24	0		No data		1:1	440	0
>75	1:2.0	6	0.1	1:1.2	46	0.2				1:1.6	586	31.1***
All sizes	1:1.2	59	0.4	1:1.1	70	0.1				1:1.3	1033	18.4***

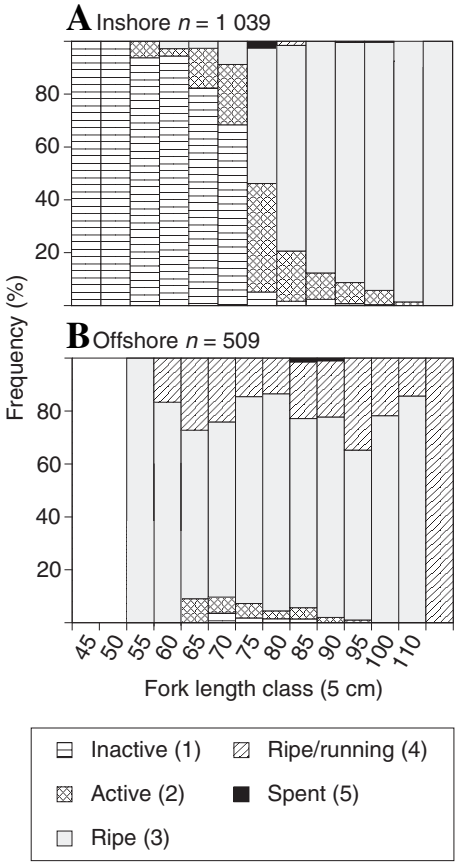

Figure 6

Percentage of macroscopic ovarian stages by 5-cm fork-length interval for *Thyrsites atun* sampled (**A**) inshore and (**B**) offshore (i.e. shorewards or seawards of the 150-m isobath) during the spawning season (June–October), 1994–97.

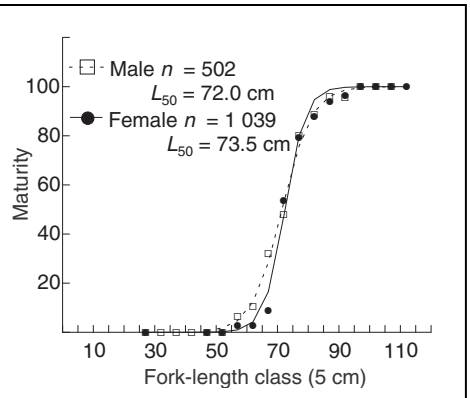

Figure 7

Percentage of mature (gonad stage 3+) *Thyrsites atun* by 5-cm fork-length class sampled during the spawning season (June–October), 1994–97. Symbols represent the observed data and the lines the fitted models. L_{50}= length-at-maturity (cm fork length); n = sample size.

noteworthy component that declined in importance with growth. In descending order. the most important prey items were as follows: lanternfish *Lampanyctodes hectoris* (IRI=46.5), euphausids *Euphausia leucens* (IRI=23), and the amphipod *Themisto gaudichaudi* (IRI=14.2) for early juveniles (5–24 cm); lanternfish (IRI=34.4), *T. gaudichaudi* (IRI=32.4), anchovies (IRI=2.8), and sardines (IRI=2.4) for juveniles (25–49 cm); anchovy (IRI=38.3), euphausids (IRI=26), and sardine (IRI=11.7) for subadults (50–74 cm); and sardine (IRI=47.4) and anchovy (IRI=38.6) for adults (≥75 cm).

In offshore waters snoek diet consisted almost exclusively of teleosts, including pelagic and demersal taxa. The most important prey items were sardine, round herring, and hake (*Merluccius* spp.) for snoek <75 cm; and hake, sardine and horse-mackerel (*Trachurus trachurus capensis*) for larger specimens. The main difference between the two offshore diets consisted in the greater importance of sardine (IRI=44.4 vs. 17.2 for snoek ≥75 cm) and the lesser importance of hake (IRI=31.8 vs. 60.8 for snoek ≥75 cm) off the western Agulhas Bank than off the west coast (Table 4). In both areas, large prey species, such as hake and horse mackerel, were more important in the larger (≥75 cm) size class.

Prey consumption

Both indices of prey consumption—proportions of stomachs containing food and mean mass of stomach contents—indicated that within each area and sampling season, adult females consumed more prey than adult males (Table 5); spatial and season trends were also evident. Two-way ANOVA with single observations revealed that differences in the mean mass of stomach contents between sexes (F= 65.9, df=1, $F_{critical}$=10.1) and between areas (F=215.5, df=3, $F_{critical}$=9.3) were both highly significant (P<0.001). Chi-square tests revealed that differences between the proportions of males and females with stomach contents were highly significant inshore on the west coast (WC) and offshore along the western Agulhas Bank (WAB) in winter–spring, but were not significant inshore on the WC in summer–autumn, or offshore on the WC in winter–spring (Table 5). Female mean stomach content mass was lowest (22.1 g) inshore on the WC in summer–autumn and highest (60.1 g) offshore on the WAB in winter–spring (spawning season). Female proportion with stomach contents was also lowest (52.5%) inshore on the WC in summer–autumn but highest (81.2%) in the same area during winter. Differences in female proportions with stomach contents between seasons inshore on the WC (χ^2=99.9, df=1), between inshore and offshore areas of the WC in winter–spring (χ^2=13.0, df=1) and between the offshore WAB and inshore WC during winter–spring (χ^2=26.3, df=1) were highly sig-

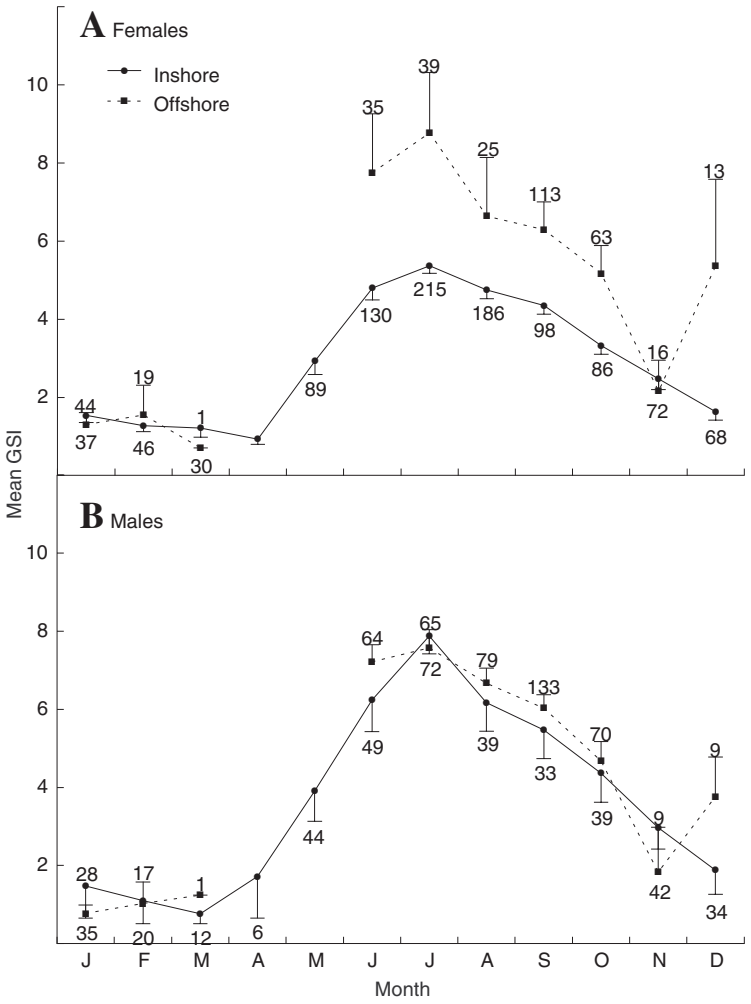

Figure 8

Mean monthly gonadosomatic indices (GSI; ±2 standard errors) for mature (≥75 cm) (**A**) female and (**B**) male *Thyrsites atun* sampled both inshore (circles) and offshore (squares), 1994–97. Inshore and offshore sample sizes are given above and below the error bars, respectively.

nificant (P<0.01), but differences between the two offshore areas—WC and WAB—in winter–spring were not. Mean stomach content mass was, nevertheless, substantially higher (60.1 g vs. 44.6 g.) offshore on the WAB than offshore of the WC during winter–spring (Table 5).

Condition

Relative condition (Kn) of adult snoek depicted a clearly seasonal cycle: highest between March and May, declining steeply through June to October (spawning season), increasing again from November through to March (Fig. 14). The proportion of stomachs without any fat was inversely related to Kn (Fig. 14): it was lowest from March to May but increased dramatically during the spawning season. The rate of fat decline was, however, higher in females than males; by September 90% of females and 58% of males had no mesenteric fat reserves.

Discussion

Crawford and De Villiers (1985) postulated that the snoek of the Benguela ecosystem comprise a single stock that undergoes a seasonal longshore migration—moving southwards into South African waters to spawn in winter and returning north, as far as southern Angola, in spring–summer. Although this theory has become widely accepted (Crawford et al., 1987; Crawford, 1995), this study showed that adult snoek are available to South African line fisher-

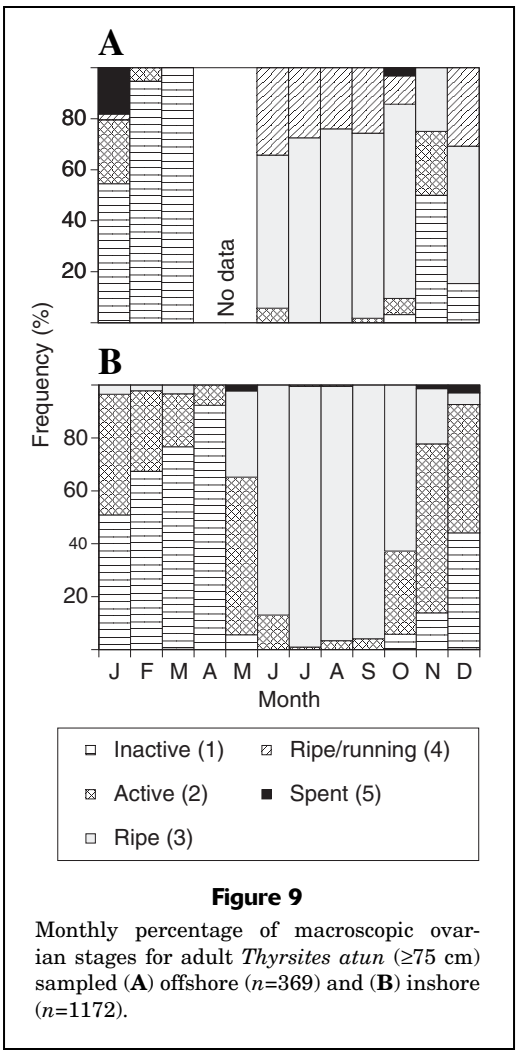

Figure 9

Monthly percentage of macroscopic ovarian stages for adult *Thyrsites atun* (≥75 cm) sampled (**A**) offshore (n=369) and (**B**) inshore (n=1172).

men throughout the year, and that the seasonal availability of adults on the trawl grounds results from an offshore spawning migration rather than southward movement from Namibian waters. Based on these results, *inter alia*, separate nursery areas and egg and larval distributions north and south of the cold upwelling cell (25–27°S) off southern Namibia, Griffiths (in press) concluded that Benguela snoek exist as two subpopulations, and have limited exchange.

The life history of South African *T. atun* is summarized by the conceptual model presented in Figure 15. Movement patterns were inferred largely from spatiotemporal trends in fishery-dependant catch and effort data. Considering that snoek is the most important line fish on the South African western seaboard and that it is a bycatch in the trawl fishery, catch trends are unlikely to have been biased by switches in targeting. Moreover, even though line-fish catches are under-reported (Sauer et al., 1997), they have been demonstrated to accurately reflect seasonal trends in the abundance of migratory species (Griffiths and Hecht, 1995). Given the offshore movement of adult fish during the spawning season and the associated ovarian condition (greater GSIs and the presence of hydrated oocytes), it is concluded that South African snoek spawn offshore between the 150- and 400-m isobaths. Although most of the inshore catch was line-caught, the absence of stage-4 females from trawls made shallower than 150 m during the spawning season (n=46, including 32 ripe [stage-3] specimens) indicates that this observation is not an artifact of gear selectivity. Spatial patterns in trawl CPUE from both fishery-independent (Fig. 2) and fishery-dependent (Fig. 11) data, collected during winter–spring, suggest an extensive spawning ground that encompasses the western edge of the Agulhas Bank and most of the South African west coast, to a point just north of Hondeklip Bay. Presence of snoek eggs and larvae (off South Africa) from the southern tip of the Agulhas Bank to Hondeklip Bay and their great abundance between the 200-m and 600-m isobaths (Olivar and Fortuño, 1991; Olivar and Shelton, 1993) corroborate offshore spawning and an extensive spawning ground. The occurrence of snoek preflexion larvae in region 6 (Wood, 1998) indicates that spawning does occur farther to the east, but the relatively low abundance of adult fish and spawning products suggests it is not an important spawning area.

The sex ratio of adults (≥75 cm) on the west coast (regions 0–3) was skewed towards males on the spawning grounds (2M:1F), and towards females further inshore (2.9F:1M), particularly during the spawning season. Based on the differential loss of intestinal fat, it is evident that the energetic demands of spawning are higher in females than in males. The higher rate of prey consumption by females during winter–spring (i.e. spawning season) than during summer–autumn and the greater prey consumption by females than by males during the spawning season indicate that they are able to enhance their spawning effort with exogenous energy. It is therefore postulated that because snoek are indeterminate serial spawners, females on the west coast move inshore between spawning events, where their principal prey—*Sardinops sajax* and *Engraulis japonicus*—are more abundant.

Females spawning off the western Agulhas Bank do not appear to move inshore to feed between spawning events, according to near equal sex ratios and low inshore catch rates in winter–spring (region 5). Although line catches in region 4 were highest during the spawning season, which at first glance may appear to be contradictory, CPUE was an order of magnitude lower than in region 3 or region 5, indicating relatively low inshore abundance at that time of the year. High female mean stomach content mass (60.1 g) and the significantly higher proportion of females than males with food (shared only with the inshore feeding ground of the WC) suggest that the offshore WAB functions as both spawning and feeding ground during winter–spring. In addition, PBSs have revealed that clupeids—adult sardine and round herring—are more abundant near the shelf edge of the WAB in winter than along the WC (Coetzee[5]), and dietary comparison (this study) showed that clupeids indeed represent a larger component of the offshore diet

[5] Coetzee, J. 2000. Personnal commun. Pelagic Section, Marine & Coastal Management, Private Bag X2, Roggebaai, 8012, Cape Town.

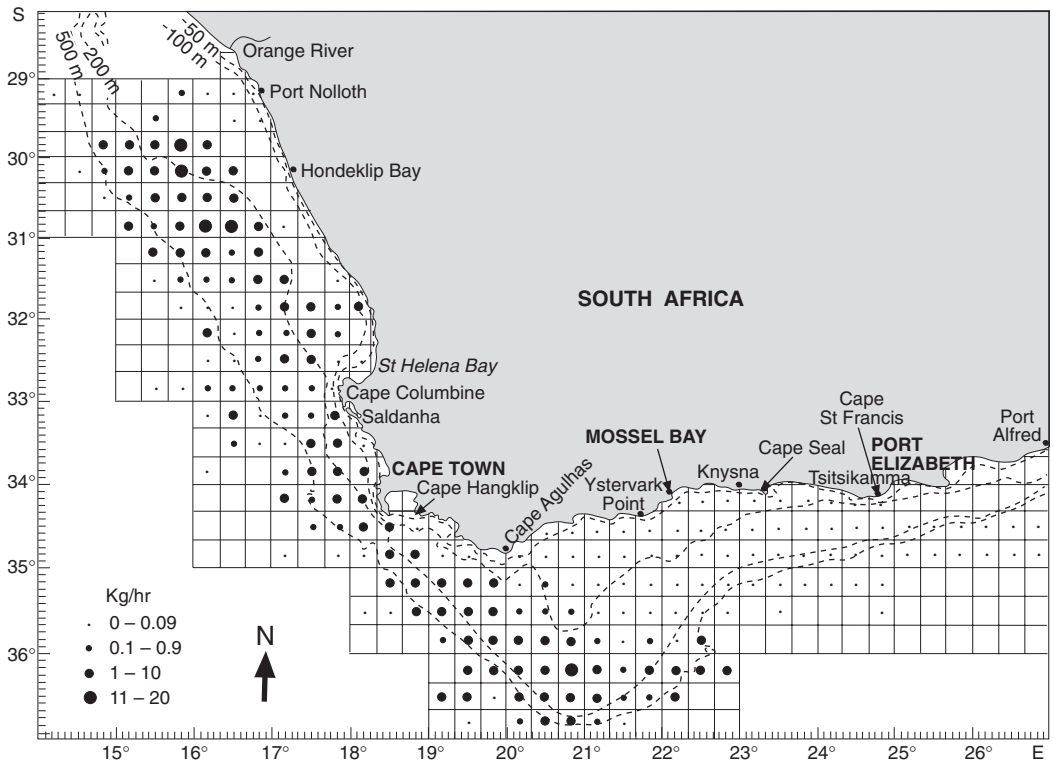

Figure 10

Catch per unit of effort (kg/h) by 20-mile block (1986–97) for *Thyrsites atun* caught by commercial trawls in the southern Benguela system during the spawning season.

of the WAB than offshore along the WC, where hake was dominant. Sex ratios and feeding patterns of adult snoek in the present study were confirmed as persistent biological features of the western Agulhas Bank by experimental trawl surveys on the spawning ground of region 4 during August 1999 and August 2000. The principal prey taxon for 1875 snoek with a sex ratio of 1M:1.2F (P<0.001) was Clupeidae (67% by weight); mean stomach content masses were 58.2 g for females and 27.6 g for males.

Even though young-of-the-year snoek were sampled (with fishing gear) in each of the seven regions, they formed a larger proportion (by mass and frequency of occurrence) of the diet of gannets at Bird Island (Lamberts Bay) than in gannets at Malgas Island. Either early juveniles are more abundant north of Cape Columbine than between Cape Columbine and Cape Infanta or they are selected at a higher frequency by gannets in the former area. Higher proportions of snoek smaller than 70 cm in the handline and pelagic-trawl catches of regions 0–2 than in catches from region 3 support the first suggestion, confirming that the area north of Cape Columbine has an important nursery function. Length frequencies of pelagically trawled, demersally trawled (<150 m), and line-caught snoek, nevertheless suggest a second nursery area to the east of Danger Point. But because handline catches in

Figure 11

Photomicrograph of transverse section of *Thyrsites atun* ovary stained with haemotoxylin and eosin, showing co-occurrence of postovulatory follicles (POF) together with primary growth (PG) and advanced yolk-stage oocytes (YO).

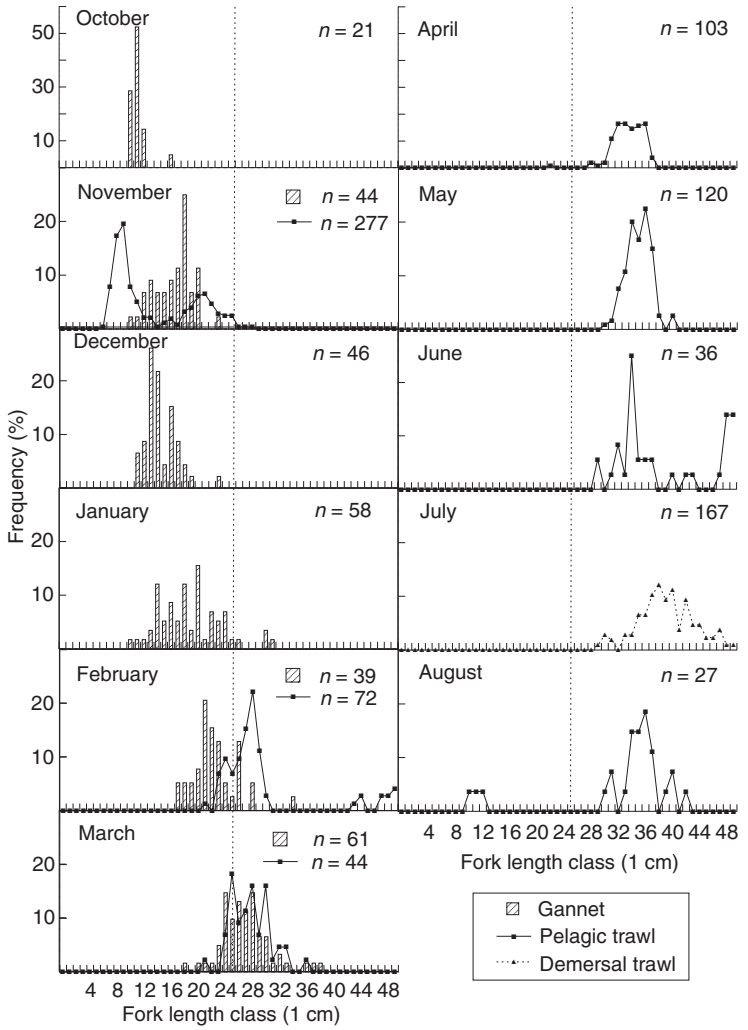

Figure 12

Monthly fork-length distributions of *Thyrsites atun* <50 cm caught by midwater trawls (1985–97), demersal trawls (1985–97), and Cape gannets (1978–97) in the southern Benguela system. *n* = sample size. Dotted line at 25 cm is included as a reference point.

regions 4 and 5 amounted to only 10% of those in regions 1and 2 (1985–97) and given that juvenile snoek made a substantially lower contribution to the diets of gannets foraging in this area, the area north of Cape Columbine is regarded as considerably more important to juvenile snoek. *Thyrsites atun* in demersal trawls made deeper than 150 m were mostly >65 cm, whereas those from shallower bottom trawls included substantial proportions smaller than this length. It is therefore concluded that the primary nursery ground is situated on the west coast, north of Cape Columbine and in water shallower than 150 m; a secondary nursery exists to the east of Danger Point. The absence of specimens <30 cm from demersal trawls, particularly those made shallower than 150 m, and their presence in pelagic trawls, indicates that 0-year-old snoek are largely epipelagic but become pelagic with growth (at ca. 8 months old).

The northward flowing Benguela Current provides a mechanism for transporting epipelagic snoek eggs and larvae (De Jager, 1955; Olivar and Fortuño, 1991) from the spawning ground to the proposed nursery areas. The Benguela current is found offshore (generally between the 150- and 400-m isobaths) and flows along the western edge of the Agulhas Bank and up the South African west coast; rate of flow is fastest (typically 25–80 cm/s) between Cape Point and Cape Columbine, where it develops into a shelf edge jet (Shannon and Nelson, 1996). Although water movement is primarily parallel to the shelf, inshore advection occurs to some degree due south of Danger Point and to a greater extent between Cape Columbine and Hon-

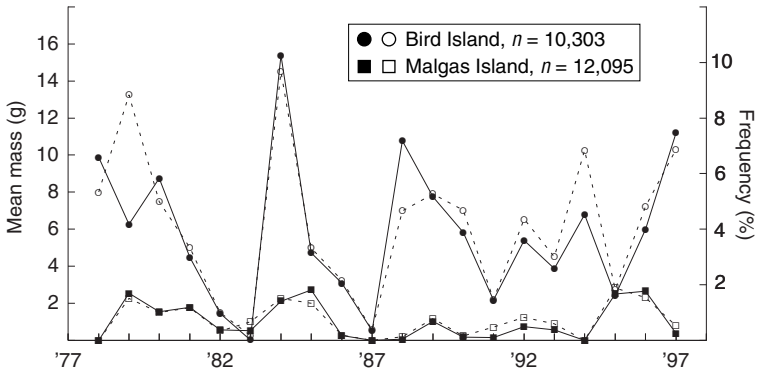

Figure 13

Annual frequency of occurrence (*%F*; dotted line) and mean mass (solid line) of *Thyrsites atun* in the stomachs of Cape gannets from Bird Island (circles) and Malgas Island (squares), 1978–97. *n*=number of gannet stomachs examined.

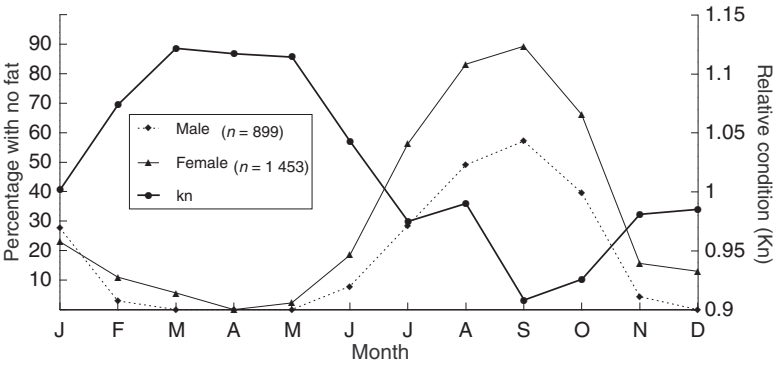

Figure 14

Mean monthly relative condition (Kn) and the proportion of adult *Thyrsites atun* (≥75 cm) without intestinal fat reserves, in the southern Benguela Ecosystem (1994–97).

deklip Bay (Shelton and Hutchings, 1990; Shannon and Nelson, 1996).

Snoek hatch about 2 days (50 hours) after fertilization (De Jager, 1955), are phytoplanktivorous from first feeding (3.5 mm and 3–4 days after hatching) until 8 mm long (standard length), after which they prey largely on the larvae of other fishes (Haigh, 1972). Total abundance of fish larvae in the southern Benguela is highest in spring and summer (Shelton, 1986); snoek larvae spawned during the winter and spring months are therefore assured of an abundant supply of food. Following northward advection in the jet current, young-of-the-year anchovy, round herring, and sardine, which share the northern nursery area with snoek, move shoreward across the shelf, with a concomitant increase in size (Armstrong et al., 1987; Roel and Armstrong 1991; Hampton, 1992; Roel et al., 1994; Barange et al., 1999; Van der Lingen and Merkle, 1999). They arrive at the coast from February through through June at total lengths of 5–11 cm, and, unlike snoek, which are found on the nursery grounds for 2–3 years, immediately begin a southwards migration back onto the Agulhas Bank, where they were originally spawned. Coupled with earlier spawning, rapid growth ensures that 0-year-old snoek are large enough (ca. 35 cm TL) to partake with the older juveniles in this seasonally abundant food source. Substantial increases in line catches during the period of clupeoid recruitment suggest that juvenile snoek follow their prey inshore. Differences in the size and age composition of catches north and south of Cape Columbine, however, indicate that they do not move southwards with them and onto the Agulhas Bank. The large contribution of lanternfish to the diets of snoek <50 cm is attributed to the fact that most of these fish were sampled during the second half of the year, i.e. when juvenile clupeoids (i.e.

Table 3

Stomach contents of snoek (*Thyrsites atun*) sampled inshore of the 150-m isobath along South African west coast (1994–97). *M* = percent mass, *F* = percent frequency of occurrence, *IRI* = percent index of relative prey importance at the species and at a higher (bold) taxonomic level. [P] = pelagic and [D] = demersal species.

Taxon and prey item	5–24 cm FL (n = 11)			25–49 cm FL (n = 212)			50–74 cm FL (n = 540)			>74 cm FL (n = 1, 069)		
	M	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*
Annelida							<0.1	0.2	**<0.1**	0	0	0
Polychaeta							<0.1	0.2	<0.1			
Crustacea	27.7	54.5	**24.7**	19.4	45.5	**12.6**	22.0	39.5	**14.3**	7.4	5.9	0.5
Amphipoda												
Themisto gaudichaudi[P]	20.9	9.1	14.2	17.8	42.0	32.4	1.42	10.9	1.0			
Brachyura												
Megalopa larvae[P]							<0.1	0.2	<0.1			
Euphausiacea												
Euphausia lucens[P]	6.8	45.5	23.0	1.3	3.6	0.2	15.0	27.4	26.0	0.3	1.6	<0.1
Isopoda												
Paridotea ungulata[P]							<0.1	<0.1	<0.1	<0.1	0.1	<0.1
Macrura												
Lobster pueruli[P]							<0.1	0.2	<0.1	<0.1	0.3	<0.1
Pasiphaea spp.[P]							<0.1	0.5	<0.1	0	0	0
Mysidacea[P]				<0.1	0.9	<0.1	0.3	1.0	<0.1	<0.1	0.1	<0.1
Stomatopoda												
Pterygosquilla armata[P]							5.0	10.4	3.3	7.1	4.5	1.1
Unidentified crustaceans				0.3	0.9	<0.1	0.1	0.6	<0.1	<0.1	0.3	<0.1
Mollusca												
Cephalopoda							0.3	2.2	**<0.1**	0.2	1.6	**<0.1**
Inioteuthis							<0.1	0.2	<0.1	0	0	0
Loligo vulgaris reynaudii							0	0	0	<0.1	0.3	<0.1
Lolliguncula mercatoris?							0.2	1.5	<0.1	<0.1	1.1	<0.1
Lycoteuthis?							0	0	0	<0.1	0.1	<0.1
Sepia australis							0.1	0.4	<0.1	<0.1	0.1	<0.1
Todaropsis eblanae							0	0	0	<0.1	0.1	<0.1
Unidentified squid							<0.1	0.2	<0.1	0	0	0
Teleostei	72.3	63.6	**75.3**	80.6	76.0	**87.4**	77.8	66.9	**85.7**	92.4	95.7	**99.5**
Engraulis japonicus[P]				6.1	10.7	2.8	30.9	19.6	38.3	26.9	44.0	38.6
Sardinops sagax[P]				8.9	6.3	2.4	18.9	6.8	11.7	43.1	33.8	47.4
Etrumeus whiteheadi[P]				5.1	1.8	0.4	6.5	3.2	1.3	2.3	3.5	0.3
Lampanyctodes hectoris[P]	68.4	9.1	46.5	37.2	21.4	34.4	0.8	1.9	0.1	0.4	1.3	<0.1
Maurolicus muelleri[P]				1.0	2.7	0.1	0.8	1.5	0.1	<0.1	<0.1	<0.1
Trachurus t. capensis[P]							4.1	2.4	0.6	3.9	6.8	0.9
Scomber japonicus[P]							0	0	0	0.5	0.1	<0.1
Lepidopus caudatus[P]							0.3	0.4	<0.1	0.1	0.5	<0.1
Thyrsites atun[P]							0	0	0	<0.1	0.1	<0.1
Sufflogobius bibartus[P]							1.3	1.0	0.1	0.1	0.2	<0.1
Gonorhynchus gonorhynchus							0	0	0	0.2	1.1	<0.1
Gnathophis capensis							<0.1	0.2	<0.1	0.3	2.9	<0.1
Merluccius spp.[D]				5.0	1.8	0.4	5.7	5.2	1.9	3.1	2.6	0.3
Clinidae[D]							<0.1	0.2	<0.1	<0.1	0.1	<0.1
Emmelichthys nitidusr[D]							0	0	0	0.5	0.1	<0.1
Spondyliosoma emarginatum[D]							0	0	0	0.3	0.2	<0.1
Unidentified Teleostei	4	54.5	16.3	17.4	35.7	28.8	8.5	29.3	15.7	10.7	33.0	11.5

Table 4

Stomach contents of snoek (*Thyrsites atun*) sampled offshore of the 150-m isobath along the west coast (regions 1–3) and the western Agulhas Bank (regions 4 and 5) (1994–97). *M* = percent mass, *F* = percent frequency of occurrence, *IRI* = percent index of relative prey importance at the species and at a higher (bold) taxonomic levels. [P] = pelagic and [D] = demersal species.

	West coast						Western Agulhas Bank					
	50–74 cm FL (n = 147)			≥75 cm FL (n = 447)			50 – 74 cm FL (n =336)			≥75 cm FL (n = 367)		
Taxon and prey item	*M*	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*	*M*	*F*	*IRI*
Annelida				<0.1	<0.1	**<0.1**						
Polychaeta				<0.1	<0.1	<0.1						
Crustacea	1.3	4.8	**0.1**	1.5	6.9	**0.1**						
Amphipoda												
Themisto gaudichaudi[P]				0.1	0.2	<0.1						
Brachyura												
Parapagurus dimorphus[D]	0.1	0.7	<0.1	0.1	0.4	<0.1						
Euphausiacea												
Euphausia lucens[P]	1.1	3.4	0.2	1.3	5.3	0.4						
Macrura												
Funchalia? [P]	<0.1	0.7	<0.1	<0.1	0.7	<0.1						
Stomatopoda												
Pterygosquilla armata[P]				0.1	0.4	<0.1						
Mollusca												
Cephalopoda				1.4	2.7	**<0.1**				1.7	1.9	**<0.1**
Lycoteuthis?				0.1	0.2	<0.1						
Sepia australis				0.1	0.4	<0.1						
Todaropsis eblanae				1.2	1.8	0.1				1.7	1.4	0.1
Unidentified squid				<0.1	0.2	<0.1				<0.1	0.5	<0.1
Teleostei	98.7	97.3	**99.9**	97.1	96.4	**99.8**	100	100	**100**	98.3	99.4	**99.9**
Engraulis japonicus[P]	0.1	0.7	<0.1	<0.1	0.2	<0.1	0.2	0.6	<0.1	0.1	0.3	<0.1
Sardinops sagax[P]	25.7	23.8	36.3	17.0	19.2	17.2	61.4	45.2	79.4	25.6	28.3	44.4
Etrumeus whiteheadi[P]	18.5	13.6	14.9	4.9	5.4	1.4	19.6	22.9	12.9	6.3	11.2	4.3
Lampanyctodes hectoris[P]	4.5	12.2	3.2	6.0	18.1	5.7				1.0	4.1	0.3
Maurolicus muelleri[P]	2.5	7.5	1.1	1.4	13.0	1.0	0.4	5.4	0.1	0.2	3.5	<0.1
Trachurus t. capensis[P]				13.2	12.8	8.8	1.4	0.6	<0.1	14.2	10.1	8.8
Scomber japonicus[P]	5.3	0.7	0.2							3.0	1.6	0.1
Lepidopus caudatus[P]	2.6	2.7	0.4	1.2	0.9	0.1				9.3	6.0	3.4
Thyrsites atun[P]										0.8	0.3	<0.1
Gonorhynchus gonorhynchus[D]							2.6	2.7	0.2	4.7	6.8	2.0
Emmelichthys nitidus[D]										<0.1	0.3	<0.1
Diaphus hudsoni[P]				<0.1	0.2	<0.1				<0.1	0.3	<0.1
Scomberesox saurus [P]							1.9	0.9	0.1	0.2	0.3	<0.1
Merluccius spp.[D] [1]	31.4	15.0	27.8	47.6	24.4	60.8	4.4	3.3	0.4	28.0	18.5	31.8
Caelorinvhus simorhynchus[D]				0.1	0.7	<0.1						
Sebastes capensis[D]	0.5	0.7	<0.1	0.4	0.4	<0.1				0.2	0.5	<0.1
Zeus capensis[D]				0.7	0.2	<0.1						
Paracallionymus costatus[D]	0.6	0.7	<0.1	1.8	3.6	0.3				1.5	1.6	0.2
Unidentified Teleostei	6.9	37.4	15.2	2.8	24.8	3.7	8.1	30.4	7.0	3.2	23.4	4.6

[1] Two species of hake occur in South African waters—*M. paradoxus* and *M. capensis*–but owing to difficulty differentiating partially digested specimens, they were not analyzed separately.

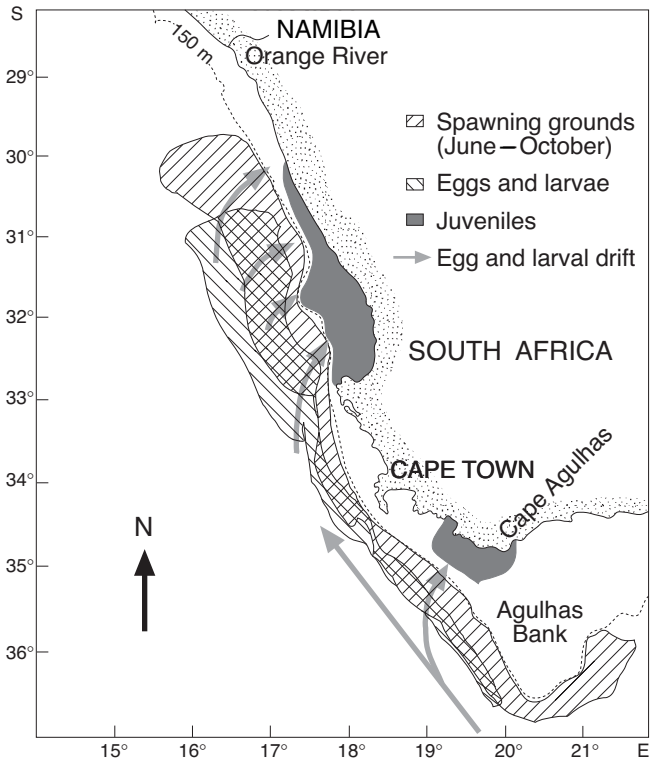

Figure 15

Conceptual model depicting the life history of *Thyrsites atun* in the southern Benguela ecosystem, including spawning grounds, distribution and transport of eggs and larvae, and the nursery areas.

Table 5

Proportions (%) of stomachs with food, and the mean mass of stomach contents for adult (>75 cm) male (M) and female (F) *T. atun* sampled on the South African west coast (WC; regions 1–3) and western Agulhas Bank (WAB; regions 4 and 5). χ^2 values were based on the frequencies of males and females with and without stomach contents (2×2 contingency tables) in each area (Yates' correction factor was applied as df =1). Significance levels are given by * (P<0.05), ** (P<0.01), and *** (P<0.001).

Area	Sex	n	%	χ^2	Mean mass (g)
Summer–autumn					
$WC_{inshore}$	M	197	50.2	0.18	13.3
	F	383	52.5		22.1
Winter–spring					
$WC_{inshore}$	M	130	52.4	6.6**	34.0
	F	729	81.2		43.0
$WC_{Offshore}$	M	374	61.8	2.5	39.0
	F	193	69.0		44.6
$WAB_{Offhore}$	M	212	49.5	15.2**	38.4
	F	336	67		60.1

those small enough to be eaten by young snoek) are least abundant inshore.

Given that the majority of the alternative prey are most abundant at some distance from the coast—euphausids between 10 and 20 km from the coast (Pillar, 1986; Hutchings et al., 1991), lanternfish, and lightfish between the 75- and 300-m isobaths (Hulley and Prosch, 1987), and mantis shrimp in the 20–200 m depth zone (Griffiths and Blaine, 1988)—it is likely that juvenile snoek move farther offshore when anchovy recruits leave the area, i.e. beyond the normal operating range of line fishermen in regions 0–2 (hence the seasonal drop in handline CPUE).

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