

## Aspects of the biology and life history of largespot pompano, *Trachinotus botla*, in South Africa

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**Abstract.** *Trachinotus botla* is an important recreational surf zone-dependent fish species distributed in the Indo-west Pacific from South Africa to Australia. In South Africa it is restricted to the northern KwaZulu-Natal coast. Biological investigations revealed that it is a fast growing species that attains a maximum age of ~7 years. Males and females sexually matured in their third year. It has a protracted summer spawning season with evidence of serial spawning behaviour. *T. botla* is an opportunistic predator with a generalist diet, with fish feeding on a wide variety of prey items particularly those that are temporally ‘superabundant’. Small fish fed predominantly on copepods and terrestrial insects, whereas larger fish consumed bivalves and crabs. Teleosts, primarily engraulids, were important components to the diet of fish of all sizes. An ontogenetic dietary shift was observed just after sexual maturity (~300-mm fork length) that is possibly linked to a change in habitat preference with larger fish foraging on deeper reefs.

**Additional keywords:** Carangidae, diet, fisheries, growth, reproduction.

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### Introduction

*Trachinotus botla* (Shaw, 1803), known as largespot pompano or wave garrrick in South Africa and common dart in Australia, is a surf zone species with a cosmopolitan distribution throughout the Indo-west Pacific ranging from South Africa to Australia (Williams 2002). Within South Africa, it is confined to the sub-tropical waters north of East London (van der Elst 1993; Smith and Heemstra 2003) and is most prevalent in the Maputaland area of northern KwaZulu-Natal. It is an important recreational shore angling species and accounts for up to 30% of the shore angling catch composition in northern KwaZulu-Natal (Mann 2008) where it is targeted by light tackle shore anglers. *T. botla* is particularly susceptible to small lures, flies and the fairly recent development (since the early 2000s) of a technique of angling known locally as ‘dropshot’ fishing where anglers fish with small lures consisting of weighted jigs inserted into soft plastic fish imitation bodies. It is also caught for use as live bait by fishers targeting larger fishes.

Although the *T. botla* shore-fishery in South Africa remains solely recreational by legislation, the Australian fishery differs in that additional harvests are made by a commercial beach seine netting sector. In Australia, *T. botla* is harvested together with a cogenere *T. copperingi* as by-catch when targeting more valuable species, such as tailor (*Pomatomus saltatrix*), flathead mullet (*Mugil cephalus*) and whiting (*Sillago ciliata*) (McPhee 1999). Although no estimates of total harvests have been made in South Africa, annual commercial harvests in southern Queensland between 1988 and 2000 were variable and ranged between 8 and 51 tonnes with 32 tonnes harvested in 2000 (Williams 2002)

and ~5 tonnes per annum in NSW (Rowling *et al.* 2010). In addition, an estimated 120 tonnes of *Trachinotus* spp. were harvested by the Queensland recreational fishery in 2005 (DEEDI 2011) and between 15 and 50 tonnes in NSW (Rowling *et al.* 2010).

Information on the life history of *T. botla* in South Africa is absent whereas in Australia it is limited to a single biological study and fishery assessment (McPhee 1999). Recent stock status assessments of Queensland fisheries define the species as having a low priority, suggesting the stock is in a reasonably healthy state (DEEDI 2011). In South Africa, a preliminary assessment by Parker *et al.* (2013) suggests that the resource is underfished. To assist in further understanding the biology of *T. botla* and to contribute towards its long-term management, this study describes aspects of its life history in South Africa. Aspects investigated include age and growth, maturity, population structure, spawning and reproductive periodicity, and a comprehensive evaluation of its diet and feeding habits.

### Materials and methods

#### General sampling

*Trachinotus botla* samples were collected every month using rod and line during daylight hours from Sodwana Bay, KwaZulu-Natal (27°32′24.6″S; 32°40′47.9″E) between May 2010 and May 2011. Fish were measured for fork length (FL) and total length (TL) to the nearest millimetre, and whole (WM) and eviscerated (EM) mass to the nearest gram. The gonads, stomachs and viscera removed, fish were sexed and assigned a

**Table 1.** Macroscopic and histological staging criteria used to assess the gonads of female and male *Trachinotus botla* from northern KwaZulu-Natal, South Africa

Class	Macroscopic description	Histological description
1. Immature	Ovaries discernible as thin transparent bands. Sex is indistinguishable. Testes discernible as thin transparent bands. Sex is indistinguishable.	Oogonia and pre-perinuclear oocytes are present on the ovary.  Spermatogonia predominant. No spermatocytes, spermatids or spermatozoa visible.
2. Juvenile/Resting	Ovaries are thread-like at the anterior, but are lobed towards the posterior. Posterior lobe is slightly opaque in appearance. Slight increase in width of testes from mid-section to posterior. Testes are white in colour.	Ovaries dominated by pre-perinuclear and early perinuclear oocytes. Few late perinuclear oocytes are present.  Seminiferous tubules start to develop and contain spermatocytes.
3. Developing	Ovaries moderate in size with lobation progressing anteriorly. Ovaries opaque in appearance and ova not visible to the naked eye. Testes increase in width to a moderate size. Testes are firm and slightly irregular in shape as folding starts to occur along the edges. White in colour with blood vessels clearly visible. No sperm present.	Characterised by oocyte stages up to the cortical alveoli stage. First appearance of primary yolk vesicle oocytes.  Spermatocytes are dominant in the outer region and spermatids dominate the inner region tubules. Seminiferous tubules and sperm ducts not fully developed.
4. Active	Ovaries large in size, and noticeably irregular in shape as a result of a distended tunica. Ova are visible to the naked eye, bright orange in colour. Tunica bursts easily with pressure. Blood vessels abundant and clearly visible. Testes enlarged and lobate in shape with a triangular cross section. Sperm extruded on cutting. Creamy white in colour.	All stages of vitellogenesis present including final egg maturation. Tertiary yolk vesicle oocytes dominate. Zona granulosa and zona radiata well developed in tertiary yolk vesicles.  Testes show all stages of spermatogenesis. The seminiferous tubules and sperm ducts are well developed and full of spermatozoa.
5. Post-spawning	Ovaries are reduced in size and flaccid. Dark orange-red in colour. Ova are not visible to the naked eye. Testes are reduced in size, flaccid and triangular in cross section. Colouration is an opaque off-white.	Predominantly pre-perinuclear oocytes.  Testes with all stages of spermatogenesis. Fewer spermatozoa are visible in the seminiferous tubules and sperm ducts. Tubules become vacuous with a high proportion of 'empty space'.

macroscopic reproductive class (Table 1) and excised gonads were weighed to the nearest 0.01 g. The stomach and gonads of each fish were stored in 10% buffered formalin and sagittal otoliths were removed, cleaned and stored in eppendorf tubes. Macroscopic gonadal staging was validated histologically where a small section of tissue was removed from a subsample of fish and prepared for histological analysis by embedding the tissue in paraffin wax, sectioned to a thickness of 5–6 µm, and stained with haematoxylin and eosin. Stomachs were weighed to the nearest 0.01 g and their contents were removed and identified to the lowest possible taxonomic level.

#### Population structure and morphometrics

The relationship between *FL*, *TL* and *EM* was described using linear regression. For the *FL*–*EM* relationship both variables were natural-logarithm transformed. Sex ratios were used to describe population structure, and a contingency table was used to test the null hypothesis that population structure did not deviate from a 1 : 1 sex ratio.

#### Age determination and growth modelling

Preliminary investigation revealed that transverse sections of otoliths (burned or unburned) did not adequately expose the growth zones. Submersing whole otoliths in methyl-salicylate BP, and viewing with a reflected light source against a black

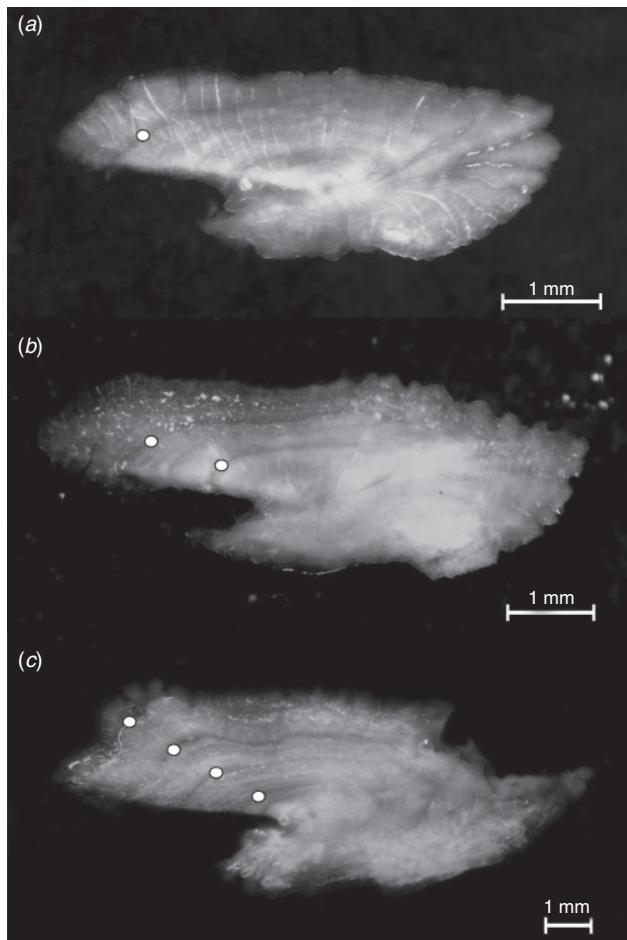
background was found to be the most suitable method of defining individual growth zones (Fig. 1), as suggested by McPhee (1999). The age of each fish was determined by counting the number of opaque zones on the otolith, starting at the nucleus and finishing at the distal otolith edge. A calibrated microscope eyepiece was used to define the nucleus edge using suspected age-zero fish. If two of the three readings agreed, then this estimate was accepted as the final age. If there was no agreement between all three readings then the otolith was rejected from further analysis.

The consistency of growth zone counts was assessed by calculating an index of average percentage error (IAPE) (Beamish and Fournier 1981) as:

$$IAPE = \frac{1}{n} \sum_{j=1}^n \left[ \frac{1}{R} \sum_{i=1}^R \frac{|X_{ij} - \bar{X}_j|}{\bar{X}_j} \right]$$

where *n* fish are aged, *R* is the number of times each fish *j* is aged, *X<sub>ij</sub>* is the *i*th age determined for the *j*th fish and  $\bar{X}_j$  is the average age calculated for the *j*th fish. A Bowker's test (Bowker 1948) was used to determine if age estimates between readers was symmetric.

The periodicity of opaque zone formation was validated using an otolith edge analysis (Campana 2001). The null hypothesis that a single growth zone is deposited annually was



**Fig. 1.** Whole sagittal otoliths of (a) 1-year-old, (b) 2-year-old and (c) 4-year-old *Trachinotus botla* viewed under reflected light on a black background while submersed in methyl-salicylate.

tested using a periodic logistic regression (Beamish *et al.* 2005) of the form:

$$\text{logit}(\theta_i) = \beta_0 + \beta_1 \sin\left(2\pi \frac{\text{MOY}_i}{PE}\right) + \beta_2 \cos\left(2\pi \frac{\text{MOY}_i}{PE}\right)$$

where  $\theta_i$  is the expected proportion of otoliths with an opaque zone present at the margin for each angular transformed month of any year  $\text{MOY}_i$ ,  $PE$  is the hypothesised (i.e. 12 for an annual cycle) or estimated monthly periodicity of growth deposition and  $\beta_0$ ,  $\beta_1$  and  $\beta_2$  are the regression coefficients. Regression parameters were estimated by non-linear minimisation of a negated binomial log-likelihood function of the form:

$$-LL = -\sum_{i=1}^{12} [m_i \ln(\theta_i) + (n_i - m_i) \ln(1 - \theta_i)]$$

where  $n_i$  is the number of otoliths examined per month and  $m_i$  represents the number of otoliths with an opaque zone present on the margin. A likelihood ratio test (LRT) was performed to test the null hypothesis that a single growth zone is deposited annually (Winker *et al.* 2010).

Growth was estimated by fitting the four-parameter Schnute model (Schnute 1981) to the observed age-at-length data of the form:

$$L(t) = \left( y_1^b + (y_2^b - y_1^b) \frac{1 - e^{-a(t-\tau_1)}}{1 - e^{-a(\tau_2-\tau_1)}} \right)^{\frac{1}{b}}$$

where  $y_1$  and  $y_2$  are the length of fish at the youngest ( $\tau_1$ ) and oldest ( $\tau_2$ ) aged fish, and  $a$  and  $b$  the growth curvature parameters. Model parameters were estimated using non-linear minimisation of negated normal log-likelihood function. An age correction factor was applied to the data, whereby 1 February was taken to be the theoretical birth date of all fish sampled. This was based on the timing of observed maximum reproductive activity. Both the Von Bertalanffy and Logistic growth models are nested within the Schnute model by respectively constraining  $b = 1$  or  $-1$ . A LRT was used to assess whether the full four-parameter Schnute model was more parsimonious than either the reduced model alternatives. Parameter variability was estimated using a parametric bootstrapping procedure (Efron 1979) with 1000 iterations. A LRT was conducted to test the null hypothesis that growth patterns between males and females were equal.

#### Reproductive biology

Sexual maturity was defined as the presence of either vitellogenic oocytes in the ovaries or the presence of well developed sperm ducts filled with spermatozoa within the testes (Table 1). Length- and age-at-50% maturity was estimated by fitting a logistic ogive to the proportion of sexually mature fish per 10 mm length class or age respectively. Only samples collected during the spawning season were included in the analyses. The logistic ogives for both length and age are described as:

$$P(\theta) = \left[ 1 + \exp\left(-\frac{\theta - \theta_{50}}{\delta}\right) \right]^{-1}$$

where  $P(\theta)$  is the proportion of mature fish in the length class or age class  $\theta$ ,  $\theta_{50}$  is the length- or age-at-50% maturity and  $\delta$  is the width of the ogive curve. Both  $\theta_{50}$  and  $\delta$  were estimated by non-linear minimisation of a negated binomial log-likelihood. Parameter variability was estimated using parametric bootstrapping with 1000 iterations. A LRT was conducted to test the null hypothesis that length- and age-at-50% were equal between the sexes.

A gonadosomatic index (GSI), only calculated for mature fish, was used as a proxy for reproductive activity and is calculated as the ratio of the gonad mass to eviscerated body mass. Spawning season was also determined by identifying those months with the highest proportion of 'Active' individuals from the macroscopic staging assessment.

#### Feeding biology

The importance of different food items to the diet of *T. botla* was assessed with three metrics. These were percentage mass (%M; the mass of a particular food item as a percentage of the total mass of the contents of that particular stomach), percentage

frequency of occurrence (%FO; number of stomachs containing particular food item expressed as a percentage of all stomachs containing food), and a relative index of importance (IRI) which was calculated as  $IRI = \%FO \times \%M$  (Hyslop 1980). Each calculated IRI was expressed as a percentage for all food items to facilitate direct comparisons between food items. Percentage by number was not incorporated into the IRI as some food items were too far digested to accurately identify individuals.

Variation in feeding intensity was investigated using a stomach fullness index (SFI) that is the ratio of the stomach content mass to the fish’s eviscerated body mass (Man and Hodgkiss 1977). Analysis of variance tested the null hypotheses that mean SFI was equal between seasons and size classes.

Principal component analysis (PCA) was used to investigate the relative importance of food items to the diet of *T. botla*, whereafter linear discriminate function analysis (DFA) was applied to classify the size classes according to their observed diets. Multivariate analyses were conducted in R (R Development Core Team 2011).

Results

Population structure and morphometrics

Of the 369 fish examined, 107 (29%) were male, 139 (38%) were female and 123 (33%) were unsexed (Table 2). Adult (>250 mm FL) sex ratio was slightly female-biased (1 : 1.42), however, the overall sex ratio of *Trachinotus botla* did not differ significantly from unity ( $\chi^2 = 2.99$ ; d.f. = 3,  $P = 0.39$ ). The relationship between FL and TL was described as  $TL\text{ (mm)} = 1.36\text{ FL (mm)} - 33.52$  ( $R^2 = 0.99$ ), whereas the length-eviscerated mass relationship was  $EM\text{ (g)} = 0.00002\text{ FL (mm)}^{2.96}$  ( $R^2 = 0.99$ ).

Age and growth

Of a total of 311 pairs of otoliths used to determine age, estimates from 273 (87.8%) were accepted. The overall IAPE was 15.1% and both reader’s age estimates were symmetrical ( $\chi^2 = 6.66$ , d.f. = 10,  $P = 0.76$ ). All otoliths interpreted from fish captured in November were found to have opaque margins, whereas the highest proportions of otoliths with translucent margins were sampled in March (41%) (Fig. 2). One opaque-translucent growth zone pair was deposited annually ( $\chi^2 = 2.32$ , d.f. = 1,  $P = 0.13$ ).

*Trachinotus botla* were found to be a fast growing, short-lived species (Fig. 3) as the oldest male and female fish were both 6 years of age and measured 434 and 495 mm FL respectively. Fish attained 132 mm FL within 2 months of their life, 30% of their maximum length, and grew almost linearly at a rate of 10% of their maximum length. Schnute’s (1981) model was found to be the most statistically appropriate ( $P < 0.01$ ) to describe the growth of *T. botla*. Male and female growth patterns did not differ significantly ( $\chi^2 = 1.47$ , d.f. = 4,  $P = 0.83$ ) from one another and all data were combined into a single growth model (Table 3).

Reproductive biology

Differences in length-at-50% maturity between males and females were notable but not statistically significant ( $\chi^2 = 9.5$ , d.f. = 2,  $P = 0.08$ ) with fish maturing at  $252.5 \pm 5.0\text{ mm FL}$  and

Table 2. Monthly size and sex distribution of *Trachinotus botla* sampled from northern KwaZulu-Natal, South Africa

Month	n	FL (mm)			Sex distribution		
		Mean	Min.	Max.	Male	Female	Unsexed
May	41	232.8	144	416	8	17	16
Jun	32	188.1	119	285	15	9	8
Jul	24	184.3	123	264	4	4	16
Aug	26	189.7	133	313	6	5	15
Sep	31	199.1	135	300	7	8	16
Oct	31	201.3	150	274	6	13	12
Nov	35	306.1	146	495	12	19	4
Dec	30	264	150	414	12	12	6
Jan	41	251.6	165	374	9	15	17
Feb	29	282.5	162	422	10	15	4
Mar	26	248.4	170	412	10	10	6
Apr	23	220.7	142	395	8	12	3

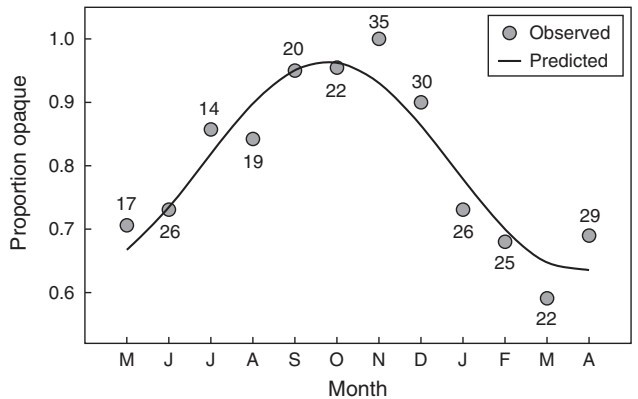


Fig. 2. Otolith edge analysis illustrating the monthly proportion of otoliths with opaque edges in *Trachinotus botla* from KwaZulu-Natal, South Africa. The solid line represents the predicted periodic regression model with an annual cycle.

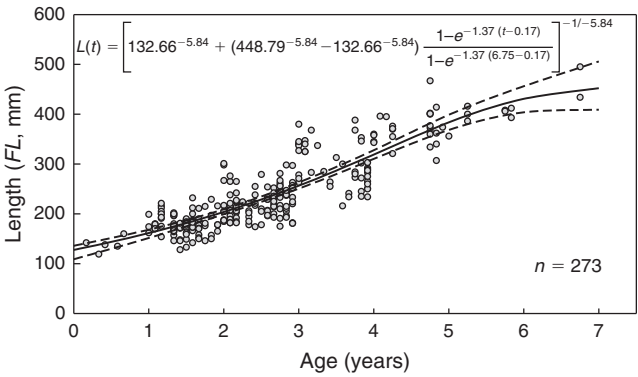


Fig. 3. Schnute (1981) growth model applied to combined sex length-at-age data for *Trachinotus botla* sampled from KwaZulu-Natal, South Africa. Dotted lines represent the 95% bootstrap confidence intervals.



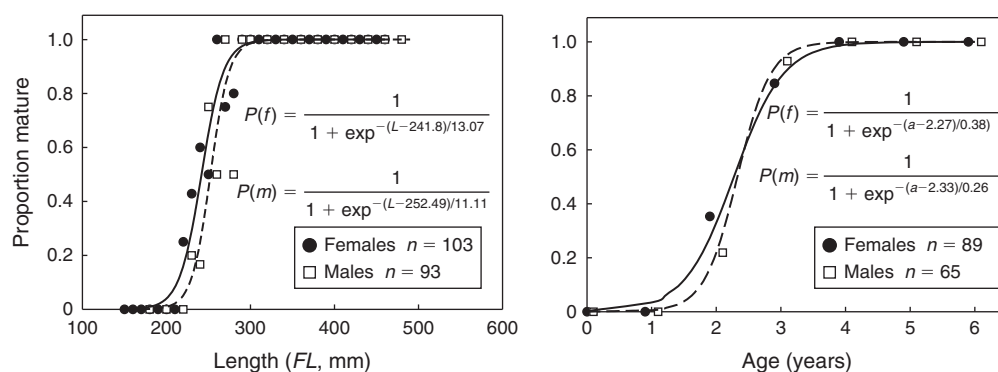
241.8 ± 5.7 mm FL respectively (Fig. 4). In contrast, age-at-50% maturity was found to be identical for males and females (2.3 ± 0.1 years). When the sexes were combined, the length-at-50% maturity was calculated as 247.2 ± 5.8 mm FL. Maturation was rapid, with all fish maturing within 70 mm (220–290 mm).

Five macroscopic classes were defined for males and females (Table 1) which were validated histologically. The proportions of the different classes exhibited a clear seasonal trend in gonad development for both sexes. Gonads in the ‘Developing’ and ‘Active’ classes dominated between November and February (Fig. 5) whereas ‘Post-spawning’ class individuals were only recorded in March, indicating a summer spawning season extending between November and February. Gonads in the ‘Juvenile/Resting’ class were the most prevalent between April and October and this class accounted for all of the gonads assessed between May and August. Similarly, mean GSI was the highest in November for females and December for males. GSI remained low between June and October for both sexes.

**Table 3.** Point estimates and summary statistics for the Schnute (1981) growth model applied to female, male and combined sex *Trachinotus botla* length-at-age data collected from northern KwaZulu-Natal, South Africa

CI, 95% confidence interval; CV, coefficient of variation; MLE, maximum likelihood estimate; SE, standard error

	Parameter	MLE	Summary statistics		
			CV	SE	CI
Females (n = 187)	a (year <sup>-1</sup> )	1.73	1.45	2.52	−0.42; 8.20
	b	−7.37	1.54	11.38	−36.33; 2.45
	L <sub>1</sub> (FL, mm)	129.45	0.09	11.47	103.35; 138.22
	L <sub>2</sub> (FL, mm)	472.38	0.07	31.28	417.46; 534.57
Males (n = 171)	a (year <sup>-1</sup> )	1.56	1.26	1.97	0.05; 7.41
	b	−6.47	1.38	8.94	−33.69; 0.74
	L <sub>1</sub> (FL, mm)	128.33	0.07	9.29	107.47; 137.78
	L <sub>2</sub> (FL, mm)	420.85	0.06	25.33	379.66–477.56
Combined (n = 276)	a (year <sup>-1</sup> )	1.37	1.38	1.89	0.06; 7.66
	b	−5.84	1.52	8.87	−35.11; 0.45
	L <sub>1</sub> (FL, mm)	132.66	0.05	6.49	116.33; 141.40
	L <sub>2</sub> (FL, mm)	448.79	0.05	22.31	408.48; 492.52



**Fig. 4.** Logistic ogives fitted to the observed proportion of mature male and female *Trachinotus botla* from KwaZulu-Natal, South Africa.

### Feeding biology

Of a total of 169 *T. botla* stomachs analysed, 34 (20.1%) were found to be empty. Fish of less than 250 mm FL had a significantly higher stomach fullness index (ANOVA,  $F = 4.22$ , d.f. = 4,  $P = 0.03$ ) than larger fish (Fig. 6). *T. botla* had a diverse diet with up to 10 different prey species found in a single stomach. The first two principal components of the PCA explained 44% of the variation among the 14 prey groups with the most important prey groups being teleosts, copepods, crab megalopae, mole crabs and mussels (Fig. 7). These five prey groups accounted for 68.3% of the ranking index in the diet of all fish investigated. Teleosts and copepods were the two most important food sources in small fish, whereas crabs and mussels were the most important food sources in larger fish (Table 4). Gastropods were the most important food source of the largest fish (>400 mm FL) examined. The DFA classified the fish sampled into two size groups – small (<300 mm FL) and large (>300 mm FL). A total of 84.8% were correctly classified, comprising a 92.7% classification rate for small fish and 50.0% for large fish.

### Discussion

Trachinoids are widely regarded as inshore species and all *Trachinotus* spp. investigated have been found to utilise the surf zone environment during some stage in their life history (McPhee 1999). Within South Africa, and presumably elsewhere, *T. botla* appears to be the only ‘permanent’ surf zone carangid species that completes its entire life cycle inshore. It is therefore unsurprising that it displays life history characteristics that are typical of surf zone specialists. These include fast growth with a short life span, a high natural mortality rate ( $M = 0.7 \text{ year}^{-1}$ , Parker *et al.* 2013), high fecundity, serial spawning (Table 5) and a diverse diet.

The growth estimates in this study are comparable to the growth of *T. botla* in Queensland, Australia (McPhee 1999), and typically similar to congeners (McPhee 1999; Mourad 1999; Muller *et al.* 2002; Murphy *et al.* 2007). Differential growth patterns between sexes occurred in larger fish and it was evident that female fish continued to grow to fruition whereas growth in male fish slowed with age. The consistency of reading otoliths was poor (IAPE = 15.1%), which may be a consequence of the

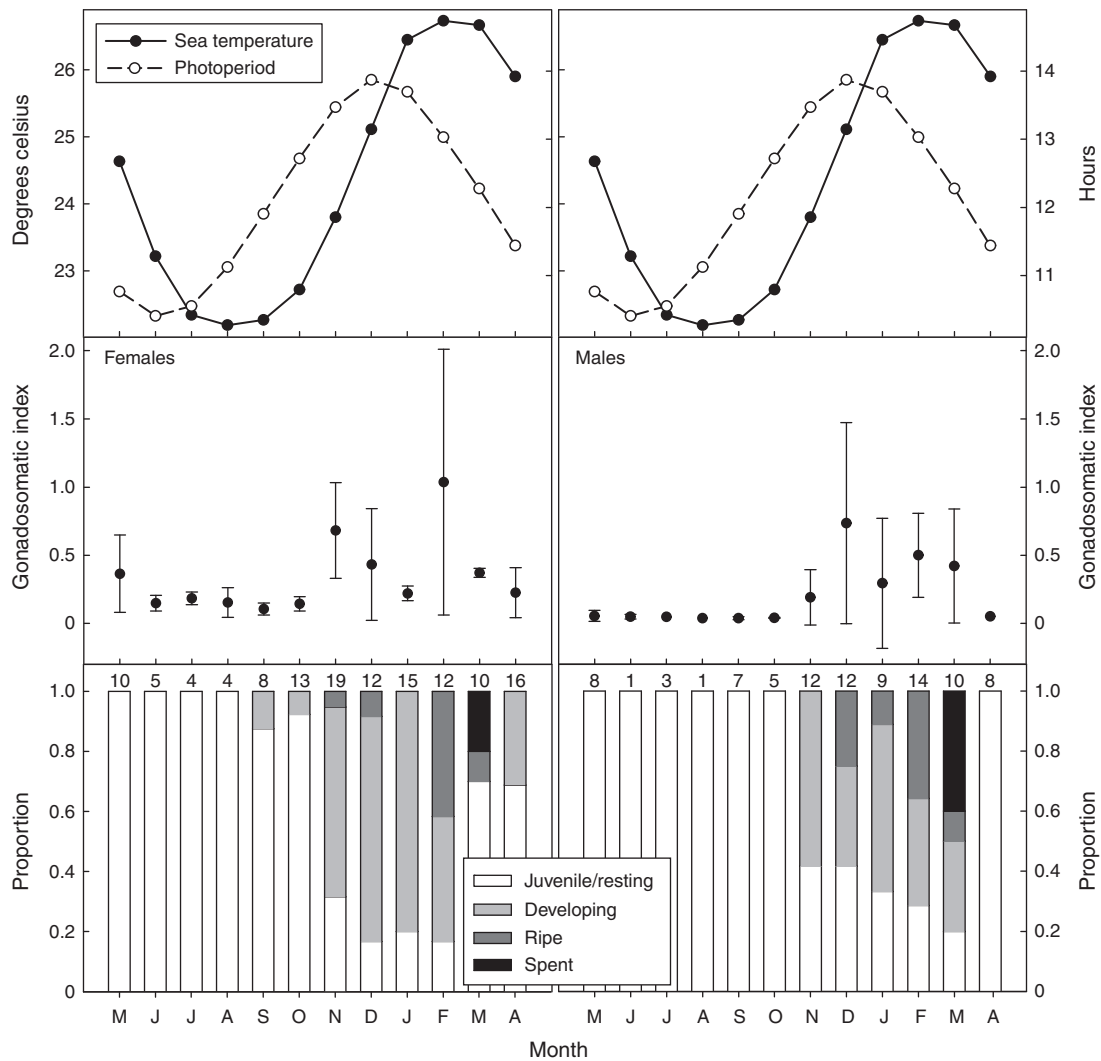


Fig. 5. Mean monthly gonadosomatic indices and observed proportions of macroscopic reproductive classes for *Trachinotus botla* sampled from KwaZulu-Natal, South Africa. Mean sea surface temperature and photoperiod for Sodwana Bay are also included.

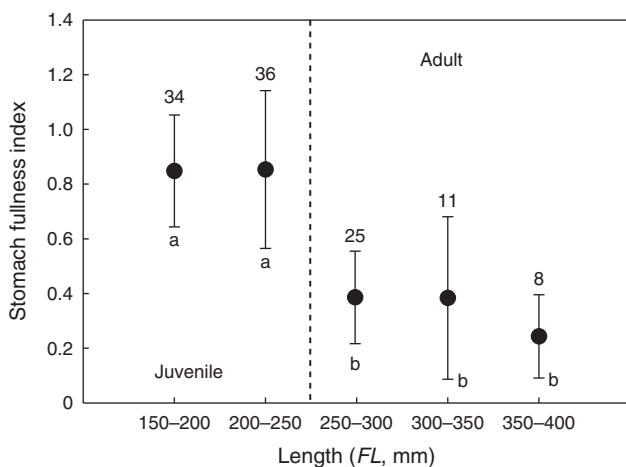
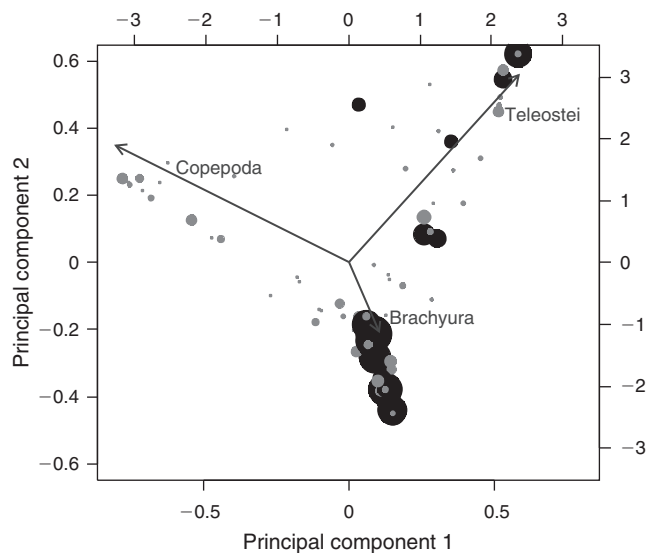


Fig. 6. Variation in stomach fullness index (SFI) as a function of length for *Trachinotus botla* sampled from KwaZulu-Natal, South Africa. Vertical bars denote 95% confidence intervals.

subtropical environment in which *T. botla* inhabits, as reduced seasonality often results in poor growth zone differentiation (Caldow and Wellington 2003; Morales-Nin and Panfili 2005). Young fish were the most problematic to age because of the inaccuracy determining the boundary between the nucleus edge and the first growth zone. Readability however improved with age with the lowest IAPE estimated in the 5-year age group.

Both macroscopic and histological examination of gonads indicated that the species has a protracted spawning season throughout the summer period (November to March) in northern KwaZulu-Natal. There was also evidence to suggest the species is likely to participate in multiple spawning events within a single protracted season with the presence of oocytes at a wide range of maturation classes. McPhee (1999) noted that *T. botla* in Australia participated in multiple spawning events and that the ovaries may alternate in producing the majority of eggs for each event. Serial spawning has also been identified in *C. ignobilis* (von Westernhagen 1974) and *C. melampygus* (Moriwake *et al.* 2001), and is indicative of a species that

inhabits a capricious environment, such as the surf zone. Serial spawning is hypothesised to be a ‘bet-hedging’ strategy whereby spawning numerous batches of eggs results in an overall reduction in risk of reproductive failure in resource poor periods (Nevoux *et al.* 2010).



**Fig. 7.** Principal component analysis ordination of 14 food items in the diet of *Trachinotus botla*. The diameters of the circles are scaled to represent the mass of each individual fish sampled. Grey circles represent small fish (<300 mm FL) and black circles represent large fish (>300 mm FL). Arrows represent the loadings of the three most important food items.

*Trachinotus botla* is an opportunistic predator that consumes a wide variety of prey items (Schleyer and Wallace 1986; McPhee 1999; Williams 2002), a characteristic typical of other surf zone specialists (Lasiak and McLachlan 1987; Brown and McLachlan 1990; Inoue *et al.* 2005). A distinct ontogenetic shift in diet was observed at ~300 mm FL and corresponds to 4.3 years of age. This dietary shift included both a change in the dominant prey items consumed and their quantity, occurred 2 years after sexual maturity and is presumably due to a change in habitat preference (see Werner and Gilliam 1984). Small fish were restricted to shallow areas of the inshore surf zone where they fed on copepods, small teleosts and mole crabs. Larger fish fed predominantly on mussels, gastropods and crab megalopa in deeper, reef-oriented habitats within the surf zone. Smaller fish also consumed significantly more food, possibly due to a combination of their higher metabolic demands and the lower protein and energy content in their diet. Evidence for megalopae and bivalves providing a higher quality food source (Timonin *et al.* 1992) is that the ontogenetic shift in diet corresponds to both the age and length at inflection of *T. botla*'s growth trajectory. Angling is considered an inherently biased sampling method (Bennett *et al.* 2009; Götz *et al.* 2009) and needs to be considered when interpreting stomach fullness as it selects for actively foraging fish.

Surf zone habitats are often referred to as ‘open’ systems as their motile faunal assemblages, such as plankton, are in constant flux. The abundance of plankton in the surf zone is determined by inshore currents and wave action, and is characterised by pulses of unsustainably high (superabundant) densities (Wooldridge 1983; Lasiak and McLachlan 1987). The ability of *T. botla* to effectively utilise ‘superabundant’

**Table 4.** Stomach contents analysis of small ( $n = 112$ ) and large ( $n = 26$ ) *Trachinotus botla* sampled in Sodwana Bay, South Africa

The importance of food items are quantified as percentages of frequency of occurrence (%FO), mass (%M) and an index of relative importance (%IRI). Values in bold indicate the three most important food items by either %FO, %M or %IRI

Food item	Small fish (123–299 mm FL)			Large fish (300–434 mm FL)		
	%FO	%M	%IRI	%FO	%M	%IRI
Amphipoda	0.89	0.04	<0.01	–	–	–
Arachnida	0.89	2.99	0.27	–	–	–
Ascidacea	0.89	<b>17.04</b>	1.51	–	–	–
Bivalvia	1.79	<b>28.07</b>	4.99	23.08	<b>14.15</b>	<b>20.84</b>
Brachyura	19.64	3.34	6.53	<b>38.46</b>	9.01	<b>22.13</b>
Cephalopoda	0.89	0.45	0.04	–	–	–
Copepoda	<b>53.57</b>	3.67	<b>19.59</b>	11.54	0.75	0.55
Gastropoda	8.04	0.85	0.68	<b>57.69</b>	3.86	14.21
Hippidae	9.82	<b>11.39</b>	<b>11.14</b>	11.54	<b>12.62</b>	9.29
Insecta	<b>24.11</b>	3.03	7.29	19.23	2.48	3.04
Isopoda	9.82	0.8	0.79	11.54	0.3	0.22
Mysidacea	16.07	0.56	0.9	7.69	0.19	0.09
Nematoda	17.86	0.49	0.87	19.23	0.02	0.03
Ostracoda	4.46	5.74	2.55	7.69	<b>18.28</b>	8.97
Penaeidea	25	3.99	9.92	11.54	1.28	0.94
Polychaeta	6.25	5.45	3.39	11.54	4.05	2.98
Teleostei	<b>50.0</b>	5.64	<b>28.06</b>	<b>34.62</b>	7.53	<b>16.63</b>
Unidentified/Mucus	9.82	1.11	1.09	7.69	0.13	0.07
<i>Velella</i> sp.	5.36	0.72	0.38	–	–	–

Table 5. A review of critical life history parameters of recreationally important carangid fishes

Species	Study area	Max. age	Max. length	Mortality rate	Age-at-maturity	Length-at-maturity	Sex ratio (M : F)	Spawning season	Evidence of serial Spawning	Reference
<i>Trachinotus botla</i>	South Africa	6	495 mm FL	$Z = 1.04 \text{ year}^{-1}$ , $M = 0.70 \text{ year}^{-1}$	2.3 year	247.2 mm FL	1 : 1.3	Summer (Nov–Feb)	Yes	Current study; Parker <i>et al.</i> (2013)
<i>Trachinotus botla</i>	Australia	6	489 mm TL	$Z = 1.75 \text{ year}^{-1}$ , $M = 1.20 \text{ year}^{-1}$	NA	361–370 mm TL	1 : 1	Summer (Oct–Apr)	Yes	McPhee (1999)
<i>Trachinotus carolinus</i>	Florida	4	635 mm TL	$M = 0.40 \text{ year}^{-1}$ , $Z = 0.40 \text{ year}^{-1}$	2 year	285–325 mm FL	NA	Feb–Sep	NA	Murphy <i>et al.</i> (2007)
<i>Trachinotus falcatus</i>	Florida	23	916 mm FL	NA	3.1 year	486–547 mm FL	NA	Summer (May–Jul)	NA	Crabtree <i>et al.</i> (2002)
<i>Caranx ignobilis</i>	Hawaii	9	1330 mm FL	NA	4 year	600 mm SL	1 : 1.4	Summer (Apr–Aug)	NA	Sudekum <i>et al.</i> (1991)
<i>Caranx melampygus</i>	Hawaii	5	710 mm FL	NA	2 year	350 mm SL	1 : 1.2	Summer (Apr–Nov)	NA	Sudekum <i>et al.</i> (1991)
<i>Caranx bucculentus</i>	Australia	8	493 mm SL	NA	NA	NA	1 : 1	All year with a peak in summer	Yes	Brewer <i>et al.</i> (1994)
<i>Seriola dumerili</i>	Mexico	15	1355 mm FL	$Z = 0.70 \text{ year}^{-1}$	NA	1090–1130 mm SL	NA	Summer (May–Jul)	NA	Manooch and Potts (1997)

prey items when the opportunity arises is a fundamental characteristic of a ‘true’ surf zone species (McFarland 1963; Keast 1977; Schleyer and Wallace 1986; Lasiak and McLachlan 1987). In particular, copepods and terrestrial insects were observed in large numbers when present in the stomachs of *T. botla*. Stomach contents of fish sampled in October had large quantities of formicid alates, which coincided with the general period of nuptial flights for these terrestrial insects in KwaZulu-Natal. Similarly, post-larval penaeid prawns were found in large numbers from stomachs sampled between May and June coinciding with peak larval recruitment of *Penaeus japonicus* and *P. indicus*, the two most common species in northern KwaZulu-Natal (Forbes and Cyrus 1991). It is unlikely that the small prey items that were consumed, particularly copepods, were individually identified and ingested. McPhee (1999) notes that *T. botla* does not possess the jaw structure associated with fish species that are able to capture zooplankton individually. Prey, such as copepods, are likely eaten non-selectively by ram suspension feeding through patches of high prey density.

Understanding the biology and life history characteristics of a species is crucial for the successful management of the fishery. *T. botla* exhibits fast growth and has a short life span; characteristics that facilitate a resource that is more suitable and better able to sustain with high levels of exploitation. In addition the *T. botla* fishery in KwaZulu-Natal is exclusively shore based and almost entirely recreational, with a limited subsistence sector. The commercial sale of the species is prohibited, and the fishery is strictly limited to rod and line angling. The nature of the fishery itself inherently limits the exploitation of the species. It is therefore unsurprising that a recent assessment revealed that the *T. botla* shore fishery of KwaZulu-Natal is in a stable state and the species is currently underexploited (Parker *et al.* 2013).

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