The life history and fishery assessment of largespot pompano, *Trachinotus botla,* in northern KwaZulu-Natal, South Africa

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Abstract

Largespot pompano, *Trachinotus botla*, is a surf zone carangid with a cosmopolitan distribution in subtropical and tropical waters. Within South Africa, the species occurs along the KwaZulu-Natal coastline where it is a popular recreational fishing target. Recreational fishing in southern Africa has developed significantly in recent years, and is now regarded as an industry with huge economic potential. The long-term contribution of South African recreational fisheries to local economies is reliant upon sustainable exploitation through effective management.

Trachinotus botla was found to grow rapidly with maximum observed age of six years. Otolith growth zone deposition was validated using edge analysis. Growth was similar between males and females until ~350 mm FL after which females continued to grow while growth in males slowed. The resulting overall sex ratio was slightly female-biased (1 male: 1.3 females). *Trachinotus botla* matures early with all fish considered to be mature at 290 mm FL, which corresponds to an age of three years. A protracted spawning season was observed ranging from November to February and there was evidence to suggest that *T. botla* is a serial spawner. Dietary analysis indicates that *T. botla* is an opportunistic predator with a catholic diet. The opportunistic utilization of “superabundant” prey items is a fundamental characteristic of the species feeding habits. An ontogenetic dietary shift was observed at approximately 300 mm FL that was linked to a shift in habitat preference.

This thesis provided the first evidence that infection by the tongue-replacing isopod, *Cymothoa borbonica*, reduces the growth rate of wild host fish populations despite not affecting the diet, feeding habits and feeding frequency of their hosts. These results also highlighted the inadequacy of condition factor as a proxy for quantifying the effects of cymothoids on their hosts, and identified the need to incorporate host age when assessing the effects of parasite infection. Information on the life-cycle of *C. borbonica*, including estimates of the hypothesized “infectious” period and its longevity were obtained through analysis of parasite infection patterns as a function of host age and length.

An assessment of the *T. botla* shore fishery of KwaZulu-Natal using historical catch data revealed that the fishery is stable. Productivity of the *T. botla* fishery increased towards the north of KwaZulu-Natal. Distinct seasonal variations in the *T. botla* fishery were also noted with catches peaking in summer months and lowest during winter. A per-recruit assessment revealed that the species is currently underexploited (SBR = 62% of pristine levels), and fishing mortality rate could be doubled before reaching the spawner biomass-per recruit target reference point of F_{SB40}. A combination of the life history characteristics of species, the nature of the recreational shore fishery together with the current management regulation of 5 fish person^{-1} day^{-1} has ensured the sustainable utilization of the *T. botla* resource in KwaZulu-Natal.

Table of Contents

Chapter 3 – The life history of largespot pompano, *Trachinotus botla*, in northern KwaZulu-Natal, South Africa

Chapter 4 – Evidence for the deleterious effects of the tongue-replacing isopod *Cymothoa borbonica* on the largespot pompano, *Trachinotus botla*

Chapter 5 – A spatio-temporal assessment of the *Trachinotus botla* shore fishery in KwaZulu-Natal, South Africa

Chapter 6 – General discussion and management recommendations

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Chapter 1

General introduction

Recreational fisheries are those where fishing is conducted by individuals for sport and leisure with a possible secondary objective of catching fish for personal consumption (Cooke and Cowx 2006). Rock-and-surf angling in South Africa is a popular recreational pastime which attracts many anglers mainly due to the high levels of accessibility to the coast and its affordability (Mann and Buxton 1997). Although recreational fisheries do not directly produce the financial benefits commonly seen in commercial fisheries, the knock-on economical and social implications of an accessible recreational fishery are considerable (Buxton & Clarke, 1991). In 1997 the South African shore angling sector was estimated to have more than 400 000 participants, contributing to 1.3% of the gross domestic product of local economies (Brouwer and Buxton 2002). These estimates have increased significantly in recent years and despite the paucity of information available, recreational fishing remains an important contributor to the GDP of many southern African countries (Potts *et al.* 2009).

It is largely recognized that a significant proportion of the recreational fishing sector is based on the non-catch related motivations related to fishing and that the benefits of recreational fishing are not directly related to the size of harvest. The willingness of participants to pay large sums of money for the opportunity to catch a single prized specimen was illustrated in an economic evaluation of an Angolan recreational fishery in 2006. The total contribution of the recreational fishery to the local economy was US$ 1007 per harvested fish and US$ 243 per harvested kg (Potts *et al.* 2009). Similarly, the coastal community of St Lucia in KwaZulu-Natal, South Africa, received US$ 1.2 million from recreational fishing in 2001 (Mann *et al.* 2002b). The recreational fishing industry in southern Africa undoubtedly has huge economical potential. To provide a sustainable benefit to local economies in developing countries, it is imperative that recreational fisheries remain healthy and sustainable in the long-term.

The environmental demands of a recreational fishery are considered to be far less than commercial fisheries. McPhee (1995) defines the requirement of a recreational fishery as the reasonable probability of an angler catching one or more fish during an outing. Declines in fish stocks attributed to recreational fisheries are predominantly disregarded by fisheries managers and there is a widespread perception that recreational fishing is a benign activity (Cooke and Cowx 2006). Drastic declines in catches in the South African and Namibian inshore fisheries as a result of recreational fishing pressure have been observed in recent years (Potts *et al.* 2009). Consequently, potential revenue has been lost as recreational anglers have begun seeking alternative destinations. Such situations are not limited to developing countries alone. An evaluation of the Australian recreational fishing industry concluded that changes to management and monitoring programs are necessary to ensure the long-term sustainability of the countries recreational fisheries (McPhee *et al.* 2002).

The term “linefish” commonly refers to commercially and recreationally important fish species which are usually caught using hook and line techniques. The earliest biological research into economically important linefish species in South Africa was initiated in 1962 (Ahrens 1964) as a result of growing concern for the sustainability of linefish resources. Since then a considerable amount of research effort has focused on aspects of the life history of the important commercial and recreational target species (Brouwer and Buxton 2002). To date, marine scientists have conducted research on over 100 linefish species (Palmer *et al.* 2008). Active management of South African shore-angling fisheries has been conducted since the 1970‟s. Fisheries management was formalized with the implementation of a comprehensive suite of national management regulations designed to limit catch and effort in 1985 (Brouwer *et al.* 1997). The regulations were subsequently revised in 1992, and have been regularly updated with continual research. Significant political changes in 1994 resulted in a shift towards the current research model of management-based research, sustainable resource use, status reports and long-term monitoring (Palmer *et al.* 2008). These agendas were later reinforced as the primary objectives of the Marine Living Resources Act (MLRA, No 18 of 1998). Currently there are two research coordinating groups dedicated to linefish research in South Africa - the South African Marine Linefish Management Association (SAMLMA) and the Marine Linefish Research Group (MLRG). SAMLMA comprises of representatives in the recreational and commercial linefishing sectors, as well as regional conservation authorities and linefish scientists. It is formally constituted interest group, which is recognized in terms of the Marine Living Resources Act as the official body representing linefish users. The MLRG comprises of approximately 50 professional scientists and students based at several academic and research organizations throughout South Africa (Palmer *et al.* 2008).

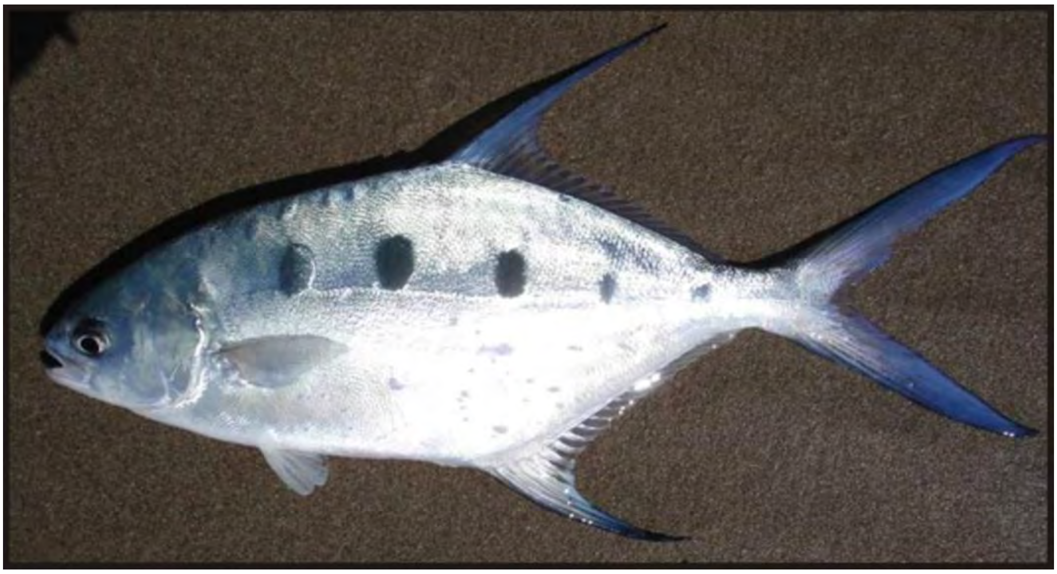

Figure 1.1: Largespot pompano *Trachinotus botla*

Largespot pompano *Trachinotus botla*

Trachinotus botla, known as the largespot pompano or wave garrick in South Africa and swallowtail dart in Australia, is one of approximately 54 carangid species inhabiting southern Africa (van der Elst 1993, Smith and Heemstra 2003). There are 19 species in the genus *Trachinotus* worldwide, four of which are found in southern African waters. These are *T. africanus, T. baillonii, T. blochii* and *T. botla. Trachinotus botla* (Figure 1.1) has been reclassified on several occasions. The species was first described by Russell in 1803 as *Botla parah*, reclassified by Shaw (1803) as *Scomber botla*, and again in 1831 as *Trachinotus russelli* by Cuvier and Valenciennes. The genus "*Trachinotus*" is derived from the term "rough back" and "*botla*" originates from the common name for "fish" in India in the early 1800‟s (van der Elst 1993, McPhee 1999). *Trachinotus* species are commonly referred to as "pompanos", derived from the Spanish "pampano" for grape leaf and is thought to be a reference to the similarities in shape between the leaf and the fish (van der Elst 1993). *Trachinotus botla* has a cosmopolitan distribution throughout the Indo-west Pacific (Williams

2002). The species has been found from South Africa to Australia, including the Madagascar, Seychelles and the Maldives. Within South Africa the species is confined to the sub-tropical waters north of East London (van der Elst 1993). *Trachinotus botla* is the most abundant pompano found along the coastline of South Africa and is most abundant in the Maputaland area of northern KwaZulu-Natal.

Trachinotus botla is an important recreational shore angling species within South Africa where it accounts for up to 30% of the shore angling catch composition in northern KwaZulu-Natal (Mann 2008). It is often targeted by light tackle angling because of its aggression and speed and is also commonly used as live bait when targeting larger fishes such as sharks and the giant kingfish, *Caranx ignobilis*.

Despite *T. botla's* importance as a recreational angling species, scientific information pertaining to its biology and life history is sparse. This thesis therefore presents the first scientific investigation in South Africa. Internationally, a single, unpublished biological study of the species was conducted off the coast of Queensland, Australia (McPhee 1995).

Thesis Outline

Biological studies form the basis of management strategies and specific biological traits determine the fundamental input parameters for stock assessments (FAO 2008). The aim of this thesis was to contribute to the understanding of all biological and life history aspects of *T. botla* and use this information to provide an assessment of its fishery. To achieve this aim, this thesis has been divided into five additional chapters.

Chapter 2 is a description of the study area, provided to give this thesis a geographical and oceanographical reference. This chapter also provides a summary of the data used in subsequent analyses.

Chapter 3 investigates the life history of *T. botla*, concentrating on age and growth, reproduction, diet and feeding behavior.

Chapter 4 provides information on the tongue-replacing isopod parasite *Cymothoa borbonica* that infects *T. botla.* This chapter investigates parasite prevalence and the fundamental characteristics of the host-parasite relationship. Insights into the life history traits of the parasite and the effects of parasitism on its host, *T. botla*, are also discussed.

Chapter 5 is an assessment of the recreational shore fishery of *T. botla* within KwaZulu-Natal. The shore fishery is described using historical catch data over the past two decades. The assessment aims to describe the current status of the *T. botla* stock, the behaviour of the resource users, and the potential impacts of varying degrees of exploitation on the resource.

This thesis concludes in Chapter 6. This chapter discusses the general findings of the thesis and provides management recommendations and future research directions.

Chapter 2

Study area

All areas sampled were located within the iSimangaliso Wetland Park (the former Greater St. Lucia Wetlands Park), a World Heritage Site that was proclaimed in December 1999 (Figure 2.1). The Wetland Park stretches along the Zululand coast from Maphelane in the south to Kosi Bay in the north, covering 220 km of coastline. The IWP encompasses the shoreline as well as the marine area within 5 kilometers of the shoreline and is a multi-zoned Marine Protected Area (MPA). Although the MPA is primarily a controlled zone, allowing for limited fishing access, three no-take "sanctuary" zones exist (DEAT 2006). Most samples were collected from Sodwana Bay (27°32'24.6" S; 32°40'47.9" E). Fish were collected using rod and reel. As the use of vehicles on the beach is prohibited beyond the 2 km zone, sampling in Sodwana Bay was conducted within 5 km north and south of Jesser Point.

Sodwana Bay (Figure 2.2) lies between tropical and subtropical zones and has warm, moist summers and mild, dry winters. Average monthly surf zone temperatures vary between 22.2 - 26.7 °C (ORI 2011). The continental shelf is relatively narrow (2.1 – 4.1 km wide) and largely encrusted with a thin veneer of corals (Celliers and Schleyer 2002). The rich coral communities found in the Sodwana Bay area are the Western Indian Ocean‟s highest latitude coral reefs (Glassom *et al.* 2006). The area has a vast diversity of ichthyofauna which accounts for nearly 85% of the 399 reef fish species endemic to the West Indian Ocean region (UNESCO 2008). It is an area of high recreational use, particularly SCUBA diving and recreational angling (Figure 2.3). In 1996 there were a total of 17 692 boat launches and 118 389 recreational SCUBA dives recorded in Sodwana Bay (Schleyer and Tomalin 2000). Shore angling effort within iSimangaliso Wetland Park is also high, and an estimated 26 213 angler-outings were recorded in 2010 (Maggs 2011).

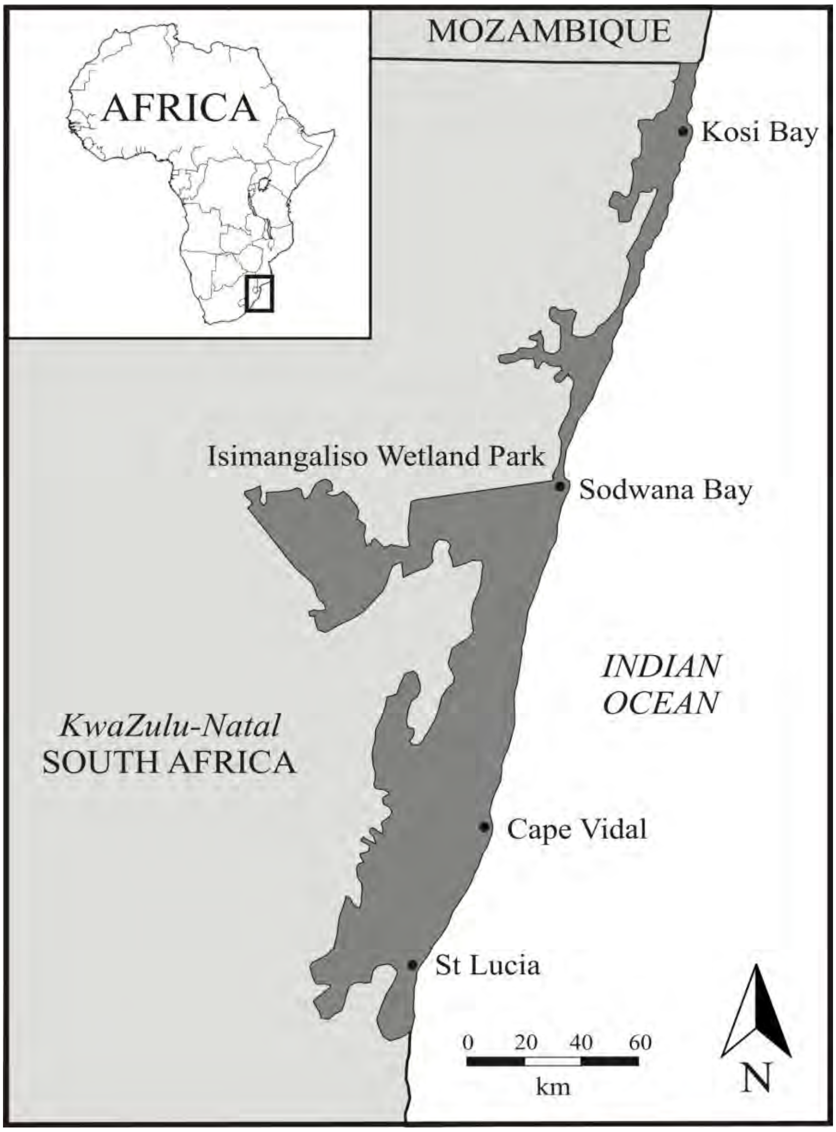

Figure 2.1: Map of the study area indicating the position of iSimangaliso Wetland Park within KwaZulu-Natal, South Africa.

The most important large-scale oceanographic feature in the study area is the Agulhas Current. Inshore current flow is predominantly southward and commonly reaches 0.5 - 0.75 m/s, but rarely exceeds the maximum (Roberts *et al.* 2006). Satellite imagery has revealed the existence of eddies which develop offshore of Mozambique and spiral southwards into South African waters with decreasing velocity. As a result, the northern inshore waters around Sodwana Bay are not as strongly influenced by the Agulhas Current as the waters further south in KwaZulu-Natal (Ramsay 1994). However, given a few consecutive days of a south – southeasterly wind, the warm Agulhas current water is retained close to shore resulting in warmer, cleaner water within the surf zone.

Figure 2.2: Aerial photograph of Jesser point, Sodwana Bay. (Panoramio 2011).

Figure 2.3: Sodwana Bay is an area of high recreational use, particularly SCUBA diving. Vehicles are permitted on the beach within a 2 km stretch north of Jesser point. (Photographs supplied by Steyn 2008)

Figure 2.4: Sandy beaches with scattered rock outcrops are the preferred habitat characteristics of *Trachinotus botla*.

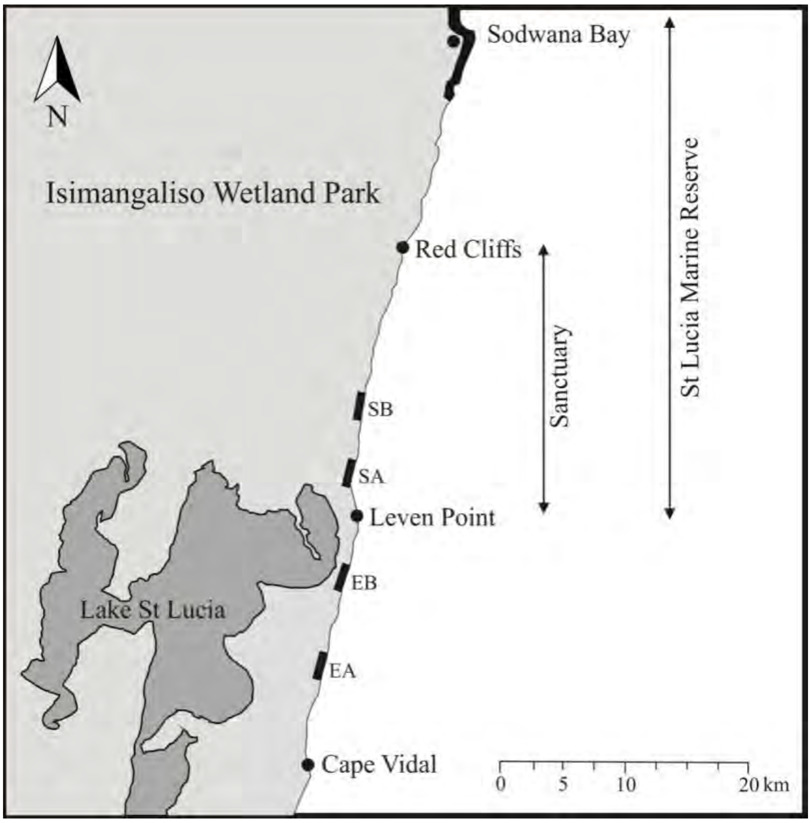

Figure 2.5: Map of the St Lucia Marine Reserve and Sanctuary showing the area sampled around Sodwana Bay. The map also indicates the St Lucia Marine Reserve fish monitoring and tagging sampling sites. The EA and EB sites are in the previously exploited area, while the SA and SB sites are within the sanctuary area. "▬" indicates areas that were sampled. Adapted from Mann (2008).

Table 2.1: Summary of the data used in this thesis.

Data	**Area sampled**	**Collection method**	**Data use**
This thesis	Sodwana Bay, St Lucia Marine Reserve Sanctuary (SA & SB), Previously exploited area (EA &EB)	Angling and collection from recreational fishermen	Biology and life history analyses, parasite analyses and stock assessment parameter estimates
National Marine Linefish System (NMLS) data	KwaZulu-Natal	Surveys of recreational shore fishermen (Maggs 2011)	Description of *Trachinotus botla* shore fishery and stock assessment parameter estimates
ORI/WWF-SA National tagging project data	South Africa	Public participation by recreational fishermen (Dunlop and Mann 2011)	Movement analyses and stock assessment parameter estimates

Samples from the Sodwana Bay area were supplemented with additional samples from the St Lucia Marine Reserve (SLMR) and data from the National Marine Linefish System (NMLS) and ORI/WWF-SA National tagging project (Table 2.1). The SLMR program, established by the Oceanographic Research Institute (ORI), aims to record species composition, size composition, catch per unit effort (CPUE) and individual fish movements in the St Lucia Marine Reserve (Mann 2008). Sampling has focused in the restricted “no take” sanctuary zone located between Red Cliffs and Leven Point and the controlled fishing stretch of coastline south of the Sanctuary zone, between Leven Point and Cape Vidal (Figure 2.5). Although the latter area is open to fishing, Mann (2008: 1) describes the area as “previously exploited” as there has been a drastic reduction in the fishing effort in the area due to lack of accessibility subsequent to the beach driving ban in 2002 that prohibited beach access to powered vehicles (Mann 2008).

Chapter 3

The life history of largespot pompano, *Trachinotus botla*, in northern KwaZulu-Natal, South Africa

Introduction

The life history of an organism typically refers to the chronological schedule of important biological events in an organism's lifetime. These events include juvenile development, sexual maturity, parental investment, senescence, and ultimately mortality. Life history strategies are largely dependent on the principles of evolutionary biology and ecology, and the variety of life histories traits exhibited are as a direct result of natural selection. King and McFarlane (2003) describe these traits as underlying determinants for a species response to proximate and ultimate environmental conditions. The role of the environment in selecting for these life history traits is particularly noticeable in unpredictable environments. Inconsistency within an environment often leads to plasticity in several life history traits, resulting in these traits changing depending on the current environmental conditions (Law 2000). Life history traits also respond and evolve to exploitation. Documented affects include an increased growth rate (Jennings *et al.* 1999), early maturation (Jennings *et al.* 1999, Gotz *et al.* 2008) and a shorter life span (Richardson 2010). If an organism is exploited its life history needs to be considered as it provides necessary information pertinent to its management (King and McFarlane 2003).

Life history theories have been simplified into recognisable concepts such as the *r*- *K*-continuum (MacArthur and Wilson 1967), "bet-hedging" (Stearns 1976) and the trilateral continuum (Winemiller and Rose 1992). Considering the complex array of variables that contribute to a species" life history, it is unlikely that any single theory would sufficiently describe it. These theories are clearly an oversimplification, but provide a conceptual ecological framework that can, if necessary, be applied in fisheries management. For example, those species with similar life-history traits can be grouped, and observed trends in one species can be extrapolated to other species within the same grouping.

The ability to accurately determine the age of a species is one of the most essential aspects of life history assessments (Bradford 1991, Morison *et al.* 1998, Sparre and Venema 1998, Campana 2001) as it provides temporal scaling for essential biological processes. Fish are generally aged by counting growth increments on calcified hard structures, with otoliths, scales and vertebrae being the most commonly used (Campana 2001).

The evolution of a particular reproductive strategy is a result of complex interactions between environmental, physiological, and phylogenetic characteristics. These may be grouped into two distinct factors - proximate causal factors (i.e. a direct cue influencing adult fish) and ultimate causal factors (i.e. developed by natural selection acting on survivorship and recruitment of larvae) (Lobel 1989). The principle goal is to time spawning periods such that physiological requirements necessary for early life-history stages of potential offspring are optimised, maximising the species chances for survival (Sheaves 2006). An understanding of a species‟ reproductive activity is essential to the classification of its life history strategy (King and McFarlane 2003).

Dietary information contributes to the knowledge of a species‟ functional niche within its ecosystem (Hyslop 1980). Niche segregation may be achieved through multiple elements including temporal, spatial and/or behavioural differences in habitat utilization (Werner and Gilliam 1984, Lasiak and McLachlan 1987). Sized-based changes in diet, otherwise known as ontogenetic dietary shifts, are well-studied (Werner and Gilliam 1984, Winemiller 1989, Dahlgren and Eggleston 2000, Garrison and Link 2000, Layman *et al.* 2005). Ontogenetic segregation suggests different ecological roles within a species based on size, and is thought to be an ecological adaptation to reduce intraspecific dietary overlap and competition (Garrison and Link 2000). Species interactions and specific behavioral patterns are often driven by the need to acquire nutrition. Understanding these interactions through dietary analysis and bioenergetics is important component of understanding the biology and life history of a species (Hansen *et al.* 1993).

Despite the structurally homogenous nature of many surf zones, its‟ physical variability influences the community composition and biomass it sustains (Beyst *et al.* 2002). Prey availability, both in quantity and quality, may be a major factor influencing the structure of fish assemblages in these dynamic ecosystems (Lasiak and McLachlan 1987). Motile faunal assemblages associated with surf zones are not discrete entities and are in constant flux (Lasiak and McLachlan 1987). The unpredictable nature of surf zones favours non-specialist feeders which are able to take advantage of a wide range of food items and the opportunistic utilization of "superabundant" prey items is common amongst surf zone teleosts (McFarland 1963, Keast 1977, Schleyer and Wallace 1986, Lasiak and McLachlan 1987)

Several carangid species inhabit the surf zone of the iSimangaliso Wetland Park, of which *T. botla* is the most common. The aim of this chapter was to describe the biology and life-history of *Trachinotus botla* from northern KwaZulu-Natal, the most south-westerly population in its global distribution. Aspects include an investigation into its age and growth, maturity, population structure, spawning and reproductive periodicity and a comprehensive evaluation of the diet and feeding habits.

Methods and materials

General sampling

Sampling was conducted between May 2010 and May 2011 and was restricted to rod and line angling from the shore. Other forms of sampling such as seine netting were prohibited to ensure the environmental impacts of the project are kept to a minimum, and sampling techniques were within the iSimangaliso Wetland Park recreational regulations. Large fish were targeted using baited hooks, and smaller fish were targeted using artificial lures. In addition, catches from recreational fishermen were collected whenever possible to supplement monthly samples. All *T. botla* retained were euthanized immediately after capture by pithing and stored on ice in an insulated box.

In the laboratory, fish were measured for fork length (FL), total length (TL), whole mass (g) and eviscerated mass (g). The gonads, gut and viscera were removed and each fish was sexed and assigned a macroscopic reproductive stage (Table 3.1). The stomach and gonads of each fish were stored in 10% buffered formalin for further analysis. The sagittal otoliths were removed, cleaned and stored in eppendorf tubes for later ageing. Each fish was checked for the presence of the tongue-replacing isopod parasite *Cymothoa borbonica*. If present the length of each parasite, from the head to the posterior tip of the pleotelson, was measured to the nearest 0.1mm with vernier calipers.

Table 3.1: Macroscopic and histological staging criteria used to assess the gonads of female and male *Trachinotus botla* sampled from northern KwaZulu-Natal between May 2010 and May 2011.

Stage	Macroscopic description	Histological description
1. Immature	Ovaries discernable as thin transparent bands. Sex not distinguishable.	Oogonia and pre-perinuclear oocytes are present on the ovary.
	Testes discernable as thin transparent bands. Sex not distinguishable.	Spermatogonia predominant. No spermatocytes, spermatids or spermatozoa visible.
2. Juvenile/Resting	Ovaries are thread-like at the anterior, but are definitively lobed towards the posterior. Posterior lobe is slightly opaque in appearance.	Ovaries dominated by pre-perinuclear and early perinuclear oocytes. A few late perinuclear oocytes are present.
	Slight increase in width of testes from mid-section to posterior. White in colour.	Seminiferous tubules start to develop and contain spermatocytes.
3. Developing	Ovaries moderate in size as the lobed posterior progresses forward. Opaque in appearance and ova not visible to the naked eye.	Characterised by oocyte stages up to the cortical alveoli stage. First appearance of primary yolk vesicle oocytes.
	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 veins and arteries clearly visible. No sperm present.	Spermatocytes are dominant in the outer region and spermatids dominate the inner region tubules. Seminiferous tubules and sperm ducts not fully developed.
4. Active/Ripe	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 and arteries abundant and clearly visible.	All stages of villetogenesis present including final egg maturation. Tertiary yolk vesicle oocytes dominate. Zona granulosa and zona radiata well developed in tertiary yolk vesicles.
	Testes enlarged and lobate in shape with a triangular cross section. Sperm extruded on cutting. Creamy white in colour.	Testes show all stages of spermatogenesis. The seminiferous tubules and sperm ducts are well-developed and full of spermatozoa.
5. Post Spawning /Spent	Ovaries are reduced in size and flaccid. Dark orange-red in colour. Ova are not visible to the naked eye.	Predominantly pre-perinuclear oocytes.
	Testes are reduced in size and flaccid. Triangular shaped cross section. Colouration is an opaque off-white.	Testes with all stages of spermatogenesis. Fewer spermatozoa are visible in the seminiferous tubules and sperm ducts. Tubules have a high proportion of empty "space".

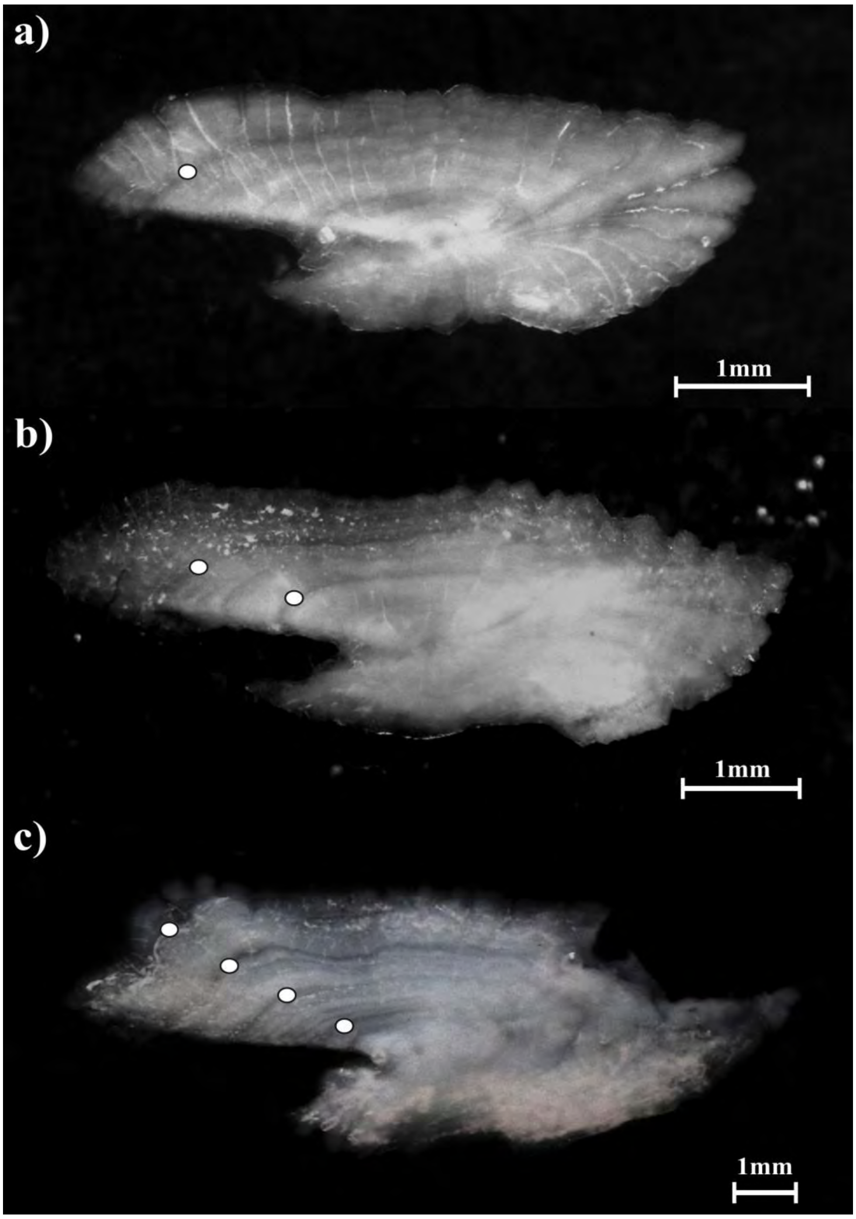

Figure 3.1: Whole sagittal otoliths of *Trachinotus botla* viewed under reflected light on a black background while submersed in methyl-salicylate. (a) 1-year old individual, (b) 2-year old individual and a (c) 4-year old individual.

Morphometrics and population structure

The relationships between fork length (FL) and total length (TL), and between FL and weight (W_t) were described using linear regression. For the length-weight regression, both variables were natural-logarithm transformed. Fulton‟s condition factor (*CF*) was calculated as:

$$CF = \frac{W}{FL^3} \times 1000$$

A students *t*-test was used to test the null hypothesis that mean male and female CF were equal.

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 and growth

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 (Figure 3.1). 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. Two independent readers were used. The author read the otoliths on two separate occasions, while the second reader undertook a single reading. Both readers had no prior knowledge of the fish size or capture date. 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 percent error (IAPE) (Beamish and Fournier 1981) as:

$$IAPE = \frac{1}{n}\sum_{j=1}^{n}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{\left|X_{ij} - \bar{X}_j\right|}{\bar{X}_j}\right] \times 100$$

where n fish are aged, R is the number of times each fish j is aged, X_{ij} is the i^{th} age determined for the j^{th} fish and X_j is the average age calculated for the j^{th} fish. A Bowker‟s test of symmetry (Bowker 1948) was used to test the null hypothesis that there is no difference in the symmetry of readings between readers.

Growth zone formation was indirectly validated using edge analysis (Campana, 2001), where the presence of either an opaque or translucent zone on the margin of each otolith was recorded and the month of capture noted. The data was then transformed into a relative frequency of all otoliths with an opaque margin per month. The periodic formation and subsequent deposition of growth zones was determined using a periodic logistic regression (Beamish *et al.* 2005) of the form:

$$Logit\ (\theta) = \beta_0 + \beta_1 \sin\left(2\pi \frac{MOY_i}{PE}\right) + \beta_2 \cos\left(2\pi \frac{MOY_i}{PE}\right)$$

where θ_i is the expected proportion of otoliths with an opaque zone present at the margin for each angular transformed month of any year MOY_i, PE is the assumed or estimated monthly periodicity of growth deposition (i.e. 12 for an annual cycle) and β_0, β_1 and β_2 are the regression coefficients. Regression parameters were estimated by non-linear minimization of a negated binomial log-likelihood function of the form:

$$-LL = -\sum_{i=0}^{11} [m_i ln(\theta_i) + (n_i - m_i) ln(1 - \theta_i)]$$

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 hypothesis that a single growth zone is deposited on a yearly basis (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:

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

where y_1 and y_2 are the length of fish at the youngest (τ_1) and oldest (τ_2) aged fish, and a and b the growth curvature parameters. An age correction was applied to the data, whereby the 1st of February was taken to be the theoretical birth-date of all fish sampled. This was based on the observed maximum reproductive activity. Parameter variability was estimated using a parametric bootstrapping procedure (Efron 1979) with 1000 iterations. A likelihood ratio test

(LRT) was conducted to test the null hypothesis that growth patterns between males and females differed significantly.

Reproductive biology

All gonads were weighed to the nearest 0.01g and a subsample of fish gonads were selected for histological analysis. These gonads were chosen according macroscopic staging and were representative of all stages for both males and females. Preparations for histological analysis involved removing small sections of tissue from the posterior of a randomly selected lobe of the gonad and embedding the tissue in paraffin wax, sectioned to a thickness of 5 – 6 µm, and stained with Haematoxylin and Eosin.

Length- and age-at-50% maturity was estimated by fitting a logistic ogive to the proportion of sexually mature fish per 10mm length class or age, respectively. The logistic ogive for both length and age is described as:

$$P(L) = \frac{1}{1 + \exp(-(L - L_{50})/\delta)}$$

where $P(L)$ is the proportion of mature fish in the length class or age class L, L_{50} is the length or age at 50% maturity and δ is the width of the ogive curve. Both L_{50} and δ were estimated by non-linear minimization of a negated binomial log-likelihood. A likelihood ratio test (LRT) was conducted to test the null hypothesis that length- and age-at-50% were equal between the sexes. A gonadosomatic index (GSI) was used as a proxy for reproductive activity and is calculated as:

$$\mathrm{GSI} = \frac{\text{gonad mass (g)}}{\text{eviscerated body mass (g)}} \times 100$$

Spawning season was determined by identifying those months with the highest proportion of ripe individuals from the macroscopic staging assessment, and corroborated with high monthly GSI.

The cyclic pattern of reproductive activity was also assessed using a periodic regression. The influence of temperature on GSI was investigated by adding mean water temperature as independent variable

$$\mathrm{GSI} = \beta_0 + \beta_1 \sin\left(2\pi \frac{MOY_i}{P}\right) + \beta_2 \cos\left(2\pi \frac{MOY_i}{P}\right) + \beta_3(T_i \times MOY_i)$$

where MOY_i is the month of the year, P is the periodicity of reproductive activity (in months) and β_0, β_1 and β_2 the regression parameters to be estimated. Parameter β_3 is the additional temperature parameter and T_i is the temperature variable for the month MOY_i. Regression parameters were estimated using non-linear least squared regression.

Feeding biology

Once in the laboratory, stomachs were weighed to the nearest 0.01 gram and their contents removed. All food items were identified to the lowest possible taxonomic group using taxonomic keys. The contents were dried in an oven for 24 hours at 50 °C, after which they were re-weighed to the nearest 0.1 mg.

Variation in feeding intensity due to either season or size was investigated using a stomach fullness index (SFI) proposed by Man and Hodgkiss (1977) of the form:

$$SFI = \frac{Mass\ of\ stomach\ contents\ (g)}{Eviscerated\ mass\ of\ fish\ (g)} \times 100.$$

ANOVA was used to test the null hypotheses that mean SFI did not differ between season and fish size.

Principal Component Analysis (PCA) was used as an exploratory data analysis approach to investigate the relative importance of food items to the diet of *T. botla*. A linear discriminate function analysis was then used to categorize the size classes according to observed dietary composition. Further assessment of the importance of food items was completed using three different methods of stomach analysis. These were percent frequency of occurrence (*%F*; number of stomachs containing particular food item expressed as a percentage of all stomachs containing food), percentage by number (*%N*; the number of individuals in each food category expressed as a percentage of the number of total individuals in all food categories), and percentage by mass (*%M*; the mass of a particular food item as a percentage of the total mass of the contents of that particular stomach) (Hyslop 1980). The importance of each food item was determined through the use of a ranking index, $RI = \%F \times \%M$ (Hyslop 1980). Each calculated *RI* was expressed as a percentage for all food items to facilitate direct comparisons between food items. Percent by number was not incorporated into the *RI* as some food items were too digested to accurately identify individuals.

Results

Morphometrics and population structure

The relationship between FL and TL was described as TL = 1.36 FL - 33.52 (R^2 = 0.99), while the length-weight relationship for both males and females was $W_t = 0.00002\ \mathrm{FL}^{2.96}$ (R^2 = 0.99). There was no significant difference in condition factor between males and females (t-test*,* df = 146*,* $p = 0.50$).

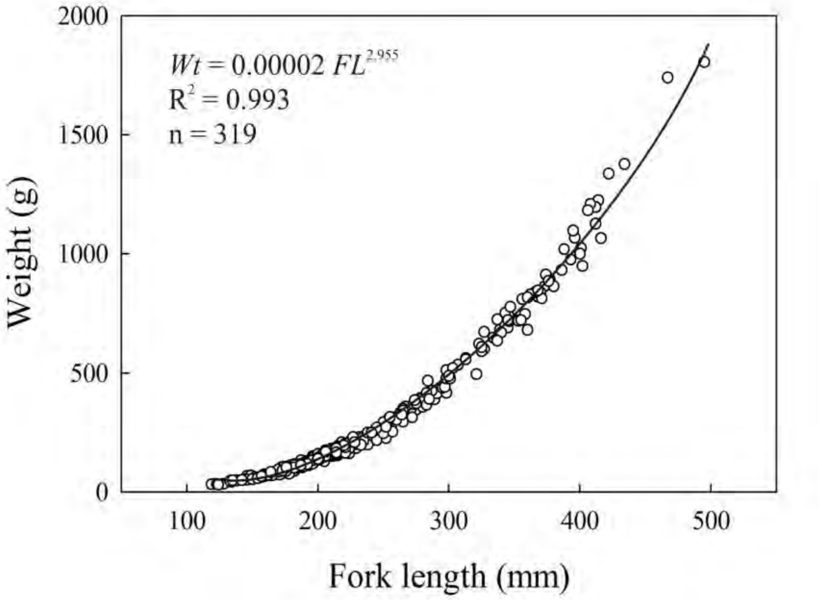

Figure 3.2: Length-weight relationships for *Trachinotus botla* sampled from Sodwana Bay, northern KwaZulu-Natal.

Of the 369 fish examined, 107 (29%) were male, 139 (38%) were female and 123 (33%) were unsexed (immature) (Table 3.2). The adult (> 250 mm FL) sex ratio was slightly female biased (1: 1.42). The proportion of male fish sampled over 400 mm FL was half of that of female fish. Female fish were also more predominant in the smallest size class (< 200mm FL). However, the overall sex ratio of *T. botla* did not differ significantly from unity (χ^2 = 5.97; df = 3, p = 0.39).

Table 3.2: Observed sex ratios of male and female *Trachinotus botla* per length class sampled from northern KwaZulu-Natal.

Fork length (mm)	Males	Females	Sex ratio
< 200	19	31	1: 1.63
200 - 299	63	71	1: 1.13
300 - 399	21	29	1: 1.38
> 400	4	8	1: 2.00

Age and growth

A total of 311 pairs of otoliths were used for age determination, 273 (87.8%) age estimates were accepted. The overall IAPE was 15.1%, but larger, older fish had a considerable lower IAPE than smaller fish (Table 3.3). A Bowker‟s test of symmetry revealed that the two reader‟s estimates were symmetrical (χ^2 = 11.89, df = 10, p = 0.29) (Figure 3.3).

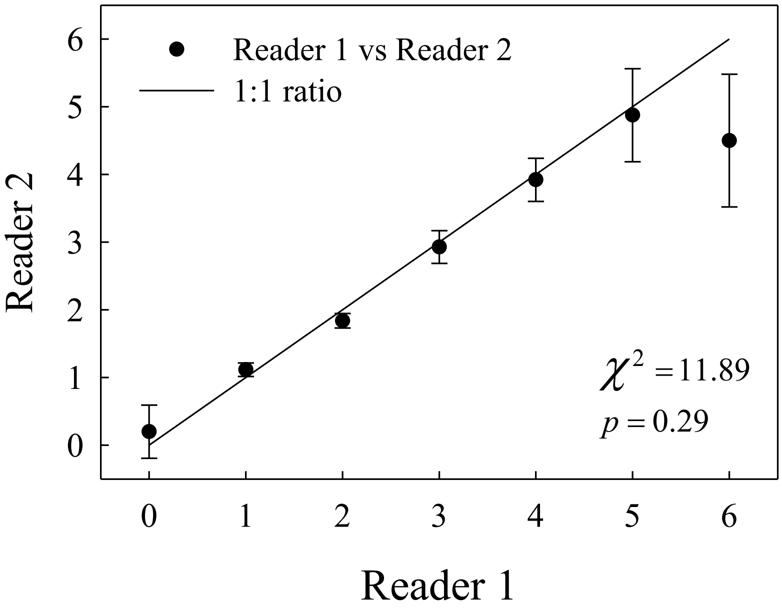

Figure 3.3: Age bias-plot describing the age estimation consistency between readers. Results of the Bowker‟s test for symmetry are also illustrated.

Table 3.3: Index of Average Percent Error (IAPE) and mean fork length (mm) for each age class of *Trachinotus botla* sampled in northern KwaZulu-Natal.

Age	Mean FL (mm)	IAPE	n
0	138.8	26.7	5
1	181.6	21.1	87
2	198.4	13	102
3	266.8	11.5	45
4	397.0	12.3	24
5	395.0	9.2	9
6	495.0	12.3	2

Edge analysis of pooled age data suggested that one hyaline and opaque ring were deposited annually (Figure 3.4 & Table 3.4). All otoliths read from fish captured in November were found to have opaque edges. The highest proportions of otoliths with hyaline edges were sampled in March (41%). Otoliths with opaque edges were more common than otoliths with hyaline edges (230 and 55 respectively).

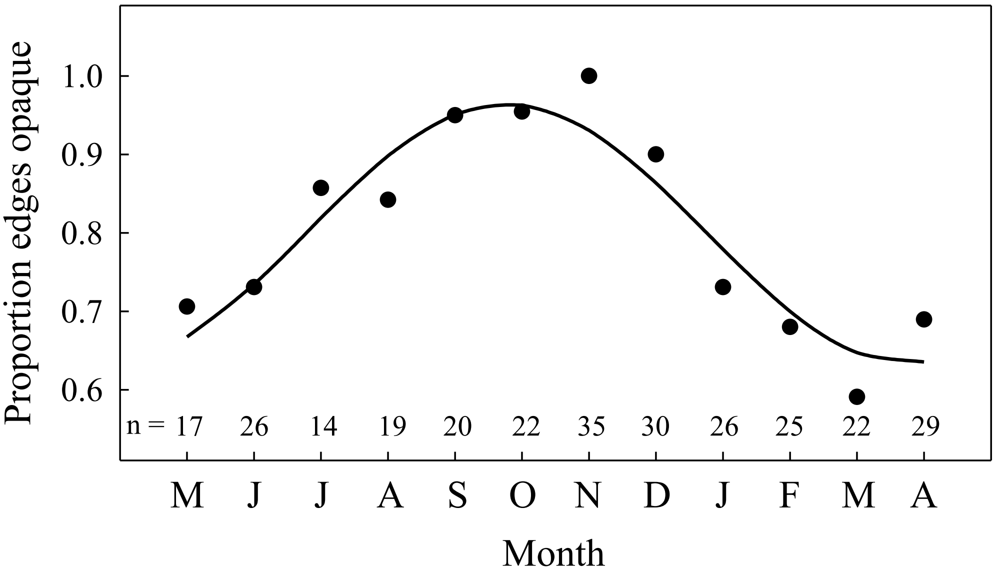

Figure 3.4: Otolith edge analysis illustrating the monthly proportion of otoliths with opaque edges in *Trachinotus botla* from northern KwaZulu-Natal. The solid line represents the predicted periodic regression model with an annual cycle.

Table 3.4: Parameter estimates from the logistic periodic regression analysis. The periodicity (PE) was estimated for the full model and fixed for the unimodal and bimodal models. *LL* values are log-likelihood estimates.

Parameter	**PR*Full***	**PR*Unimodal***	**PR*Bimodal***
β_0	0.82	0.80	0.77
β_1	-0.11	-0.01	0.07
β_2	-0.12	-0.17	0.01
PE (months)	10.09	12	6
Parameters	4	3	3
LL	-123.84	-124.14	-137.62
2(ΔLL)		0.61	26.95
p-value		0.44	<0.01

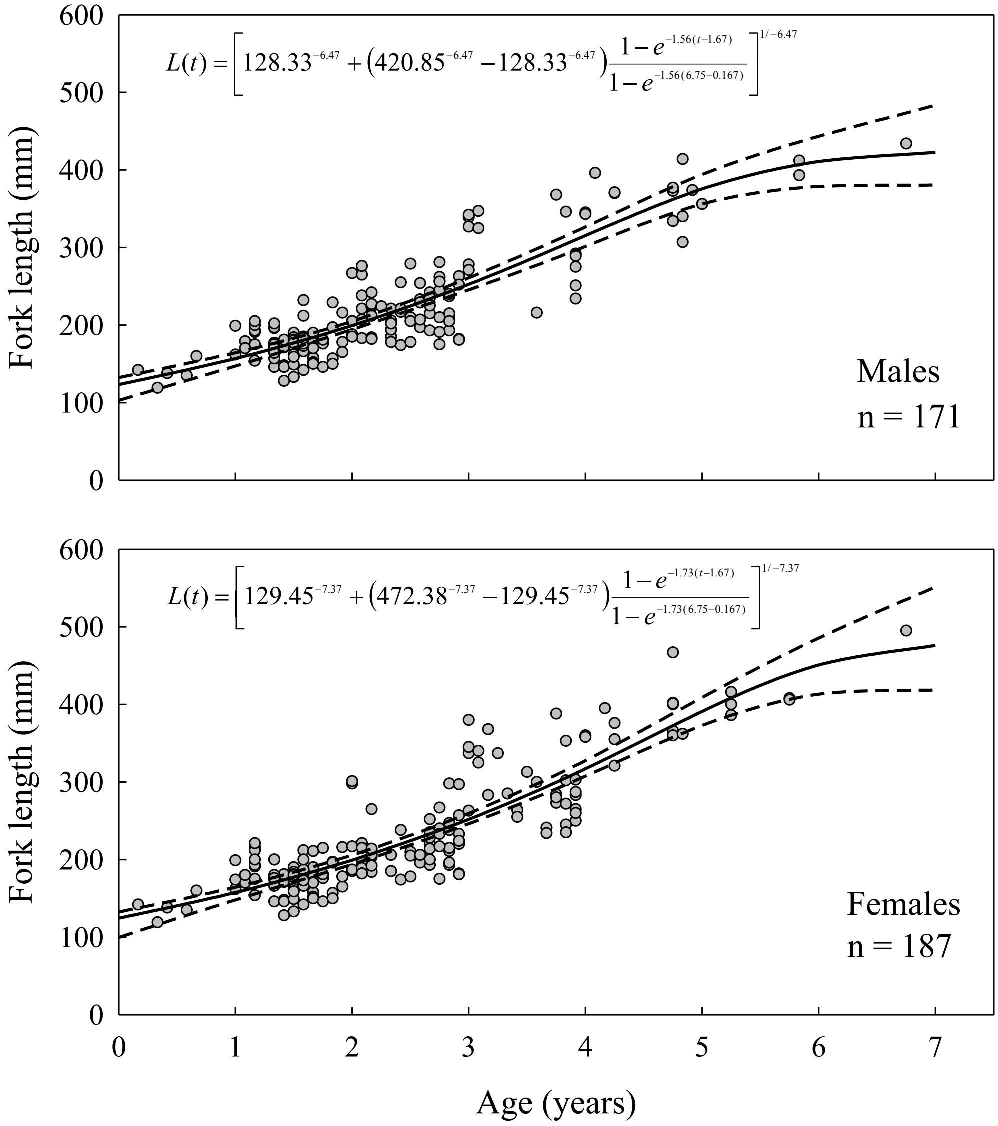

Figure 3.5: Schnute growth models for male and female *Trachinotus botla* sampled from Sodwana Bay, northern KwaZulu-Natal. Dotted lines represent the 95% confidence intervals of the fitted models using parametric bootstrapping.

Table 3.5: Point estimates and summary statistics for the Schnute growth models of female, male and combined sex *Trachinotus botla* from northern KwaZulu-Natal, South Africa. MLE = maximum likelihood estimate, CV = coefficient of variation, SE = standard error and CI = 95% confidence interval.

			Summary Statistics		
	Parameter	MLE	CV	SE	CI
Females (n = 187)	*a (year* $^{-1}$*)*	1.73	1.45	2.52	-0.42 - 8.20
	b	-7.37	1.54	11.38	-36.33 - 2.45
	L_1(mm FL)	129.45	0.09	11.47	103.35 - 138.22
	L_2 (mm FL)	472.38	0.07	31.28	417.46 - 534.57
Males (n = 171)	*a (year* $^{-1}$*)*	1.56	1.26	1.97	0.05 - 7.41
	b	-6.47	1.38	8.94	-33.69 - 0.74
	L_1(mm FL)	128.33	0.07	9.29	107.47 - 137.78
	L_2 (mm FL)	420.85	0.06	25.33	379.66 - 477.56
Combined (n = 276)	*a (year* $^{-1}$*)*	1.37	1.38	1.89	0.06 - 7.66
	b	-5.84	1.52	8.87	-35.11 - 0.45
	L_1(mm FL)	132.66	0.05	6.49	116.33 – 141.40
	L_2 (mm FL)	448.79	0.05	22.31	408.48 - 492.52

Figure 3.5 illustrates the age and growth of both male and female *T. botla* using Schnute"s growth model, which described the growth better than a linear model (LRT, df = 2, $p > 0.05$). The oldest female fish was 6 years old (495 mm FL) and the oldest male was also 6 years old (434 mm FL). Growth between males and females did not differ significantly (LRT, df = 4, $p > 0.05$) and were combined. Summary statistics for the Schnute"s growth function parameters derived from a parametric bootstrap procedure with 1000 iterations are presented in Table 3.4.

Reproductive biology

Oogenesis

The first recognisable stages of female reproductive cell structure were oogonia and pre-perinuclear ooctyes (Figure 3.6). Pre-perinuclear oocytes were generally polygonal in shape, had a large cytoplasm to nucleus ratio and had highly basophilic cytoplasm when stained with Haematoxylin and Eosin (H&E). Two other types of perinuclear oocytes were present in the primary growth phase - early- (EPO) and late-perinuclear (LPO) oocytes. Early-perinuclear oocytes were larger in size, more ovoid in shape and had a slightly less basophilic cytoplasm than the pre-perinuclear oocytes. Late-perinuclear oocytes were the largest of all the perinuclear oocytes. Increase in the size of these cells was accompanied by the cells becoming more circular. Late-perinuclear oocytes were characterized by numerous nucleoli grouped against the nuclear wall. During the primary yolk vesicle stage the cortical alveoli formed at the periphery of the oocyte. Cortical alveoli were clear and became larger and more numerous as the oocyte progressed, and filled the entire cytoplasm before the onset of vitellogenesis. Oocytes in the secondary yolk vesicle stage were characterised by the appearance of acidophilic secondary yolk vesicles at their periphery, staining red in H&E. Tertiary yolk vesicle oocytes were characterised by an increase in size and number of yolk vesicles. The yolk vesicles and cortical alveoli occupied the entire central section of the cytoplasm. The nucleus was centrally positioned and irregular in shape and the zona radiata and zona granulosa were well developed and prominent. As the oocyte developed further the nucleus migrated from the centre of the oocyte to the periphery, marking the completion of vitellogenesis. Post spawned ovaries resembled that of juvenile/resting fish. Oocytes were predominantly pre-perinuclear and were packed tightly within the ovary.

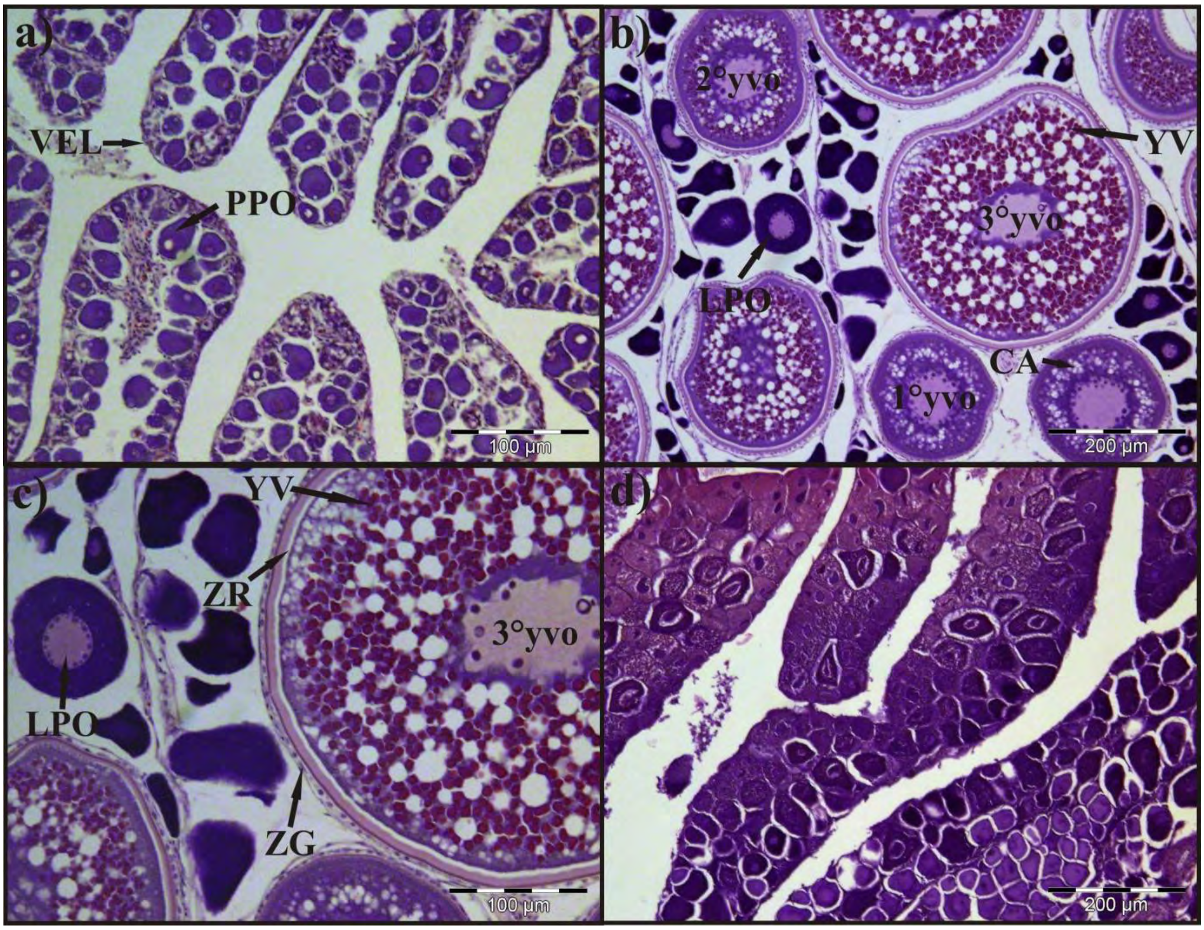

Figure 3.6: Transverse sections through ovaries of *Trachinotus botla* illustrating oogenesis. (a) The general structure of juvenile female showing the first signs of oogenesis, where the lamellae are dominated by pre-perinuclear oocytes (PPO). The pre-perinuclear oocytes grouped in ovigerous lamellae which are enveloped by a vascular epithelial lining (VEL). (b) Presence of early perinuclear oocytes and the development of cortical alveoli (CA) in the periphery of late-perinuclear oocytes (LPO). All three stages of yolk vesicle oocytes (primary, secondary and tertiary) are present. (c) During vitellogenesis the zona granulosa (ZG) and zona radiata (ZR) are well-developed. Enlarged acidophilic yolk vesicles (YV) are clearly visible in the tertiary yolk vesicle oocytes. (f) Post-spawning ovary where all mature oocytes have been released. Only pre-perinuclear oocytes remain in the ovaries.

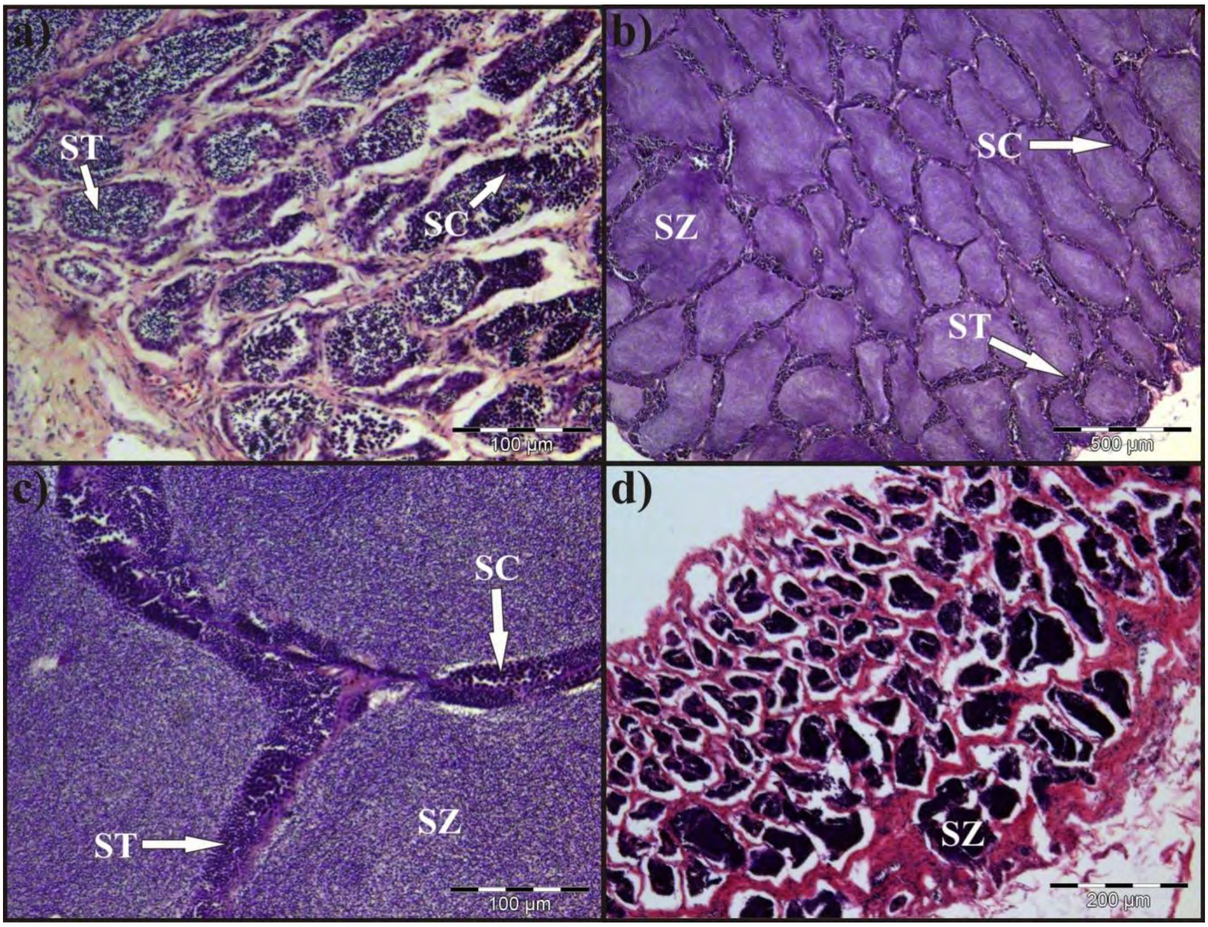

Figure 3.7: Transverse sections through testes of *Trachinotus botla* illustrating spermatogenesis. (a) The structure of a juvenile male with minimal reproductive activity. The first signs of spermatogensis are apparent with the development of spermatocytes (SC). Spermatocytes dominate the periphery regions of the testes, and the inner region mainly consists of spermatids (ST). Prior to spawning, "nests" of spermatocytes are visible which are surrounded by spermatids. (b) A fully ripe male gonad exhibiting large amounts of spermatozoa (SZ) in the seminiferous tubules and minimal unoccupied space. (c) Spermatocytes (SC) and spermatids (ST) are collected on the edges of the seminiferous tubules, and the centres of the tubules are completely filled with spermatozoa (SZ). (d) Post-spawned male gonad with decreasing amounts of spermatozoa (SZ) in the seminiferous tubules.

Spermatogenesis

Testes were regular in formation, with a number of seminiferous tubules leading into numerous secondary sperm ducts and finally into the main sperm duct (Figure 3.7). Spermatogonia were visible in the early stages of reproductive development and progressed through mitotic division to give rise to Spermatocytes. Spermatocytes were the largest germ cells and the most basophilic, staining dark blue. These cells were predominant in the periphery of the testes of developing fish. Spermatocytes gave rise to spermatids, which were smaller and less basophilic. Spermatocytes and spermatids were restricted to the periphery of the seminiferous tubule of ripe fish. The smallest and least basophilic germ cells were the spermatozoa. These cells filled the seminiferous tubules, secondary sperm ducts and the main sperm duct of ripe fish. The amount of spermatozoa in the testes decreased rapidly as fish progressed from ripe to spent. This process started at the periphery of the testes.

Histological validation of macroscopic staging

Histological analysis validated the macroscopic staging criteria, with discrepancies between the two found to be minimal. The "spent" category was the most problematic, and a small number of female individuals which were described as "spent" macroscopically were revealed to be in the tertiary stage of vitellogenesis (Tables 3.6 & 3.7).

Table 3.6: Histological validation of gonads for female *Trachinotus botla*. „„+‟‟ indicates the presence of the cell type in question, while „„+++‟‟ represents prevalent or abundant cell types.

	Oogonia	Pre-perinuclear oocytes	Early perinuclear oocytes	Late perinuclear oocytes	Primary yolk vesicle	Secondary yolk vesicle	Tertiary yolk vesicle
Immature	+	+++					
Juvenile/Resting	+	+++	+				
Developing		+	+++	+++			
Active/Ripe			+	+	+	+++	+++
Post spawning	+	+++					

Table 3.7: Histological validation of gonads for male *Trachinotus botla*. „„+‟‟ indicates the presence of the cell type in question, while „„+++‟‟ represents prevalent or abundant cell types.

	Spermatogonia	Spermatocytes	Spermatids	Spermatozoa
Immature	+	+		
Juvenile/Resting	+	+++		
Developing		+++	+++	
Active/Ripe		+	+	+++
Post spawning			+	+

Maturity

Males and females had similar sexual maturity patterns (Figure 3.8) with fish maturing at 252.5 ± 5.0 mm FL and 241.8 ± 5.7 mm FL for males and females, respectively. Age-at-50% maturity was identical for males and females (2.3 ± 0.1 years). Neither length- or age-at-50%-maturity was significantly different between females and males (LRT, df = 2, $p > 0.05$). When the sexes were combined, the length-at-50% maturity was calculated as 247.2 ± 5.8 mm FL. The rate at which maturity was obtained was rapid, with all fish maturing within 70 mm (220 – 290 mm).

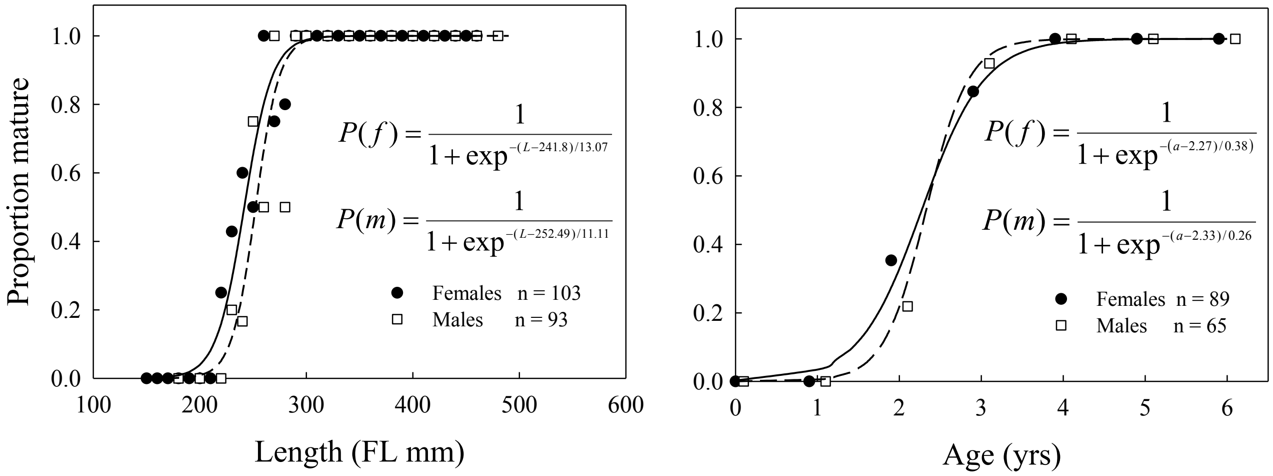

Figure 3.8: Logistic ogives fitted to the observed proportion of mature male (□) and female (●) *Trachinotus botla* from northern KwaZulu-Natal.

Reproductive seasonality

Five macroscopic stages were defined for both males and females (Table 3.1) and the proportions of these different stages suggested a clear seasonal trend in gonad development for both sexes. Gonads in the “developing” and “ripe” stages were dominant between November and February (Figure 3.9). Alternatively, “spent” stage individuals were only recorded in March. This indicates a spawning season which ranges from November to February. Gonads in the “juvenile/resting” stage were the most prevalent between April and October. This stage accounted for all of the gonads assessed between May and August. The reproductive activity period was longer in female fish (September-April) than males (November-March). GSI corroborated the macroscopic staging of a summer spawning period as the highest mean GSI were recorded in November for females and December for males. Average GSI remained low between June and October for both sexes.

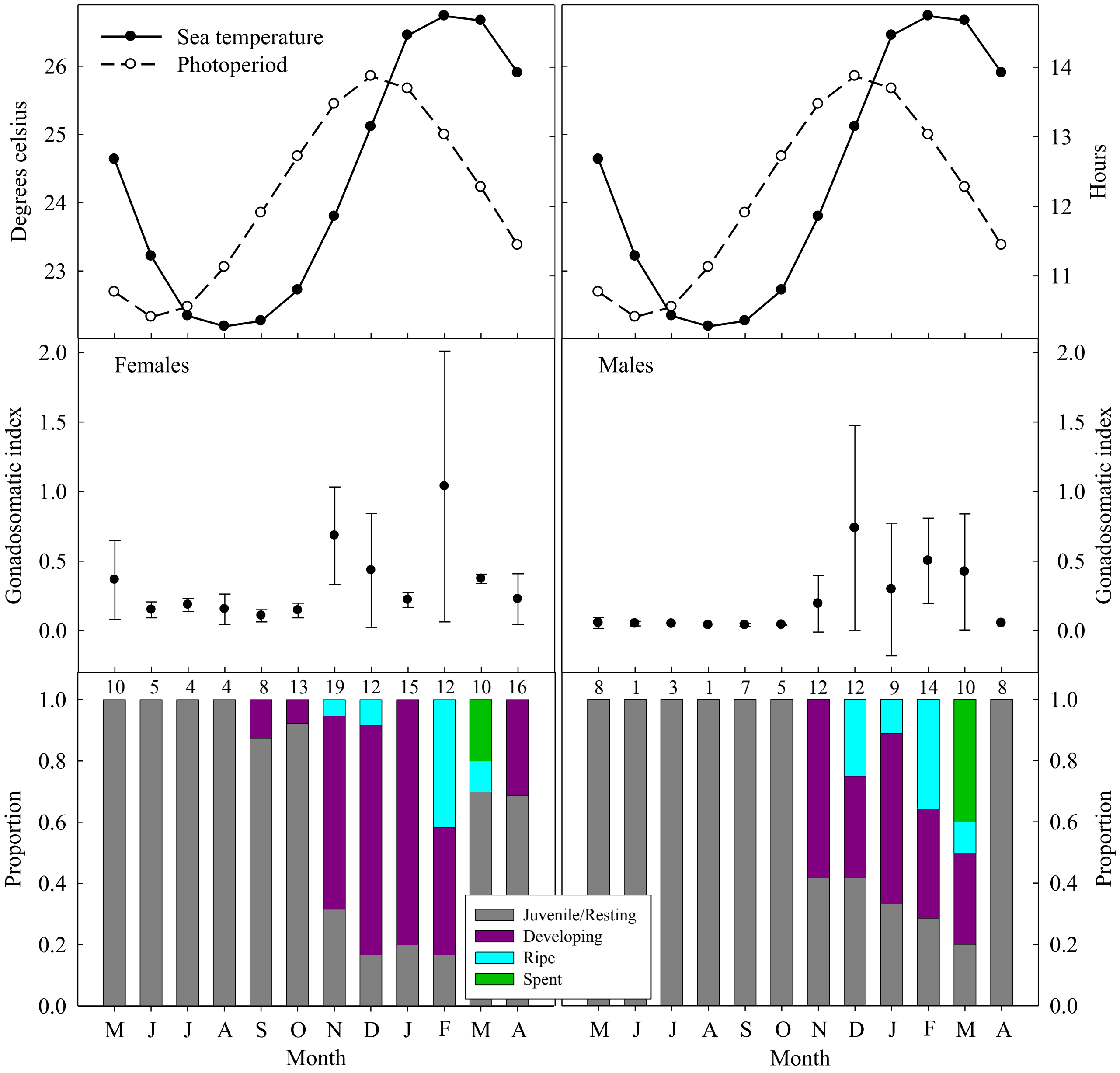

Figure 3.9: Observed monthly proportion of the different macroscopic reproductive stages and mean gonadosomatic indices for *Trachinotus botla* sampled from northern KwaZulu-Natal between May 2010 and April 2011. Surf zone water temperatures and photoperiod for Sodwana Bay over the same period are included. Numbers indicate sample sizes.

Reproductive activity and associated environmental factors

Reproductive activity of *T. botla* was strongly correlated to two major environmental factors - surf zone water temperature and photoperiod (Figure 3.9). Photoperiod reached a maximum value of 13.9 hours in December that corresponded with the first peak in GSI. This peak was followed by a relative dip in GSI in January. A second peak in GSI was observed in February, which corresponded with the maximum mean water temperature of 26.7 °C. The initiation of reproductive activity appeared to be strongly related to surf zone temperatures. In contrast, the termination of reproductive activity is more closely correlated with decreasing photoperiod than water temperature.

The gonadosomatic index was cyclic with a period of 10.9 months and not significantly different from an annual cycle of 12 months (LRT, $\gamma = 0.26$, $p = 0.61$). The bimodal ($PR_{bimodal}$) model which had a fixed period of 6 months ($P = 6$) was significantly different from the full model (LRT, $\gamma = 22.90$, $p < 0.05$). Water temperature was incorporated as an independent variable in the periodic regression which best described the cyclic period of GSI, confirming the importance of temperature in the spawning of *T. botla*.

Feeding intensity

Of the 169 *T. botla* stomachs analysed, 34 (20.1%) were found to be empty. Smaller fish (<250 mm FL) had a higher stomach fullness index (SFI) than larger fish (>250 mm FL) (Figure 3.10). This difference was not statistically significant and the average SFI in all length classes were found to be statistically similar (ANOVA, $p > 0.05$). Fish sampled in autumn (Mar – May; SFI = 1.11) and winter (Jun – Aug; SFI = 0.76) had a higher mean stomach fullness index than those sampled in spring (Sep – Nov; SFI = 0.47) and summer (Dec – Feb; SFI = 0.48) (Figure 3.11). These differences were not statistically significant (ANOVA, $p > 0.05$).

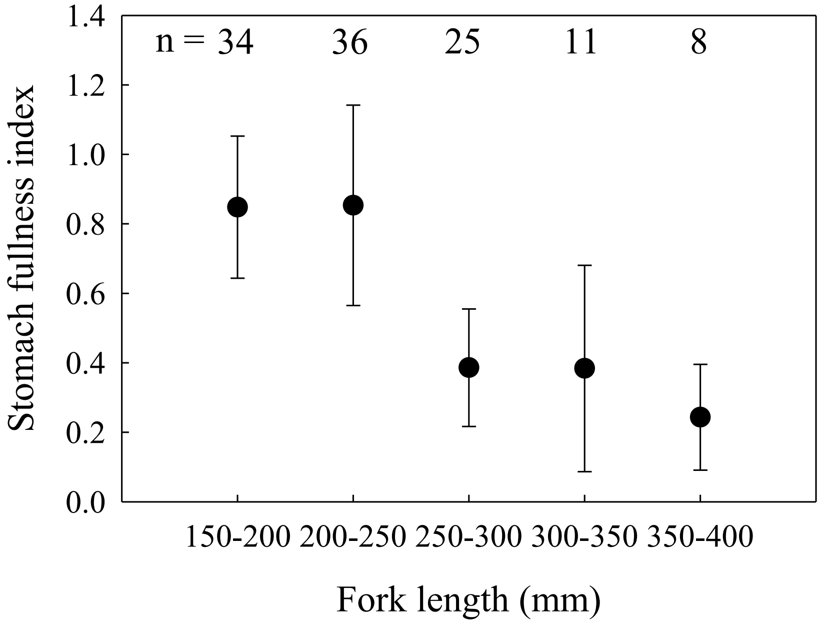

Figure 3.10: Variation in stomach fullness index (SFI) as a function of length for *Trachinotus botla* sampled from northern KwaZulu-Natal. Vertical bars denote 95% confidence intervals.

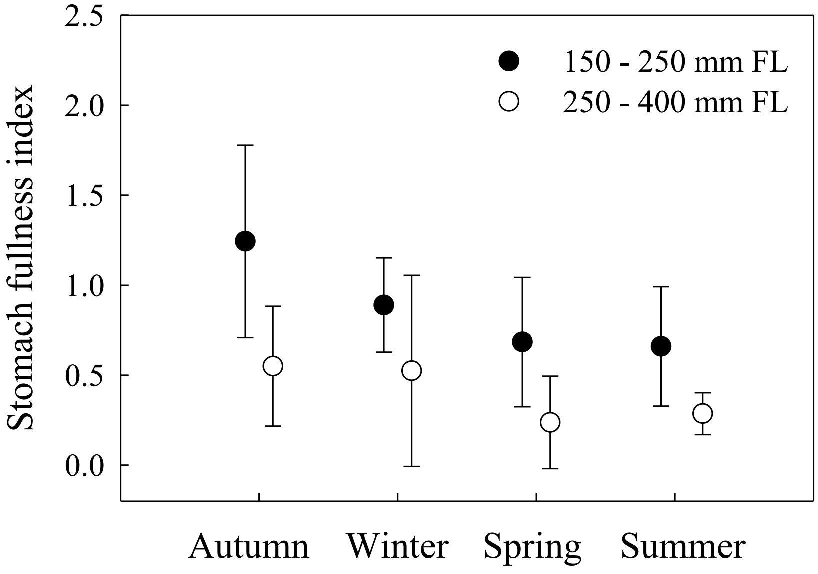

Figure 3.11: Seasonal variation in stomach fullness index (SFI) for *Trachinotus botla* sampled from northern KwaZulu-Natal. Vertical bars denote 95% confidence interval.

Dietary analysis

Principle Component Analysis (PCA) revealed that the first two principal components explained 44% of the variation among the 14 prey variables considered (Table 3.8). All variables except two (Copepoda and Mysidacea) had positive loadings in the first principle component (PC1). The second principal component (PC2) accounted for 18.1% of the variability among prey items, and the majority of the variables were negatively loaded. Teleostei and Copepoda were the most significant variables in both PC1 and PC2 (Figure 3.12). Fish were grouped into two size groups based on linear discriminate function analysis - small (<300mm FL) and large (>300mm FL). A total of 84.8% were correctly classified, comprising of 92.9% correct classification of small fish and 50.0% correct classification of large fish.

Table 3.8: Principal Component Analysis (PCA) of 14 food groups related to the diet and feeding behaviour of *Trachinotus botla,* sampled from northern KwaZulu-Natal. Bold numerals indicate prey items with a |PC| > 0.2.

	Principal Component	
	1	**2**
Variance explained	25.48%	18.13%
Cumulative variance explained	25.48%	43.61%
Eigenvectors		
Teleostei	**0.52**	**0.76**
Copepoda	**-0.84**	**0.41**
Brachyura	0.09	**-0.29**
Penaeidea	0.05	**-0.23**
Hippidae	0.07	**-0.21**
Gastropoda	0.03	-0.12
Insecta	0.02	-0.08
Ostracoda	0.01	-0.07
Bivalvia	0.02	-0.05
Nematoda	0.02	0.02
Isopoda	<0.01	-0.03
Polychaeta	0.01	-0.02
Mysidacea	-0.01	-0.01
Velella sp.	<0.01	-0.01

Relative importance of food items

Trachinotus botla had a catholic diet with up to 10 different prey species found in a single stomach. Only small amounts food matter was considered unidentifiable. Matter which was considered to be congealed mucus and digestive fluids was commonly found in the majority of stomachs examined and was a likely consequence of whole stomach preservation. This matter was excluded from the analysis. The most important prey items fish (Teleosts), copepods (Copepoda), crabs (Brachyura), mole crabs (Hippidae) and mussels (Bivalvia). These five components attributed to 68.3% of the ranking index (RI) in the diet of all fish studied (Figure 3.13). Teleostei and Copepoda were the two most important food sources in small fish (< 300 mm FL) (Table 3.9) and Brachyura and Bivalvia were the most important food source in larger fish (>300 mm FL) (Table 3.10). Terrestrial insects were significant prey of small fish, while Gastropods were the most important food source of large fish (>400 mm FL).

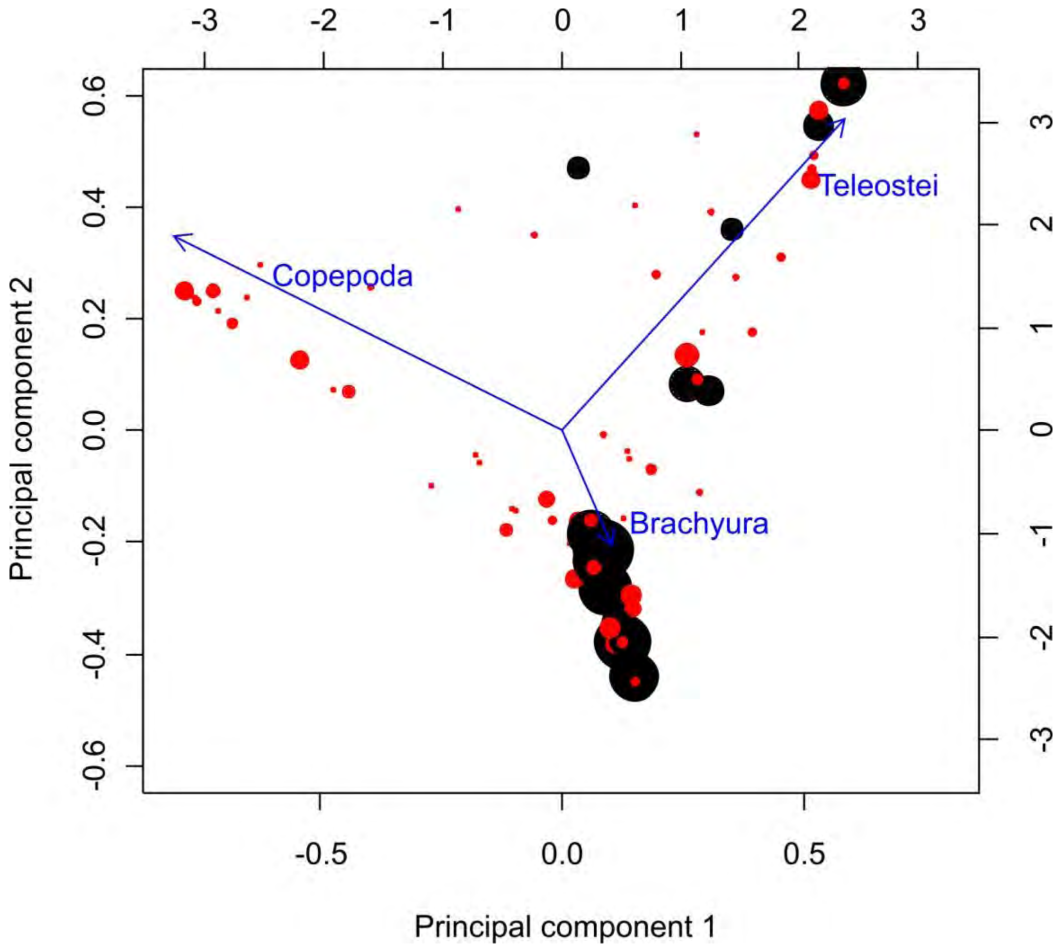

Figure 3.12: Principal Component Analysis ordination of 14 food items in the diet of *Trachinotus botla*. The diameters of the circles are a scaled to represent the mass of individual fish. Red circles represent small fish (<300 mm FL) and black circles represent large fish (>300 mm FL). Arrows represent the loading of the three most important food items.

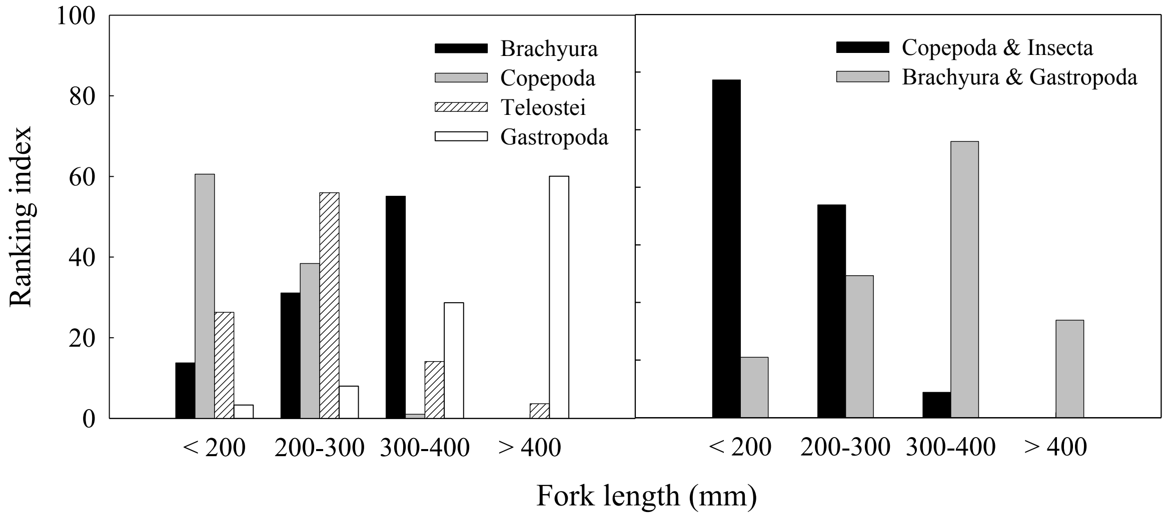

Figure 3.13: The relative importance of four dominant food items in the diet of *Trachinotus botla* per length class, sampled from northern KwaZulu-Natal, South Africa.

Table 3.9: Prey items found in the stomachs of 112 *Trachinotus botla* (123 – 299 mm FL) sampled in Sodwana Bay between May 2010 and April 2011.

Food item	Freq. Occurrence	Percentage Number	Mass	IRI
Teleostei	50.00	5.92	5.64	28.06
Copepoda	53.57	75.67	3.67	19.59
Hippidae	9.82	0.20	11.39	11.14
Penaeidea	25.00	5.59	3.99	9.92
Insecta	24.11	4.14	3.03	7.29
Brachyura	19.64	0.75	3.34	6.53
Bivalvia	1.79	-	28.07	4.99
Polycheata	6.25	0.15	5.45	3.39
Ostracoda	4.46	-	5.74	2.55
Ascidiacea	0.89	0.01	17.04	1.51
Mysidacea	16.07	5.32	0.56	0.90
Nematoda	17.86	0.59	0.49	0.87
Isopoda	9.82	0.45	0.80	0.79
Gastropoda	8.04	-	0.85	0.68
Velella sp.	5.36	0.10	0.72	0.38
Arachnida	0.89	0.01	2.99	0.27
Cephalopoda	0.89	0.01	0.45	0.04
Amphipoda	0.89	0.01	0.04	<0.01
Unidentified/Mucus	9.82	1.07	1.11	1.09

Table 3.10: Prey items found in the stomachs of 26 *Trachinotus botla* (300 – 434 mm FL) sampled in Sodwana Bay between May 2010 and April 2011.

Food item	Freq. Occurrence	Percentage Number	Mass	IRI
Brachyura	38.46	9.30	9.01	22.13
Bivalvia	23.08	-	14.15	20.84
Teleostei	34.62	13.18	7.53	16.63
Gastropoda	57.69	-	3.86	14.21
Hippidae	11.54	2.71	12.62	9.29
Ostracoda	7.69	-	18.28	8.97
Insecta	19.23	29.84	2.48	3.04
Polycheata	11.54	1.16	4.05	2.98
Penaeidea	11.54	1.94	1.28	0.94
Copepoda	11.54	31.01	0.75	0.55
Isopoda	11.54	2.71	0.30	0.22
Mysidacea	7.69	2.33	0.19	0.09
Nematoda	19.23	4.65	0.02	0.03
Unidentified/Mucus	7.69	1.16	0.13	0.07

Discussion

Trachinotus botla is a fast growing species that has a relatively short life span not exceeding six years of age. These estimates are comparable to the growth of *T. botla* in Queensland, Australia (McPhee 1995), and typically similar to congenerics (McPhee 1995, Mourad 1999, Muller *et al.* 2002, Murphy *et al.* 2007). Age determination of the Florida pompano (*T. carolinus*) revealed similar results as species reached a maximum age of seven years old (Muller *et al.* 2002, Murphy *et al.* 2007). In contrast, one species, permit *T. falcatus*, has been known to live to a maximum age of 23 years (Crabtree *et al.* 2002).

The consistency of reading otoliths was relatively poor (IAPE = 15.1%), particularly for a short-lived species. This inconsistency may be a result of reading whole otoliths, the subtropical environment, or both. Manipulation of otoliths was often required to create the optimal angle of the reading surface, introducing additional bias. A total of 28 (11.1%) otolith pairs were immediately rejected upon first reading, the majority of which were completely transparent. The IAPE for fish under two years of age was almost double that of fish over three years of age. Similarly, a substantial decrease in IAPE was observed between ages one and two years (21.1% and 13.0%, respectively). The increase in readability of otoliths from fish greater than one year of age indicates the inaccuracy involved in defining the boundary between the nucleus edge and the first growth zone. The lowest IAPE was observed in the five year age group, substantiating that as the fish age their otoliths become more readable. It must however be noted that IAPE is a measure of reproducibility and not aging accuracy (Campana 2001).

Edge analysis validated that a single growth zone was deposited per year. The highest proportion of otoliths with opaque edges occurred towards the end of spring (November), and the highest proportion of otoliths with transparent edges occurred in the beginning of autumn (March) suggesting that there is a "lag" period between the decrease in growth during winter and the subsequent detection of the opaque zone deposition. The validation findings were comparable to that of McPhee (1995) who applied the same technique to *T. botla* in Australia. Edge analysis is the most applied method of growth zone validation. It is also the most likely method to be misused (Campana 2001). Ideally a more reliable method of validation, such as mark-recapture of a chemically tagged fish, should be used to ensure accurate results.

Both male and female *T. botla* reached a maximum age of six years and there was no evidence to suggest a difference in growth rate between male and female *T. botla* in the first three years. Differential growth patterns appeared thereafter, and it was evident that female fish continued to grow while growth in male fish decreased. As a result, females reached a larger size than males. It is common for female individuals of a species to attain greater sizes than their male counterparts. This is a phenotypic expression of evolutionary life-history traits, as males do not limit the species reproductive output. Female fecundity generally increases exponentially with increasing fish size (Stearns 1976, Werner and Gilliam 1984, Jakobsen *et al.* 2009), therefore larger females would have the ability to produce more offspring and increase their reproductive success.

Table 6.1: A review of critical life-history parameters of recreationally important fishing species belonging to the Carangidae.

Species	**Study Area**	**Longevity**	**Max. length**	**Mortality estimates**	**Age-at-50%-maturity**	**Length-at-50%-maturity**	**Sex ratio (M:F)**	**Spawning season**	**Evidence of serial Spawning**	**Reference**
Trachinotus. botla	South Africa	6	495 mm FL	$Z = 1.04$ year^{-1} $M = 0.70$ year^{-1}	2.3 yrs	247.2 mm FL	1:1.3	summer (Nov - Feb)	Yes	Current Study
Trachinotus. botla	Australia	6	489 mm TL	$Z = 1.75$ year^{-1} $M = 1.20$ year^{-1}	NA	361 - 370 mm TL	1:1	summer (Oct - April)	Yes	McPhee (1995)
Trachinotus. carolinus	Florida	4	635 mm TL	$M = 0.40$ year^{-1} $Z = 0.40$ year^{-1}	2 yrs	285 - 325 mm FL	NA	Feb - Sept	NA	Murphy *et al.* (2007)
Trachinotus. falcatus	Florida	23	916 mm FL	NA	3.1 yrs	486 - 547 mm FL	NA	summer (May - July)	NA	Crabtree *et al.* (2002)
Caranx. ignobilis	Hawaii	9	1330 mm FL	NA	4 yrs	600 mm SL	1:1.4	summer (Apr - Aug)	NA	Sudekum *et al.* (1991)
Caranx. melampygus	Hawaii	5	710 mm FL	NA	2 yrs	350 mm SL	1:1.2	summer (Apr - Nov)	NA	Sudekum *et al.* (1991)
Caranx. bucculentus	Australia	8	493 mm SL	NA	NA	NA.	1:1	all year, peak in summer	Yes	Brewer *et al.* (1994)
Seriola. dumerili	Mexico	15	1355 mm FL	$Z = 0.70$ year^{-1}	NA	1090 - 1130mm SL	NA	Summer (May – July)	NA	Manooch & Potts (1997)

Point estimates for length-at-50% maturity for both males and females were similar while age-at-50% maturity was identical for both sexes. All fish reached sexual maturity before 290 mm FL, which corresponds to an age of three years. Knife edge maturity curves suggest maturation occurs rapidly. This is similar to findings of *T. botla* in Australia (McPhee 1995). Similarly, *T. carolinus* from north America reaches 100% maturity by two to three years of age (Crabtree *et al.* 2002, Main *et al.* 2007).

The overall sex ratio was slightly female biased (1 male: 1.3 females) and size dependent with large fish (> 400mm FL) being the most skewed with a sex ratio of two females for every male sampled. Small fish (< 200mm FL) exhibited an unusually skewed sex ratio (1 male: 1.6 females) when compared to adjacent length classes. This is probably a result of the inability to accurately define gonad structure in juvenile fish. Distinguishing between a juvenile female gonad and an immature gonad was easier than a juvenile male gonad and an immature gonad. Therefore some juvenile male fish may have been misidentified as immature (unsexed) fish, distorting sex ratios.

Both macroscopic and histological examination of the gonads of *T. botla* indicated that the species has a protracted spawning season throughout the summer period (November to March) in northern KwaZulu-Natal. The GSI results corroborated the spawning period. *Trachinotus* spp. have been known to have prolonged spawning periods during spring and summer. Some species are able to spawn throughout the year, but this behaviour generally occurs at lower latitudes (Main *et al.* 2007). These trends indicate that the species is a serial spawner which is likely to participate in multiple spawning events within a single season; particularly the two distinct periods. The protracted spawning season and presence of oocytes at a wide range of maturation stages corroborated this spawning behaviour. McPhee (1995) suggested that *T. botla* in Australia participated in multiple spawning events and that a considerable proportion of left and right ovaries were significantly unequal in weight. McPhee (1995) therefore suggested that the number of ova shed during a single spawning event is unequal for each ovary, and ovaries may alternate in producing the majority of eggs for each event. Serial spawning, particularly two distinct spawning events, is common within the carangids and has been identified in *C. ignoblis* (von Westernhagen 1974) and *C. melampygus* (Moriwake *et al.* 2001). This spawning behaviour is indicative of species that inhabit fickle environments, such as the surf zone, and may be considered "bet-hedging". This behaviour is based on the notion that the probability of total reproductive failure as a result of investment during resource poor periods is reduced through spawning numerous batches of eggs at different times (Nevoux *et al.* 2010).

Reproductive activity in *T. botla* appears to be associated with both water temperature and photoperiod, similar to the majority of marine teleosts (Johannes 1978, Pankhurst and Porter 2003). Photoperiod is commonly viewed as the principal environmental determinant of reproductive development and acts as the primary role in regulating the overall reproductive cycle (Pankhurst and Porter 2003). Temperature acts as a secondary cue that interacts with the photoperiod signal so as to synchronize the final stages of reproductive development with optimal environmental conditions (Pankhurst and Porter 2003). The timing of spawning is generally interpreted as a mechanism for ensuring that larvae hatch into environmental conditions that improve their survival (Bromage *et al.* 2001). In the case of *T. botla*, spawning may be timed so that planktonic prey are most abundant when offspring reach their initial predatory stages.

Trachinotus botla is an opportunistic predator that consumes a wide variety of prey items, which is in agreement with other feeding studies on the species (Schleyer and Wallace 1986, van der Elst 1993, McPhee 1995, Williams 2002). Overall, Teleostei (primarily Engraulidae) were the dominant food item across all length classes. Smaller fish (<300 mm FL) fed predominantly on calanoid copepods, mole crabs, postlarval penaeid prawns, and terrestrial insects. Larger fish (>300 mm FL) were more dependent on crabs, mussels and gastropods. A decrease in mean feeding intensity (SFI) was noted with an increase in fish size. This is possibly due to small individuals needing to consume a relatively greater quantity of food more regularly than larger individuals as zooplankton are a poor source of dietary protein and energy when compared to crabs or mussels (Timonin *et al.* 1992).

A distinct ontogenetic shift in diet at ~300 mm FL was clearly evident. Given that both resource utilization and predation risk are generally related to body size, many species will undergo extensive ontogenetic shifts in diet and/or habitat use (Werner and Gilliam 1984). The marked partitioning of food resources based on fish size creates complex ecological interactions in natural communities, most notably a decrease in intraspecific resource competition (Werner and Gilliam 1984). Ontogenetic shifts are not necessarily limited to food resources. In the case of *T. botla* it seems that the shift in diet may be a consequence of an ontogenetic shift in habitat use, or vice versa. Larger fish are undoubtedly found in deeper water than their smaller counterparts (D. Parker, pers. obs.). Larger fish were also more abundant over rocky reef habitats, while smaller fish tended to remain in predominantly sandy surf zones. This movement from a shallow, sandy habitat to a deeper more rock/reef orientated habitat is highlighted in the stomach contents of individuals. Notably, the rock/reef orientated species such as mussels and several crab species in the stomachs of larger individuals. The physical attributes needed to successfully feed on prey items such as crabs and mussels also dictates the point at which diet shifts occurs. A significant amount of force is required to crush mussels and gastropods. It would be expected that larger, stronger and more robust morphological feeding apparatus would be favoured (Richardson 2010).

Surf zone habitats are often referred to as “open” systems, and their motile faunal assemblages such as plankton are in constant flux. The ability of *T. botla* to effectively utilize “superabundant” 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*. Analysis of stomach contents of fish sampled in October revealed large quantities of formicid alates coinciding with the general period of nuptial flights for these terrestrial insects in KwaZulu-Natal. Similarly, postlarval penaeid prawns were found in large numbers in stomachs analysed from late-May and June. This coincides with the peak larval recruitment of the two species common in northern KwaZulu-Natal - *P. japonicas* and *P. indicus* (Forbes and Cyrus 1991). It is unlikely that the small prey items which were consumed, particularly copepods, were individually identified and eaten. McPhee (1995) highlights the fact 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.

To conclude, *T. botla* is a fast growing, short-lived and early maturing species. Growth was similar between males and females until a point (±350 mm FL), after which, females continued to grow while growth in male fish was slowed. The species has a protracted spawning season ranging from November to February. Two definite peaks in GSI and the presence of different gonad stages during this period indicate that the species is a serial spawner. The sex ratio was slightly female-biased (1 male: 1.3 females), which increased with size. *Trachinotus botla* is an opportunistic predator with a catholic diet, feeding on a wide variety of prey items. Teleosts played an important role in the diet of fish of all sizes. Small fish also fed on copepods and terrestrial insects, while large fish depended largely on mussels and crabs as a source of nutrients. The opportunistic utilization of “superabundant” prey items is a fundamental characteristic of the species feeding habits. An ontogenetic dietary shift was observed at ~300 mm FL or 3 years of age, probably due to a shift in habitat preference. The observed biological and life history characteristics are indicative of a opportunistic species according to Winemiller and Rose (Winemiller 2005) and is a likely adaption suited to the stochastic nature of the surf zone environment.

Chapter 4

Evidence for the deleterious effects of the tongue-replacing isopod *Cymothoa borbonica* on largespot pompano, *Trachinotus botla*

Introduction

Parasites are fundamental components of any aquatic ecosystem (Scholz 1999, Marcogliese 2005). Examination of parasites at the community level can provide insight into the population dynamics and community structure of the ecosystem (Marcogliese and Cone 1997) as well as food web structure, function and ecosystem biodiversity (Marcogliese 2005). Besides direct losses caused by mortality, parasites may alter host growth, behaviour, resistance to other stressors, susceptibility to predation and decrease reproductive ability (Scholz 1999). The significance of these impacts is often overlooked, as the understanding of parasites and their interactions with wild fish populations is often hindered by the lack of data.

Cymothoids are a group of crustaceans that typically parasitize teleosts. They have a cosmopolitan distribution in tropical and temperate regions (Brusca 1981). Members of the genus *Cymothoa* are ectoparasites that exhibit numerous host attachment sites including skin, fins, branchial or buccal cavities, and are also known to burrow into the musculature (Bakenhaster *et al.* 2006). Species infesting buccal and gill chambers are likely to originate from a more advanced phyletic lineage within the genus than species attaching on the outer epidermis (Brusca and Gilligan 1983). Despite the variability in site attachments, cymothoids often exhibit high host-specificity (Brusca 1981, Bunkley-Williams and Williams 1998). There are currently 48 recognised *Cymothoa* species three of which, *C. borbonica*, *C. eremita* and *C. rotundifrons*, have been recorded from the south-western Indian Ocean (Hadfield *et al.* 2011). *Cymothoa borbonica* has been recorded off the coast of several African countries, including South Africa (Barnard 1920) and Mozambique (Barnard 1926), and the islands of

Madagascar (Trilles 1979), Reunion (Monod 1934), Mauritius (Trilles 1975) and the Maldives (Stebbing 1904).

Table 4.1: A review of the cymothoid isopod parasites that have been found to infect carangids.

Parasite species	Host species	Study area	Reference
Cymothoa borbonica	*Trachinotus botla*	South Africa	Current study
Cymothoa oestrum	*Caranx hippos*	Venezuela	Bunkley-Williams *et al*., (2006)
Cymothoa oestrum	*Caranx* spp.	Curaçao	Kensley & Schotte (1989)
Cymothoa oestrum	*Elagatis bipinnulatus*	Colombia	Bunkley-Williams *et al*., (2006)
Cymothoa spinipalpa	*Chloroscombrus chrysurus*	Brazil	Costa *et al*., (2011)
Cymothoa spinipalpa	*Oligplites saurus*	Brazil	Thatcher *et al.* (2007)
Ceratothoa imbricatus	*Trachurus declivis*	Australia	Maxwell (1982)

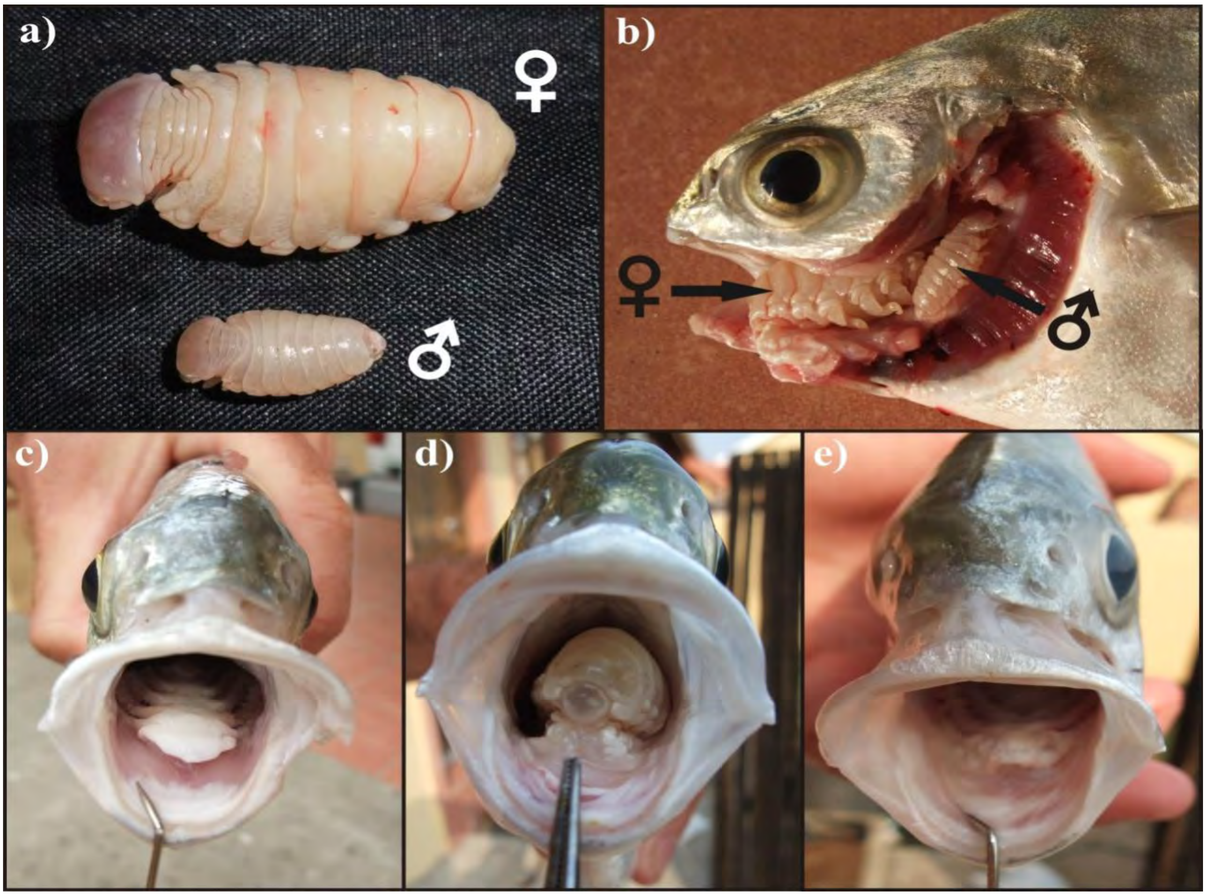

Figure 4.1: a) Male and female *Cymothoa borbonica* sexual dimorphism, b) their position within the host‟s buccal cavity where the larger female attaches itself to the basihyal while the smaller male attaches to a gill raker, c) an uninfected host fish, *Trachinotus botla*, with an intact and functional basihyal, d) an infected fish with *C. borbonica* attached to its basihyal, and e) a host fish with a damaged and deformed basihyal structure as a result of infection by *C. borbonica*.

Major knowledge gaps still exist in the fields of taxonomy, biology, epizootiology and control of fish parasites (Scholz 1999). Ecological studies on *Cymothoa* spp. are restricted to documenting parasite prevalence (Marks *et al.* 1996, Chavez-Lopez *et al.* 2005) and life history (Bakenhaster *et al.* 2006). Few studies have focused on their impacts (Brusca and Gilligan 1983, Colorni *et al.* 1997). As a consequence, there is a lack of knowledge regarding cymothoids and their interaction with their hosts within the natural environment. Literature on the effects of cymothoids on cultured fish is more abundant due to logistical convenience (Sievers *et al.* 1996, Horton and Okamura 2001) and it is recognized that stocking fish at high densities under cultured conditions may lead to stress that could augment the parasite‟s effects (Horton and Okamura 2001). Therefore extrapolation of such effects to wild host populations is limited.

Cymothoids are generally protandrous hermaphrodites and usually occur in a male-female pairing (Bakenhaster *et al.* 2006). Species infesting the buccal cavity (Figure 4.1) enter the gills of the host as males after a short "infectious" free-living manca stage. They later transform into functional females on the host's basihyal, and await the attachment of another male (Brusca and Gilligan 1983). Copulation occurs within the host‟s buccal cavity (Brusca and Gilligan 1983) and most females produce between 300-600 eggs per marsupium (Bakenhaster *et al.* 2006). There is evidence that cymothoids are sanguivorous, and feed intermittently on the host‟s blood vessels at the site of attachment (Brusca and Gilligan 1983) with Colorni *et al.* (1997) noting the occasional presence of erythrocytes in the intestinal lumen of the adult isopod parasites. Documented pathogenic effects of cymothoid infections on their finfish hosts include mortality, tissue damage, anaemia, a decrease in mean weight and length, and inhibited growth (Marks *et al.* 1996, Sievers *et al.* 1996, Horton and Okamura 2001, Leonardos and Trilles 2003).

This chapter presents basic information on *C. borbonica* and a description of the host-parasite relationship with *Trachinotus botla*. The chapter quantified parasite prevalence throughout the size and age classes of its host species, and investigated impacts including changes in feeding and growth. It was hypothesized that parasite infection would affect the feeding habits and diet of fish, and therefore, may impede its host‟s growth and condition.

Methods and Materials

General Sampling

Trachinotus botla were collected using rod and line from Sodwana Bay between May 2010 and May 2011. All fish were examined for the intrabuccal presence of *C. borbonica*. Infected fish were recorded, measured (FL mm) and weighed (g). Their sagittal otoliths were removed for age determination, a sample of dorsal muscle tissue excised for later stable isotope analysis, and the stomachs removed for later diet analyses. The parasites were removed from the fish‟s buccal cavity and the length of each parasite (from the head to the posterior tip of the pleotelson) was measured to the nearest 0.1mm using vernier calipers.

Dorsal muscle tissue samples were dried in an oven at 60° C to a constant weight. The dried muscle was ground into a fine powder, weighed to the nearest 1 ± 0.05 mg and placed in 8 × 5 mm tin foil capsule for stable isotope analysis. The age of each fish was determined by counting the number of opaque zones on whole otoliths submersed in methyl-salicylate BP, using a reflected light source against a black background. The stomachs were weighed to the nearest 0.01 gram and their contents were removed. All food items were identified to the lowest possible taxonomic group using taxonomic keys. A more detailed account of the methodology used in ageing and diet analysis is described in Chapter 3.

Data analysis

The relationship between the length of the female and male parasites, as well as the relationship between the length of the female parasite and its host fish, were calculated using linear regression. Parasite prevalence was described as the proportion of hosts infected with one or more *C. borbonica* individuals. Prevalence as a function of either age (*a*) or length (*l*) was estimated using a modified logistic ogive in the form of:

$$P(x) = \frac{\theta_{max}}{1 + exp^{\left[ln\,(19)\times\left(\frac{x\,-\,\theta_{50}}{\theta_5 -\,\theta_{50}}\right)\right]}}$$

where x is either the fork length of the fish (mm) or its age (years), θ_{max} is the estimated maximum infection proportion and θ_{50} and θ_5 are the estimated lengths, or ages, where 50%

and 5% of the population is infected, respectively. Parameter variability was estimated using parametric bootstrapping (Efron 1979) with 500 iterations.

Condition factor of infected and non-infected fish was calculated as: $CF = \frac{W}{L^b} \times 1000$ where W is the weight (g), L is the fork length (mm) and b is the growth exponent from the length-weight regression. The null hypothesis that mean CF differed between infected and uninfected fish was assessed using a t-test.

The null hypotheses that mean fork length (mm) and mean eviscerated mass (g) differed per age class was assessed using t-tests. Linear regressions were fitted to length and age data for infected and uninfected fish and the difference in the slopes was assessed using ANCOVA.

Variation in feeding intensity was investigated using a stomach fullness index (SFI) proposed by Man and Hodgkiss (1977) as:

$$SFI = \frac{Mass\ of\ stomach\ contents\ (g)}{Eviscerated\ mass\ of\ fish\ (g)} \times 100.$$

The null hypothesis that SFI differed between infected and uninfected fish was assessed using a t-test.

Stable isotope samples were analyzed using a Europa Scientific INTEGRA isotope ratio mass spectrometer. Isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were obtained in parts per thousand (‰) relative to Vienna Dee Belemnite (VPDB) and atmospheric nitrogen standards as:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = \left({}^{\mathrm{R}_{sample}}\!\big/_{\mathrm{R}_{standard}} - 1 \right) \times 1000$$

where R is the isotopic ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. A Hotelling‟s T^2 test was used to test the null hypothesis that the distance between $\delta^{13}C$ and $\delta^{15}N$ centroid positions differed significantly from zero for infected, uninfected and basihyal damaged fish.

Results

Parasite characteristics

A total of 369 fish were examined for *C. borbonica*, of which 164 (45%) were found to be infected. Female parasites were significantly larger than males (t-test; $t = 27.32$; df = 234, $p < 0.01$) and ranged in size from 14.1 – 32.5 mm with a mean length of 24.5 ± 2.3 mm. Males ranged from 8.5 – 19.4 mm with an average length of 13.1 ± 3.9 mm. There was a significant correlation between the length of female and male parasites (R^2=0.44) (Figure 4.2). Similarly, the relationship between the length of female parasites and their host was significantly correlated (R^2=0.62).

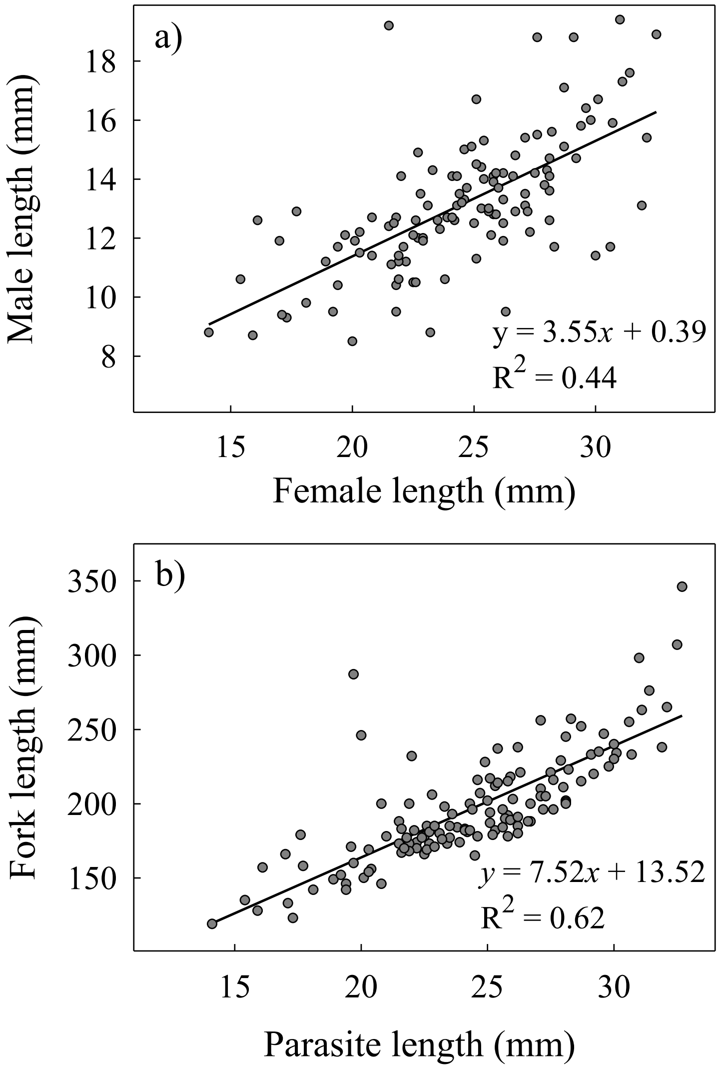

Figure 4.2: The linear relationships between a) the length of male and female *Cymothoa borbonica,* and b) the length of the female parasite and the length of its host fish, *Trachinotus botla*, sampled from northern KwaZulu-Natal.

Parasite prevalence

Parasite prevalence was dependent on both fish length and age (Table 4.2). Smaller fish were the most susceptible to infection by *C. borbonica* and the highest infection rates (67%) were found in fish less than 200 mm FL (Figure 4.3). A sharp decrease in this rate was observed between 200 mm FL and 400mm FL, and no parasites were found in fish over 400 mm FL. Similar trends were observed when comparing infection at age of *T. botla,* and prevalence decreased with an increase in age. The highest parasite prevalence was observed in fish less

Table 4.2: Total number of *Trachinotus botla* found to be infected by *Cymothoa borbonica* from Sodwana Bay, northern KwaZulu-Natal. Parasite prevalence is described as a proportion of all the fish sampled, per age cohort and length class.

Age	Total sampled	Observed proportion infected	Fork length (mm)	Total sampled	Observed proportion infected
0	5	0.80	100 - 150	22	0.64
1	88	0.59	150 - 200	133	0.68
2	102	0.48	200 - 250	107	0.45
3	46	0.17	250 - 300	45	0.22
4	25	0.04	300 - 350	25	0.08
5	8	0	350 - 400	25	0
6	2	0	>400	12	0

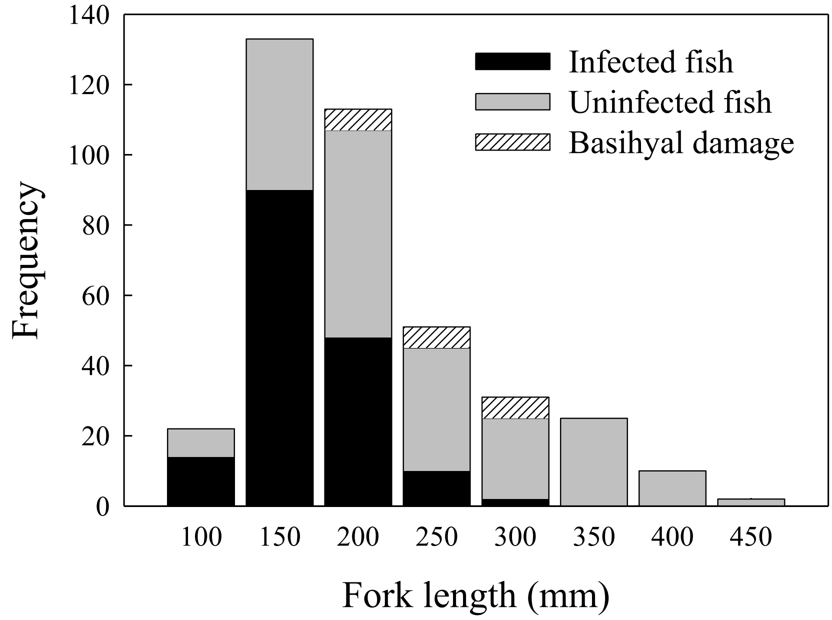

Figure 4.3: Length frequency of sampled fish categorized into fish infected by *Cymothoa borbonica*, uninfected fish, and those fish with basihyal damage as a result of possible previous infection.

than one year of age. In contrast, only a single fish greater than three years of age was infected. A total of 18 (4.9%) fish were observed to have considerable damage to their basihyal without the presence of a parasite. The damage was attributed to a recent parasite infection. Fish with basihyal damage had a size range of 224 – 347 mm FL, and an age range of 2 – 4 years.

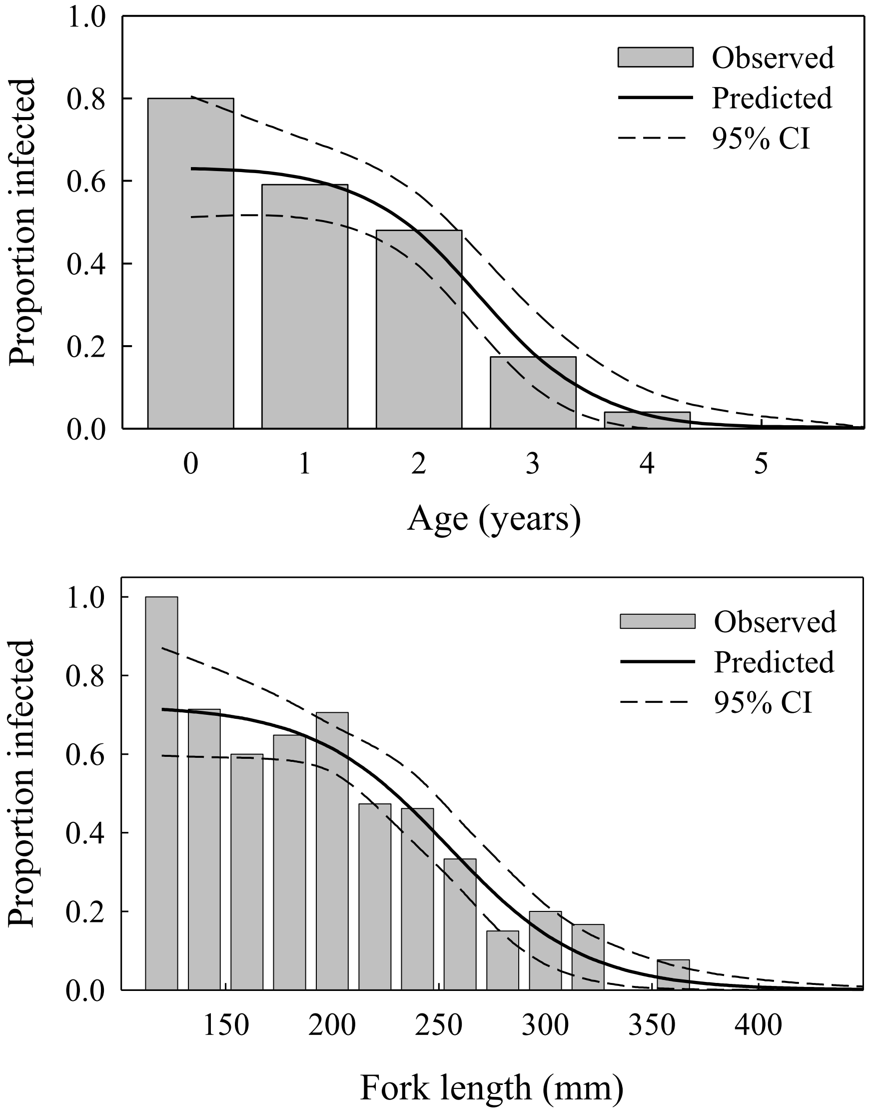

Figure 4.4: Observed and predicted (± 95% CI) proportion of *Trachinotus botla* which were infected by *Cymothoa borbonica.* Proportions are described in relation to age (years) and fork length (mm) of the host.

Effects of parasite infections

Host fish had considerable physical damage to their basihyals (Figure 4.1e). This was characterized by a marked decrease in the size of the basihyal, deformation of its shape and a roughened surface. In severe cases, the basihyal structure was completely absent. Male parasites attached to the cartilaginous gill rakers, and no obvious damage to the gill filaments of the host was observed. The area within the buccal cavity of infected fish was drastically reduced when compared to uninfected fish, as it was occupied by the female parasite (Figure 4.1d). Additional area was occupied by the male parasite towards the gill region. Mean condition factor of infected ($CF = 0.22$) and uninfected ($CF = 0.22$) fish did not differ significantly (t-test; $t = 0.31$, df = 323, $p = 0.76$).

Effects on growth

Parasite infection had a severe impact on the growth of *T. botla* which were greater than 1 year of age. There was no evidence that the growth of younger fish was affected. Mean fork length (mm) of infected fish greater than one year differed significantly from uninfected fish. Similarly, large differences were observed between the mean eviscerated mass of infected and uninfected fish over the age of one year (Table 4.3 and Figure 4.5). The growth rate of fish infected by *C. borbonica* was significantly lower than that of uninfected fish (ANCOVA*;* $t = 2.88$, df = 165, $p = <0.01$).

Table 4.3: Comparison of mean fork length (mm) and eviscerated mass (g) of fish infected by *Cymothoa borbonica* and uninfected fish, categorized according to age.

	Mean length (FL mm)			Mean eviscerated mass (g)		
Age	Host fish	Non-host fish	*p* (t-test)	Host fish	Non-host fish	*p* (t-test)
1	181.51	178.52	0.56	99.98	95.17	0.58
2	207.21	226.33	0.01*	145.98	197.75	0.02*
3	258.50	307.28	<0.01*	283.03	495.73	<0.01*

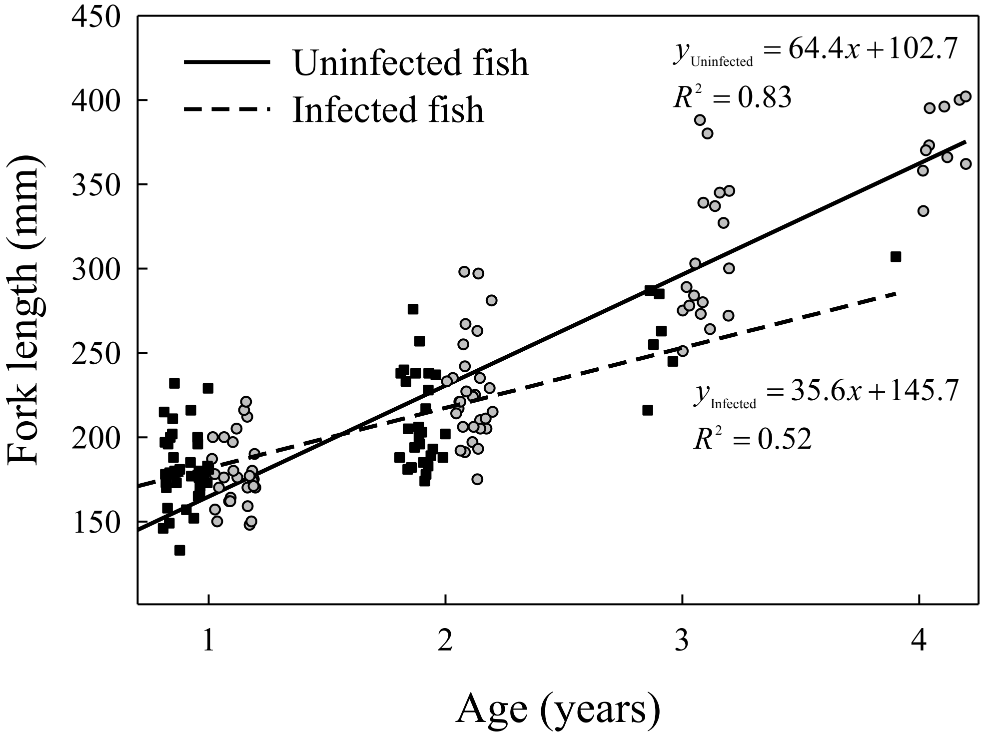

Figure 4.5: Age at length data for *Trachinotus botla* infected by the parasitic isopod *Cymothoa borbonica* (■) and uninfected fish (○). Linear regressions are presented for infected (dashed) and uninfected (solid) fish.

Effects on diet

Diet and feeding analysis (Chapter 3) indicated that small *T. botla* (<300 mm FL) were largely dependent on teleosts and copepods as their prey sources. There was no evidence to suggest parasite infections affected feeding habits. Stomach fullness index (SFI) did not differ significantly between infected and uninfected fish (t-test; df = 122, *p* = 0.19). Stable isotope analysis revealed similar carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) enrichment values for infected fish, uninfected fish and fish with basihyal damage (Figure 4.6). Further analysis confirmed that the distance between $\delta^{13}C$ and $\delta^{15}N$ centroid positions did not differ significantly from zero for infected and uninfected fish (Hotelling‟s T^2: $f = 0.08$, df = 51, p = 0.92). This was confirmed using a residual permutation procedure (RPP) ($p = 0.93$).

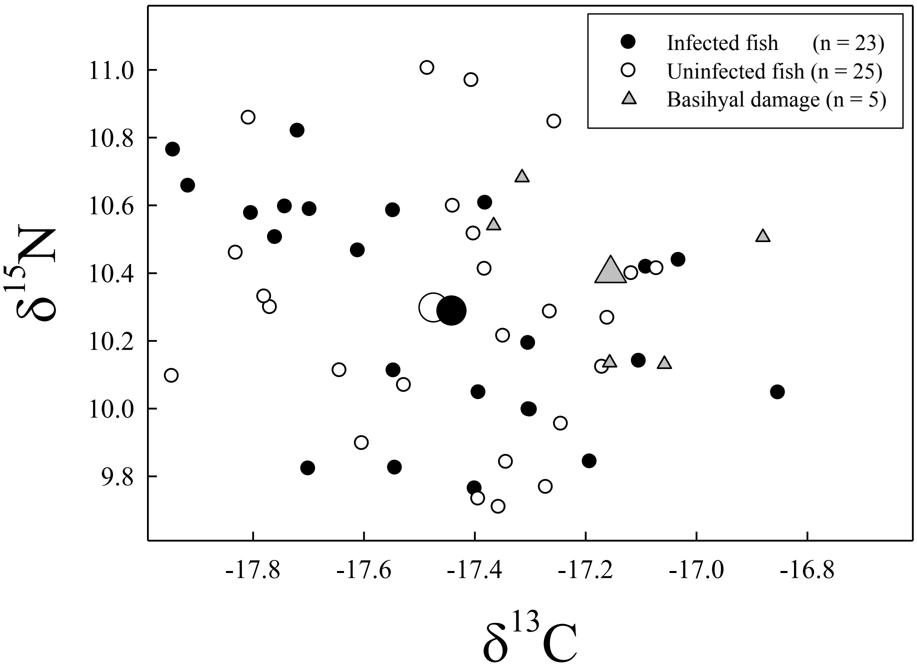

Figure 4.6: Dispersion of $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of *Trachinotus botla* infected by the tongue replacing parasite (*Cymothoa borbonica*), uninfected fish and fish with observed basihyal damage sampled from northern KwaZulu-Natal. The larger symbols represent the mean centroid position for their respective groups.

Discussion

Cymothoa borbonica almost always occurred in a male-female pair, with a few exceptions where only the female was present. It is assumed that in most cases where only a female occurred, there was a male present which may have got dislodged during capture or handling. The correlation between the length of the isopod and the length of its host suggests that recruitment occurs early in life and the parasite grows symbiotically with its host. The consistent parasite growth may be a result of the spatially restricted environment of the hosts" buccal cavity, as lengths of external cymothoid parasites do not always correlate with their host lengths (Bunkley-Williams and Williams 1998). The consistent presence of a male-female pair, as well as the high degree of correlation between the lengths of these pairs, is a result of a highly evolved parasitic life history. In general, cymothoids are protandrous hermaphrodites (Brusca 1981, Horton and Okamura 2001, Bakenhaster *et al.* 2006), but behaviour and intraspecific interactions may exert strong influence on sexual determination. It is suggested that in some *Cymothoa* spp., the female releases pheromones to stimulate the neurosecretory system of conspecific males. The result is an extended production of androgen in the nearby male, thus prolonging their masculinity and affecting their growth (Raibaut and

Trilles 1993). This evolutionary adaptation optimizes reproductive opportunity as it ensures a 1:1 sex ratio in a species where parasite intensity is limited to two parasites per host.

Parasite prevalence in *T. botla* was high and 45% of all fish sampled were parasitized. However, this average value may be misleading as prevalence varied greatly according to fish size. Small fish had a much higher prevalence rate than their larger counterparts, and a significant decrease in prevalence was observed in fish over 300 mm FL. The decrease in parasite prevalence with increased host size or age is common within *Cymothoa* spp. (Marks *et al.* 1996, Horton and Okamura 2001, Bakenhaster *et al.* 2006) and may be due to the death of the parasites and not the death of infected fish. The observed basihyal damage, and subsequent regeneration of the basihyal which was observed in some individuals, suggests that the host fish may outlive the isopod parasite. Such prevalence patterns, accompanied by consistent correlations between parasite and host size, indicate variable host susceptibility. Particularly a "window" period where the host is highly susceptible to the parasite, after which susceptibility dramatically decreases until they are eventually "immune" to infection. This is surprising given that the life-cycle of *C. borbonica* (Figure 4.7) includes an "infectious" free-living manca stage, which would suggest infection occurred randomly on contact or ingestion. Unfortunately an accurate estimation of the susceptibility period was not possible as prevalence data is limited to fish > 119 mm FL due to sampling gear restrictions. If it is assumed that parasite prevalence will follow an asymmetrical distribution and observed prevalence is highest within the smallest fish cohort sampled (0 - year old fish), the infection period must occur within the first year of the host"s life (<120 mm FL). The loss of the parasites and subsequent basihyal damage was only observed in fish 2 – 3 years old, suggesting that this damage is repaired over time. *Cymothoa borbonica* therefore has a life-cycle period of no greater than three years. Bakenhaster *et al.* (2006) substantiate that *Cymothoa* spp. have short life-cycles by revealing that *Glossobius hemiramphi* complete their life cycle within a single year.

The mechanisms responsible for host specificity are often complex and include physical, chemical and behavioural components (Buchmann and Lindenstrøm 2002). In ectoparasites, chemical stimuli emitted from the host and the anatomical structure of host"s epidermal surfaces play a particularly important role in host selection and successful attachment

(Buchmann and Lindenstrøm 2002). As mentioned, susceptibility to *C. borbonica* is limited to a specific host size, despite its free-living manca phase. This can be explained by a combination of preferred diet and, ultimately, the anatomical structure of the fish‟s gills at the period of infection. The free-living *Cymothoa* manca are likely to "mimic" the physical characteristics of copepods that are the most important food item of small fish (Chapter 3). Diet alone could not result in the definitive prevalence patterns observed, as copepods were also observed in the stomach contents of larger fish. Ultimately it is the anatomical structure of *T. botla* which determine parasite infection. Thin gill arches and minimal space between gill rakers, as found in juvenile fish, seem to facilitate the successful attachment of *C. borbonica* to their host.

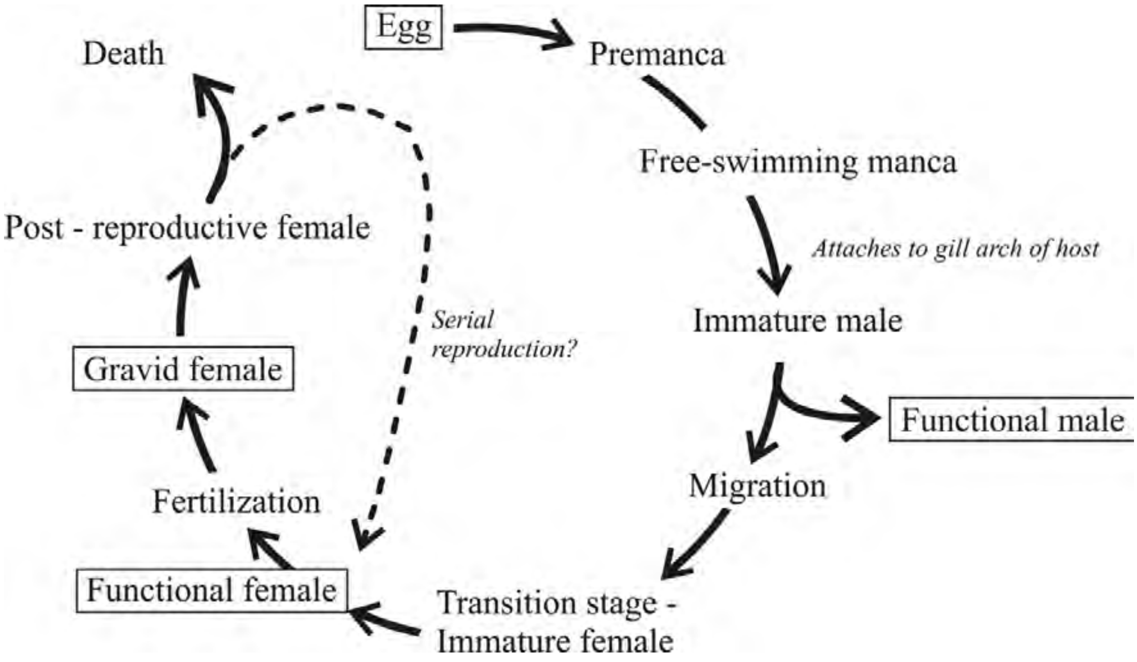

Figure 4.7: Hypothesized life-cycle of the parasitic isopod *Cymothoa borbonica* found to inhabit the buccal cavity of *Trachinotus botla* from northern KwaZulu-Natal. Life stages in boxes were observed. Adapted from Bakenhaster *et al.* (2006).

Parasite infection had obvious detrimental effects on their hosts. These included severe basihyal damage and a loss in buccal cavity volume as result of female parasite attachment. The hypothesis is that the female isopod may serve as a mechanical and functional replacement for the host‟s basihyal (Brusca and Gilligan 1983). Stomach fullness index was found to be statistically similar between fish infected by *C. borbonica* and uninfected fish, suggesting that feeding frequency of *T. botla* is not affected by the presence of the isopod parasites. Similar results were documented by Marks *et al.* (1996), where infection by *Lironeca ovalis* had little effect on the mass of stomach contents of *Pomatomus saltatrix***.** Their study concluded that infection by *L. ovalis* did not impair the host‟s feeding ability. There is also potential for minor damage to gill filaments in close proximity to the site of attachment of male parasite. Colorni *et al*. (1997) found evidence of histological damage to the gill rakers and filaments upon which the parasite rests its abdomen. The damage was a consequence of the isopod beating its pleopods for respiration. While this aspect was not examined in this chapter, further investigation is necessary to determine the effects of such damage on respiration in *T. botla*.

The results clearly indicate that growth in infected fish is slower than growth of uninfected fish. This trend only becomes noticeable towards the second year of the host‟s life, and is increasingly pronounced until the parasites finally detach from the host. The impacts of parasitism therefore appear to be cumulative. This suggests a minor nutritional or oxygen deficiency, compounded over long periods of time, is the likely cause for the inhibited growth in parasitized fish. There is, however, no evidence to suggest that these deficiencies may result in mortality. Condition factor has widely been used as a proxy for fish health (Froese 2006) and subsequently to quantify the effect of parasites on their host (Colorni *et al.* 1997, Horton and Okamura 2001). Despite the significant inhibition of growth recorded in parasitized *T. botla*, there was no significant difference in condition factor between infected and uninfected fish. The efficacy of condition factor with regard to quantifying parasitic effects, particularly in cymothoids, is questionable and must be applied with caution. The uniform or proportional stunting (slowed growth) of infected fish is not accounted for when analysing condition factor. Similarly, Williams and Bunkley-Williams (2000) concluded that condition factor was not a sufficiently sensitive metric to assess isopod impairment in many hosts, and incorporating host age into analyses is essential to demonstrate the effects of parasitism.

Stable isotope analyses have been commonly used to infer trophic characteristics of communities and general food web structures (Layman *et al.* 2007, Jackson *et al.* 2011). The stable isotope ratios in an organism‟s tissues are derived from all trophic pathways available to the organism and culminate in a distinct trophic "signature" (Layman *et al.* 2007). This "signature" is generally described in a spatial context using bivariate plots of carbon and nitrogen ratios. Recent advances in quantitative analyses of stable isotope data (Layman *et al.* 2007, Turner *et al.* 2010, Jackson *et al.* 2011) has allowed for the statistical comparison of an individual species" niche within a community. These methods facilitated the direct trophic niche comparison between fish infected by *C. borbonica* and uninfected fish. The objective of the stable isotope analyses was to determine if parasite infection required a long-term modification in diet to ensure host survival. Statistical analyses revealed no significant differences in the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios in bivariate space between infected and uninfected fish. This implies that both infected and uninfected fish occupy the same trophic niche within their ecosystem. It is therefore unlikely that there is a modification in diet or feeding habits of the host fish despite the obstruction of its buccal cavity. Fish exhibiting basihyal damage had higher carbon ratios than the other two groups. This can be attributed to the difference in mean fish size between the sampled groups and consumption of more $\delta^{13}C$ enriched prey.

The stable isotope analyses, combined with stomach fullness index (SFI) analysis, suggests there is no modification in diet and/or feeding habits of *T. botla* due to infection by *C. borbonica*. This host-parasite relationship has the characteristics of an adaptive co-evolutionary strategy. The co-evolution enables the host to maintain its feeding ability while the parasite grows to sexual maturity and reproduces.

Biological information on the genus *Cymotha* and the results from this chapter suggest that the isopod parasite *C. borbonica* is a highly evolved organism. Host specificity within cymothoids is known to be variable, with some species showing a tendency to be specific to ecological "groupings" such as schooling species as opposed to taxonomic specificity (Colorni *et al.* 1997). Host-specific parasites are more evolved than generalist parasites as their development is based on the unique life-cycle of their host. This is evident when analysing the life histories of *T. botla* and *C. borbonica* simultaneously. A clear ontogenetic dietary shift occurs in *T. botla* at ~300 mm FL (Chapter 3), which coincides with the mean length period when basihyal damage was observed in the host species. This dietary modification involves a shift from small, "soft" prey items (Copepoda and Teleostei) to larger items with hard external structures (Brachyura and Bivalvia). The ability to consume the larger, harder prey items is likely to be significantly reduced if the isopod parasites were still present, possibly resulting in host mortality. Alternatively, if the parasite is unable to cope with the mastication associated with the consumption of hard prey they may become detached from the hosts‟s basihyal. Whatever the reason, *Cymothoa borbonica* has evolved to exploit the period before this ontogenetic dietary shift.

To conclude, this chapter has provided the first evidence that *C. borbonica* infections reduce the growth rates of wild host fish populations. The inhibited growth patterns of infected fish are likely a result of nutritional and/or oxygen deficiency through buccal obstruction that is compounded over time. Despite this obstruction, the parasite does not seem to affect the diet, feeding habits or feeding frequency of their hosts. Further investigation into the effects of parasite presence on host bioenergetics, nutrition and respiration is needed to identify the cause of the observed growth inhibition. The results have also highlighted the inadequacy of condition factor as a proxy for quantifying the effects of cymothiods on their hosts. Furthermore, information has been provided into the life-cycle of *C. borbonica*, including an estimate of the hypothesized “infectious” period and its longevity. The chapter has emphasized the adaptive, evolutionary strategy employed by the cymothoids which produce unique host-parasite interactions that results in the optimal exploitation of a targeted period of the host‟s life cycle.

Chapter 5

A spatio-temporal assessment of the *Trachinotus botla* shore fishery in KwaZulu-Natal, South Africa

Introduction

Marine resources are in a steady state of crisis globally due to overfishing. The proportion of fish stocks estimated to be underexploited or moderately exploited declined from 40% in the mid-1970s to 15% in 2008. In contrast, the proportion of overexploited, depleted or recovering stocks increased from 10% to 32% (FAO 2010). In South Africa, the local fisheries were declared to be in a state emergency in 2000 in terms of the MLRA (Palmer *et al.* 2008). In 2001, total allocated commercial effort in the linefishery was reduced from 2600 to 732 permits and a new linefish management protocol was implemented as a means to manage stocks sustainably (Palmer *et al.* 2008).

Rock-and-surf angling is a popular pastime which attracts many anglers in South Africa, mainly due to the high levels of accessibility and affordability (Mann and Buxton 1997). In 1997, the shore angling sector was estimated to have more than 400 000 commercial and recreational participants, contributing to 1.3% of the gross domestic product of local economies (Brouwer and Buxton 2002). The recreational fishing industry continues to grow, and the linefish species of South Africa have been exposed to an increase in fishing effort over the past two decades (Brouwer *et al.* 1997). The need for relevant, long-term research and subsequent development of management strategies which promote sustainable marine resource use is necessary. Fishery assessments form the basis of management strategies as they provide decision-makers with information pertaining to the resource‟s status, determination of sustainable harvesting levels, and advice on the merits of alternative management strategies (King 2007).

One of the major obstacles of fishery assessments is the availability of accurate data, and inadequate and erroneous scientific information often leads to poor management decisions. There are two sources of information used in assessing a fishery – scientific survey data and fishery catch and effort data. The importance of fisheries independent scientific surveys of marine stocks has grown in the last few decades. Surveys are an efficient means of monitoring fish populations and understanding temporal and spatial dynamics (Pennington and Stromme 1998). Scientific surveys are expensive to conduct and often countries do not have the financial or human resources to collect information in this manner. Similarly, information on species that are perceived to have low economic value (i.e. recreational species) is less likely to be collected through scientific surveys. These fisheries are often termed “data-poor”, and depend largely on fisheries-dependent catch statistics for assessment.

Catch statistics provide information on captured fish, as well as the quantity of effort it took to produce the catch. This enables the calculation of a relative abundance index and catch-per-unit-effort (CPUE) that has been widely used in fisheries assessments in South Africa (Brouwer *et al.* 1997, Penney *et al.* 1999, Brouwer and Buxton 2002, Mann *et al.* 2002b, Mann and Pradervand 2007). CPUE data alone provides inadequate information needed for the comprehensive assessment and management of a fishery (Hampton *et al.* 2005, Maunder *et al.* 2006). If the age composition of the catches is known, or can be calculated using age-length keys, then fully age-structured models can be applied. These models provide estimates for mortality levels and subsequently the historical and current levels of abundance (King 2007). Incorporating these estimates into stochastic models which describe the underlying dynamics associated with population fluctuations provides fisheries scientists with an essential tool for predicting outcomes based on hypothetical scenarios (King 2007).

Age-structured, or dynamic pool models such as per-recruit analysis, incorporate the effects of growth, mortality and recruitment on a stock. A per-recruit model, be it from a yield per-recruit (YPR) or spawner biomass per-recruit (SBR) perspective, assumes a steady-state situation in which all input parameters are temporally invariant. For YPR, the total yield in any one year from all age classes is therefore assumed to be the same as the yield from a single individual over its entire life span (Sparre and Venema 1998). This assumption is unreasonable, as it would theoretically be impossible to overfish a stock if recruitment remained constant, as YPR would never reduce to zero (Richardson 2010). Alternatively, SBR (Beverton and Holt 1957) focuses on providing estimates to maintain reproductive capacity of a stock within safe biological levels (Butterworth *et al.* 1989). SBR analyses address the threat of recruitment overfishing (i.e. harvesting too many large adult fish so that future recruitment is depleted to levels that cannot sustain the population), which is thought to be the leading cause of stock collapse in many species (Myers *et al.* 1994, Richardson 2010). In South Africa, per-recruit analyses are recommended in the linefish management protocol as an appropriate method for assessing the status of the linefish species harvested by commercial, recreational and subsistence fishers (Griffiths *et al.* 1999). Subsequently, the SBR analysis technique has been employed on many stock assessments of popular South African linefish species (Booth 1997, Chale-Matsau *et al.* 2001, Mann *et al.* 2002a, Götz 2005, Richardson 2010).

This chapter provides a spatial and temporal assessment of the *T. botla* shore fishery of KwaZulu-Natal using historical catch and effort data, and presents an estimate of current stock status. It is hypothesized that a “recovery” period would be detectable in the fishery after the 2002 beach vehicle driving ban. The driving ban is thought to have affected the behaviour of resource users, particularly with regards to the spatial distribution of fishing effort. Effort may have shifted to be concentrated in areas in close proximity to public beach access, particularly in Maputaland where access areas are dispersed. Evidence of localised overexploitation is expected in these areas of concentrated fishing effort. Seasonal fishing patterns are also expected within the Maputaland fishery, and recreational angling effort is likely to increase over the holiday periods in remote areas.

Methods and materials

Fishery trends

Catch and effort data were obtained from the National Marine Linefish System (NMLS). While the database included data from 1985 to 2010, only data from 1987 were used as accuracy of previous two years was questionable. A total of 15 designated survey sites were identified in KwaZulu-Natal, from Bhanga Nek in northern Maputuland to Trafalgar on the South Coast (Figure 5.1). Catch-per-unit-effort (CPUE) was calculated as the number of fish caught per angler outing (fish.outing^{-1}), and was assumed to be a relative index of abundance. Seasonal abundance trends were described throughout the designated survey sites to provide a spatio-temporal overview of the *T. botla* shore fishery of KwaZulu-Natal.

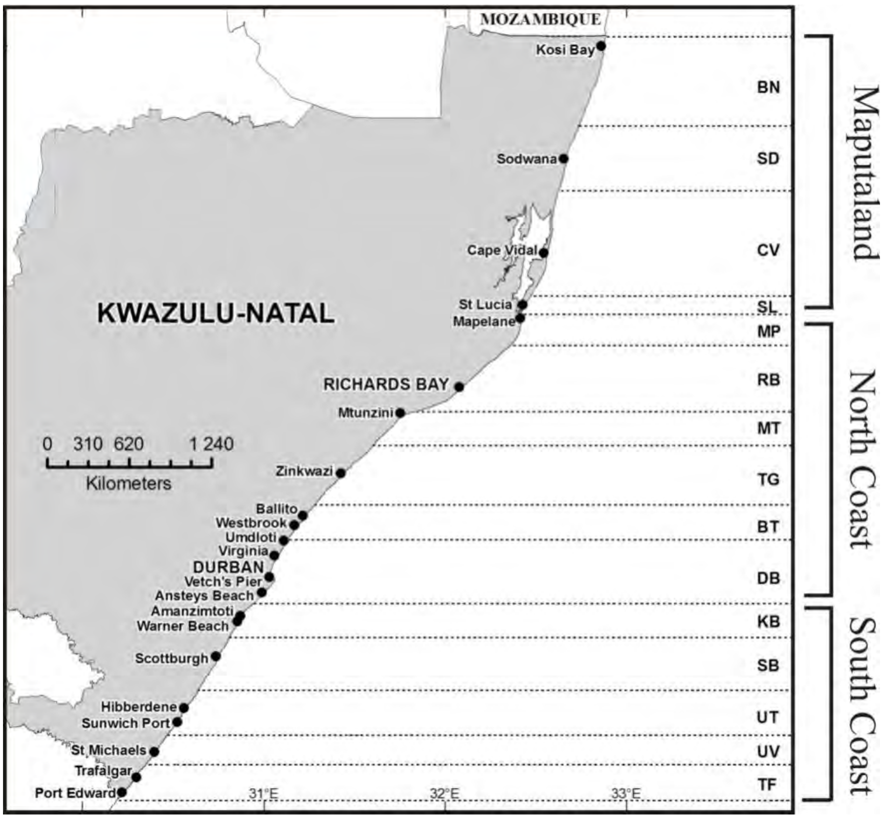

Figure 5.1: Designated survey sites for the National Marine Linefish System (NMLS) program along the Kwazulu-Natal coastline. Adapted from ORI (2011).

Movement

Movement analysis was based on data from the ORI/WWF-SA Tagging project that included 2391 tagged fish and 46 recaptures reported nationally. The ORI/WWF-SA Tagging project was initiated by the Oceanographic Research Institute (ORI) in 1984 and has become a successful national collaborative environmental project. The project issues its members, which are volunteer anglers, with tagging kits which include small plastic dart tags and a hollow, needle-like applicator. The species of fish, tag number, length (FL or TL), date, locality and name of the angler are recorded on a card and returned to ORI for capture onto a database. If a tagged fish is recaptured the same information is recorded and sent for capture onto the database. Time at liberty and distance moved can therefore be calculated. Tagging is generally restricted to larger fish (± 300 mm FL).

Per-recruit analysis

Sex independent growth, maturity and the length-weight relationship parameters were obtained from Chapter 3, and summarized in Table 5.1. Spawner biomass-per-recruit (SBR) and yield-per-recruit (YPR) were calculated as a function of both fishing mortality (*F*) and age-at-selectivity (S_a) as:

$$\mathrm{SBR}(F, S_a) = \sum_{a=0}^{t_{max}} W_a \, \tilde{N}_a \psi_a$$

and

$$\mathrm{YPR}(F, S_a) = \sum_{a=0}^{t_{max}} W_{a+1/2} \, \tilde{N}_a \frac{S_a F}{(M + S_a F)} \left[1 - e^{-(M + S_a F)}\right]$$

respectively, where *F* is the instantaneous rate of fishing mortality on fully selected fish, t_{max} is the maximum observed age, *M* is the instantaneous rate of natural mortality, S_a the selectivity at age *a*, W_a the mass of fish at age *a*, ψ_a the proportion of mature fish at age *a* and $\tilde{N}_a$ is the relative number of fish at age *a* calculated recursively as:

$$\tilde{N}_a \begin{cases} 1 & \text{if } a = 0 \\ \tilde{N}_{a-1} \, e^{-M - S_{a-1} F} & \text{otherwise} \end{cases}$$

Table 5.1: Parameter estimates which were used in the per-recruit analyses of *Trachinotus botla* from KwaZulu-Natal.

Parameter	**Estimate**	**Description**
L_1	132.66 mm FL	Average length of youngest fish
L_2	448.79 mm FL	Average length of oldest fish
a	1.37 year^{-1}	Growth curvature parameter
b	-5.84 year^{-1}	Growth curvature parameter
t_1	0.17 years	Known minimum age
t_2	6.75 years	Known maximum age
M	1.04 year^{-1}	Asymptotic natural mortality rate
F	0.27 year^{-1}	Asymptotic fishing mortality rate
t_{max}	6 years	Observed maximum age
a	0.00002 g mm^{-1}	Length-weight regression parameter
b	2.96	Length-weight regression parameter
ψ	2.31 years	Age-at-50%-maturity
δ_ψ	0.33 year^{-1}	Inverse rate of maturity
S	2.03 years	Age-at-50%-selectivity
δ_S	0.14 year^{-1}	Inverse rate of selectivity

Selectivity

Hook selectivity was estimated by assuming that it was sigmoidal and that 100% selection was achieved at the peak of the age-frequency distribution. Selectivity was, therefore, modelled by fitting a logistic ogive to the normalised ascending limb of the age-frequency distribution as:

$$S_a = \frac{1}{1 + \exp^{-(a - a_{50})/\delta}}$$

where S_a is the hook selectivity on a fish of age a, a_{50} is the age-at-50%-selectivity and δ is the parameter which determines the inverse rate of selectivity. Model parameters were estimated using non-linear regression.

Mortality rate estimates

Total mortality (Z) and natural mortality (M) rates were calculated as the inverse-variance weighted mean of linearized catch-curve (Ricker 1975) and survival was calculated using the Chapman Robson (1960) estimator. For total mortality, this was applied to the length-frequency data obtained from Sodwana Bay and from a long-term monitoring project being conducted in the St Lucia Marine Reserve north of Cape Vidal (B. Mann, ORI, unpublished data). The natural mortality estimate was calculated using the same methodology applied to data collected from the "no take" marine sanctuary zone within the St Lucia Marine Reserve. Length frequencies were converted to age-frequencies using a normalised age-length key. For the catch-curve analysis, Z_{cc} and its asymptotic standard error, SE_{Zcc}, were estimated from the negated slope of a linear regression fitted through the natural logarithm-transformed descending limb of the age-frequency data. Alternatively, the Chapman and Robson (1960) estimator is defined as:

$$Z = -\log_e\left(\frac{1 + \bar{a} - {}^{1}\!/_{n}}{\bar{a}}\right)$$

where $\bar{a}$ is the mean age at and older than the peak of the age-frequency distribution, and n is the number of fish in this sample.

Results

Description of the fishery

Trachinotus botla catch and effort data from the shore fishery between 1987 and 2010 indicated that the fishery has remained relatively stable since 2000. Annual catches ranged from 860 individual fish in 1994 to 2354 individuals in 1995, while effort ranged from 186 731 outings in 1987 to 96 462 outings in 1996. Both catch and effort for *T. botla* was unevenly distributed across the KwaZulu-Natal coastline. Cape Vidal produced the highest catches (10 734 fish recorded) and was almost double that of the second highest location, Durban (5 481 fish). Effort was particularly high in Durban,

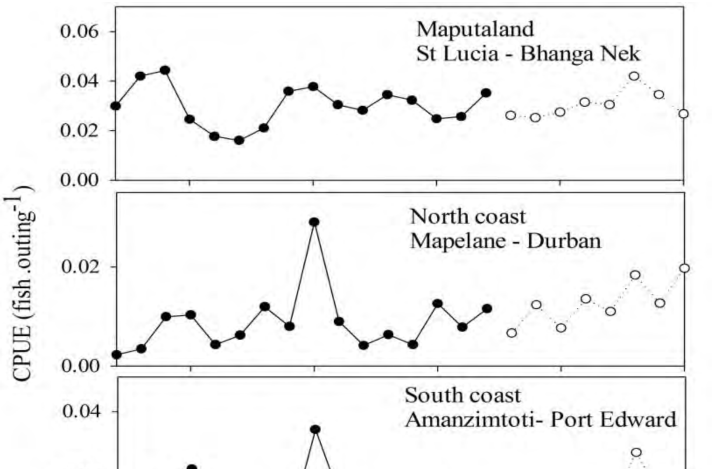

Figure 5.2: Contour plot of annual CPUE data for the *Trachinotus botla* shore fishery at each designated NMLS survey site in KwaZulu-Natal from 1987 – 2010. The graph also displays the mean annual CPUE for the combined areas of Maputaland, North coast and South coast. Unshaded circles indicate post beach driving ban data.

an urban centre, and its immediate surroundings. St Lucia and Cape Vidal also recorded relative large amounts of fishing pressure. CPUE records displayed a latitudinal trend, and areas north of St Lucia had much higher mean annual CPUE records than those areas south of St Lucia (Figure 5.2). Distinct seasonal variations occur within the fishery (Figure 5.3). Catch records of *T. botla* peak in the summer months despite the majority of effort being concentrated in the winter months in KwaZulu-Natal. Increases in CPUE with the onset of summer are first exhibited in the months of September and October in the far north region of KwaZulu-Natal (CV, SD and BN). Mean annual CPUE after the implementation of the beach

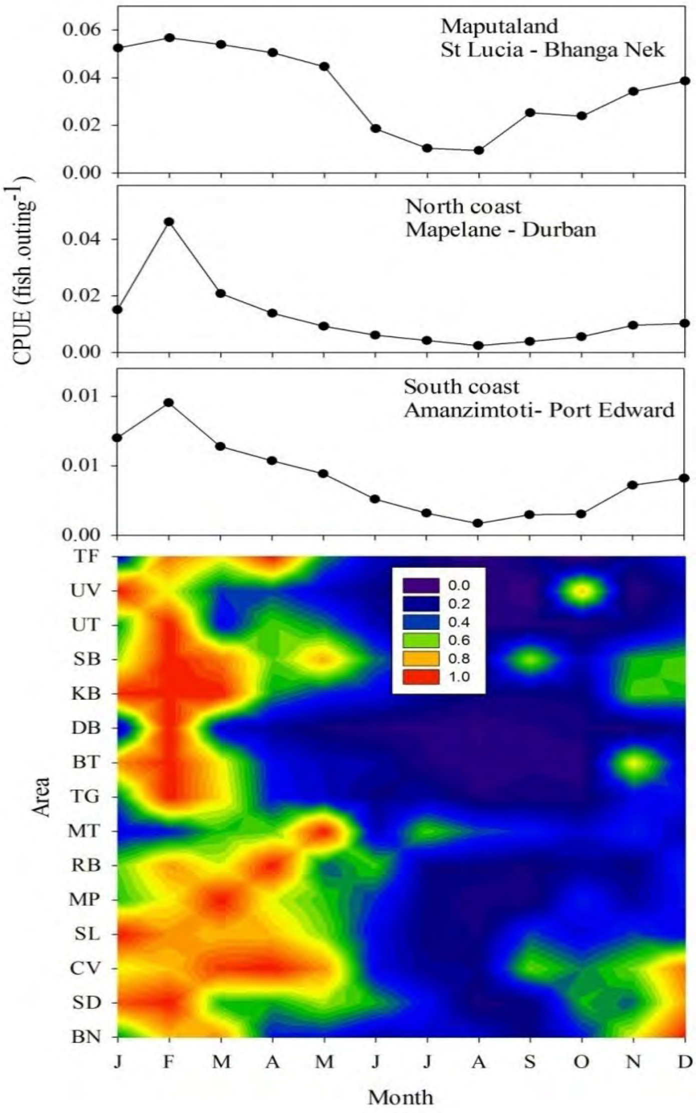

Figure 5.3: Contour plot of CPUE data by month for each designated NMLS survey site between 1987 and 2010. The data is described as a proportion of the maximum CPUE recorded for the site. The graph also displays the mean monthly CPUE for the combined areas of Maputaland, North coast and south coast.

driving ban appeared to have increased but this trend was not significantly different to that from before the ban due to the high variability in mean CPUE values (ANCOVA; $t = 0.97$, df $= 23$, $p = 0.34$).

Movement

A total of 2391 *T. botla* were tagged along the coastline of South Africa, of which 46 (1.88%) were recaptured. The average time at liberty was 208 days, with a maximum of 1236 days. Distance moved averaged 7 km, and 78% of all fish recaptured were within 1 km of their release site. Two fish were observed to have made significant northeast movements of 114 km (Sanctuary area A to Kosi Bay) and 107 km (Christmas Bay to Kosi Bay). Both of these fish were sexually mature (335 and 401 mm FL) when released and were at liberty for 301 and 299 days, respectively. The median distance moved along the coastline in a northeast and southwest direction was 13 km and 1 km, respectively.

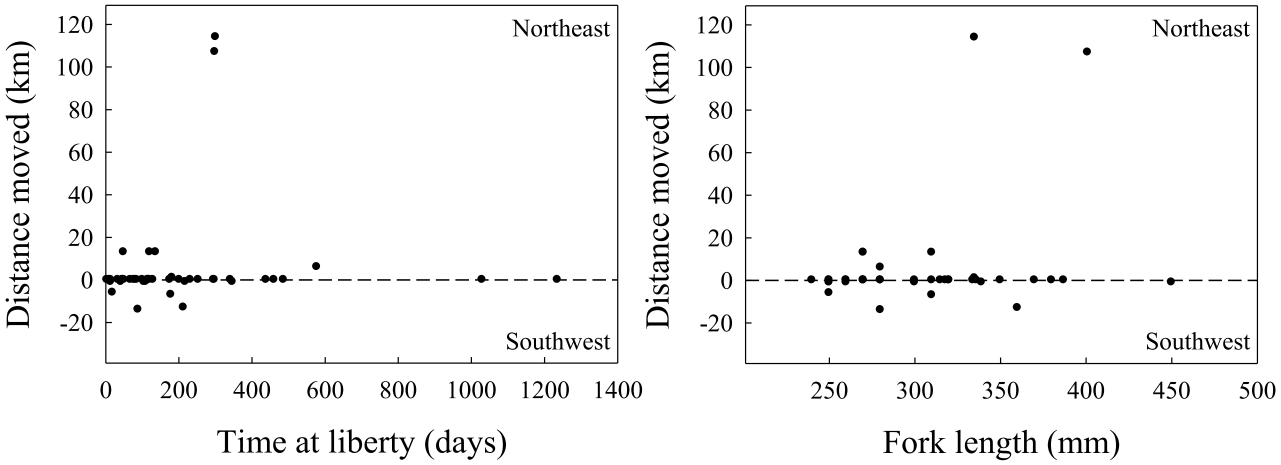

Figure 5.4: Movement patterns of *Trachinotus botla* tagged in South Africa. Movement is described as the distance from the tagging site to recapture site, as either a function of time or length. Positive values depict movements in a northeast direction, while negative values depict movements in a southwest direction.

Mortality

The total mortality estimate for Sodwana bay was 1.32 y^{-1} ($Z_{CR} = 1.26$ y^{-1}, $Z_{CC} = 1.37$ y^{-1}), and the total mortality estimate for the St Lucia Marine Reserve was 1.30 y^{-1} ($Z_{CR} = 1.27$ y^{-1},

Z_{CC} = 1.55 y^{-1}). These were calculated as inverse-variance weighted means of the independent estimates provided by the two methods applied. Subsequently, the total mortality for *T. botla* was estimated as $Z = 1.31 \pm 0.04\ y^{-1}$. Natural mortality for *T. botla* was estimated as $M = 1.04 \pm 0.04\ y^{-1}$ and was calculated as the inverse-variance weighted mean of the two independent methods applied to data from the Sanctuary zone ($Z_{CR} = 1.03\ y^{-1}$, $Z_{CC} = 1.13\ y^{-1}$). Fishing mortality was estimated as $F = 0.27\ y^{-1}$ (Figure 5.5).

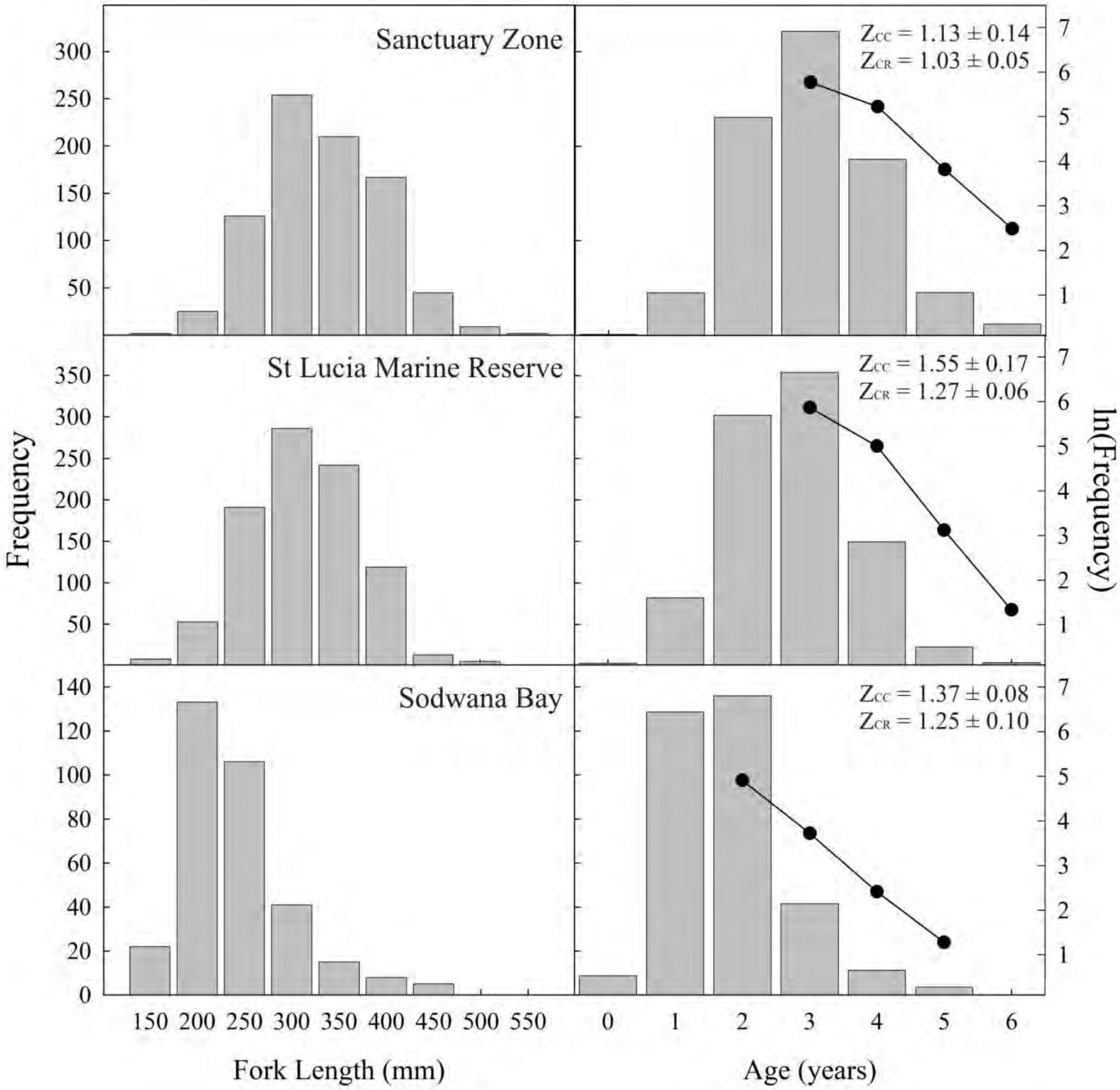

Figure 5.5: Length- and age-frequency distribution of *Trachinotus botla* from the different data sources. Plots describing ln(frequency) are incorporated into the age-frequency graphs. Estimates of *Z* are provided from linearized catch-curve analysis (Z_{CC}) and the Chapman and Robson estimator (Z_{CR}).

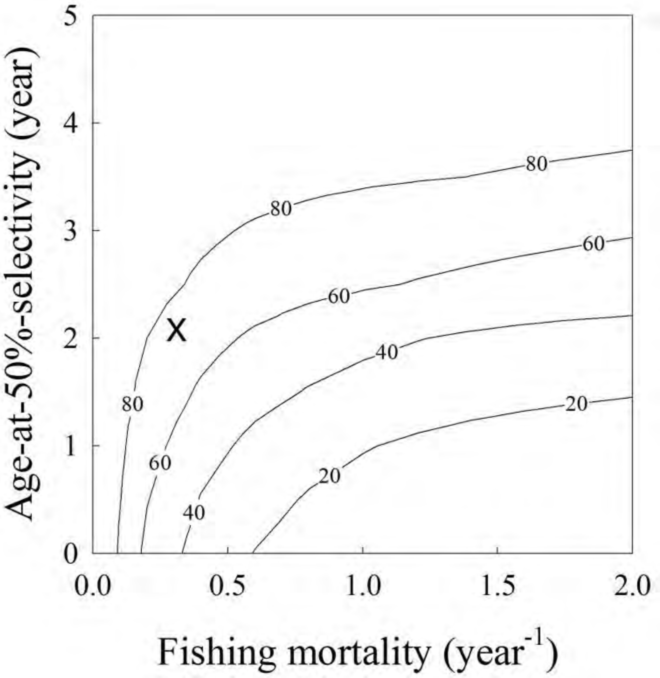

Figure 5.6: Isopleth plot describing the response of spawner biomass-per-recruit to different combinations of fishing mortality (*F*) and age-at-50%-selectivity (*S*) for *Trachinotus botla* sampled in KwaZulu-Natal. *M* = 1.04. "X" denotes current status.

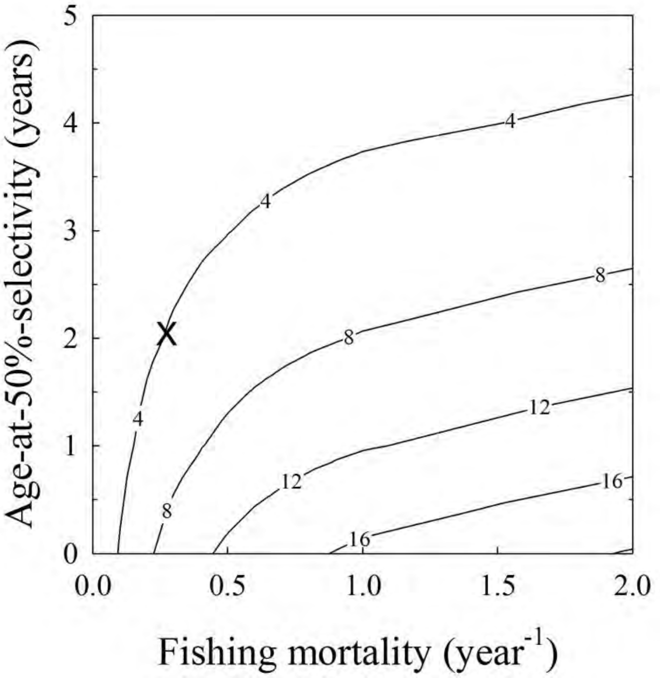

Figure 5.7: Isopleth plot describing the response of yield-per-recruit to different combinations of fishing mortality (*F*) and age-at-50%-selectivity (*S*) for *Trachinotus botla* sampled in KwaZulu-Natal. *M* = 1.04. "X" denotes current status.

Per-recruit analyses

The per-recruit analyses estimated that SBR was currently at 75% of pristine levels and YPR was estimated to be 4.05 grams. Isopleth diagrams describing the response of SBR and YPR to different values of fishing mortality (*F*) and age-at-50%-selectivity (*S*) are presented in Figures 5.6 and 5.7, respectively. The response isopleths shows that at low values of *S*, maximum SBR was attained at correspondingly low values of *F*. At high values of *F* (>1.5y^{-1}) SBR was largely dependent on *S* and the effects of increased fishing effort became negligible.

Table 5.2: The response of *Trachinotus botla* spawner biomass-per-recruit target reference points to three natural mortality (*M*) scenarios.

M(yr^{-1})	F_{max}	$F_{current}$	$F_{0.1}$	F_{SB50}	F_{SB40}
0.94	∞	0.24	1.05	0.72	1.11
1.04	∞	0.27	1.29	0.84	1.32
1.14	∞	0.31	1.59	0.99	1.6

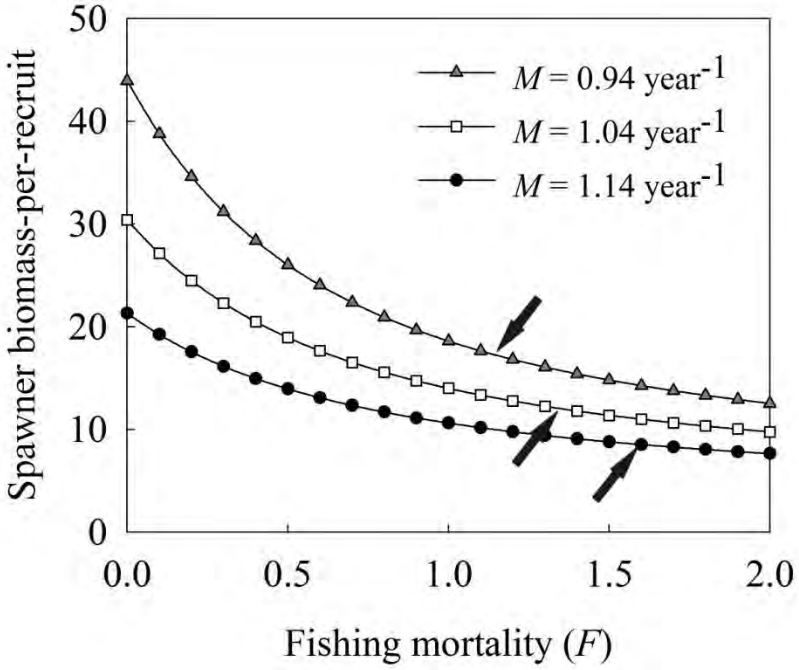

Figure 5.8: Spawner biomass-per-recruit as a function of fishing mortality (*F*) for *Trachinotus botla* under three natural mortality scenarios. Arrows indicate the point at which the target reference point (SB_{40}) is reached.

Sensitivity of the SBR model to M

The effects of alternative natural mortality (*M*) scenarios on both YPR and SBR were assessed and are summarised in Figure 5.8 and Table 5.2. In all three natural mortality scenarios, the level of fishing effort required for a marginal yield ($F_{0.1}$) strategy was higher than the effort needed to reduce SBR to half that of an unexploited stock (F_{SB50}), but lower than the effort needed to reduce SBR to 40% of an unexploited stock (F_{SB40}). Maximum fishing mortality (F_{max}) increased monotonically in all scenarios.

Discussion

Trachinotus botla abundance increased northwards with Cape Vidal, Sodwana Bay and Bhanga Nek having considerably higher mean annual CPUE than any other sites along the coast. These trends highlight the tropical nature of the species, and its affinity to the warmer waters of northern KwaZulu-Natal (van der Elst 1993, McPhee 1995, Heemstra and Heenstra 2004). The *T. botla* shore fishery of KwaZulu-Natal has shown long-term stability with regards to catch rate with peak catches occurring over the summer months despite shore angling efforts for the region peaking during winter. The increase winter angling effort coincides with the period when shore anglers target species such as *Pomatomus saltatrix*, *Lichia amia and Sarpa salpa*. *Pomatomus saltatrix* is the most important shore angling species caught in KwaZulu-Natal (Mann 2000), and *L. amia* is regarded as one of the most popular gamefish in the South African recreational angling sectors (Van der Elst *et al.* 1993). Few shore anglers target *T. botla*, particularly in southern KwaZulu-Natal, and the sporadic catches indicate that the species is predominantly by-catch. The species can be targeted along the northern Maputaland coastline, but is widely viewed as a by-catch species throughout the shore angling fraternity.

Shore angling effort in KwaZulu-Natal was concentrated in two distinct areas - Durban and its surroundings, and the area between Cape Vidal and St Lucia. Accessibility undoubtedly drives the large fishing effort observed around Durban, as the city has an estimated human population of over 3 million (SSA 2008). The Cape Vidal and St Lucia regions are sparsely populated in comparison. These regions are located within the Isimangaliso Wetland Park, a holiday location that was proclaimed a World Heritage Site in 1999 with ~1 million visitors entering the park in 2002 for recreational purposes (UNESCO 2008).

The low tag recapture rate of *T. botla* is indicative of a large population (or high tagging mortality and/or tag shedding). The use of recaptured fish to describe movement patterns in this chapter was limited, as only 46 individuals were recaptured. It was however evident that most of the population resides within a relatively small area, while a small proportion of the population exhibit the tendency for large scale movements. The two fish that undertook large-scale movements were large (335, 401mm FL) and mature. The likelihood of an individual moving large distances increases with an increase in size as the energetic cost of movement decreases (Roff 1988). While the size range of recaptured fish was narrow (240 – 450 mm FL) as a result of sampling protocol, the possibility of smaller individuals undertaking similar large-scale movements cannot be disregarded. Both large-scale movements were in a northerly direction along the coastline. Excluding these two recaptures, no directional movement trends in the other fish were noted. No trend between distance moved and time at liberty was observed to indicate gradual diffusion movement behaviour within the species. Similarly, there was no evidence to support the hypothesis that movement may be related to spawning. A tagging study of *T. botla* in Queensland, Australian had comparable results. Most fish (49.3%) were recaptured less than 1.6 miles from their release site and few fish moved more than 40 miles (McPhee *et al.* 1999). Movement was described as spatially over-dispersed with possible ranging tendencies, and each fish has the potential to move a great distance (McPhee *et al.* 1999).

Similar movement trends have been displayed in reef-associated species such as *Chrysoblephus laticeps* (Kerwath *et al.* 2007), *Dichistius capensis* (Attwood and Bennett 1994) and *Caranx melampygus* (Holland *et al.* 1996). Kerwath *et al.* (2007) noted that it is possible that some individuals are more prone to moving than others. A more parsimonious hypothesis is that all fish are predetermined to stray from their home range at some stage of their life. The authors highlight the importance of defining the home range as it may then be used as statistically significant concept against which movement can be compared. This may be difficult in surf zone species such as *T. botla* as its environment is dynamic and can be altered over extremely short time periods. This is particularly true in times of adverse weather and rough sea conditions. The paucity of constant visual cues for defining a home range suggests that *T. botla* may rely on other factors, such as prey availability (McPhee 1995). Prey items within a surf zone are generally motile and unevenly distributed (temporally and spatially) (Lasiak and McLachlan 1987). Individuals may move when prey encounter rates in their home range falls below a critical level, and continue to move until suitable concentrations of prey items are relocated. This hypothesis may explain the apparently random observed movement patterns.

The promulgation of a beach vehicle ban in January 2002 has lead to large decreases of shore angling effort in areas that are not directly adjacent to beach access areas (Mann and Pradervand 2007). This regulation has effectively created numerous undefined refugia where fishing exploitation has been drastically reduced, in some cases to being negligible. It can be argued that the same regulation has merely shifted the fishing effort to more accessible areas, concentrating effort into a fraction of the original fishing area. In doing so, accessible areas have endured fishing efforts which are unsustainable. This may lead to localised overexploitation. Movement patterns of *T. botla* display a degree of residency and localised overexploitation of the species in accessible areas must be taken into consideration. Mann and Pradervand (2007) found that *T. botla* CPUE increased within the St Lucia Marine Reserve north of Cape Vidal. In contrast, long-term CPUE trends in Sodwana Bay (± 45 km north of Leven point) show a steady decline from 1987 to 2010. Sodwana Bay remains the only beach in South Africa where driving is permitted within a 2 km stretch without a recognised permit. As such, the vast majority of the shore angling effort is localised within the 2 km stretch of beach. This highlights the susceptibility of the species to localised overexploitation, and the importance of Marine Protected Areas (MPA) in marine conservation. MPA"s are regarded as a fundamental component of the precautionary approach to fisheries management (Clark 1996). One of the primary benefits of MPAs is the exportation of larvae, recruits and adult fish into adjacent fishing grounds; described as the "spillover" effect (Clark 1996, Attwood *et al.* 1997, McClanahan and Mangi 2000). The spillover could influence a large area as larvae have the potential to disperse over considerable distances (Zeller *et al.* 2003).

The selection of any stock assessment methodology is largely based on data availability. In the case of *T. botla*, a per-recruit assessment approach was adopted as the only data available are catch and life-history data together with length frequency distributions. Current SBR was estimated as 75% of pristine levels and current yield-per-recruit was estimated as 4.05 grams. Yield is less important than spawner biomass in this particular situation, and the assessment focused on the possibility of recruitment overfishing. It is generally accepted that the risk of recruitment overfishing is greatly increased at SBR levels below 25% of pristine (F_{SB25}), known as the limit reference point. Ideally, fisheries are aimed to be managed at SBR levels of 40% of pristine (F_{SB40}), known as the target reference point (Butterworth *et al.* 1989, Hilborn and Ludwig 1993, King 2007). Based on the current mortality and selectivity estimates the target reference point would be reached if fishing mortality increased to 1.32 year^{-1}, which is almost five times greater than the current fishing mortality estimate. The management protocol for the South African linefishery recommends classifying linefish species into four management categories based on per-recruit reference points. A fishery would be considered to be collapsed if $F_{current} \leq F_{\mathrm{SB25}}$, overexploited if $F_{\mathrm{SB25}} < F_{current} \leq F_{\mathrm{SB39}}$, optimally exploited if $F_{\mathrm{SB40}} < F_{current} \leq F_{\mathrm{SB50}}$ or underexploited if $F_{current} > F_{\mathrm{SB50}}$ (Griffiths *et al.* 1999). The assessment suggests that the levels of stock exploitation of *T. botla* shore fishery of KwaZulu-Natal remain relatively low, and that the species is currently underexploited.

Although recruitment into the fishery (2.03 years) occurs before maturity, the risk of recruitment overfishing will remain relatively low if the age-at-50%-selectivity is >2 years. Increases in *F* are accompanied by relatively sharp decreases in spawner biomass per-recruit when age-at-50%-selectivity is <2 years of age. A sensitivity analysis revealed that when age-at-maturity coincides with the age-at-50%-selectivity (2.3 years), the stock would be far more resilient and the chance of recruitment overfishing will decrease dramatically ($F_{\mathrm{SB40}} = 3.86$).

The suitability of the per-recruit analyses approach as an effective assessment tool has previously been questioned (Booth and Buxton 1997, Richardson 2010). Although the per-recruit analyses has limitations (Norris 1991), a fundamental understanding of these limitations will increase its effectiveness as an assessment tool. The quality and reliability of input parameters is of paramount importance, and should be obtained from unexploited populations where possible (Götz *et al.* 2008, Richardson 2010). Richardson (2010) explains that few biological fish studies have the luxury of sampling unexploited populations, as without a comparable exploited population the outcomes have no meaningful management value. It is essential to acknowledge that exploitation may alter biological traits such as maturation and longevity – parameters on which per-recruit assessments are based. Decision makers should err on the side of caution when interpreting assessments based on parameters from exploited populations. Richardson (2010, page 119) emphasized the importance of accurate and reliable input parameters, particularly estimates of *M*, by stating that "if the accurate estimation of *M* is precluded then the SBR assessment results are likely to have very little meaning". A sensitivity analysis confirmed the importance of accurate estimates of natural mortality. Pristine estimates of SBR varied greatly depending on values of *M*, and subsequently altered reference point estimates. An overestimation of *M* significantly increased the fishing mortality needed to reach the target reference point at it assumes a more productive resource. It is clear that decisions based on inaccurate estimates of *M* could easily result in the overexploitation of a stock.

The assessment outcomes are not surprising given the life history traits of the species. *Trachinotus botla* exhibits fast growth, early maturation and has a short life span; all characteristics that facilitate a resource that is more suitable, and better able to cope with high levels of exploitation. In comparison, the fishery of Florida pompano (*T. carolinus*) in North America is considered to be overexploited despite having similar life history traits to *T. botla* (Muller *et al.* 2002, Murphy *et al.* 2007). Although the species may be biologically similar, the two fisheries differ fundamentally. The Florida pompano is a valuable commercial species that fetches US\$10.kg^{-1}, as well as a popular recreational species. The fishery is largely boat-based and the use of gillnets was openly permitted until 2001, after which the technique was restricted to licensed commercial fishermen (Muller *et al.* 2002). In contrast, 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. It is clear that the nature of the fishery itself inherently limits its exploitation.

To conclude, the *T. botla* shore fishery of KwaZulu-Natal appears to be in a stable state. The stock assessment showed that the species is currently underexploited (SBR = 75% of pristine levels), and fishing pressure could be increased. A notable finding was that if age-at-50%-selectivity was increased to be on par, or above age-at-50%-maturity, the resilience of the population to exploitation would be increased. The importance of accurate input parameter estimates, particularly *M*, was highlighted as a fundamental limitation of the per-recruit analyses. Per-recruit analyses are suitable for short-term predictions (Booth and Buxton 1997), but it is recommended that other age-structured models are incorporated in the future to provide a more accurate and comprehensive assessment.

Chapter 6

General discussion and management recommendations

Introduction

Carangidae include a diverse group of fishes known by common names such as jacks, trevallies, amberjacks, pompanos, scads, kingfish, pilotfish and rainbow runners. Carangids are found in all tropical and subtropical marine waters of the world, with a few, such as horse mackerels and leervis, occur in temperate regions (Honebrink 2000). Carangids within South Africa, with the exception of the temperate Cape horse mackerel *Trachurus capensis*, are predominantly found off the coast of KwaZulu-Natal and generally become more abundant towards Mozambique. Their habitat utilisation is broad and ontogenetic habitat shifts are a fundamental life history characteristic of many species (Smith and Parrish 2002).

The surf zone is utilised by all *Trachinotus* spp. during some stage in their life history (McPhee 1995). Within South Africa, and maybe elsewhere, *T. botla* appears to be the only "permanent" species that completes its entire life-cycle within the surf zone. A large majority of trachinotids use multiple habitat types throughout their life. *Trachinotus blochii, T. falcatus* and *T. carolinus* have all been documented to inhabit estuarine waters at some period (Blaber and Cyrus 1983, Adams *et al.* 2006, Main *et al.* 2007). The Florida pompano, *T. carolinus*, is unique in that spawning occurs offshore and juveniles recruit into the surf zone. Adults later move into estuaries and coastal waters (Murphy *et al.* 2007). The confinement of *T. botla* to the surf zone is rare amongst carangids and a number of hypotheses may explain this behaviour. First, ichthyoplankton surveys conducted in large estuaries in northern KwaZulu-Natal suggest that *T. botla* larvae may not reach the estuarine environment (Harris and Cyrus 2000, Harris *et al.* 2001). The reasons for this are unknown, as *T. botla* larvae was identified to occupy the surf zone adjacent to the St Lucia estuary mouth in KwaZulu-Natal (Harris and Cyrus 1996). Second, if *T. botla* larvae were to reach the estuarine environment it is possible that the species may be intolerant of the physicochemical parameters, particularly salinity and turbidity. *Trachinotus botla* is a visual predator that may be turbidity-limited, and are unable to feed efficiently without sufficient water transparency (McPhee 1995).

Spawning seasons for most carangids are fairly protracted and generally peak during summer. *Trachinotus* spp. reach sexual maturity at a relatively small sizes, with the exception of *T. falcatus* that matures at approximately 500 mm FL and grows to over a meter (Crabtree *et al.* 2002). The vast majority of *Trachinotus* spp. mature at approximately 200 mm FL. This appears to be an adaptive strategy that compensates for high juvenile mortality as a consequence of the stress that the inconsistent surf zone environment places on recruitment (Lemos *et al.* 2011). A similar argument is applicable when explaining the serial spawning behaviour of *T. botla.* More environmental variability would correspond to a higher probability of individuals encountering poor resource conditions and therefore lower probability of successful reproduction and survival. Fish therefore partake in multiple spawning events in an attempt to overcome the high probability of reproductive failure if spawning is synchronous.

Carangids have been divided into three groups according to feeding habits - carnivorous, represented by the genera *Caranx* and *Seriola*; planktivorous, such as *Decapterus* and *Selar*; and molluscivorous, such as *Trachinotus* (Cruz Esalona and Abitia Cardenas 2004). As with other regions worldwide, *Caranx* spp. are considered to be apex predators within South African marine waters (Best *et al.* 1997). Carangids also exhibit a wide variety of feeding behaviours that are idiosyncratic. Major (1978) studied predation behaviour of small *C. ignobilis* on Hawaiian anchovies and noted evidence of mutualistic hunting. Small groups (three to five individuals) had more success hunting schooling prey than fish that hunted individually. Parrish (1993) also noted increased predatory success by kingfish (*C. caballus*) when hunting in groups of three to five, especially when disrupting schools of prey fish and orienting to the detached individuals. Alternatively, island jack *Carangoides orthogrammus* has been observed "rooting" in the sand for crustaceans and fishes (Myers 1991). The pilotfish (*Naucrates ductor*) forms a commensal relationship with sharks, rays, and other large fishes and feeds on scraps of the host"s food as well as consuming ectoparasites from the host"s body (Smith-Vaniz 1986). The examples suggest that defining a "typical" carangid based on its feeding behaviour is impractical, although similarities between certain species are evident.

Within this thesis, two distinct trends were observed in the feeding behaviour of *T. botla* (Chapter 3). The first is the ontogenetic dietary shift that occurs at ~300 mm FL. The diet of smaller fish consisted mainly of copepods, mole crabs, postlarval prawns and terrestrial insects. Larger fish were more dependent on crabs, mussels and gastropods. Remarkably similar feeding patterns have been exhibited by *T. falcatus* that also undergoes a shift in diet at 350 mm FL (Finucane 1969). Ontogenetic dietary shifts are common in carangids, and are often linked to shifts in habitat. Examples of this behaviour include *C. ignobilis* (Sudekum *et al.* 1991), *C. sexfasciatus* (Blaber and Cyrus 1983, Myers 1991) and *S. dumerili* (Badalamenti *et al.* 1995). The second distinct trend observed in the feeding behaviour of *T. botla* is its opportunism. The species utilizes "superabundant" prey items, particularly copepods, postlarval penaeids and terrestrial insects. These prey items are likely to have been consumed by ram suspension feeding, as *T. botla* does not possess the jaw structure associated with fish species that are able to capture zooplankton individually (McPhee 1995). Ram suspension feeding has been identified in at least 50 fish species in sixteen families (Sazima 1998). The nature of this indiscriminate feeding behaviour has been thoroughly examined in two other carangids - *P. dentex* (Sazima 1998) and *S. dumerili* (Sanderson *et al.* 1996).

Studies relating to the parasitic isopod *Cymthoa* spp. have been largely restricted to occurrence records and morphological features. There are relatively few ecological studies describing parasite-host relationship of *Cymothoa* spp., and those that have been published are based on small sample sizes and/or captive populations. There is even less information regarding parasitic isopods infecting carangids (Table 4.1). No literature was found to link cymothoids to fish within the genus *Trachinotus* and this chapter provided the first evidence that *C. borbonica* infections stunt growth in wild fish. The long term effects of infection on the *T. botla* population are unknown, and there are no data available regarding the reproductive capabilities of infected individuals. The high prevalence rates observed in *T. botla* do, however, suggest that the parasitic isopods are fundamental components of their hosts" aquatic environment.

The **Trachinotus botla** *shore fishery*

Knowledge of the biology and life-history characteristics of a species is crucial for the successful management of the fisheries that harvest it. This thesis presents the first information regarding the life-history and fishery assessment of *T. botla* in South African marine waters. In doing so, it provides the first opportunity to propose management recommendations that are species-specific. In line with the principles of the Marine Living Resources Act (MLRA, 1998), the Department of Agriculture, Forestry and Fisheries is mandated to adhere to the following objectives and principles. These are a) the need to achieve optimum utilisation and ecologically sustainable development of marine living resources, b) the need to conserve marine living resources for both present and future generations, and c) the need to apply precautionary approaches in respect of the management and development of marine living resources.

Incorporation of the precautionary approach with respect to fisheries management into the MLRA ensures that the decision making process focuses on the nature and level of risks and uncertainties. Fisheries management is inherently complicated and the majority of these complications stem from the uncertainties associated with scientific processes such as stock assessments. The application of the precautionary principle in the fishing sector became established as a reaction to the lack of ability to guarantee the sustainability of resources being exploited (Fernando 2005).

A number of recreationally important linefish species within South Africa have been shown, using per-recruit analyses, to be mainly over-exploited or collapsed. These include *Scomberomorus commerson* (Govender 1995), *Argyrosomus japonicus* (Griffiths 1997), *Pomatomus saltatrix* (Govender 1997), *Atractoscion aequidens* (Hutton *et al.* 2001) and *Lichia amia* (Smith 2008). Fortunately, the *T. botla* resource of KwaZulu-Natal appears to be in stable and underexploited with current SBR at 75% of pristine levels. The current fishing mortality rate is estimated at $F = 0.27$ year^{-1} and could be theoretically increased by a magnitude of four before the target reference point (F_{SB40}) is met. Similar assessment results were found for *Sarpa salpa* (Van der Walt and Govender 1996) and *Neoscorpis lithophilus* (Mann *et al.* 2002a), both of which are important recreational shore angling species in KwaZulu-Natal. Mann *et al*. (2002a) concluded that the management regulation of a bag limit of five fish person^{-1}day^{-1} was sufficient to ensure its sustainable utilization of *N. lithophilus* at the time of assessment. In contrast, Van der Walt and Govender (1996) proposed that the minimum size limit of 150 mm TL was serving little purpose in protecting *S. salpa*. The authors concluded that the species was in no need of any restrictive regulations at the time, but should the stock of *S. salpa* show a declining trend a bag limit restriction would be the most appropriate management option (Van der Walt and Govender 1996).

According to the guidelines proposed by the Food and Agriculture Organization (FAO 2001), which use life history traits to classify finfish species by productivity, *T. botla* is a high-productivity category fish. The guidelines predict that a cumulative 10-year-rate-of-decline of 83%, and a corresponding average annual rate-of-decline of 16% would be needed to reduce the current population level down to a SBR of 20% within ten years (FAO 2001). For these reasons it is believed that the current management regulation in place for this species (i.e. a bag limit of five fish person^{-1}.day^{-1}) is sufficient to ensure its sustainable utilisation.

Table 6.1: Current South African management regulations for carangids that are important to recreational angling. – indicates the absence of a regulation. DAFF (2011).

Common name	Scientific name	Size limit (TL)	Bag limit (fish person^{-1}day^{-1})
Garrick (Leervis)	*Lichia amia*	70 cm	2
Kingfishes	*Caranx spp.*	-	5
Largespot Pompano	*Trachinotus botla*	-	5
Scads	*Decapterus spp.*	-	-
Southern Pompano	*Trachinotus africanus*	-	5
Talang queenfish	*Scomberoides commersonnianus*	-	-
Yellowtail	*Seriola lalandi*	-	10

Management recommendations

Recreational fisheries in South Africa are open-access and direct control on the total catch is not possible as the number of fishermen cannot be controlled (Attwood and Bennett 1995). Restricting the CPUE of anglers through the use of daily bag limits reduces the mortality of fish indirectly. Alternatively, the use of minimum size limits may ensure fishing mortality is limited to a selected proportion of the population. The primary reason for the application of a size limit in a recreational species is to allow individual fish to spawn at least once before capture (King 2007). The majority of important recreational fishing species have a minimum legal size limit in South Africa. Currently, *T. botla* has no minimum size limit. Well-publicised and enforced size limits are a means of encouraging a conservation ethic within the fishing community (McPhee 1995, King 2007). An age-at-50%-selectivity sensitivity analysis (Chapter 5) provided insight into the population response to the implementation of a minimum size limit. Increasing the age-at-50%-selectivity to align it with the age-at-50%-maturity resulted in a considerable increase in the fishing mortality needed to reach the target reference point (F_{SB40}) from 1.32 year^{-1} to 3.86 year^{-1}. A minimum size limit, which corresponded to the age-at-50%-maturity (247 mm FL, 303 mm TL), would significantly decrease the chance of recruitment overfishing.

Consideration of the resource users is a fundamental part of formulating management strategies. Table 6.2 illustrates the percentage of total catch below potential minimum size limits, calculated using data from Sodwana Bay and the SLMR "previously exploited" zone. A minimum size limit of 30 cm TL would reduce the harvestable catch of *T. botla* by 29%.

Table 6.2: The proportion of total catch of *Trachinotus botla* which would be below the proposed minimum size limits.

Proposed minimum size limit (cm TL)	Percentage of total catch below proposed minimum size
20	3.4
25	13.5
30	29.0
35	50.1
40	68.3
45	84.1

In reality this value is likely to be far lower, as fish below this size are of little use to recreational fishermen apart from live bait for targeting larger species (D. Parker, pers. obs.). Alternatively, a minimum size limit > 30 cm TL would likely find little support among anglers and result in high levels of non-compliance. As previously stated, the current management regulation in place for this species (i.e. a bag limit of five fish person^{-1}day^{-1}) appears to be sufficient enough to ensure its sustainable utilization. If, in future, there is increasing exploitation of *T. botla* (i.e. increasing fishing mortality) to a point whereby the stock status is unknown, the implementation of a minimum size limit of 30 cm TL would be recommended. This recommendation is likely encourage a conservation ethic within the fishing community without negatively affecting the recreational fishery users, who are the primary users of the resource. Further studies into the impact of implementing a minimum size limit on subsistence fishermens" livelihoods would be recommended before implementation.

Future research

It is generally accepted that fisheries are dynamic and require constant revision. South Africa, unlike many southern African countries, is in a fortunate position in that it possesses the infrastructure and capacity to monitor various linefish species such as *T. botla*. Programmes such as the National Marine Linefish System (NMLS) and the ORI/WWF-SA national tagging programme provide the means for periodic revision of the *T. botla* shore fishery. It is recommended that the *T. botla* fishery be reassessed every 6 years, based on the lifespan of the species.

Finally, from an ecological perspective, it is suggested that the relationship between *C. borbonica* and *T. botla* be further investigated, specifically the effects of parasite presence and the cause of the observed growth inhibition and the long term consequences for the *T. botla* population.

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