The biology of *Boopsoidea inornata* (Castelnau, 1861) and life history comparisons within the Sparidae

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Fransmadam, *Boopsoidea inornata* (Castelnau, 1861), photographed by author in the laboratory at UCT

Declaration of Authorship

I, Hend Ensair declare that the thesis entitled "The Biology of *Boopsoidea inornata* and Life History Comparisons within the Sparidae" and the work presented in it are my own and has been generated by me as the result of my own original research. I confirm that: This work was done wholly or mainly while in candidature for a research degree at this University. Where I have consulted the published work of others, this is always clearly attributed. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work. I have acknowledged all main sources of help; Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself. None of this work has been published before submission.

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Abstract

South African marine ichthyofauna has remarkable diversity across a range of biogeographic zones from cold-temperate to subtropical. Two families stand out here, both with high diversity and high rates of endemism to the region, namely Sparidae and Clinidae. The Sparidae are of greater interest because of their commercial importance, and conversely, their conservation status. Several are listed as threatened by the IUCN. The Sparidae is also the family with the greatest plasticity in life history characteristics of any vertebrate family, as they include gonochorism, rudimentary hermaphrodites, and both kinds of sequential hermaphrodites. Life history characteristics are known determinants of the resilience of fish species to fishing, and more generally of their response, either positive or negative, to any form of disturbance.

Life history characteristics of most of the species of Sparidae, in South Africa and worldwide, have been studied, particularly those of commercial and conservation importance. Omissions include those that are small, with little commercial importance. This is an oversight, as there is much to be learned about life history strategies by studying the full spectrum of variation in the family, and particularly those variants which produce numerically, and therefore ecologically, significant population sizes. In this thesis, I study the life history and parasite community of one of South Africa's most abundant seabreams in separate chapters. In the last chapter I take a fresh perspective on life history variation among fishes, by comparing four sympatric seabreams to describe the several dimensions along which life history trade-offs can occur without the confounding influences of environment and phylogeny.

Boopsoidea inornata (Castelnau, 1861) is endemic to South Africa. Eight hundred and seventeen fishes were sampled from four locations: False Bay, Struisbaai, Goukamma and Port Elizabeth from 2012 to 2014. They ranged in size from 130 to 310 mm fork length. The diet of *B. inornata* was investigated in False Bay and Struisbaai using Prey-Specific Index of Relative Importance (%PSIRI). *B. inornata* is an omnivore, with a preference towards small sand- and reef-dwelling prey and has only limited intake of algae and small fish. Age and growth were assessed using sectioned otoliths. A clear seasonal pattern of band formations deduced from the frequency of opaque margins show that B. *inornata* lay down one opaque and one transparent band per year. *B. inornata* is a small species (L_{∞}= 222.7 mm) with high longevity (t_{max}= 37). It is a rudimentary hermaphrodite. The ovaries hold up to 8000 vitellogenic eggs, which equates to an average 19 eggs per gram of body mass. This value is low compared with other seabream species. *B. inornata* females spawn repeatedly during the year, although there is more spawning

activity in spring, than in other months. The sex ratio is heavily skewed towards females (1:3.35). The presence of post-ovulatory follicles together with hydrated oocytes indicates that the species is an indeterminate batch spawner. Length at 50% maturity was calculated based on gonads collected throughout the spawning season. Females mature at 178 mm FL, compared to 185 mm FL for males. Female GSI greatly exceeds male GSI, and, together with the sex ratio, suggests a polygamous mating system.

One hundred and fifty *B. inornata* were collected from False Bay, Struisbaai, Goukamma and Port Elizabeth to investigate associated parasite assemblages. Eighty six percent of the sample was infected by parasites. Parasites infecting *B. inornata* have never before been recorded. Nineteen parasite taxa were found infecting *B. inornata* across all localities and included myxozoan, monogenean, digenean, cestode, nematode, copepod and isopod representatives. Three species of digenean metacercaria showed high prevalence of infection in *B. inornata* across all four localities. These included a *Stephanostomum* sp. infecting the gill arches of 61%, and two unidentified digeneans. The unidentified digenean metacercariae- 2 was found in the kidneys and musculature of 59% of the total sample and the unidentified digenean metacercariae-1 was found infecting the hearts of 47% of the total sample. Overall parasite assemblages were significantly different amongst all localities, with no significant difference in parasite assemblages among size classes, age classes or sex within localities.

Fish life history is affected by environmental and biological factors but is also constrained by phylogenetic influences on morphology and physiology. In an attempt to expose the nature and extent of life history trade-offs, I compared four closely related and sympatric seabreams, namely *Spondyliosoma emarginatum*, *Pachymetopon blochii*, *Rhabdosargus globiceps* and *Boopsoidea inornata*. I contend that only by eliminating or reducing as far as possible the effect of environment, habitat and phylogeny can we expose real trade-offs. Samples of each species were obtained in every season from the south-western Cape, South Africa, to obtain measures of total length, mass, gonadosomatic index and condition. *S. emarginatum* is a nest-guarding, short-lived, protogynous hermaphrodite. *P. blochii* is a resident, group-spawner, engaging in sperm competition. *R. globiceps* is a moderately long-lived migrant with a sex ratio of 1:1, that also engages in sperm competition over a short spawning season. *B. inornata* is a polygamous, long-lived resident with low annual fecundity, but a protracted spawning season. Although all four species are *periodic* strategists, life history trade-offs exist between several sets of variables, namely semelparity vs iteroparity, age-at-maturity vs maximum size, annual fecundity vs longevity, length of spawning season vs parental care, and length of spawning season vs migration. The efficiency of the sequential hermaphrodite strategy which allows every

fish to spawn as a female until they are large enough to act as a male makes one question the rarity of this strategy. I argue that halving of the female life-span compromises the *periodic* strategy, and that hermaphroditism is at odds with migration. The latter rests on the assumption that the migrant social structure is based on cooperation, for feeding, defence and navigating in schools, whereas the hermaphrodite social structure is based on aggression and dominance hierarchies which requires residency and territoriality. No clear adaptive reason for the divergence among the sympatric species can be identified, although competition among the young is a candidate. This comparison reveals a wide range of options available to seabreams and shows how disparate life histories can be equally adaptive under identical conditions. More generally I have shown how a variety of life-history traits, such as migration, sex-ratio, reproductive strategy and somatic growth form interact to define a life-history.

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CHAPTER 1

General introduction

1. General description

The Sparidae family (collectively referred to as seabreams) is one of the most commercially important marine fish families along the South African coast. The family comprises 35 genera, with 133 species and subspecies described (Smith *et al.* 2003, Heemstra and Heemstra 2004). Seabream species classification remains unclear, however, as molecular phylogeny does not align with the present classification based on morphology (Hanel and Sturmbauer 2000, Orrell *et al.* 2002, Chiba *et al.* 2009, Santini *et al.* 2014). Sparidae are divided into six subfamilies: Boopsinae, Denticinae, Diplodinae, Pagellinae, Pagrinae and Sparinae, but these are not monophyletic (Orrell *et al.* 2002). Geneticists recognised two major clades with the Sparidae (Santini *et al.* 2014) and admitted the Centracanthids (*Spicara* spp.) into the family (Orrell *et al.* 2002, Chiba *et al.* 2009).

Morphological classification of seabreams has used dentition and external characteristics to separate species. Sparidae are physically characterised by an oblong body shape, moderately deep and compressed, a large head, often with a steep upper profile, the snout and supraorbital areas are scale less, the mouth is often small with upper jaw, 24 vertebrae, preoperculum is scaled without spines on the margin, a single dorsal fin with 10-13 spines, three spines in the anal fin and overall are highly variable in colour (Carpenter and Niem 2001). Species are distinguished most effectively by characteristic grooves in the upper part of the pre-maxilla (Hanel and Tsigenopulo 2011).

Several biological studies have been conducted on aspects of the life history of seabreams in South Africa (Nepgen 1977, Buxton and Clarke 1989, Buxton and Garratt 1990, Smale and Punt 1991, Mann and Buxston 1992, 1996, 1997, 1998, Garratt 1993, Garratt *et al.* 1993,

Bennett 1993a,b, Van der Walt and Beckley 1997, Van der Walt and Mann 1998, Griffiths *etal.* 2002, Brouwer and Griffiths 2005a,b, Mann *et al.* 2005, Fairhurst *et al.* 2007, Tunley *et al.* 2009, Attwood *et al.* 2010). Forty-one species of seabreams are found in South Africa, 25 of which are endemic. Fish species of this family are of aquaculture, commercial and recreational importance (Smith and Heemstra 1986).

1.2 Distribution

Seabreams have a broad geographical distribution across the continental shelves, found on a variety of bottoms reaching 450 m depths in tropical, subtropical and temperate waters (Froese and Pauly 2012). Seabreams mostly inhabit subtropical localities, with approximately 76 species in 33 genera restricted to subtropical areas. The highest seabream diversity is found around the Southern African region, specifically in the temperate Cape region of South Africa, with 17 genera. Forty-four species have distributed themselves along the cool and warm temperate southern African coastal shelf (Hanel and Tsigenopoulos 2011). The Eastern Atlantic Ocean and Mediterranean Sea have the second highest diversity (together with 9 genera), the Western Indian Ocean has 9 genera on its own. The Eastern Central Atlantic Ocean and the Indian-West Pacific Oceans have just 4 and 5 genera respectively. In the tropics they are usually in deep water. The closely related Lethrinidae (emperors) and Lutjanidae (snappers) replace seabreams in shallow tropical seas.

1.3 Habitat

This family can occur in rocky and sandy bottom habitats near to shore or on offshore reefs at common depths ranging from 1 to 150 m (Heemstra and Heemstra 2004). Fish in this family are mainly found in coastal marine habitats but do occur, though less frequently, in fresh or brackish waters during breeding seasons (Mann and Buxton 1992). Twenty-two species are found in South Africa waters that are dependent on estuaries in the juvenile phase of their life cycles (Wallace *et al.* 1984, Heemstra and Heemstra 2004, Nelson *et al.* 2016). SCUBA

observations have shown that larger fish of most species occur in low densities on reefs in deeper water (Buxton and Smale 1984), young and small fish are usually seen in aggregations or schools and occur in shallower waters. Some species show little or no substrate preferences as adults, but others are confined to distinct habitat types (Hanel and Tsigenopulo 2011).

1.4 Feeding

The evolutionary adaptation of the jaw has enabled fish in this family to derive various specialized feeding strategies. The development of the pharyngeal jaw structure and heterodontic teeth of this family have allowed these fish to react rapidly to environmental changes and enabled them to exploit a variety of ecological niches. Herbivory is another adaptation to prey availability, a niche which has allowed for the existence of many South African seabreams (Vandewalle *et al.* 1995). Benthivory which is the most common form of feeding for this family, required the formation of molariform teeth. This adaptation allows fish to prey on hard-shelled invertebrates and in so doing expand their feeding ranges to hard–substrate benthic habitats (Vandewalle *et al.* 1995). In a competitive system, species that are able to harness both niches effectively are perhaps granted an adaptive niche of their own, such as the generalist seabreams of the Boopsinae, which are considered to be an omnivorous subfamily (Hanel and Tsigenopoulos 2011).

1.5 Age and growth

Sectioned otoliths provide more accurate age estimates of seabreams than whole otoliths and have been used extensively for South African seabreams by counting the annual periodicity of growth zone deposition (Buxton and Clarke 1986, 1989, 1992, Smale and Punt 1991). The occurrence of single annuli, comprised of one opaque and one translucent zone per year, has been reported for seabream otoliths (Pulfrich and Griffiths 1988, Mann and Buxton 1997, Pajuelo et al. 2006). Most seabreams produce opaque zone deposition of discontinuous or slow growth, coinciding with the spawning season during spring and summer, and the translucent zone appears to form during the months following the spawning season in South Africa (Mann and Buxton 1996). The timing of zone formation is controlled by a combination of endogenous and environmental factors (Ferrel *et al.* 1992, Mann and Buxton 1996, Brouwer *et al.* 2003). The von Bertalanffy growth model is useful to compare growth amongst seabreams and has been used extensively to describe the growth of Southern African seabreams (Buxton and Clarke 1989 1991, Horvath *et al.* 1990, Smale and Punt 1991, Garratt *et al.* 1993). Southern African seabreams are variable with respect to growth and maximum length. Ages range between short-lived, *Sarpa salpa,* of maximum 6 years (Van der Walt and Mann 1998), to long-lived with slower growth, *Petrus rupestris* of 54 years (Andrews *et al.* 2018), with the typical seabreams living to at least 16 years (Buxton 1993).

1.6 Reproduction

Seabreams have the most diverse sexual strategies of any fish family (De Mitcheson and Liu 2008), and by extension, any vertebrate family. Hermaphrodites find its most complex expression in seabream, while some develop male and female gonads simultaneously. Hermaphrodites either change from males to females (protandrous) or females to males (protogynous) as they grow larger, but there are also cases of simultaneous hermaphrodites and rudimentary hermaphrodites leading to secondary gonochorism (Buxton and Garratt 1990, De Mitcheson and Liu 2008). Sex-changing fishes often have bimodal length-frequency distributions and the sex ratios of protandric sparids may be skewed towards the males. In the case of protandric species, size or age at which sex change occurs is not genetically determined but is rather influenced by changing population conditions (Munday *et al.* 2006). Most seabreams representing sexual dimorphism and paired spawning are sequential protogynous or rudimentary hermaphrodites (Buxton 1990). Early records compiled by Garratt (1985) showed that there were six protogynous species around South Africa which includes three species of the *Chrysoblephus* genus, seven rudimentary hermaphrodite and nine gonochoristic

species. However, these groupings are far from exact as is evident from the conflicting descriptions of reproductive styles of particular species, and the fact one species can exhibit different strategies in separate populations, as is the case with *Acanthopagrus berda* (see De Mitcheson and Liu 2008).

Seabream spawning seasons are thought to be related to the water temperature, initiated by an increase in water temperature and finishing when water temperatures decrease. If this is correct, then seabreams spawn mostly during spring and summer (Brown-Peterson and Thomas 1988, Nieland and Wilson 1993, Brown-Peterson *et al.* 2002, Nieland *et al.* 2002). They are multiple spawners with an ovarian development that is asynchronous (Buxton and Clarke 1986, Buxton and Clarke 1991, Buxton 1993), leading to the occurrence of both regular and frequent spawning events during a single reproductive season (Wallace and Selman 1981). A reproductive season for seabreams can last between 60-150 days, resulting in a high fecundity (ca. 0-4-3.2x10^6 eggs kg^{-1} of body weight). For example, the common dentex, *Dentex dentex*, spawns from March to June for a period of around 90 days, thus producing around 0.76-1.50 million eggs per kg in the Mediterranean Sea (Abellan 2000). The black porgy, *Acanthopagrus schlegelii*, on the other hand, seems to be a lot less fecund with a mean annual fecundity of 0.18-0.47 million eggs per kg, and a spawning time span which only lasts around 30 days between February and March in Japan (Gonzalez *et al.* 2008).

Their eggs and larvae are, with only one exception (*Spondyliosoma* spp), pelagic The eggs range from 0.8-1.2 mm diameter and each egg has a single oil globule ranging from 0.1-0.26 mm, while the newly hatched larvae are 2 mm long with unpigmented eyes (Breder and Rosen 1966, Brownell 1979, Musick 1999a, Brouwer and Griffiths 2005a, Attwood et al. 2010). Some species recruit in estuaries even though adults of those species occur in the open ocean at depths in excess of 50 meters (Griffiths *et al.* 2002). Another example of distinct nursery grounds is provided by the South African *Petrus rupestris*, which as juveniles remain in shallow waters (Smale and Punt 1991).

1.7 The sub family Pagellinae

The subfamily Pagellinae, defined on morphological characters, incorporates three genera, *Lithognathus, Pagellus* and *Boopsoidea.* Genetic analyses show a close association between these genera and *Gymnocrotaphus, Spicara* and *Pachymetopon.*

Lithognathus spp. have a silvery body that often has dark crossbars, the eye diameter is much less than the snout length and there are no scales between the eyes, and fairly large scales cover the rest of the body. *Lithognathus* spp. have a single outer series of teeth and two larger and more inner series of small molars. Three species appear only in shallow water in South Africa, namely, *Lithognathus aureti* (Holtzhausen 1999), *Lithognathus lithognathus* (Bennett 1993b) and *Lithognathus mormyrus* (Heemstra and Heemstra 2004).

All *Pagellus* species have a pink body colouration. Of the four species only one, *Pagellus bellottii natalensis,* is found in South Africa. It has no scales between the eyes, no preopercale flange and has small pointed teeth (Smith and Heemstra 1986).

The genus *Boopsoidea* has only one known species, *Boopsoidea inornata* (Smith and Heemstra 1986). The eye diameter is bigger than the snout length, it too has no scales between the eyes and the head length is three quarters of the body depth. The mouth is small and there are no dark crossbars present on its body (Smith and Heemstra 1986, Van der Elst and De Freitas 1988).

1.8 B. inornata

The biology and ecology of *B. inornata* has not been published, but an unpublished student project and some taxonomic and field guides list useful parameters and life history information (Trow 1982, Smith and Heemstra 1986, Van der Elst 1988). *B. inornata* is endemic to South Africa and widely distributed from False Bay to Aliwal Shoal (Smith and Heemstra 1986, Le Chanteur and Griffiths 2002). The habitat of adults are rock reefs at depths from 5-34m (Trow 1982, Buxton and Smale 1984, Van der Elst 1988). The habitat of juveniles is shallow subtidal

reefs and gullies (<5 m), particularly those covered in coralline algae (Buxton and Smale 1984, Beckley and Buxton 1989). The eggs and larvae are pelagic and have been found in shelf waters at Tsitsikamma (Mann 2013).

The maximum length recorded for the species is approximately 40 cm total length (Van der Elst 1988), maximum weight has been established at 580 g (Penrith 1972). The diet composition and feeding intensity of *B. inornata* has been studied qualitatively at two localities around South Africa, the Transkei and Algoa Bay (Trow 1982) and False Bay (Le Chanteur and Griffiths 2003). *B. inornata* has been classified as a supra-benthic invertebrate predator that feeds on a wide range of small sand and reef-dwelling prey. The spawning season is extended and occurs in spring and summer (Van der Elst 1988). Although the flesh of this species is tasty, its small size makes it of limited commercial value, being utilized only as a fish bait (Penrith 1972, Van der Elst 1988).

1.9 Parasites infecting seabreams

All species of fishes are infected by parasites (Kellogg 1913, Olson 1987, Rohde 1993). Parasitism has the potential to affect growth, reproductive strategies and survival strategies of fish populations (Johnson and Chase 2004). Seabreams are host to a variety of metazoan parasites (Pérez-del Olmo *et al.* 2008). Globally the parasites of seabreams are well studied, but most research has been done in the Mediterranean and North Atlantic, motivated partly by their aquaculture importance (Sasal *et al.* 1999, Power *et al.* 2005, Pérez-del Olmo 2008, Pérez- del Olmo *et al.* 2007, Marzoug *et al.* 2012).

Historically there are very few studies on marine parasites in South Africa, although this is changing as the importance of parasites, both to commercial fisheries and fish biology is becoming better appreciated (Reed 2015). The most research on parasites infecting seabream hosts in South Africa has been by Bray (1984 and 1987) and Avenant-Oldewage (1994) who described numerous species from mostly the Trematoda and Copepoda. The effects of these parasites on their hosts are understudied with just a few, such as the common parasitic isopod

Anilocra capensis, infecting the Hottentot (*Pachymetopon blochii*) showing some physiological effects (Wright *et al.* 2001). Nothing is known of the parasites of *B. inornata*.

1.10 The puzzle of seabream life history variation

The variability within the seabreams has drawn the attention of several authers. The reproduction, morphology and diet of the seabreams are among the most variable of all fish families (Stergiou & Karpouzi 2002, Orrell et al. 2002, de Micheson & Liu 2009). South Africa, with its rich seabream fauna and sharp gradient in oceanographic conditions from cool temperate to subtropical, is an excellent place to study life history variation and its causes. Why, for example, do some species migrate in schools, while others hold territories? Why is longevity so variable? Why do some maintain separate sexes while others are sequential hermaphrodites? More puzzling is why these variable strategies exist in the same place and in such morphologically similar species.

1.11 Thesis outline

Chapter 2 covers the life history of *B. inornata* sampled in four areas across its range: False Bay, Struisbaai, Goukamma and Port Elizbeth. It covers the diet composition and feeding intensity, morphometrics, age and growth and reproduction parameters.

Chapter 3 describes the parasite fauna of *B. inornata*, exploring temporal and spatial variation in four localities around the coast of South Africa. The implications of the parasite findings with regard to movement and connectivity are discussed.

Chapter 4 is a comparison of four sympatric seabream life histories. In this chapter I consider the variation in life history parameters among phylogenetically very similar species in the same habitat. In so doing, I eliminate these influences as far as is possible, to examine the extent and dimensions of unforced variation on life histories. In particular, I examine the nature of life history trade-offs and consider among other factors, seasonality, longevity, fecundity and gender differences. I speculate on the adaptive advantages and disadvantages of sequential hermaphroditism, polygamy and migration, and question how such variable strategies can present themselves under identical conditions.

Chapter 5 is a short synthesis of my work and its main contributions.

CHAPTER 2

Diet, Age, Growth and Reproductive Biology of *Boopsoidea inornata*

Abstract

The life-history of *Boopsoidea inornata* (Sparidae) is investigated in this chapter. *B. inornata* individuals were sampled from False Bay (109), Struisbaai (663), Goukamma (22) and Port Elizabeth (23) in South Africa from 2012 to 2014. Fish ranged in size from 130 to 310 mm FL. The diet of 199 *B. inornata* was investigated in False Bay and Struisbaai. Prey-Specific Index of Relative Importance (%PSIRI) was calculated at the levels of classes and phylum. Prey items were removed from stomachs and 1390 individual prey items, from 17 classes in 12 phyla were identified. Arthropoda (30.6%), Echinodermata (29%), the two algal phyla (Rhodophyta and Chlorophyta) (12.8%), Annelida (11.7%) and Chordata (6%) dominated the diet composition. Slight dietary differences were observed between locations and between seasons. False Bay stomachs contents were slightly more variable. The age and growth of *B. inornata* were determined from readings of sectioned sagittal otoliths. A total of 817 otoliths were read independently by three readers. Close agreement was reached on 415 fish which were used to model the age-length relationship. Average percent error (APE), co- efficient of variation (CV) and index of precision (D) values were 17%, 12% and 4% respectively. Maximum estimated ages for males and females were 36 and 37 years respectively. Females matured (t_{50}) at 1.6 years whereas males matured (t_{50}) at 3.3 years. Von Bertalanffy growth parameters ranged from 0+ to 37 years old (L_{∞}=222.7 mm; K=0.292 y^{-1}; t_0=-3.58). The growth performance of *B. inornata* was found to be high at ϕ' =4.16. False Bay fish get larger than Struisbaai fish, although the growth rate is the same ($F=2.62$, $df=3.500$, $p<0.05$). A protracted spawning season was identified on the basis of gonad maturity staging, but the peak months were from July to October. The maximum monthly GSI values are relatively low in males (1.16) compared with females (3.62). The sex ratio was 1:3.35, males:females. The presence of postovulatory follicles together with hydrated oocytes indicated that the species is an indeterminate batch spawner. *B. inornata* is a rudimentary hermaphrodite. Length at 50% maturity was calculated based on gonads collected throughout the spawning season. Females matured at a smaller size, 178 mm FL, compared with males, at 185 mm FL. *B. inornata* is a long-lived early maturing periodic strategist. The mating system is likely to be polygamous. *B. inornata* is a slow-growing, long-lived periodic strategist.

2. Introduction

Boopsoidea inornata is among the most numerous inshore reef fishes of the Agulhas Bank, but very little is known of its biology. It is an obviously small-bodied species which is known to contribute to the diet of larger fish (e.g. Smale 1988), and is expected to play an important role as predator and prey.

2.1 Diet

Diet information contributes substantially to our understanding of species ecology, trophic relationships, food webs, and ultimately the flow of energy through ecosystems (Ainsworth *et al.* 2010). An understanding of feeding variability among fish species is essential to increase the accuracy of results or predictions of how predators impact population dynamics and also how they cause indirect ecological effects through diversity of hunting tactics and intensity of predation (Alonzo *et al*. 2003). Many ecosystem models use dietary information as a proxy for the interactions among species and top predators, and such information is considerably important to understanding an ecosystem (Christensen 1995, Walters *et al.* 1997, Yodzis 1998).

Trophic level estimation helps to quantify the effects of fishing and therefore evaluate its impact on marine ecosystems (Pauly and Christensen 2000). Competition among predators and on the other hand between predators and fisheries can be assessed through studies of diet (Furness and Tasker 2000). Prey numbers would be decreased through direct competition with other predator species or through competition with fisheries. The overexploitation of prey species has been directly linked to a decrease in top predators (Furness and Tasker 2000). Species- specific diet data obtained from stomach content analysis is not only useful in trophic ecosystem modelling but is also valuable for ecosystem-based fishery management (Yodzis 1994).

Stomach content analysis remains a universal technique for sampling the diets of fishes (Hyslop 1980). Diet analysis aims to determine whether a particular food category is present in the diet and to determine the most frequently consumed prey, and also aims to determine the level of importance of items in a diet (Ainsworth *et al.* 2010). More complex dietary analyses have been carried out for different purposes. For example, feeding habit variations were investigated in relation to (1) age and size (Scharf *et al.* 2000), (2) intra- and inter-specific relationships (Crespin de Billy *et al.* 2000), (3) spatial effects, and (4) seasonal or diurnal patterns (Fraser and Metcalfe 1997). In these studies, the methods employed to quantify the importance of prey items in the diet of fishes included counts, frequency of occurrence, and volume or weight of individual prey items (Hyslop 1980, Mohan and Sankaran 1988, Costello 1990, Cortès 1997).

Descriptions of the dietary importance of prey has been done using a number of methods. The gravimetric method, providing average percent weight (*%W*), records the total mass of a prey category in stomachs containing one or more individuals of each prey category and then expressed as percentage weight of all stomachs. The volumetric method, providing average percent volume (*V%*), records the total volume of a prey category within stomachs containing one or more individuals of each prey category and expressed as percentage of all stomachs (Hyslop 1980). The numerical method, providing Average percent number (*%N*), records the total number of prey items of each food category expressed as an average percentage over all stomachs. Percent frequency of occurrence (*%FO*) records the number of non-empty stomachs containing one or more individuals of certain species (Hunt and Carbine 1951, Hyslop 1980).

The use of individual diet measures can create an unrealistic impression of which prey items are preferred, for example *%N* used alone can create a bias towards a certain prey item if the predator has consumed large quantities of a small organism. One of the more widely used compound indices in fish diet studies is the index of relative importance (Pinkas *et al.* 1971, Cortès 1997). Characterization of fish diets from stomach content analysis commonly involves the calculation of multiple relative measures of prey quantity (*%N*, *%FO*, *%W* or V%) and their combination in the standardized Index of Relative Importance (*%IRI*). However, Prey-

specific index of relative importance *(%PSIRI*) has shown by Brown *et al.* (2012) to be stronger than the traditional index of relative importance (*IRI*). It is useful for more balanced treatment of the relative measures of prey quantity, shows less erroneous behaviour across taxonomic levels of identified prey and still presents prey-specific measures with the *%FO* though using *%N* and *%W* or *V%* as separate compound indexes to summarize relative importance. *%PSIRI*is comparable between studies when different criteria and methods are used for diet analysis (Brown *et al.* 2012).

As *B. inornata* often occurs in large numbers on coastal reefs it may have ecological importance in terms of predatory influence on many small invertebrates and vertebrates living near or on the reefs. This species is also a common prey item for larger predatory reef fish (Smale 1988). Trow (1982) studied the diet of *B. inornata* from the Transkei and Algoa Bay region, and found primarily a benthic feeding habit, although planktonic and epi-benthic invertebrates were ingested too. In these regions *B. inornata* consumes small crustaceans and ascidians regularly. Trow (1982) suggested that *B. inornata* has a crepuscular or nocturnal feeding habit, although the basis for this suggestion is not clear. The diets of 17 of the most abundant supra-benthic reef fish species in False Bay were studied by Le Chanteur and Griffiths (2003). Their study examined the diet of *B. inornata* and concluded that this species is a small benthic invertebrate predator that feeds on a broad range of taxa. The list includes amphipods primarily, reef and sand dwelling species, but also ostracods, isopods and sessile invertebrates, including soft corals and small solitary ascidians. The species also occasionally feed in the water column on some mysids and juvenile fishes. Van der Elst (1988) provides the only other account of *B. inornata's* diet, although the source of his information is unclear.

B. inornata is listed as omnivorous, feeding on crustaceans, polychaetes worms, and small pieces of seaweed which may be ingested simply for associated epiphytic organisms (Van der Elst, 1988). Penrith (1972) made observations of the behaviour of several seabream species, among which was *B. inornata*. He noted this species aggregates above high-relief reefs where

wave turbulence cause fragments of algae to be washed about. These fragments were seen to be eaten readily.

2.2 Age and Growth

Understanding the dynamics of fish populations is an integral part of the management of fishery resources and biological studies (Ricker 1973). Age and growth are two of the most important biological variables, providing the time component in rate calculations such as growth and mortality, which are essential parameters for most stock assessment models (Campana 2001). Interpreting growth patterns which relate to annual growth cycles in fishes requires the use of various methods pertaining to specific calcifying structures (Campana and Thorrold 2001). The great diversity of life history patterns among species and dynamic environmental conditions that increase variation in fish growth and ultimately affect the growth increments on the several calcified structures, are often the cause of difficulties when estimating the age of fish species (Campana 2001).

The age of fish is usally determined by counting the number of annually formed growth zones, which form in response to seasonal variation in environmental conditions, which are a result of the proportion of protein and calcium deposited during alternating periods of slow and fast growth (Campana and Neilson 1985). Selecting the most suitable calcified structure is one of the main problems facing age estimation. Campana and Thorrold (2001) estimated that well over 1 million fish were aged worldwide in 1999, most of those using scales and otoliths, that proved to be the most reliable indicators of age.

The use of scales and otoliths has been criticized because the age of older fish are frequently underestimated (Beamish and Mcfarlane 1983, Carlander 1987). Otoliths are considered to be the most accurate structure for ageing as they have a higher priority in utilization of calcium (Carlander 1987). Furthermore, otolith growth is not directly linked to somatic growth (Simkiss

1974), while the growth of scales is. Otoliths are not routinely used in every situation because fish must be killed to extract them and this affects the market value of the fish, and the preparation of otoliths is relatively expensive.

Transverse otolith sections, whole otoliths surfaces, and dyed and burnt otoliths are used, depending on which method provides the better distinction of the annual growth zone. Some authors have reported that using whole otoliths might lead to underestimated ages (especially among slowly growing and older fish because of the difficulties in detecting the outer rings as a result of the allometric growth of the otolith). Otolith sections reveal all of the growth zones, and are therefore read in preference to whole otoliths (e.g., Brouwer and Griffiths 2004, Beamish and McFarlane 1987).

There are numerous factors that influence the growth of fish. It is important to determine the periodicity of zone formation for accurate ageing (Beamish and Mcfarlane 1983, Newman *et al*. 1996). Likewise, confirming the growth increment periodicity, and determining the precision of repeated estimates on the same growth structure is an important step towards achieving an accurate age estimate (Campana 2001). Underestimates of age and the consequent over estimation of growth can lead to the collapse of fisheries (Campana *et al.* 1990).

Traditionally age determination methods have been validated by the recapture of chemically tagged (OTC-oxytetracycline) and aged fish (usually fish less than one year old) followed by an evaluation of new growth ring deposits from a known time at liberty (Campana 1999). Another method that is better suited to long-lived fishes is the bomb radiocarbon technique that incorporates specific radioisotopes with known half-lives into the otolith during its growth (Campana and Jones 1998). This method was recently applied to a South African seabream species (Andrews *et al.* 2018). There are no guarantees that if growth has been validated for one species that the same validation applies to other species or other populations and stocks. Young fish and old fish show variation in the rate of growth ring deposition, and so validating techniques must be specific to fish of different sizes.

Marginal increment analysis (MIA) is also used in validation studies (the marginal increment

is the distance outside the outermost opaque zone). When the opaque and translucent zones are formed annually the marginal increment should undergo a measurable decline at one time of the year. MIA is performed at a relatively low cost although it is considered the most difficult technique for age validation (Campana 2001).

Tag-recapture studies performed by Brouwer and Griffiths (2004) and Potts and Cowley (2005) using OTC led to the validation of the annual ring deposition in four seabream species; namely *Argyrozona argyrozona*, *Cymatoceps nasutus*, *Cheimerius nufar* and *Chrysoblephus laticeps*. Another method for validating periodicity is chemical marking or labelling of otoliths known as fluorchrome marking (Lang and Buxton 1993).

2.3 Reproduction

Information relevant to the reproduction of a species, such as the length and age at first maturity, fecundity and spawning period are relevant for stock assessments. The annual total egg production and larval viability of a stock is referred to as the stock reproductive potential (Trippel 1999). To increase reproductively active offspring, fish species follow different reproductive strategies (Balon 1984, Ware 1984). Stock reproductive potential is controlled by environmental and ecological factors such as temperature, predation, food availability and the synchrony between larval emergence and environmental conditions (Mertz and Myers 1994). These factors may drive variations in reproductive strategies (Robertson 1990).

Variables related to annual reproductive potential are linked to the size and age structure of population. It is important to establish a reliable estimate of total egg production because

larger and older spawners may have higher relative fecundity and higher egg quality and may spawn more frequently than small and young females (Fitzhugh *et al*. 2012, Marshall *et al*. 2003). Fecundity is the number of eggs spawned by an individual female fish either annually or from a single spawning event. The abundance of planktonic fish eggs combined with fecundity has been used to estimate the size of adult fish stocks, sex ratio and proportion of females spawning (Lockwood *et al.* 1981).

Sex ratios and maturity schedules have been demonstrated to vary spatially (Adams *et al.* 2000). The temporal pattern of reproduction through a fish's life is determined by the combination of multiple environmental cycles such as the light-dark, tidal, semilunar, lunar and seasonal cycles (Yamahira 2004). Gonadosomatic values (GSI) increase and peak as an indication that the spawning season has begun. Ovaries develop oocyte atresia and post- ovulatory follicles (POF) indicating the end of the spawning season (Hunter and Goldberg 1980). The spawning season varies in terms of duration, even among individual fish (so synchronization of spawning periods is vital for reproductive success) and is related to water temperature and fish health. Two types of spawning seasons are the restricted spawning season, more common in high latitudes, and extended spawning, common in temperate and tropical seas (Lowerre-Barbieri *et al.* 2011).

Three of the reproductive spawning strategies for fish are 1) synchronous (all eggs released once in a season or lifetime), 2) group synchronous (two separate population of eggs can identify in ovaries with regards to size. Larger population will be spawned in current breeding seasons, while the smallest population will be spawned in breeding seasons to come, and 3) asynchronous multiple spawners, where fish release eggs repeatedly throughout the season (it characterized by homogenous mixture of eggs stage). Extended spawning seasons are typical of indeterminate spawners with asynchronous oocyte development patterns (Hunter *et al.* 1985, Murua *et al.* 2003). Reproduction in most fishes is cyclic although the length of cycle is very variable (Hamlett and Koob 1999).

Most fish species release a large number of pelagic eggs. There is a trade-off between the quantity and quality of eggs, with some fish producing small quantities of large eggs while

others produce small eggs in large quantities. A form of parental care is the production of eggs that are richer in yolk that can improve the chances of offspring survival (Mcmillan 2007).

Fish generally have separate sexes. Hermaphroditism is considered abnormal but is the dominant strategy in some families. The Sparidae have some of the most diverse modes of sexuality, including gonochorism sequential hermaphroditism (protogyny and protandry), as well as rudimentary hermaphroditism (Buxton and Garratt 1990).

2.4 Aims of this Chapter

The aims of this chapter are to provide a comprehensive description of the life history of *B. inornata*. In this chapter I (1) provide a qualitative and quantitative description of diet, (2) assess the variability in diet in relation to biological and environmental factors, (3) describe longevity, growth rate and length and age–at-maturity, and (4) describe the reproductive strategy.

2.5 Methods

2.5.1 Sampling Regions

Struisbaai lies within the Agulhas bioregion east of Cape Agulhas and is the most southern tip of Africa (Figure 2.1). Reefs in this region host a number of economically important South African endemic fish that include reef-dwelling *Sparidae*. The bottom type is mostly sandy with areas of rocky reef. *B. inornata* was caught only on the rocky reefs which are between 12 and 20 m deep. Fish were captured by baited hook fishing. Anecdotal evidence from local fishermen suggests that *B. inornata* are present on rocky reefs during the day but are absent during the night.

False Bay is a wide southward opening bay located south-east of Cape Town in the Western Cape of South Africa at 34° 15` S, 18° 40` E. The bay is approximately 35 km long and 30 km wide and has extensive reefs down to 40 m. Surface temperatures vary between 14℃ and 22℃ (Dufois and Rouault 2012). False Bay is important for various commercial fisheries (Sink *et al.* 2012) as the bay is ideally positioned between the cool, nutrient–rich waters of the west coast and the warmer subtropical, nutrient–poor waters of the east coast. Both systems influence the hydrodynamic processes within the bay. Due to the dynamic nature of False Bay, its reefs and banks boast a great number of South African endemic fish, including those of the reef-dwelling seabream family (Tunley *et al.* 2009). Within False Bay, 20 species of *Sparidae* have been identified (Day *et al.* 1970). *Pachymetopon blochii* (30.6%), *Sarpa salpa* (17.7%) and *B. inornata* (16.1%) are the most abundant species (Le Chanteur and Griffiths 2003).

Goukamma Marine Protected Area (MPA) is situated along the warm temperate South African South Coast. It covers an 18 km stretch of shoreline and extends one nautical mile offshore. The area of MPA is approximately 40 km^2 and includes rocky platforms, sandy beaches, an estuary (Goukamma River), sub tidal rocky reefs and sub tidal sandy and muddy substrates. The variety of reefs in and around Goukamma MPA hosts a number of endemic temperate fish species. *Chrysoblephus laticeps* and *Boopsoidea inornata* are the most abundant species in this area (Götz *et al.* 2009a,b). No fishing is allowed from boats in the MPA.

Port Elizabeth is located within Algoa Bay, the Algoa Bay is the largest of several half-heart-shaped bays found on the southeast coast of South Africa. The bay is flanked on the western side by Cape Recife (34°02`S, 25°42`E) and on the eastern side by the less prominent Cape Padrone (33°46`S, 26°28`E). Over most of Algoa Bay the depth is less than 50 m (Karczmarsk *et al.* 1999). Fish were caught on Riy Bank within Algoa Bay.

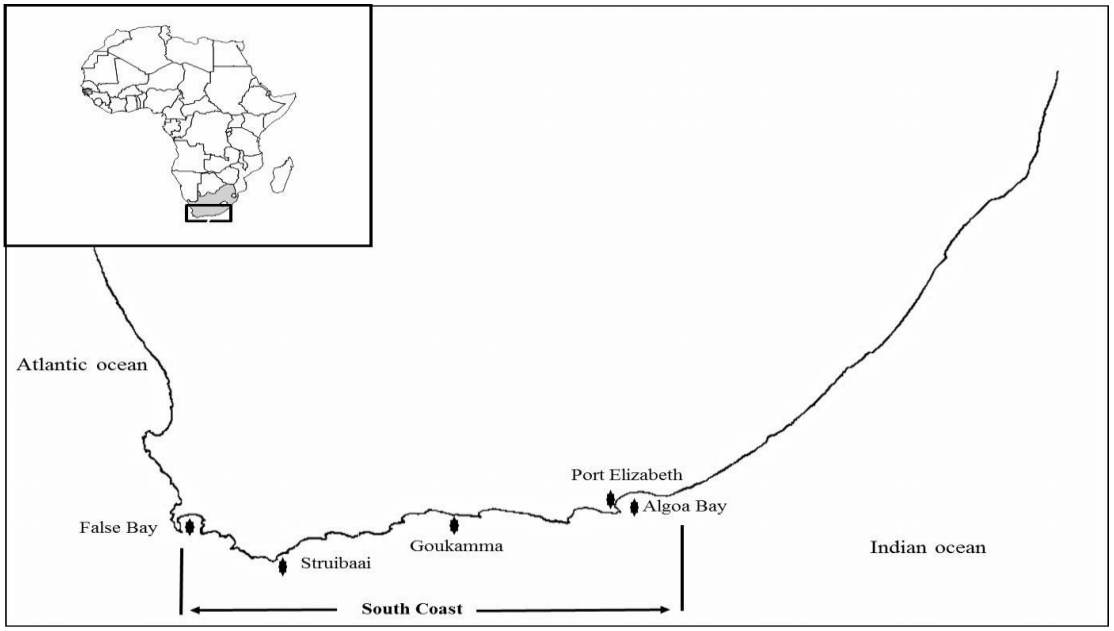


Figure 2.1: Sampling locations where *Boopsoidea inornata* were taken in False Bay, Struisbaai, Goukamma and Algoa Bay

2.5.2 Sample Collection

Eight hundred and seventeen specimens of *B inornata* were obtained from Struisbaai, False Bay and Goukamma and Port Elizabeth over periods of three years, one year, one month and one month respectively (Table 2.1). Fish were caught by hook and line from a boat and transferred to an ice-chest. In the laboratory the fish were dissected, and the following data were recorded for each specimen: the total body length (TL) was measured to the nearest mm, the fork length (FL) to the nearest mm, and whole mass and gutted mass (W) to the nearest 1.0 g. The weight of the gonads was taken to the nearest 0.1 g. Gonads were preserved in 10% buffered formalin for histological analysis. Weight of stomachs was taken to the nearest 1 g and preserved in 10% buffered formalin for later examination. The otoliths were removed and stored dry.

Table 2.1: Sample size of *B. inornata* sampleds in South Africa

Years	2012		2013		2014		
Months	Struisbaai	False Bay	Struisbaai	False Bay	Struisbaai	Goukamma	Port Elizabeth
January	11		32	14			
February	1		43				
March				17	45		
April			25	14	24	22	23
May	22		57	10			
June	2		76	12			
July	7		47				
August	4	15	33				
September		12	17				
October	69	10	33				
November		5	57				
December	58						

2.5.3 Stomach Content Analysis

Of the 817 specimens, 199 stomachs, excluding from fish caught in Goukamma and Port Elizabeth, were removed for diet analysis. These 199 stomachs were made up from a subsample of 5 to 10 stomachs per sampling event which took place over a one-year period at Struisbaai and False Bay.

Stomachs were removed from preservative and weighed to the nearest 0.1 g. Stomach were opened and the contents were emptied into a petri dish and grouped into recognizable taxa. Prey items were identified to the lowest possible taxonomic level using taxonomic keys and field guides (Day 1974, Branch *et al.* 2010). The number of individual animals per group was counted or estimated. Algae and colonial organisms, which could not be counted, were scored 1 for abundance. Each taxonomic group was added to a measuring flask to record its volume.

If bait used to capture line-caught specimens was found in the stomachs it was removed from the counts and volume calculations.

Average percent volume (*%V*) is the relative volume of each pery item in the total volume of

non- empty stomachs.

$$\%V_{ij} = \frac{100 * V_i}{\sum_i Vi} \quad \text{..... Eq.1}$$

$$\%V_i = \frac{\left[\sum_{j=1}^{n} \%V_{ij}\right]}{n} \quad \text{..... Eq.2}$$

Where $\%V_i$ is the abundance by volume of prey category i in stomach sample j, and n is the total number of stomachs.

Average percent number (*%N*) is the relative abundance of prey items in the total number of non-empty stomachs.

$$\%N_{ij} = \frac{100 * N_i}{\sum_i Ni} \quad \text{..... Eq.3}$$

$$\%N_i = \frac{\left[\sum_{j=1}^{n} \%N_{ij}\right]}{n} \quad \text{..... Eq.4}$$

Where $\%N_i$ is the abundance by counts of prey category i in stomach sample j, n_i is the number of stomachs containing prey i.

Percent prey-specific volume *(%PV*) is the average volume of a specific prey item in the total volume of stomachs containing that specific item.

$$\%PV_i = \frac{\left[\sum_{j=1}^{n} \%V_{ij}\right]}{n_i} \quad \text{..... Eq.5}$$

Percent prey-specific number (*%PN*) is the average number of a specific prey item in the total number of stomachs containing that specific item.

$$\%PN_i = \frac{\left[\sum_{j=1}^{n} \%N_{ij}\right]}{n_i} \quad \text{Eq.6}$$

Percentage frequency of occurrence (*%FO*) is the frequency of occurrence of prey items in the total number of non-empty stomachs.

$$FO_i = \frac{n_i}{n} \quad \text{Eq.7}$$

Prey-specific index of relative importance (*%PSIRI*) was calculated using the following equations (Brown *et al.* 2012).

$$\%PSIRI_i = \frac{\%FO_i * (\%PV_i + \%PN_i)}{2} \quad \text{Eq.8}$$

The trophic level of *B. inornata* was calculated by multiplying the %PSIRI of each prey item by the trophic level of that prey item, as is typically done in assessing the trophic level of fish species (e.g. Pauly 1999). Primary producers and detritus were assigned a score of 1, herbivores were assigned a score of two, and so on. The diet descriptions of each species were taken from Branch *et al.* (2010).

Multivariate techniques (PRIMER 6) were used to describe and compare the percentage volumes for the various prey items consumed by *B. inornata* in each location (Clarke and Warwick 2001). Percentage volume data were square-root transformed to prevent super-abundant prey species from dominating the analysis. A resemblance matrix was calculated using the Bray-Curtis index of similarity, and the group average procedure was used to construct a Multidimensional Scaling Plot (MDS). Permanova model was used to test the effect of sex, season and length. Length was represented as four 25 mm bins of fork length starting

with 150 to 174 mm. Similarity Percentages (SIMPER) was used in a one-way analysis to identify which prey items were responsible for the variation between areas.

The Shannon-Wiener diversity index was used to measure average species diversity per fish.

$H` = -\sum p_i In(p_i)$ Eq.9

Where p_i is the proportion of individuals calculated for of the i^{th} prey species. Shannon-Wiener diversities were average across areas.

2.5.4. Morphometric and meristic analysis

All 817 fish were used to describe the relationship between whole weight (W) in grams and fork length (FL) in millimetres. Data were log-transformed. A linear regression was carried out to estimate constants α and β and the 95 % confidence intervals around each parameter by using least squares regression analysis (Zar 1984). The regression was fitted for all fish together and then separately for each area.

$W = aFL^{\beta}$ Eq.10

Fulton's condition index was not suitable for *B. inornata* as this species does not display isometric growth. An alternative condition factor introduced by Le Cren (1951) was used instead:

$K_{rel} = \frac{W}{\alpha L^{\beta}}$ ..... Eq. 11

Because the male and female growth curves differed significantly, different parameters applied to each sex. Each sex therefore had an average condition factor of 1.0 across all areas. Sex was used as a factor in a two-way ANOVA model to test for seasonal differences in condition, for each area separately.

The stomach Fullness Index (SFI), (Blegvad 1917) was calculates as follows:

$$SFI = \frac{\text{stomach mass(g)}}{\text{fish mass(g)}} \times 1000 \quad \text{Eq.12}$$

The Kruskal-Wallis non-parametric test (Kruskal and Wallis 1952) was used to test the effect of *Season* on the *SFI* of mature fish for each sex, for all areas combined, because the combined assumptions of homoscedasticity and normality were not met.

2.5.5 Analysis of Age and Growth

Sagittal otoliths were removed using metal forceps, cleaned and stored dry. The right otolith from each pair was chosen and the position of the nucleus was estimated and marked. Otoliths were embedded in clear casting resin and sectioned between 0.25 mm to 0.35 mm in thickness through the nucleus using twin rotating diamond wafering blades. The sections were mounted on glass slides with DPX mountant and viewed at 10× magnification with transmitted light. Photomicrographs were taken through the stereomicroscope. Counts of opaque rings were made from the photomicrographs.

Each otolith was read independently by three readers. The count started at one year, with the first ring after the first translucent band around the nucleus (Figure 2.2). Disagreement among readers often stemmed from misinterpretation of the first translucent band, and hence the limits of the nucleus, which could vary in width, presumably due to variation in date of birth. Failure to recognise an opaque ring after the limit of the nucleus was interpreted as an age 0+ fish. Bands were often not complete, which could also lead to discrepancies. Most disagreement was caused by unclear patterns in the early years. Older rings, particularly after 10 years, were

read more consistently.

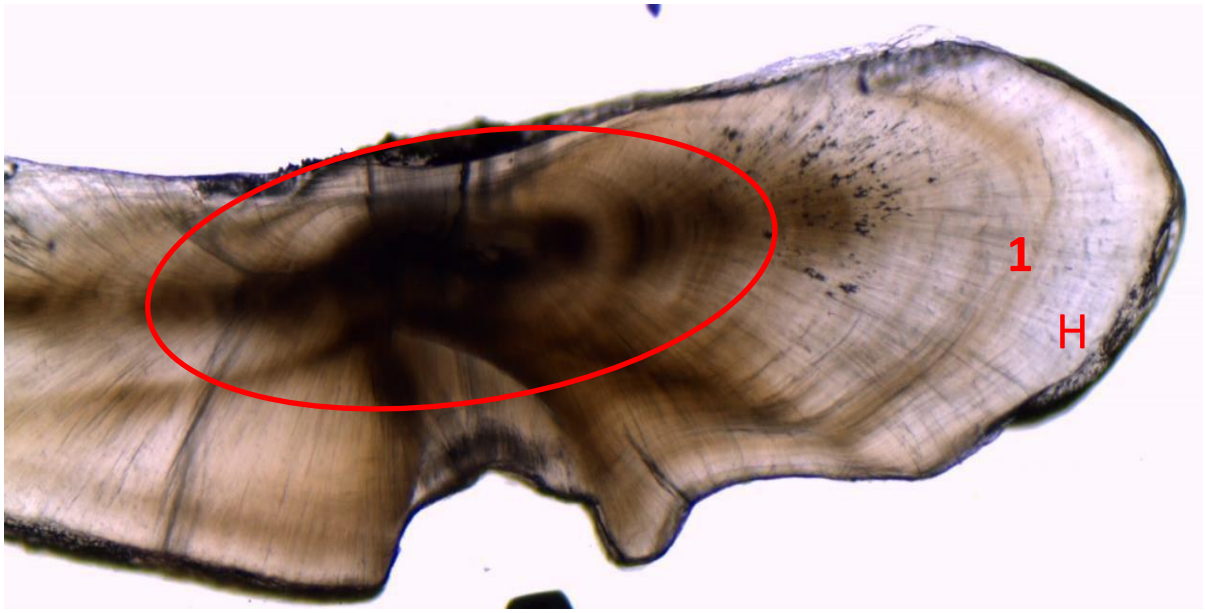


Figure 2.2 :A photograph of a transverse section of an otolith of a one-year old *Boopsoidea inornata* caught in December, showing the nucleus (red oval), the first opaque ring (1) and a hyaline margin (H).

The edge of the otoliths younger than 10 years was identified as either hyaline or opaque. In older fish the banding was too close to yield a readable edge. A marginal zone analysis was conducted each in order to identify in which months the growth zone was formed.

The percentage variation (*%V*) between the counts was determined as followed:

$$\%V = \frac{maximum\ age\ estimate - minimum\ age\ estimate}{average} * 100 \quad \text{Eq.13}$$

For samples where *%V* was 10% or less, the median of the three counts was accepted. Residuals were calculated as the difference between each age estimate and the average of all three estimates for each fish. Residuals were used to calculate three indices of precision.

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

$$\mathrm{APE} = 100\% \times \frac{1}{R}\sum_{i=1}^{R}\frac{|Xij - Xj|}{X_J} \quad \text{Eq.14}$$

Where R is the number of times each fish 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 (Beamish and Fournier 1981).

Precision of age estimates was determined by estimating the coefficient of variation (*CV*), which expresses, as a percentage, the standard deviation of replicated age counts per fish as a fraction of the mean (Campana, 2001). The *CV* is given by the equation:

$$CV = 100\% \times \frac{\sqrt{\sum_{i=1}^{R}\frac{(X_{ij} - X_j)^2}{R-1}}}{X_j} \quad \text{Eq.15}$$

And the index of precision (*D*) (Chang 1982) by:

$$D = \frac{CV}{R} \quad \text{Eq.16}$$

These indices were calculated for all fish and the average values per index were presented. A single age estimate for each fish was derived from the mean of the ages, rounded up or down to the nearest whole number. Both the APE and the *CV* were calculated for each otolith. An average *APE* and *CV* computed over all otoliths for a given method then provided an index of the precision for each method.

The magnitude of the discrepancies among the three readings was used to reject or accept a particular fish sample. The procedure used a combination of two methods, which was necessary because the species spanned a very wide range of ages. Firstly, a particular sample was accepted if two readings were identical and the third differed by no more than one year. The *%V* of the remaining fish were used as the second criterion. If the *%V* was 10% or less, then the sample was accepted. The modal estimate was used.

The growth of *B. inornata* was estimated by fitting the three-parameter Von Bertalanffy growth function (VBGF) (Ricker 1975) to male and female fish:

$$L_t = L_\infty(1 - e^{-K(t-t0)}) \quad \text{Eq.17}$$

Where L_t is the fork length-at-age t, L_∞ is the theoretical asymptotic fork length, K is the growth coefficient, t_0 is the age-at-zero length and t is the estimated age of the fish in years. Model parameters were estimated by minimising the residual sum-of-squares (Haddon 2001). Using the analysis of residual sum-of–squares procedure (Haddon 2001) differences in growth models between sexes and areas were tested. The procedure involves fitting the model to the pooled data set and then separately for each factor (area or sex). The F-statistic was calculated as:

$$F = \frac{\frac{RSS_p - \sum_i RSS_i}{DF_p - \sum_i DF_i}}{\left(\frac{\sum_i RSS_i}{\sum_i DF_i}\right)} \quad \text{Eq.17}$$

Where the RSS_p is the sum-squared residuals for the pooled data, RSS_i is the sum-squared residuals for each individual dataset (i), DF_p and DF_i are the degrees of freedom and were computed as (n - 3), where n is the total number of data points in all datasets. If the probability of the F-statistic fell below 0.05 then the pooled model was rejected in favour of separate models.

The growth performance index (ϕ`) was estimated to compare the values of growth parameters obtained in the present study with those reported by other authors for species in the same clade of the Sparidae. This index was calculated as follows (Munro and Pauly 1983)

$$\phi` = \log K + \log L_\infty \quad \text{Eq.18}$$

$Log_{10}k$ was plotted against $\log_{10}L_\infty$ for all species including *B. inornata*. For some species the

length estimates were given in total length TL. In these cases, TL was converted to FL using published equations, but where none exist, I used as formula typical of the Sparidae:

$$FL = TL \times 0.9 \quad \text{Eq.19}$$

Growth parameters were compared among species within and between the taxonomic clades proposed by Santini *et al.* (2014).

Length at 50 % maturity (L_{50}) was calculated by fitting a logistic ogive to the observed proportion of mature fish per 10 mm length class. The three-parameter logistic ogive is described by the equation:

$$\psi(L) = m_{\infty}\left(1 + e^{\left(-\frac{L-L_{50}}{\delta_L}\right)}\right)^{-1} \quad \text{Eq.20}$$

Where $\psi(L)$ is the predicted proportion of mature fish in each size class, L is the midpoint of each size class, L_{50} is the length-at-50% maturity (stage 3+), δ_L is the width of the ogive curve, *and* m_{∞} is asymptotic maturity. The maximum likelihood estimates of these parameters were obtained by minimizing the negative binomial log-likelihood function
(Winker *et al.* 2012, Eq. 19).

$$-\mathrm{In}(L) = \sum_l (x_l \mathrm{In}(\hat{P}_l) + (n_l - x_l)\mathrm{In}(1 - \hat{P}_l)) \quad \text{Eq.21}$$

Where L is the likelihood of the data, x_l is the number of mature fish in size class l, n_l is the total number of fish in size class a, and $\hat{P}_l$ is the predicted proportion of mature fish in size class a. The same procedure was used to fit the model to the number of mature vs immature fish were taken during the spawning season in each one-year age class.

2.5.6 Reproduction

Gonads were staged macroscopically on a scale of 1 to 6 (Table 2.2).

Table 2. 2:Classification and description of macroscopic maturity stages of the gonads of *B. inornata*.

Maturity Stages		Female	Males
Stage 1	Immature/resting	Orange-pink in colour, ovary lobes are thin, translucent and threadlike in shape, no oocytes are visible.	Thin and translucent white, ribbon-like, triangular in section.
Stage 2	Active/early maturation	Ovary lobes are rounded in section and much larger in size than in immature fish.	Whitish/beige, firm to the touch.
Stage 3	Maturing	Ovary lobes are rounded in section; small opaque oocytes are visible and fill the entire ovary.	White and occupying the majority of the abdominal cavity, sperm is present in the main duct, but does not exude
Stage 4	Late maturation	Orange-yellow in colour, ovaries are much larger than stage 3 and fill the greater proportion of the abdominal cavity; translucent oocytes can be seen between opaque oocytes.	Softer in touch but otherwise similar to the previous stage, sperm exudes when lightly squeezed
Stage 5	Ripe	Ovaries are as large as stage 4, flaccid yellow with patches of red, the hydrate eggs are prominent	Sperm flows freely when lightly squeezed. Testes are soft and breakable.
Stage 6	Spent	Ovaries are small and flaccid, red in colour; residual eggs can be seen through the wall.	Testes reduced in size, firm to the touch and pale pink in colour.

The sex ratio was calculated as the ratio between otal number of males to total number of females. A chi-square test was used to determine whether the sex ratio differed significantly from the expected ratio of 1:1.

Gonadosomatic index (*GSI*) was determined by the relationship:

$$GSI(\%) = \frac{\text{gonad mass(g)}}{\text{fish mass(g)} - \text{gonad mass (g)}} \times 100 \quad \text{.....Eq.22}$$

Ovaries (n = 46) were selected for histological analysis based on their macroscopic gradings: 5 in stage 1, 5 in stage 2, 5 in stage 3, 6 in stage 4, 21 in stage 5, 4 in stage 6. An approximate 3 mm section was cut from the middle of each ovary. Sections were soaked in 70% ethyl alcohol for two days to dehydrate them before embedding in paraffin wax.

Five to ten µm sections were cut from the wax using a microtome. The sections were stained with Mayer`s haematoxylin and Eosin – phloxin stain and finally mounted with Entellan. Histological classification of oocyte development followed Hunter and Macewicz (1985).

Five ovaries from Struisbaai and three ovaries from False Bay were determined by the naked eye to be in ripe stage. These were removed by careful dissection and weighed to the nearest gram before being preserved in 10 % formalin. Three subsamples from the anterior, middle, and posterior of the ovarian lobe (left or right) were removed and weighed to the nearest 0.001 g. Oocytes were suspended in water in a petri dish (Brouwer and Griffiths 2005a) and viewed under a Leica EZ4D dissecting microscope at 8X magnification. An image of each sample was captured using image analysis software (Image J). The number of oocytes was counted, and the horizontal diameter measured for each oocyte. A frequency histogram was produced for each ovary to determine the distribution of oocyte size.

The same five ovaries from Struisbaai and three ovaries from False Bay used to describe ovarian organisation were used to determine potential fecundity. For each ovary the number of advanced oocytes, including hydrated oocytes, just prior to spawning was estimated by the gravimetric method (Hunter *et al.* 1985).

$F_{Potential}$ and F_{Batch} were obtained by applying the following formula:

$$F_i = \frac{[\sum_i \frac{O_i}{W_i}]}{n} * W_{Ovary} \quad \text{..... Eq.23}$$

Where (F_i) was the estimated potential fecundity or the batch fecundity for a pre-spawning specimen i, (O_i) is the number multiplying advanced oocytes, (W_I) is the weight of subsamples, (n) is the number of subsamples and (W_{Ovary}) is the weight of the whole ovary.

The relationship between potential fecundity or batch fecundity with fork length and with mass was discribed and tested by the linear regression procedure.

2.5.7 Abdominal Fat

Abdominal fat was scored on a scale of 0 to 3 (Table 2.3) (Attwood *et al.* 2010). Fat strings refer to deposits of fat visible on the mesenteric tissue. The abdominal fat score of males and females was averaged per quarter year for each sex.

Table 2.3:Abdominal fat stages in *B. inornata*.

Fat	Description
0	No fat visible on abdominal organs
1	Fat strings thin (<5 mm) but clearly visible
2	Fat strings swollen, obscure up to 50 % of abdominal organs
3	Fat obscures > 50 % of abdominal organs and lines the dorsal surface of gas bladder

2.6 Results

2.6.1 Diet

Of 199 specimens examined 11 (5.5%) had empty stomachs, 8 (4%) stomachs contained only well-digested or unidentifiable prey and the remaining 180 (90.4%) stomachs contained identifiable prey items. The analyses of stomach contents led to the identification of 1390 individual prey items, from 17 classes in 12 phyla.

PSIRI scores revealed that Arthropoda and Echinodermata were almost equally dominant phyla, at 30 and 29% respectively, but the full list of phyla also included Cnidaria, Bryozoa, Annelida, Nemertea, Sipuncula, Platyhelminthes, Mollusca, Chordata, Chlorophyta, Rhodophyta (Table 2.4). Together, the two algal Phyla scored 12.8 on the PSIRI scale.

The dominant orders of animal prey, in order of importance were Cornatulida (, Amphipoda, Phiurida, Mysida, Enterogona and Isopoda.

The bulk of the prey are small invertebrates, either sessile filter-feeders or mobile benthic herbivores and predators. Of all the species, 22.6% were sessile, 68.8% were free living benthic animals and 8.5% were pelagic. Following the descriptions in Branch et al. (2010), the most common prey species can be described as follows: *Themisto gaudichaudii* (Amphipoda) is a pelagic predator of fish larvae and zooplankton; *Amaryllis macrophthalmus* is a scavenger dwelling on macroalgal holdfasts and under boulders; *Mesodopsis major* is a common mysid in kelp forests. *Ciona intestinalis* is an introduced sea-squirt common in harbours.

The trophic level of *Boopsoidea inornata* is 3.31. Using the classification scheme proposed by Stergiou and Karpouzi (2002), this species is an omnivore with a preference for animals.

The intestines of examined fish were not examined as they contained only well-digested or unidentifiable prey, but shells of fifteen abalone, *Haliotis parva*, were found in two fish from Struisbaai on account of their large volume. This is considered a rare abalone, one which is not harvested. No *Haliotus* spp. were found in stomachs, and therefore not included in the diet list.

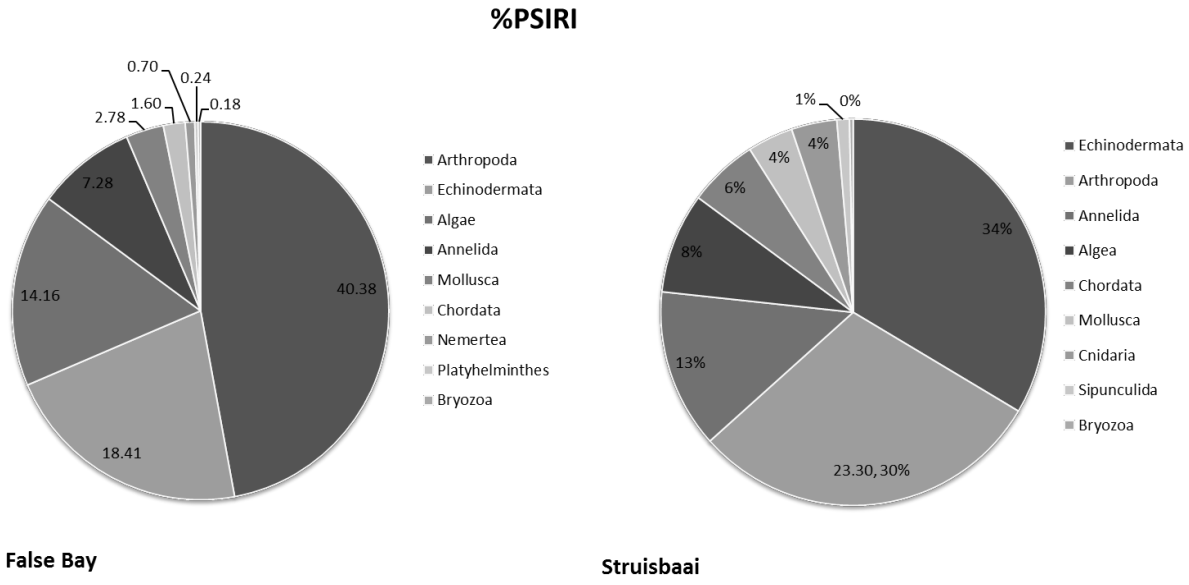


Figure 2.3: Prey-specific index of relative importance (*%PSIRI*) of main prey species in the overall diet of *B. inornata*.

Table 2.4:Diet composition of *B. inornata* by occurrence (*O*) and percent frequency of occurrence *(%FO*), percent prey-specific number (*%PN*), percent number (*%N*), percent prey-specific volume (*%PV*), percent volume (*%V*), and prey-specific index of relative importance (*%PSIRI*).

Phyla	Subphylum	Class	Order	Species	*O*	*%FO*	*%PN*	*%N*	*%PV*	*%V*	*%PSIRI*
Cnidaria		Anthozoa	Alcyonacea	*Sinularia gravis*	8	4.44	35.13	0.73	39.25	1.43	1.65
			Actiniaria	*Anthostella stephensoni*	1	0.56	33.33	0.07	66.67	0.59	0.28
			Zoanthidea	*Isozoanthus capensis*	1	0.56	50	0.07	50	0.04	0.28
		Hydrozoa	Anthomedusae	*Velella velella*	3	1.67	39.02	0.59	54.08	1.13	0.78
		Total			13	7.22	37.03	1.5	45.61	3.18	2.98
Platyelminthes		Turbelllaria	Polycladida	*Planocera gilchristi*	1	0.56	33.33	0.07	40	0.88	0.2
Nemertea			Unidentified		3	1.67	30	0.29	30.1	0.4	0.5
Sipuncula		phascolosomatidae	Golfingiida	*Golfingia capensis*	5	2.7	30.5	0.73	32.7	0.95	0.88
Annelida		Polychaeta	Eunicida	*Marphysa elitueni*	5	2.78	62.98	0.8	55.69	2.78	1.65
				Lysidice natalensis	2	1.11	27.5	0.29	49.48	1.1	0.43
				Total	7	3.89	52.84	1.1	55.69	3.88	2.11
			Spionida	*Polydora* spp	2	1.11	62.12	0.88	39.8	0.73	0.57
			Unidentified		37	20.56	43.33	6	44.55	10.28	8.58
		Total			46	25.5	45.6	8.17	46.04	10.3	11.7

Table 2.4: Continu

Phyla	Subphylum	Class	Order	Species	*O*	*%FO*	*%PN*	*%N*	*%PV*	*%V*	*%PSIRI*
Arthropoda	Crustacea	Malacostraca	Mysida	*Mesodopsis* sp.	36	20	57.84	42.3	45.17	3.95	10.3
			Decapoda	Unidentified Brachyura	2	1.1	55	0.15	50.95	1.85	0.59
			Isopoda		21	11.67	42.28	6.22	33.11	1.6	4.4
			Amphipoda	*Themisto gaudichaudii*	3	1.67	68.75	1.45	38.73	0.29	0.9
				Amaryllis macrophthalmus	5	2.78	46.85	2.75	22.6	0.58	0.96
				Unidentified	43	23.89	48.63	14.97	34.46	3.6	9.92
				Total	49	27.2	51.37	18.37	27.13	4.44	11.74
		Hexanauplia	Harpacticoida		10	5.56	23.35	1.76	14.64	0.39	1.06
		Maxillopoda			1	0.56	75	0.44	40	0.29	0.32
		Ostracoda			13	7.22	41.31	3	13.08	0.71	1.96
		Total			88	49.44	74	71.01	51	9.19	30.6
Bryozoa		Gymnolaemata	Cheilostomata	*Jellyella tuberculate*	2	1.11	37.5	0.15	69.88	1.02	0.6
Mollusca	Pelecypoda	Bivalves			8	4.4	54.9	0.81	58.6	1.87	2.52
		Gastropoda		Eggs- unidentified	1	0.56	100	0.07	100	1.46	0.56
			Trochoidea	*Gibbula multicolour*	4	2.22	29.5	0.72	25.88	0.44	0.62
			Patellogastropoda	*Scutellastra obtecta*	1	0.56	66.67	0.15	20	0.07	0.24
			Littorinimorpha	*Cypraea erosa*	6	3.33	19.17	0.44	46.62	3.15	1.1
		Total			19	10.5	44.16	2.25	51.9	4.85	5.03

Table 2.4: Continu

Phyla	Subphylum	Class	Order	Species	*O*	*%FO*	*%PN*	*%N*	*%PV*	*%V*	*%PSIRI*
Echinodermata				*Amphipholis squamata*	11	6.11	43.34	1.37	46.33	3.58	2.74
		Ophiuroidea	Ophiurida	*Ophiactis carnea*	4	2.22	45.31	0.72	44.69	1.94	1
				Unidentified	21	13.89	51.83	2.82	55.21	10.1	7.43
				Total	35	19.44	51.23	4.76	51.08	15.62	10.47
		Echinoidae		Unidentified	3	1.67	77.78	0.22	77.78	2.63	1.3
		Crinoidea	Comatulida	*Comanthus wahlbergi*	45	24.44	49.28	3.18	66.18	19.75	14.11
				Annametra occidentalis	6	3.33	45.73	0.43	46.57	1.61	1.54
				Total	50	27.78	48.9	3.6	61.21	21.37	15.99
		Holothuroidea			7	3.89	44.12	0.59	37.32	0.63	1.58
		Total			**79**	**43.33**	**60.65**	**9.37**	**73.2**	**40.26**	**29**
Chordata	Tunicate	Ascidiacea	Enterogona	*Ciona intestinalis*	21	11.67	38.04	1.76	43.89	6.77	4.78
	Vertebrata	Osteichthyes		Unknown	2	1.11	58.33	1.91	96.08	2.56	0.86
		Total			**23**	**12.78**	**39.81**	**1.95**	**48.43**	**9.33**	**5.64**
Chlorophyta					18	10	29	1.3	40.86	4.06	3.51
Rhodophyta					33	18.33	47.33	2.42	53.43	4.79	8.75
Algae		**Total**			**48**	**26.67**	**42.95**	**1.5**	**0.48**	**8.85**	**12.8**

Diet analysis revealed 28 species in stomachs from fish caught in Struisbaai and 21 species in stomachs of fish caught in False Bay (Figure 2:3). Permanova model of the effects of sex, area, season and length, showed that only area and length significantly affected diet (Table 2.5). The dissimilarity among locations was due to the total absence of Littorinimorpha in Struisbaai, while brittlestars, red algae and Ascidiacea were abundant. There was a total absence of soft corals in False Bay diets, however, Crinoidea, green algae and Mysida were numerous.

Length had weaker effect. Ascidians, crinoids and brittlestars increased consistently in prevalence with body size, but errant polychaetes, mysids and amphipods became progressively less prevalent as fish size increased. There was no consistent trend in the prevalence of algae with body size.

Table 2.5: The results of a Permanova model on the effects of four exaplanatory variables on *Boopsoidea inornata* diet composition.

Variable	DF	SoSqs	MEANSQ	F	R^2	P
SEX	2	0.544	0.27202	0.66513	0.00731	0.88
AREA	1	1.155	1.15542	2.82519	0.01552	0.003
FLCAT	1	0.851	0.85102	2.08088	0.01143	0.027
SEASON	1	0.714	0.71395	1.74572	0.00959	0.063
RESIDUALS	174	71.161	0.40897		0.95614	
TOTAL	179	74.425			1	

There was no significant difference in the diversity of individual diet between False Bay and Struisbaai, as measured by the Shannon-Wiener diversity index (t=1.2, p=0.11). When measured as species richness however, a marginally significant difference was found. False Bay fish had 2.39 species per stomach and Struisbaai fish had 2.02 species per stomach (t=2.04, p=0.04).

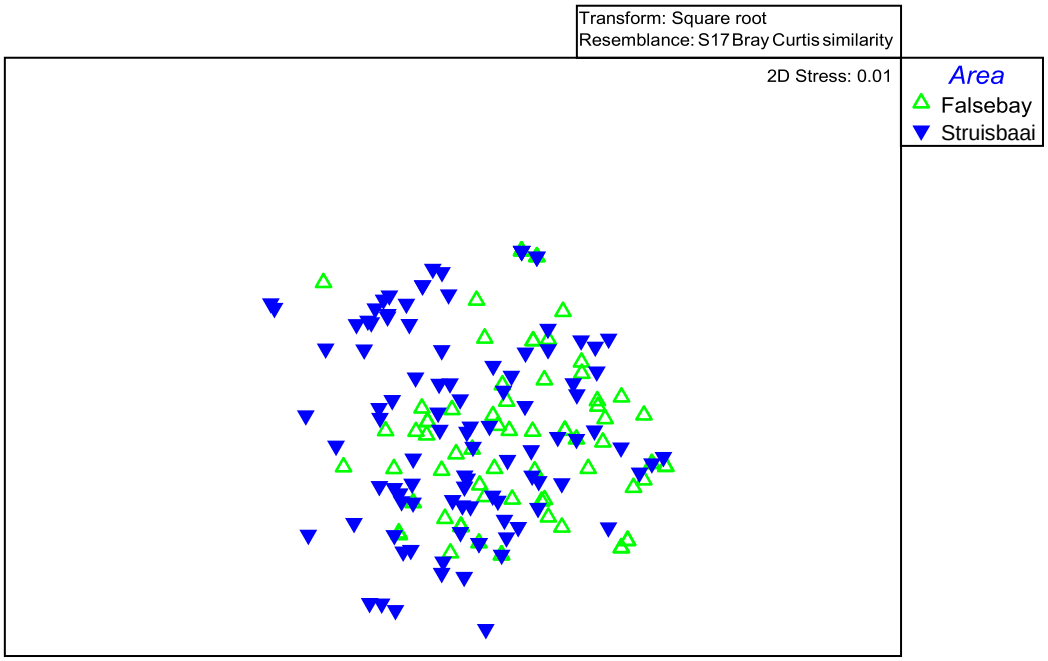


Figure 2.4: A two-dimensional MDS plot showing similarity between prey composition at the two sample locations.

The diets of *B. inornata* in the Transkei, Algoa Bay and False Bay have been described by Trow (1982) and Le Chanteur and Griffiths (2003) and compared with the diets of *B. inornata* caught in False Bay and Struisbaai during this study (Appendix 2.1).

The stomach fullness index SFI of individual mature fish ranged from 2.7 to 672 for females and from 5.49 to 376 for males. For both sexes the maximum average SFI was in the first quarter: 111±8.81 for females and 103±12.9 for males. Third quarter averages were 85±8.1 and 59±7.7, respectively. (Figure 2.5)

The Kruskal-Wallis rank test revealed that there was a significant difference in mature female and males SFIs among the seasons (W=15.7, X^2 =7.8, df = 3, $p < 0.05$) and (W=13.1, X^2 = 7.8, df = 3, $p < 0.05$) respectively. An interesting feature of the sex-specific SFI data is the low value for males in the third quarter, substantially lower than any other quarter for males, and lower than all female averages.

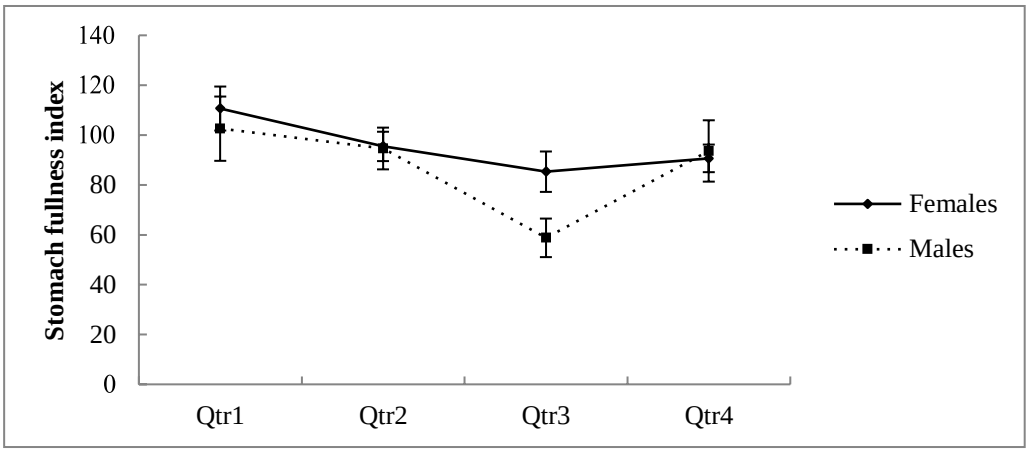


Figure 2. 5: Average Stomach fullness index (SFI) in the mature female and males in *B. inornata*, in each quarter. Quarter 1 represents the period from January to March.

2.6.2 Morphometric and meristic analysis

A total of 817 *B. inornata* (130–310 mm FL) were sampled (Figure 2.6). Of these, 76% were female, 23% were male and <2% had male and female gonads. The samples originated from False Bay (13.3%), Struisbaai (81.3%), Goukamma (2.6%) and Port Elizabeth (2.8%) (Table 2.6).

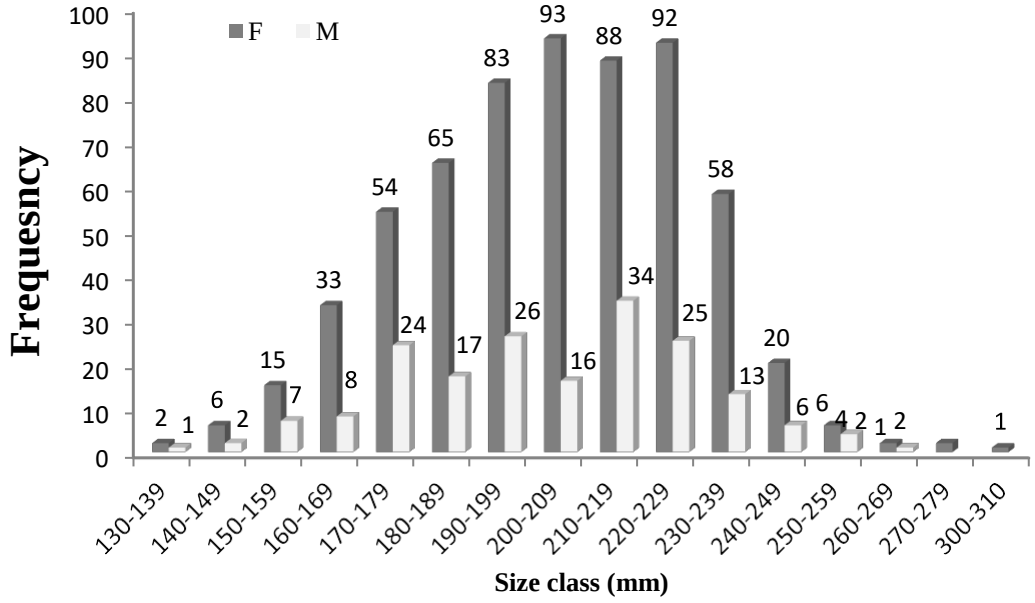


Figure 2.6:The number of males and females of *B. inornata* sampled in the various size classes.

Table 2.66:Sample size, size range of *B. inornata* samples broken down by sex.

Location	Sample size			FL range (mm)		
	♂	♀	♂+♀	♂	♀	♂+♀
False Bay	11	92	6	130-259	140-279	160-259
Struisbaai	149	508	6	140-269	130-310	170-209
Goukamma	12	9	1	210-259	180-229	212
Port Elizabeth	12	11		180-139	190-229	

Total length (mm) was related to fork length (mm) as follows (Figure 2.7):

FL (mm)=0.902 TL (mm) + 0.767 mm; n=817, r^2=0.986 Eq. 24

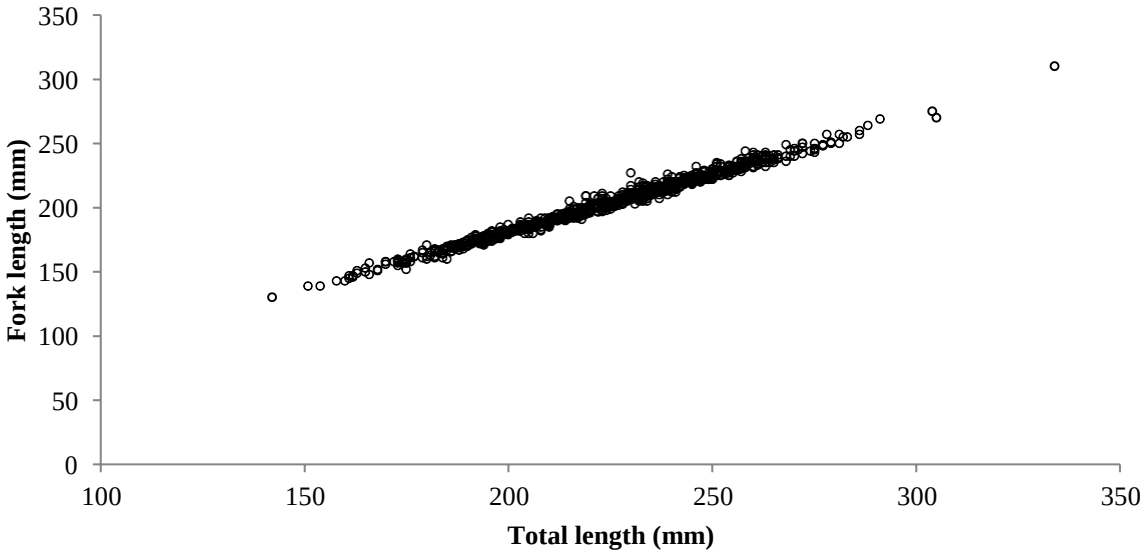


Figure 2.7:The linear relationship between fork length and total length of *B. inornata*

The length weight relationships for each region (Figure 2.8 and 2.9) were:

False Bay: $W_F = 9.38x10^{-5} FL^{2.740}$; n=109, r^2=0.976. . Eq. 25

Struisbaai: $W_S = 5.757x10^{-5}FL^{2.818}$; n=663, r^2=0.959. Eq.26

Goukamma: $W_G = 1.25x10^{-4}FL^{2.686}$; n=22, r^2=0.911. Eq.27

Port Elizabeth: $W_P = 9.102x10^{-5} FL^{2.730}$; n=23, r^2=0.936. Eq.28

The comined-area equation is:

Combined: $W=5.732x10^{-5}FL^{2.821}$; n=817, r^2=0.957. Eq.29

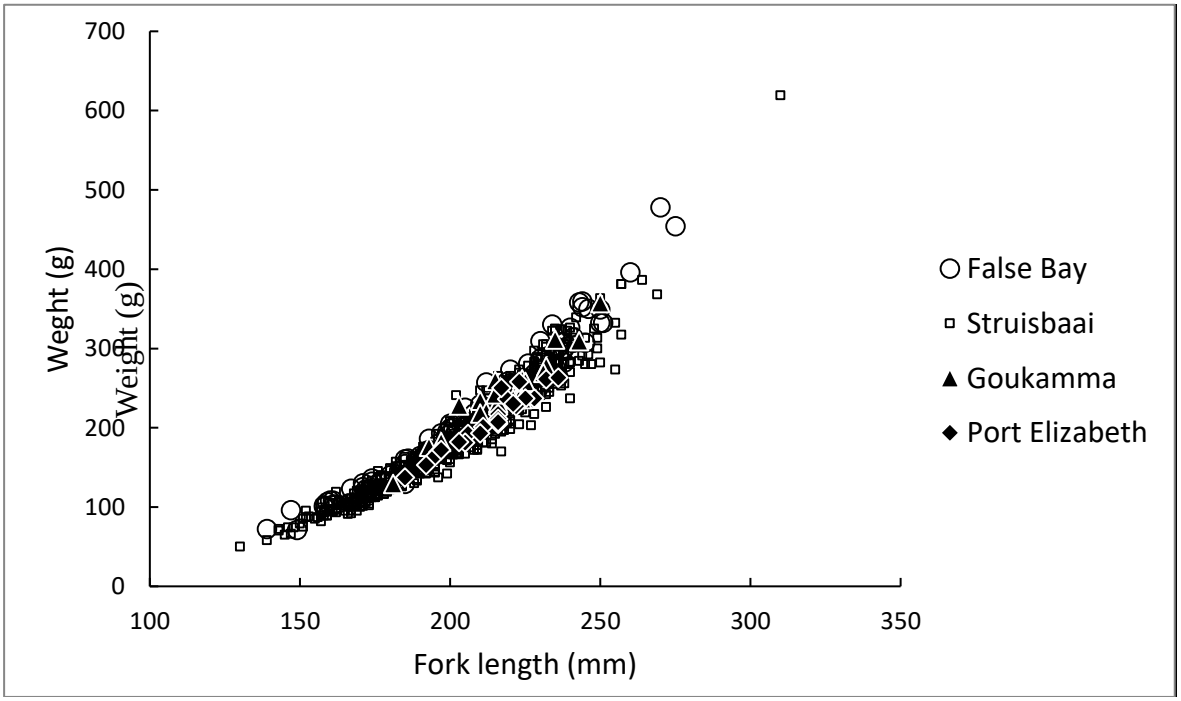


Figure 2.8: The plot of weight vs fork length of *B. inornata*.

Pair-wise comparisons revealed no statistical difference between slopes among the areas when tested with two-way, one tailed t-tests. Overall, the exponent was 2.82 (SE=0.02) which was significantly smaller than 3.0. *B. inornata* display hypoallometric growth.

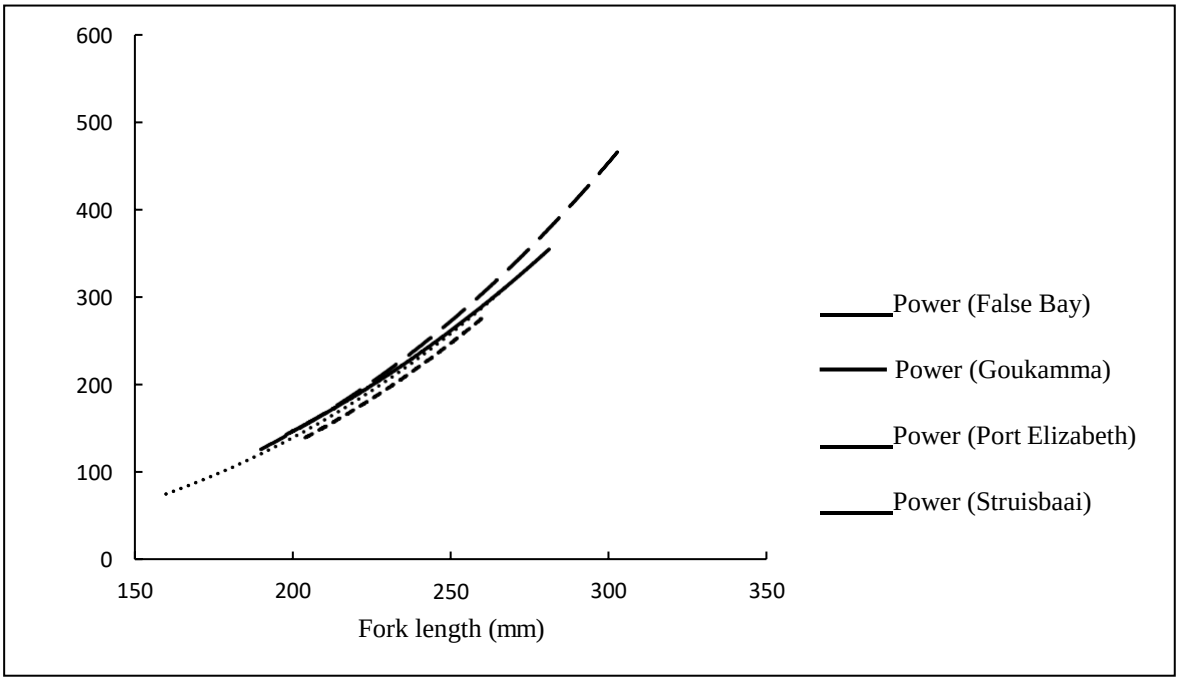


Figure 2.9: Regression of weight vs fork length of *B. inornata* sampled in Aprial.

There was a significant difference in the length-weight relationships between males and females (t=2.21, p=0.027). The female relationship was

$W = 5.020 \times 10\text{-}5\ FL^{2.846}$, n=620, r^2=0.953 Eq. 30

For males it was

$W = 8.91 \times 10^{-5}\ FL^{2.664}$; n=184, r^2=0.967. Eq. 31

The exponent for females was 2.85(SE = 0.025) whereas for males it was 2.74 (standard error = 0.037).

The average condition of individual *Boopsoidea inornata* ranged from 0.76 to 1.31, and the standard deviation was 0.074. This dispersion is in effect the standard deviation of the monthly residuals about the length-weight relationship. Variations in the condition factor can be ascribed to season and area. Across all areas it was evident that there was a seasonal effect in female condition, but that a seasonal effect in male condition was less clear.

A test of seasonality in the Struisbaai fish, which were most comprehensively sampled, showed no effect of sex ($F=0.69$, $p=0.41$), but a strong seasonal effect ($F=13.42$, $p=1.8 \times 10^{-8}$) and a significant, but weak, interaction between season and sex ($F=2.98$, $p=0.03$). The lack of a sex effect was expected as the condition index was normalised to the length-weight function for each sex. The seasonal effect was due only to a low 4^{th} quarter condition, and the sex- seasonal interaction was due to the male condition being greater than the female condition in the fourth quarter. Overall, it can be interpreted that the variation is mostly ascribed to low female condition in the 4^{th} quarter (Figure 2.10).

Among False Bay females there was no seasonal effect. The third and fouth quarter condition of females was lower than in the first half of the year, but the effect was not significant ($F=2.36$, $p=0.076$).

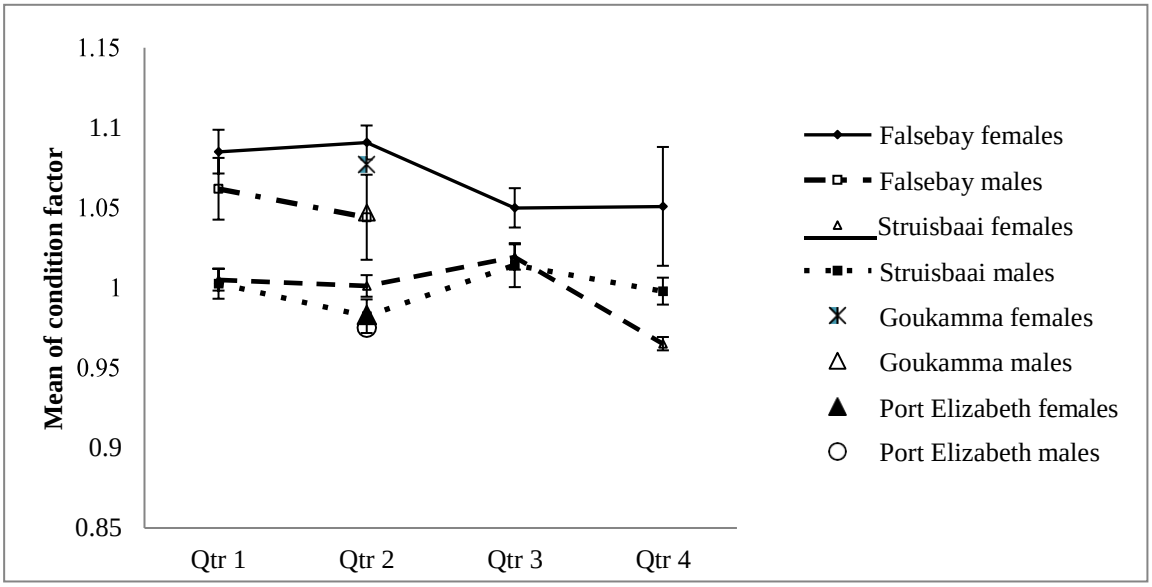


Figure 2.10:The average condition factor of *B. inornata* in each quarter by sex and by area. Quarter 1 represents the months from January to March. Error bars indicate one standard error.

2.6.3 Age and growth

Of the 817 otolith samples, 15 were broken and not sectioned. Of the remining 802, the *APE*, *CV* and D value were 13%, 9% and 3% respectively. Of the total otoliths examined, 415 yielded useful age estimates and 388 were discarded because they failed to meet the criteria outlined in section 2.5.5.

Photographs of sectioned otoliths of a variety of ages are presented in Appendix 2.2. The sectioned otoliths displayed clear growth zones, the hyaline (light) bands, interspersed with (dark) bands. The first complete hyaline and opaque ring after the nucleus was accepted as the first complete year of growth. Thereafter each subsequent opaque band marked the passing of another year. Counts were made on the left and right side of the sectioned nucleas, usually along the margin of the sulcus, to obtain a good estimate.

A clear seasonal pattern of band formation was deduced from the frequency of opaque margins in otoliths of fish younger than ten years (Figure 2.11). The frequency of opaque margins increased from a minimum in January to a maximum in June. It was assumed each opaque zone represented an annulus. Of the 802 otoliths, 290 were not used for the marginal zone analysis, either because they were older than 10 years, or because the margin was unreadable.

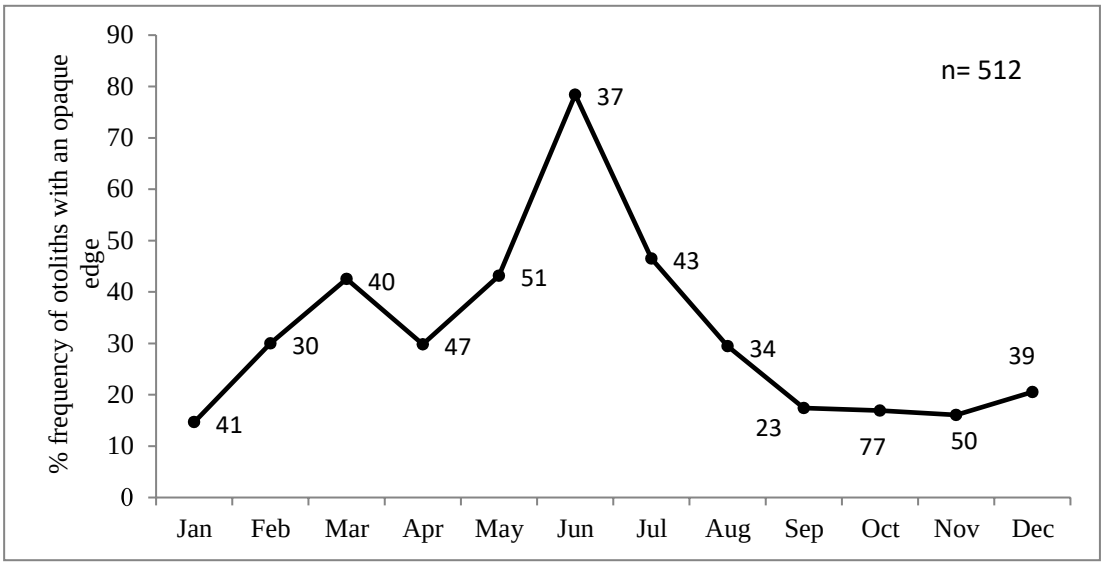


Figure 2.11:The proporation of opaque bands per month. The numbers indicate the number of otoliths for which there was majority agreement on the edge.

The estimated age of fish ranged from 0 to 37 years. The age-length key is continuous from 130 to 257 mm FL (Appendix 2.3). The oldest male was estimated at an age of 36 years and 220 mm FL. The oldest female was estimated to be 37 years old at a fork length of 232 mm. The 2, 3 and 4-year classes exhibited the most variation, with fish ranging in from 150 to 239 mm FL.

A von Bertalanffy growth curve was fitted to the fork length vs age data of 415 *B. inornata* (Figure 2.12). The parameters of the von Bertalanffy growth curve were also calculated for male and female fish separately, and for both sexes combined, including the six-intersex fish (Table 2.7). The estimates for each sex were remarkably similar, and it was not deemed

necessary to subject the difference to statistical tests. However, growth differences between areas were more substantial.

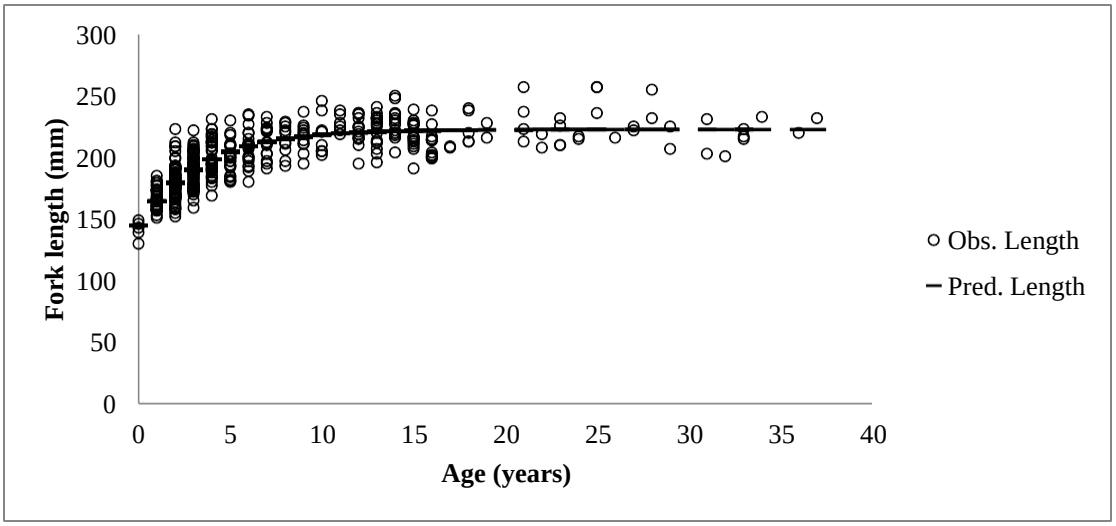


Figure 2.12: Size-at-age data for *B. inornata* with the best-fit von Bertalanffy model.

Table 2.7 : Parameters of the von Bertalanffy growth curve for males, females and all fish combined of *B. inornata.*

Sex	L∞	k(years-1)	t_0(years)	N
Males	221.0	0.290	-3.62	92
Females	223.0	0.288	-3.69	317
All fish	222.7	0.292	-3.58	415

The model of growth for the two areas, False Bay and Struisbaai, were significantly different (Figure 2.13) ($F=10.91$, $df=3,391$, $p=6.7\times10^{-7}$). To test which of the parameters, L∞ or k, differed between the areas, the ARSS test was run again, first fixing the k and estimating L∞ separately for the two areas, and then fixing L∞ and estimating k for the two areas. False Bay individuals grew significantly bigger than Struisbaai individuals ($F=10.91$, $df=3,391$, $p=9.6\times10^{-7}$). The difference in L∞ was 20 mm. Struisbaai individuals grew marginally faster

than False Bay individuals (F=10.91, df=3,391, p=9.1x10^{-5}). The difference in growth rates was 0.015 y^{-1} (Table 2.8).

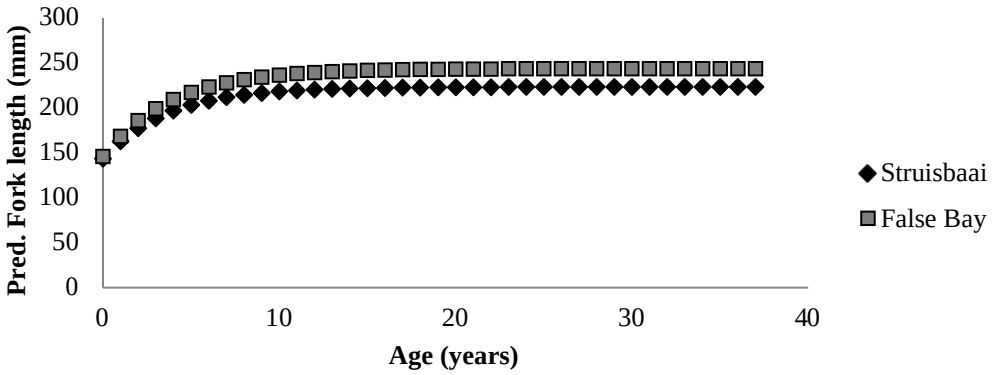


Figure 2.13:Discrepancies of predicted length-at-age between False Bay and Struisbaai.

Table 2.8: Parameters of the von Bertalanffy growth curve for all fish of *B. inornata* collected at False Bay and Struisbaai.

Location	L∞	k(years-1)	t0(years)	N
False Bay	243	0.261	-3.48	52
Struisbaai	223	0.276	-3.72	342

The growth parameters of *B. inornata* were the most extreme among those in the same taxonomic clade within the Sparidae (Santini *et al.* 2014). (Appendix. 2.4) (Figure 2.14). The ϕ` value was 4.16, which was lower than that of the other members of the clade. It had a higher growth rate but a smaller L_{inf} than the other species.

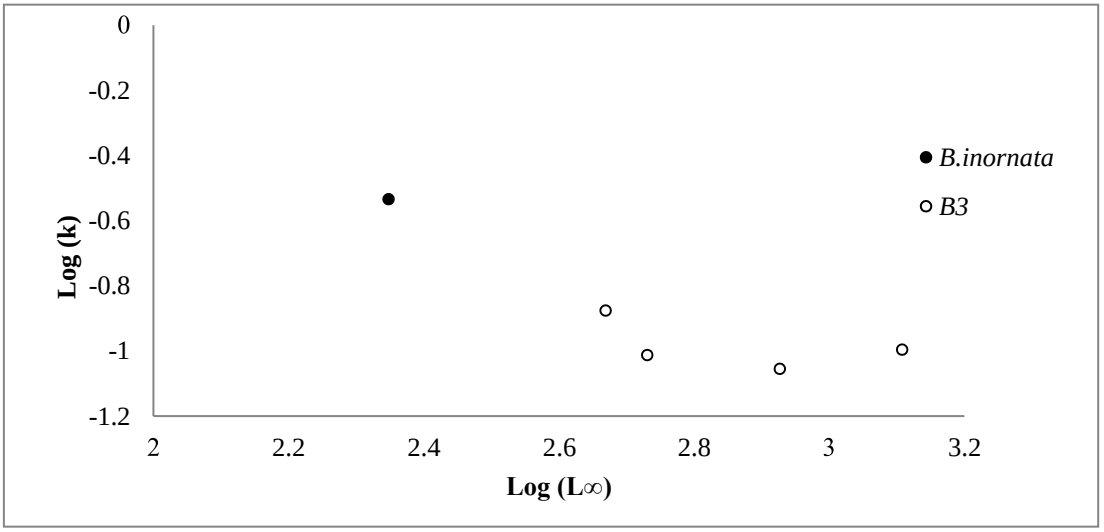


Figure 2.14:Comparison of growth performance among five species in the taxonomic clade labelled B3 by Santini *et al*. (2014). The species are: *Lithognathus lithognathus*, *Lithognathus aureti*, *Pachymetopon blochii*, *Pachymetopon aeneum*, *Boopsoidea inornata*.

The size-at-50% maturity was estimated for males at 185 mm FL (δ_L=17.1mm; Figure 2.15). and for females at 178 mm FL (δ_L=11.2mm, Figure 2.16). The smallest mature male and females observed in the sample were 157 mm FL and 151 mm FL respectively. The size-at-50% maturity was estimated for all fish combined at 179 mm FL (δ_L=13.3mm). The estimated asymptotic maturity (m_∞) was 0.63 for males, 1.00 for females and 0.9 for all fish combined.

The males of *B. inornata* matured at 3.3 years old, while females matured earlier at 1.6 years of age. The age-at-50% maturity was estimated for all fish combined to be at 1.87 years old.

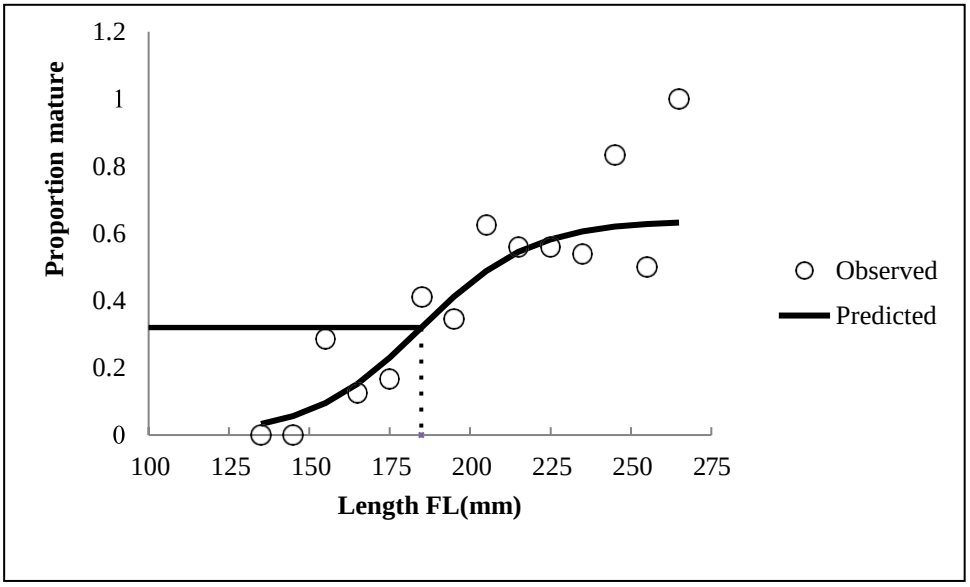


Figure 2.15: A plot of the proportion of male *B. inornata* that are mature per 10 mm size class, with the best-fit model. The dashed line indicates the size-at-50% maturity.

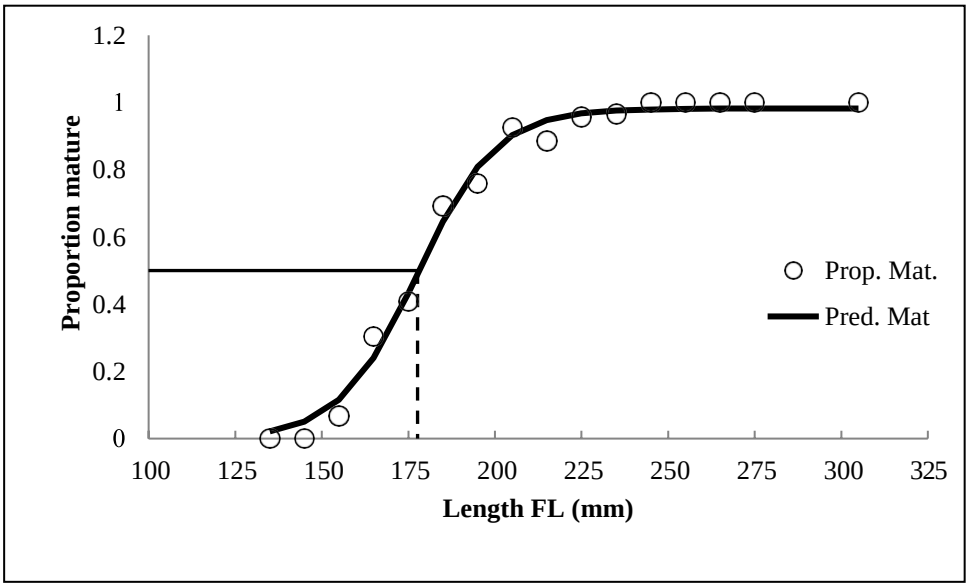


Figure 2.16:A plot of the proportion of female *B. inornata* per 10 mm size class, with the best- fit model. The dashed line indicates the size-at-50% maturity.

2.6.4 Reproduction

Out of the 817 *B. inornata*, 620 were females, 184 were males and 13 were hermaphrodites. Macroscopic observation showed that 13 mature fish had testes and ovaries. The testes were in a posterior position, whereas the ovaries were anterior. The ovaries in these fish were weakly developed in each case (Figure 2.17). Excluding hermaphrodites, the overall ratio of males to females (1:3.35) was significantly different from expected (1:1), ($X^2 = 236.43$, $df = 1$, $p < 0.05$). Struisbaai and False Bay showed a significant departure from the expected ratio of 1:1 ($X^2=196.16$, $df = 1$, $p < 0.05$) and ($X^2=63.69$, $df = 1$, $p < 0.05$) respectively. Goukamma and Port Elizabeth show no divergence from the expected sex ratio of 1:1, ($X^2=0.42$, $df = 1$, $p > 0.51$) and ($X^2=0.04$, $df = 1$, $p > 0.83$) respectively, although samples sizes at these localities were small.

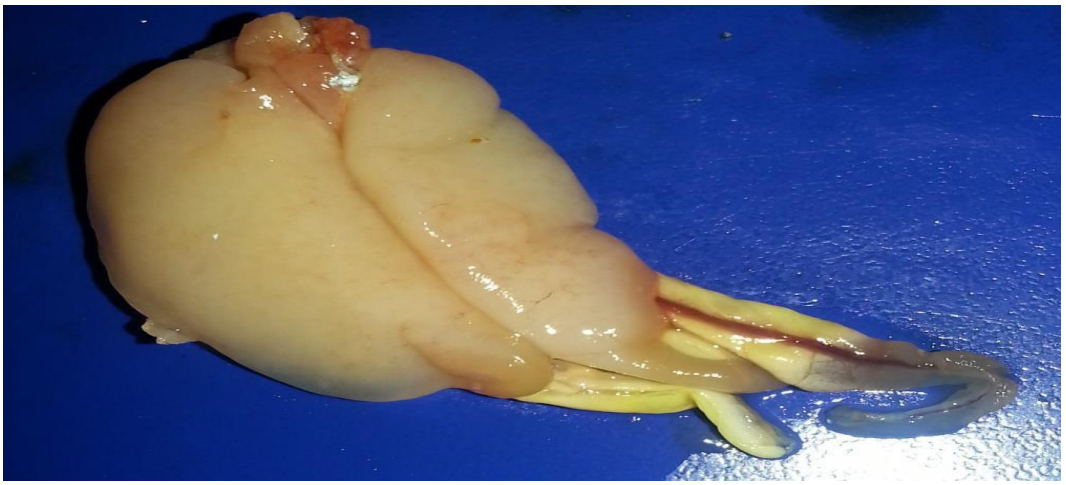


Figure 2. 17:Gonads of a hermaphroditic *B. inornata*: In each case the testes were better developed than the ovaries.

Individual GSIs ranged from 0.03 to 10.24% for females and from 0.02 to 3.79% for males.

The maximum monthly average GSI values among all areas, for females, was in August

(3.62±0.34%), and a minimum (0.72±0.13%) in November (Figure 2.18). August and September seem to be the primary spawning months. The maximum monthly average GSI values for males remain low for most of the year (0.78±0.02) was in August (1.16±0.37) but October (1.11±0.24) was almost as high. September and November were both low. Compared with the female GSI values, male values were relatively low and only started to increase one month after the females. Secondary spawning peaks are evident in December and January, and March, April (Figure 2.20).

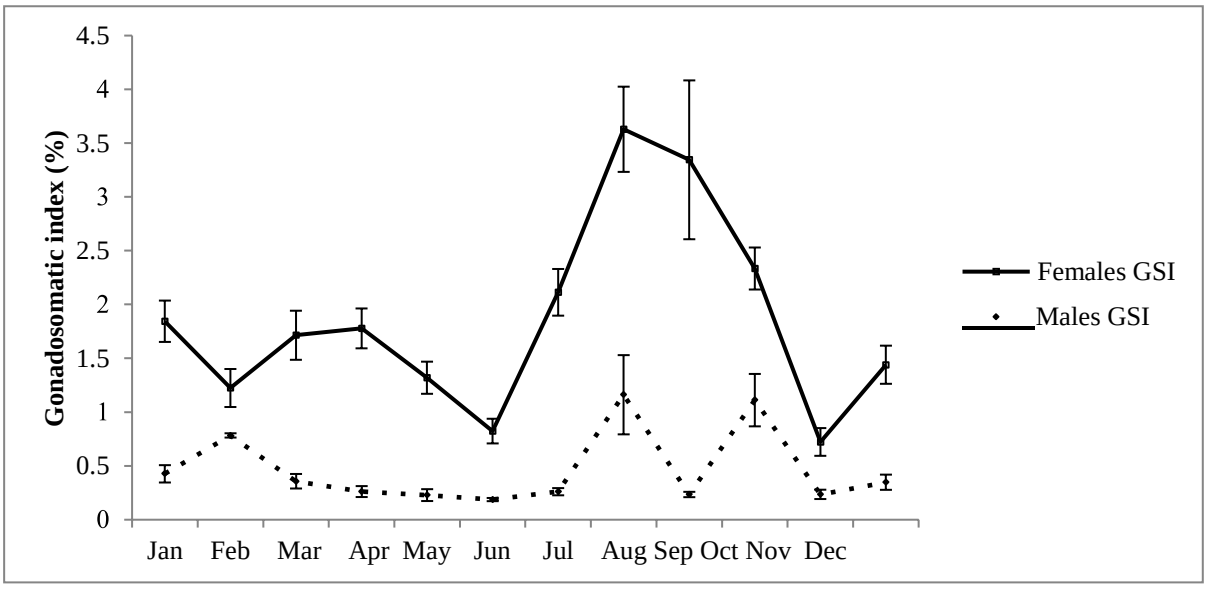


Figure 2. 18:Monthly variation in the gonadosomatic index in male and female in *B. inornate*. Error bars indicate one standard error.

The average monthly GSI values for females in False Bay were the highest among all areas, ranging from 1.59±0.52 to a peak of 4.38±1.19 in September. The female range at Struisbaai was 0.51±0.05 to 3.57±0.45 with the peak in August. Females in Goukamma and Port Elizabeth were collected only in April and mean GSI values for those two locations were 1.45±0.38 and 1.06±0.11 respectively.

Males were found in False Bay only from March to May and a peak in mean GSI was noted for April (1.04±0.44). Males in Struisbaai showed a peak in average GSI in August (1.16±0.36) and October (1.11±0.24). Port Elizabeth males were only sampled for the month of April but showed the lowest average GSI values amongst the four locations sampled (0.18±0.32). (Figure 2.19).

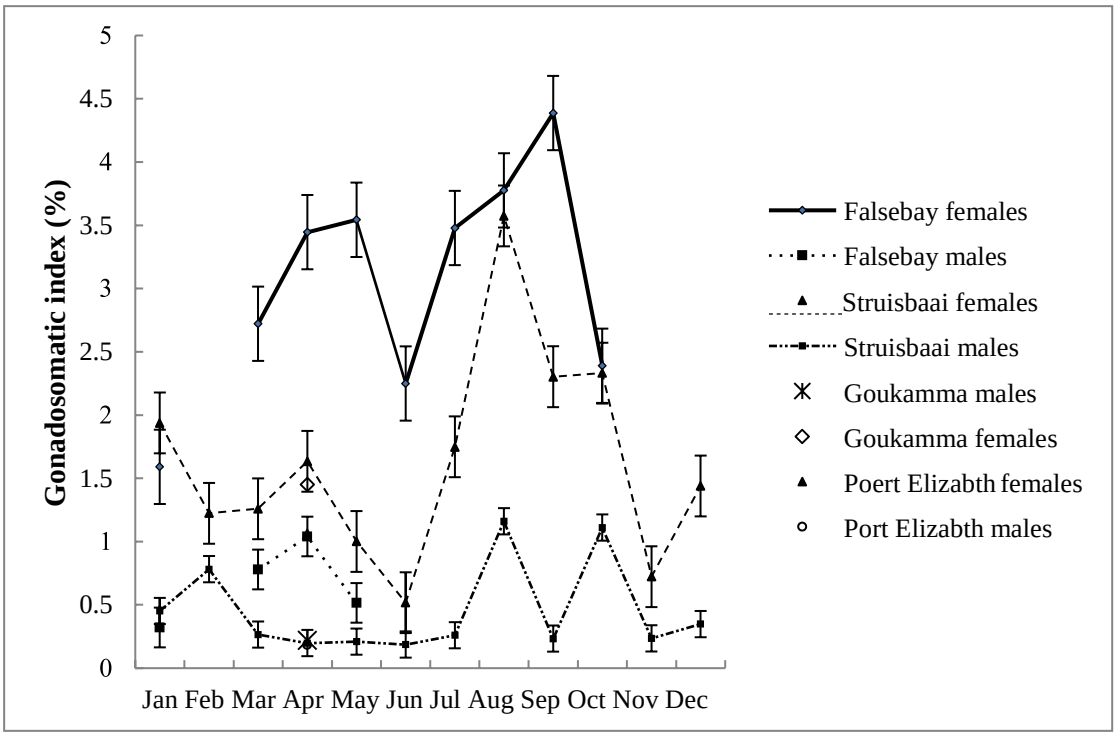


Figure 2.19:Monthly variation in the gonadosomatic index in female and males of *B. inornata* in Struisbaai, False Bay, Goukamma and Port Elizabeth.

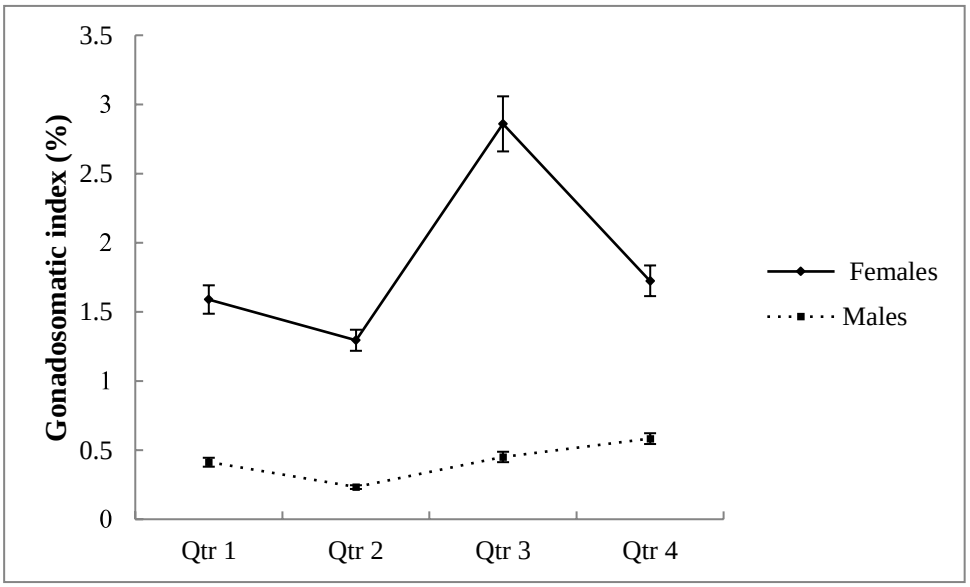


Figure 2.20:Average gonadosomatic index (GSI) of *B. inornata*, in each quarter by sex Quarter 1 represents the period from January to March.

These results were also reflected by the monthly changes in the frequency of the different maturity stages of gonads of *B. inornata*. Fish with mature ovaries were found throughout the year, however, in the months January, March, August and September more than 50% of the sampled females had ripe gonads. The highest occurrence of spent gonads was in June and October at 36.7 % and 23 % respectively. November was dominated by inactive gonads, when immature/resting and active/early maturation stages accounted for 52 % of the sample, while the active stage dominated in May and July at 59.7% and 61.4 % respectively (Figure 2.21). Only inactive (n=103) and active testis stages (n=81) were found for males. No males with free-flowing sperm were encountered. Inactive testes dominated in the month of September (Figure 2.22). Active testes dominated in February and August. The majority of inactive males were present during April and July, while January and March were dominated by active males.

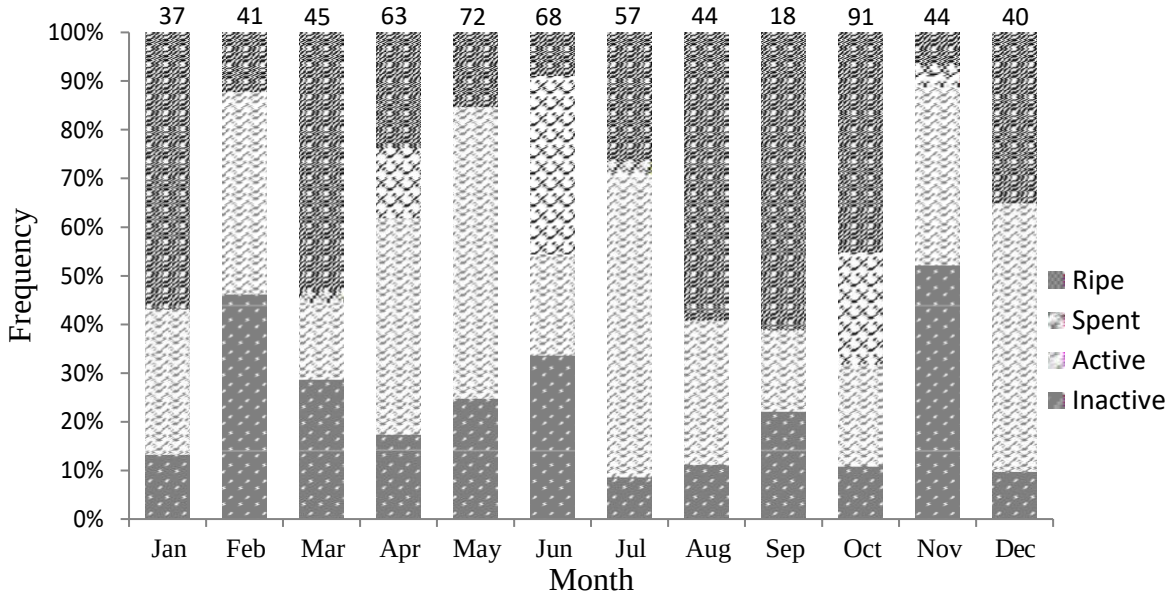


Figure 2.21:Relative percentage frequency of ovary stages in *B. inornata* per month. Sample sizes are listed above.

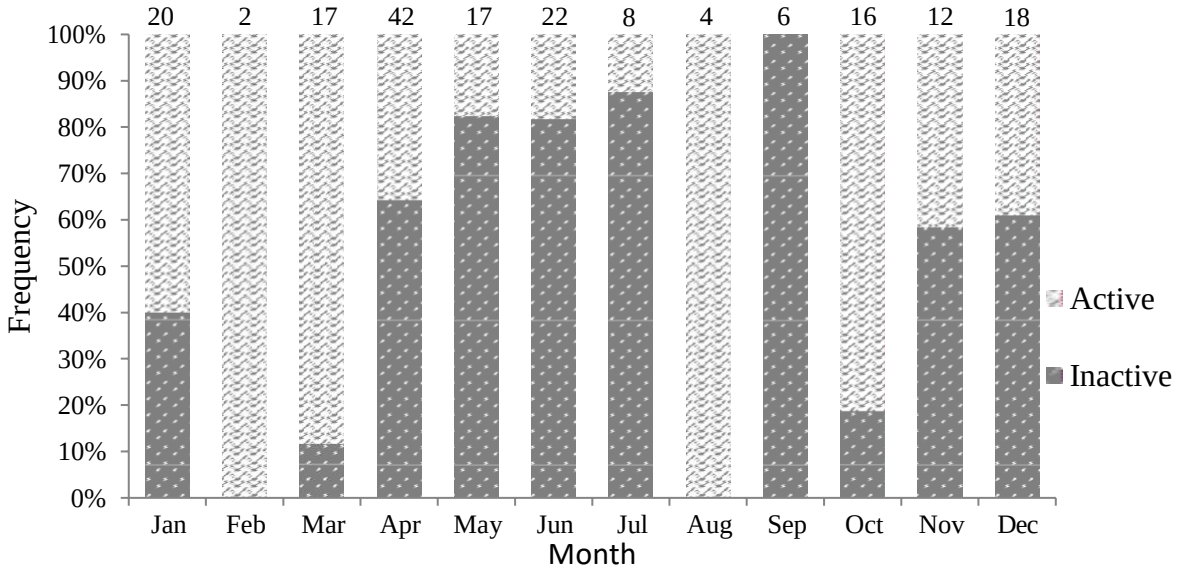


Figure 2.22:Relative percentage frequency of testis stages in *B. inornata* per month. Sample sizes are listed above.

Ovaries in *Boopsoidea inornata* were assigned to one of six developmental stages according to macroscopic and histological observation. Macroscopic variations were related to gonadal morphology whereas histological variations reflected oocyte composition. Histological descriptions of each stage are given below.

Stage (1) Immature or resting: Only previtellogenic oocytes are present in this stage. These are small spherical cells, each with thin indistinct peripheral cytoplasm (c), large nucleus (n), nucleolus (m) and balbiani bodies (b) (Figure 2.23-1).

Stage (2) Active and early maturing: This early stage of maturation is characterized by the first appearance of yolk vesicles and granular cortical alveoli vesicles (ca). Oil droplets (o) are few in number, small in size and at the periphery of the cytoplasm (Figure 2.23-2:3).

Stage (3) Maturing: This stage is characterized by early vitellogenic oocytes. Oil droplets accumulate and increase in number in the cytoplasm and yolk globules (y) appear in the peripheral region and increase in number in the cytoplasm (Figure 2.23-4:5:6).

Stage (4) Late maturation: This stage is characterized by late vitellogenic oocytes. Yolk globules become larger and are scattered in the cytoplasm. Oil droplets begin to fuse with one another around the nucleus. The oocyte wall consists of a zona radiate (z) and is coated with a follicular epithelial layer (Figure 2.23-7).

Stage (5) Ripe: The nucleus is located in the peripheral region of cytoplasm and the oil droplets have increased in size and are intermixed with the yolk globules. The yolk globules (y) enlarge and fuse with each other. After germinal vesicle breakdown, the oocytes are still within their follicular cell (f) (Figure 2.23-8:9).

Stage (6) Spent: The stage is characterized by disintegration of the nucleus. Yolk globules fuse to form the yolk plate (yp) (Figure 2.23-10:11). Disorganization of the follicular cell and

spent stage is noted by the appearance of empty follicles. A new generation of small oocytes (So) can be seen. Postovulatory follicles (POF`s) were present in the ovaries in different stages indicating that spawning had occurred recently (Figure 2.23-12).

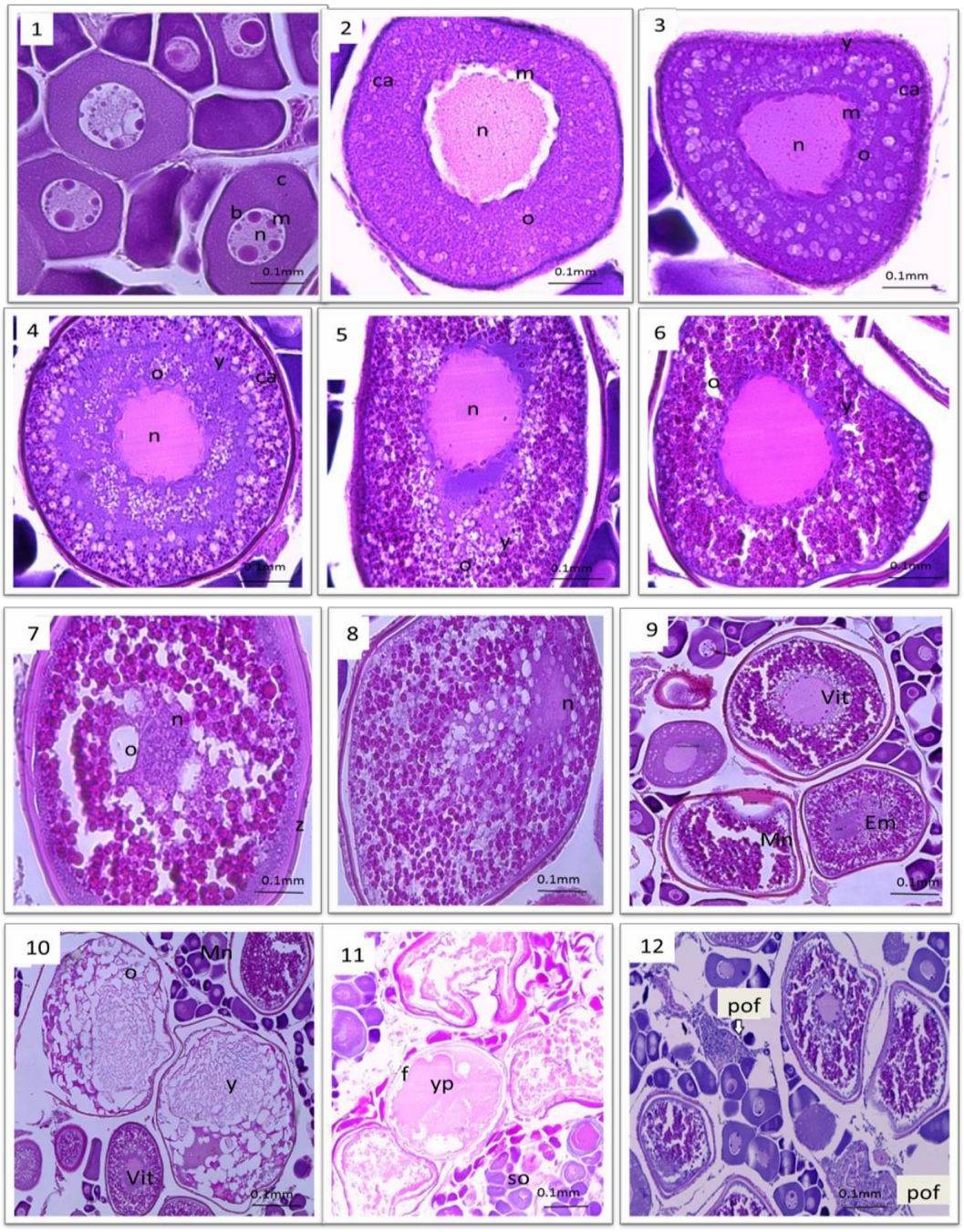


Figure 2.23:Histological sections through ovaries of *B. inornata* various stages of maturation(1) Immature, (2,3) Active and early maturing, (4,5,6)Maturing, (7)Late maturation, (8,9)Ripe, (10,11)Spent, (12) early postovulatory follicles (Pof) cytoplasm (c), large nucleus (n), nucleolus (m), balbiani bodies (b), cortical alveoli vesicles (ca), oil droplets (o), yolk globules (y), zona radiate (z), vitellogenic (Vit), early migration (Em), migration (Mn), follicular cell (f), hydrated yolk plate (yp), small oocytes (So).

Previtellogenic oocytes (<477 µm) accounted for 48.9 % of oocytes in mature ovaries. Vitellogenic oocytes between 478 and 881 µm diameter, including oocytes with an early yolk (yolk vesicle or cortical alveoli) formation stage and a late yolk formation stage, accounted for 50.4% of oocytes. Migratory nucleus oocytes and hydrated oocytes were always ≥ 882 µm in diameter and translucent, with faint segmentation. These accounted for only 0.005% of oocytes. Hydrated oocytes of *B. inornata* are spherical in shape, characterized by a smooth chorion, homogenous yolk and a single visible oil droplet (Figure 2.24).

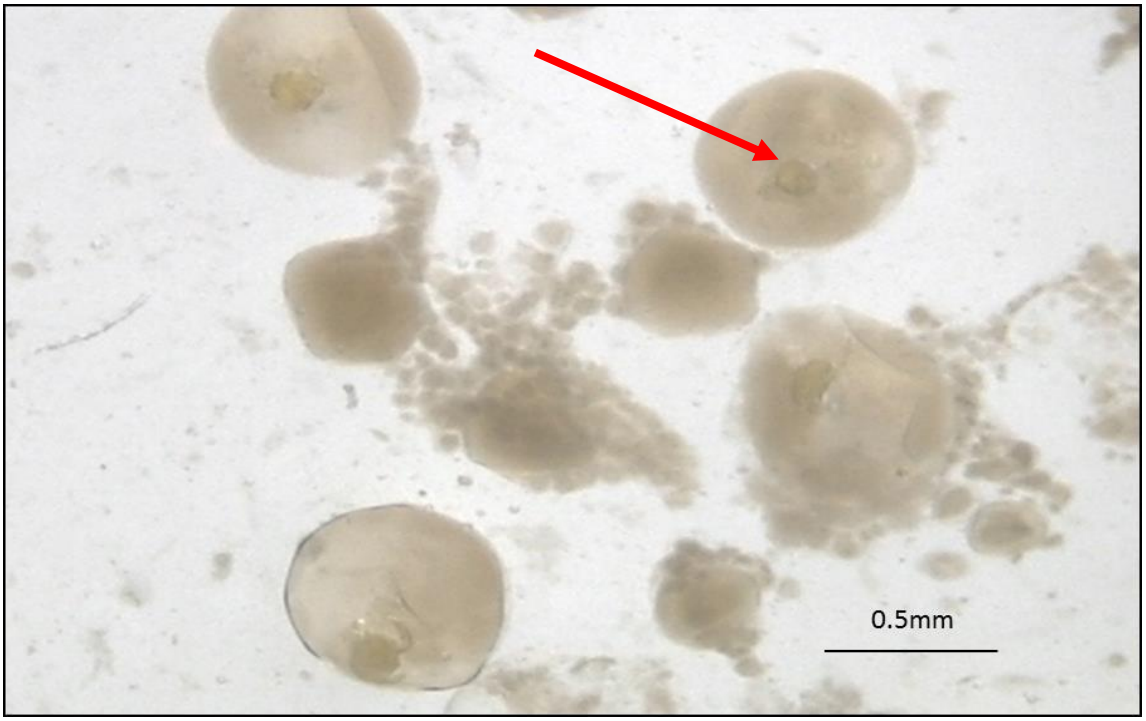


Figure 2.24: Hydrated oocytes of *B. inornata* with smooth homogenuos yolk and a large single droplet (shown by arrow).

The image-analyser generated oocyte size distributions of five females from Struisbaai and three females from False Bay (Figure 2.25). Ripe ovaries from Struisbaai were composed of 51% previtellogenic oocytes (40-477 µm) and 48% vitellogenic oocytes between (478 and 981 µm) (48%) and 1% hydrated oocytes between (982 and1209 µm). Ripe ovaries from False Bay were composed of 45.2% previtellogenic oocytes (122-477 µm), 54.1% vitellogenic oocytes between 478 and 975 µm (54.1%) and 0.5% hydrated oocytes between

(895 and 1145 µm).

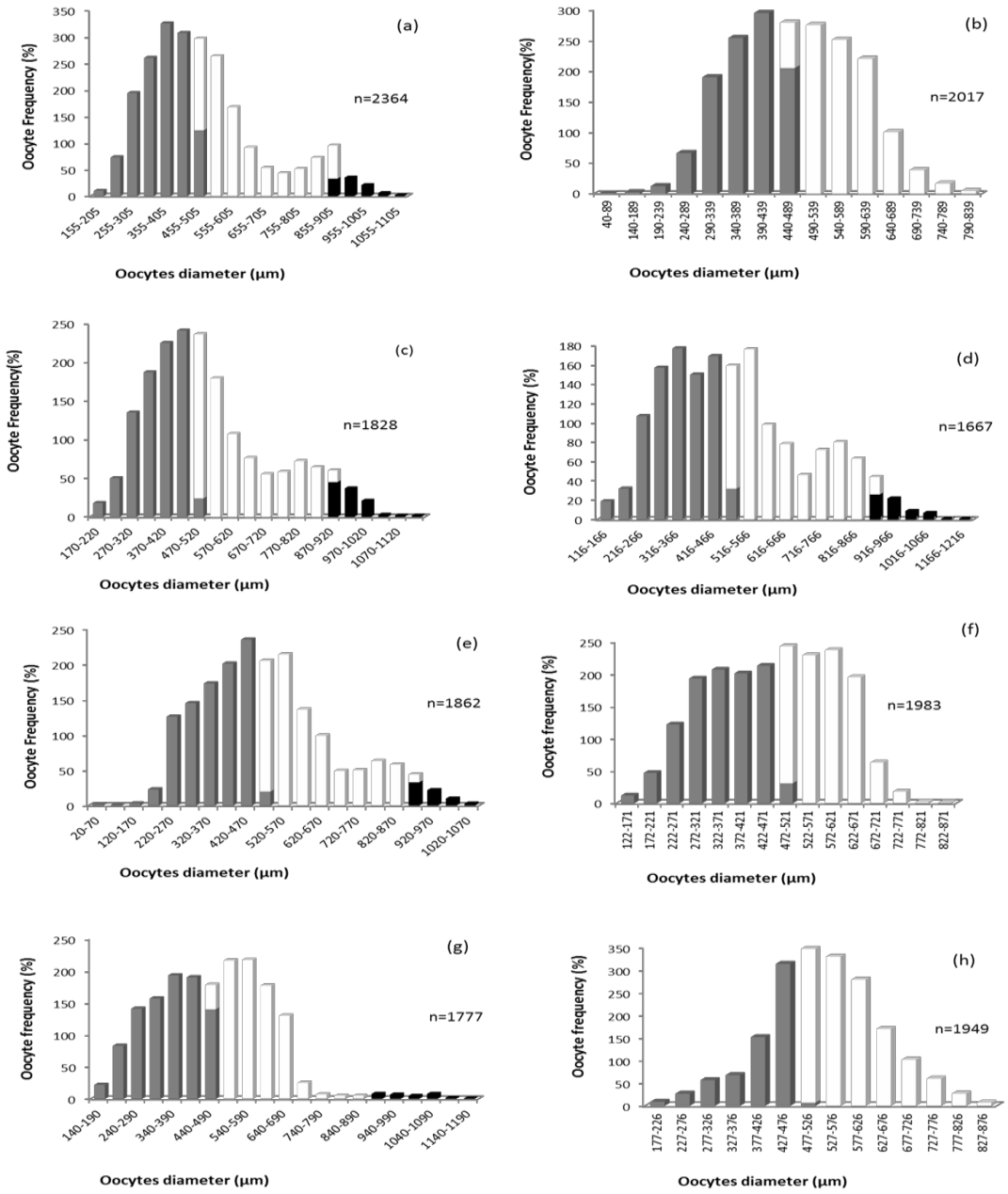


Figure 2.25: Size frequency distributions of oocytes within the ripe ovaries of eight *B. inornata* caught in Struisbaai (a: e) and False Bay (f:h). The white column indicates vitellogenic oocytes, grey indicates pre-vitellogenic oocytes and black indicates hydrated oocytes, the numbers of oocytes are indicated.

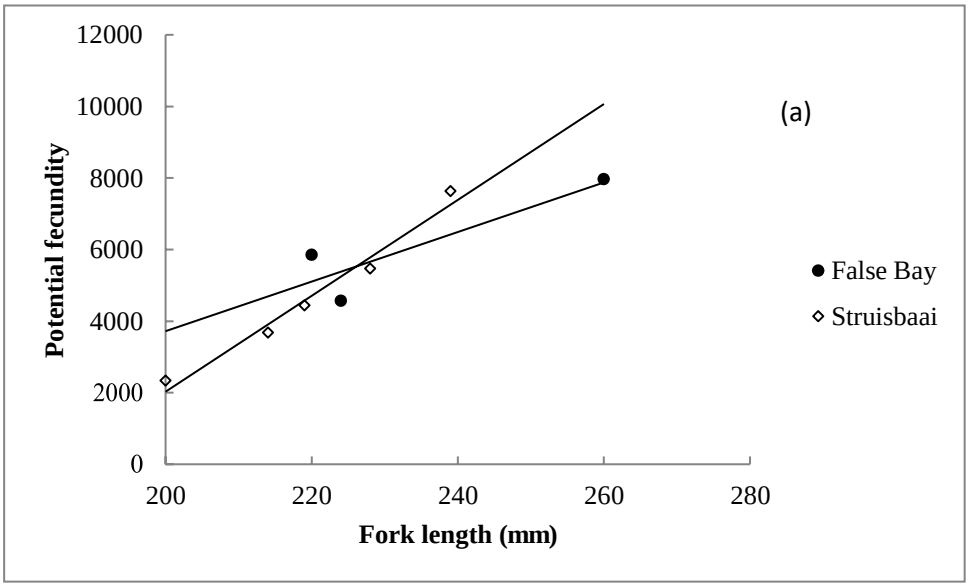
The relationship between potential annual fecundity and fork length and mass were described.

Based on the estimates of annual fecundity from eight mature females from two areas, it was

revealed that the annual fecundity for *B. inornata* ranged from 2333 eggs to 7959 eggs for fish of 200 and 260 mm fork length respectively and 176 to 396 g respectively. This equates to 19.06 eggs per gram of fish body mass. Fecundity was positively correlated with fork length and fish mass (Figure 2.26. a, b). Potential fecundity was compared between Struisbaai and False Bay from regressions, against fork length and mass. There was no significant difference between the coefficient of potential fecundity from the two locations (t=2.19, p=0.094). Fecundity in the two areas is thus adequately described by the same relationships:

Combined: P_F = 69.311 FL- 10143, n=8, r^2 =0.816. Eq.32

Combined: P_F = 21.254 W-389.12, n=8, r^2 =0.926. Eq.33



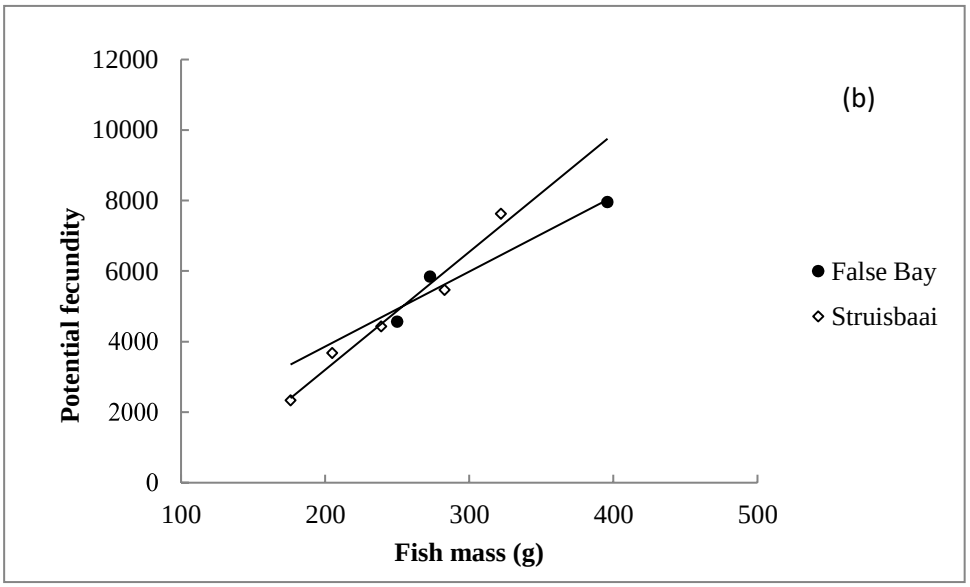


Figure 2.26:The relationship between potential fecundity and (a) fork length and (b) fish mass for eight *B. inornata* caught in Struisbaai and False Bay.

Ovaries that contained oocytes in the early hydration phase were examined to estimate batch fecundity. From Struisbaai four females had hydrated oocytes, and one ovary from False Bay. Although postovulatory follicles (POFs) were found in all the ovaries. In False Bay, a female (FL of 239 mm and weight of 273 g) had an estimated batch size of 137 eggs. In Struisbaai a female (FL of 228 mm and weight of 283 g) had more than 634 eggs per batch. There is a positive correlation of batch fecundity with fish length, and fish mass (Figure 2.27. a, b).

Struisbaai: P_F = 15,54 FL-2978.8, n=4, r^2=0.877 Eq.34

Struisbaai: P_F = 4.054 W-548.6, n=4, r^2=0.924 Eq.35

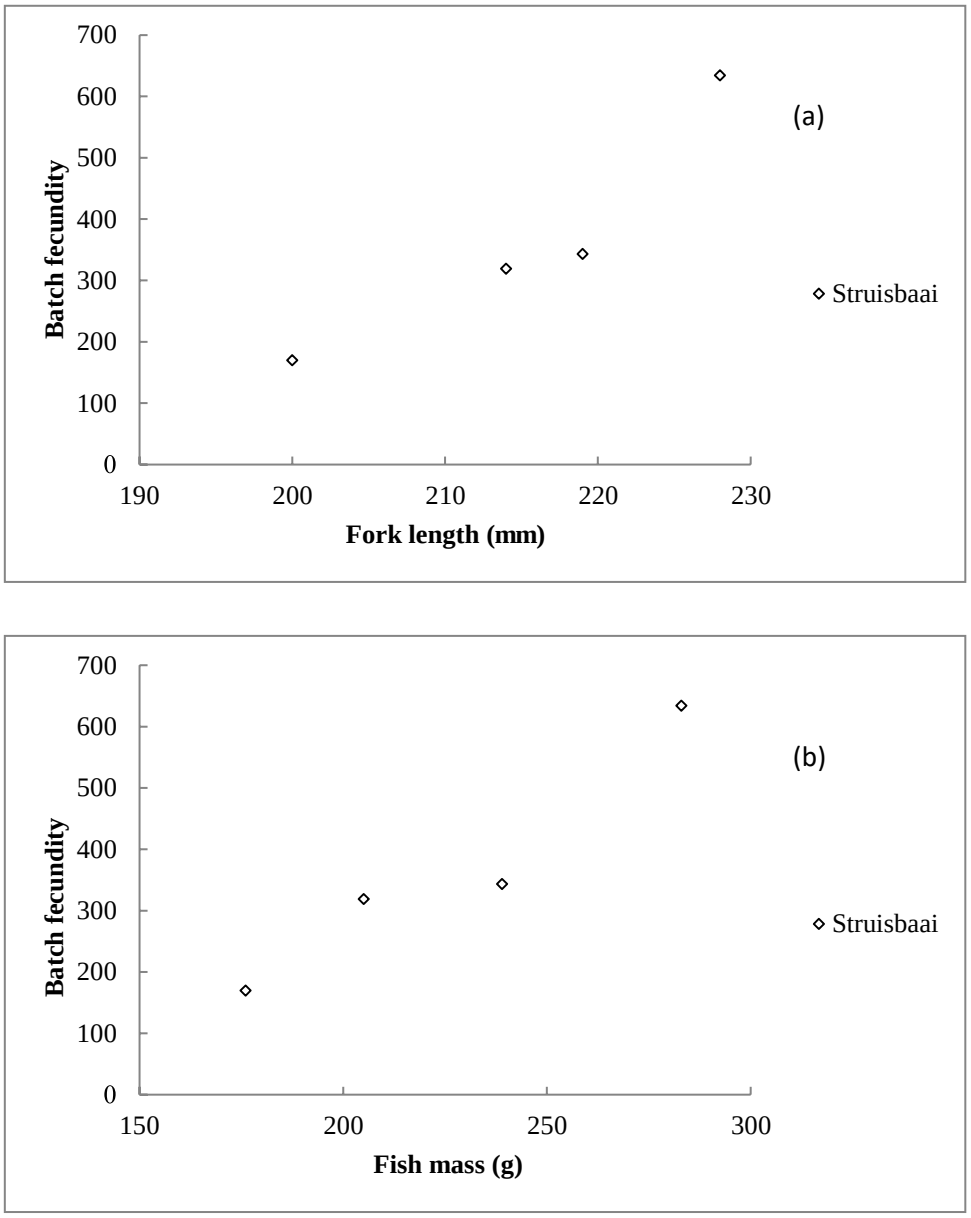


Figure 2.27:Relationship between batch fecundity and (a) fork length and (b) fish mass for four *B. inornata* caught in Struisbaai.

The range in the average seasonal abdominal fat score was 0.77 and 0.57 for females and males respectively. The abdominal fat for females showed a peak in the second quarter and a minimum in the fourth quarter. The male abdominal fat peaked in the third quarter and a minimum in the fourth quarter (Figure 2.28). The average quarterly fat of males and females

tracked each other closely. Both sexes substantially replenished fat reserves in the first quarter, immediately after the spawning season.

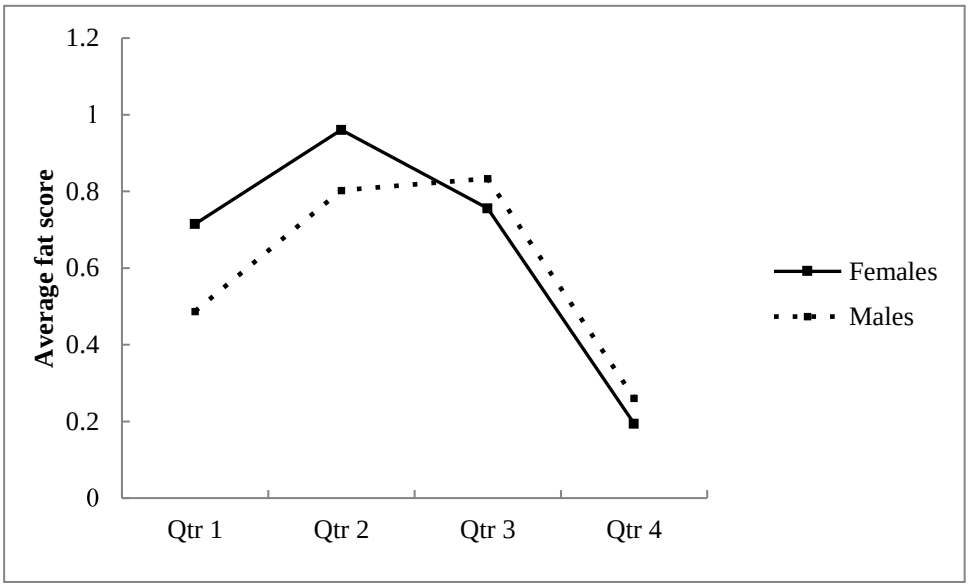


Figure 2.28:Average fat score of *B. inornata* in each quarter by sex. Quarter 1 represents the period from January to March.

The abdominal fat in False Bay fish was the highest among all areas. Typically, it was one level higher in False Bay than Struisbaai, for males and females (Figure 2.29). The trend in fat with respect to ovary and testes stage was similar in False Bay and Struisbaai. For both sexes, immature fish had low fat and inactive/resting fish had the greatest amount of fat. The fat content diminished consistently with ovary development. Fat was highest for stage 2, but diminished at progressively higher stages of gonad development. Insufficient samples from the other two sites were available for a comparison by sex, area and gonad stage (Figure 2.30).

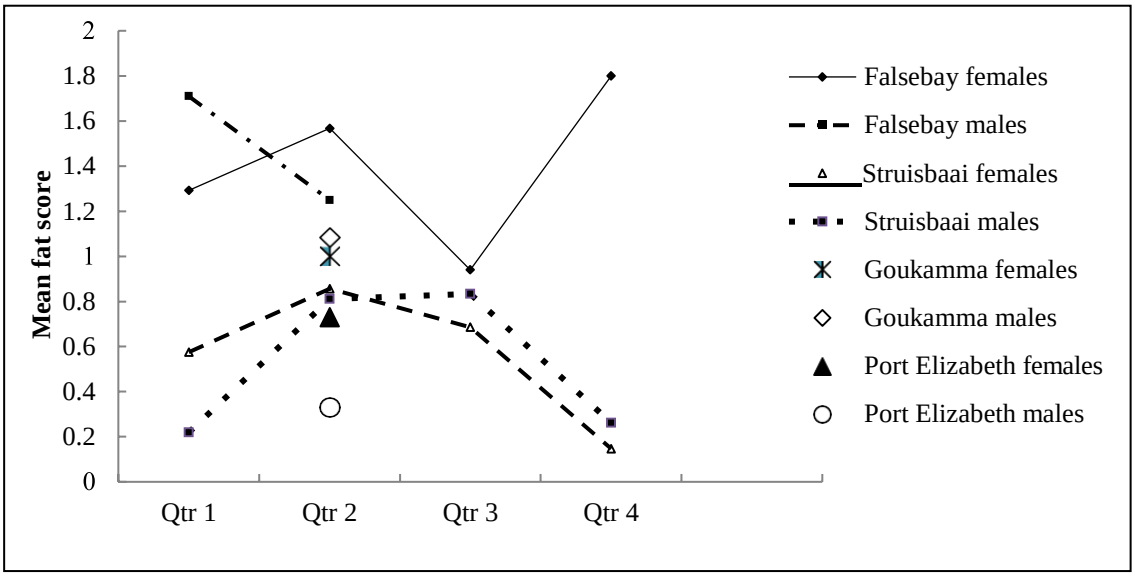


Figure 2. 29:Average fat score of *B. inornata* caught in Struisbaai, False Bay, Goukamma and Port Elizabeth, in each quarter by sex. Quarter 1 represents the period from January to March.

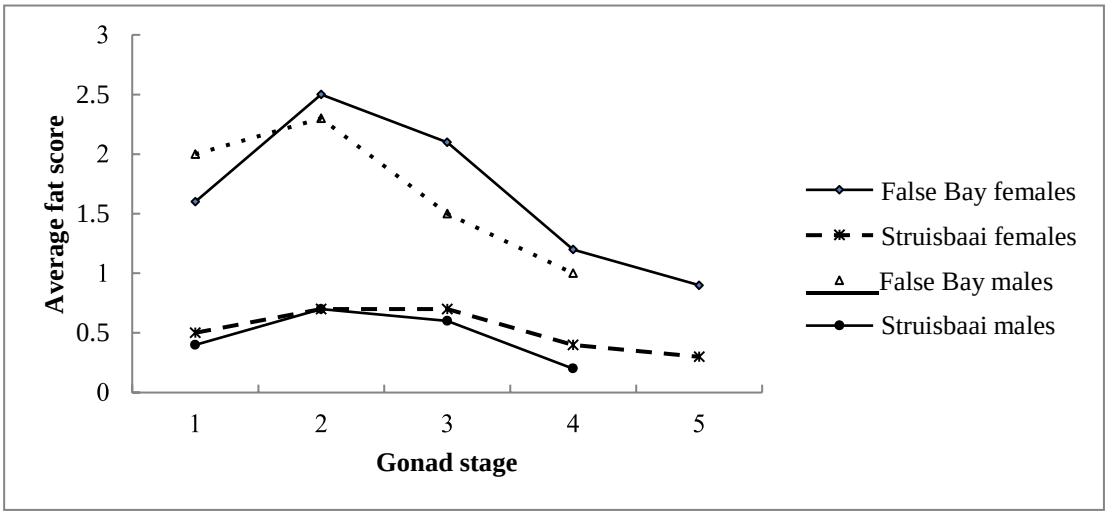


Figure 2.30:Average fat score and gonad stage of *B. inornata* caught in Struisbaai and False Bay in each quarter by sex. Quarter 1 represents the period from January to March.

2.7. Discussion

2.7.1 Diet

Analysis of the diet showed that the *B. inornata* is an omnivore, with a preference towards small sand- and reef-dwelling prey and only limited intake of algae and small fish. The majority of prey items comprised sessile and mobile animal prey of benthic origin, suggesting that *B. inornata* forages predominantly in benthic habitats. The dominant orders of animal prey, in order of importance, were Cornatulida, Amphipoda, Phiurida, Mysida, Enterogona, and Isopoda.

B. inornata stomachs were filled with a wide range of prey items. There is no significant difference in the variety of diet among seasons or sex. Gut content samples from Struisbaai and False Bay were different but in neither case was there seasonal variability. Crinoids dominated in Fale Bay and ophiuroids dominated in Struisbaai. Echinoidae, Patellogastropoda, Maxillopoda, Anthozoa, Zoanthids, Trochoidea, and Alcyonacea had little importance in Struisbaai, these groups were absent totally from the diets of False Bay fish. Overall, the Struibaai diet was more variable, perhaps reflecting greater invertebrate diversity in the warmer waters of Struisbaai. This difference suggests that the species is a generalist feeder.

Organisms with tough exteriors, particularly ascidians, crinoids and ophiuroids dominated the dioet of large fish, whereas small, free swimming and soft bodied organisms such as crustacea and polychaetes were more prevalent among the smaller fish. Large fish had a greater variety of prey than small fish. Scharf et al., (2000) found that, among 18 marine fish species examined, a wider size-range of prey was consumed by larger fish than small fish.

The results from False Bay are largely in agreement the diet studies conducted in the Eastern Cape by Trow (1982). The single exception is the low importance of Ascidiacea in this False Bay, whereas ascidiacea accounted for up to 50% by frequency of occurrence in the east. Trow

(1982) hypothesised that *B. inornata* feed on ascidiacea to ingest attached epiphytic organisms. Le Chanteur & Griffiths (2003) also showed a low frequency of ascidacea in the diet of *B. inornata* collected in False Bay.

Sparidae typically consume a wide range of benthic prey and a substantial amount of plant material (Stergiou and Karpouzi 2002). Le Chanteur & Griffiths (2003) reported that the diet of *B. inornata* was most similar to the sympatric *Spondyliosoma emarginatum* and *Pachymetopon blochii*, due to the abundance of a small, benthic invertebrate in all their diets. Like these other two, *B. inornata* is a generalist.

2.7.2. Age and Growth

The parameters of the von Bertalanffy growth model reveal that *B. inornata* is a long-lived, slow-growing species. The growth rates of *Sparidae* range from 0.042 y^{-1} for *Acanthopagrus butcheri* to 0.921 y^{-1} for *Spicara smaris*. The sex-combined growth rate for *B. inornata* is 0.292 y^{-1}, falling between the growth rates *Polystegonus undulosus* (0.277y^{-1}) and *Peturus rupestris* (0.378y^{-1}), and is roughly average value for the family.

The great diversity in Sparidae is reflected in theoretical asymptotic length (L_∞) and maximum ages (t_{max}) attained. Maximum size ranges over an order of magnitude from 128 mm FL for *Spicara smaris* to 1283 mm FL for *Lithognathus lithognathus* and maximum age from 6 years for *Sarpa salpa* and *Pagellus bellotti natalensis* to 50 years for *Lithognathus aureti*. *B. inornata* can therefore be regarded as a small species (L_∞= 222.7 mm) of high longevity (t_{max}= 37).

The estimated asymptotic length of *B. inornata* is considerably smaller than the largest fish observed in this study (L_{max} = 310 mm), which therefore reflects great variation in growth. Sparid growth tends to be very fast in the first few years of their life, slowing down considerably afterwards. Some authors report that early growth of sparids may not be adequately represented by the von Bertalanffy growth model (Morison et al., 1998, Gonçalves et al., 2003)

By using the calculated growth parameters K and L_∞ from published data for different species in the Sparidae family one can estimate ϕ`, a growth performance index. ϕ` is considered a useful tool for comparing the growth of different populations of the same species and of different species belonging to the same family (Sparre & Venema 1998, Munro & Pauly 1983). For Sparidae the ϕ` values range from 3.75 for *Dentex macrophthalmus* to 5.75 for *Peturus rupestris*. A higher ϕ` value indicates faster growth. Due to a high K value and low L_∞, the growth rate for *B. inornata* tends to be slow, ϕ`= 4.16, and falls between *Pagellus erythrinus* (ϕ`= 4.17) and *Boops boops* (ϕ`= 4.15).

Sparidae in general are found to be mature at lengths of 30-84% of L_∞ and ages of 8% to 44% of t_{max}. For *B. inornata* the length at 50% maturity for males and females is 185 mm FL (70% of L_∞) and 178 mm FL (58% of L_∞) respectively. For all sexes combined the length at 50% maturity is 180 mm FL, or 82% of L_∞. It can be concluded that *B. inornata* mature at a large size relative to the estimated asymptotic length, second largest among all *Sparidae* after *Polystegonus undulosus* that matures at 84% of L_∞.

The age at 50% maturity for males and females is 3.29 years (9 % of t_{max}) and 1.6 years (4.3% of t_{max}) years respectively. For all sexes combined the age at 50 % maturity is 1.87 years (5% of t_{max}). *Chrysoblephus gibbiceps*, with maximum age of 48 years, showed the same degree of maturity at an early age (8% of t_{max}). In these species the growth rate slows dramatically after maturity.

Of the 33 papers on sparid age and growth reviewed by Brouwer & Griffiths (2004) only four provided any measure of precision of aging, and none showed information on average percent error (APE) for *B. inornata*. In the current study *B. inornata* were difficult to age with a poor precision indicated by an APE of 17%. In comparison, *Polystegonus undulosus*, with maximum age of 20 years, showed the same degree of precision (18.2%). For short-lived *Sparidae* it has been shown that the APE is lower, *Sarpa salpa* with maximum age of 6 years has an APE of

3.9% (van der Walt & Beckley 1997). However, this trend does vary as *Argyrozona argyrozona*, with a maximum age of 27 years, has a low APE of 5.3%. The difficulty of ageing long-lived fish is a result of the slowing or cessation of somatic growth as fish age that results in a narrowing of spacing between growth rings (Beamish 1979).

The results showed that there was a significant difference in estimated asymptotic length of *B. inornata* between locations, False Bay (L_∞ = 243 mm) was higher than Struisbaai (L_∞ = 223 mm). Fish from False Bay grew at a similar (statistically inseperable) rate (k = 0.261y^{-1}) to those from Struisbaai (k = 0.276 y^{-1}). The reason for this could be attributed to differences in the quantity and quality of food, the hydrographic conditions (it is cooler in False Bay), and the higher prevalence and infection intensity values of parasites in Struisbaai versus False Bay (chapter 3). Larger maximum sizes in the west compared to the east have been found for other South African seabreams *Spondyliosoma emarginatum* (Tunley et al. 2009) and *Rhabdosargus globiceps* (Griffiths et al. 2002; Attwood et al. 2010), implying a systematic reason for differences in growth.

2.7.3 Reproduction

Although fish with ripe gonads were observed throughout the year, evidence suggests that *B. inornata* spawn most frequently from July to October with a peak in August. During this period mature females were spawning repeatedly. Less intense studies on the species confirm a long spawning season. Mann et al., (2015) observed that *B. inornata* had ripe gonads throughout the year and van der Elst (1981) reported that species spawns through spring and summer. There is no clear difference in spawning season between areas.

Lorenzo et al., (2002) reports that the values of gonadosomatic index (GSI) for males were commonly lower than those for females on reviewing the reproductive biology of the sparidae, but this pattern is not universally followed. The GSI of female and male *B. inornata* differ

substantially. Females invest more energy into their gonads than males. The gonado- somatic values at peak spawning were much greater in females (mean 1.75) than the males (mean 0.41) which is a characteristic of protogyny. This may be related to a reduction in male numbers leading to less sperm competition. Buxton & Garratt (1990), in their comparison of protogynous species and rudimentary hermaphrodites, reported that GSI in females is always much greater than in males for protogynous species but that gonad size is similar for rudimentary hermaphrodites. But as I will discuss later, *B. inornata* is not protogynous.

Females and males in False Bay had the highest GSI when compared with other locations. As with the growth difference, this could again be reflective of better feeding conditions in the west, and confirms that *B. inornata* is prioritising gonad development above somatic growth, as would be expected for a small species that matures early.

A reduction in the volume of abdominal fat in *B. inornata* coincides with its peak breeding season. Abdominal fat is likely used in the development of eggs and sperm, as was found to be the case for another seabream, *Pagrus pagrus* (Aristizabal 2007). Fat content may therefore be used as an indicator of spawning potential over the season and with knowledge of population size it may serve as index of total egg production (Morimoto 1996, Marshall et al., 1999).

An increase in abdominal fat after the spawning season preceded an increase in condition factor. Condition of the fish does not drop dramatically during spawning, the reason for this could be due to high feeding activity of this fish during and immediately after spawning. Because *B. inornata* has a protracted spawning period, and food is available year-round in the warm temperate region, they probably eat while their gonads develop. Such is the case with *P. pagrus* (Aristizabal 2007). One possible and important exception is related to the difficulty of catching male fish with ripe testes. Their absence in the sample could indicate they do not feed during spawning, and this might provide a clue to their spawning behaviour. A different method of capture may yield ripe males.

When the GSI and condition factor are compared, it seems that condition is weakly affected by the sexual cycle. June (one month before spawning season) has the minimum condition factor for both sexes, condition factor then recovers during the spawning season to levels equivalent in April and May (maturation phase). *B. inornata* are broadcast spawners, as is typical of the family (Beckley and Buxton 1989).

Most seabreams spawn in spring, but the length of the season varies considerably. The spawning season for two sparid species (*Spondyliosoma* spp) that lay eggs in a nest, are in spring, whereas *P. blochii* are biannual spawners, in late autumn–early winter and again in summer (Pulfrich & Griffith 1988).

Many South African seabreams were reported as gonochorists by Penrith (1972). According to microscopic examination of gonads, the present study found a number of characters that appear to be distinctive to rudimentary hermaphrodites with occasional expression of protogyny as evidenced by individuals with degenerating ovaries and developing testes, rather than true gonochorists. Males and females have a similar size, typical of seabreams that maintain separate sexes.

The *B. inornata* population seems to consist of mostly true males and true females, as well as hermaphrodites, though hermaphrodite fish represent a minor part of the population. Sex ratios of protogynous hermaphroditic Sparidae are typically skewed towards females, in an unexploited population the expected ratio is 1:2 up to 1:4 and in an exploited population can favour females to a much higher degree, up to 1:19 (Garratt 1985, Buxton 1993, Pajuelo & Lorenzo 1996, 1998). The sex ratio of *B. inornata* was heavily skewed to females (1:3.3), more so in the west than the east. Two possible explanations here are (i) sex determination is temperature dependant and (ii) males either die young or migrate to warm water. The idea that sex-ratios can be adjusted to suit the economy of a polygamous system has been rejected (Hamilton 1967). Hamilton did outline some conditions which might violate the assumptions of Fisher's principle (e.g. viscous populations and local competition), but none of these could

be argued to apply to seabreams.

Temperature affects sex determination in only a few fish species (Ospina-Alvarez and Piferrer 2008). No evidence of this has been found among the Sparidae, but where it exists, high temperatures produce more males than low temperatures (Helfman et al. 2009). The two small samples in the east had sex ratios not significantly different from 1:1. A larger sample size might have revealed a different result, because at both sites in the west males were vastly

outnumbered, and more so in the cooler False Bay. Differential mortality or movement might seem more plausible, but there is no evidence to back this up whatsoever.

The smallest mature males and females captured were 201 mm in fork length and 198 mm in fork length respectively. This similarity in size of males and females is a characteristic of rudimentary hermaphrodites. Fifty per cent of the population were sexually mature (L_{50}) when males and females reached 185 mm FL and 178 mm FL respectively.

The macroscopic method gives a good understanding about development of the gonads by defining each maturation stage, especially with species that have unknown reproductive styles. The majority of marine fishes release pelagic eggs that generally float freely in seawater, most of them in upper surface layers (Ahlstrom & Moser 1980). Pelagic eggs are small in size, ranging from 0.6 to 4.0 mm in diameter, with a mean of 1 mm (Kendall et al., 1984) and a median of 1.1 mm (Chambers & Leggett 1996). They are spherical in shape, usually having a smooth chorion and the yolk can be either segmented or homogenous. Most pelagic fish eggs have a single oil droplet, though some may have two or more oil droplets or even lack an oil droplet (Ahlstrom & Moser 1980). These characteristics could be identified in the eggs of *B. inornate*, which are spherical in shape with an average egg size of 0.61 and with a smooth chorion. The yolk is homogenous and has a single oil droplet. Hydrated eggs for sparids in South African are between 0.8-1.25 mm in diameter (Brownell 1979) these measurements agree with the results of the present study in which hydrated eggs of *B. inornata* range from 0.88-1.20 mm in diameter.

The presence of oocytes in different stages of maturation is usually considered to be evidence of serial spawning (Hunter & Goldberg 1980, Melo & Armstrong 1991). Histological evidence of ripe ovaries that contained oocytes in different stages of maturation suggests that the oocyte development is asynchronous and that *B. inornata* is a serial spawner. The

presence of post-ovulatory follicles together with vitellogenic oocytes is evidence that *B. inornata* is also a batch spawner that spawns irregularly, as do many *Sparidae* species.

B. inornata is characterized by a continuous oocyte size distribution and as such has an indeterminate fecundity. There is no hiatus between previtellogenic and vitellogenic oocytes, which reflects the continuous maturation of oocytes throughout spawning. Consequently, the previtellogenic oocytes will progress through to maturity during spawning and contribute to the standing stock even after spawning (Hunter et al., 1985). Potential fecundity is positively related to the size of mature females in spawning season (Hunter et al., 1985, Collins et al., 1998). Fecundity in fishes is variable among individual species (Sadovy 1996).

In my study potential fecundity is linear and increases markedly with length and weight. Batch fecundity is positively related to the size of mature females. There is no significant difference between False Bay and Struisbaai, as females had the same batch fecundity at the same size. The estimation of the annual fecundity of species with indeterminate fecundity requires a combination of data on batch fecundity, spawning season duration and spawning frequency (Murua et al., 2003). The potential fecundity of indeterminate species can be estimated as the product of number of eggs per batch and the number of batches per years (Fitzhugh et al., 2012). *B. inornata* is a typical indeterminate spawner that spawns a small number of eggs comparing with the total number present (Hunter et al., 1985), as a result most of vitellogenic oocytes remain in the ovary during the spawning period and will probably constitute the pool of oocytes to be spawned at the next spawning event.

In summary, *B. inornata* has indeterminate fecundity; a protracted spawning period and a low maximum mean monthly GSI. The low GSI in males combined with a skewed sex ratio suggests polygyny. Males might fight for access to females, implying that its reproductive effort is channelled to aggression rather than sperm production. *B. inornata* is a classical periodic strategist (Winemiller 2005). It is unusual in that it spawns early and lives long. It forgoes a large size in favour of early maturation.

2.8. Conclusion

It is interesting that after several decades of intensive studies of seabreams in southern Africa, no biological data could be found for one of the most abundant species, *B. inornata*, except for two studies of its diet (Trow 1982, Le Chanteur and Griffiths 2003). The omission may relate to its small body size, and consequent low value to fisheries. Nevertheless, this small body size signals an outlier in terms of life history, which may help to explain some of the life history trade-offs in the family.

This small seabream has a diet that is typical of the family. It is primarily a benthic feeder: omnivorous, but with a preference for animal prey.

Also *B. inornata* showed a significant difference in estimated asymptotic length between locations. In this feature it is not alone. *S. emarginatum* and *R. globiceps* both show a gradient in body size and growth rate from the South Western Cape to the eastern Agulhas Bank, reflecting the direct and indirect influences of water temperature and food availability.

The unusual feature of the species is its small body-size coupled with high longevity, high life-time fecundity. The species is polygamous, as evidenced by a strongly skewed sex ratio and low male GSI, but the species is a rudimentary hermaphrodite. The incidence of hermaphroditic expression was low, around 1.2%. The seabreams are known to be plastic with respect to sexual strategy, including gonochorism and all varieties of hermaphrodites. *B. inornata* displays some of the features of protogyny, i.e. low male GSI and low male: female sex ratio and might represent a strategy that is intermediate between gonochorism and protogyny.

2.9.1. Appendix 2.1

Appendix 2. 1:Diet comparison for *B. inornata* caught off False Bay and Struisbaai (present paper) and different areas in South Africa. By percent frequency of occurrence (*%FO*), percent volume (*%V*): (*V*), dry mass (M).

Sources	Le Chanteur and Griffiths 2003		Trow 1982					Present paper			
Areas	False Bay		Transkei and Algoa Bay					False Bay		Struisbaai	
	%FO	*%V*	*%FO*	*V*	*%V*	*M*	*%*	*%FO*	*%V*	*%FO*	*%V*
Algae	12	2.7	37.6	1.71	3.7	0.39	3.8	35.62	3.75	20.56	7.67
Chlorophyta	10	1.7	-	-	-	-	-	21.92	7.61	1.87	1.8
Rhodophyta	6	1	-	-	-	-	-	17.81	3.1	18.69	5.88
Ochrophyta	2	0.1	-	-	-	-	-	-	-	-	-
Ascidiacea	20	7.7	53.5	13.1	28.1	2.28	24	9.59	4.88	13.8	7.97
Vertebrata (fish)	2	<0.1	2.9	0.43	0.9	0.046	0.4	1.37	3.76	0.93	1.8
Crustacea		63.4		6.48	13.9	1.935	18.7	60.27	13.74	41.12	13.55
Amphipoda	86	30.6	37.6	1.15	2.5	0.253	2.4	31.51	3.79	24.3	4.86
Isopods	40	9.4	13.5	1.09	2.3	0.185	1.8	21.92	2.05	4.76	1.32
Ostracoda	50	14.4	7.1	0.06	0.1	0.006	0.1	8.22	0.5	6.54	0.84
Cirripedia	12	1.6	8.2	0.57	1.2	0.249	2.4			0.93	0.48
Pycnogonida	2	0.1	5.9	0.72	1.6	0.14	1.4	-	-	-	-
Panaeid Prawn	2	5	-	-	-	-	-	-	-	-	-
Leptostraca	8	0.2	-	-	-	-	-	-	-		
Mysida	16	0.6	14.1	0.39	0.8	0.054	0.5	23.29	5.73	17.76	2.82
Decapoda	6	1.4	21.2	2.41	5.2	1.009	9.7			0.93	3
Copepoda	2	<0.1	2.3	0.02	0.1	0.003	0.1	9.59	0.62	2.8	0.24
Unidentified crustacean	-	-	10	6.48	1.7	0.137	1.7	-	-	-	-
Echinodermata	22	8.5	9.4	0.63	1.4	0.186	1.8	38.36	43.25	47.66	40.35
Holothuroidea	-	-	-	-	-	-	-	1.37	0.02	5.56	1.02
Crinoidea	22	8.5	-	-	-	-	-	35.62	32.3	22.43	14.39

Appendix 2.1: Continued

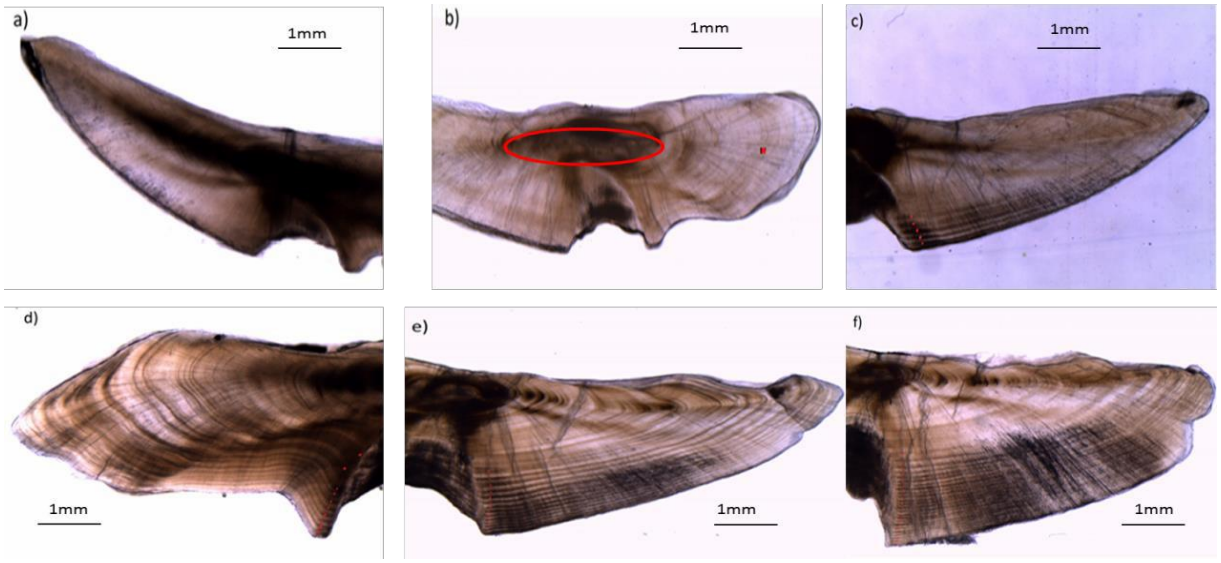
Sources	Le Chanteur and Griffiths 2003		Trow 1982					Present paper			
Areas	False Bay		Transkei and Algoa Bay					False Bay		Struisbaai	
	%FO	*%V*	*%FO*	*V*	*%V*	*M*	*%*	*%FO*	*%V*	*%FO*	*%V*
Echinoidae	-	-	-	-	-	-	-			2.8	4.32
Brittlestars	-	-	-	-	-	-	-	15.07	7.79	22.43	20.62
Mollusca	10	0.4	13.6	7.33	15.8	0.762	7.4	12.3	10.32	9.35	5.34
Cephalopoda	-	-	1.8	6.47	14	0.608	5.9	-	-	-	-
Bivalves	2	<0.1	-	-			-	4.11	1.5	4.67	2.1
Whelk-like	4	<0.1	-	-	-	-	-	-	-	-	-
Limpets	6	0.3	-	-	-	-	-			0.93	0.12
Winkles	-	-	-	-	-	-	-			3.74	0.72
Opisthobranchia	-	-	-	-	-	-	-	0.93	2.4	-	-
Cowies	-	-	-	-	-	-	-	8.22	8.08		
Cnidaria	-	-	-	-	-	-	-			12.15	5.55
Hydroza	6	0.3	-	-	-	-	-			2.8	1.86
Opisthobranchia	-	-	-	-	-	-	-			0.93	2.4
Cowies	-	-	-	-	-	-	-	8.22	8.08		
Cnidaria	-	-	-	-	-	-	-			12.15	5.55
Hydroza	6	0.3	-	-	-	-	-			2.8	1.86
Actiniaria	-	-	-	-	-	-	-			0.93	0.96
Zoanthidea	-	-	-	-	-	-	-			0.93	0.06
Alcyonacea	20	-	9.4	0.92	2	0.732	7.1			7.48	2.34
Polychaeta	18	10.8	27.1	3.64	7.9	0.787	7.6	21.92	15.69	28.04	15.11
Errantia	16	10.3	-	-	-	-	-	6.85	8.25	1.87	1.08
Sedentaria	2	0.5	-	-	-			1.37	0.19	0.93	1.08
Unidentified polychaeta	-	-		-	-			13.7	6.1	25.23	12.95
Sipuncula	-	-	2.3	0.41	0.4	1.148	1.4			4.67	1.56

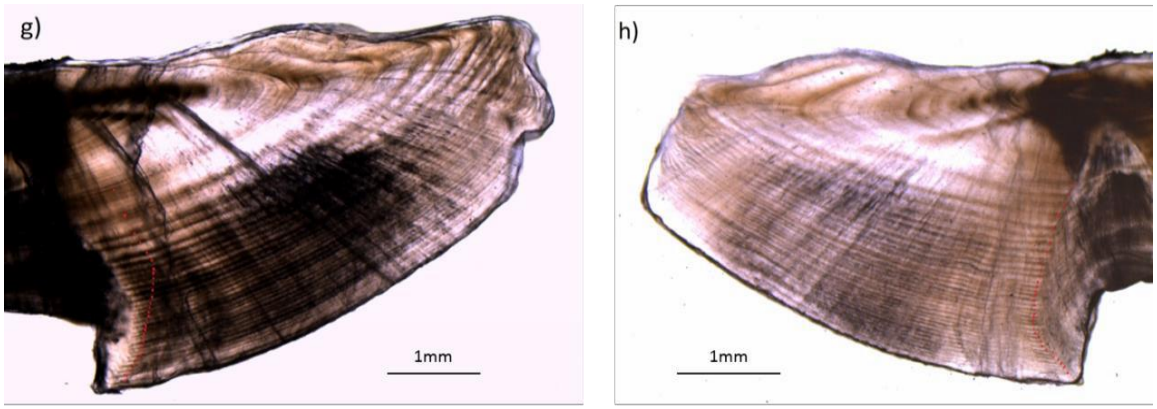
Appendix 2.1: Continued

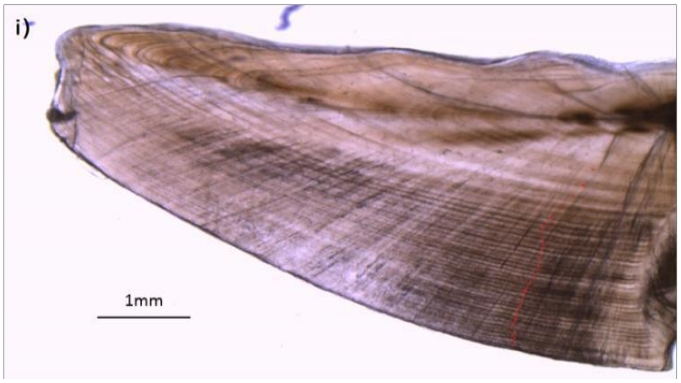
Sources	Le Chanteur and Griffiths 2003		Trow 1982					Present paper			
Areas	False Bay		Transkei and Algoa Bay					False Bay		Struisbaai	
	%FO	*%V*	*%FO*	*V*	*%V*	*M*	*%*	*%FO*	*%V*	*%FO*	*%V*
Turbelllaria	-	-	-	-	-	-	-	1.37	2.25		
Nemertea	-	-	2.9	2.03	4.4	0.088	0.8	4.11	1.03		
Bryozoa	2	<0.1	22.3	3.66	7.9	1.079	10.4	1.37	0.38	0.93	1.44
Insecta	-	-	3.5	0.07	0.1	0.006	0.1	-	-		

2.9.2. Appendix 2.2

Appendix 2. 2:Images of otoliths with rings counts denoted by red dots and the nucleus by red cycle. (a) 0 year, (b) 1year, (c) 5years, (d) 10 years, (e) 15years, (f) 25years, (g) 31years, (h) 36 years and (i) 37years.







2.9.3. Appendix 2.3

Appendix 2. 3:Combined age-length key for male, female and hermaphroditic *B. inornata*.

FL(mm)	Age(years)																																
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	21	22	23	24	25	26	27	28	29	31	32	33	34	36	37
130-139	2																																		
140-149	3																																		
150-159		9	5	1																															
160-169		10	15	1	1																														
170-179		7	26	15	1																														
180-189		2	19	10	6	5	2																												
190-199			14	17	10	5	4	2	2	1			1	1		1	1																		
200-209			4	12	4	7	5	2	1	1	3			2	1	2	4	2				1							1	1	1				
210-219			1	2	8	4	5	4	2	4	1	1	5	3	2	6	4		2	1	1	1	2	2		1						2			
220-229			1	1	2	1	3	5	5	4	3	3	4	4	4	4	1		1	1	1		1				2		1			1		1	
230-239					1	2	2	1	2	1	1	2	4	6	4	2	1		1		1		1		1			1		1			1		1
240-249											1			1	1				1																
250-259															1						1				1			1							

2.9.4. Appendix 2.4

Appendix 2. 4: Comparison of growth and maturity values of Sparidae species, estimated for different regions of the world, grouped by taxonomic clade proposed by Santini *et al*. 2014.tmax= maximum age (years), L_{max}= Maximum fork length (mm), L∞= theoretical asymptotic length (mm), K, t_0 von Bertanffy growth parameters, L50 = FL Species	Sex	Tmax	Lmax	L∞	K	t0	L50	L50/L∞	t50	t50/tmax	Φ`	Santini *et al.* 2014	Locality	Reference
Dentex maroccanus	Females	-	405	330	0.2	-0.5	130	39%	2	-	4.33	A1	Atlantic, Algeria	Mohdeb and Kara 2015
Dentex macrophthalmus	Females	38	608	309	0.06	-5.43	166	54%	7.7	20%	4.33	A1	Atlantic, Angola	Potts *et al.* 2010
Pterogymnus laniarius	Combined	16	405	379	0.13	-1.78	257	68%	5.2	33%	4.27	A2	South Africa	Booth and Buxton 1997
Petrus rupestris	Combined	33	1300	1223	0.37	-0.75	575	47%	7.2	22%	5.75	A2	South Africa	Mann 2013
Polystegonus undulosus	Combined	20	900	832	0.22	-0.17	700	84%	8.8	44%	5.28	A2	South Africa	Mann 2013
Cymatoceps nasutus	Combined	45.5	1099	1089	0.05	2.88	530	49%	10	22%	4.77	A2	South Africa	Mann 2013
Chrysoblephus cristiceps	Combined	22	655	655	0.08	-2.35	365	56%	7.7	35%	4.54	A2	South Africa	Mann 2013

Argyrozona argyrozona	Combined	30	720	623	0.08	-1.96	292	47%	4	13%	4.49	A2	South Africa	Mann 2013
Chrysoblephus puniceus	Female	11	522	406	0.18	-2.25	240	59%	2.5	23%	4.48	A2	South Africa	Mann 2013

Appendix 2.4: Continud.

Species	Sex	tmax	Lmax	L∞	K	t0	L50	L50/L∞	t50	t50/tmax	Φ`	Santini *et al.* 2014	Locality	Reference
Chrysoblephus laticeps	Combined	17	512	425	0.14	-1.69	172	41%	2.5	15%	4.42	A2	South Africa	Mann 2013
Chrysoblephus gibbiceps	Combined	48	675	430	0.11	-3.79	249	58%	3.9	8%	4.31	A2	South Africa	Mann 2013
Chrysoblephus anglicus	Combined	17	720	650	0.08	-1.85	360	55%	7	41%	4.55	A2	South Africa	Mann 2013
Argyrops spinifer	Combined	25	630	524	0.22	-0.44	267	51%	2.4	10%	4.78	A3	Arabian Gulf	Grandcout *et al.* 2004
Dentex dentex	Females	28	900	771	0.1	-2.87	311	40%	3	11%	4.78	A3	Mediterranean, Spain	Morales-Nin and Moranta 1997
Dentex gibbosus	Combined	16	900	911	0.14	-0.11	-	-	-	-	5.09	A3	Atlantic Islands, Canary	Pajuelo and Lorenzo 1995
Pagrus pagrus	Combined	17	819	576	0.14	-0.99	204	36%	-	-	4.67	A3	Atlantic Islands, Canary	Pajuelo and Lorenzo 1996
Cheimerius nufar	Combined	22	675	839	0.06	-2.16	250	30%	3.5	16%	4.66	A3	South Africa	Mann 2013
Pagrus Auriga	Combined	18	837	714	0.08	-1.49	348	48%	-	-	4.61	A3	Atlantic Islands, Canary	Pajuelo *et al.* 2006

Appendix 2.4: Continud.

Species	Sex	tmax	Lmax	L∞	K	t0	L50	L50/L∞	t50	t50/tmax	Φ`	Santini *et al.* 2014	Locality	Reference
Pagellus erythrinus	Combined	-	630	270	0.2	-1.62	-	-	-	-	4.17	A3	Atlantic, Portugal	Coelho *et al.* 2010
Calamus proridens	Combined	10	297	306	0.25	-1.69	132	43%	1	10%	4.36	B1	Atlantic, Mexico	Tyler-Jedlund 2009
Archosargus probatocephalus	Combined	26	622	490	0.26	-0.42	-	-	-	-	4.79	B1	Atlantic, USA	Dutka-Gianelli and Murie 2001
Calamus nodosus	Combined	17	414	461	0.17	-0.87	-	-	-	-	4.56	B1	Atlantic, USA	Horvath *et al.* 1990
Spondyliosoma cantharus	Combined	10	630	390	0.24	-0.11	156	40%	2	20%	4.56	B2	Atlantic Islands, Canary	Pajuelo and Lorenzo 1999
Sarpa salpa	Combined	6	405	224	0.55	-0.51	145	65%	1.9	32%	4.44	B2	South Africa	Mann 2013
Boopsboops	Combined	16	274	252	0.22	-1.42	141	56%	2	13%	2.14	B2	Atlantic, Portugal	Monteiro *et al.* 2006
Spicara smaris	Females	7	180	128	0.92	-3.52	-	-	-	-	4.18	B2	Mediterranean, Greece	Vidalis and Tsimenidis 1996
Spicara maena	Combined	8	270	223	0.53	-0.08	-	-	-	-	4.42	B2	Adriatic sea	Dulčić *et al.* 2000
Lithognathus lithognathus	Combined	30	1238	1283	0.1	-0.22	585	46%	6	20%	5.25	B3	South Africa	Mann 2013
Pachymetopon blochii	Combined	12	486	538	0.09	-0.43	202	38%	4	19%	4.44	B3	South Africa	Mann 2013

Appendix 2.4: Continud.

Species	Sex	tmax	Lmax	L∞	K	t0	L50	L50/L∞	t50	t50/tmax	Φ`	Santini *et al*. 2014	Locality	Reference
Lithognathus aureti	Combined	50	800	846	0.08	-2.76	495	59%	9.7	19%	4.79	B3	South Africa	Mann 2013
Boopsoidea inornata	Combined	37	310	223	0.29	-3.58	183	82%	1.87	5%	4.16	B3	South Africa	This study
Pachymetopon aeneum	Combined	12	540	467	0.13	-0.24	225	48%	5	42%	4.46	B3	South Africa	Mann 2013
Lithognathus mormyrus	Combined	12	335	360	0.19	-0.94	196	54%	3	25%	4.4	B4	South Africa	Mann 2013
Sparus sarbs	Combined	-	-	375	0.16	-	-	-	-	-	4.35	B5	Arabian Gulf	El-Agamy 1989
Rhobdosargus sarba	Combined	16	720	745	0.16	-0.99	234	31%	2.5	16%	4.44	B5	South Africa	Radebe *et al.* 2002
Sparus aurata	Combined	-	630	538	0.15	-1.71	-	-	-	-	4.63	B5	Adriatic Sea	Kraljević and Dulčić 1997
Pagellus acarne	Combined	8	378	297	0.22	-0.87	175	59%	3	38%	4.28	B5	Atlantic Islands, Canary	Pajuelo and Lorenzo 1999
Sparodon durbanensis	Combined	31	1029	1021	0.09	-0.7	350	34%	5.4	17%	4.97	B5	South Africa	Mann 2013
Pagellus bogaraveo	Females		738	446	0.1	-2.29	-	-	-	-	4.29	B5	South Africa	Chilari *et al.* 2006 and Micale *et al.* 2002

Appendix 2.4: Continud.

Species	Sex	tmax	Lmax	L∞	K	t0	L50	L50/L∞	t50	t50/tmax	Φ`	Santini et al. 2014	Locality	Reference
Acanthopagrus bifasciatus	Combined	21	450	325	0.23	-2.2	219	67%	2	10%	4.39	B6	Arabian Gulf	Grandcout *et al.* 2004
Acanthopagrus vagus	Combined	16	675	500	0.07	-2.99	207	41%	3.6	23%	4.27	B6	South Africa	Mann 2013
Acanthopagrus australis	Combined	-	693	266	0.51	-0.32	-	-	-	-	4.55	B6	Pacific, Australia	Pollock 1982
Acanthopagrusberda	Combined	14	675	500	0.07	-2.99	225	45%	5.6	40%	4.27	B6	South Africa	James *et al.* 2003
Acanthopagrus butcheri	Females	-	540	545	0.04	-5.21	-	-	-	-	4.09	B6	Australia	Morison *et al.* 1998
Pchymetopon gronde	Combined	38	572	461	0.15	-1.64	300	65%	5.5	14%	4.51	B7	South Africa	Mann 2013
Diplodus vulgaris	Combined	14	379	250	0.4	-0.34	159	64%	-	-	4.39	B7	Atlantic, Portugal	Gonçalves *et al.* 2003
Diplodus cervinus hottentotus	Combined	33	480	397	0.14	-2.14	280	71%	6	18%	4.36	B7	South Africa	Mann 2013
Diplodus sarguscapensis	Combined	21	360	309	0.24	-1.04	160	52%	3	14%	4.37	B7	South Africa	Mann 2013
Spondyliosoma emarginatum	Females	8	312	289	0.22	-3.82	235	81%	3	37%	4.26	-	South Africa	Fairhurst *et al.* 2007

CHAPTER 3

Parasite communities of *Boopsoidea inornata*

Abstract

A preliminary survey of parasites infecting *Boopsoidea inornata* from four localities in South Africa was conducted. One hundred and fifty *B. inornata* were collected from False Bay, Struisbaai, Goukamma and Port Elizabeth during 2014 to 2015. Nineteen parasite taxa were found infecting *B. inornata* across all localities. Six of these were identified to class level: five belonging to trematode digenean metacercariae: Hemiuridae, Diplostomidae, Digenean "tetracotyle" metacercaria, two belonging to unidentified metacercaria and one to Cestoda. Thirteen parasites were identified to genus level: the trematode *Stephanostomum* sp., monogenean *Pricea* sp. and *Diplozoon* sp., nematodes *Anisakis* sp. and *Cucullanus* sp., copepods *Hatschekia* sp., *Nothomobolochus* sp., *Clavellissa* sp. and *Nerocila* sp., myxozoans *Kudoa* sp. and *Davisia* sp. and the protozoan *Goussia* sp. *Stephanostomum* sp. infected the gill arches at an overall prevalence of 61%, the unidentified digenean metacercaria-2 infected the kidney and musculature of 59% of fish, the unidentified digenean metacercaria-1 infected the heart of 47% of the sample and the nematode *Anisakis* sp. infected the gonads, liver, body cavity and stomach of 25% of *B. inornata* sampled. Results indicate that no significant difference in parasite assemblage among size classes, age classes and sex, overall and within localities. There was a significant difference in species diversity between individual hosts from False Bay and Struisbaai. The Shannon- Wiener index showed a low species diversity, peaking at just 1.12 species in Struisbaai. Goukamma and Port Elizabeth showed no significant difference in diversity with a Shannon-Wiener value peaking at 2.0 in Goukamma. Discriminant function analysis (DFA) showed an overall correct classification rate of 66% with the highest probability of correctly predicting the origin of *B. inornata* based on parasite assemblage being in False Bay where 73% accuracy was observed. Results showed significant spatial differences in parasite assemblages.

3. Introduction

Globally parasites comprise over 30% of all species amongst identified animal phyla (De Meeûs and Renaud 2002). They are an important component of ecosystems contributing to biodiversity and food web connectivity in surprising ways that are constantly being discovered as research in this field grows. South Africa is well known for its highly diverse marine environment with more than 13000 marine species described from around the country (Griffiths *et al.* 2010). Amongst these, very few parasite species are listed, and infact were totally ommited from the South African list of 'Census of Marine Life' survey that took place nine years ago. The efforts of South African marine parasitologists during the last eight years have estimated the number of marine fish parasite taxa to only about 311 (Irfan Nunkoo pers. comm. 2019).

Reviewing the history of discovery of marine fish parasites in South Africa, Smit and Hadfield (2015) showed that research on marine parasites has steadily increased over the last 200 years. The first description of a marine parasite was completed by Leach (1818) who described the parasitic isopod, *Anilocra capensis* from hottentot *Pachymetopon blochii* off Cape Point (Smit and Hadfield 2015). Subsequently K.H. Barnard (1914a, 1914b, 1920, 1925a, 1925b,1926, 1948, 1955a, 1955b, 1957), H. B. Fantham (1918, 1919, 1930, 1938) and Rodney Bray (1974, 1978,1983, 1984, 1985, 1986a, 1986b, 1987, 1990, 1991) were amongst early pioneering researchers who made a lot of progress into exploring marine parasite diversity in South Africa. These authors laid the path for future marine parasitological taxonomists in South Africa and who have since dominated research in this field. As a result, the majority of research conducted in marine fish parasitology in South Africa has focused on taxonomy, with well known taxonomists such as Hadfield *et al.* (2014 a, b), Smit and Davies (2001, 2004, 2005 and 2006), and Dippenaar and Olivier (1999 and 2004), to mention just a few, contributing largely to our current knowledge on the diversity of marine fish parasites in South Africa.

Despite the efforts of taxonomists, very few records exist for studies examining entire parasite communities, associated with specific marine fish hosts, and throughout their distribution range

in South Africa. Equally few studies have examined the ecological and physiological effects of parasites within marine ecosystems in South Africa (Reed 2015). The first publication describing some aspects of metazoan parasite fauna infecting a single host species in South Africa was by Payne (1986). This author recorded a number of conspicuous parasites infecting th commercially valuable fish species, South African kingklip (*Genypterus capensis*), including the large parasitic copepod *Sphyrion laevigatum* that has intrigued fishermen for decades. Several years later González and Moreno (2005) and González *et al.* (2006) studied patterns of ecto- and endoparasitic fauna infecting the false jacopever or Cape redfish *Sebastes capensis* within its distribution range in the Northern and Southern Hemispheres. Yeld and Smit (2006) studied biogeographical variation in parasites communities associated with two species of cat shark *Haploblepharus pictus* and *H. edwardsii* around the coast of South Africa. These authors examined spatial and temporal variation in parasite communities infecting these sharks around the coast of South Africa which included the discovery of a new trypanosome species, *Trypanosoma haploblephari* infecting the blood of the sharks.

Several years later a series of publications focused on parasites of marine commercial fishes and their use as biological tags for stock discrimination started to appear. Reed *et al.* (2012) conducting the first survey of parasites infecting South African sardine, (*Sardinops sagax*) in an attempt to identify suitable parasites for use as biological tags. The use of parasites as biological tags has successfully been implemented in many parts of the world (Mackenzie and Abaunza, 1998; Timi, 2007; Mackenzie and Hemmingsen 2015) but had yet to be attempted in South Africa. The basis of this applied method of parasitology lies in understanding parasite communities associated with fish species throughout their distribution ranges. In South Africa, the first attempts of using this method coincided, in most cases, with the first surveys of parasite communities infecting marine commercial fishes.

Soon after Reed *et al.* (2012), Le Roux (2013) studied parasite communities of Cape horse mackerel (*Trachurus capensis*) from the coasts of South Africa and Namibia. The results of this study revealed significant differences between parasite assemblages infecting these fishes living in the northern and southern Benguela. Bowker (2013) followed on from this study to investigate

parasite assemblages of two species of mackerel (*Trachurus trecae* and *T. capensis*) in the northern and southern Benguela ecosystem, showing significant differences in parasite assemblages between *T. trecae* and *T. capensis* within the northern Benguela, and between small and large *T. capensis* and immature males and females within the same species in the northern and southern Benguela. Morris *et al.* (2015, 2016) examined different aspects of spatial variation in the parasite's assemblage of *Callorhinchus capensis* (St Joseph shark) from several localities along the west coast of South Africa. Both studies found that the component community of parasites infecting this species of shark included a high prevalence of the cestode *Gyrocotyle plana* infecting the spiral valve, and two species of monogeneans infecting the gills, *Callorhynchicotyle callorhynchi* and *Callorhinchicola multitesticulatus.* These studies also identified few spatial variations occurring amongst parasite assemblages between localities with an apparent close evolutionary relationship between *G. plana* and *C. capensis*. Kohler (2015) surveyed the parasite community of short-nose spiny dogfish *Squalus acutipinnis* from the west, south and east coasts of South Africa, and examined their suitability as indicators for trace metal concentrations. She recorded very few parasites, with only two species found infecting these sharks (*Anisakis* sp. and *Sphytius* sp.). These parasites were not suitable as heavy metal bio-indicators because of their low abundance. van der Lingen *et al.* (2015) and Weston *et al.* (2015) confirmed that parasite biotags can be used for stock discrimination of *Sardinops sagax* of the west and south coast of South Africa. Additionally, Nunkoo *et al.* (2016) surveyed metazoan parasites of snoek (*Thyrsites atun*) off South Africa and reported 16 parasite taxa including nine new host records and four new locality records. He also identified the myxozoan *K. thyrsites*, nematode *Anisakis* sp., copepod *N. fradei*, and cestode *M. uncinatus* as potential biological tags. Nunkoo *et al.* (2017) described the first ever record of metazoan parasite fauna from oilfish *Ruvettus pretiosus* Cocco, 1829 (Perciformes: Gempylidae) in South African waters and most recently Mackintosh *et al.* (2018) described the macroparasites of angelfish *Brama brama* (Bonnaterre, 1788) in the southern Benguela Current ecosystem.

The importance of understanding parasite communities associated with fishes of commercial value in Africa was emphasised by Reed (2015) who reviewed parasite studies of commercially

important marine fishes in sub-Saharan Africa (e. g. Senegal, Nigeria and South Africa). Her review discussed how parasite data could contribute to the improvement of fisheries management and stock assessment studies. Also, that parasite data can act as indicators of environmental pollution as well as provide clues to the condition of fish hosts under certain pressures. Parasites are not only useful indicators in fish stock assessments. For instance, pollution can increase parasitism when it negatively affects host defence mechanisms which leads to increased host susceptibility or by simply increasing the population densities of suitable intermediate and final hosts (Marcogliese 2002). In addition, parasites are often more sensitive to variations in the environment than their hosts and could themselves be affected by certain pollutants with their absence being an indication of disturbance to a particular environment. Thus, many papers have described the effects of anthropogenic impacts on parasite communities (Mackenzie *et al.* 1995, Williams and Mackenzie 2003).

In South Africa, a number of studies have examined use of fish parasites as early warning systems for heavy metal pollution, especially in freshwater systems (Retief *et al.* 2006). One study is known from the marine environment. Morris *et al.* (2016) investigated parasites as early warning systems for heavy metal pollution in two species of shark in South Africa. Concentrations of metals were found in the tissue of the parasite *Gyrocotyle plana* infecting the spiral valve of *Callorhinchus capensis* and the nematode *Proleptus obtutsus* infecting the stomach of *Rhinobatos annulatus* and *Rhinobatos blochii*. Arsenic, manganese, lead, titanium and zinc showed accumulation in *G. plana* and at magnitudes higher than those in surrounding environment and ranging between 2 to 6 times the concentration of the surrounding host`s tissues.

Including parasite data in fish biology studies is an important component that has been ignored in the past. Knowing the details of parasite species associated with a particular fish host not only improves our understanding of parasite diversity, but also contributes to an improved understanding of host-parasite relations. These may contribute to better understanding host biology, ecology, endemism, distribution and susceptability to environmental change.

3.1 Parasites of Sparidae in South Africa

Not many fishes from the family Sparidae have been surveyed for parasitic infection in South Africa. A few records exist of parasites documented sporadically, some of which are listed in (Table. 3.1). The parasite fauna of the South African endemic sparid, *B. inornata* has not yet been surveyed.

Table 3.1: Some common parasites recorded from Sparidae in South Africa

Parasite class	Parasites species	Host in South Africa	Site of infection	Locality	Reference
Trematoda	*Cotylogaster basiri*	*Rhabdosargus sarba*	Rectum	Durban, Kwazulu-Natal	Bray (1984)
Trematoda	*Elstia stossichianum*	*Sarpa sarpa*	Intestine	Durban, Kwazulu-Natal	Bray (1984)
Trematoda	*Steringotrema pagelli*	*Spondyliosoma emarginatum*	Intestine	Algoa Bay, Eastern Cape	Bray (1984)
Trematoda	*Pseudaephnidiogenes rhabdosargi*	*Rhabdosargus sarba*	Stomach	Durban, Kwazulu-Natal	Bray (1985)
Trematoda	*Pachycreadium obovatum*	*Sparodon durbanesis*	Intestine	Blue Hole, Port Elizabeth	Bray (1987)
Trematoda	*Allopodocotyle recifensis*	*Pterogymunus laniarius*	Intestine	Cape Recife	Bray 1987
Trematoda	*Helicometra fasciata*	*Pachymetopon blochii*	Intestine	Blue Hole, Port Elizabeth	Bray (1987)
Branchiura	*Argulus kosus*	*Sarpa salpa*	Skin of dorsal fin	Kosi Bay	Avenant-Oldewage (1994)
Isopoda	*Anilocra capensis*	*Pachymetopon blochii*	Above operculum, posterior-dorsally to the eyes	False Bay	Wright et al. (2001)

3.2 Aims of this Chapter

This chapter describes the parasite fauna associated with *B. inornata* from four localities in South Africa (False Bay, Struisbaai, Goukamma, Port Elizabeth) and provides basic infection statistics, the effect of fish size, age and sex on parasitic infection, and investigates spatial and temporal variation in infections between these four localities.

3.3 Methods

3.3.1 Sample Collection and Processing

150 specimens of *Boopsoidea inornata* were collected from False Bay, Struisbaai, Goukamma and Port Elizabeth and examined for parasites from April 2013 to June 2015 (Table 3.2). These consisted of subsamples of four fish per sampling event from the total sample size (see chapter 2). Samples were collected monthly in Struisbaai and False Bay over a one-year period (except in Struisbaai for January 2015 and False Bay in November 2014 due to difficult sampling conditions). Samples were also collected simultaneously on the 28th April 2014 in both Goukamma and Port Elizabeth (Table 3.2)

Table 3.2: Sample locations of *B. inornata* collected for parasitological analyses off South Africa from 2013 to 2015.

Location	Dates caught	Number of fishes per sample
False Bay	24-July-2013 to 20-June-2014	43
Struisbaai	4-April-2013 to 28-June-2014, February 2015	62
Goukamma	28-April-2014	22
Port Elizabeth	28-April-2014	23

Subsequent to collection, *B. inornata* individuals were kept on ice, bagged, labelled and transported to the Department of Biological Sciences laboratory at the University of Cape Town for storage and later dissection. All samples were frozen at -20^{0}C and allowed to thaw to room temperature prior to dissection. Once thawed, every *B. inornata* was measured (FL, cm) weighed (g) and sexed as per methods in Chapter two.

All external surfaces (skin, fins) were closely examined for the presence of parasites. Gills, eyes and viscera were removed, placed in Petri dishes and examined for parasites using a Leica EZ34 dissecting microscope (magnification 10x to 63x).

The body cavity and internal organs (heart, liver, stomach wall, intestine, gonads, kidney, musculature and spleen) were seperated and studied by naked eye for, encysted or encapsulated parasites. The heart, liver, stomach wall, intestine, gonads, kidney, musculature and spleen were examined by preparing a wet, temporary mount from a small piece of tissue on a microscope slide from each organ and viewed a using compound microscope (Leica DM750) at 400x -1000x magnification.

Any parasites observed and collected were preserved in 10% formalin or in 70% ethanol. Micrographs were taken using a compound microscope (Leica DM750 at 400x -1000x magnification) or a Nikon DS Camera Control Unit DS-5m Camera head in combination with a Nikon stereoscopic Zoom Microscope SMZ 1500. Most parasites were identified to the genus level by expert parasitologist, Dr Ken MacKenzie from the University of Aberdeen in Scotland.

3.3.2 Data Analysis

The level of parasitic infection was quantified by using prevalence, mean intensity and mean abundance according to Bush *et al.* (1997), where “prevalence” is the proportion of infected hosts among all the hosts examined (Eq. 1), “the mean intensity” is the mean number of parasites found infected a single host (Eq. 2) and “the mean abundance” is the mean number of particular parasite individuals in a sample of infected hosts (Eq. 3).

$$Prevalence = \frac{Number\ of\ hosts\ infected\ of\ particular\ parasite\ sp}{Number\ of\ hosts\ examind\ for\ that\ parasite\ sp.} \quad \text{Eq.1}$$

$$Mean\ intensity = \frac{The\ total\ number\ of\ parasites\ of\ particular\ host\ sp}{Number\ f\ hoats\ infected\ with\ that\ parasite} \quad \text{Eq.2}$$

$$Mean\ abundance = \frac{The\ total\ number\ of\ parasite\ of\ particular\ host\ sp}{Total\ number\ of\ hosts\ (infected+unifected)} \quad \text{Eq.3}$$

A categorical scale was necessary to use as some parasites identified were too small and too numerous to count using the compound microscope. The geometric mean was calculated for each of these categories (Table 3.3; Eq 4).

Table 3. 3: Categorical scale used to indicate the relative estimate of parasites found.

Scale	Number of parasites in field of view	Geometric mean for each range
X0	0	0
X1	1 to 10	3.16
X10	11 to 100	33.1
X100	101 to 1000	317.8

The Geometric mean was used to compare different items, with each item having multiple properties and different numerical ranges.

Geometric mean= $\sqrt[N]{a_1 a_2 a_3 \dots \dots a_N}$ Eq.4

3.3.3 Multivariate Analyses

Differences in parasite assemblages identified between localities were analysed using Primer 6, version 6.1.5 software package. A square-root, transformed to prevent super-abundances, and a Bray-Curtis similarity coefficient was used to calculate a resemblance matrix, which formed the basis of a multi-dimensional scaling (MDS) plot to analyse differences between the four localities (Port Elizabeth, Goukamma,, Struisbaai and False Bay) overall, between False Bay and Struisbaai, and between the four localities during autumn only because two of the four localities (Goukamma and Port Elizabeth) were sampled in autumn only.

A one-way Analysis of Similarities (ANOSIM) test was used to separately test for the differences in parasite assemblage between size class, age class and between sexes amongst the four localities (Port Elizabeth, Goukamma, Struisbaai and False Bay) overall, between False Bay and Struisbaai, and between the four localities during autumn only. The significance of infections amongst different size classes and age classes were tested using One- and Two-way ANOSIM, this was then repeated for differences in parasite assemblage between annual collections in False Bay and Struisbaai between season sex and size class.

Species accumulation curves (SACs) were used to determine how parasite communities inter act the region of study and evaluate species richness in the different regions. The Shannon-Wiener diversity index was used to measure species diversity per fish infected among sampling locations using just the number of known parasite assemblage not parasites counted by categorical scale (Table 3.3).

The most prevalent parasite species were selected for use in Discriminant Function Analysis (DFA), to classify between *B. inornata* from four regional groups as was conducted by Melendy *et al.* (2005) and McClelland and Melendy (2011).

3.4 Results

150 *Boopsoidea inornata* were collected from four locations in South Africa and examined for parasitic infections from 2013 to 2015. Overall fish size ranged from 139 to 270 mm, and were grouped into three size classes, small (139-199 mm), medium (200-219 mm) and large (220-270 mm). Fish age ranged from 0 to 33 years and they were classified into three groups: young (0-4 years), medium (4-10 years) and old (11-33 years). A 102 samples were discarded because they failed to meet the criteria outlined in section 2.5.5 in chapter 2. (Table 3.4).

Table 3.4**:** Location, number, size and age ranges of *Boopsoidea inornata* samples collected in South Africa from 2013 to 2015 (48 = total sample size). N = sample size.

Location	N	Age range (Years)	Size range (FL)	Overall Prevalence of parasites
False Bay	18	0 to 4	149-231	84% (36/43)
Struisbaai	13	2 to 33	193-231	95% (59/62)
Goukamma	7	6 to 31	189-238/	100% (22/22)
Port Elizabeth	10	5 to 22	185-219	100% (23/23)

Amongst the 150 samples of *B. inornata* examined, 129 were infected by parasites (86% prevalence) with 19 parasitic species recorded in total. Due to the difficulty of identifcation of these parasites and the general lack of information available of marine parasite diversity in South Africa, 13 of the parasite taxa collected were identified to genus level and six to class level (Table 3.5) (Figures 3.1 to 3.4). The most prevalent parasite taxa amongst all samples were the digeneans, with *Stephanostomum* sp. (61%) found infecting the gills, unidentified digenean metacercaria-2 (59%) found infecting the kidneys and muscle and unidentified digenean metacercaria-1 (47%) found infecting the heart.

Amongst fish examined from False Bay, overall prevalence was 84% (36/43) and ten parasites taxa were found. The most prevalent parasites were the unidentified digenean metacercaria-1 (56%) digenean metacercaria-2 (33%) and digenean “tetracotyle”- metacercaria (23%). Overall 95% (59/62) of fish examined from Struisbaai were infected by parasites, with 12 parasite taxa identified. Again, the most prevalent parasite taxa were the digeneans *Stephanostomum* sp. (81%) unidentified digenean metacercaria-2 (60%) and unidentified digenean metacercaria-1 (40%). Among fish examined from Goukamma, 100% (22/22), were infected by parasites and ten parasite taxa were found. The most prevalent parasite were the digeneans *Stephanostomum* sp. (95%) unidentified digenean metacercaria-2 (77%) and a nematode from the genus *Anisakis* sp. (77%). Twenty-three fish were examined from Port Elizabeth, all of which were by infected parasites (100%). Twelve parasite taxa were identified, and the most prevalent parasites were

unidentified digenean metacercaria-2 (91%), *Stephanostomum* sp. (74%) and a coccidean from the genus *Goussia* sp. (61%).

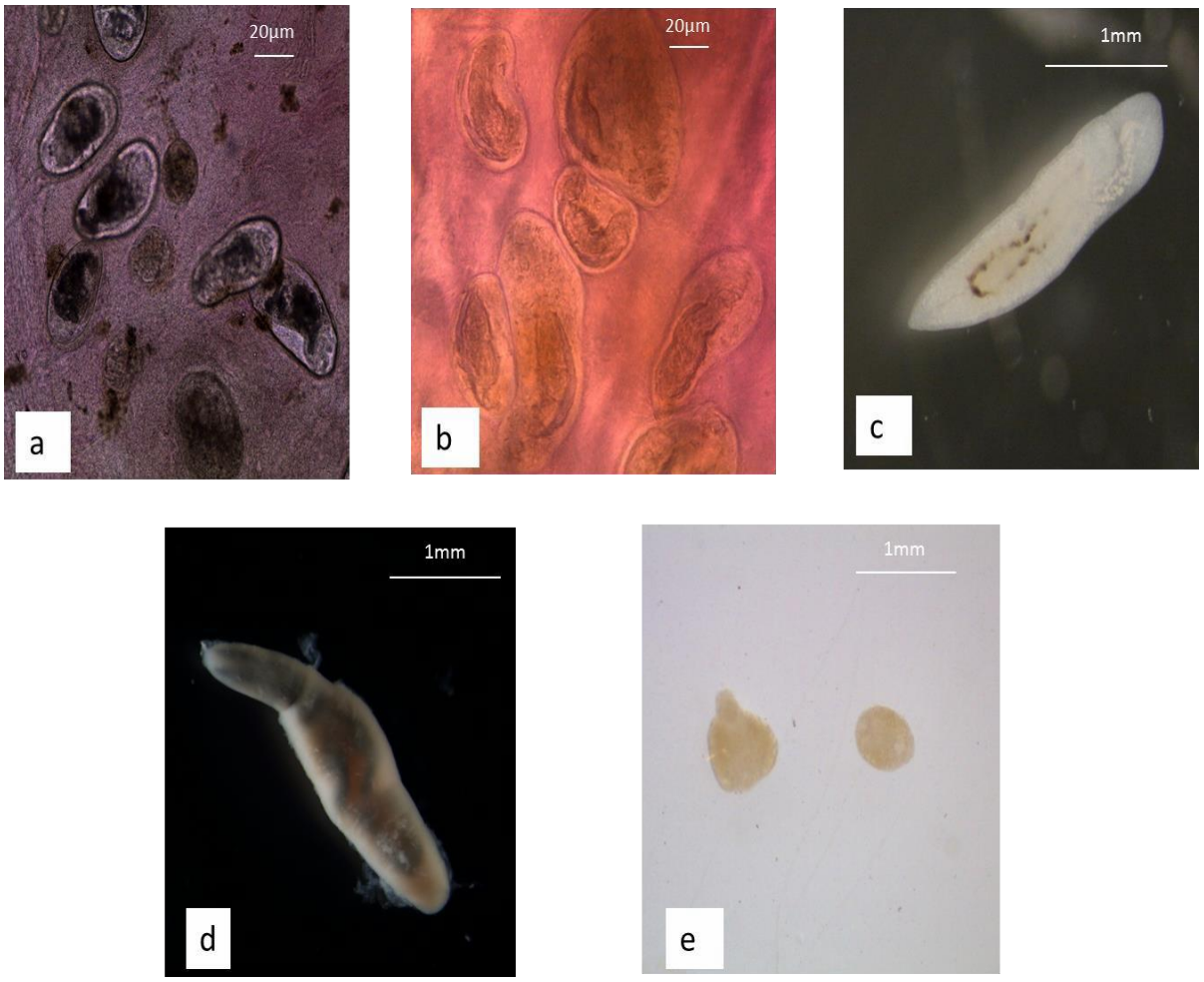


Figure 3.1: Trematoda species observed in organs of *B. inornata* collected off South Africa (2013 to 2015) : (a) unidentified digenean metacercariae-2 found in the kidney, (b) unidentified digenean metacercariae-1 found in the heart. (c) diplostomid larvae found in the eyes (only found in Struisbaai) (d) hemiurid larvae found in the gills (only found in Port Elizabeth). (e) digenean "tetracotyle" metacercaria found in the eyes.

Table 3. 5: Parasites species found infecting *Boopsoidea inornata* (n=150) from False Bay, Struisbaai, Goukamma and Port Elizabeth (2014 and 2015) including body location, prevalence (P %), mean intensity (MI) and mean infection abundance (MA).

Class	Species	Body location	False Bay (n=43)			Struisbaai (n=62)			Goukamma (n=22)			Port Elizabeth (n=23)		
			P (%)	MI	MA	P (%)	MI	MA	P(%)	MI	MA	P(%)	MI	MA
Monogenea	Diplozoon sp.	Gills	-	-	-	-	-	-	4.55	1	0.05	8.7	1.5	0.13
	Pricea sp.	Gills	-	-	-	1.61	2	0.03	-	-	-	-	-	-
Trematoda	Diplostomid larvae	Eyes	-	-	-	1.61	1	0.02	-	-	-	-	-	-
	Hemiurid larvae	Gills	-	-	-	-	-	-	-	-	-	4.35	3	0.13
	Unidentified Digenean metacercaria 1	*Heart	55.8	77.4	43.2	40.3	24.1	9.73	45.4	101	45.7	47.8	97.1	46.4
	Unidentified Digenean metacercaria 2	*Kidney - *Muscle	32.5	25.6	8.3	59.6	41.2	24.6	77.2	262	203	91.3	111	101
	Digenean “tetracotyle”-metacercaria	Eyes	23.2	1.4	0.33	3.23	1	0.03	-	-	-	8.7	1.5	0.13
	Stephanostomum sp	Gills	9.3	3	0.28	80.6	16.4	13.2	95.45	8.19	7.82	73.9	8	5.91
Nematoda	*Anisakis* sp.	Gonad - liver -Body cavity - Stomach	4.65	4.5	0.21	14.5	1.56	0.23	77.2	7.71	5.95	39.1	2.11	0.83
	Cucullanus sp.	Intestinal	-	-	-	1.61	2	0.03	-	-	-	-	-	-
Copepoda	*Hatschekia* sp.	Gills	-	-	-	-	-	-	9.09	3	0.27	26	2.5	0.65
	Nothomobolochus sp.	Gills	2.33	1	0.02	-	-	-	-	-	-	-	-	-
	Clavellissa sp.	Gills	6.98	1.33	0.09	9.68	1.67	0.16	9.09	1	0.09	17.3	1.35	0.22

Table 3.4: Continued

Class	Species	Body location	False Bay (n=43)			Struisbaai (n=62)			Goukamma (n=22)			Port Elizabeth (n=23)		
			P (%)	MI	MA	P (%)	MI	MA	P(%)	MI	MA	P(%)	MI	MA
Sporozoa	*Goussia* sp. (1)	*Liver	6.98	3.16	0.22	4.84	118	5.71	9.09	160	14.5	30.3	15.9	4.87
	Goussia sp. (2)	*Gonad- Muscle	-	-	-	14.5	6.49	0.94	13.6	3.16	0.43	60.8	38.4	24.4
Malacostraca	*Nerocila* sp.	Caudal fin	-	-	-	-	-	-	4.55	1	0.05	-	-	-
Castoda	Cestoda larvae	Body cavity	-	-	-	-	-	-	-	-	-	13	2	0.26
Myxosporea	*Kudoa* sp.	*Muscle	2.33	3.16	0.07	-	-	-		-	-	-	-	-
	Davisia sp.	*Kidney	2.33	3.16	0.07	-	-	-	-	-	-	-	-	-

*Modal mean infection based on scale in (Table 3.2)

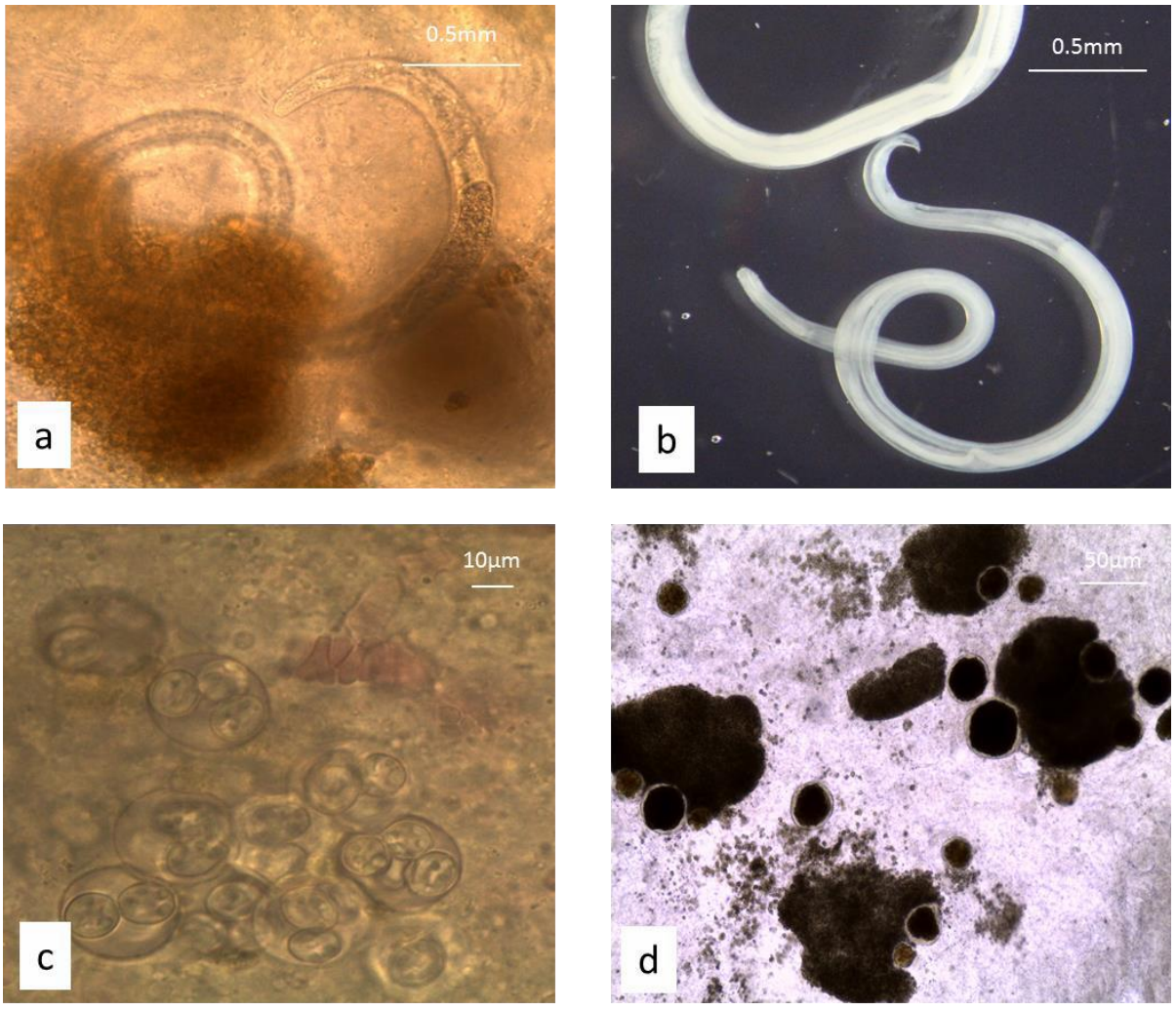


Figure 3.2: Parasitic species observed in organs of *B. inornata* collected off South Africa (2013 to 2015), (a) *Anisakis* sp. found in the liver. (b) *Cucullanus* sp. found in the intestines and found only from Struisbaai. (c) *Goussia* sp. (1) found in the liver. (d) *Goussia* sp. (2) found in the gonads.

Figure 3.3: Parasites species found in *B. inornata*, Copepoda (a) *Hatschekia* sp. found in the gills and (b) *Clavellisea* sp. found in the gills. (c) *Pricea* sp. found in the gills, only from Struisbaai. (d) *Nerocila* sp. found in the tail, only from Goukamma.

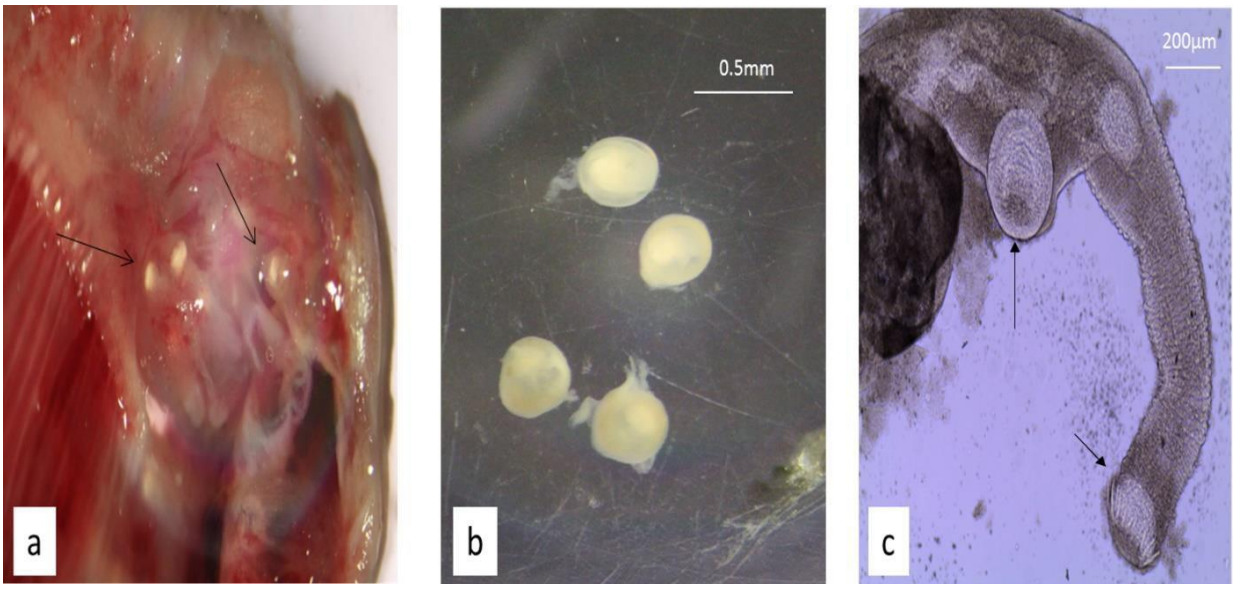


Figure 3.4: Trematoda species observed in organs of *B. inornata* collected off South Africa (2013 to 2015) (a) *Stephanostomum* sp. cysts were observed inside the gill arches (arrows), (b) *Stephanostomum* sp. (oval cysts with fine transparent walls) were isolated from gill arches, (c) ventral view of anterior extremity and ventral sucker of *Stephanostomum* sp (arrows).

The cluster and MDS analysis revealed strong similarity within regional groups (Figure 3.5, a, b), with only False Bay showing some indication of separation. However, the 2D stress factor suggests poor representation of samples.

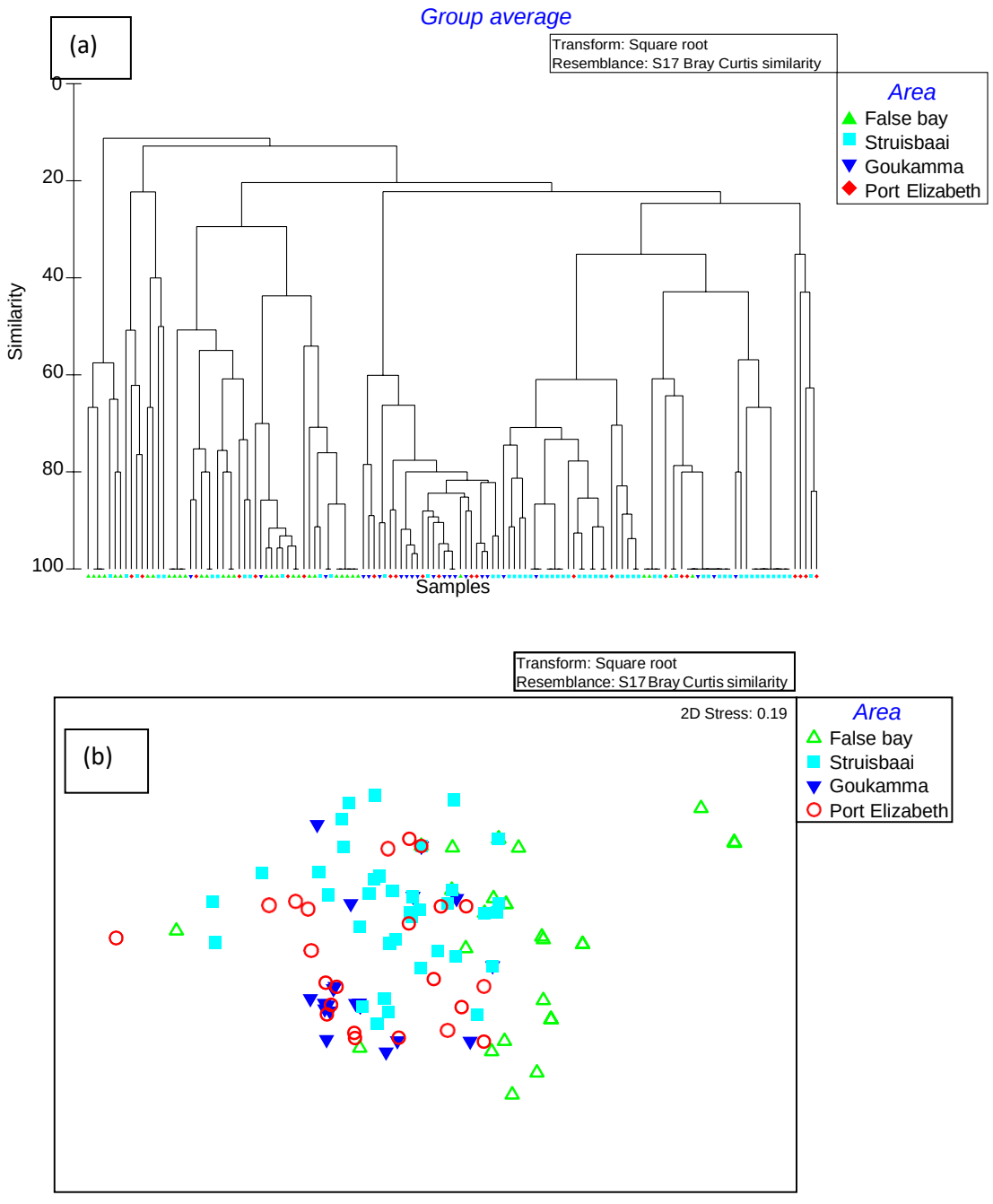


Figure 3. 5: Dendrogam (a) and MDS (b) diagram showing the separation of *B. inornata* from each area on the basis of the parasite assemblage regional groups in South Africa (2013 to 2015).

One and two-way ANOSIM showed that there was a significant difference in parasite assemblages between localities, but no difference in parasite assemblages among size classes, age classes or sex in infected individuals within each locality (Tables 3.6 and 3.7). The SIMPER analysis indicated that the average similarity among infected individuals within False Bay (14.4%) was less than the other locations, followed by Port Elizabeth (20.3%), Struisbaai (24.3%) and Goukamma (37.6%).

Table 3.6: One-way analysis (ANOSIM) of differences in parasite assemblages of *Boopsoidea inornata* in different regions, size classes, sex and age classes in South Africa (2013 -2015)

Factor	Level	R	P
Location	4	0.215	0.001
FLcat	3	0.013	0.099
Sex	2	-0.032	0.855
Age cat	3	0.025	0.103

Table 3.7:Two-way (ANOSIM) differences in parasite assemblages of *Boopsoidea inornata* infecting different areas, size and age class in South Africa (2013 -2015).

Factor (1)	Level	R	P	Factor (2)	Level	R	P
Location	4	0.234	0.001	FLcat	3	-0.19	0. 697
Location	4	0.176	0.001	Age cat	3	-0.034	0. 077

Parasite assemblages identified among regions in autumn showed that there was a significant difference in parasite assemblages identified between all locations. Two-way ANOSIM showed that there was no significant difference in parasite assemblages among size classes and age classes during autumn (Table 3.8).

Table 3. 8: Two-way (ANOSIM) differences in parasite assemblages of *Boopsoidea inornata* infecting different areas, size class and age class in autumn (April to June) in South Africa (2013 -2015).

Factor (1)	Level	R	P	Factor (2)	Level	R	P
Location	4	0.216	0.001	FLcat	3	-0.04	0. 816
Location	4	0.292	0.001	Age cat	3	-0.083	0. 143

There was a high dissimilarity in parasite assemblages between Goukamma and Port Elizabeth (75.26%) due to the abundance of *Stephanostomum* sp. and *Goussia* sp. 1 in Goukamma, whereas *B. inornata* from Port Elizabeth showed more abundance of *Goussia* sp 2. Autumn samples from Struisbaai and False Bay showed a high dissimilarity index of 90.05 % due to an abundance of unidentified digenean metacercaria-1, the low frequency of *Stephanostomum* sp. and the total absence of *Goussia* sp. 1 in False Bay.

Seasonal assessment of variation in parasite assemblages from Struisbaai and False Bay throughout the entire sampling period showed that these were significantly different (Table 3.9). Parasite assemblages in False Bay varied from those in Struisbaai with a dissimilarity index of 91.06%. The dissimilarity between these locations was due to the high abundance of the unidentified digenean metacercaria-1 in False Bay, and the high abundance of unidentified digenean metacercaria- 2, *Stephanostomum* sp. and *Goussia* sp. (1) in Struisbaai.

Table 3.9: One-way analysis of similarities (ANOSIM) in parasites assemblages of *Boopsoidea inornata* from False Bay and Struisbaai for season, sex and size class in South Africa (2013 -2015)

Factor	Level	R	P
Location	2	0.319	0.001
Season	4	0.063	0.075
Sex	2	-0.075	0. 935
FLcat	3	-0.003	0. 518
Age cat	3	-0.043	0.081

There was a significant difference in the diversity of parasites species between False Bay and Struisbaai, as measured by the Shannon-Wiener diversity index (t=-1.8, p=0.036). When measured as species richness, False Bay had 0.46 parasites species per infected fish while Struisbaai had significantly higher infection of 1.12 parasites species per fish (t=-5.68, p=6.13).

Goukamma and Port Elizabeth showed no significant difference in the diversity of parasite species (t=0.12, p=0.45). When measured as species richness, similarity was found between Goukamma, with 2.0 parasites species per infected fish, and Port Elizabeth, with 1.95 parasite species per infected fish (t=0.16, p=0.43). A species accumulation curve (SACs) for parasites infecting *B. inornata* estimated a total species richness of 19 parasite taxa (Figure 3.6). After estimating the species richness by extrapolating the curve to its asymptote at each level of sampling, the SACs chart showed a slow slope with a late asymptote for the 150 examined hosts.

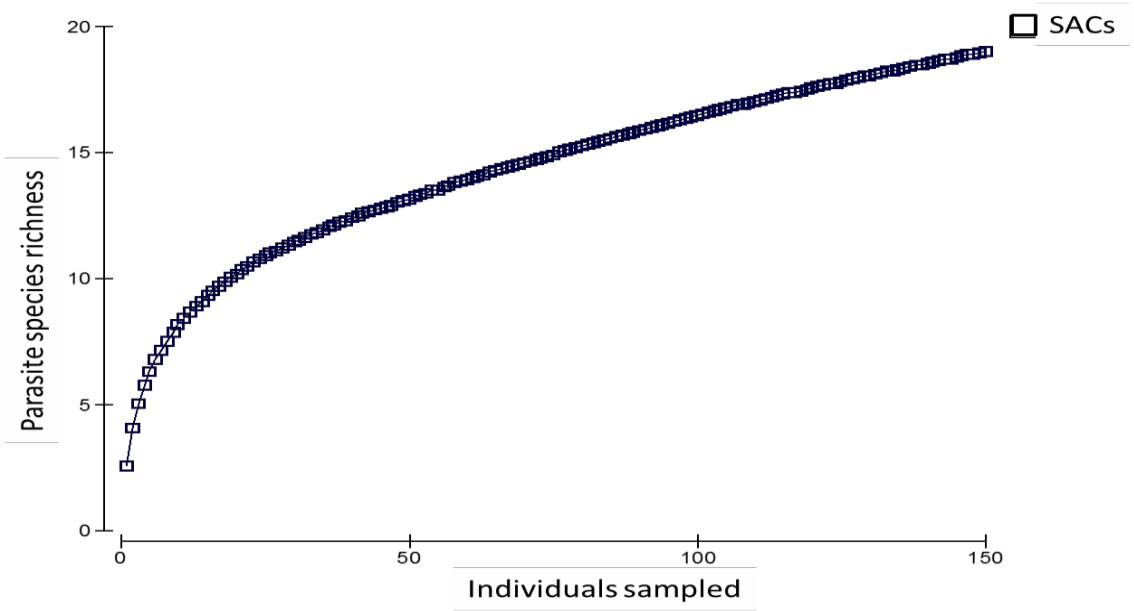


Figure 3.6: Parasite species accumulation curves for *B. inornata* from four localities in South Africa in 2013 to 2015.

Discriminant function analysis (DFA) showed an overall correct classification rate of 66% for accurately predicting the locality of *B. inornata* from their parasite assemblage. The probability of predicting the locality origin of *B. inornata* correctly was the highest for False Bay at 73%

accuracy, while Goukamma, Port Elizabeth and Struisbaai were 66%, 64% and 63% accurate respectively (Figure 3.7).

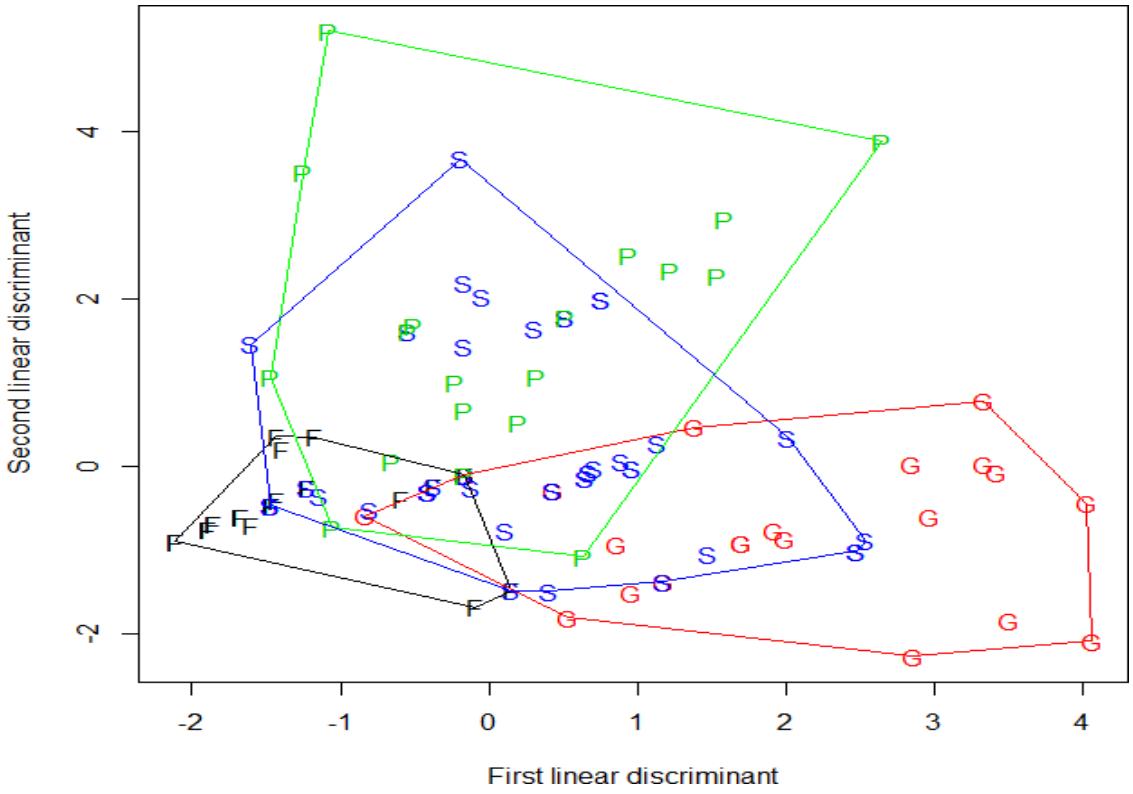


Figure 3. 7: A plot of the two linear discriminant functions showing the separation of hosts from each area on the basis of the parasite assemblage. F: False Bay, G: Goukamma, P: Port Elizabeth and S: Struisbaai in South Africa (2013 -2015)

3.5 Discussion

The results presented in this chapter represent the first survey of parasites infecting *B. inornata* and also the first investigation into the entire community of parasites associated with species from the family Sparidae across four localities in South Africa. Most research on parasites infecting sparids in South Africa comprise taxonomic studies on specific taxonomic groups (Reed 2015). Due to the lack of general taxonomic information available for marine parasite species in South Africa, no

parasitic taxa collected here were identified to species level. Amongst the 19 species recorded, 13 were identified to genus and six to class. In addition, the focus of this thesis was on the biology of *B. inornata*, and the survey of parasites associated with this species was included to address questions of population structuring and movement and to examine broad spatial and temporal patterns associated with variations in parasite assemblages.

Despite the lack of species level identification, it was apparent that *B. inornata* has a diverse parasite community showing some specific patterns of infection. In particular three species of digenetic trematode metacercariae showed high prevalence of infection across all four localities. These included a *Stephanostomum* sp. (Figure 3.1:4) infecting the gill arches and two unidentified digeneans, namely unidentified metacercaria-2 infecting the heart and unidentified digenean metacercaria-1 infecting the kidneys. Larval forms of the nematode, *Anisakis* sp. were the fourth most abundant parasite and were frequently observed in the liver, gonads, stomach and general body cavity. The fifth most abundant species was another digenean trematode metacercaria (a tetracotyle-type metacercaria) found infecting the eyes of *B. inornata* most commonly in False Bay and Struisbaai. This species resembles *Cardiocephaloides* sp. recorded from the eyes of South African sardine (*Sardinops sagax*) that has been used as a biological tag for sardine stock assessment (Weston *et al.* 2015)

Metacercarial larval stages such as those species recorded in *B. inornata* are frequently the most common parasitic infections in marine fishes. Digenetic trematode life cycles tend to include several hosts, with molluscs (gastropods, bivalves and prosobranch snails) being first intermediate hosts to cercarial stages, metacercarial stages generally infecting fish as second intermediate hosts and piscivorous birds or predatory fish the final host (Paperna 1995) (Figure 3. 1). Campbell *et al.* (1980) recorded helminth life cycles in 52 species of deep-living benthic fishes and highlighted the specificity of parasite species for intermediate and final hosts that were useful to link prey and predators. *Stephanostomum* sp. are harmful gill parasites that may cause gill lesions and produce respiratory disorders (Kennedy 2007). Numerous investigations concerning the parasites in sparid fishes from the Mediterranean Sea showed high digenean species diversity (Bartoli *et al.* 2005).

Pérez-del Olmo *et al.* (2007) examined the patterns of composition and structure of parasite communities in *Boops boops* and found that it hosts a large number of metazoan parasites (67 species). Bartoli and Bray (2004) described *Stephanostomum euzeti* from the gill arches of *Boops boops*. González *et al.* (2004) reported seven metazoan parasites from *Dentex dentex* that were found in the gills, one of them being a *Stephanostomum* sp.

Very little research has been conducted on the diversity of *Stephanostomum* sp. in South Africa, with just a few species on record. Bray (1985) described three digeneans from this genus from marine fishes off South Africa. *Stephanostomum* sp. was described from the gill membrane of *Merluccius capensis*. Bray (1985) also identified *S. solontschenki* and *S. ditrematis* from the rectums of *M. capensis* and *Megalaspis cordyla* respectivley.

The high prevalence of digenetic trematode species recorded from *B. inornata* across all localities may be related to the proportion of molluscs that contributed 5% PSIRI to the diet of *B. inornata*, with bivalves contributing up to half that percentage along with some undigested abalone shells that were found in the intestines of Struisbaai fish. Although most digenetic trematode cercaria actively seek and infect fish hosts via boring throught the skin, *B. inornata* may be more susceptable to these infections whilst spending time feeding on molluscs and hence being in the close vicinity to free swimming cercaria released from the mollusc hosts. Some infections may also also occur via consumption of molluscs, although this is not the usual route.

The life cycle of nematodes from the genus *Anisakis* tend to involve several hosts, with crustaceans (copepods, amphipods etc) being the first intermediate hosts, generally followed by fishes and cephalopods as paratenic hosts, and marine mammals as final hosts (Figure3. 2). Most stages are infective via consumption of an infected host, except for the very first stage where free swimming larvae infect small crustaceans. The high prevalence of *Anisakis* sp. infecting *B. inornata* is likely a consequence of the diet of these fish as they feed extensively on crustaceans which contributed 30.60% *PSIRI* of their diet (see chapter 2).

Members of the genus *Anisakis* are known to be highly pathogenic causing loss of appetite and emaciation and even mortality in heavily infected fish and other hosts (Williams *et al.* 1994). Most concerningly, the nematodes from this genus, *Anisakis*, are able to successfully infect humans, as our bodys are physiologically similar the natural final hosts of many *Anisakis* species, namely marine mammals. Humans infected by nematodes from the genus *Anisakis* become ill with a disease called Anisakiosis, which causes a number of severe gastro-intestinal problems and allergic reactions (Hochberg *et al.* 2010). Through changing diet preferences in society, especially the consumption of raw or poorly cooked fish, there has become an increased awareness of fish parasites as a health risk to humans.

Few studies on the diversity of marine nematodes are known from South Africa, with most records being incidental accounts forming part of studies usually examining the biology of a particular fish species (Reed 2015). Some records do exists, such as Hennig (1974) who described the effects of *Anisakis* sp. infection on *Engraulis encrasicolus*, Hecht (1976) who reported *Anisakis* sp. infection statistics in *Trachurus capensis* around the Eastern Cape coast of South Africa, and Botha (1986) who surveyed *Anisakis* sp. and post-larval stages of the trypanorynch cestode *Hepatoxalyn trichiuri* in two species of Cape hakes, *M. capensis* and *M. paradoxus*.

3.5.1 Host biological characteristics

Host size, age, sex and diet composition are considered useful sources of variation for explaining differences in parasite richness among component communities and infra-communities (Rohde 1984, Williams *et al.* 1994). Despite, the wide range of age classes (0-33 years) for *B. inornata* infected with parasites there was unexpectedly no significant correlation of fish size and mean parasite assemblage infection statistics. The same results were seen for size classes, season and sex effect on susceptibility to infection in *B. inornata*. Hemmingsen *et al.* (2000) found that the age and sex differences in the occurrence of some metazoan parasites could be related to differences in feeding behaviour between male and female fish. *Boopsoidea inornata* did not support this hypothesis since there was no significant difference in the prey composition among size and sex (see chapter 2).

3.5.2 Spatial variation

The results of the present study showed a significant spatial difference in infection of all parasites infecting *B. inornata* from the four localities, False Bay, Struisbaai, Goukamma and Port Elizabeth. Fish infected by *Stephanostomum* sp. showed random distribution of infection, with the False Bay fish having the lowest prevalence and infection intensity values. *Boopsoidea inornata* infected by the unidentified digenean metacercariae-2 showed gradually increasing prevalence and infection intensity from False Bay to Port Elizabeth. In contrast unidentified digenean metacercaria-1 showed relatively similar prevalence and infection intensity across all localities.

The significant variation in parasite assemblages between localities is likely due to oceanographic conditions around the coast of South Africa, with False Bay, on the west coast of South Africa, being separated from the eastern coast localities (Struisbaai, Goukamma and Port Elizabeth) by a biogeographical break region known as the Agulhas Bank. Such potential isolation of *B. inornata* host populations may allow for the evolution of unique parasite assemblages.

The spatial distribution of some parasites was isolated to one locatily, whilst others, such as the digenean "tetracotyle" metacercaria (*Cardiocephaloides* sp.) showed discontinuous distribution in both infection intensity and prevalence between localities (Table 3.5). Mackenzie *et al.* (2008) reported that when parasite fauna of two host populations collected from two different geographic areas are significantly different, the life history of those fish populations may also be different. A good example of this application were the studies by Reed *et al.* (2012), van der Lingen *et al.* (2015) and Weston *et al.* (2015) who all utilised a parasite biotag, a "tetracotyle" metacercaria (*Cardiocephaloides* sp.), to elucidate the number of populations of *S. sagax* in South Africa. Weston *et al.* (2015) subsequently tested the multiple stock hypothesis for *S. sagax* in South Africa by examining this same digenean metacercaria (*Cardiocephaloides* sp.), to provide convincing evidence of discrete stocks.

According to the results in this chapter, the different level of prevalence and intensity of infections in *B. inornata* could be related to spatial variation in environmental conditions, whilst the variation observed in parasite assemblages seasonally may be influenced by different feeding habits and prey types through different seasons (see Chapter 2). Marcogliese (2002) reported that the variation among local habitats also affects parasite species composition and the variations in spatial distribution of different benthic invertebrate taxa reflect the distribution of parasites that use them as intermediate hosts. Most molecular studies on the geographic ranges of fish helminth parasites have shown that the greatest diversity exists in those host species with relatively small geographic ranges (Jousson *et al.* 2000).

3.5.3 Parasite species richness

The parasitic assemblage in *B. inornata* was diverse from an early age and did not increase with fish size, perhaps as a result of diverse feeding habits in young fish. There was a significant difference in species richness between individual hosts from the False Bay and Struisbaai. The Shannon-Wiener diversity index showed a low species richness, peaking at just 1.12 species in Struisbaai. Goukamma and Port Elizabeth showed no significant difference in diversity with a Shannon-Wiener value peaking at 2.0 in Goukamma. In contrast, discriminant function analysis (DFA) related 73% of the probability of correctly predicting the origin of *B. inornata* from parasite counts to False Bay, attributable to this locality having the lowest parasite diversity and richness.

Boopsoidea inornata may have parasite species rich component common to isolationist infracommunities with low transmission rates. Infra-communities were recognised as the sub-populations of parasites living within an individual host (Poulin 2001). Isolationist communities consist of fewer species and those mostly with limited colonisation abilities. A species accumulation curve is vital to understanding the spatial compositions of species and predicting species richness (Moreno and Halffter 2000). The species accumulation curve for parasites infecting *B. inornata*

showed slow initial slope with the curve reaching a late asymptote, reflecting the relatively high abundance of a few species (19 parasite taxa with 150 individuals).

3.6 Conclusions

A diverse parasite community of 19 taxa infects *B. inornata*. Most of the parasite species are new host records and some could only be identified to genus level. A significant difference in parasite community structure between fish from False Bay and Struisbaai was found, which implies a very low rate of mixing of hosts between these sites. The results of this study contribute to the body of knowledge of parasites on South African marine fish.

CHAPTER 4

Life history trade-offs among four sympatric seabreams

Abstract

Fish life history is affected by environmental and ecological factors but is also constrained by phylogenetic influences on morphology and physiology. True life history trade-offs can be exposed in a comparison of closely related species which are subject to identical environmental conditions, and which have similar diets. I compare the life histories of four closely related and similar-sized, sympatric, omnivorous seabreams which share the same physical habitat, namely *Spondyliosoma emarginatum*, *Pachymetopon blochii*, *Rhabdosargus globiceps* and *Boopsoidea inornata*. Samples of each species were obtained in every season from the south-western Cape, South Africa, to obtain measures of total length, mass, gonadosomatic index and condition. *S. emarginatum* is a nest-guarding, short-lived, protogynous hermaphrodite. *P. blochii* is a resident, group spawner, engaging in sperm competition. *R. globiceps* is a moderately long-lived migrant with a sex ratio of 1:1. *B. inornata* is a polygamous, long-lived resident with low annual fecundity, but a protracted spawning season. Although all four species are periodic strategists, life history trade-offs are evident between annual fecundity and longevity, migration and spawning season length, hermaphroditism and bet-hedging and hermaphroditism and migration. No clear adaptive reason for the divergence can be identified, although competition among the young is a candidate. The comparison reveals a wide range of options available to seabreams and shows how disparate life histories can be equally adaptive under identical conditions.

4. Introduction

The extent of life history variation among teleost fishes is remarkable. Strategies range from annual fecundity in the millions and no parental care, to those that hardly differ from the conservative chondrichthyans strategy of single-digit annual fecundity, high longevity, late-maturation and live-bearing. Stark life history contrasts exist between deep phylogenetic lineages among fish, which suggests low plasticity in life histories. Life histories are easily manipulated by artificial selection, yet they appear to be conservative in wild populations.

Life history divergence in the teleosts is broadly delineated by orders and families, but also by habitat. For example, life history parameters of species of the short-lived Clupeiformes as a group differ substantially from those of long-lived Gadiformes and Scorpaeniformes. Although this might suggest heritability of such traits, the members of each order also occupy typical niches that differ substantially from those of other orders, making it difficult if not impossible to explain the conservatism of traits within many lineages (Parsons *et al.* 2017). The study of the causes of life history variation requires examinations within species or closely related species, which might exhibit adaptive radiation.

The role of life history traits in ongoing adaptive radiation in fishes has received much recent interest (Morrongiello *et al.* 2012, Burgess and Marshal 2014, Parsons *et al.* 2017). Productivity and habitat predictability are assumed to be important drivers of life history variation. The apportionment of resources to annual fecundity, growth and longevity is shaped by local availability of resources, and its predictability, among other factors. Life histories vary along environmental gradients (Leggett and Carscadden 1978, Morrongiello *et al.* 2012). Fish productivity by way of growth and reproduction is a complex function of the ecosystem, in which competition, food availability and seasonality are among the most important drivers. Consequently, broad geographical location and depth affects condition, growth and reproduction in fishes (Lloret *et al.* 2002).

Another, perhaps equally important, influence on life history is predation (Roff 1991). This influence has applied value in fisheries management. Fish populations vary in their resilience to the added

predation caused by fishing, largely as a function of life history traits. The productivity and resilience of fish populations are expected to be at least partially related to life history attributes (Rochet *et al.* 2000, Winemiller 2005). Modeling studies confirm the critical role of life history in population dynamics of marine fish (Bjørkvoll *et al.* 2012). Easily measured life history parameters are now used as predictors of productivity and resilience in teleosts and chondrichtyes and have been used in criteria to evaluate the conservation status of fish species and the sustainability of fisheries (Musick 1999b). They may also be used as surrogates for time-series of population-level abundance data when setting harvest strategies (King and McFarlane 2003). These relationships may have policy, legal and market implications.

It is important that the various life history parameters exhibit strong covariance – including some well described trade-offs, such as the inverse relationship between fecundity and parental care (Sargent and Gross 1986). The negative correlation of such variables might promote life history variation among species in similar circumstances.

The evolution of life history traits depends not only on selective pressures imposed by the environment, but crucially also the plasticity in the trait. One marine family which offers excellent, if not overwhelming, material for investigating life history divergences and covariances among traits is the Sparidae. This family has the most variable set of reproductive strategies, including gonochorism, protandry, protogyny and rudimentary hermaphroditism, among all vertebrate families (Atz 1964). Unusually strong environmental gradients of temperature and community structure exist along the South African coast, between the cold upwelling coast of the west and the subtropical Indian Ocean coral reefs in the west (Branch and Branch 2018). South Africa has 42 species of seabreams, the most of any region in the world, spread along this ecotone. Unsurprisingly, there is much life history variation in this closely related group of fishes in South Arica, and with it an excellent opportunity to study life history adaptations and consequences.

In this chapter I examine how different strategies can prevail among taxonomically and ecologically similar fish species in exactly the same habitat and location. The massive flexibility in the seabreams

seem to offer multiple solutions to the same problem. The four seabreams (steentjie, *Spondyliosoma emarginatum*), (hottentot, *Pachymetopon blochii*), (white stumpnose, *Rhabdosargus globiceps*) and (frans madame, *Boopsoidea inornate*) are sympatric in the south-western Cape (Day 1974, Penney 1991, Le Chanteur and Griffiths 2002), occupy the same habitat and have massive dietary overlap. Stationary baited underwater camera surveys, for example, have frequently recorded combinations of three of these species in a single hour (de Vos *et al.* 2015, Roberson *et al.* 2015). Despite being of the same clade in the Sparidae family (Santini *et al.* 2014), of similar maximum size and of similar trophic level, their life histories, and in particular their reproductive strategies, are divergent. In these four species I expect to find a natural exhibition of pure life history trade-offs, unconfounded by environmental and ecological conditions.

The focus of this chapter is perfectly framed by the final paragraph of Winemiller and Rose's (1992) excellent paper on life history strategies among North American fishes, which I repeat here. Finally, we point out that a variety of fishes with divergent life history strategies frequently co-exist in the same habitats. The feeding niche probably determines a large proportion of the total environmental variance experienced by an organism. Inherited design constraints, including the morphological features required for trophic function, in particular microhabitats, place restrictions on the evolution of life history features. A diversity of life history strategies is consequently observed among species that perceive the same environment very differently from another. As a consequence, management efforts designed to abate a problem for a given species may sometimes have unintended effects on sympatric species that exhibit alternative strategies.

Unfortunately, member species of the Sparidae feature heavily in the IUCN list of threatened fishes (Comeros-Raynal *et al.* 2016), as do other diverse coastal families in tropical and subtropical settings, such the Carangidae, Serranidae, Lutjanidae and Lethrinidae. The management of species in these families are not tailored to individual life history variation, but usually take effect as a blanket strategy, such as effort control, gear limitation or zonation. Such species are frequently included in bycatch lists of commercial fisheries (Attwood *et al.* 2011, prawn trawl). As Winemiller and Rose (1992) point out, the resilience of co-occurring species to a common fishing strategy could vary substantially.

I will describe and attempt to explain the variance and co-variance in easily measured life history parameters of four abundant, sympatric and very similar seabreams, on the premises that the species niches are similar and that their morphologies are similar. These premises will be examined as a prelude to a hypothesis that life history trait co-variance can result in a range of substantially different life histories with equal adaptive value.

4.1 Methods

4.1.1 Fish samples

The analyses reported here draws heavily on data already reported in the primary literature and chapter 2 of this thesis (Fairhurst *et al.*2007; Tunley *et al.*2009; Attwood *et al.* 2010). These were augmented by additional samples as indicated in Table 4.1 and described below.

Fish were caught by hook and line at three locations in the south-western Cape over the period 2005 to 2016: Saldanha Bay, False Bay and Cape Agulhas (Table 4.1, Figure 4.1). Immediately upon capture the fish were transferred to a container with sea water and clove oil (concentration 20mg/l) and later transferred to an ice chest. Fish were either dissected fresh, or frozen and then later dissected.

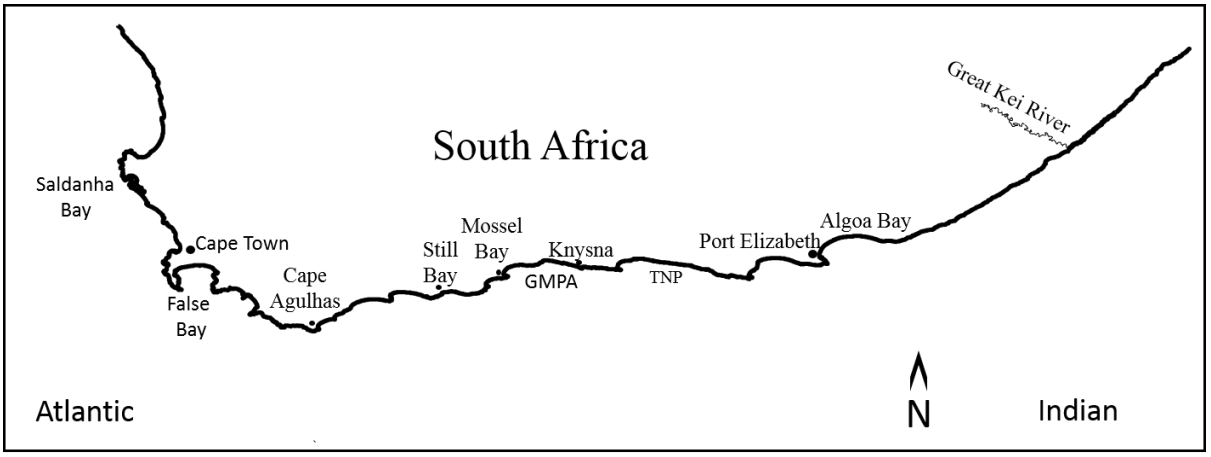


Figure 4.1: Geographic distribution of the sampling site southern Africa: Saldanha Bay, False Bay, Cape Agulhas, Goukamma (GMPA) and Algoa Bay

Table 4.1: The locality and number of records of fish measurements and dissections used in this study per source

Source	Locality	*Rhabdosargus globiceps*	*Pachymetopon blochii*	*Spondyliosoma emarginatum*	*Boopsoidea inornata*
Fairhurst *et al.* 2007	Saldanha Bay			369	
Tunley *et al.* 2009	Saldanha Bay and Cape Agulhas			319	
Attwood *et al.* 2010	Saldanha Bay	989			
Chapter 2 this thesis	False Bay, Cape Agulha, GMPA and Algoa Bay				817
Unpublsihed False Bay samples	False Bay	158	318	127	

4.1.2 Measurements and dissections

A standard protocol was used for the measurement and dissection of all species, as described in Chapter 2. The total body length to the nearest mm, the fork length to the nearest mm, whole mass, and gutted mass to the nearest 0.1 g. The viscera were exposed to remove the stomach and gonads. Sex and sexual maturity were macroscopically assigned to one of six developmental maturity stages (Chapter 2). Gonads were staged on a 1 to 7 scale for *R. globiceps*, *S. emarginatum* and *P. blochii* (Attwood et al. 2010) and on a 1 to 6 scale for *B. inornata* (Chapter 2). The weights of the gonads were measured to the nearest 0.1 g. Stomach contents were identified to the lowest taxonomic level possible and each taxon was measured volumetrically.

4.1.3 Data analysis

Length-weight regressions were performed on each species using the least squares linear regression procedure on ln-transformed data (Froese, 2006). A species was classified as iso-metric if the confidence interval of the estimate of b included 3.0. Otherwise, it was hyper-allometric if the entire

confidence interval was greater than 3.0, and hypo-allometric if it was below 3.0. The predicted weight of each fish was used as the denominator in the calculation of the condition index (K).

$$k = \frac{W}{\alpha L^{\beta}} \quad \text{..... Eq.1}$$

Where a and b are the length-weight regression parameters, L is length (mm) and W is weight. The gonadosomatic index (GSI) was calculated as follows:

GSI = Gonad weight / (fish weight - gonad weight) Eq.2

The GSI was averaged across all fish at each gonad stage for each sex. GSI was also averaged for all mature fish per quarter. A two-tailed equal variance t-test was used to test for differences between male and female GSI at the highest stages of development (ripe and ripe-and-running). A one-way ANOVA was used to test for differences between female GSI during each quarter, for each species separately. Two-way crossed, random effects ANOVA tests were used to test for differences in GSI between sexes, seasons and the inter-action of sex and season. Dietary information for the four species has been reported at various taxonomic levels in the primary scientific literature. A relatively course-scale comparison of diet at the level of class is provided here. Other life history parameters were extracted from published sources and compared in a table. A comparison of age and growth was accomplished by plotting ln(K) against ln(L∞) of each species.

4.2 Results

4.2.1 Sex and size distribution of samples

R. globiceps was equitably sampled throughout the year in Saldanha Bay from 2003 to 2010 (Table 4.2, Figure 4. 1). Of 1145 fish, 456 were male, 650 female, six hermaphrodites and 34 immatures. The sex ratio was therefore 1:1.42 male: female. Sizes ranged from 154-472 mm FL.

P. blochii were sampled across the seasons in False Bay, but most heavily in autumn and winter. The fourth season was relatively under-sampled (Table 4.2, Figure 4. 1). Of the 317 fish, 120 were male and 188 females. Seven were unsexed juveniles and two had ovaries and testes. The sex ratio was therefore

1:1.56 male: female. Sizes ranged from 126-365 mm FL.

S. emarginatum were sampled at Saldanha Bay, False Bay and Struisbaai. This species was more heavily sampled in the second part of the year (Table 4. 2, Figure 4. 1). The species is a protogynous hermaphrodite. Fish that had developing testes and degenerating ovaries were classed as males. The sex ratio was 1:2.6 male: female. Sizes ranged from 124-313 mm FL.

Table 4.2: The seasonal distribution of seabream samples used in this comparison

Species	Jan – Mar	Apr - Jun	Jul - Sep	Oct – Nov
Rhabdosargus globiceps	259	292	373	222
Pachymetopon blochii	62	88	142	16
Spondyliosoma emarginatum	76	58	261	254
Boopsoidea inornata	162	284	137	2211

4.2.2 Length-weight regressions

Length and weight were most strongly correlated for *B. inornata* (Table 4.3), but weakest for *S. emarginatum*. Residual variation ranged between 1.4% and 4.2%, much of which is explained as variation in condition, as described below in relation to the spawning cycle. The slopes of the relationships indicate isometric growth in *R. globiceps* and *P. blochii*, hyper-allometric growth in *S. emarginatum* and hypo-allometric growth in *B. inornata*.

Table 4.3: The results of power regressions of weight (g) against total length (mm) for four species of seabreams. The parameters a and b belong in the formula $Length = a\,Mass^b$. Isometric growth was indicated if b was not statistically different from 3, whereas a value significantly above 3.0 indicated hyper-allometric growth and a value significantly below 3.0 indicated hypo-allometric growth.

Species	Max length	A	B	R2	Growth form
Rhabdosargus globiceps	520 mm	0.0000092	2.99	0.978	Isometric
Pachymetopon blochii	400 mm	0.0000265	2.95	0.959	Isometric
Spondyliosoma emarginatum	346 mm	0.0000071	3.16	0.958	Hyper-allometric
Boopsoidea inornata	334 mm	0.0000573	2.81	0.986	Hypo-allometric

4.2.3 Gonadosomatic index

The maximum GSI differs between sexes to varying degrees and direction among the species (Figure 4.2). In *P. blochii* and *R. globiceps* there was no difference in GSI between the sexes (Table 4.4).

P. blochii showed higher stage 6 GSI in males than females, but this difference was not significant. In the other two species, female GSI exceeded male GSI.

Table 4.4: The results of t-tests of the difference between ripe female and male GSI. Stage 5 gonads were used for the test, but due to a lack of ripe *B. inornata males*, stage 4 was used for that species.

Species	Female GSI	Male GSI	DF	t	P
Rhabdosargus globiceps	0.054	0.051	113	1.0821	0.2815
Pachymetopion blochii	0.062	0.060	63	0.444	0.658
Spondyliosoma emarginatum	0.075	0.016	95	6.492	3.8×10^{-9}
Boopsoidea inornata	0.016	0.009	122	4.24	4.25×10^{-5}

In *R. globiceps* female GSI peaked at 5%. In *P. blochii*, the male GSI was the highest, reaching a 9.3% average in stage 6, whereas in females it was only 6.1%. The difference between sexes was most stark in *S. emarginatum*, in which female GSI reached 7.5% and 10% for stages 5 and 6 respectively, whereas males of stage 5 were below 2% and males of stage 6 were never encountered. Females of *S. emarginatum*, achieved the highest average and individual GSI of any sex of any of the four species. Similar sex-related variance was evident in *B. inornata*, although for this species the female GSI was considerably lower (3.5%) than that of *S. emarginatum*. Male *B. inornata* was lower than that *S. emarginatum* males, judging from stage 4 testes. More developed testes were not encountered for this species.

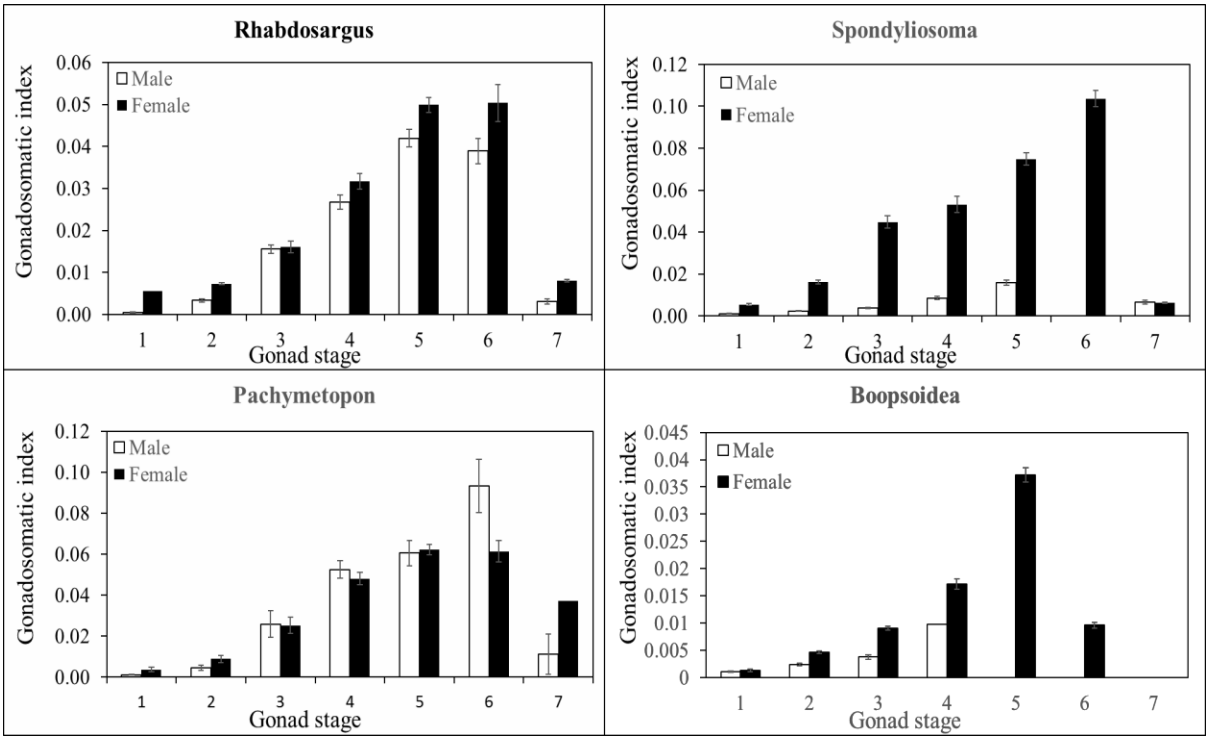


Figure 4.2: Average gonadosomatic index of *R. globiceps*, *S. emarginatum*, *P. blochii* and *B. inornata*, in each gonad stage by sex. Error bars indicate one standard error.

The GSI pattern across the seasons also showed variation among the species (Figure 4. 3, Table 4. 5). Variation was seen in the timing of the peaks, the length of the peaks and the depth of the cycle. Male and female GSI always varied in concert, so only female patterns were compared among seasons.

The strongest cycle was seen in the *S. emarginatum*. A strong peak was in quarter three, more than double the next highest quarter (four). The GSI was the lowest in season one. Average *B. inornata* GSI also peaked in quarter three, but its elevation did not greatly exceed the other three seasons. The quarters had a more equitable GSI value than for *S. emarginatum*. Average GSI in *R. globiceps* was highest in quarters three and four, and lowest in season two. The two highest seasons were about three times as high as the two low seasons. Average GSI in *P. blochii* was highest in season two, but season three also had a strong GSI. Seasons 1 and 4 were similarly low. The two highest seasons were about three times as high as the low seasons.

Average GSI in *P. blochii* was highest in season two, but season three also had a strong GSI. Seasons 1 and 4 were similarly low. The two highest seasons were about three times as high as the low seasons.

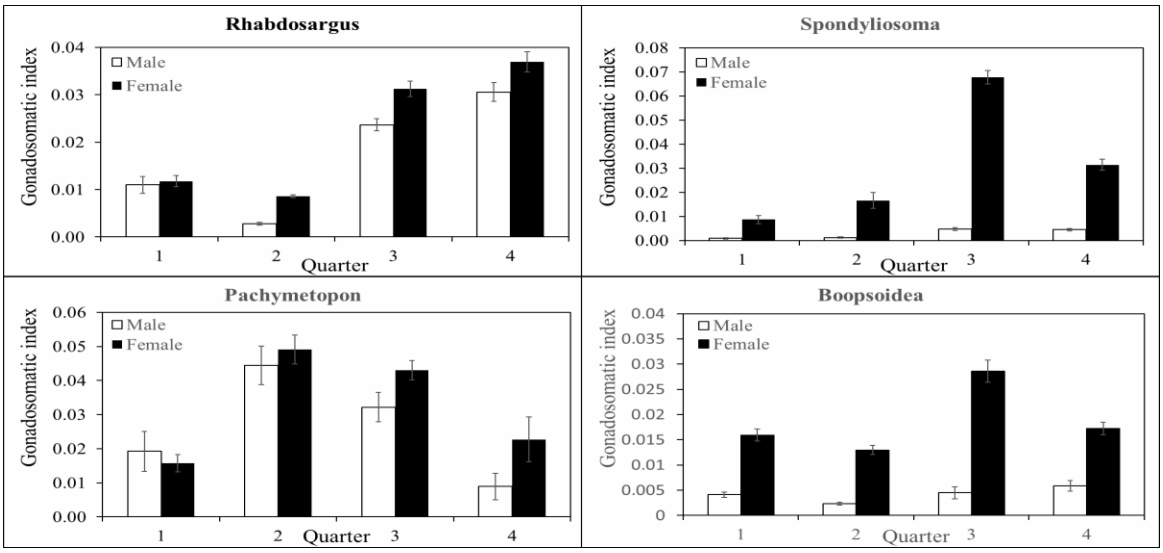


Figure 4.3:Average gonadosomatic index (GSI) of *R. globiceps*, *S. emarginatum*, *P. blochii* and *B. inornata*, in each quarter by sex. Quarter 1 represents the period from January to March. Error bars indicate one standard error.

Table 4.5: Results of one-way ANOVA models of female GSI with season as the only explanatory variable. Season was significant for each species.

Species	DFGroup	DFResidual	MSGroup	MSResidual	F	P
R. globiceps	3	578	0.077	0.005	15.08	1.84 x 10-9
P. blochii	3	184	0.010	0.000	15.67	4.03 x 10-9
S. emarginatum	3	468	0.078	0.001	75.3	2.2 x 10-16
B. inornata	3	616	49.3	2.17	22.70	5.91 x 10-17

The peak average quarterly female GSI did not reach the same level as the average GSI for ripe- running fish for any of the four species. A crude measure of the seasonal concentration of spawning is the variability of the average GSI among the quarters. If each quarter had the same average GSI (i.e. zero variability), then spawning is spread evenly across the year, but if the GSI is vastly greater in one season than any of the other three (highest variability), then spawning is most concentrated. Therefore, to measure the temporal concentration of spawning, I calculated the coefficient of variation of quarterly GSI for each species and found the order of variability to be: *B. inornata* (cv = 29%), *P. blochii* (42%), *R. globicespecies* and *S. emarginatum* (73%).

The average GSI alone is a not true representation of spawning. The females need to be ripe to indicate spawning. The proportion of females that were ripe in every season was used as another measure of the spawning intensity in that season. As a means of displaying the different strategies among the four species, I plotted the seasonal proportions of females that were ripe against the average female GSI for ripe and running fish (Figure 4. 3). *B. inornata* and *P. blochii* group together in that their spawning is spread over a longer period (covering 3 seasons) but at a lower intensity than the other two species. *B. inornata* rests from spawning in season 2, whereas P. *blochii* rests in season

1. *R. globiceps* and *S. emarginatum* restrict their spawning to one quarter, albeit different seasons. *R. globiceps* spawns in Season 4, whereas *S. emarginatum* spawns in season 3. Of the four species, *B. inornata* has the lowest and *S. emarginatum* has the highest female GSI in ripe females. The maximum GSI of *S. emarginatum* is almost treble that of *B. inornata*.

4.2.4 Condition Factor

Condition varied by season for all species in concert with the GSI, but the sex effects were more complicated (Figure 4.4, Table 4.6). In *R. globiceps* and *P. blochii*, there was no significant difference in condition among the sexes, and no interaction between sex and season. The only significant variation in these two species was among seasons, *P. blochii* condition peaked in season one and two, whereas *R. globiceps* condition peaked in season three. In both these species, the peaks in condition preceded the quarters that had the highest GSI. *P. blochii* condition decreased from season one (very little spawning) to season four at the end of a protracted winter spawning season.

Table 4.6: Results of two-way ANOVA models of condition, with season, sex and their interaction as explanatory variables for each seabream species. Significant factors are typed in bold.

Species	DF	Sum Sq	Mean Sq	F value	P
Boopsoidea inornate					
Quarter	3	0.18721	0.062404	13.4218	1.656×10^{-8}
Sex	1	0.00321	0.003208	0.6900	0.406
Season x Sex	3	0.04159	0.013862	2.9814	0.030
Residuals	649	3.01750	0.004649		
Rhabdosargus globiceps					
Quarter	3	0.502	0.1676	34.016	$<2 \times 10^{-16}$
Sex	1	0.002	0.0023	0.464	0.495
Season x Sex	3	0.007	0.0025	0.516	0.671
Residuals	974	4.800	0.0049		
Pachymetopon blochii					
Quarter	3	0.188	0.0628	5.602	0.0009
Sex	1	0.002	0.0026	0.239	0.6247
Season x Sex	3	0.034	0.0116	1.034	0.3774
Residuals	300	3.363	0.0112		
Spondyliosoma emarginatum					
Quarter	3	0.322	0.107	13.938	8.07×10^{-9}
Sex	1	0.157	0.157	20.347	7.654×10^{-6}
Season x Sex	3	0.113	0.038	4.909	0.0221
Residuals	660	5.050	0.008		

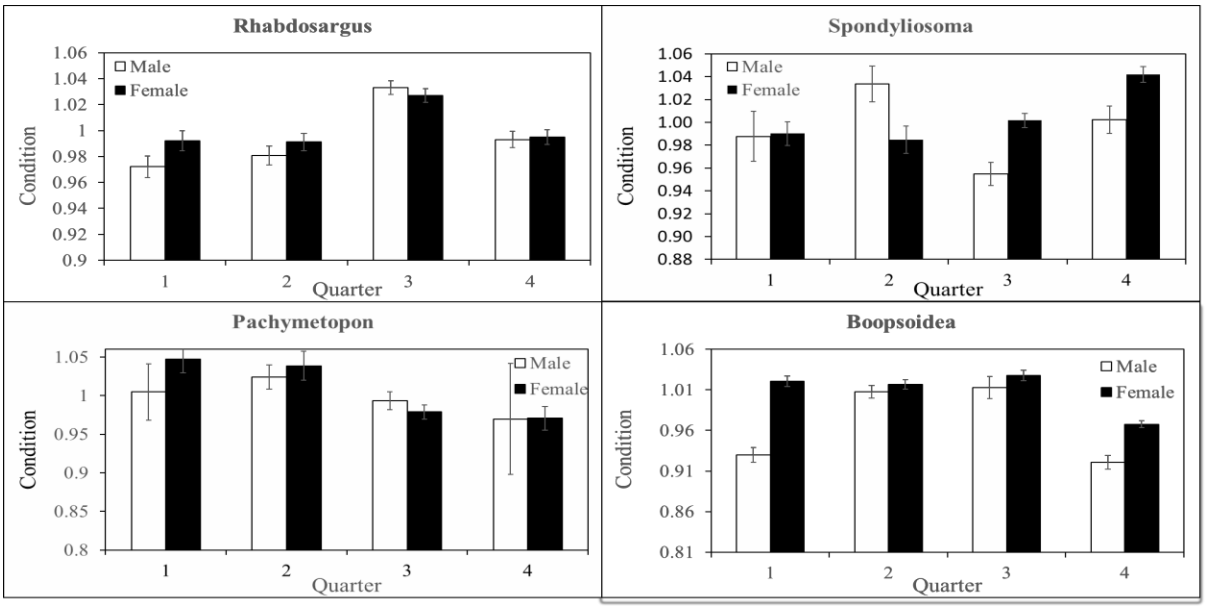


Figure 4.4: The average condition factor of *R. globiceps*, *S. emarginatum*, *P. blochii* and *B. inornata*, in each quarter by sex. Quarter represents the months from January to March. Error bars indicate one standard error.

In contrast, significant interactions between sex and quarter were found for *S. emarginatum* and *B. inornata*. Despite having the greatest GSI among any species, female *S. emarginatum* did not display strong variation in condition among seasons. Highest condition was seen in the summer season following spring spawning. *S. emarginatum* was the only species with a sex effect on condition. Not only was the male condition cycle stronger overall, it was also out of phase with that of the females, as seen by a significant sex-season interaction effect. The males accumulated condition in the second quarter, ahead of the spawning season, and well above that of the females. In the spawning season (season three) it loses condition dramatically, falling well below that of females, and at a time when female condition is recovering.

B. inornata female condition was similar across seasons 1 to 3, but dropped substantially in season 4, between the two spawning peaks. Male condition did not vary among the seasons. Overall there was no seasonal cycle in variation, nor a sex difference, but a significant interaction term showed that male and female variation was also out of phase. The decline in female condition in season 4 was not

matched by a decline in male condition. On the other hand, the male condition was lowest in seasons 2 and 4, the seasons with least ripe females.

4.2.5 Seasonality and intensity of spawning

The proportion of females that were ripe and running in every quarter was used as a measure of the spawning intensity in that quarter. As means of displaying the different strategies among the four species, I have plotted the seasonal proportions of ripe females per species against the female GSI for ripe and running fish (Figure 4.5). It is immediately apparent that *B. inornata* and *P. blochii* group together in that their spawning is spread over a longer period (covering 3 seasons) but at a lower intensity than the other two. *B. inornata* rests in Season 2, whereas *P. blochii* rests in season 1. *R. globiceps* and *S. emarginatum* have far shorter spawning seasons than the other two. *R. globiceps* spawns in Season 4, whereas spawns in season 3. Of the four species, B. *inornata* has the lowest and *S. emarginatum* has the highest female GSI in ripe and ripe and running fish. The maximum GSI of *S. emarginatum* is almost treble that of *B. inornata*.

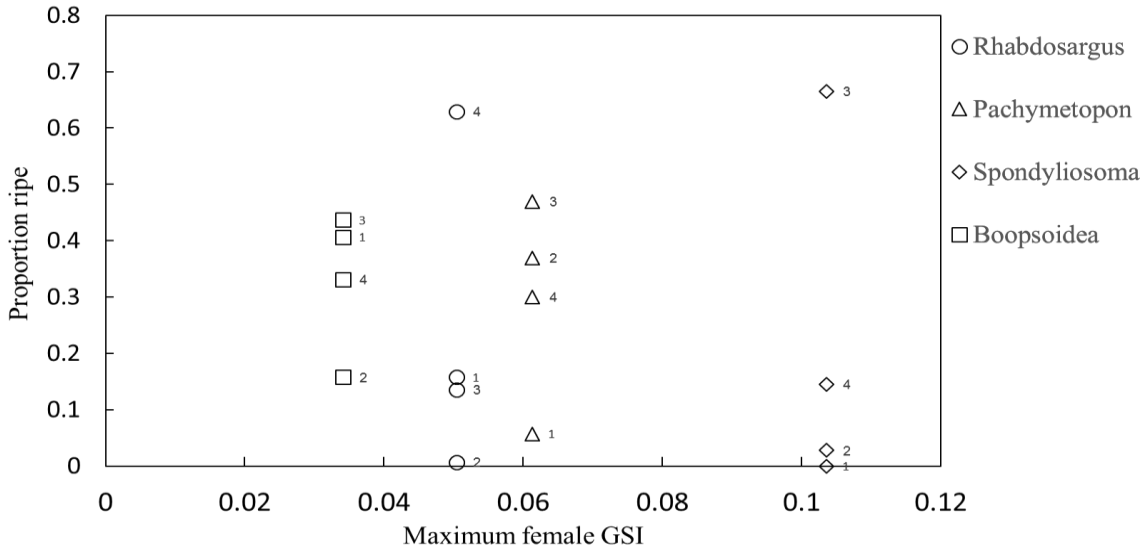


Figure 4.5: The proportion of females ripe and running fish of R. globiceps, S. emarginatum, P. blochii and B. inornata versus the maximum female GSI for ripe and running fish.

4.2.6 Life history parameters

A range of other life history parameters have been drawn from existing sources and reproduced here to facilitate comparison (Table 4.7). A comparison of growth performance is achieved by plotting growth rate against maximum length (Figure 4.6). The four species spread out on this plot: *B. inornata* has highest growth but smallest size, whereas *R. globiceps* has slowest growth and largest maximum size. Many of these parameters have been alluded to in the text above, but the diet information has not. Diets are compared in Appendix 4.4.1. All four species are classed as omnivores with a preference for invertebrates.

Table 4.7:Life history parameters of four South African seabreams. Data were drawn from Fairhurst *et al*. 2007, Tunley *et al*. 2009, Pulfrich and Griffiths 1988, Griffiths *et al*. 2002 and Attwood *et al*.2010.

Parameter	*Rhobdosargus globiceps*	*Pachymetopon blochii*	*Spondyliosoma emarginatum*	*Boopsoidea inornate*
L∞(FL)	343	538	289	223
k (y-1)	0.24	0.09	0.74	0.29
Max age (y)	21	12	8	37
Age-at-maturity (y)	2	4	3	1.87
Sex ratio M:F	1:1.42	1:1.56	1:2.6	1:3.3

Log e(K)

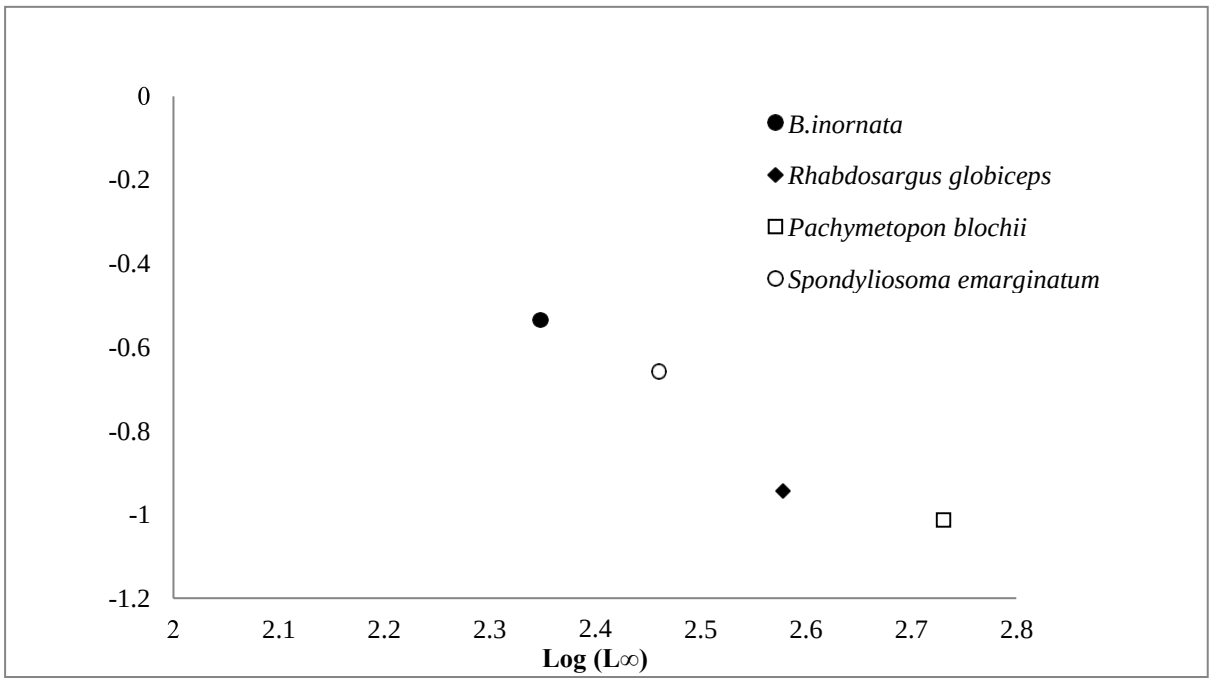


Figure 4. 6:Comparison of growth performance among four species.

4.3 Discussion

Convergence of fish life histories, irrespective of phylogeny, is expected to occur among species in similar environments (Ibañez *et al.* 2009, Mims *et al.* 2010, Winemiller *et al.* 2015). In this chapter I examine the reverse phenomenon, namely variance in life histories among close relatives in identical environments and similar niches. This approach is not an attempt to challenge the idea of convergence but is rather directed at exposing the nature of trade-offs. If several life histories are employed by physically similar, close relatives under identical conditions, then the differences in their life history parameters should reflect the partial or full extent of trade-offs and should reveal the dimensions along which these could occur. Comparing life histories of species from different environments, different niches or different phylogenies, cannot reveal true trade-offs when confounded by one of these variables. What I examine here is also different from intraspecific plasticity in life history characteristics among separate populations, or over long time periods, which experience different selection pressures.

The study of life history variance is important for understanding adaptation to changing environments, and perhaps speciation by way of reproductive isolation in the absence of physical separation. It may also be of value for fisheries management (King and McFarlane 2003).

Many studies of fish life history variation focussed on bi-dimensional trade-offs – e.g. somatic growth vs early maturation (Rochet *et al.* 2000), clutch size vs parental care (Elgar 1990), egg size vs egg number (Morrongiello *et al.* 2012) or the extent of bet-hedging along the semelparous - iteroparous continuum (Crespi and Teo 2002). More ambitious studies have attempted a synthesis of life history variation among fish taking several dimensions and phylogenies into account. The r-K selection theory, for example, is a model that groups animal traits onto a continuum from high fecundity and low parental care to low fecundity and high parental care (McArthur and Wilson 1967). Although the model fails in several respects (Stearns 1977), it is still widely used in predicting how population dynamics might vary in a given situation. Balon (1975) grouped all fishes into 32 reproductive guilds, based on life history and environmental parameters, and suggested that these guilds vary in their invasion potential.

Winemiller and Rose (1992) provided a more comprehensive synthesis of life history variation across marine and freshwater fishes and showed that all fish species fall within a three-dimensional continuum based on a combination of life history traits. The extreme (or pure) forms are referred to as *opportunists*, *equilibrium* strategists and *periodic* strategists, but real fishes are a combination of two or three of these. The variables they looked at included various age and growth parameters, mortality, fecundity and parental care. In my examination of four species, I consider all of these and the sexual strategy, social organisation and the possibility of migration, which are categorical variants. The trade-offs associated with the switch to hermaphroditism has never been explicitly investigated.

The selection of closely related sympatric fish species with similar body-size and shape was a deliberate attempt to explore the variability in life history attributes under identical conditions and constraints. The large variation among the species cannot be explained by variances in temperature, seasonality, predation pressure, habitat, body structure or ancestry. I postulate that the four species presented here exhibit a degree of life history variation that reflects true alternative life histories and trade-offs of component parameters unforced by ancestry or environment. It may of course be possible that competition has driven some of this variation, and the extent to which such competition can be relieved by alternate life histories needs to be considered.

I would like to add diet and trophic position to the above list of similarities, as the four species are all

classified as omnivores with a preference for animal prey, following the scheme of Stergiou and Karpouzi (2002), but close examination reveals differences that may be important. At the level of the class, there is a substantial overlap in the taxonomy of the dietary organisms, yet there is variance in the diets. The dentition alone suggests differences. *R. globiceps* has incisors and molars indicating a durophagous diet. It is the only species that extends its range into deep water, where there is no access to algae. The other three species have incisors and no molars. Omnivory is a feature of all four species, but plant material plays its strongest role in the diet of *Pachymetopon blochii*, which may have a bearing on the timing of spawning and condition cycles. I consider diet as a potential driver of life history, so these variations are important. For example, a herbivore might be expected to have a different production cycle than a piscivore, due to differences in the seasonal availability of the food sources.

Trophic morphology was initially used for the classification of the seabreams, but genetic analyses have now shown this to be a false character (Hanel and Sturmbauer 2000). Relationships in the seabreams do not mirror trophic morphology, and indeed several morphologies evolved separately in the seabreams. Dentition is not a conservative characteristic in seabreams (Orrell *et al.* 2002). The four species studied here diverged from a common ancestor approximately 42 mya (Santini *et al.*2014). The most closely related among the four are *B. inornata* and *P. blochii*, which diverged 30 mya, and the ancestor of *S. emarginatum* was likely the first to split from that of the other three (Santini *et al.*2014).

My contention that the four species are sympatric also needs interrogation. Stationary camera surveys provide the most precise position data for this comparison. Cameras detected all four species in False Bay, Betty's Bay, Struisbaai and Stilbaai in the 6 to 30 m range (de Vos *et al.* 2014, Roberson *et al.* 2015). At Tsitsikamma all species were encountered in one stationary camera survey (Parker 2015), and in another only *R. globiceps* was absent, but all four were found there in angling surveys (Burger 1990, Parker 2015). *R. globiceps* is known to range considerably further east than Tsitsikamma (Smale and Buxton 1985). *P. blochii* is not found east of Tsitsikamma. Heyns-Veale *et al.* (2016) found that despite overlaps in depth, *P. blochii*, preferred deeper reefs there compared to either *B. inornata* or *S. emarginatum*. This pattern likely reflects a more cold-water preference. There is no information to suggest that it forgoes herbivory in deepwater at this location, yet this is likely what truncates its

eastward distribution. *B. inornata* and *S. emarginatum* were found together on the shallow reefs in Goukamma MPA, which Götz *et al.* (2009a) explained by way of dietary separation, on the basis that only *B. inornata* ate Porifera, albeit infrequently. No depth distinction among the species is evident between False Bay and Stilbaai (de Vos *et al.* 2014, Roberson *et al.* 2015).

There is a strong reef association among all four species. The depth ranges overlap enormously, from 5 to 50 m, although *R. globiceps* frequents soft sediment areas too and is trawled down to 80 m. *R. globiceps* recruits in lagoons and estuaries, which gives it the largest depth and habitat range of the four species. Tag data and catch data shows that it has a migratory component to its life cycle (Kerwath *et al.* 2008). The migration is typically inshore (summer) to offshore (winter), although some variations are likely among the four populations described by Griffiths *et al.* (2002). *P. blochii* movement is unknown, although its young recruit on shallow reefs than where the adults are found (Mann 2013). *S. emarginatum* and *B. inornata* are resident (Tunley *et al.*2009, Mann 2013).

Camera footage confirms that habitat sharing occurs at the micro-habitat (<10 m) level. Stationary cameras have frequently detected combinations of three of the species in a single hour. These data suggest that not only are the ranges (the smalles single area that encompasses the known distribition of adults) massively overlapping – each species' range overlaps at least by 50% with any other of the three species – but that the physical areas occupied overlap strongly along 300 km of coastline. These four species are in frequent visual contact with each other. Heyns-Veale *et al.* (2016) suggested that species with similar diets are predicted to occupy different areas, but the case in question suggests otherwise. Although not an exact match on either variable, I contend that both the diet and the habitat of these four sympatric seabreams are remarkably similar, and sufficiently so to suggest that all, or at least some combinations, must be in competition, over all or at least some of their ranges.

4.3.1 Physical and behavioural comparisons

Within the seabreams, we see huge variation in size, even within genera, e.g. *Polysteganus* and *Lithognathus*. Being closely related does not ensure physical similarity, but these four seabreams are similar sized and shaped fishes. They are often confused in fisheries catch records. The four seabreams do not have identical maximum sizes, but all can be regarded as small seabreams (L_{inf} < 400 mm).

Similar body depths, the blunted heads, small terminal or slightly underslung mouths, and weakly forked caudal fins speak of strong, but not high-speed swimmers. Their feeding behaviour and escape strategies are probably quite similar. In particular, it would be difficult to argue *a priori* that they suffer different adult mortality rates in the same areas. Colourations vary from the light brown in *P. blochii*, bronze in *B. inornata*, to silver/grey with tinges of blue and red in *S. emarginatum* and silver in *R. globiceps*, but all blend into the background rather than stand out. The last two have vertical bars, which likely accords with their more frequent use of soft sediment habitats. All four species occur in shoals, but the organisation varies from mixed sized, aggregations in *P. blochii*, to fish of similar size in schools for *R. globiceps.* Male *S. emarginatum* are obviously territorial in the breeding season, but no such behaviour has been documented for any of the other three species.

4.3.2 Reproductive strategy

Spondyliosoma emarginatum, like its northern hemisphere congener *S. cantharus*, is a protogynous hermaphrodite. Although protogyny is a common feature in the Sparidae family, what sets the species of this genus apart from the rest of the family is the habit of laying eggs in a nest (Fairhurst *et al.*2007). The males guard the nest (Zsilavecz 2005). In all other seabreams, eggs are discharged into the water column. The other three species compared in this study are rudimentary hermaphrodites and maintain separate sexes.

None of the species have a 1:1 sex ratio. Females always predominate, but to varying degrees. The determination of sex ratio in sequential hermaphrodites is problematic because the selectivity of the fishing gear will influence the balance of sexes in the sample. If the gear is poor at catching small fish, then the larger sex will be over-represented. Comparisons of sex ratios between populations of the same species of sequential hermaphrodite have frequently exposed the strong role of fishing mortality on the gender balance, which is therefore another confounding factor. *S. emarginatum* is not subjected to even moderate fishing pressure as it is not a popular table fish. The ratio of 1:3.6 is comparable to that found by Fairhurst *et al.* (2007) and is similar to those of other unharvested populations of protogynous hermaphrodites (Buxton 1993, Götz *et al.*2008).

Among the three species with separate sexes, the ratios are highly variable. Sex ratios in *R. globiceps* and *P. blochii* are similar, but males are vastly outnumbered in *B. inornata*. In the case of the latter the sex ratio is the average across four sites, which are widely divergent in water temperature. The possibility of water temperature influencing determination of sex cannot be discounted. The male to female sex ratio at the extremes of the range of *B. inornata* are 1:1 (warm end of range) and 1:7 (cold end of the range). Although temperature determination of sex has not been confirmed in any seabream, it is known among other perciform fishes (Pavlidis *et al.* 2000, Devlin and Nagahama 2002). In these cases, males are more commonly produced at high temperature.

A 1:1 sex ratio among Sparidae is not typical (Mann 2013). Sex-ratio selection is facilitated by polygenic control of sex determination. Fisher's principle states that a 1:1 sex ratio is characteristic of populations in which both sexes have equal parental expenditure. *R. globiceps* and *P. blochii* are close to this scenario. Deviations from 1:1 are difficult to explain, and polygamy itself does not offer a mechanism for deviation from 1:1 (Hamilton 1967). Selective mortality or sex specific distribution may offer explanations, but I have no evidence to suggest that either of these are important factors.

The higher female to male ratios in S. *emarginatum* and *B. inornata* might suggest commonality in their breeding strategies, but one is a nest guarding, protogynous hermaphrodite and the other a broadcast spawning rudimentary hermaphrodite. In both cases, the low male GSI suggests that one male spawns with multiple females.

4.3.3 Length-weight regressions

Length appears to be an excellent predictor of mass in all four species, but close examination of the correlation coefficient indicates potentially important differences. *S. emarginatum* is hyper-allometric, indicating that it grows in mass faster than what is predicted by the cube of the length. A search of b values for other species of Sparidae shows that sequential hermaphrodites (of both types) are, with few exceptions, hyper-allometric (Figure 4.7). In contrast, those with separate sexes are either isometric or hypo-allometric. The significance of the pattern does not indicate causation, but it does suggest a pattern in which the sexual strategy and the growth form are linked. This link will be revisited after

consideration of conditions needed for sequential hermaphroditism.

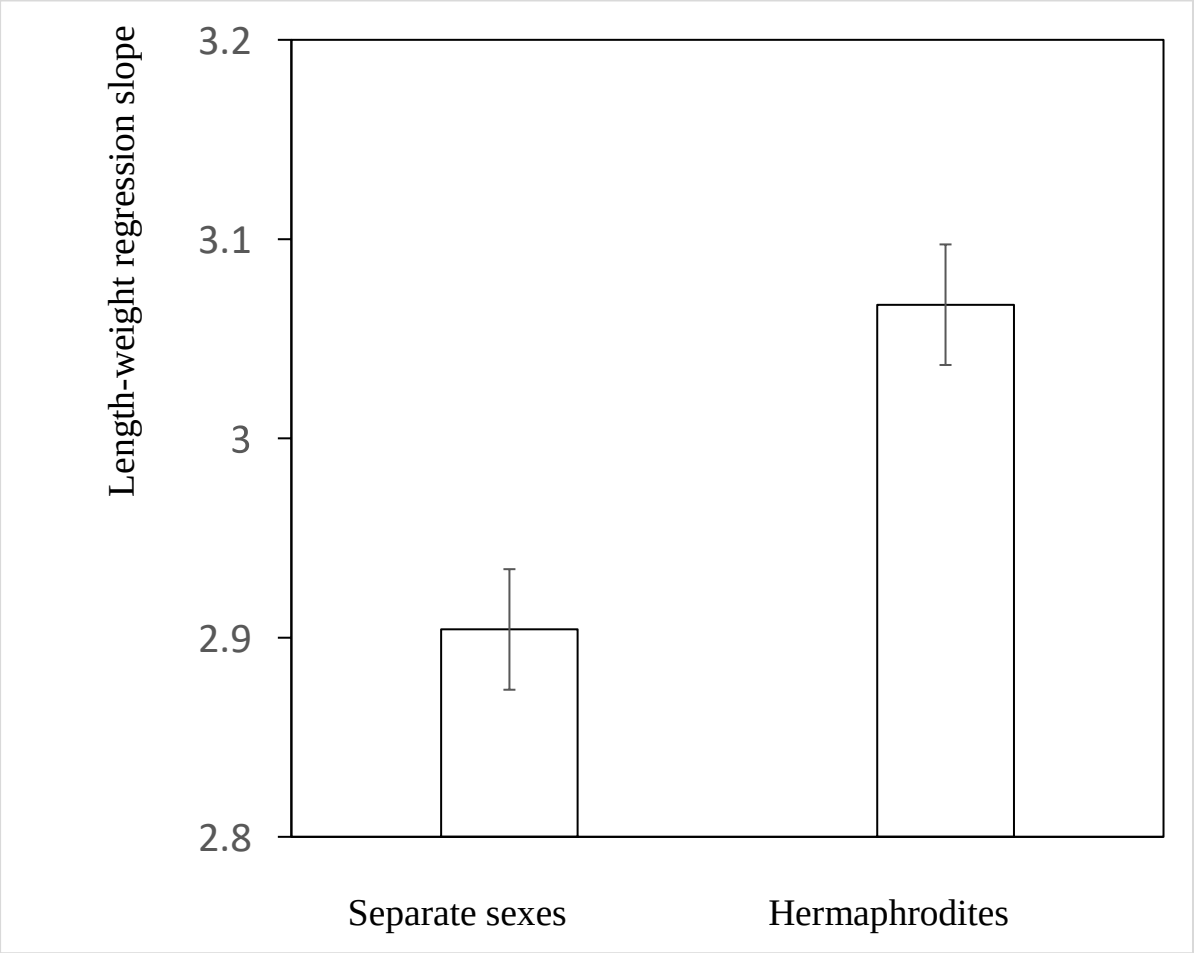


Figure 4. 7: The mean (error bars indicate s.e.) length-weight regression slope of Sparidae species that have separate sexes and sequential hermaphrodites. Included in this analysis are: *Argyrops spinifer, Cheimerius nufar, Chrysoblephus gibbiceps, Boopsoidea inornata, Polysteganus undulosus, Chrysoblephus puniceus, Rhabdosargus holubi, Argyrozona argyrozona, Lithognathus lithognathus, Pagrus aurata, Lithognathus aureti, Pachymetopon blochii, Petrus rupestris, Rhabdosargus sarba, Diplodus capensis, Pterogymnus laniarius, Cymatoceps nasutus, Sparodon durbanensis, Rhabdosargus globiceps, Pachymetopon grande, Acanthopagrus berda, Polysteganus coeruleopunctatus, Lithognathus mormyrus, Chrysoblephus cristiceps, Chrysoblephus laticeps, Spondyliosoma emarginatum, Sarpa salpa.*

4.3.4 Investment in gonads: differences among sexes

Buxton and Garratt (1990) made the observation that protogynous hermaphrodites in the Sparidae have low GSI in males compared to females, whereas among gonochorists the GSI is more equitable. They provide, as examples, data from one hermaphrodite (*Chrysoblephus laticeps*) and one gonochorist (*Sparadon durbanensis*). The GSI differences between the sexes of *S. emarginatum* confirm at least part of their theory, assuming that GSI is a proxy of sperm production. Male gonad investment is seemingly low among protogynous hermaphrodites.

Among the gonochorists, the GSI is equitable between the sexes in *P. blochii* and *R. globiceps*, but not so in *B. inornata* in which male GSI is far lower than that of females. The hypothesis might require further testing among the Sparidae, although evidence among Labridae and Scaridae is consistent with Buxton and Garratt's observation (Choat and Robertson 1975, Robertson and Warner 1978).

Robertson and Warner (1978) suggest that large testes are associated with intense sperm competition among those species with separate sexes. This would seem to be the case for *R. globiceps* and *P. blochii*. Both these species have near-equitable GSIs between sexes, and the most equitable sex ratios. It is almost counter-intuitively that the more males there are, the more sperm production is required. The case of *B. inornata*, with diminutive male GSI, suggests a lack of sperm competition with a sex ratio heavily skewed in favour of females – over most of its range. The sex ratio and the difference between the GSI of the sexes therefore appear to be linked. In species where males are less abundant, male investment, at least in gonads, is concomitantly lower. I postulate therefore that spawning in *B. inornata* follows a polygamous pattern in which a male has access to several females, perhaps on an exclusive basis.

The absence of sperm competition in *B. inornata* could be due to one of two situations or both. In the case of the protogynous hermaphrodite the males are fewer and larger than the females. On the basis of numbers alone there should be no necessity for sperm competition. The sex ratio is a function of the age at sex change, which is known to depend on mortality rates in protogynous hermaphrodite

Sparidae (Buxton 1993, Götz *et al.* 2008, Tunley *at al* 2009). The skewed sex ratio may be a sufficient explanation of the low testis size in *B. inornata*.

The cost of reproduction is of course not limited to gametogenesis. A condition for polygamy is that at least one sex is free of parental care. Among seabreams there is no evidence of parental care by any sex, except by the males of the two *Spondyliosoma* species. Reduced investment in testes by *S. emarginatum* is likely offset by the energy expended on nest building and egg guarding (Sargent and Gross 1986). *S. emarginatum* males aggressively defends their nests against intruders of its own and other species, including attacks on human divers 100 times their mass (Zsilavecz 2005)! In the case of *S. emarginatum,* the male expenditure on reproduction comes after that of the female.

The possibility of aggressive behaviour among male *B. inornata* in securing access to a harem might well offset the lower investment in testes. If this is correct, and in contrast to *S. emarginatum,* male *B. inornata* expend their energy on reproduction by way of spermatogenesis and courtship fighting before spawning.

The polygamous models of *B. inornata* and *S. emarginatum* differ in that one is rudimentary hermaphrodite and the other a protogynous hermaphrodite. The failure of the male to reproduce would be most detrimental to the fitness of a member of the *B. inornata* species. However, a failure to reproduce as a male in *S. emarginatum* is less problematic if such a fish had a successful run as a spawning female. Could it be argued that competition among male *B. inornata* is more critical, and perhaps therefore more energy demanding? I predict, in the absence of observations on the spawning of *B. inornata*, that males of this species engage in aggressive courtship battles to secure access to females.

4.3.5 Investment in gonads: differences among species

The differences in GSI among the species also require explanation. Why should species with similar diet and identical habitat show a three-fold variation in female GSI among ripe females? The frequently cited observation that high parental care is matched with low fecundity offers no explanation here. *S. emarginatum* is the only species with parental care (by the male) yet its females have the largest mass-

specific ovaries. Longevity offers a better explanation. *S. emarginatum* is the shortest lived of the four species, and it has the largest female GSI. In fact, their life as a female is very short, as sex change occurs at around age 4 (Fairhurst *et al.* 2007), giving each fish only two or three seasons of egg production. In contrast, *B. inornata* is the longest lived and has the lowest GSI. Among the two other rudimentary hermaphrodite species, *P. blochii* has a higher female GSI than *R. globiceps,* and it is shorter lived. Longevity and maximum GSI are clearly traded-off.

Differences in ovary size might therefore simply be a matter of bet-hedging, as the four species spread out along the semelparous – iteroparous dimension. The early maturing *S. emarginatum* is the shortest-lived seabream, alongside *Boops boops* (Monteiro *et al.* 2006) and *Sarpa salpa* (van der Walt and Beckley 1997). The long-lived *B. inornata* shares its longevity (38 years) with *Chrysoblephus gibbiceps*, which also has very low GSI (van Zyl 2013). Only the large *Petrus rupestris* (Andrews *et al.* 2018) and *Pagrus auratus* get older, among the seabreams.

The comparison of GSI among species, as a measure of fecundity, is problematic as the frequency of spawning and batch size might vary among the species and therefore affect the annual fecundity. All of the species are batch spawners and have indeterminate fecundity, and the seasonality imposed on each is identical, and so for these reasons I concur with Buxton and Garratt (1990) that gonad size is a useful index of fecundity but note that the length of the spawning season must be considered too.

4.3.6 Length and timing of the spawning season

The season for spawning in *S. emarginatum* is the shortest of all the four species and may therefore also explain the high female fecundity. Spawning is a short intense process in this hermaphrodite. The shortness of the season is not characteristic of protogynous hermaphrodites, as others engage in a longer spawning season, such as the sympatric *Chrysoblephus laticeps* (Buxton 1990, Götz 2005). The reason for the short season in *S. emarginatum* is most likely the habit of preparing nests and defending eggs. *S. emarginatum* males are effectively confined to their nests for the purpose of defence before, during and after spawning. Their confinement will reduce their feeding options drastically and the defence against intruders is likely to be energy demanding. It is therefore doubtful that a male *S. emarginatum*

can sustain a protracted spawning season. A trade-off exists here between the duration of parental care and energy intake (Rangeley and Godin 1992), and by extension growth and fecundity.

B. inornata's low GSI can also be explained by its long spawning season, covering three quarters of the year, but at low intensity. *P. blochii* also spawns over three quarters of the year, but at low intensity. Although *P. blochii* and *R. globiceps* might share a similar mating system, the spawning of the latter occurs predominantly in one quarter of the year. As *P. blochii* is the more herbivorous species - 19% of its diet is algae by volume (Pulfrich and Griffiths 1988), it would be expected that seasonal algal production would be limiting across the year, compared to invertebrate prey. Instead, the explanation for this difference in spawning season might lie in the movement behaviour of the species. *R. globiceps* is a migratory species, which leaves the feeding ground for a spawning area. These fish spend winter in cold, deep water and spawning occurs in early spring (Griffiths *et al.* 2002, Attwood *et al.* 2010). Being a strongly schooling and migratory species, it likely spawns over a short period when all the fish are together. Spawning would likely occur in an aggregation, which demands the high male GSI.

The timing of spawning is also not entirely uniform among the species. Peak spawning is winter for *P. blochii*, early spring for *S. emarginatum*, and mid-spring for *R. globiceps*. *B inornata* spawning is also centered on spring but is drawn out across the year. Timing to first feeding, swimbladder inflation and flexion in *R. globiceps* is recorded at 4 day post hatch (DPH), 6 DPH and 14 DPH respectively at 20 °C (Russell 2013). If the same pattern exists for the other species, one could assume that feeding would need to commence within two weeks of hatching. It is unclear what the very young fish feed on, but 5 cm *R. globiceps* feed on zooplankton (Bennett 1989). Young *S. emarginatum*, *P. blochii* and *B. inornata* rely heavily on algae (Le Chanteur and Griffiths 2003). The dentition confirms a split between *R. globiceps* and the rest and may explain the slightly later spawning in that species as their young rely on zooplankton. The habit of recruiting in estuaries also confirms the reliance on plankton rather than macrophytes for *R. globiceps*.

Autumn is the month of least sexual activity for all species except *P. blochii*, for which it is summer. *P. blochii* is known as winter spawner, following the building of gonads in summer when algae are most abundant.

4.3.7 Condition Factor

Investment in reproduction can occur before spawning (gametogenesis, territorial battles, nest building), during spawning (courtship) and after spawning (parental care). The investment cycle, as evidenced by condition loss, need not be aligned in the sexes. In *P. blochii* and *R. globiceps* the condition cycle does not vary between the sexes. Both sexes in these species expend their energy during gametogenesis and in roughly equal amounts – there being no territoriality, courtships battle nor parental care. Males in these two species compete through the production of sperm.

Condition varies between the sexes in *S. emarginatum* and *B. inornata*. Such variation suggests that the investment in reproduction by the sexes is not synchronised, and that male expenditure either precedes or lags that of the female. In *B. inornata* the annual drop in condition precedes that of the female, which suggests courtship battles. The fact that ripe and running males of *B. inornata* were never caught with baited hooks (Chapter 2), suggests that they are pre-occupied with courtship, above feeding, when their testes are ripe – unlike the case in *P. blochii* and *R. globiceps*. In *S. emarginatum* the decline in condition of the male's lags that of females which corresponds with male parental care. Although I cannot provide evidence in support of the courtship battle hypothesis for *B. inornata*, parental care among *S. emarginatum* is well known. *S. emarginatum* males build condition massively in autumn ahead of the winter spawning and nest defense.

In all species except *B. inornata*, female condition varies among seasons and female condition peaks in the season prior to peak spawning. The weak cycle in *B. inornata* reflects low annual spawning output and a lengthy spawning season. In contrast the cycle is strong in *S. emarginatum*, as one would expect with a short, intense spawning season.

4.3.8 Dimensions of life history trade-offs

Of more interest than the scale of the trade-offs are the dimensions long which they occur. With an opportunity to explore dimensions with only four species, further constrained by looking only at a few basic measurements, one will naturally only get a subset of all possible dimensions. Nevertheless, it is surprising to see at least four axes of variation in the comparison.

i. Semelparous-iteroparous.

None of the four species are truly semelparous, but there is a 7-fold variation in their reproductive lifespans. *S. emarginatum* spawns over a maximum of six season (three as females), *P. blochii* for 15, *R. globiceps* for 18 and *B. inornata* for 35. Do the recruits of these four species experience markedly different mortality profiles? I can only answer this question partially. *S. emarginatum* eggs are benthic, and the costly nest guarding habit more than likely reduces the mortality on the early life stages. This may be the trade-off. For pelagic eggs of the other three species, this first week is the most perilous, when filter feeders can reduce the cohort by two orders of magnitude in a week (Jennings *et al* .2009). *P. blochii* recruits are seen in abundance on the same shallow reefs as the adults, but *R. globiceps* have distinct nursery grounds and are strongly shoaling. *B. inornata* juveniles are nowhere abundant and do not shoal.

Not only are the number of reproductive years an important factor but also the length of the spawning season. *S. emarginatum* has the shortest season, and nest guarding could again be used as the explanation for its reduced perception of risk. Or equally it could be the cost of maintaining a nest, as suggested earlier. Perhaps nesting behaviour makes the species more vulnerable to predation, thereby truncating its life. Zsilavecz's (2005) observations of male *S. emarginatum* bravely fighting off intruders, surely suggests a penalty by way of adult mortality. One could imply a trade-off between parental care and adult mortality. The adult places itself at risk, to increase the survival of its offspring. There is no gender stereotyping here, as every *S. emaginatum* will get its turn to be the heroic male. In contrast, the pelagic spawners cast their eggs in the current, and live a long life. The adults pass the risk to their offspring.

The spawning season of *R. globiceps* is also short. I suggest that the trade-off here is migration, which I view as a surrogate for parental care. The adults of both sexes spend energy and increase mortality risk to place their eggs appropriately for the juveniles to reach a nursery ground, either estuaries on south coast (Griffiths *et al.* 2002) or moderately wave exposed shores on the west coast (Clarke 1995). As migration takes adults away from feeding grounds (Kerwath *et al.*2008), it cannot be a protracted process, i.e. spawning must happen quickly so that they can return to feeding grounds. *P. blochii* or *B. inornata* do not leave their reefs and as a result the risk for spawning in such locations must be high, as such reefs are carpeted with filter-feeders trying to catch their eggs. *P. blochii* or *B. inornata* spawning seasons are longer in compensation.

ii. Age at maturity vs maximum size

Much less variation is seen along this well documented dimension among the four species chosen for this study, than is found in the family as a whole. Age at maturity is either two or three in the four species studied. In the seabreams *L. lithognathus* and *P. rupestris*, however, we see late maturity (>6 y) coupled with massive body size (>25 kg). Their large size necessitates a different dietary niche, which would complicate the study of trade-offs. This is a proper trade-off, but it likely includes an influence on diet with implications for morphology and dentition. Large fish need an abundant source of protein – and the low calorific value of the invertebrates and algae eaten by the four species in this comparison is likely insufficient to sustain massive growth rates.

iii. Fecundity

Neither total nor life-time fecundity estimates are available for all species, but it would appear that life-time fecundity is not likely to vary as much as would be suggested by variation in female GSI. I have used GSI as an indication of batch fecundity (West 1990, Gunderson 1997). *S. emarginatum* attain the highest average female GSI in the spawning season, followed by *P. blochii*, *R. globiceps* and lastly *B. inornata*. The number of spawning seasons (spawning years x spawning seasons) in the life of a fish in each of these species follows the reverse order: *S. emaginatum* has the least and *B. inornata* the most. Because these closely related species have very similar ovarian structure and

oocyte size, their relative life-time fecundity is indicated approximately by the product of the GSI in the spawning season and the number of spawning seasons. Seabreams have been found to be indeterminate batch spawners, without exception (Chapter 2, Brouwer and Griffiths 2005). The trade-off appears to be between batch fecundity and the number of batches, such that total life-time fecundity is broadly similar among the four species. Gunderson (1997) reported a strong positive correlation between GSI and natural mortality, which must therefore be considered as a trade-off. His samples included 28 fish species across a number of families and, importantly, included a variety of maximum sizes, from 17 cm to 130 cm. Natural mortality is also a function of size. The four fish in this study, as I previously argued, are similar in size, body design and niche, and therefore not likely to vary much with regard to natural mortality in the same environment. For this reason, I do not consider natural mortality to explain the large variation in GSI among these four fish.

iv. Gonochorism vs protogynous hermaphroditism

The habit of changing sex among certain fishes is intriguing, but particularly so in seabreams. This family, like no other, has a mix of protandrous, protogynous and gonochoristic fishes (Buxton and Garratt 1990). Under what circumstances should a species show sex change? Warner (1988) informed us that the answer is straightforward: "*if the product of survival to a particular age and fecundity at that age increases with age faster in one sex than the other, then an individual that changes sex will have a higher life-time reproductive success than one that does not*". Is this answer useful when trying to understand why one of the four sympatric seabreams should be protandrous, while the remainder are rudimentary hermaphrodites? If I extended this comparison to include *Sarpa salpa* and *Diplodus capensis*, it would need to explain why we see protandry and protogyny in closely related, sympatric species. It is significant that the remaining species are rudimentary hermaphrodites, rather than gonochoristic, as it implies that they have the ability to change sex, should it be advantageous. Indeed, even within a seabream species we see different strategies among populations (De Mitcheson and Liu 2008). I contend that sex change in *S. emarginatum*, was simply a response to nesting behaviour and benthic eggs, which provided the size-advantage for males needed to meet Ghiselin's (1969) requirement of protogyny. But this explanation does not hold for other protogynous hermaphrodites,

such as *Chrysoblephus laticeps*.

In a polygamous mating system, where males compete for females, not all males will get to reproduce every year, and some might never reproduce. Such males are at a Darwinian disadvantage. The inefficiency of this system can be eliminated if the fish turn to protogyny, or if the sex ratio is altered. Polygamy might be the system that favoured the development of protogyny in three *Chrysoblephus* species (Buxton and Garratt 1990). The heavily skewed sex ratio, and the low male GSI in *B. inornata*, suggest a lack of sperm competition and polygamy by a rudimentary hermaphrodite. Without much knowledge of the polygenic control of sex determination and hermaphroditism, it would seem reasonable to suggest that a shift in the sex-ratio and shift to hermaphroditism are equally possible and equally likely, except for the Fischers principle which stands against the former option.

S. emarginatum and *B. inornata* eliminated this inefficiency in different ways, and selection has also driven them to have very different longevity. There is no clear link between longevity and reproductive type in the Sparidae. Short and long-lived examples of both reproductive types exist, e.g. *Crenidens crenidens* (Ahmed 2012) and *Petrus rupestris* (Smale 1988) are short- and long-lived species with separate sexes, respectively, whereas *Sarpa salpa* (Van der Walt and Mann 1998) and *Cymatoceps nasutus* (Mann *et al.* 2015) are short- and long-lived sequential hermaphrodites, respectively.

Whereas sex-change and heavily skewed sex ratios might seem odd to humans, I find that the lack thereof, at least in fish which are obviously predisposed to such strategies, needs scrutiny. I unfortunately have no simple explanation for its relative rarity. The maintenance of separate sexes in *R. globiceps* and *P. blochii* is curious, because it appears to be wasteful. Their males produce far more sperm than is needed.

I propose that for a seabream which adopts a migratory life-style such as *R. globiceps*, protogynous hermaphroditism is disadvantageous. The large migrant seabreams *Lithognathus lithognathus* (Bennett and Griffiths 1986, Bennett *et al*. 2017) and *Chrysoblephus gibbiceps* (Van Zyl 2013) maintain separate sexes, whereas their resident congeners (*L. aureti, L. momorus* and C. *laticeps*) are hermaphrodites (Holtzhausen 1999, Kallianiotis *et al*. 2005, Kerwath *et al.* 2000). A possible link between residency and hermaphroditism is the need to develop a social hierarchy among one or the other sex. Without any

compelling evidence outside the Sparidae, I would speculate that social hierarchies are more easily developed in a resident species, where fish can maintain aggression toward conspecifics as they do not rely on group cohesion. Migrants work cooperatively, usually in schools, for protection, feeding, navigation and swimming efficiency (Roff 1988). Migrants cannot also be aggressive toward each other, and for this reason sexual selection works more effectively by way of sperm competition – the male that collected the most energy produces the most sperm and has the greatest chance of fertilisation success. The migrant male competes without being aggressive to its conspecifics.

The link between movement behaviour and sexual strategy is backed up by the difference in growth parameters (Figuer 4.7). The difference in average slope is significant (n_1=15, n_2=11, t=3.65, P = 0.001). The hyper-allometric growth pattern of hermaphrodites suggest a robust fish with a sedentary life, whereas the hypo-allometric growth pattern of gonochorists suggests a long-streamlined fish adapted for migration.

The need for spawning migrants to maintain separate sexes may be because male and female fish migrate in schools, and for that reason need to be similar sized to travel long-distances at similar velocity. The sexes of sequential hermaphrodites are of unequal size and would not likely school very easily.

The reason for *P. blochii* maintaining separate sexes, a sex ratio only slightly less than one, and large testes, as opposed to a hermaphrodite model, is not easily explained as not all the facts are available. The movement behaviour of the species is unknown, other than an ontogenetic movement from shallow to deep reefs. Nevertheless, the co-existence of rudimentary hermaphrodites and protogynous hermaphrodites on the same reefs shows that these divergent strategies are equally adaptive.

v. Extent of variation on the life history triangle

Winemiller's (2005) triangular life history model depicts fish history strategies as lying somewhere along a continuous triangular plane between three pure strategies, namely Opportunist, Periodic and Equilibrium. How do the four seabreams spread out in the triangle? The axes of the model are juvenile survivorship, generation time, and fecundity. Low juvenile survivorship, high generation time and high fecundity characterise the *Periodic* strategy, which is the best description of each of the four species in this study, regardless of their differences. There is a spread within this corner of the triangle, however, mostly along the axis corresponding to generation time. The generation times (using the formulation provided by Simpfendorfer 2005), are 3.4 y (*S. emarginatum*), 8.0 y (*P. blochii*), 9.5 y (*R. globiceps*) and 10.1 y (*B. inornata*). Juvenile survivorship is lower in *S. emarginatum* than in the other three, on account of nest guarding, but life-time fecundity probably similar for each.

An important consequence of sequential hermaphroditism is that it effectively halves the number of years over which an individual can lay eggs and can make finding a mate difficult. Whereas a gonochoristic population is split into two sexes over all ages, the sequential hermaphrodite genders are split by age. Consider the case where a population produces one good year of recruitment after five consecutive bad years. As the cohort develops and becomes sexually mature, the gonochoristic fish in that cohort will spawn with each other and contribute to recruitment, thereby stabilizing the population. But in the sequential hermaphrodite, spawning within the cohort is impossible, as they are all the same sex, so there is no possibility of building on a good year of recruitment, particularly if such years are few and far between. In the hermaphrodite, spawning can only take place between cohorts, but if there are no good cohorts of the one sex, spawning will fail. The advantage of the *periodic* strategy is that only one or two good cohorts are needed to keep the recruitment high, as those cohorts will breed year after year, but in hermaphrodites this strategy is badly compromised

De Mitcheson and Liu (2008) found in their review that sequential hermaphrodites are common on tropical reefs, but rare in high latitudes and practically unknown in the pelagic environment. I contend

that the high variability of these last two environments requires a *Periodic* strategy and therefore precludes sequential hermaphroditism. Sequential hermaphroditism compromises the *Periodic* strategy. Bet-hedging is therefore traded off with the efficiency of hermaphroditism.

vi. Why are the strategies different?

Four life history patterns present themselves as successful among closely related, similar sized fish in the same area and habitat. I propose that this variation is reflective of true-life history trade-offs, as there is no environmental factor, or phylogenetic constraint, to explain their differences. Nevertheless, it still useful to consider why the divergence exists – just because they can be different, does not mean they must be different. In one possibility, the ancestors of each arrived at a common location, but failed to converge in their life histories, settling instead on different, but apparently equally successful strategies. In another, they evolved divergent life histories sympatrically, driven by competition. Competition might account for the differences, particularly at the juvenile stage. Whereas, I argue that the adults overlapped in diet and habitat, the vulnerable juvenile stages are separated in space (*R. globiceps*), habitat (*S. emarginatum*) and timing (winter-spring for *P. blochii*, and spring-summer for *B. inornata*).

4.4.1 Appendix

Appendix 4.1:Diet comparison between *R. globiceps, S. emarginatum, P. blochii and B. inornate* (present paper) in different areas in South Africa. By percent frequency of occurrence (*%FO*).

Species and Sources	*Rhabdosargus globiceps* (Buxton and Kok 1983)	*Pachymetopon blochii* (Pulfrich and Griffihs 1988)	*Spondyliosoma emarginatum* (Le Chanteur and Griffiths 2003)	*Boopsoidea inornata* Chapter 2 this Thesis
Areas	Mossed Bay and Algoa Bay	Dyer Island	False Bay	False Bay and Struisbaai
	%FO	%FO	%FO	%FO
Algae	-	34.19	8	26.6

Rhodophyta	-	-	4	18.3
Chlorophyta	2.3	-	4	10
Phaeophyta	1.2	-	-	-
Chordata				
Ascidiacea	-	1.78	10	11.6
Vertebrata (fish)	-	0.13	2	1.11
Arthropoda				
1. Crustacea	-	-	96	49.49
Amphipoda	3.5	64.3	96	27.2
Isopods	10.4	14.79	22	11.6
Ostracoda	-	9.63	22	7.22
Cirripedia	-	2.58	10	0.56
Tanaidacea	2.3	0.41	2	-
Megalopa	1.2	2.85	-	-
Mysida	-	9.63	10	20
Anomura	1.2	-	-	-
Stomatopods	-	2.58	2	-
Macrura	1.2	-	-	-
Copepoda	-	-	-	5.56
Decapoda	-	4.48	4	1.1
Cumacea	-	-	2	-
Unidentified crustacean	20.7	-	-	-
2. Pycnogonids	-	2.17	-	-

Appendix 4.1: Continued.

Species and Sources	Rhabdosargus globiceps (Buxton and Kok	Pachymetopon blochii (Pulfrich and	Spondyliosoma emarginatum (Le Chanteur and	Boopsoidea inornata Chapter 2 this

	1983)	Griffihs 1988)	Griffiths 2003)	thesis
Areas	Mossed Bay and Algoa Bay	Dyer Island	False Bay	False Bay and Struisbaai
	%FO	%FO	%FO	%FO
Mollusca	-	30.0	28	10.5
Gastropods	2.3	-	28	4.3
Pelecypods	11.5	-	-	-
Cephalopods	1.2	-	-	-
Bivalvia	-	-	6	4.4
Platyelminthes				
Polychaeta	-	13.98	6	25.5
Erantia	-	-	4	3.89
Sedentaria	-	-	2	1.11
Chaetopteridae	31.0	-	-	-
Echiuroids	-	0.27	-	-
Unidentified polychaete	9.1	-	-	20.56
Bryozoans	-	-	4	1.11
Echinodermata	-	3.0	6	43.3
Ophiuroids	5.8	2.17	-	19.44
Branching	-	-	4	-
Echinoidea	2.3	0.54	-	1.67
Criniods	-	2.31	6	27.78
Holothurians	-	0.14	-	3.89
Cnidaria				
Hydroids	-	29.58	22	1.67
Anemones	-	0.54	-	4.44
Gorgonacea	-	-	16	-
Nematodes	-	2.85	-	-
Sipunculids	-	1.90	-	2.7

Eggs	-	2.40	4	-
Unidentified remains	28.7	45.18	-	-

CHAPTER 5

Broadening perspectives on fish life histories

5. Conclusion

The study of *Boopsoidea inornata* was an interesting and necessary addition to the already rich information on the Sparidae. I believe it was overlooked for its small size and commercial insignificance, but it turned out to be a fascinating addition - a life history quite different from those already described. It is small and long-lived, with a broad spawning period. Having traded this for low annual fecundity, the species is a very much a *periodic* strategist, but not one that reaches the large sizes seen elsewhere in the family. It matures early, whereas the large ones mature late. Competition might have restricted its diet to invertebrates with low calorific content, and therefore a lack of protein to sustain a high growth rate.

B. inornata is a very conspicuous and numerous species on inshore reefs. It is very successful in South Africa, but it is not represented outside the region (nor is its genus), unlike several other small seabream genera that have pan-African distributions (*Acanthopagrus*, *Crenidens*, *Diplodus*, *Lithognathus*, *Polysteganus* and *Salpa*). This fact might point to a poor colonising ability. The species is too small to have been tagged (the tagging programme in South Africa discourages tagging of fish smaller than 1 kg), but the parasite study revealed a surprising degree of differentiation in the parasitic community over relatively short spatial scales. This surely suggests a low movement rate. Spatial variation in parasite communities of other small seabreams in South Africa have not yet been studied, and hence no direct comparison can be made. However, migratory fish species in South Africa have greater parasite uniformity (*Brama brama*, *Scomber japonicus*, *Thyrsites atun* and *Trachurus capensis*).

Another fact that suggests a residential life style is the reproductive characteristic of the species. I argue that *B. inormata* is a polygamist. Low male GSI points to lack of sperm competition, but there is no sequential hermaphroditism here. In a polygamous system, males are likely to aggressively secure access to females. In this case, such behaviour can only be speculated, but an additional fact – the

skewed sex ratio – suggests that aggression might be mitigated to some extent. However, Fischer's principle predicts a 1:1 ASR (Adult sex ratio) ratio, and it very difficult to think of a mechanism that would cause this ratio to be different. Indeed, experiments on silversides *Menidia menidia* showed how a population responded to a disturbance by restoring the sex ratio to 1:1 (Conover and Van Voorhees. 1990). A shift in the sex-ratio towards females should reduce the extent of, but not eliminate, the need for male aggression. The possibility of temperature control on sex determination, as suggested by the east-west shift in sex ratio needs further study for its many obvious implications.

The role of males is frequently overlooked in fisheries studies, which understandably tend to focus more on ovarian production than spermatogenesis. The size of the testes alone gives a clue of the type of spawning that may prevail and the social structure. The condition cycles also provide a hint at the same processes. The polygamous and sequential hermaphrodite had male and female cycles significantly out of synchrony, which can only attest to the existence of a male reproductive effort other than spermatogenesis. Courtship battles assist reproduction in assuring that the strongest genes are propagated. Nest guarding gives the young an important reprieve from otherwise high juvenile mortality.

Stergiou and Karpouzi (2002) found that the seabreams had the most diverse diet of any family in the Mediterranean. The dental morphology of the family is highly variable, with evidence of convergent evolution among lineages within the family (Orrell *et al.* 2002). Above all, seabream sexual strategies are the most variable of any vertebrate family, with gonochosrism, protogyny and protandry in the same genera (De Mitcheson and Liu 2008). This family provides excellent material for the study of life-histories.

The exhibition of life histories provided by four sympatric seabreams highlighted the variety of dimensions among which trade-offs can occur. Although I make the case that the variation measured is unaffected by phylogeny and environment, subtle differences in both these aspects are evident, but not sufficient to explain the extent and dimensions of the variation. I propose that this comparison provides evidence that multiple solutions to a single problem are possible, and that this serves as a counter-phenomenon to convergence and parallel evolution. This work needs to be repeated in other parts of the world and on other taxa.

Apart from the already well-described trade-offs involving fecundity, longevity and parental care, my work sheds some light on the advantages and disadvantages of sequential hermaphroditism. I propose that it is the efficiency of the mating system that gives sequential hermaphrodites the advantage. A male that can first act as a female, before he can get females of his own, is at a Darwinian advantage over a permanent male. But the interesting question here is why this strategy is not more common. *B. inornata* highlighted the value of the periodic strategy – the most common marine strategy among fish. The truncation of the female egg-producing life in sequential hermaphrodites might provide the clue here, as it compromises the ability of the population to overcome the variability that is so ubiquitous in the sea. Sequential hermaphrodites predominate at low latitudes on stable reefs and is absent in the variable pelagic realm (De Mitcheson and Liu 2008).

I suggest that this trade-off provides a satisfactory explanation for the apparent equivalence of success of sequential hermaphroditism in *S. emarginatum* and the separate sexes of *P. blochii* and *B. inornata*, in a region of the world that sits between the stability of the tropics and the more variable, seasonally pulsing mid-latitudes. These three species with markedly different life histories form the tightest grouping in Le Chanteur and Griffiths' (2003) analyses of species associations in False Bay. Migratory behavior sets *R. globiceps* slightly apart in their analysis, because of its temporary absence on the reefs. The migratory life-style also involves trade-offs – the energy needed for migration comes at a cost in terms of fecundity and length of spawning season (Roff 1988) and, I suggest, precludes hermaphroditism due to the need to maintain group cohesion. *R. globiceps* has the strongest schooling tendency of the four species I compared. Migration is more common in seasonal habitats of the high latitudes and the variable pelagic zone.

Regardless of whether my hypothesising has merit, the comparison highlights the range of options available to fish, and suggests that the study of trade-offs, typically involving only growth, fecundity, age at maturity and parental care, needs to be expanded to include categorical factors such as the various sexual strategies and movement behaviours.

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