Parasite assemblages of Cape horse mackerel (*Trachurus capensis* Castelnau, 1861) from the northern and southern Benguela.

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Minor dissertation

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DECLARATION

1. I know that plagiarism is wrong. Plagiarism is to use another's work and pretend that it is one's own work.

2. For this dissertation the Harvard convention for citation and referencing has been used. Each contribution to and quotation in, this dissertation from the work(s) of other people has been attributed, and has been cited and referenced.

3. This dissertation is my own work.

4. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work.

Jessica Le Roux **Date**

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CONTENTS

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Abstract

A survey of parasites infecting Cape horse mackerel, *Trachurus capensis* Castelnau, 1861, from both the southern and northern Benguela ecosystems was conducted to test the hypothesis of discrete stocks in each subsystem. One hundred and twenty five *T. capensis* of two size classes were collected off the coasts of South Africa and Namibia and their bodies and organs were examined for parasitic infections. Differences in parasite assemblages between smaller and larger *T. capensis* within each subsystem, between *T. capensis* of each size class from the two subsystems, and between larger fish collected in different seasons within the southern Benguela, were assessed. A total of twenty-nine parasite species were found infecting *T. capensis*. Ten of these were identified to species level (*Ceratomyxa australis, Davisia donecae, Ectenurus lepidus, Gastrocotyle trachuri, Goussia cruciata, Lernanthropus trachuri, Nybelinia lingualis, Rhadinorhynchus cadenati, Scolex pleronectis* and *Tergestia laticollis*), three to genus level *(Anisakis* sp., *Caligus* sp. and *Kudoa* sp.). Significant spatial differences in *T. capensis* parasites were observed, with larger fish differing in infection intensity and abundance of *Anisakis* sp. and infection intensity of *L. trachuri*. Significant spatial variation in parasites was also observed in smaller fish, which differed in *Anisakis* sp. abundance, *L. trachuri* infection intensity and abundance, *G. trachuri* abundance and *G. cruciata* infection intensity and abundance. Significant fish size effects on *T. capensis* parasites were also observed in both subsystems. *Anisakis* sp. infection intensity and abundance and *G. cruciata* abundance differed significantly between larger and smaller fish from the southern Benguela. Larger and smaller fish from the northern Benguela differed in *G. cruciata* infection intensity and abundance, *G. trachuri* abundance and *L. trachuri* abundance. No seasonal differences in parasites of larger *T. capensis* from the southern Benguela were observed. By using a discriminant function analysis parasite abundance data correctly assigned 92% of larger fish and 96% of smaller fish to their respective southern and northern Benguela sub-populations or stocks. These results show that analyses of parasites can be used to infer population structure and support the hypothesis of distinct *T. capensis* stocks in the northern and southern Benguela subsystems.

List of Figures

Figure 16: Monogenea parasites found in *Trachurus capensis* Castelnau, 1861: *Gastrocotyle trachuri* found on the gill (MacKenzie, 2012). Found in *T. capensis* from both the southern and northern Benguela.

Figure 17: Myxozoan species found in *Trachurus capensis* Castelnau, 1861: (A) *Ceratomyxa australis* in the gall bladder, (B) *Davisia donecae* found in the kidney and (C) *Kudoa* sp. found in the muscle (Al Quraishy. 2011). (A) and (B) found in *T.capensis* from both the southern and northern Benguela. (C) found only in *T. capensis* from the southern Benguela.

Figure 18: Nematoda parasites found in *Trachurus capensis* Castelnau, 1861: *Anisaki*s sp. (stained using Mexican red fabric dye) found in the body cavity (MacKenzie, 2012). Found in *T. capensis* from both the southern and northern Benguela.

Figure 19: Trematoda parasites found in *Trachurus capensis* Castelnau, 1861: (A) Digenea 2 found in the intestine, (B) Digenea 3 found in the pyloric caeca, (C) *Ectenurus lepidus* (stained using Mexican red fabric dye) found in the stomach (MacKenzie, 2012), (D) *Tergestia laticollis* (stained using Mexican red fabric dye) found in the intestine (MacKenzie, 2012) and (E) *Nybelinia lingualis l*arvae found in the kidney (Pascual et al., 1996). (D) and (E) found only in *T. capensis* from the southern Benguela. (A), (B) and (C) found in *T. capensis* from both the southern and northern Benguela.

Figure 20: Unknown parasite species found in *Trachurus capensis* Castelnau, 1861: (A) Unknown 10 found in the liver, (B) Black spot deposits found on the gonads and (C) Unknown 1 found in the body cavity. (A) and (B) found in only in *T. capensis* from the northern Benguela and (C) found in *T. capensis* from both the southern and northern Benguela.

Figure 21 (previous page): Comparisons of prevalence (%) of all parasite species found in *Trachurus capensis* Castelnau, 1861 from the southern and northern Benguela. (A) larger southern Benguela fish caught in August 2012 and larger northern Benguela fish caught in August 2011, (B) smaller southern Benguela fish caught in August 2012 and smaller northern Benguela fish caught in August 2011, (C) larger southern Benguela fish caught in August 2012 and smaller southern Benguela fish caught in September 2012, (D) larger northern Benguela fish caught in August 2011 and smaller northern Benguela fish caught in August 2011 and (E) larger southern Benguela fish caught in March 2012 and larger southern Benguela fish caught in August 2012. Note that the x-axes are not uniform.

Figure 22: Box and whisker plots showing mean (*modal) infection intensity of six parasite species in *Trachurus capensis* Castelnau, 1861 from the southern and northern Benguela. (A) *Anisakis* sp., (B) *Gastrocotyle trachuri,* (C) *Lernanthropus trachuri,* (D*) *Goussia cruciata,*. (E) **Davisia donecae* and (F) **Ceratomyxa australis.*

Figure 23: Box and whisker plots showing mean (*modal) parasite abundance of six parasite species in *Trachurus capensis* Castelnau, 1861 from the southern and northern Benguela.
(A) *Anisakis* sp., (B) *Gastrocotyle trachuri,* (C) *Lernanthropus trachuri,* (D) **Goussia cruciata,* (E) **Davisia donecae* and (F) **Ceratomyxa australis.*

List of Tables

Chapter 1: Introduction and Literature Review

Overview

Upwelling systems are very nutrient rich, stimulating high primary productivity and in turn supporting higher trophic species (Hutchings et al., 2009). The Benguela current found on the western coast of southern Africa is one of these highly productive upwelling systems. An additional feature of the Benguela is the Luderitz upwelling cell, which is located roughly offshore between the borders of South Africa and Namibia (Lett et al., 2007). The Benguela is divided into north and south subsystems by the Luderitz upwelling cell. This extreme upwelling cell brings very cold water to the surface and causes a physical and subsequent biological boundary which is thought to provide an effective barrier to pelagic organisms due to cold and offshore advection. It is unclear how strong this boundary is and if particular species are able to move across it.

Trachurus capensis Castelnau, 1861 is found within the Benguela system. The distribution of the adult population of *T. capensis* in South African waters is found mostly along the south coast of South Africa especially on the Agulhas Bank while on the west coast juveniles dominate (Hecht, 1990). However, Mc Laverty (2012) also identified the presence of a small adult population in the St. Helena Bay area on the west coast. In South Africa *T. capensis* is targeted using mid-water trawls. *Trachurus capensis* juveniles are caught as by-catch in the pelagic purse-seine fishery while adults are caught as by-catch in the hake (*Merluccius capensis*) directed demersal trawl in South Africa (DAFF, 2012). In Namibian waters smaller sized *T. capensis* are found in the north near Kunene River and adults everywhere further offshore (Krakstad, 2001; Mundjulu, 2009). In Namibian waters *T. capensis* has the highest biomass and the highest catch of all fish species found there. The pelagic purse-seine and mid-water trawl both target *T. capensis* in Namibian waters. This fishery constitutes a significant amount of the national wealth of Namibia.

Trachurus capensis is not only economically important but ecologically significant in the Benguela ecosystem as well. Due to their large biomass, they exert a top-down control on prey species such as euphausiids, polychaetes, chaetognaths, squid, various other crustaceans and fish, and a bottom-up control on predators such as Cape hakes, *Merluccius capensis* and *M. paradoxus,* as well as fish such as snoek, *Thyrsites atun*, and marine mammals (Pillar et al., 1998).

There has been some debate over whether the south and west coast populations of *T. capensis* in South African waters formed separate stocks, but genetic work by Naish (1990) showed that these stocks are seemingly not genetically distinct. Currently there are two recognised stocks of *T.*

capensis within the Benguela system, these being the southern Benguela population and northern Benguela population, divided largely by the Luderitz upwelling cell. However, little is known about the mixing between these stocks and whether these are indeed biologically separate stocks. Although it is strongly believed that there are southern and northern Benguela stocks of *T. capensis* and these are managed as separate stocks, further testing may be required. Mixing is important to understand, as fluctuations in one stock could lead to changes in another. It is also possible that the increase in abundance of larger *T. capensis* on the west coast is the result of the southward movement of fish from the northern Benguela (Barange et al., 1998). It is important to understand the structure of the stocks of *T. capensis* as well as the levels of mixing and integrity of these stocks for the purpose of fisheries management.

Naturally any economically important fish species requires sensible management strategies and the more information available about the distribution and stock structure of a species, the better management strategies can be implemented. Stock identification will become more essential due to an emphasis on management that now considers stock complexity within areas that were previously thought to contain a single stock (Stephenson, 1999). "This new emphasis on stock complexity is necessary if management is to comply with a precautionary approach to fisheries management" (Stephenson, 1999).

Methods used to determine stock structure include the analysis of distribution and abundance data, morphological variations, variations in life history traits and genetic information. Stock structure can also be inferred from the results of tagging studies, which use either artificially implanted tags or naturally occurring tags, such as parasites.

The main application of parasitology in fisheries science is the determination of population structure and stock discrimination. This is called using a parasite as a biological tag or "biotagging" (MacKenzie and Abaunza, 1998; Mosquera et al., 2003). Different parasite species, communities and different levels of infection can be used to infer population characteristics and structure. Therefore, having a complete understanding of parasite species infecting *T. capensis* could contribute to determine population structure.

Parasitic species infecting fishes from the genus *Trachurus* have been well documented throughout the world and have been used in applied marine studies as part of multidisciplinary approaches to stock discrimination (MacKenzie et al., 2008). In particular a lot of work has been done on the parasites of *Trachurus trachurus* Linnaeus, 1758. As an example the HOMSIR project (Horse Mackerel Stock Identification Research) was a multidisciplinary international project that aimed at determining the stock structure of *T. trachurus* in European waters. The HOMSIR project integrated

information from a variety of different approaches to identify stocks. These included methods using molecular markers, levels of genetic variability, estimation of gene flow between populations, body morphometrics, otolith shape analysis, parasites as biological tags and lastly, life history traits such as growth, reproduction and distribution (Campbell, 2008). MacKenzie et al. (2008) used the parasitic species to confirm the three sub-populations found in the Mediterranean Sea by comparing mean parasite abundances of two parasite species. Much less is known about parasitic species associated with other *Trachurus* species.

Project aims

The aims of this project were to complete surveys of all parasite species infecting *T. capensis* in southern Africa and to assess if there is a difference between parasite assemblages in *T. capensis* in the southern and northern Benguela. This will provide more information to help determine if indeed the southern Benguela and northern Benguela populations are separate stocks. The null hypothesis is that there is no difference between the southern Benguela and northern Benguela parasite populations of *T. capensis*. This project also assessed if there is a difference in parasite assemblages between *T. capensis* size classes within each system and if seasonality plays a role in changing parasite assemblages in the southern Benguela.

Literature review

Pelagic species

Small to medium pelagic fish dominate catches in coastal and oceanic upwelling systems (Fréon et al., 2005). These fish provide a considerable amount of income for many developing countries due to their abundance especially in the four major upwelling regions, despite their typically low commercial value (Fréon et al., 2005; Worm et al., 2009). Pelagic fish move freely in the water-column where they spend the majority of their time. While this is the case for most, a few species (e.g., horse-mackerel and mackerel) feed on, or near the bottom of the ocean floor. Small to medium pelagic species often represent the majority of fish biomass in marine ecosystems, especially in the very productive eastern boundary currents (Worm et al., 2009). A total of 186 fish species are exploited by world pelagic fisheries, however 50% of total pelagic landings are represented by only seven species (*Engraulis ringens, Clupea harengus, Sardinops melanostictus, Sardinops sagax, Scomber japonicus, Mallotus rillosus,* and *Trachurus murphyi*) (Fréon et al.,

2005). Most fisheries that target small to medium pelagic species are able to make large catches with efficient gear because of the shoaling behaviour of pelagic fishes. Purse-seining is the most efficient method for catching surface schooling small pelagic species, while semi-pelagic trawls and bottom trawls are used to catch other small and medium-sized pelagic fish (Fréon et al., 2005).

The genus *Trachurus* Plumier, 1801

"Mackerel" is a common name used for a grouping of a number of different pelagic fish species. This grouping is not particularly clear, however, it does include four families. These are, *Scombridae* which is considered the true mackerel family and has about 30 species, the family *Gempylidae* also known as snake mackerel which has approximately 5 species, *Hexagrammidea* which has two species and lastly the *Carangidae* family, otherwise known as Jack mackerel, constitutes 15 species from the genus *Trachurus* (Table 1). There have been many changes to the systematics of the genus *Trachurus* over the decades, currently 15 species are recognised (Suda et al., 1995).

Table 1: List of species of the genus *Trachurus* Plumier, 1801 including their scientific and common names (adapted from Suda et al. (1995)).

Species name	**Common name**
Trachurus aleevi Aleevi, 1956	Unknown
Trachurus capensis Castelnau, 1861	Cape horse mackerel
Trachurus declivis Jenyns, 1841	Greenback horse mackerel
Trachurus delagoa Necrassov, 1970	African scad
Trachurus indicus Necrassov, 1966	Arabian scad
Trachurus japonicus Temminck and Schlegel, 1844	Japanese jack mackerel
Trachurus lathami Nichols, 1920	Rough scad
Trachurus longimanus Norman, 1935	Crozet scad
Trachurus mediterraneus Steindachner, 1868	Mediterranean horse mackerel
Trachurus murphyi Nichols, 1920	Chilean jack mackerel
Trachurus novaezelandiae Richardson, 1842	Yellowtail horse mackerel
Trachurus picturatus Bowdich, 1825	Blue jack mackerel
Trachurus symmetricus Ayres, 1855	Pacific jack mackerel
Trachurus trachurus Linnaeus, 1758	Atlantic horse mackerel
Trachurus trecae Cadenat, 1950	Cunene horse mackerel

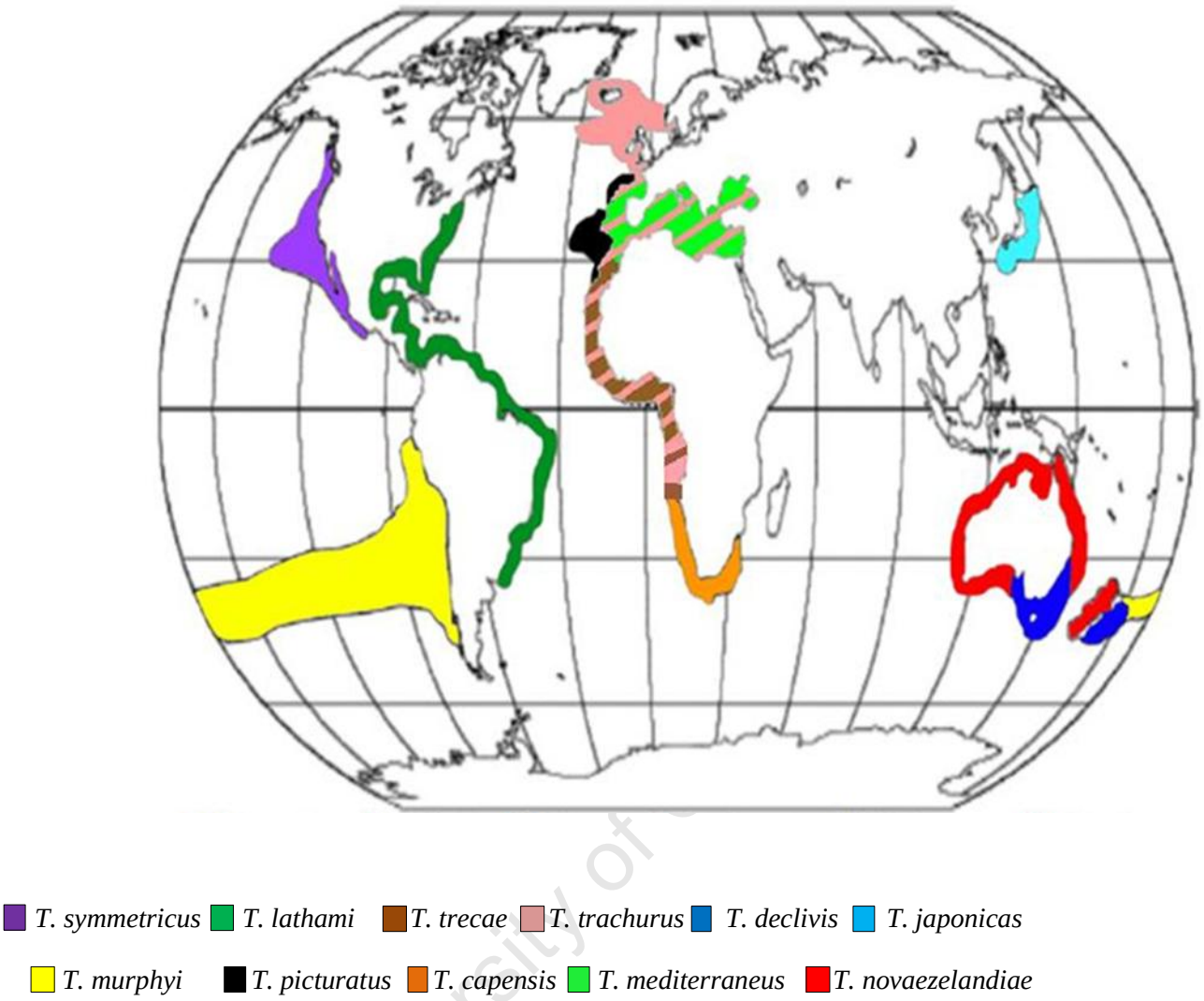


Figure 1: Map showing the distribution of 11 species from the genus *Trachurus* Plumier, 1801 (adapted from Cárdenas et al. (2005)).

The species of the genus *Trachurus* are widely distributed and are found along the coasts and throughout temperate, tropical and subtropical seas (Cárdenas et al., 2005) (Figure 1). There has been some debate on the number of *Trachurus* species. Nekrasov (1976) considered *T. capensis* to be a subspecies of *T. trachurus*, therefore reducing the number of recognised species to 14 (Cárdenas et al., 2005). While, some believed *T. capensis* to be its own species others recognized that the current status of *Trachurus longimanus* in the genus is questionable given that it is considered a synonym of *Trachurus picturatus* (Cárdenas et al., 2005).

Most of the 15 *Trachurus* species have commercial significance with the total catch growing significantly since 1974 (Suda et al., 1995) (Table 2). *Trachurus murphyi* has the highest catch of all species from the genus *Trachurus* and is found in the south Pacific off the coasts of Chile and Peru. While the majority of this catch is caught by Chilean fisheries, China and Peru also have a large stake in the total catch (FAO, 2012). *Trachurus trachurus* is among the most important fishing resources in Iberian waters (Murta, 2000) and is targeted by a large number of nations. *Trachurus japonicas* is economically important to Japan, China and Taiwan (FAO, 2012). *Trachurus capensis* is caught by vessels from Namibia, Poland, Russian Federation, South Africa, Spain and the Ukraine. Namibia catches the greatest proportion of the global total catch of *T. capensis (*FAO, 2012).

Table 2: World catch data of all species from the genus *Trachurus* Plumier, 1801 (2001-2010) showing highest to lowest catch in tons (FAO, 2012).

Species of Trachurus	**Year**									
	2001	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**
Trachurus murphyi	2 528 924	1 750 078	1 797 415	1 936 200	1 754 995	1 992 783	1 992 410	1 468 293	1 287 178	728 301
T. capensis	354 046	386 361	404 930	352 965	360 389	334 928	233 400	223 156	233 505	231 396
T. japonicus	235 874	229 539	317 332	308 198	403 348	328 781	380 178	260 265	216 586	206 210
T. trachurus	249 953	211 752	208 810	205 434	218 957	210 817	204 357	184 340	243 467	206 785
T. trecae	81 771	65 937	39 155	37 821	31 434	34 102	37 276	46 837	16 208	15 912
T. medierraneus	20 459	23 924	23 326	23 779	18 782	19 687	28 129	26 773	24 929	18 595
T. declivis	7 730	6 301	27 378	26 095	1 991	21 566	23 386	411	469	284
T. picturatus	1 509	5 675	4 013	4 076	2 303	4 177	5 502	5 692	5 698	4 707
T. lathami	412	458	1 042	770	1 456	1 290	2 609	1 912	1 938	1 724
T. symmetricus	3 839	1 026	231	2 302	608	1 500	2 443	426	270	705
Others	407 970	345 948	278 128	379 048	465 588	389 421	346 897	411 753	411 722	458 203

The Benguela ecosystem

Two species in the genus *Trachurus* are found in the Benguela ecosystem, these being *T. capensis* and *T. trecae*. The Benguela is one of the four major eastern boundary upwelling systems in the world (Boyer and Hampton, 2001; Axelsen et al., 2004). Due to the south-easterly winds that push surface water offshore, upwelling occurs and brings cold, nutrient rich water with it (Hutchings et al., 2009). It is also important to note that there are two stratified subtropical boundary regions, on either side of the Benguela upwelling region (Hutchings et al., 2009). Firstly the Angola-Benguela front which shifts seasonally, can be described as a subtropical transition zone located between the equatorial Atlantic and the upwelling system. Secondly, the Agulhas current in the south which brings warm temperate water to the south coast of South Africa (Lett et al., 2007; Hutchings et al., 2009) (Figure 2).The Benguela is subdivided at 26^0S by the powerful Luderitz upwelling cell (Lett et al., 2007; Hutchings et al., 2009). The southern Benguela region is typified by a seasonal, pulsed wind-driven upwelling with warm Agulhas water offshore (Hutchings et al., 2009). The southern Benguela if further divided into two regions, the west coast of South Africa which experiences coastal upwelling and the south coast of South Africa which is a temperate shelf region. The northern Benguela shelf is a typical coastal upwelling system with equator-ward winds, cold water, high plankton biomass and moderate to high fish biomass (Hutchings et al., 2009).

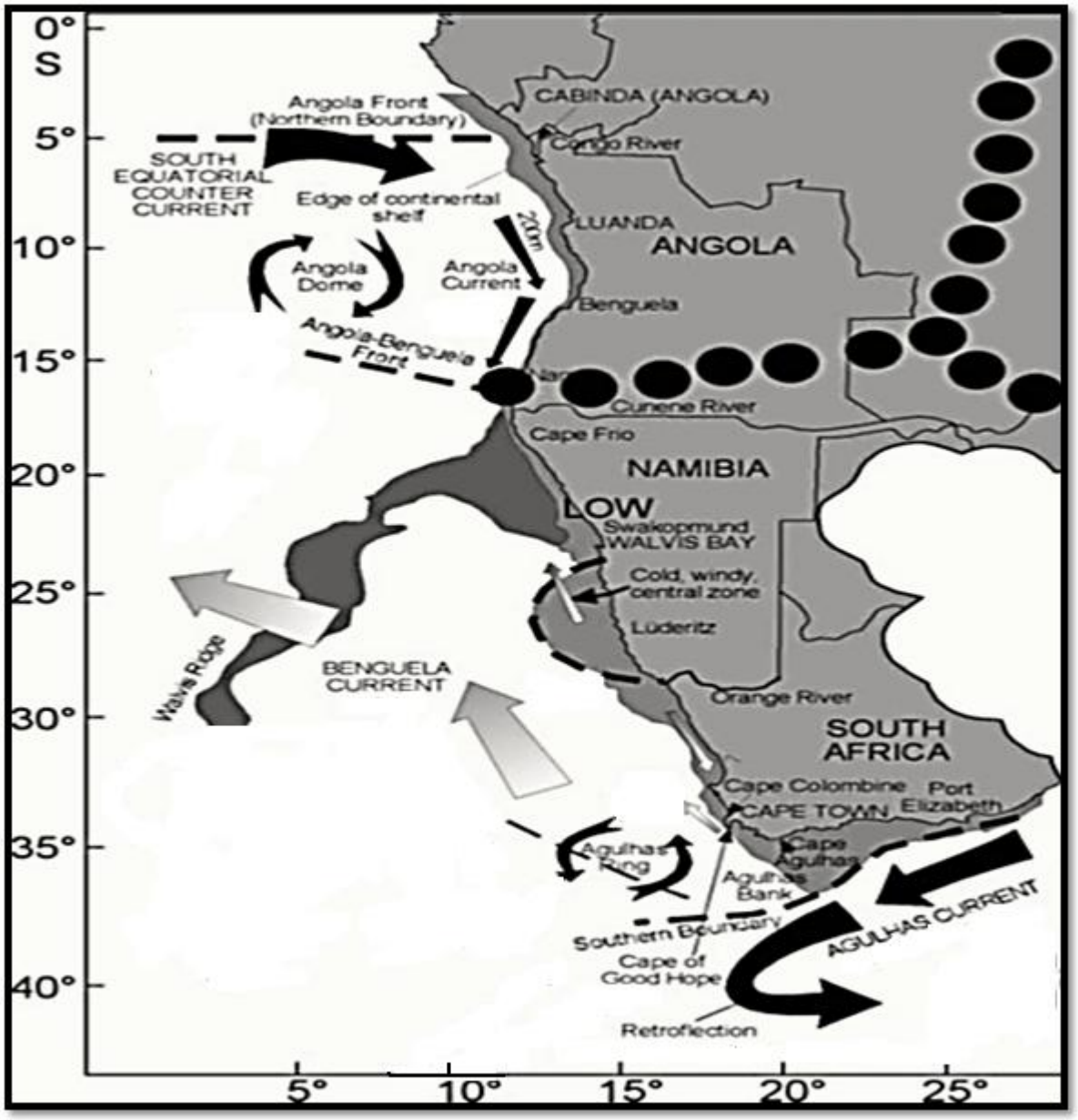


Figure 2: The Benguela upwelling ecosystem depicting large scale oceanic features. Warm tropical water is advected southwards in the Angola and Agulhas Currents to form intense mixing areas on the northern and southern boundaries of the Benguela (adapted from Hutchings et al., 2009).

***Trachurus capensis* Castelnau, 1861**

Trachurus capensis (Figure 3) is an important species in the Benguela ecosystem (Figure 5). Found along both the South African and Namibian coasts, *T. capensis* is distributed from Port Alfred on the south coast of South Africa to the northern border of the Benguela (being Tombwa in southern Angola) (Axelsen et al., 2004).

In South Africa the largest concentrations of adult fish are found on the Agulhas Bank, at the continental shelf break (Barange et al., 1998). Barange et al. (1998) examined the distribution of *T. capensis* by analysing pelagic surveys on the south and west coasts of South Africa, which showed differences in the distribution of *T. capensis* by size-class. Recruits (total length less than 10 cm) were generally limited between the Orange River mouth and Mossel Bay, whereas the majority of adults (larger than 30 cm) were east of Mossel Bay and juvenile fish (10-20 cm) were concentrated inshore along the coasts of the western and southern Cape (Barange et al., 1998) (Figure 4). The distribution of *T. capensis* does have some seasonality as *T. capensis* appear to be more widespread in summer months compared to winter months, when they tend to move south (Barange et al., 1998). Mc Laverty (2012) showed that *T. capensis* show a clear eastward shift with age as described by Barange et al. (1998), however Mc Laverty (2012) also identified the presence of a small adult population in the St. Helena Bay area on the west coast (Figure 7). It was also discovered that the extent of the south coast recruitment is much greater than previously thought (Mc Laverty, 2012).

Trachurus capensis also shows size-specific (or size-based) distribution patterns in Namibian waters with the smaller sized fish being found North near the Kunene River and the adults being found further offshore at the 200 to 500m isobaths (Figure 8) (Krakstad, 2001; Mundjulu, 2009). The main concentrations of fish are found in the north from around 17°00'S to 20°00'S (Krakstad, 2001). Axelsen et al. (2004) describe an expected migration of adult fish from Namibia to South Africa waters and also a return of juvenile fish from South African waters suggesting *T. capensis* from the southern and northern Benguela are not separated at Luderitz.

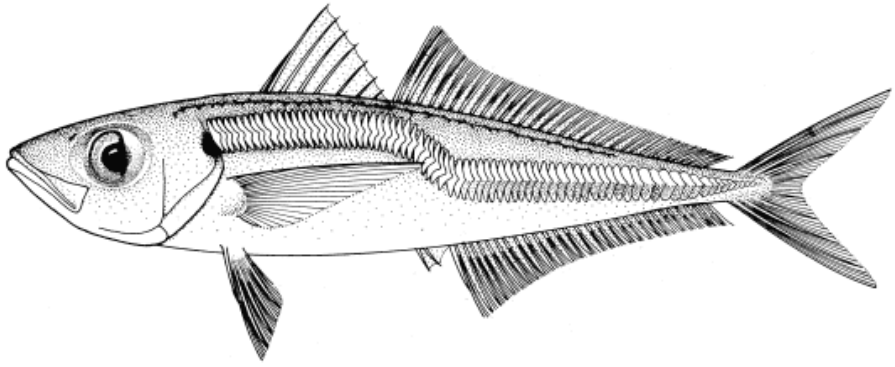


Figure 3: Drawing of *Trachurus capensis* Castelnau, 1861 (FAO, 2013).

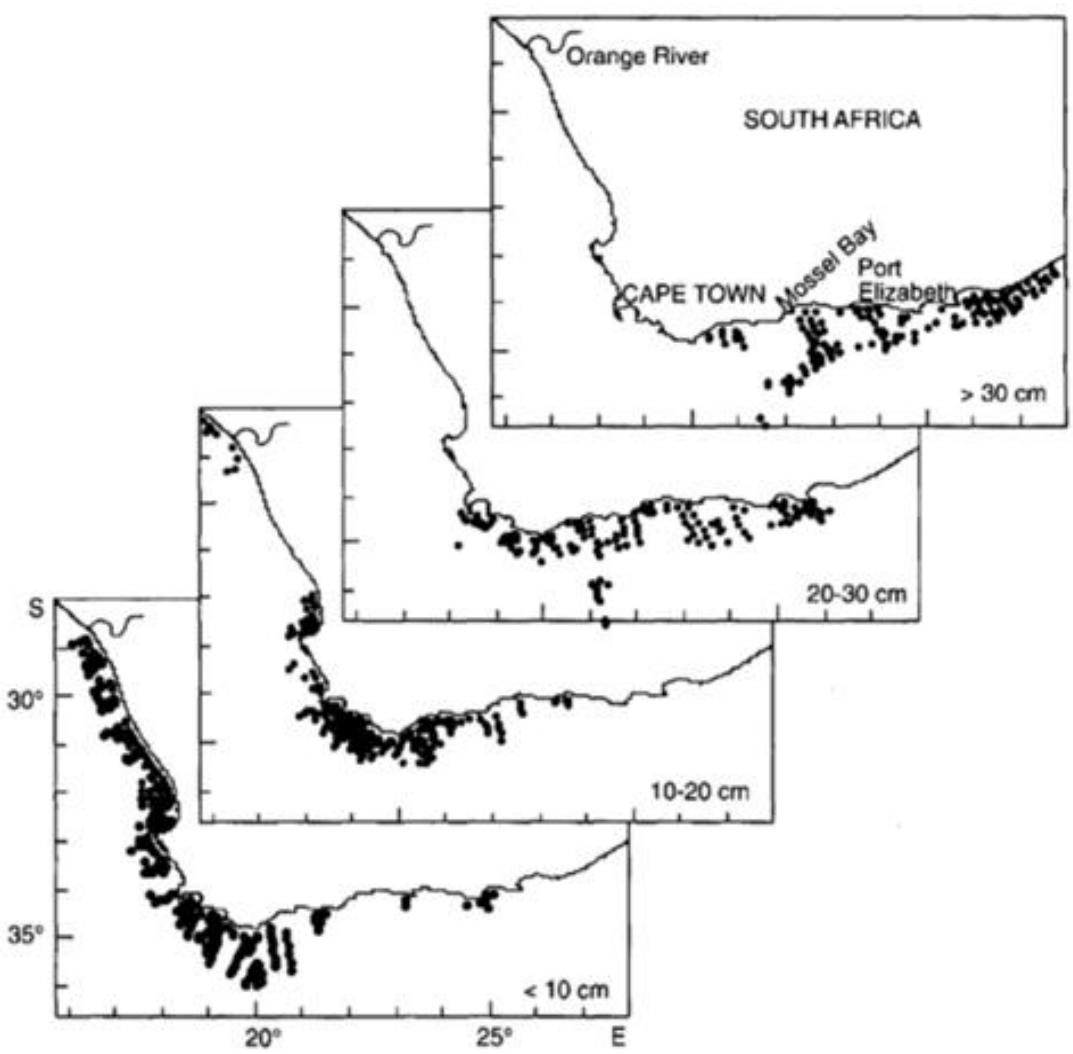


Figure 4: Distribution of the *Trachurus capensis* Castelnau, 1861 in South African waters by size class derived from all acoustic/midwater trawl surveys carried out in the period 1984-1996 (Barange et al., 1998).

During the day, *T. capensis* generally remain close to the sea bed but rise up off the sea bed at night and perform a nocturnal vertical migration into mid-water (Pillar et al., 1998; Axelsen et al., 2004). This migration often complicates fishing methods as well as acoustic surveys of abundance. The reason for this daily migration was initially thought to be purely as a result of feeding strategies, however more recent evidence suggests the migration may be caused by the thermal variations in the water (Pillar et al., 1998; Axelsen et al., 2004). Other suggested reasons for the migration are predation avoidance and or energy benefits (Pillar et al., 1998;

Krakstad, 2001). As there are a multitude of causal factors involved, vertical migration may vary spatially and temporally in South African waters.

Off Namibia, 95% of the diets of adult *T. capensis* comprise euphausiids, whereas off the west coast of South Africa the species feeds opportunistically on euphausiids, polychaetes, chaetognaths, squid, various other crustaceans and fish (Boyer et al., 2001). These fish are an important component of the ecological system as they are a food source for top predators. The species represents an important food resource for fish, especially the Cape hakes *Merluccius capensis* and *M. paradoxs* as well as for marine mammals (Crawford, 1989; Pillar et al., 1998). On the south coast of South Africa, *T. capensis* constitute up to 60% of the day time diet of large hake, while snoek (*Thyrsites atun),* cetaceans and the Cape fur seal (*Arctocephalus pusillus pusillus)* are also identified as predators of *T. capensis* (Pillar et al., 1998).

The South African fishery for *Trachurus capensis* Castelnau, 1861

Currently, *T. capensis* is caught in three South African fisheries, the mid-water-trawl and as by-catch in the hake-directed demersal trawl and small pelagic purse-seine fisheries. Historical catches of South African *T. capensis* from 1950 to 2010 have varied greatly (Figure 5). The *T. capensis* fishery is managed in terms of a Precautionary Maximum Catch Limit (PMCL). The PMCL has fluctuated between 22 000 and 54 000 tons since 1990 (DAFF, 2012). The PMCL has been maintained at 44 000 tons in recent years and accommodates both mid-water-directed and by-catch in the hake-directed demersal trawl sector (DAFF, 2012; Mc Laverty, 2012). Currently the F. V. Dessert Diamond catches 85% of the allocated PMCL (Mc Laverty, 2012). 12 500 metric tons of the PMCL of 44 000 metric tons is allocated to the demersal trawl fleet which catches adult by-catch on the south and west coasts (Mc Laverty, 2012). Juvenile *T. capensis* are by-catch in the surface pelagic purse-seine fishery on the west coast where a 5 000 tons precautionary upper catch limit (which is not part of the PMCL) is enforced (DAFF, 2012; Mc Laverty, 2012). Management of the *T. capensis* resource in South African waters is hampered by a lack of data, particularly the lack of suitable time-series of abundance indices (DAFF, 2012). Estimates of both the adult and juvenile stocks are uncertain due to the high variability in acoustic estimates

(Kerstan and Leslie, 1994; Berange et al., 1998). This is often due to the vertical migration of the *T. capensis* and so the index most likely underestimates the size of the resource (DAFF, 2012). Consequently, less is known about the status and productivity of the resource in comparison to other South African resources such as hake, sardine and anchovy (DAFF, 2012).

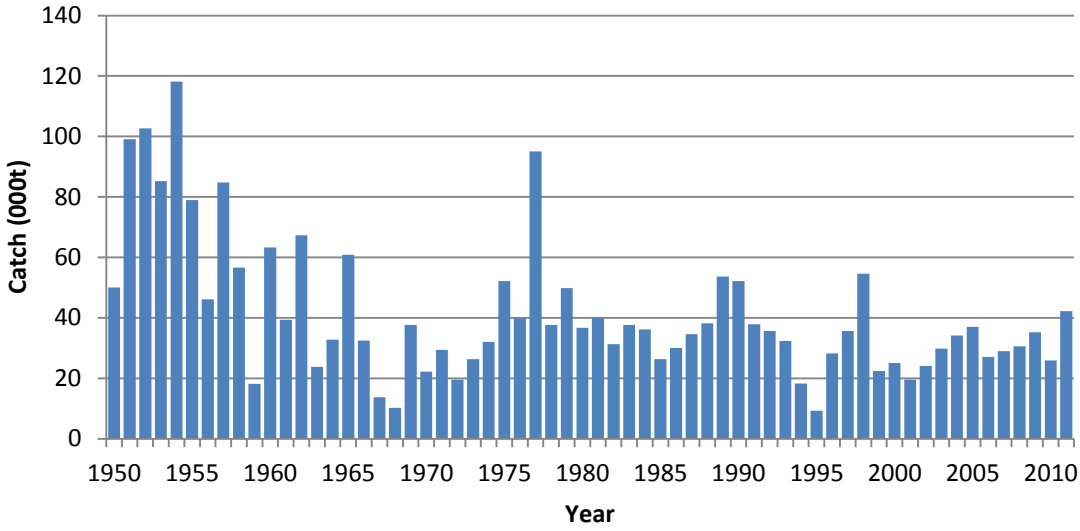


Figure 5: Historical catches of South African *Trachurus capensis* Castelnau, 1861 (in 000s of tons) from 1950 to 2010 (Roux et al., in press).

The Namibian fishery for *Trachurus capensis* Castelnau, 1861

Fisheries have contributed considerably to the national exports and income, and they constitute a significant component of national wealth since Namibia's independence in 1990 and the establishment of an Exclusive Economic Zone (Wilhelm et al., 2008). *Trachurus capensis* is the second highest economic contributor to the fishing industry after Cape hake in Namibia even though it has the highest stock volume and catch of all fish species in Namibian waters and this is because of its low market value (Mundjulu, 2009; Kirchner et al., 2010). In 2006, the landed value for fishmeal and frozen fish was N$7 116 (1US$ ~ N$7.10) and N$2 000 per ton respectively, resulting in a total landed value of about N$800 million for *T. capensis* (Kirchner et al., 2010).

Pelagic purse-seine and mid-water trawl fisheries catch *T. capensis* in Namibian waters (Boyer and Hampton, 2001; Kirchner et al., 2010). The *T. capensis* landed are generally sold as frozen whole product or converted to fishmeal (Kirchner et al., 2010). Catches were small

in the first years of exploitation (1960s), averaging 64 000t annually (Figure 6). The acoustic survey estimates are used as a relative index and form part of a data set used in an age-structured production model to determine the state of the stock (Axelsen et al., 2003; Kirchner et al., 2010). A Total Allowable Catch (TAC) of 500 000t was set in 1980, but only for the non-local mid-water trawl fleet, leaving catches by the local purse seine fleet unrestricted until 1992 (Kirchner et al., 2010). In 2008, the stock was thought to be under severe stress and estimated to be at a level of about one-third of Maximum Sustainable Yield, so TACs were decreased from 360 000 to 230 000t (Kirchner et al., 2010). Since then, the acoustic survey estimates and the Catch Per Unit Effort (CPUE) series have shown a remarkable improvement in stock biomass. Indeed, the CPUE data for 2009 and 2010 are higher than ever recorded (Kirchner et al., 2010). Some 10–15% of the TAC is now generally allocated to the purse-seine fleet, which catches mainly smaller fish (generally less than 17 cm), most of which are immature (Kirchner et al., 2010).

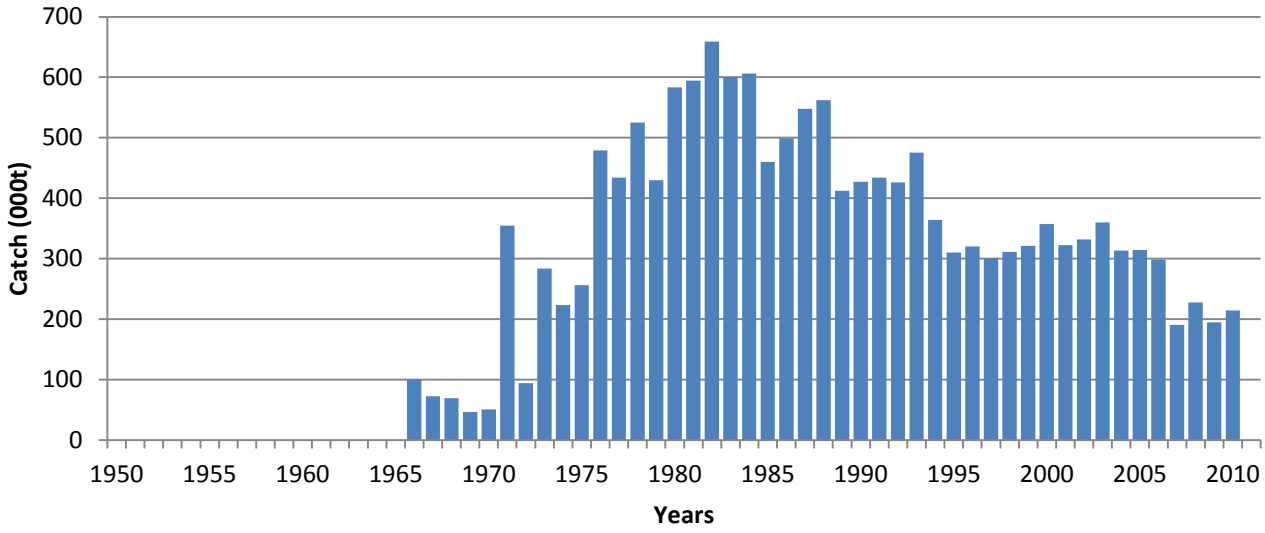


Figure 6: Historical catches of Namibian *Trachurus capensis* Castelnau, 1861 (in 000s of tons) from 1950 to 2010 (Roux et al., in press).

Life history of *Trachurus capensis* Castelnau, 1861

Very little research has been conducted on the life history strategy and basic ecology of *T. capensis*. *Trachurus capensis* appear to have two major spawning peaks in South African waters, although the timing seems to vary between the eastern and western Agulhas Bank (Naish et al., 1991; Barange et al., 1998). Peak spawning was documented in June and

November for the eastern bank, whereas August to February is the main spawning period on the western Bank (Barange et al., 1998; Mc Laverty, 2012). According to new research, spawning occurs indeterminately and intermittently in batches throughout the year with two peaks May to August and October to January (Mc Laverty, 2012). It is likely that *T. capensis* recruit in the numerous bays on the south coast of South Africa. During summer, a substantial proportion of the eggs and larvae from the western and central Agulhas Bank would be transported northwards in the shelf-edge jet current along the west coast (Barange et al., 1998) (Figure 7). Once mature the fish move offshore and move back to the south coast and Agulhas Bank. Hecht (1990) conducted macro- and microscopic examinations of the gonads showing that the fish begin to mature at 29 cm. The sex ratio of a sample of the population was 1:1 (Hecht, 1990). An eastward migration was noted, which may take more than a year to complete, and is probably enhanced in winter by the prevailing easterly flow (Barange et al., 1998). Once matured, fish enter the spawning cycle. *Trachurus capensis* older than 3-4 years seem to have an affinity for the shelf-edge region of the eastern Agulhas Bank (Hecht, 1990; Barange et al., 1998). The distribution patterns of *T. capensis* described here suggest that migratory routes may take several years to complete, with old fish migrating more extensively than juvenile fish (Barange et al., 1998). Migrations are ecologically significant as they can affect spawning and foraging success, which is influenced by environmental conditions in the particular area. The biomass of *T. capensis* on the west coast is approximately five times smaller than that on the south coast (Barange et al., 1998).

The small adult population in St. Helena Bay observed by Mc Laverty (2012) suggests not all recruits from the west coast return to the Agulhas Bank. Large fish (greater than 10 cm TL) are common across the Agulhas Bank, with larger size classes (greater than 20 cm TL) often found further east, emphasizing the eastward shift with age (Mc Laverty, 2012) (Figure 7).

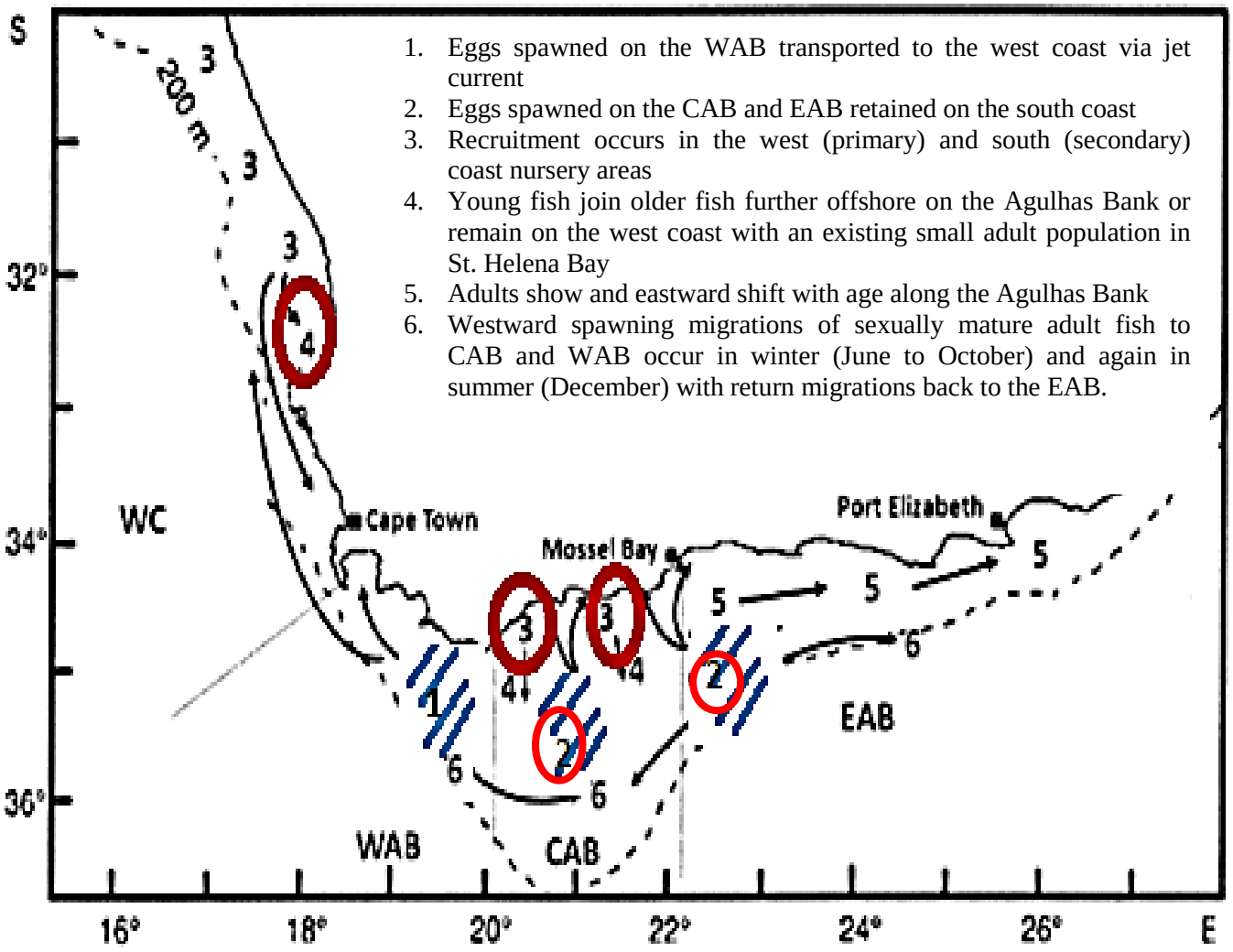


Figure 7: Updated (from Barange et al., 1998) diagram of the life history strategy of *Trachurus capensis* Castelnau, 1861 in the southern Benguela (Mc Laverty, 2012). WAB, CAB and EAB = western, central and eastern Agulhas Bank, respectively, and WC = west coast (separated by lines). Blue areas indicate spawning areas while the red circles indicate main changes to *Trachurus capensis* life history proposed by Barange et al. (1998).

The life history strategy of *T. capensis* in Namibian waters is mostly the same as *T. capensis* in the southern Benguela; however, distributions are different (Figure 8). Surveys of eggs and larvae off Namibia show that spawning is concentrated in the north in the mixing zone of warm oceanic water and cool coastal water, between October and March. The timing of spawning is closely linked with the duration and intensity of mixing (Boyer et al., 2001). Spawning that occurs in the north results in higher numbers of recruits found in the north near the Kunene River mouth. Juvenile *T. capensis* live inshore of the 100m isobaths and when mature they move northwards and offshore to spawn (Boyer and Hampton, 2001; Krakstad, 2001). Adults generally occur north of 21^0S but migrate southwards especially in winter (Boyer and Hampton, 2001; Krakstad, 2001) (Figure 8).

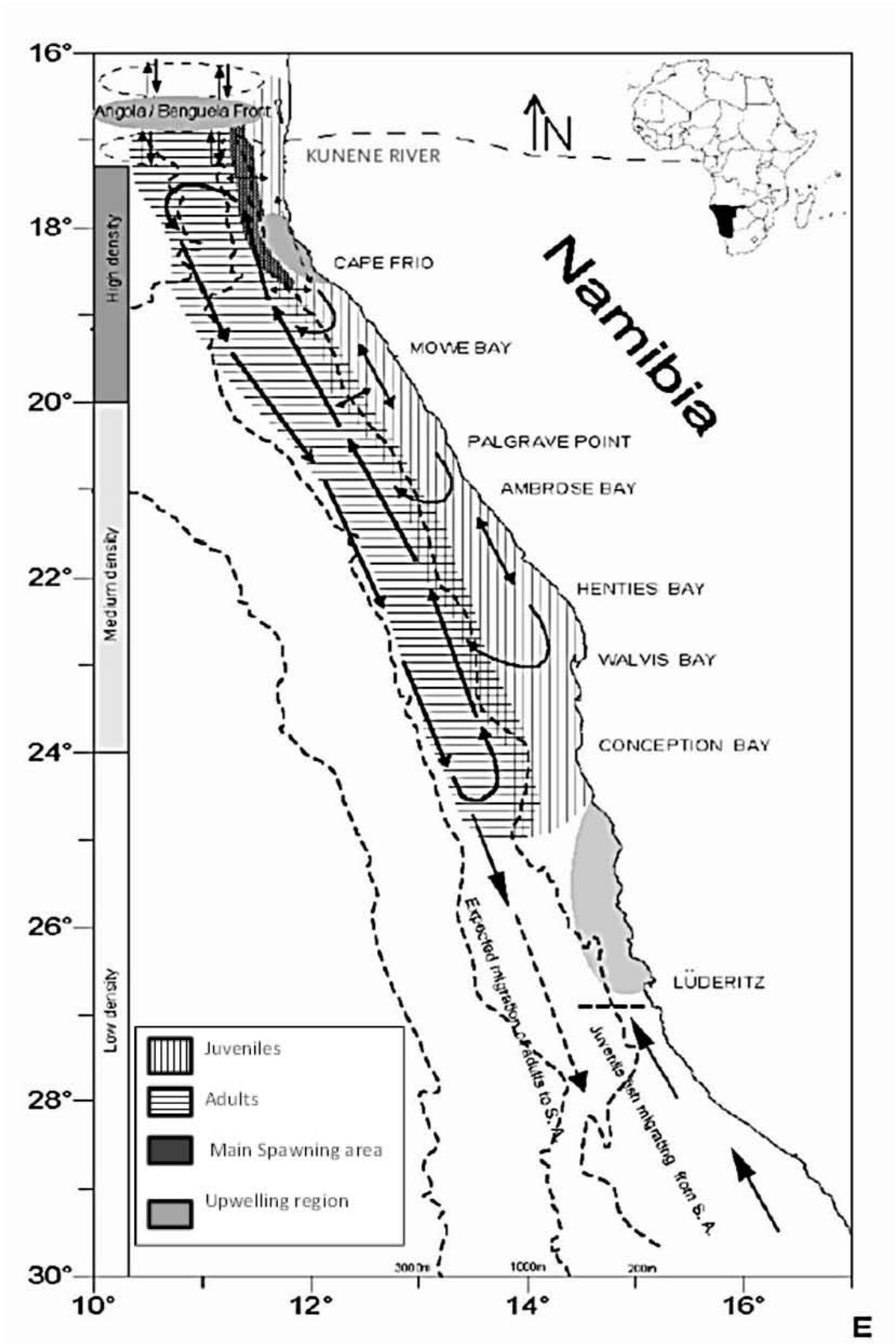


Figure 8: Map depicting the distribution of *Trachurus capensis* Castelnau, 1861 at different life stages off Namibia (Axelsen et al., 2004).

Trachurus capensis **Castelnau, 1861 population structure in southern Africa**

A stock is a fisheries management concept, akin to a "sub-population" in the ecological sense (Baldwin et al., 2012). Species have geographic limits to their distribution and many have a tendency to form structured discrete stocks or sub-populations. These discrete sub-populations have at least some degree of reproductive isolation either in space or time (Campbell, 2008). The isolation often leads to genetic and morphological differences and exposure to different parasite species (Campbell, 2008). "A stock can be defined as a group of individuals of a particular species whose genetic characteristics, and usually life history characteristics, are more similar to each other than other stocks" (Waldman, 2005).

It is essential to determine boundaries of populations of economically important fish species, therefore stock identification is needed (Waldman, 2005). "The stock concept was introduced to better understand the vulnerability of sub-populations within specific species to over-fishing, and to help delineate which fishing areas and components were most at risk of being over-fished" (Baldwin et al., 2012). Due to its economic importance *T. capensis* is subject to active resource management. Therefore knowledge of the population stock structure is important as the basic unit used in fishery management is a stock and so stock identification is a priority for exploited populations (Abaunza et al., 1995; Begg and Waldman, 1999) for example *T. capensis*. The knowledge of the stock distribution and population structure is essential for management measures to be put in place that will allow for sustainable exploitation of species (Campbell, 2008).

There are two stocks or sub-populations of *T. capensis* that are currently assumed around the coast of southern Africa. One stock in the southern Benguela, extending from south of the Orange River mouth to as far east as East London, and the other in the northern Benguela (de Villiers, 1977; Draganik, 1977; Crawford, 1989; Hecht 1990, Naish 1990, Naish et al. 1991, Pillar et al., 1998; Boyer and Hampton, 2001). They are managed as two stocks due to the presence of the Luderitz upwelling cell (Agenbag and Shannon, 1988; Axelsen et al., 2004). However, according to Axelsen et al., (2004) there does appear to be some mixing between these stocks (Figure 8). In the past it was assumed that *T. capensis* off the west and south coast of South Africa were separate stocks due to catch distributions (Barange et al., 1998). However, Naish (1990) concluded, on the basis of mitochondrial DNA analysis, that *T. capensis* from the South African south and west coast were not genotypic separate stocks. This stock on the south and west coast of South Africa was expected to be genetically

separated from the northern Benguela stock by the environmental barrier that is the Luderitz upwelling cell (Figure 2) (Hecht, 1990; Naish et al. 1991; Mc Laverty, 2012). However, recent genetic studies involving mitochondrial DNA have however found no genetic indication that Namibian and South African *T. capensis* are genotypic stocks (Axelsen et al., 2004). This does not mean these stocks cannot be phenotypic stocks. It is thought that this thermal barrier could limit the possibility for species to move from the southern to the northern Benguela and vice versa (Axelsen et al., 2004; Lett et al., 2007). Lett et al. (2007) found that the combination of a surface hydrodynamic and a subsurface thermal barrier could limit the possibility for species to be transported from the southern to the northern Benguela, but that this was dependent on species tolerance to low temperatures (Lett et al., 2007). The degree of mixing of *T. capensis* between southern and northern Benguela stocks is not known but stocks are currently considered separate, at least for management purposes (Krakstad, 2001). Differences in spawning season and the indication of a spawning migration support the two-stock hypothesis (Hecht, 1990; Axelsen et al., 2004). Naish (1990) also concluded that there was a limited exchange of fish between the southern and northern Benguela stocks. The question of integrity of stocks and levels of mixing are important because changes in the population on the west coast could be linked to stock fluctuations in the northern Benguela stock (Barange et al., 1998). It is also possible that the increase in abundance of larger sized fish of South African *T. capensis* from 1993 to 1996 on the west coast may have been the result of southward migrating Namibian *T. capensis* (Barange et al., 1998). However, there is still much uncertainty in this regard and uncertainty about the actual biological stock structure of *T. capensis*. It is suggested that research effort directed at improving the understanding of exchanges between southern and northern Benguela populations and stock structure of *T. capensis* is vital (Barange et al., 1998).

The use of parasites in fisheries management

The use of parasitological data for investigating population structure and stock discrimination of commercial pelagic fish species is well documented (Mosquera et al., 2003; Shukhgalter et al., 2007). Parasites have also been used as indicators of a variety of different aspects of fish biology (MacKenzie, 1993; Abaunza et al., 1995; MacKenzie and Abaunza, 1998). A reduction or increase in levels of parasitic infection will serve as an early warning that changes in the environment are occurring (MacKenzie, 1993; MacKenzie, 1999). As

many parasites have complex life cycle interactions with a variety of hosts, the assemblage of parasites within a host can potentially reflect that host's trophic position (Marcogliese, 2005). The use of parasites as biological tags in population studies has been long established and used on marine fish, mammals and invertebrates. One of the prerequisites to rational management of fisheries is the precise identification and definition of fish stocks although this can be difficult (Mosquera et al., 2003). Aside from stock structure, information about the past movements of fish can be obtained from using parasites as biological tags (MacKenzie and Abaunza, 1998; Mosquera et al., 2003). MacKenzie (1987) discusses three types of studies one can perform using parasites as biological tags. These include stock separation, seasonal migration and recruitment studies. The first publication describing the use of parasites as biological tags in a population studies of a purely marine organism appeared over 60 years ago being a study carried out by Herrington et al., (1939) where stocks of redfish off the USA coast where analysed using parasitic species (MacKenzie, 2002; Mosquera et al., 2003).

The theory of using parasites as biological tags is based on the fact that fish become infected with a parasite only when the fish is in the endemic region of that particular parasite (MacKenzie and Abaunza, 1998; MacKenzie et al., 2008). If the fish is caught outside that region one can infer that the fish was in the parasite's endemic region at some point in its lifecycle (MacKenzie and Abaunza, 1998; MacKenzie et al., 2008). If there is data on the maximum life span of a parasite that has been found in a fish then this can enable calculation of how long it has been since the fish left the parasite's endemic region (MacKenzie and Abaunza, 1998; MacKenzie et al., 2008). This all involves focusing on species identification of parasites, but the different levels of infection can also be used to infer population characteristics (MacKenzie et al., 2008). A methodology has been published by MacKenzie and Abaunza (1998) for studies that use parasites as biological tags for stock discrimination. MacKenzie and Abaunza (1998) describe two main types of methods, namely selecting a few of the most appropriate parasites or looking at the entre parasite community. In the case where the first method is used, it is important to note that not all parasite species are suitable for this method of stock discrimination. There have been discussions around several criteria which will help to assess if a parasite has value as a biological tag (MacKenzie, 1993; MacKenzie and Abaunza, 2005). Having different levels of infection in different areas, not being easily detachable from the host, as well as being easily detectable and identifiable are some of these criteria. Other criteria include the parasite having low pathological effects,

simple life cycles and persisting in the host for a long period of time. The infection should have limited inter-annual variability and the parasite should occur at a high prevalence but there should be no parasite reproduction on or in the host. Carballo et al. (2012) used differences in parasite community structure to identify ecological stocks of *Odontesthes Smitti*. Either localised distributions of parasites, differences in community structure found by analysing prevalence data as well as analysing differences in levels of infection (abundance or intensity) can be used to infer stock structure with an extremely high degree of accuracy (MacKenzie, 2002).

There is generally a lack of information on parasite biology and ecology as it is very complex and this is a limiting factor for their use as biological tags (MacKenzie et al., 2008). Some of the more common parasites are more prevalent in older fish and therefore there is an age-related effect (MacKenzie et al., 2008). Another problem is that parasite infection levels can vary from year to year as well as intra-annually. Thus due to seasonality, sampling fish at different times may cause errors in the results. The identification of parasites is often difficult and there is even debate among taxonomist regarding certain species (MacKenzie and Abaunza, 1998). However, there have been an increasing number of publications which deal with parasites as biological tags in population studies (MacKenzie et al., 2008). As a result one can surmise that this method is receiving much recognition for its value. A consequence of the fragility of small pelagic fish, aggravated by their small size, is the difficulty in tagging them. As few small pelagic species survive tagging, especially when external tags are used, parasitology may be the only alternative (Mosquera et al., 2003). Another issue with artificial tags is that there is that it is likely that abnormal behaviour will occur due to the capture and handling of the fish (MacKenzie and Abaunza, 1998). The method of using parasites as biological tags can resolve these issues. This method is also much less expensive as there is no need to go out and capture and release fish but instead simply obtain fish from a commercial vessel that is already involved in the catch of that particular species (MacKenzie and Abaunza, 1998).

As discussed above the method of using parasites as biological tags has its benefits as well as its limitations and this can be said for the variety of different techniques. These other methods used to assess stock structure include; morphometric and meristic analyses, genetic analysis, artificial tags and studies that relate biological parameters to life cycles (MacKenzie and Abaunza, 1998). Therefore, it is not that one is more superior to another method, but rather

that these techniques can and should be used in combination with one another (Campbell, 2008) as was done in the multidisciplinary HOMSIR project.

Parasite fauna of the genus *Trachurus* Plumier, 1801

The majority of parasitological studies done on Jack mackerel species have been done on *T. trachurus.* MacKenzie et al. (2004) developed a checklist of protozoan and metazoan parasites of *T. trachurus* (see Appendix). The HOMSIR was a multidisciplinary international project which aimed at determining the stock structure of *T. trachurus* in European waters. In the HOMSIR project, a total of 1919 *T. trachurus* from 38 localities (Morocco to southwest Norway and the Mediterranean) were examined for parasites (Figure 9). Sixty eight different parasite taxa were found, 58 of which have been identified to species level, and includes 11 new host records and two possibly new species of myxosporean (see Appendix). MacKenzie et al. (2008) used spatial variations in the mean parasite abundance of two parasitic species to confirm the three sub-populations found in the Mediterranean Sea. The composition of the parasite fauna illustrates the importance of *T. trachurus* as an intermediate host for helminth parasites maturing in piscivorous fish and mammals.

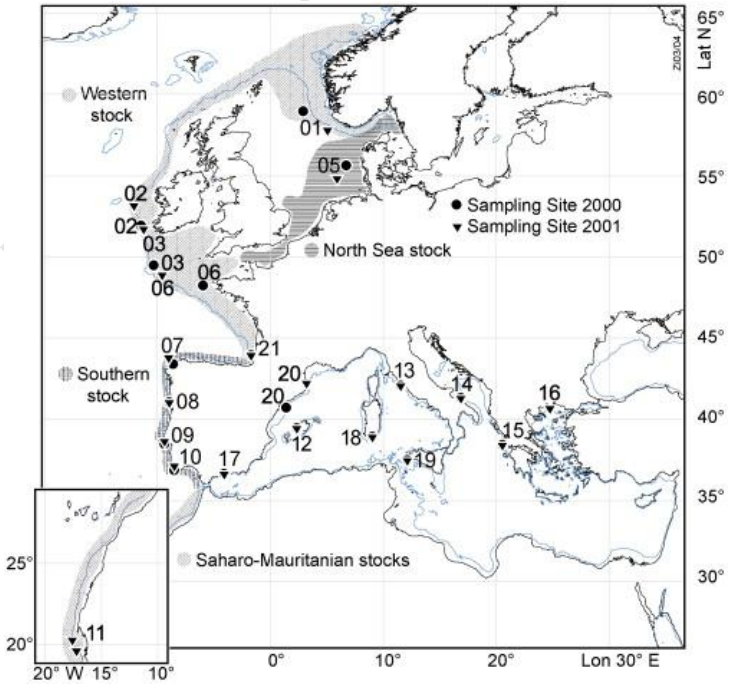


Figure 9: Sampling stations of the HOMSIR project (Abunza, 2003).

Parasites of some other *Trachurus* species have been well documented and have also been used in bio-tagging projects. For example Costa et al. (2012) did a study on the helminth parasites of *T. picturatus* from Madeira Island, Atlantic Ocean, Portugal. 103 fish were sampled and examined between January and February 2005. Only six parasite species were found; *Heteraxinoides atlanticus*, *Pseudaxine trachuri*, Unidentified Digenean, *Nybelinia lingualis*, *Anisakis* sp. and *Bolbosoma vasculosum*. All of which were found in very few fish except *Anisakis* sp. which was found in 24.3% of fish sampled and *Nybelinia lingualis* which was found in 37.9% of those fish sampled (Costa et al., 2012).

George-Nascimento (2000) compared the composition of the metazoan parasite communities within two fishing zones along the Chilean coast to determine the population structure of the *Trachurus murphyi* in these two geographical locations. Fifteen taxa of parasites were found in the 3946 fish examined between 1990 and 1996. The same taxa were found in both fishing zones. However, *T. murphyi* from northern Chile had a higher parasite abundance of cymothoid isopods, *Ceratothoa* sp., whereas those from southern Chile had more *Rhadinorhynchus trachuri, Hysterothylacium* sp. larvae, and *Anisakis* type I larvae. There were significant differences in composition of parasite communities between years in each fishing zone, presumably as a result of the increase in offshore catches since 1994. These results reinforce the hypothesis that more than one ecological stock of *T. murphyi* exists in the south eastern Pacific and contradict the current assumption of a single stock in the management of this heavily exploited fish species.

The only previous work done on the parasites of *T. capensis* from the southern Benguela is that of Hecht (1976). This was merely an aside to the focus of his research on the biology of six trawl caught species of which *T. capensis* was one. In dissecting *T. capensis* from the south east coast of South Africa, Hecht (1976) found two parasite species, namely *Anisakis* sp. larvae and *Nybelinia* sp. larvae. The *Anisakis* sp. was found on and in the gonads and ovaries as well as in the liver of the fishes while the *Nybelinia* sp. was found in and on the gonads. Hecht (1976) found that the gonads were heavily infested with *Anisakis* sp. throughout the year although a peak was noted from December to April i.e. when the gonads were in the early active stages of seasonal development. It was found that during this peak the *Anisakis* sp. weighed up to 65. 8% of the total gonad mass (Hecht, 1976; Hecht, 1990).

Gaevskaya and Kovaleva (1980) examined *T. capensis* from the northern Benguela for parasites and compared them to parasites found in *T. trachurus* from the North Sea. The

parasites (including helminths and protozoa) of *T. capensis* off the coast of Namibia are listed in their publication (Table 3). The parasite fauna of the southern species (*T. capensis*) includes two protozoan and 20 helminth species; that of the northern species includes four protozoan and 36 helminth species. Both species have retained the typical parasites of carangids and the parasites with a wide range of hosts. The differences in the parasite faunas of these two fish are attributed to changing trophic links which occurred when the territorial range of the two subspecies became separated.

Table 3: Parasite species found infecting *Trachurus capensis* Castelnau, 1861 in Namibian waters (adapted from Gayevskaja and Kovaljova (1980)).

Class	**Parasite species**
Myxozoa	*Ceratomyxa australis* Gayevskaja and Kovaljova, 1979
	Davisia donecae Gayevskaja and Kovaljova, 1979
Trematoda	*Stephanochasmus imparaspine* Linton, 1905
	Zoogonus rubellus Olsson, 1868
	Lasiotocus tropicus Manter, 1940
	Ectenurus lepidus Looss, 1907
	Didymozoidae gen. sp. (larvae)
Monogenea	*Gastrocotyle trachuri* Beneden et Hesse, 1863
	Heteraxinoides atlanticus Gayevskaja and Kovaljova, 1979
	Pseudaxine trachuri Perona and Perugia, 1889
	Heteraxine sp. Dillon and Hargis, 1965
	Cemocotyle trachuri
Cestoda	*Gilquinia* sp. 1.
	Tentaculariidae gen. sp. 1
	Nybelinia lingualis (larva) Curvier, 1817
	Nybelinia sp. 1.
	Scolex pleuronectis
Acanthocephala	*Corynosoma strumosum*
	Anisakis sp. 1.
	Paranisakis sp. 1.
	Contracaecum sp. (larvae)
Copepoda	*Lernanthropus trachuri*

Chapter 2: Materials and methods

Sample collection and processing

Five samples (Table 4) of *Trachurus capensis* Castelnau, 1861 from the southern Benguela were caught by the commercial fishing vessel F.V. Dessert Diamond off the coast of Port Elizabeth in March, August and September 2012, and those from the northern Benguela were caught by the research vessel FRS Dr Fritjof Nansen that covered the Namibian coast in August 2011 (Figure 10). The southern and northern Benguela where the fish were caught have largely differing environmental conditions for example sea surface temperature (Figure 10). Samples were caught in September or August except for sample one which was caught in March and could therefore be used to analyse seasonality. Seventy-eight fish from the southern Benguela and 47 fish from the northern Benguela were examined.

Table 4: Collection details of samples of *Trachurus capensis* Castelnau, 1861 analysed.

No.	Sample size	Name	Location	Size class	Size range	Date caught
1	27	Larger *SB March	southern Benguela	Larger	336-462 mm	28 March 2012
2	26	Larger *SB August	southern Benguela	Larger	291-335 mm	1 August 2012
3	25	Smaller *SB	southern Benguela	Smaller	186-221 mm	11 September 2012
4	22	Larger *NB	northern Benguela	Larger	305-434 mm	9 August 2011
5	25	Smaller *NB	northern Benguela	Smaller	205-260 mm	24 August 2011

*SB-southern Benguela and NB-northern Benguela.

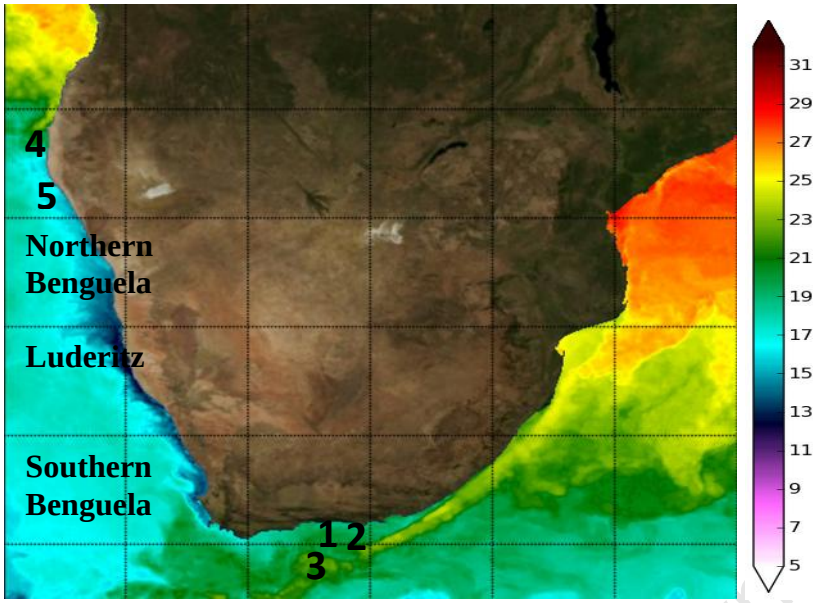


Figure 10: Sea surface temperature map (degrees Celsius) of southern Africa in summer (24 November 2011) from ODYSSEA in both the southern and northern Benguela with sampling stations 1 to 5 indicated (European Space Agency, 2012).

The fish were individually frozen in labelled bags at sea and were transferred to storage freezers in the Zoology Department, University of Cape Town. Prior to examination, fish were thawed, measured (Total length and caudal length) to the nearest 1mm and weighed to the nearest 0.1g and full parasitological examinations internally and externally were carried out on the specimens. Firstly, the skin, fins and mouth were examined for external parasites. Then the operculum, nostrils, eyes and gills were removed from the fish and examined for parasites underneath a dissecting microscope (Leica EZ4) (Figure 11 A) at magnifications ranging from 10x to 63x, after which the fish was then cut open along the ventral line and the internal organs were removed. At this point the specimen was sexed and then the body cavity was then checked for parasites.

Wet mounts of a small piece of tissue from the gonads, kidneys, spleen, heart, liver, gall bladder and ventral muscle were examined for parasite infection under a compound microscope (Leica DM750) at magnifications ranging from 400x to 1000x. The tissue was always removed from a similar position in each fish and a similar amount of tissue was examined in each instance (approximately 0.5cm^2). The stomach, intestines and pyloric caeca were examined for parasites under a dissecting microscope (Leica EZ4) at magnifications ranging from 10x to 63x (Figure 11 B). Selected parasites were preserved in either 70%

alcohol or 10% formalin. Micrographs of certain parasitic species were taken using a Nikon DS Camera Control Unit DS-U2 and DS-5M Camera head in combination with a Nikon Stereoscopic Zoom Microscope SMZ1500. In the case where parasites were difficult to see in detail to identify due to their transparency, they were stained using Mexican red fabric dye as described by Berland (2005).

All parasite species found had the following information recorded: species, location in host and the number found. In cases where it was impossible to accurately count parasites, a scale (Table 5) was used to estimate their abundance. Because these were found on a small sample examined under a compound microscope (Leica DM750) on a microscope slide they were therefore not exact counts especially in the case where there were too many to count.

Figure 11: (A) Photograph of a dissecting microscope (Leica EZ4) and petri-dishes with eyes, gills, stomach and intestine of *Trachurus capensis* and (B) Searching for parasites using a dissecting microscope (Leica EZ4) in the University of Cape Town Wet Lab.

Parasites were identified as far as possible with the help of Prof. Ken MacKenzie (University of Aberdeen) and Dr. Cecile Reed (University of Cape Town) as well as using the literature (Gaevskaya and Kovaleva, 1980; Gibson and Bray, 1986; Radujkovic and Euzet, 1989 and Campbell, 2005).

Table 5: Scale used to estimate parasite abundance.

Scale	Number of parasites
x0	0
x1	1 to 10
x10	11 to 100
x100	101 to 1000
x1000	1001 plus

Data analysis

Prevalence, mean parasite abundance and mean infection intensity were calculated for all parasites found. These have been defined by Bush et al (1997) as follows; prevalence-"number of fish infected divided by the number of fish examined, expressed as a percentage"; mean infection intensity-"total number of parasites found divided by the number of fish infected" and mean parasite abundance-"total number of parasites found divided by the total number of fish examined" (Bush et al., 1997).

The entire parasite community was analysed in terms of prevalence values. Wilcoxon matched pairs tests were done to compare parasite communities from different fish samples, particularly to compare southern and northern Benguela parasite prevalence values, as well as parasite prevalence values between size classes in both the southern and northern Benguela and in different seasons in the southern Benguela.

In terms of mean infection intensity and mean parasite abundance, features of the data presented difficulties with the parasite assemblage approach. Although a range of parasite species were found in *T. capensis* from the southern and northern Benguela, many of them occurred rarely. Therefore only the more common species were chosen for analysis in terms of parasite abundance and infection intensity. These species were selected as they were the closest match the established criteria as set out by MacKenzie (1993) and MacKenzie and Abaunza (2005). Infection intensity and parasite abundance of selected parasite species was compared between fish from the southern and northern Benguela. Comparisons of infection intensity and parasite abundance of selected parasite species were also made between size classes and seasons in the southern Benguela. In all cases both normality and homoscedasticity were rejected and therefore non-parametric tests were used. Mann-Whitney U tests were used as described by Morrison (2002).

The selected common species were used in a discriminate function analysis (DFA). To minimize the influence of host length, fish of the same size class were compared. A standard DFA as used by Melendy et al. (2005) and McClelland and Melendy (2011) was used to select the parasite abundances which best distinguished between fish from the two different parts of the Benguela. All statistical procedures were performed with Statistica 10 (StatsSoft, 2011) and/or Excel. All statistical tests were considered significant at $p<0.05$.

Chapter 3: Results

Sample characteristics

Southern Benguela fish ranged from 18 to 49 cm and show a clear bimodality in their size distribution (Figure 12 A). Northern Benguela fish ranged from 20 to 44 cm and also show a clear bimodality in their distribution (Figure 12 B).

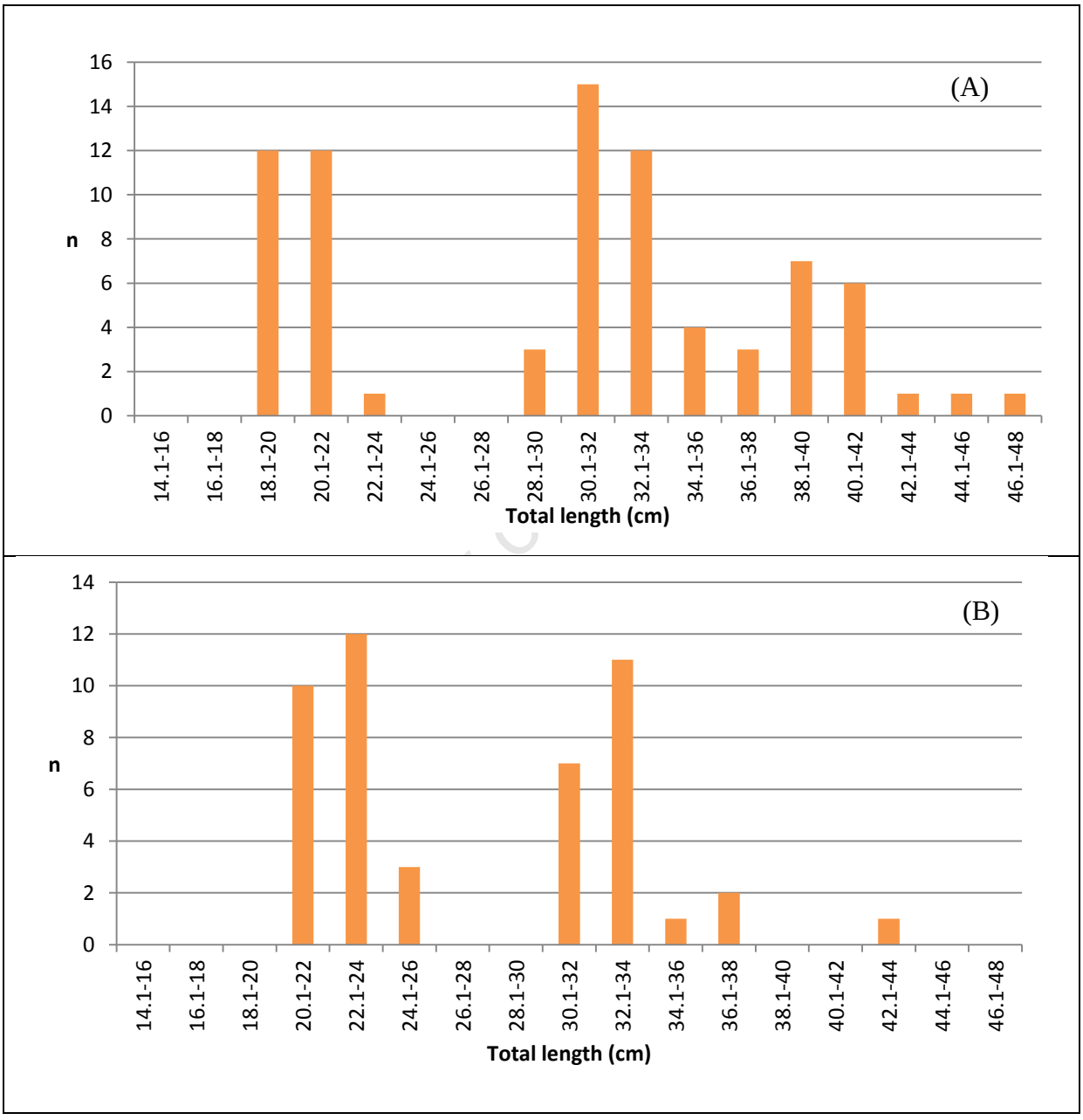


Figure 12: (A) Length frequency (cm) of southern Benguela *Trachurus capensis* Castelnau, 1861 (n=78) caught in March, August and September 2012 and (B) Length frequency (cm) of northern Benguela *Trachurus capensis* Castelnau, 1861 (n=47) caught in August 2011.

The bimodality in both the southern and northern Benguela samples (Figure 12), allowed these two size classes to be compared. The larger size class represents fish ranging from 29-47 cm in total length, while the smaller fish represents fish ranging from 18-26 cm in total length. There were two samples of larger fish in the southern Benguela (one collected in August and one in March) which allowed for an assessment of seasonal changes in parasite assemblages.

Parasite assemblages

A total of 21 parasite taxa were recorded from the 78 southern Benguela fish examined (Table 6), the most prevalent being the Nematode *Anisakis* sp. (85.9%) followed by the Monogenean *Gastrocotyle trachuri* (56.4%) and the Coccidean *Goussia cruciata* (44.9%). *Anisakis* sp. has a mean infection intensity of 25.28 parasites in the southern Benguela *T. capensis* examined. In the 47 northern Benguela fish examined, 24 parasite species were found (Table 7), the most prevalent being *Anisakis* sp. (83%), *Goussia cruciata* (72.3%) and Copepod *Lernanthropus trachuri* (34%). *Anisakis* sp. has a mean infection intensity of 15.79 parasites in the northern Benguela *T. capensis* examined. Most parasite species were found in two or three sites on *T. capensis* in both the southern and northern Benguela except for *Anisakis* sp. which was found in a wide variety of sites in *T. capensis*.

Table 6: Parasite species found infecting *Trachurus capensis* Castelnau, 1861 (n=78) from the southern Benguela (samples 1-3 see Table 4), including site, prevalence (%), mean infection intensity (±Std error) and mean parasite abundance (±Std error). * Indicates modal mean infection based on the scale in Table 5 (therefore no standard error). Unknown species in the northern and southern Benguela refer to the same species.

Class	Parasite species and author	Site	Prevalence (%)	Mean infection intensity	Mean parasite abundance
Acanthocephala	*Rhadinorhynchus cadenati* Golvan and Houin, 1964	Gonads	3.8	2.33 (±0.75)	0.09 (±0.49)
Cestoda	*Grillotia* sp. plerocescoide Muller, 1788	Intestine, pyloric caeca, stomach	3.8	1 (±0)	0.04 (±0.19)
	Scolex pleronectis Thelohan, 1892	Intestine	2.6	1 (±0)	0.03 (±0.16)
Coccidea	*Goussia cruciata* Thelohan, 1892	Liver, spleen, gall bladder	44.9	*x10	*x1
Copepoda	*Caligus* sp.	Left operculum	1.3	1 (±0)	0.01 (±0.11)
Monogenea	*Gastrocotyle trachuri* Beneden et Hesse, 1863	Gills	56.4	2.16 (±0.04)	1.22 (±0.45)
Myxozoa	*Ceratomyxa australis* Gayevskaja and Kovaljova, 1979	Gall bladder	14.1	*x1	*x1
	Davisia donecae Gayevskaja and Kovaljova, 1979	Kidney, spleen	19.2	*x10	*x10
	Kudoa sp.	Muscle	7.7	*x1	*x1
Nematoda	*Anisakis sp.*	Body cavity, gall bladder, gonads, intestine, liver, stomach, pyloric caeca	85.9	25.28 (±0.89)	21.71 (±21.23)
Trematoda	Digenea 1	Gills	5.1	1.25 (±0.25)	0.06 (±0.30)
	Digenea 2	Intestine, pyloric caeca	3.8	5.67 (±2.34)	0.22 (±1.28)
Trematoda	Digenea 3	Stomach	1.3	3 (±0)	0.04 (±0.34)
	Ectenurus lepidus Looss, 1907	Stomach	9.0	2.57 (±0.5714)	0.23 (±0.56)
	Nybelinia lingualis Curv., 1817	Kidney and gonads	5.1	1.25 (±0.25)	0.06 (±0.30)
	Tergestia laticollis Rudolphi, 1819	Intestine, pyloric caeca, stomach, gills	16.7	4.54 (±1.4833)	0.76 (±2.73)
Unknown	Grey deposits	Intestine, pyloric caeca	15.4	*x1000	*x100
	Unknown 1	Body cavity	1.3	2 (±0)	0.03 (±0.11)
	Unknown 3	Liver	1.3	*x1000	*x10
	Unknown 4	Intestine, pyloric caeca, stomach	30.8	4.25 (±0.4779)	1.31 (±113.96)
	Unknown 9	Spleen	1.3	1 (±0)	0.01 (±0.11)

Table 7: Parasite species found in *Trachurus capensis* Castelnau, 1861 (n=47) from the northern Benguela (samples 4-5 see Table 4), including site, prevalence (%), mean infection intensity (±Std error) and mean parasite abundance (±Std error). * Indicates modal mean infection based on the scale in Table 5 (therefore no standard error). Unknown species in northern and southern Benguela refer to the same species.

Class	**Species**	**Site**	**Prevalence (%)**	**Mean infection intensity**	**Mean parasite abundance**
Acanthocephala	*Rhadinorhynchus candenati* Golvan and Houin, 1964	Gonads	2.1	5 (±0)	0.11 (±0.74)
Cestoda	*Grillotia* sp. plerocescoide Muller, 1788	Gonads, liver, muscle	6.4	1 (±0)	0.06 (±0.25)
	Scolex pleuronectis Muller, 1788	Gall bladder	2.1	1 (±0)	0.02 (±0.15)
Coccidea	*Goussia cruciata* Thelohan, 1892	Liver, spleen, gall bladder	72.3	*x100	*x100
Copepoda	*Lernanthropus trachuri* Brian, 1903	Gills	34	1.4 (±0.1356)	0.48 (±0.65)
Monogenea	*Gastrocotyle trachuri* Beneden et Hesse, 1863	Gills	21.3	1.5 (±0.0714)	0.32 (±0.52)
Myxozoa	*Ceratomyxa australis* Gayevskaja and Kovaljova, 1979	Gall bladder	10.6	*x1	*x1
	Davisia donecae Gayevskaja and Kovaljova, 1979	Kidney, spleen	23.4	*x100	*x10
Nematoda	*Anisakis* sp.	Stomach, intestine, pyloric caeca, gonads, body cavity	83	15.79 (±2.599)	13.10(±20.30)
Trematoda	Digenea 1	Gills	6.4	2 (±0)	0.13 (±0.34)
	Digenea 2	Pyloric caeca	2.1	3 (±0)	0.06 (±0.44)
	Digenea 3	Pyloric caeca, intestine, gills	8.5	2 (±0.7071)	0.17(±0.70)
	Ectenurus lepidus Looss, 1907	Stomach, liver, intestine	6.4	1 (±0)	0.06 (±0.25)
Unknown	Black spot deposits	Body cavity, gills, stomach, intestine, gonads, liver	4.3	*x1000	*x100
	Grey deposits	Intestine, pyloric caeca	34	*x100	*x100
	Unknown 1	Body cavity	4.3	1 (±0)	0.04 (±0.21)
	Unknown 2	Gonads, stomach	4.3	2 (±1)	0.09 (±0.46)
	Unknown 3	Liver	2.1	*x100	*x1
	Unknown 4	Pyloric caeca	2.1	1 (±0)	0.02 (±0.15)
	Unknown 5	Stomach, gills	6.4	1 (±0)	0.06 (±0.25)
	Unknown 6	Gills, intestine	23.4	13.36 (±0.4798)	3.12 (±1.82)
	Unknown 7	Pyloric caeca	4.3	1 (±0)	0.04 (±0.20)
	Unknown 8	Stomach	2.1	1 (±0)	0.02 (±0.15)
	Unknown 10	Gonads, liver, kidney, heart	4.3	4 (±1)	0.17 (±0.77)

Micrographs

Micrographs of parasite species belonging to Acanthocephala, Cestoda, Coccidea, Copepoda, Monogenea, Myxozoa, Nematoda, Trematoda and Unknown taxa are shown (Figure 13-20). *Grillotia* sp. plerocescoide (Figure 13) found in the stomach is rather different from the other parasites seen in *T. capensis* due to the three large tentacles. *Goussia cruciata* (Figure 14) sporocysts have a cross-shaped symmetrical disposition (Diouf et al., 2000; Gestal and Azevedo, 2005). The sporocyst wall is made up of a thick inner layer with transverse striations and a multi-lamellated outer layer (Gestal and Azevedo, 2005). It is unclear which species of *Caligus* (Figure 15 A) was found, however the abdomen and two legs are clearly visible. The head of *Lernanthropus trachuri* (Figure 15 B) fused with first thoracic segment, second and third thoracic segments are fused and covered by a dorsal plate which extends posteriorly to cover the genital segment, and sometimes the abdomen. The mature stage of *Gastrocotyle trachuri* (Figure 16) begins with asymmetrical development and the principal adhesive organ is clamps (Llewellyn, 1959). *Ceratomyxa australis* (Figure 17 A) has symmetrical spores that are slightly curved with rounded ends with the polar capsules arranged at the anterior pole. The spores of *Ceratomyxa australis* (Figure 17 A) are small and have a short spore length giving them a narrower appearance compared to the more broadly rounded spores of *C. cottoidii* (Reed et al., 2007). The polar capsules of *C. australis* are also more teardrop-shaped compared to the almost spherical polar capsules of *C. cottoidii* (Reed et al., 2007). *Davisia donecae* (Figure 17 B) consists of a spore with a central capsule that is spherical or oval in shape and a definite septum sets off lateral appendages from the central region (Meglitsch, 1959). The *Kudoa* sp. (Figure 17 C) that was seen in this study had spores that were quadrangular, but rounded under pressure. The polar capsules were pear-shaped and had equal lengths while the valvegenic nuclei are located in the tips of valves. *Anisakis* sp. (Figure 18) generally have a simple digestive tube with a total length is 10 to 29 mm and its width is 0.44 to 0.54 mm (Sakanari and McKerrow, 1989). *Anisakis* sp. are encapsulated in flat spirals. Many species of Digenea have two suckers, an anterior oral and a ventral sucker. These features cannot be seen on the micrographs of Digenea 2 and 3 (Figure 19 A and B) and hence these were not identified further. *Ectenurus lepidus* (Figure 19 C) can be described as a fluke with the oral and ventral suckers close together. It has a tail and winding vitellaria which are confined in mid-body and do not extent to the tail (Figure 19 C). *Tergestia laticollis* (Figure 19 D) is somewhat similar in appearance to *Ectenurus lepidus* except without a tail. Unknown 10 (Figure 20 A) was found in the liver of *T. capensis* and can be

described as having one central spore and two smaller polar spores. Black spot deposits (Figure 20 B) were found on the gonads of *T. capensis* and were unidentifiable. It is unclear if in fact these are a parasite species or not and they are distinctly larger than most parasites found on *T. capensis* and had a solid structure. Unknown 1 (Figure 20 C) could be described as a large white worm like parasite although it had very little characteristic features, an oral sucker was present.

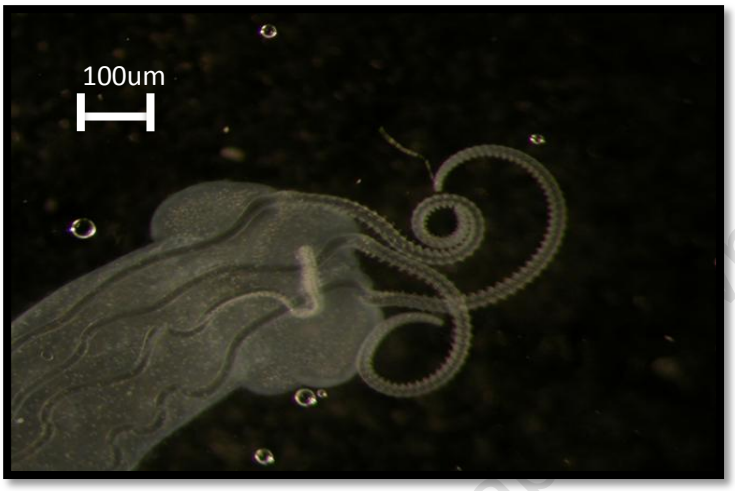


Figure 13: Cestoda parasites found in *Trachurus capensis* Castelnau, 1861: *Grillotia* sp. *plerocescoide* found in the stomach (MacKenzie, 2012). Found in *T. capensis* from both the southern and northern Benguela.

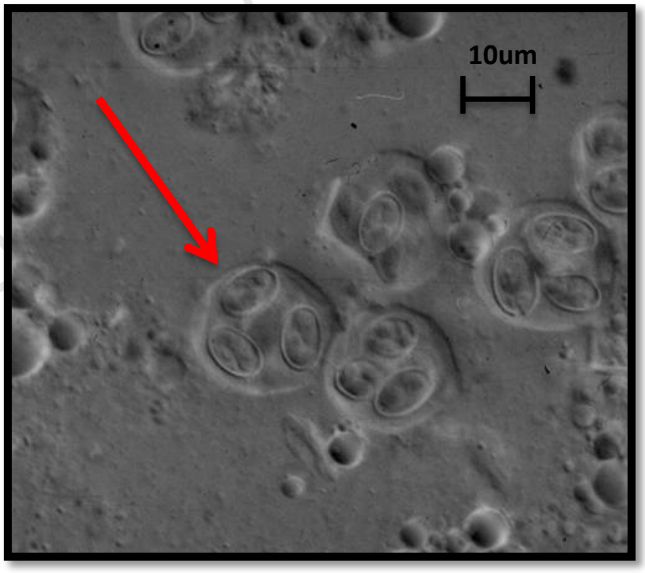


Figure 14: Coccidea parasites found in *Trachurus capensis* Castelnau, 1861: *Goussia cruciata* found in the liver (MacKenzie, 2012). Found in *T. capensis* from both the southern and northern Benguela.

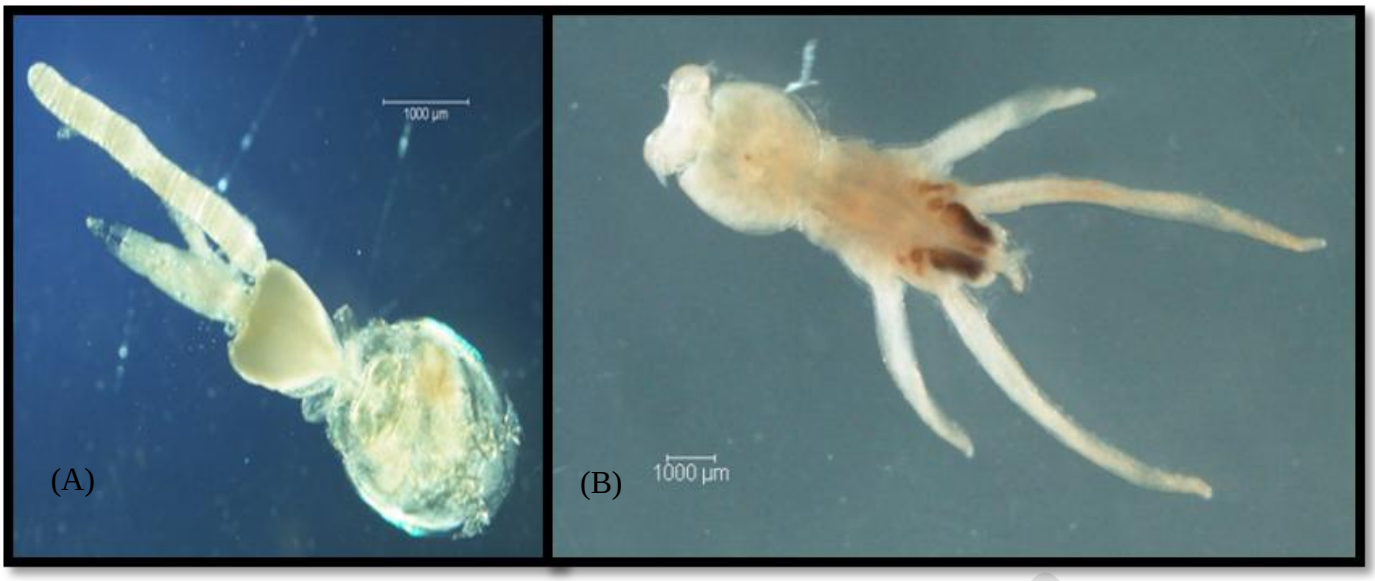


Figure 15: Copepoda species found in *Trachurus capensis* Castelnau, 1861: (A) *Caligus* sp. found on the left operculum and (B) *Lernanthropus trachuri* found on the gills. (A) found only in *T. capensis* from the southern Benguela and (B) found only in *T. capensis* from the northern Benguela sample.

Figure 16: Monogenea parasites found in *Trachurus capensis* Castelnau, 1861: *Gastrocotyle trachuri* found on the gill (MacKenzie, 2012). Found in *T. capensis* from both the southern and northern Benguela.

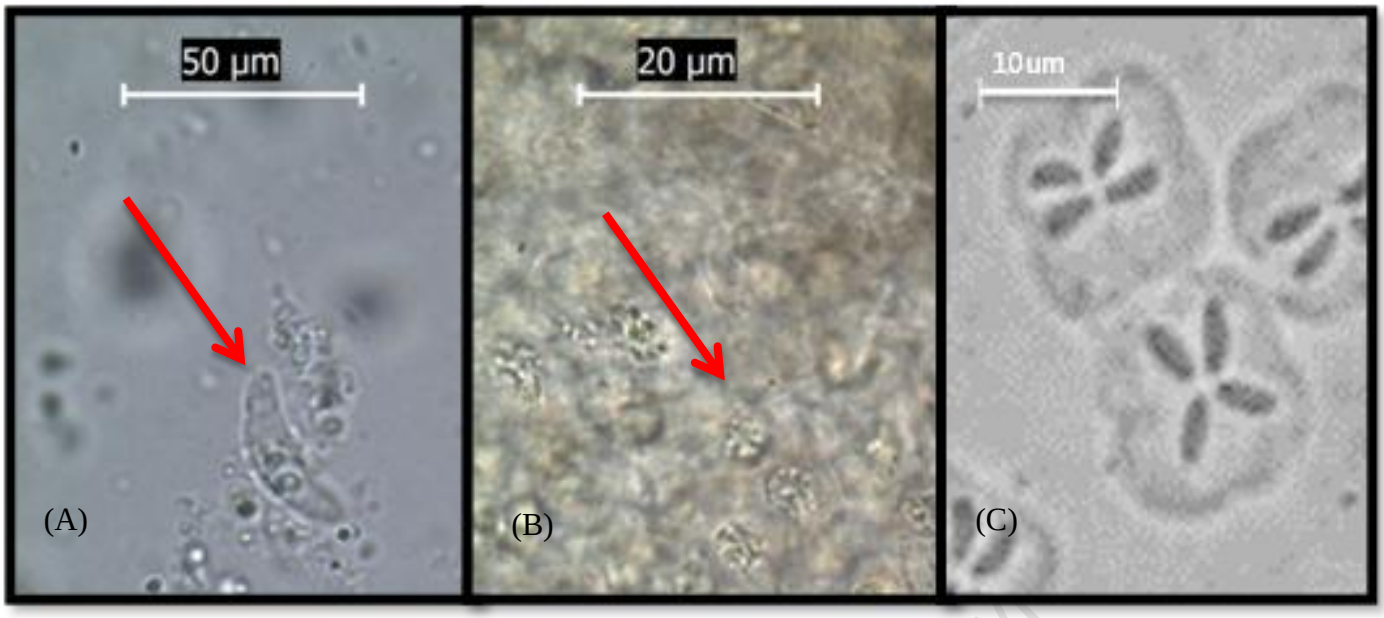


Figure 17: Myxozoan species found in *Trachurus capensis* Castelnau, 1861: (A) *Ceratomyxa australis* in the gall bladder, (B) *Davisia donecae* found in the kidney and (C) *Kudoa* sp. found in the muscle (Al Quraishy. 2011). (A) and (B) found in *T. capensis* from both the southern and northern Benguela. (C) found only in *T.capensis* from the southern Benguela.

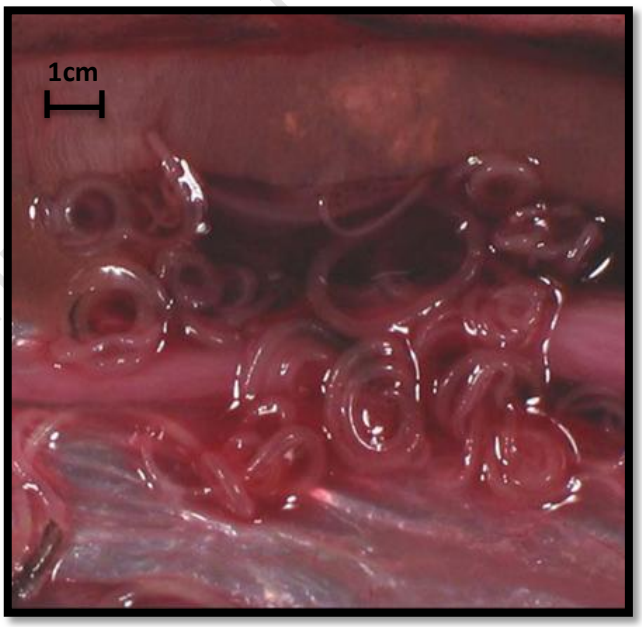


Figure 18: Nematoda parasites found in *Trachurus capensis* Castelnau, 1861: *Anisakis* sp. (stained using Mexican red fabric dye) found in the body cavity (MacKenzie, 2012). Found in *T. capensis* from both the southern and northern Benguela.

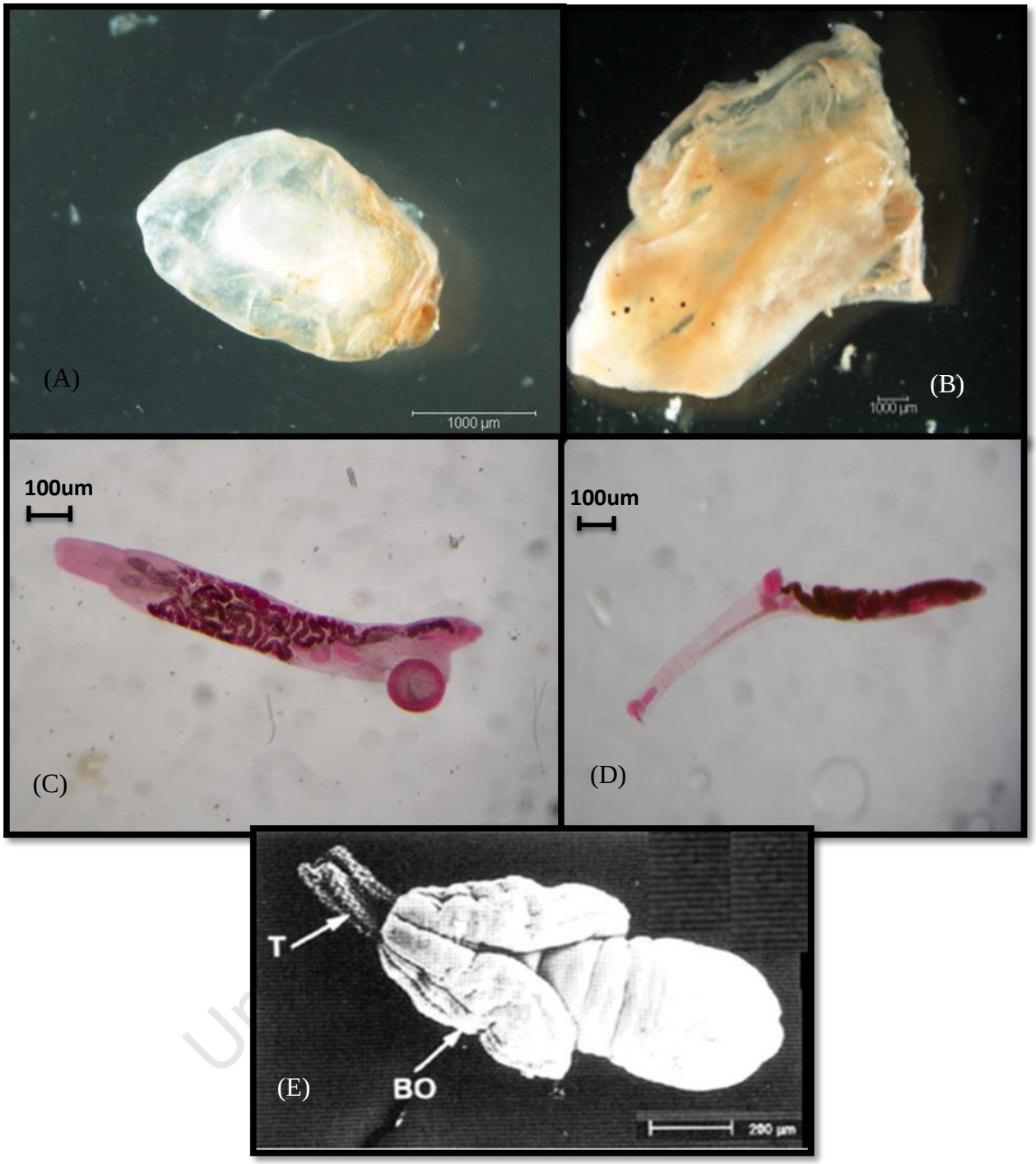


Figure 19: Trematoda parasites found in *Trachurus capensis* Castelnau, 1861: (A) Digenea 2 found in the intestine, (B) Digenea 3 found in the pyloric caeca, (C) *Ectenurus lepidus* (stained using Mexican red fabric dye) found in the stomach (MacKenzie, 2012), (D) *Tergestia laticollis* (stained using Mexican red fabric dye) found in the intestine (MacKenzie, 2012) and (E) *Nybelinia lingualis l*arvae found in the kidney (Pascual et al., 1996). (D) and (E) found only in *T. capensis* from the southern Benguela. (A), (B) and (C) found in *T. capensis* from both the southern and northern Benguela.

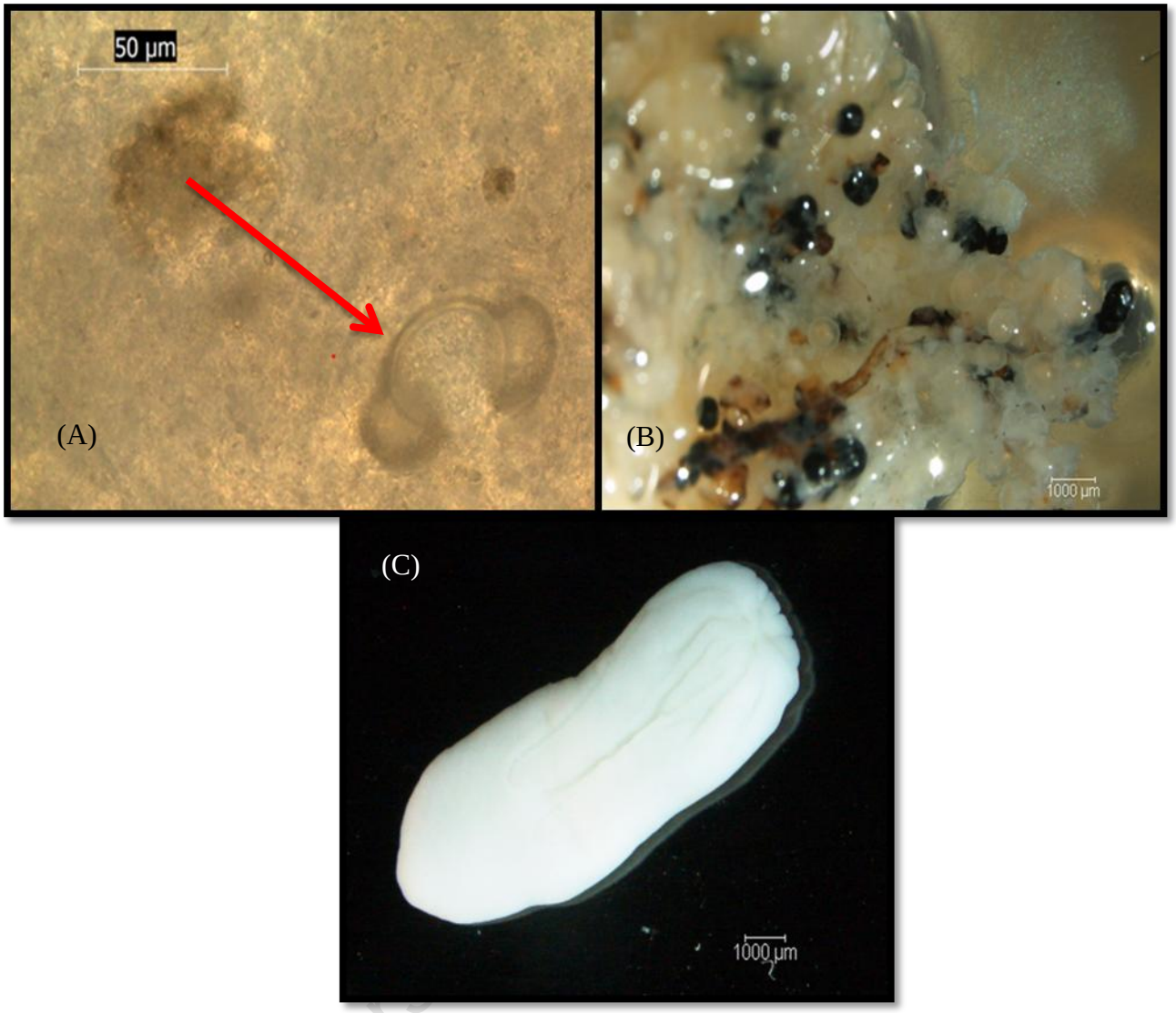


Figure 20: Unknown parasite species found in *Trachurus capensis* Castelnau, 1861: (A) Unknown 10 found in the liver, (B) Black spot deposits found on the gonads and (C) Unknown 1 found in the body cavity. (A) and (B) found in only in *T. capensis* from the northern Benguela and (C) found in *T. capensis* from both the southern and northern Benguela.

Localised parasite species

Kudoa sp. (7.7% prevalence) and *Tergestia laticollis* (16.7% prevalence) were found in both larger and smaller fish from the southern Benguela and in neither size class from the northern Benguela. *Nybelinia lingualis* (5.1% prevalence) was only found in the larger fish from the southern Benguela. The smaller fish from southern Benguela had no unique parasite species. Two parasite species were unique to the larger fish caught in March 2012 in the southern

Benguela namely, *Caligus* sp. and Unknown 9, however, both found in only 1.3% of the southern Benguela fish sampled.

Lernanthropus trachuri was found in both larger and smaller fish from the northern Benguela and in not in either size class from the southern Benguela. This copepod was found in 34% of northern Benguela fish sampled. There were some parasite species that were only found in the smaller fish from the northern Benguela, namely Unknown 5, Unknown 6, Unknown 7 and Unknown 8. These were found at prevalence of 6.3%, 23.4%, 4.2% and 2.1% respectively. There were also some parasite species that were only found in the larger fish from the northern Benguela namely, Unknown 10, Unknown 2 and Black spot deposits. These each had prevalence values of 4.26%.

Parasite community structure

Parasite community structure was compared using prevalence (%) data, and the only significant difference was between larger fish and smaller fish from the southern Benguela (Table 8).

Table 8: Comparisons of prevalence (%) of all parasite species found in *Trachurus capensis* Castelnau, 1861 using Wilcoxon Matched Pairs Test to compare southern and northern Benguela fish, fish of differing sizes within each system and seasonality in the southern Benguela. Significant differences are indicated in bold.

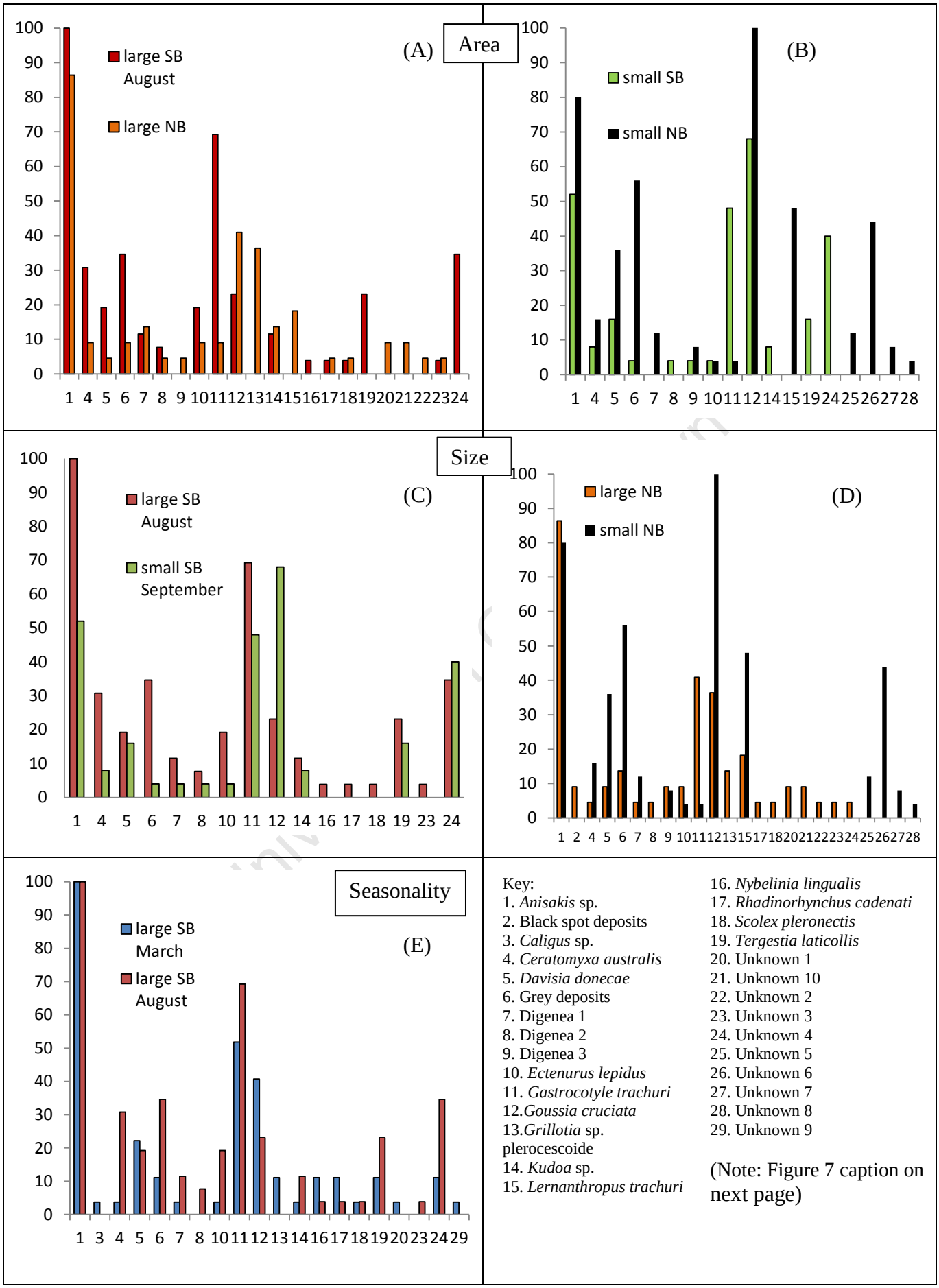
Test	Comparison	Z value	P value
larger SB August vs larger NB	North vs South (larger)	1.19	0.24
smaller SB vs smaller NB	North vs South (smaller)	1.56	0.12
larger SB August vs smaller SB	Size (SB)	**2.33**	**0.02**
larger NB vs smaller NB	Size (NB)	0.46	0.65
larger SB March vs larger SB August	Seasonality	1.53	0.13

Although not significantly different, the area comparison for the larger fish shows that the southern Benguela has higher prevalence values for most parasites. An interesting exception is *Goussia cruciata*, which is more prevalent in the northern Benguela. There are eight parasite mismatches (found in one sample and not the other) in these two samples (Figure 21 A). In contrast, the area comparison for the smaller fish shows that the northern Benguela has higher prevalence values including for *Goussia cruciata* (Figure 21 B). The exception here is *Gastrocotyle trachuri* which is more prevalent in the southern Benguela.

There was a significant difference between the prevalence values of parasites found in the larger and smaller *T. capensis* from the southern Benguela. The larger fish had four more parasite species than the smaller fish in the southern Benguela (Figure 21 C), but these however were all found at very low levels. *Nybelinia lingualis, Rhadinorhynchus candenati, Scolex pleronectis* and Unknown 3 were all only found in one fish each in larger fish from the southern Benguela caught in August. There is a large difference in prevalence values with regard to *Anisakis* sp., *Ceratomyxa australis*, Grey deposits, *Gastrocotyle trachuri* and *Goussia cruciata*. It is clear that prevalence across all parasite species in higher in the larger fish except in Unknown 4 and most notably in *Goussia cruciata* (Figure 21 C).

When comparing size classes from the northern Benguela it can be seen that 10 parasite species were found in the larger fish that were absent from the smaller fish, while the smaller fish had 4 species that were absent from the larger fish. However, the difference in community structure was not significantly different. The larger fish had higher prevalence values when compared to the smaller fish in the northern Benguela for *Anisakis* sp., Digenea 3, *Ectenurus lepidus* and *Gastrocotyle trachuri* (Figure 21 D). However, the smaller fish had higher prevalence values than the larger fish for the majority of the comparisons. Prevalence values for *Goussia cruciata* and *Lernanthropus trachuri* were much higher in the smaller fish, while there is less of a difference for *Ceratomyxa australis, Davisia donecae*, the Digeneans found as well as the Grey deposits (Figure 21 D).

Seasonal differences in parasite community structure are insignificant and prevalence values do not appear to differ much. *Anisakis* sp. is found in 100% of fish caught in both August and March. However some differences can be seen in that August has mostly slightly higher prevalence values except for *Goussia cruciata* and *Davisia donecae* (Figure 21 E).



Key:
1. *Anisakis* sp.
2. Black spot deposits
3. *Caligus* sp.
4. *Ceratomyxa australis*
5. *Davisia donecae*
6. Grey deposits
7. Digenea 1
8. Digenea 2
9. Digenea 3
10. *Ectenurus lepidus*
11. *Gastrocotyle trachuri*
12. *Goussia cruciata*
13. *Grillotia* sp. plerocescoide
14. *Kudoa* sp.
15. *Lernanthropus trachuri*
16. *Nybelinia lingualis*
17. *Rhadinorhynchus cadenati*
18. *Scolex pleronectis*
19. *Tergestia laticollis*
20. Unknown 1
21. Unknown 10
22. Unknown 2
23. Unknown 3
24. Unknown 4
25. Unknown 5
26. Unknown 6
27. Unknown 7
28. Unknown 8
29. Unknown 9

(Note: Figure 7 caption on next page)

Figure 21 (previous page): Comparisons of prevalence (%) of all parasite species found in *Trachurus capensis* Castelnau, 1861 from the southern and northern Benguela. (A) larger southern Benguela fish caught in August 2012 and larger northern Benguela fish caught in August 2011, (B) smaller southern Benguela fish caught in August 2012 and smaller northern Benguela fish caught in August 2011, (C) larger southern Benguela fish caught in August 2012 and smaller southern Benguela fish caught in September 2012, (D) larger northern Benguela fish caught in August 2011 and smaller northern Benguela fish caught in August 2011 and (E) larger southern Benguela fish caught in March 2012 and larger southern Benguela fish caught in August 2012. Note that the x-axes are not uniform.

Selected parasite species

The six selected parasite species include *Anisakis* sp., *Gastrocotyle trachuri, Davisia donecae, Goussia cruciata, Ceratomyxa australis* and *Lernanthropus trachuri.* Mean infection intensity and mean parasite abundance of these were compared between fish from the southern and northern Benguela, size classes within each subsystem and in different seasons in the southern Benguela.

Anisakis sp. infection intensity was highest in the larger fish from the southern Benguela collected in August 2012 with a mean of almost 35 parasites, while smaller fish from the southern Benguela had the lowest mean infection intensity (Figure 22 A). *Anisakis* sp. infection intensity was similar for both larger and smaller fish in the northern Benguela at around 17 parasites (Figure 22 A). *Gastrocotyle trachuri* had the highest mean infection intensity in the smaller southern Benguela fish while the smaller northern Benguela fish had the lowest (Figure 22 B). *Lernanthropus trachuri* had zero mean infection intensity in all southern Benguela fish as it was not found there, however, in the northern Benguela the smaller fish had a higher mean infection intensity (Figure 22 C). *Goussia cruciata* mean infection intensity was found at either x1 or x10 for all fish except for the smaller fish from the northern Benguela, which was found at x100 (Figure 22 D). *Davisia donecae* was found at x10 in terms of mean infection intensity in all fish samples except for larger fish caught in March in the southern Benguela and smaller northern Benguela fish where the mean was x100 (Figure 22 E). *Ceratomyxa australis* had the highest mean infection intensity of x10 parasites, in the larger northern Benguela fish as well as larger southern Benguela fish caught in March (Figure 22 F).

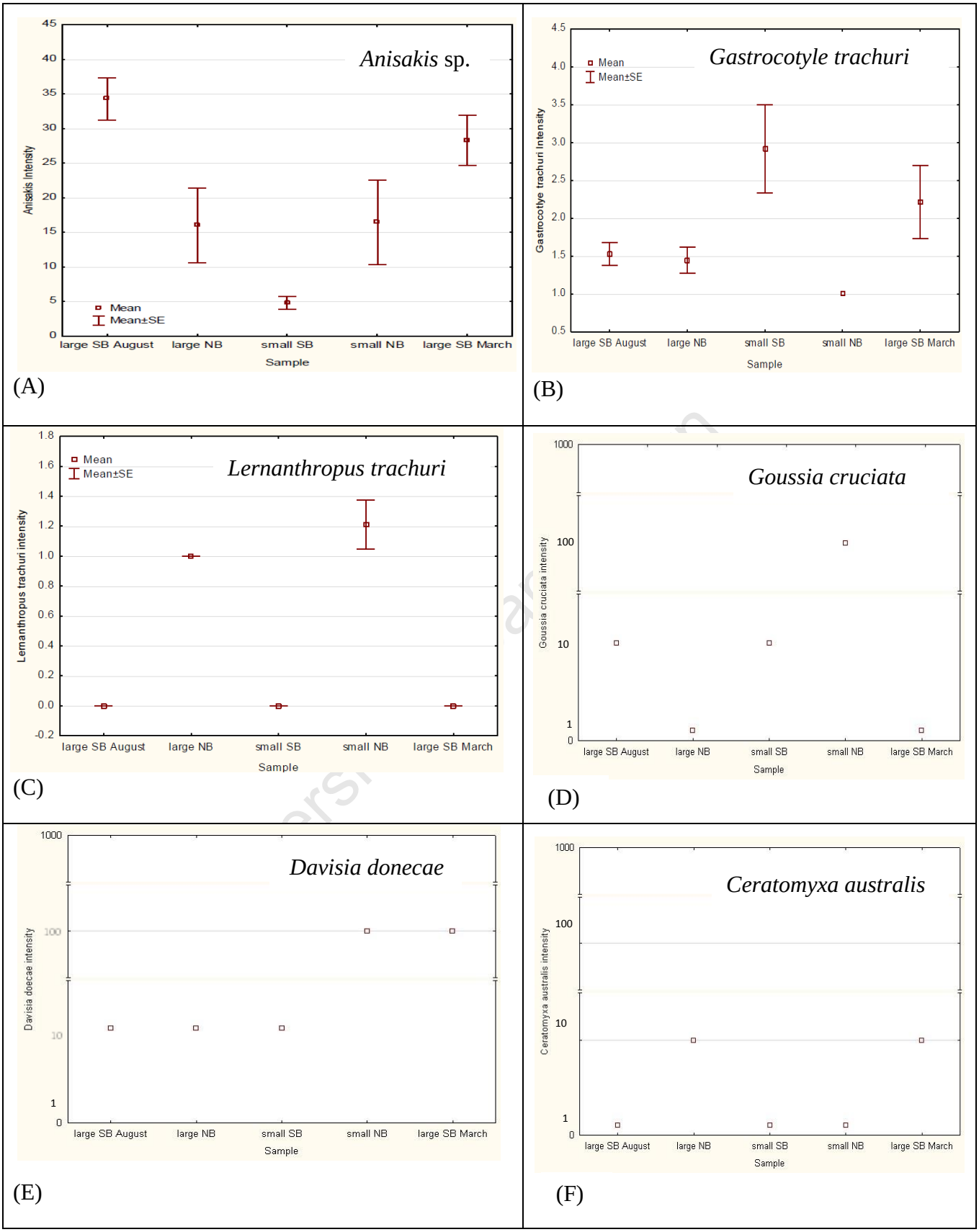


Figure 22: Box and whisker plots showing mean (*modal) infection intensity of six parasite species in *Trachurus capensis* Castelnau, 1861 from the southern and northern Benguela. (A) *Anisakis* sp., (B) *Gastrocotyle trachuri*, (C) *Lernanthropus trachuri*, (D) **Goussia cruciata*, (E) **Davisia donecae* and (F) **Ceratomyxa australis.*

Results from the Mann-Whitney U tests indicate that *Anisakis* sp. showed an area effect in the larger fish but not in the smaller fish (Table 9). *Goussia cruciata* also showed an area effect in the smaller fish. *Lernanthropus trachuri* infection intensity is significantly different and therefore showed an area effect in both the larger and smaller fish (Table 9).

In terms of comparing infection intensity, *Gastrocotyle trachuri, Davisia donecae* and *Ceratomyxa australis* showed no significant difference in any of the comparisons (Table 8). *Anisakis* sp. infection intensity on the other hand showed a significant size effect in the southern Benguela. *Goussia cruciata* showed a significant size effect in the northern Benguela. None of the six selected parasites showed significant differences in terms of infection intensity with regard to seasonality.

Table 9: Mann-Whitney U Test of infection intensity for six selected parasite species.

Infection Intensity Tests	**Comparison**	***Anisakis* sp.**		***Gastrocotyle trachuri***		***Lernanthropus trachuri***		***Goussia cruciata***		***Davisia donecae***		***Ceratomyxa australis***	
		Z value	**P value**	**Z value**	**P value**	**Z value**	**P value**	**Z value**	**P value**	**Z value**	**P value**	**Z value**	**P value**
larger SB August vs larger NB	NB vs SB (larger)	**4.13**	**<0.001**	0.19	0.85	**-3.14**	**0.001**	0.06	0.95	0.58	0.56	0.00	1.00
smaller SB vs smaller NB	NB vs SB (smaller)	-1.80	0.07	0.00	1.00	**-5.62**	**<0.001**	**-3.56**	**<0.001**	-0.11	0.92	0.69	0.49
larger SB August vs smaller SB	Size (SB)	**4.92**	**<0.001**	-1.84	0.07	0.00	1.00	-1.13	0.26	0.00	1.00	-0.13	0.90
larger NB vs smaller NB	Size (NB)	0.50	0.62	0.00	1.00	-0.28	0.78	**-3.45**	**<0.001**	-0.82	0.41	0.00	1.00
larger SB March vs larger SB August	Seasonality	1.09	0.28	-0.65	0.51	0.00	1.00	-1.64	0.10	1.36	0.17	0.00	1.00

The mean *Anisakis* sp. parasite abundance of the large southern Benguela from August as well as March was approximately 30 parasites while the mean *Anisakis* sp. parasite abundance for both larger and smaller fish from the northern Benguela was approximately 15 *Anisakis* sp. parasites (Figure 23 A). The smaller fish from the southern Benguela had a mean *Anisakis* sp. parasite abundance of less than 5 parasites. *Gastrocotyle trachuri* mean parasite abundance is highest in the small southern Benguela and lowest in the northern Benguela regardless of size as both are less than 1 (Figure 23 B). *Lernanthropus trachuri* mean parasite abundance was highest in the smaller fish from the northern Benguela at around 0.9 individuals, while the larger fish had around 0.2 individuals (Figure 23 C). *Trachurus capensis* from the southern Benguela had zero mean parasite abundance of *Lernanthropus trachuri. Goussia cruciata* (Figure 23 D) was the same in terms of mean parasite abundance (X1) across the larger fish samples except for smaller northern Benguela fish and smaller southern Benguela fish which had a mean parasite abundance of x100. *Davisia donecae* had the highest mean parasite abundance in the sample from March in the southern Benguela followed by the smaller fish from the northern Benguela (Figure 23 E). *Ceratomyxa australis* mean parasite abundance was found at x1 for all fish samples (Figure 23 F).

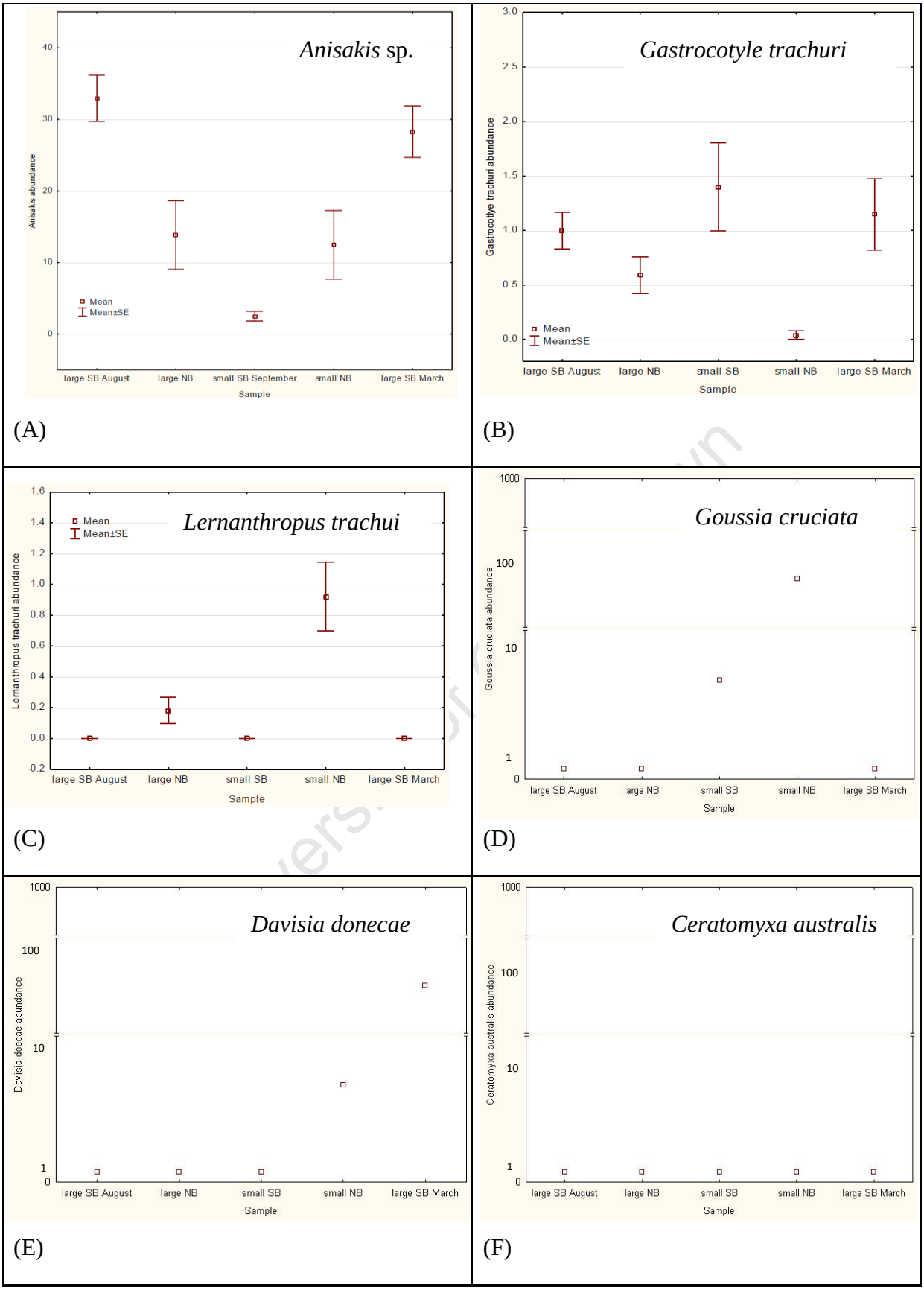


Figure 23: Box and whisker plots showing mean (*modal) parasite abundance of six parasite species in *Trachurus capensis* Castelnau, 1861 from the southern and northern Benguela. (A) *Anisakis* sp., (B) *Gastrocotyle trachuri*, (C) *Lernanthropus trachuri*, (D) **Goussia cruciata*, (E) **Davisia donecae* and (F) **Ceratomyxa australis.*

Davisia donecae and *Ceratomyxa australis* showed no significant difference in any of the comparisons of mean parasite abundance. *Anisakis* sp. had a significant area effect in both larger and smaller fish (Table 10). *Goussia cruciata*, *Gastrocotyle trachuri* and *Lernanthropus trachuri* showed an area effect in the smaller fish only (Table 10).

Goussia cruciata parasite abundance showed a significant size effect in the southern and northern Benguela, while *Lernanthropus trachuri* parasite abundance only showed a size effect in the northern Benguela (Table 10). *Anisakis* sp. parasite abundance on the other hand showed a significant size effect in the southern Benguela but not the northern Benguela. None of the six selected parasites showed a significant difference in terms of parasite abundance with regard to seasonality in the larger fish caught in the southern Benguela.

Table 10: Mann-Whitney U Test of parasite abundance comparisons for six selected parasite species.

Abundance Tests	**Comparison**	***Anisakis* sp.**		***Gastrocotyle trachuri***		***Lernanthropus trachuri***		***Goussia cruciata***		***Davisia donecae***		***Certaomyxa australis***	
		Z value	**P value**	**Z value**	**P value**	**Z value**	**P value**	**Z value**	**P value**	**Z value**	**P value**	**Z value**	**P value**
large SB August vs large NB	North vs South (large)	**4.19**	**<0.001**	1.52	0.13	-1.07	0.29	-0.73	0.46	0.63	0.52	1.48	0.13
small SB vs small NB	North vs South (small)	**-2.37**	**0.02**	**2.74**	**0.006**	**-2.90**	**0.003**	**-4.76**	**<0.001**	-1.24	0.21	-0.44	0.66
large SB August vs small SB	Size (SB)	**5.72**	**<0.001**	0.26	0.79	0.00	1.00	**-3.05**	**0.002**	0.17	0.87	1.37	0.17
large NB vs small NB	Size (NB)	0.97	0.33	**2.20**	**0.02**	**-2.12**	**0.03**	**-5.47**	**<0.001**	-1.67	0.09	-0.62	0.54
large SB March vs large SB August	Seasonality	0.82	0.41	0.53	0.59	0.00	1.00	1.03	0.30	0.32	0.75	-1.64	0.10

Discriminant Function Analysis

A standard DFA was undertaken on *Anisakis* sp., *Gastrocotyle trachuri, Lernanthropus trachuri, Goussia cruciata, Davisia donecae and Ceratomyxa australis* to assess whether T. capensis from the southern and northern Benguela could be distinguished using abundance data of these six parasites. The DFA was done separately for each size class so to eliminate the size effect.

Larger fish

Only three of the six parasite species were found to be significant in terms of classifying fish into their relative stocks namely, *Anisakis* sp., *Lernanthropus trachuri* and *Ceratomyxa australis* (Table 11).

Table 11: Results of a standard discriminant function analysis of parasite abundances in larger *Trachurus capensis* Castelnau, 1861. Parasites that made a significant contribution to the DFA are shown in bold.

Parasite species	**F score**	**P value**	**Standardized coefficient of canonical variable**
Anisakis sp.	**18.35**	**0.0001**	0.92
Gastrocotyle trachuri	1.97	0.17	0.33
Lernanthropus trachuri	**9.01**	**0.004**	-0.69
Goussia cruciata	0.78	0.38	-0.32
Davisia donecae	0.98	0.33	0.34
Ceratomyxa australis	**5.33**	**0.02**	0.63

Parasites that were significant in the DFA were used in a model which correctly classified 91.67% of all larger fish to their source location (Table 12).

Table 12: Classification of larger *Trachurus capensis* Castelnau, 1861 into southern and northern stocks as revealed by discriminant function analyses of parasite abundance of three parasite markers.

Location	**Southern**	**Northern**	**% correct**
Southern	24	2	92.3
Northern	2	20	90.9
Total	26	22	91.7

Smaller fish

Parasite species found to be significant in terms of classifying fish into their relative stocks were *Lernanthropus trachuri* and *Goussia cruciata* (Table 13).

Table 13: Results of a standard discriminant function analysis of parasite abundances in smaller *Trachurus capensis* Castelnau, 1861. Parasites that made a significant contribution to the DFA are shown in bold.

Parasite species	**F score**	**P value**	**Standardized coefficient of canonical variable**
Anisakis sp.	0.10	0.75	-0.08
Gastrocotyle trachuri	1.65	0.21	0.21
Lernanthropus trachuri	**61.93**	**<0.001**	-1.24
Goussia cruciata	**96.73**	**<0.001**	-1.39
Davisia donecae	0.58	0.45	-0.21
Ceratomyxa australis	0.25	0.62	0.09

Parasites that were significant in the DFA were used in a model which correctly classified 96 % of all smaller fish to their source location (Table 14).

Table 14: Classification of smaller *Trachurus capensis* Castelnau, 1861 into southern and northern stocks as revealed by discriminant function analyses of intensities of two parasite markers.

Location	**Southern**	**Northern**	**% correct**
Southern	25	0	100.0
Northern	2	23	92.0
Total	27	23	96.0

Chapter 4: Discussion and conclusion

Summary

A comparison of parasite assemblages in terms of prevalence of infection, infection intensity and parasite abundance between southern and northern *Trachurus capensis* Castelnau, 1861 was completed. Comparisons were also made between two size classes within each subsystem as well as between seasons for larger fish in the southern Benguela. There was no significant difference in parasite community structure (assessed using prevalence data) in any of the comparisons except for between larger and smaller *T. capensis* in the southern Benguela. There were significant differences in mean infection intensity and mean parasite abundance of several parasite species between southern and northern Benguela fish. This was the case for both smaller and larger fish suggesting that the parasite assemblages are not the same across the *T. capensis* population in southern Africa. Hence the parasite data supports the hypothesis of discrete *T. capensis* stocks in the southern and northern Benguela. There were significant differences in mean infection intensity and mean parasite abundance of several parasite species between larger and smaller fish from both the southern and northern Benguela. This suggests that size of the fish, in this case total length, is related to the level of parasitic infection. Prevalence, infection intensity and parasite abundance did not differ between March and August in larger fish in the southern Benguela, suggesting no seasonal effect on parasite infection in *T. capensis.* In summary, 17 tests showed significant differences suggesting there are spatial differences as well as size differences in parasite assemblages, however, no seasonality tests showed significant results (Table 15).

Table 15: Summary of tests that show significant differences between *Trachurus capensis* parasites in the southern and northern Benguela, size classes in each system and seasonally in the southern Benguela.

Tests	**Significant difference**
NB vs SB (larger fish)	*Anisakis* sp. infection intensity and parasite abundance *Lernanthropus trachuri* infection intensity
NB vs SB (smaller fish)	*Lernanthropus trachuri* infection intensity and parasite abundance *Goussia cruciata* infection intensity and parasite abundance *Anisakis* sp. parasite abundance *Gastrocotyle trachuri* parasite abundance
Size (southern Benguela)	Community structure-prevalence *Anisakis* sp. infection intensity and parasite abundance *Goussia cruciata* parasite abundance
Size (northern Benguela)	*Goussia cruciata* infection intensity and parasite abundance *Gastrocotyle trachuri* parasite abundance *Lernanthropus trachuri* parasite abundance
Seasonality	None

Parasite species

There are seven recognised species of *Anisakis*, five of which were found in *Trachurus trachurus* Linnaeus, 1758 by Mattiucci et al. (2008), namely *A. simplex*, *A. pegreffii*, *A. physeteris*, *A. typica* and *Anisakis* sp.. MacKenzie et al. (2004) (see Appendix) only found three species of *Anisakis* in *Trachurus trachurus; A. simplex, A. pegreffii* and *A. sphyseteris*. Mixed infections by the two sibling species *A. pegreffii* and *A. simplex* were found in the same individual hosts caught along the Iberian coast and in the Albor´an Sea (Mattiucci et al., 2008). The statistically significant differences evidenced in the relative proportions of these two sibling species between the samples indicated discrete sub-structuring of populations of *T. trachurus* in Mediterranean and Atlantic waters (Mattiucci et al., 2008), and these results confirm that *Anisakis* species are good biological tags to be used in fish stock assessment studies (Mattiucci et al., 2008). *Anisakis* sp. in *T. capensis* has been previously recorded in fish from the northern Benguela by Gayevskaja and Kovaljova (1980) as well as in fish from the southern Benguela by Hecht (1976), although those studies were unable to identify this parasite to species level. This was also the case for this project as morphologically *Anisakis* sp. are extremely similar and genetic study is needed to identify to species level.

MacKenzie et al. (2004) found *Gastrocotyle trachuri* on the gills of *T. trachurus*, as did Gayevskaja and Kovaljova (1980) on the gills of *T. capensis* in Namibian waters. Gayevskaja and Kovaljova (1980) also found *Davisia donecae* in *T. capensis* in Namibian waters.

Goussia cruciata was found in *T. trachurus* as part of the HOMSIR project (MacKenzie et al., 2004) (see Appendix), and has also been found to infect *Trachurus mediterraneus, Trachurus picturatus* off the west coast of France and in the Aegean Sea (Abollo et al., 2001; Gestal and Azevedo, 2005). It was not however found by Hecht (1976) or Gayevskaja and Kovaljova (1980), and has therefore not likely been recorded on *T. capensis* prior to this. Therefore *T. capensis* is a new host record for *Goussia cruciata.* *Goussia cruciata* is found in the liver of its host in most cases; however, infection might spread to other organs in chronic infections in larger fish. In the 2005 study by Gestal and Azevedo, macroscopic lesions were not observed in livers infected by *Goussia cruciata.* Nevertheless, large agglomerations of oocysts and decrease of functional parenchyma as well as an inflammatory reaction occurred with heavy infections (Gestal and Azevedo, 2005). In *T. trachurus* pathological changes in *Goussia cruciata* infected liver parenchyma were moderate but the most heavily infected fish did have prominently reduced livers (Abollo et al., 2001). Where Coccidian infections have been examined, there has been a general agreement that they are pathogens of considerable importance in wild fisheries (Abollo et al., 2001). No pathological effects were noted in this project, however, this was not investigated in any detail.

Ceratomyxa australis was first identified in *T. capensis* in Namibian waters by Gayevskaja and Kovaljova (1980), where it was found it in the gall bladder and has now been recorded in fish from the southern Benguela as part of this project. It has not been recorded in *T. trachurus* as of yet. The genus *Ceratomyxa* is one of the largest as well as oldest genera of Myxozoa and has at least 70 named species (Meglitsch, 1959).

Lernanthropus trachuri has been found in *T. trachurus* (MacKenzie et al., 2004), in *T. picturatus* in the Atlantic Ocean, off Portugal (Costa et al., 2012), in *T. murphyi* from South America (Oliva, 1999), as well as in *T. mediterraneus* from the Turkish coast. *Lernanthropus trachuri* was found to occur in *T. capensis* in Namibian waters by Gayevskaja and Kovaljova (1980). This was also true for this study, however, it was notably absent from fish from the southern Benguela. The genus *Lernanthropus* is the most common genus of parasitic copepods, with over 100 species, all of which are found on the gill of marine teleosts.

Lernanthropus is distributed along the coasts of Italy, Nice, Algeria, Senegal, Namibia, Chile, Peru, Sahara coast, Buenos Aries, Senegal (Oktener and Trilles, 2004).

Kudoa sp. was found in *T. trachurus* by MacKenzie et al. (2004) (see Appendix) but was not identified further, and Campbell (2005) described *Kudoa nova* found in *T. trachurus.* Neither Hecht (1976) nor Gayevskaja and Kovaljova (1980) found any *Kudoa* sp. in *T. capensis*. Therefore this is most likely a new host record for the genus *Kudoa.* Currently, there are over 75 described species belonging to the genus *Kudoa* (Pascual et al., 2012), and these can be highly variable in shape and the size of their pseudocysts and spores (Pascual et al., 2012). Genetic studies are often needed to identify *Kudoa* to species level, especially when the species are phylogenetically close. *Kudoa nova, K. paniformis, K. dianae, K. miniauriculata, K. alliaria* and *K. rosenbuschi* all have four polar capsules (as did the *Kudoa* sp. found in this project) and are phylogenetically closely related (Pascual et al., 2012).

Tergestia laticollis was found in *T. trachurus* (see Appendix) but has not previously been described in *T. capensis.* Therefore, *T. capensis* represents a new host record. *Nybelinia lingualis* is found in *T. trachurus* as well as *T. capensis* (Hecth, 1976; Gayevskaja and Kovaljova, 1980).

Stock discrimination

Trachurus capensis from the southern Benguela had noticeably higher prevalence values for *Gastrocotyle trachuri, Ceratomyxa australis***,** *Anisakis* sp. and *Ectenurus lepidus* compared to *T. capensis* from the northern Benguela. The larger southern Benguela fish have significantly higher *Anisakis* sp. infection intensity as well as parasite abundance compared to larger northern Benguela fish. However, in the larger fish *Lernanthropus trachuri* infection intensity was significantly higher in northern Benguela fish but this is simply because it is a localised parasite and was not found in any southern Benguela fish.

The northern Benguela *T. capensis, Goussia cruciata* was more prevalent compared to the southern Benguela *T. capensis*. More significant differences were found between southern and northern fish when comparing fish of a smaller size. In the smaller fish comparison, *Lernanthropus trachuri* infection intensity and parasite abundance, *Goussia cruiata* infection intensity and parasite abundance and *Anisakis* sp. parasite abundance were all significantly higher in the northern Benguela fish. However, *Lernanthropus trachuri* infection intensity

and parasite abundance was significantly higher in northern Benguela fish because it is a localised parasite and was not found in any southern Benguela fish. The exception here is *Gastrocotyle trachuri,* which had significantly higher parasite abundance in the southern Benguela fish.

In the larger fish *Anisakis* sp. parasite abundance had the highest F score and is therefore the best parasite for discriminating between fish from different source locations and hence for identifying fish in terms of their stocks. This seems clear as *Anisakis* sp. was the only significantly different parasite in the larger fish in terms of parasite abundance. Although *Lernanthropus trachuri* and *Ceratomyxa australis* had significant F scores in the DFA these were much lower than *Anisakis* sp.. *Goussia cruciata, Gastrocotyle trachuri* and *Davisia donecae* proved ineffective at classifying fish into stocks. In the classification undertaken on the smaller fish, *Goussia cruciata* preformed the best with the highest F score. This score was far greater than any other F score regardless of size class. In the smaller fish *Lernanthropus trachuri* had the second best F score while the other four parasite parasite abundances proved insignificant. As the smaller fish had greater differences in parasite abundances between stocks and therefore higher F scores, a 96% correct classification into source location was achieved. These high classification rates proved that the parasite can be used to infer stock structures and supports the hypothesis that northern and southern Benguela *T. capensis* are indeed two separate stocks.

Anisakis sp. had significantly different abundances when southern and northern fish were compared in both the smaller and larger fish and had great discriminatory power in the larger fish, and are therefore particularly useful as biotags. *Anisakis* species were useful in stock discrimination studies such as the HOMSIR project, as well as studies by Choua et al. (2011) which used *Anisakis* in a stock identification study of *Scomber australasicus,* and Mattiucci et al. (2008). This further suggests that this is a good parasite species to select as a biological tag.

Kudoa sp., *Tergestia laticollis, Nybelinia lingualis* as well as *Caligus* sp. and Unknown 9 were only found in the southern Benguela fish. *Caligus* sp. and Unknown 9 were, however, both found at only 1.3% prevalence and their absence in northern Benguela fish could therefore simply be a result of the small sample size. *Kudoa* sp. and *Tergestia laticollis* both have a new host record in *T. capensis*. *Nybelinia lingualis* has been found in northern

Benguela *T. capensis* in 1980 by Gaevskaya and Kovaleva and is therefore only a localised parasite species in this project.

The copepod *Lernanthropus trachuri* was found in 34% of northern Benguela fish sampled but was completely absent from the southern Benguela fish and therefore shows a very strong discrimination between stocks. *Lernanthropus trachuri* is presumably endemic to the northern Benguela. Unknown 5, Unknown 6, Unknown 7 and Unknown 8 were also completely absent from the southern Benguela fish. These were found in 6.38%, 23.40%, 4.26% and 2.13%, respectively in northern Benguela fish. However, it is difficult to deduce much from this as these parasites are still unidentified. Also Unknown 10, Unknown 2 and Black spot deposits were also localised in the northern Benguela, but each of these had prevalence values of only 4.26% and therefore are insignificant.

Differences in parasite assemblages could be because a particular parasite is endemic to one region, as appears to be the case with *Lernanthropus trachuri*. Isolation of two stocks often leads to exposure to different parasite species (Campbell, 2008). However, another reason could be due to the differing environments between the southern and northern Benguela where the fish were caught (Figure 10). The south coast of South Africa which is a temperate shelf region and the northern Benguela shelf is a typical coastal upwelling system (Hutchings et al., 2009). Boyer et al. (2001) discussed the differences in the diet of T. capensis from Namibian and South African and this could influence parasite assemblages. "The species composition and abundance of parasites may differ between fish stocks due to biogeography, differential environmental tolerances of parasites, differences in availability of intermediate hosts, and different life history characteristics of the fish stocks themselves." (Begg and Waldman, 1999). Therefore there are a variety of reasons that the parasite assemblages are different in the two subsystems and perhaps the two stocks are not completely isolated from one another or discrete. However, the differences in parasite assemblages from *T. capensis* in the two subsystems are clearly significant.

Size effect

There is a significant size effect with regard to parasite community structure, infection intensity, and parasite abundance. In the southern Benguela a size effect was seen in the prevalence values, with larger fish having significantly higher prevalence values for the majority of the common parasites especially *Anisakis* sp., *Certomyxa australis* and *Gastrocotyle trachuri*. This seems in line with the literature as these species appear to show a cumulative effect with increasing size and are therefore more likely to be found as host size increases. *Goussia cruciata,* which has a much higher prevalence in the smaller fish, is the exception. This finding is contrary to the literature which suggests a cumulative effect with age or size which would more than likely result in higher prevalence values with increased host size. It is unclear why this would occur but one suggestion is that this group of small T. capensis simply had a higher than normal infection of *Goussia cruciata* and therefore a larger sample is needed to rule this out.

In the southern Benguela fish a significant size effect was seen with regard to *Anisakis* sp. in terms of infection intensity as well as parasite abundance. Infection intensity and parasite abundance was much higher in the larger size class. Results from another study done by Choua et al. (2011) on *A. pegreffii* and *A. simplex* in *Scomber australasicus* showed that parasite abundance was significantly higher in both larger (greater than 450 g) and older (greater than 3 years old) fish. A cumulative effect was noted for a variety of species of *Anisakis* sp. (Costa et al., 2012). *Goussia cruciata* abundance was significantly higher in the smaller fish, and this is contrary to other studies which suggest parasite abundance should be higher in large individuals. In *T. trachurus* the number of oocysts showed a cumulative effect as parasite counts increased with increasing total length and weight of fish, but did not change with host sex or sexual maturity (Abollo et al., 2001). Diouf et al. (2000) showed a clear increase in the prevalence of *Eimeria* (now *Goussia*) *baueri* in parallel with the age of fish hosts. However, *T. capensis* is a new host record and perhaps this pattern is attributed to something host specific, or simply a small sample size. Although not statistically significant, there is a slight size effect with regard to parasite community structure. The larger fish again had higher prevalence values for species such as *Aniskis* sp. and *Gastrocotyle trachuri.* However many species had a higher prevalence values in the smaller fish; and this was the again the case for *Goussia cruciata* as well as for *Lernanthropus trachuri, Ceratomyxa australis* and *Davisia donecae.*

In the northern Benguela, *Goussia cruciata* parasite abundance as well as infection intensity was significantly higher in the smaller fish. Again this is contrary to what was expected. *Gastrocotyle trachuri* parasite abundance was significantly higher in larger fish. Llewellyn (1962) showed that *G. trachuri* are most common on young *T. trachurus*, much less frequent on 2- and 3-yr-old fish, and probably even rarer on still older fish. In the first two years nearly all fish were infected with *Gastrocotyle trachuri* with the mean parasite abundance of 12 individuals per fish. But in the third and fourth years the prevalence falls to about half and mean parasite abundance to two (Llewellyn, 1962). Therefore the results from this study seem contradictory to what is suggested in the literature, as prevalence and parasite abundance was higher in larger fish. *Lernanthropus trachuri* abundance was also significantly higher in smaller fish.

Seasonality

Hecht (1976) found a peak in *Anisakis* sp. parasite abundance and infection intensity of infection from December to April when the gonads were in the early active stages of seasonal development in *T. capensis* from the South African coast. This was not found in the present study as *Anisakis* sp. parasite abundance and infection intensity from March and August were not significantly different and were found in 100% of fish caught in March and August in the southern Benguela. In spring the number of parasites of *Gastrocotyle trachuri* on *T. trachurus* at Plymouth increased, perhaps due to juvenile's maturing over winter and therefore increasing the reproductive capacity of the population (Llewellyn, 1962). Larvae of *Gastrocotyle trachuri* on *T. trachurus* are common in May; only adults are found in July and August (Llewellyn 1959; Rohde, 1979). This was not found in the present study and *Gastrocotyle trachuri* parasite abundance and infection intensity from March and August were not significantly different. Neither community prevalence showed seasonality nor did parasite abundance or infection intensity of all the six selected parasites. However, it is difficult to assess seasonality from this study as only larger fish from the southern Benguela were compared in terms of season.

Conclusion

The argument for a two stock hypothesis is that there are biological differences between the southern and northern *T. capensis*, and that the Luderitz upwelling cell separates these stocks (Agenbag and Shannon, 1988; Axelsen et al., 2004). Furthermore, differences in spawning season and the indication of a spawning migration, support the two-stock hypothesis (Hecht, 1990). However, there does appear to be some mixing between these stocks (Axelsen et al., 2004). Genetic studies involving mitochondrial DNA have however found no indication that Namibian and South African *T. capensis* are genotypic stocks (Axelsen et al., 2004). The multitude of opinions and results is the reasoning behind this stock discrimination assessment using parasites as biological tags as it provides another approach so to provide a multidisciplinary stock discrimination assessment. "The strongest inferences on stock structure are drawn from a suite of complementary techniques that cover multiple aspects of the biology of a fish species." (Begg and Waldman, 1999).

Significant differences in infection intensity and parasite abundance of *Anisakis* sp., *Gastrocotyle trachuri, Goussia cruciata, Lernanthropus trachuri* between the southern and northern Benguela fish suggests that these are indeed separate stocks. The DFA and classification matrix reinforces the hypothesis of separate stocks as the parasite abundance data was able to correctly classify individual fish with up to 96% accuracy. The DFA also suggests that *Lernanthropus trachuri* and *Anisakis* sp. are good parasites to classify the individual fish into source location, indicating they are perhaps the best biological tags. The presence of *Lernanthropus trachuri* in a fish suggests the fish is from the northern Benguela, however, its absence from a fish does not suggest it is from the southern Benguela as it is not found in all northern Benguela fish. Hence, more than one parasite species is needed to classify the fish into source location. These results show that certain parasites can be used to discriminate between *T. capensis* from the southern and northern Benguela, which supports the hypothesis that there are discrete stocks**.** Localisation of parasites is also worth mentioning as another attribute of the data that supports the two stock hypothesis. The null hypothesis is therefore rejected as there is a significant difference between the South African and Namibian parasite populations of *T. capensis*. It is important to note that this information should be seen in the context of other studies that have used different methods to try determine the stock structure of *T. capensis*, as a holistic approach is essential (Begg and Waldman, 1999).

This study shows definite size effects relating to parasite communities of *T. capensis.* However, this appears to be rather complex and not simply that prevalence, infection intensity and parasite abundance increase with size. The cumulative effect is only seen on some parasites and in some cases it was clear that infection intensity and parasite abundance was higher in the smaller fish (e.g. *Goussia cruciata*). There appears to be no seasonality in the parasite loads of *T. capensis* in the southern Benguela in terms of community structure, infection intensity and parasite abundance.

Constraints and future research

A larger sample size and more capture sites would have been more beneficial for this project, however due to time constraints the 125 fish examined was the maximum output that could be achieved. A much larger number of parasite species were found infecting *T. trachurus* in the HOMSIR study (see Appendix) and this could be due to the much larger sample size as well as the fact that fish were taken from a larger variety of environments. It is important to note that there could be some inter-annual effects on the parasite loads of *T. capensis*, *a*s the fish from the southern Benguela were from 2012 while the northern Benguela fish were caught in 2011.

As the sampling areas from the southern Benguela were rather far east the northern and southern Benguela regions are very different in terms of oceanographic characteristics. This is because the south coast of South Africa does not experience the intense upwelling seen in the northern Benguela. This would most likely result in these fish having different parasites species. Perhaps samples from the west coast of South Africa would have been more beneficial; however, all commercial fishing of *T. capensis* takes place off the south coast of South Africa as most *T. capensis* is found off the south coast. Difficulties in identifying parasites to species level were experienced and this was a short coming of this project as better identification would provide more accurate data and more detailed information for those who will refer to this work. Preserved parasite species samples have been sent to experts to assist in the identification process.

From this study one can see that more research is needed on the seasonality of parasite community structure, infection intensity and parasite abundance as this was only tested in the southern Benguela and perhaps seasonality is more apparent in the northern Benguela. Due

to the new information that an adult population of *T. capensis* is now present on the west coast (Mc Laverty, 2012), it would be most beneficial to obtain samples of these specimens and compare their parasites to both northern Benguela fish as well as to the fish caught off the south coast of South Africa. It would be beneficial to obtain fish from the west coast of South Africa as this is still the southern Benguela but is more similar environmentally to the northern Benguela than the south coast of South Africa. This would allow the ruling out of simply environmental conditions as the reasoning for differences in parasite assemblages. Genetic work on the *Anisakis* sp. larvae would also be beneficial so to ascertain if these were all indeed one single species. Genetic markers obtained from multilocus allozyme electrophoresis are a precise tool in the identification of larval specimens of these *Anisakid* Nematodes (Mattiucci et al., 2008). Future work could also include parasitological examinations on co-occurring *Trachurus trecae* in the northern Benguela and comparing data to that of *T. capensis* in the same region. If parasite assemblages of *T. capensis* and *T. trecae* in the northern Benguela are more similar to each other than parasite assemblages of *T. capensis* from the southern Benguela, this would strengthen the two stock hypothesis. Other work that could be undertaken is an assessment of the physiological effects parasites have on these fish for example the effect *Goussia cruciata* infection has on the liver.

References

Abaunza, P., Villamor, B. and Perez, J. R., 1995, 'Infestation by larvae of *Anisakis simplex* (Nematode: Ascaridata) in horse mackerel, *Trachurus trachurus*, and Atlantic mackerel, *Scomber scombrus*, in ICES Divisions VIIIb, VIIIc and IXa (N-NW of Spain)', *Scientia Marina* **59** (3-4): 223-233.

Abunza, P., 2003, 'HOMSIR: Horse Mackerel Stock Identification Research', 2003, viewed 6 September 2012, from www.homsir.com/.

Abollo, E., Calvo, M. and Pascual, S., 2001, 'Hepatic coccidiosis of the blue whiting, *Micromesistius poutassou* (Risso), and horse mackerel, *Trachurus trachurus* (L.), from Galician waters', *Journal of Fish Diseases* **24**: 335-343.

Agenbag, J. J. and Shannon, L. V., 1988, 'A suggested physical explanation for the existence of a biological boundary at 24°30′S in the Benguela system, South African', *Journal of Marine Science* **6** (1):119-132.

Al Quraishy, S., Koura, E., Abdel-Baki, A. S., Bashtar, A. R., El deed, N., Al Rasheid, K. and Abdel Ghaffar, F., 2011, 'Erratum to: Light and electron microscopic studies on *Kudoa pagrusi* sp. N. (Myxosporea: Multivalvulida) infecting the heart of sea bream *Pagrus pagrus* (L.) From the Red Sea', *Parasitology Research* **108** (6): 1593-1594.

Axelsen, B. E., Krakstad, J. O. and Bauleth-D`Almeida, G., 2004, Aggregation dynamics and diel vertical migration in Cape horse mackerel *(Trachurus trachurus capensis)* in the Namibian Benguela. Implications for acoustic abundance estimation. in: Sumaila, U. R., Steinshamn, S. I., Skogen, M. D., Boyer, D. (eds.), *Ecological, Economic and Social Aspects of Namibian Fisheries*, pp.135-164, Eburon, Delft.

Axelsen, B. E., Bauleth-D'Almeida, G. and Kanandjembo, A., 2003, 'In situ measurements of the acoustic target strength of Cape horse mackerel *Trachurus trachurus capensis* off Namibia', *African Journal of Marine Science* **25** (1): 239-251.

Baldwin, R. E., Banks, M. A. and Jacobson, K. C., 2012, 'Integrating fish and parasite data as a holistic solution for identifying the elusive stock structure of Pacific sardines (*Sardinops sagax*)', *Reviews in Fish Biology and Fisheries* **22**:137–156.

Barange, M., Pillar S. C. and Hampton, I., 1998, 'Distribution patterns, stock size and life-history strategies of Cape horse mackerel *Trachurus trachurus capensis*, based on bottom trawl and acoustic surveys', *South African Journal of Marine Science* **19** (1): 433-447.

Begg, G. A., and Waldman, J. R., 1999, 'An holistic approach to fish stock identification', *Fisheries Research* **43**, 35–44.

Berland, B., 2005, Whole mounts, Occasional Publication No. 1, Institute of Oceanography, pp. 54, Kustem, Malaysia.

Boyer, D. C. and Hampton, I., 2001, 'An overview of the living marine resources of Namibia', *South African Journal of Marine Science* **23** (1): 15-35.

Bush, A. O., Lafferty, K. D., Lotz, J. M. and Shostak, A. W., 1997, 'Parasitology meets ecology on its own terms', *The Journal of Parasitology* **83** (4): 575-583.

Campbell, N., 2005, 'The myxosporean parasitofauna of the Atlantic horse mackerel, *Trachurus trachurus* (L.) in the North-East Atlantic Ocean and Mediterranean Sea', *Acta Parasitologica* **50** (2): 97–101.

Campbell, N., 2008, 'Population studies of horse mackerel (*Trachurus trachurus* (L.)) and herring (*Clupea harengus* (L.)) using parasites as biological tags', PhD thesis, Fishing and Fisheries Sciences and Management, University of Aberbeen.

Carballo, M. C., Cremonte, F., Navone, G. T. and Timi, J. T., 2012, 'Similarity in parasite community structure may be used to trace latitudinal migrations of *Odontesthes Smitti* Along Argentinean Coasts', *Journal of Fish Biology* **80**:15-28.

Cárdenas, L., Hernández, C. E., Poulin, E., Magoulas, A., Kornfield, I., and Ojeda, F. P., 2005, 'Origin, diversification, and historical biogeography of the genus Trachurus (Perciformes: Carangidae)', *Molecular Phylogenetics and Evolution* **35** (2): 496-507.

Choua, Y., Wang, C., Chena, H., Chena, H., Chenc S. and Shiha, H., 2011, 'Parasitism between *Anisakis simplex* (*Nematoda: Anisakidae)* third-stage larvae and the spotted mackerel *Scomber australasicus* with regard to the application of stock identification', *Veterinary Parasitology* **177**: 324−331.

Costa, G., MeloMoreira, E. and Pinheiro de Carvalho, M. A. A., 2012, 'Helminth parasites of the oceanic horse mackerel *Trachurus picturatus* Bowdich 1825 (Pisces: Carangidae) from Madeira Island, Atlantic Ocean Portugal', *Journal of Helminthology* **86**: 368-372.

Crawford, R. J. M., 1989, 'Chapter 12 Horse Mackerels and Saury', in Payne, A. I. L. and Crawford, R. J. M. (eds.), *Oceans of life off southern Africa*, pp. 122-129, Vlaeberg, Cape Town.

De Villiers, G., 1977, 'A preliminary review of trends in south african catches and abundance of horse mackerel (*Trachurus trachurus capensis*)'. *Collection of Scientific Papers* **4**: 99-104.

Department of Agriculture, Forestry and Fisheries (DAFF), 2012, Status of the South African marine fishery resources, Republic of South Africa.

Diouf, M., Benajiba, M. H. and Senhaji. M., 2000, '*Goussia cruciata* (Thelohan, 1892) a hepatic coccidian parasite of the horse mackerel *Trachurus trachurus (*Linnaeus, 1758) from the Mediterranean coasts of northern Morocco', *Bulletin of European Association of Fish Pathology* **20** (6): 219-221.

Draganik, B., 1977, 'Horse mackerel (*Trachurus Trachurus* L.) fishes in the Southeast Atlantic'. *Collection of Scientific Papers* **4**: 25-34.

European Space Agency, 2012, 'Flying Thermometers', view on the 20 January 2013, from http://phys.org/news/2012-07-thermometers.html.

Food and Agricultural Organisation (FAO), 2012, Fisheries and Aquaculture Information and Statistics Service. FAO yearbook. Fishery and Aquaculture Statistics. 2010. Miscellaneous pelagic fishes. B-37. pp. 264-291.

Food and Agricultural Organisation (FAO), 2013, 'Species fact sheet *Trachurus capensis'*, view on 27 January 2013, from http://www.fao.org/fishery/species/3105/en.

Fréon, P., Cury, P., Shannon, L. and Roy. C., 2005, 'Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A Review', *Bulletin of Marine Science* **76** (2): 385–462.

Gaevskaya, A. V. and Kovaleva, A. A., 1980, 'Reasons for the similarities and differences between the parasite faunas of two subspecies of *Trachurus trachurus* in the Atlantic Ocean', *Biologicheskie Nauki* **198** (6): 52-56.

George-Nascimento, M., 2000, 'Geographical variations in the Jack Mackerel *Trachurus symmetricus murphyi* populations in the Southeastern Pacific Ocean as evidenced from the associated parasite communities', *The Journal of Parasitology* **86** (5): 929-932.

Gestal, C. and Azevedo, C., 2005, 'Ultrastructure of *Goussia cruciata* (Apicomplexa: Coccidia) infecting the liver of horse mackerel, *Trachurus trachurus* (L.), from Ibero-Atlantic waters', *Journal of Fish Diseases* **28**: 125–132.

Gibson, D. I., and Bray, R. A., 1986, 'The *Hemiuridae* (Digenea) of fishes from the north-east Atlantic', *British Museum of Natural History* **51** (1).

Hecht, T., 1976, 'The general biology of six major trawl fish species of the Eastern Cape coast of South Africa, with notes on the demersal fishery, 1967 – 1975', PhD thesis, University of Port Elizabeth.

Hecht, T., 1990, 'On the life history of Cape horse mackerel *Trachurus trachurus capensis* off the south-east coast of South Africa', *South African Journal of Marine Science* **9** (1): 317-326.

Herrington, W., 1939, 'Observations on the life history, occurrence and distribution of the redfish parasite Sphyrion lumpi'. United States Department of Commercial Bureau of Fishing., Miteo Report, 7855: 1-12.

Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, C. H., Bartholomae, H. M. S., van der Plas, A. K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R.G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J.C. and Monteiro, P. M. S., 2009, 'The Benguela current: an ecosystem of four components', *Progress in Oceanography* **83**: 15–32.

Kerstan, M. and Leslie, R. W., 1994, 'Horse mackerel on the Agulhas Bank - summary of current knowledge', *South African Journal of Science* **90** (3): 173-178.

Kirchner, C., Bauleth-D'Almeida, G. and Wilhelm, M. R., 2010, 'Assessment and management of Cape horse mackerel *Trachurus capensis* off Namibia based on a fleet-

disaggregated age-structured production model', *African Journal of Marine Science* **32** (3): 525-541.

Krakstad, J. O., 2001, 'The Namibian horse mackerel stock -Summary of resource and management', viewed 10 September 2012, from http://193.190.8.15/ dspace/handle/.

Lett, C., Veitch, J., van der Lingen, C. D. and Hutchings, L., 2007, 'Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems', *Marine Ecology Progress Series* **347**: 247–259.

Llewellyn, 1959, 'The larval development of two species of *Gastrocotylid* Trematode parasites from the gills of *Trachurus trachurus', Journal of Marine Biology* **38**: 461-467.

Llewellyn, 1962, 'The life history and population dynamics of Monogenean gill parasites of *Trachurus trachurus'*, *Journal of Marine Biology* **42**: 587-600.

MacKenzie, K. and Abaunza, P., 1998, 'Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods', *Fisheries Research* **38**: 45-56.

MacKenzie, K. and Abaunza, P., 2005, 'Parasites as biological tags'. In: Cadrin, S. X., Friedland, K. D. and Waldman, J. R. (eds.), *Stock Identification Methods: Applications in Fisheries Science*, pp. 211-226. Elsevier Academic Press, MA, USA.

MacKenzie, K., 1987, 'Parasites as indicators of host populations', *International Journal of Parasitology* **17**:345–352.

MacKenzie, K., 1993, 'Parasites as biological indicators', *Bulletin of the Scandinavian Society for Parasitology* **1**: 1-10.

MacKenzie, K., 1999, 'Parasites as pollution indicators in marine ecosystems: a proposed early warning system', *Marine Pollution Bulletin* **38** (11): 955-959.

MacKenzie, K., 2002, 'Parasites as biological tags in population studies of marine organisms: an update', *Parasitology* **124**: 153-163.

MacKenzie, K., 2012, Personal photographs.

MacKenzie, K., Campbell, N., Mattiucci, S., Ramos, P., Pinto, A. L. and Abaunza, P., 2008, 'Parasites as biological tags for stock identification of Atlantic horse mackerel *Trachurus trachurus'*, *Fisheries Research* **89**:136-145.

MacKenzie, K., Campbell, N., Mattiucci, S., Ramos, P., Pereira, A. and Abaunza, P., 2004, 'A checklist of the protozoan and metazoan parasites reported from the Atlantic horse mackerel, *Trachurus trachurus* (L.)', *Bulletin of European Association of Fish Pathology* **24** (4): 180-184.

Marcogliese, D. J., 2005, 'Parasites of the superorganism: Are they indicators of ecosystem health?', *International Journal for Parasitology* **35**: 705–716.

Mattiucci, S., Farina, V., Campbell, M., MacKenzie, K., Ramos, P., Pinto, A. L., Abaunza, P. and Nascetti, G., 2008, '*Anisakis* spp. larvae (Nematoda: Anisakidae) from Atlantic horse mackerel: Their genetic identification and use as biological tags for host stock characterization' *Fisheries Research* **89**:146–151.

Mc Laverty, K. J., 2012, 'A re-evaluation of the life history strategy of Cape horse mackerel, *Trachurus capensis* in the southern Benguela', MSc thesis, Department of Zoology, University of Cape Town.

Mcclelland, G. and Melendy, J., 2011, 'Use of parasites as tags in delineating stocks of Atlantic cod (Gadus morhua) from the southern Gulf of St. Lawrence and the Cape Breton Shelf', *Fisheries Research* **107**: 233–238.

Meglitsch, P. A., 1959, 'Some Coelozoic Myxosporidia from New Zealand Fishes I. General and family Ceratomyxidae', *Transaction of the Royal Society of New Zealand* **88** (2): 265-356.

Melendy, J., Mcclelland, G. and Hurlbut, T., 2005, 'Use of parasite tags in delineating stocks of white hake (*Urophycis tenuis*) from the southern Gulf of St. Lawrence and Cape Breton Shelf', *Fisheries Research* **76**: 392–400.

Morrison, D.A., 2002, 'How to improve statistical analysis in parasitology research publications', *International Journal for Parasitology* **32:** 1065–1070.

Mosquera, J., de Castro, M. and Go´mez-Gesteira, M., 2003, 'Parasites as Biological Tags of Fish Populations: Advantages and Limitations', *Comments on Theoretical Biology* **8**: 69–91.

Mundjulu, I. E., 2009, 'Trends in the fishery and population traits of the Namibian stock of Cape horse mackerel *Trachurus trachurus capensis* (Castelnau, 1861)', MSc thesis, International Fisheries Management, Norwegian College of Fishery Science, Institute of Aquatic Bio-Sciences, University of Tromso.

Murta, A. G., 2000, 'Morphological variation of horse mackerel (*Trachurus trachurus*) in the Iberian and North African Atlantic: implications for stock identification', *ICES Journal of Marine Science* **57**: 1240–1248.

Naish, K. A., 1990, 'The stock identification of the Cape horse mackerel, *Trachurus trachurus capensis* (Pisces: Carangidae)'. M.Sc. thesis, Rhodes University.

Naish, K. A., Hecht, T. and Payne, A. I. L., 1991, 'Growth of Cape horse mackerel *Trachurus trachurus capensis* off South Africa', *South African Journal of Marine Science* **10** (1): 29-35.

Oktener, A. and Trilles, J. P., 2004, 'Three new parasitic copepod species for the Parasite fauna of marine fish of Turkey', J*ournal for Black sea and Mediterranean environment* **10**: 71-80.

Oliva, M. E., 1999, 'Metazoan parasites of the Jack mackerel *Trachurus murphyi* (*Teleostei, Carangidae*) in a latitudinal gradient from South America (Chile and Peru)', *Parasite* **6** (3): 223.

Pascual, S., Abollo, E., Yurakhno, V. and Gaevskaya, A., 2012, 'Molecular Characterization Of *Kudoa Nova* (Myxosporea: Multivalvulida) Infecting the Round Goby *Neogobius Melanostomus* from the Sea Of Azov', Морський Екологічний Журнал **70**.

Pascual, S., Arias, C. and Guerra, A., 1996, 'First record of the trypanorhynchidean parasite *Nybelinia lingualis* Cuvier, 1981 in the squid Tadaropsis eblanae (Cephalopoda: Ommastrephidae)', *Science Marine* **60** (4): 553-555.

Pillar, S. C. and Barange, M., 1998, 'Feeding habits, daily ration and vertical migrationof the Cape horse mackerel off South Africa', *South African Journal of Marine Science* **19** (1): 263-274.

Radujkovic, B. M., and Euzet, L., 1989, 'Parasites des poissons marins du Monténégro: Monogènes', *Acta Adriatica* **30** (51): 135.

Reed, C. C., Basson, L., Van As, L. L. and Dyková, I., 2007, 'Four new myxozoans (*Myxosporea: Bivalvulida*) from intertidal fishes along the south coast of Africa', *Folia Parasitologica* **54**: 283–292.

Rohde, K., 1979, 'A Critical evaluation of intrinsic and extrinsic factors responsible for niche restriction', *The American Naturalist* **114** (5): 648-671.

Roux, J. P., van der Lingen, C., Gibbons, M. J., Moroff, N. E., Shannon, L. J., Smith, A. D. M. and Cury, P. M., In Press, 'Jellification of marine ecosystems as a likely consequence of overfishing small pelagic fish: lessons from the Benguela', *Bulletin of Marine Science.*

Sakanari, J. A. and McKerrow, J. H., 1989, 'Anisakiasis', *Clinical Microbiology Review* **2** (3): 278.

Shukhgalter, O. A. and Rodjuk, G.N., 2007, 'The use of parasitological data in population studies of the commercial pelagic fishes from the central-east Atlantic', *ICES Council Meeting* 13: 1-5.

StatSoft, Inc., 2011, STATISTICA (data analysis software system), version 10. www.statsoft.com.

Stephenson, R. L., 1999, 'Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units', *Fisheries Research* **43** (1): 247-249.

Suda, Y., Machii, T. and Orrego, H., 1995, 'Some fishery and biological aspects of Jack Mackerel, genus *Trachurus* (Carangidae)', *Scientia Marina* **59** (3-4): 571-580.

Waldman, J. R., 2005, 'Definition of stocks: an evolving concept', in: Cadrin, S. X., Friedland, K. D., Waldman, J. R. (eds.), *Stock identification methods. Applications in fisheries science*, pp. 7–16, Elsevier Academic Press, San Francisco.

Wilhelm, M. R., Durholtz, M. D. and Kirchner, C. H., 2008, 'The effects of ageing biases on stock assessment and management advice: a case study on Namibian horse mackerel', *African Journal of Marine Science* **30** (2): 255-261.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D., Rosenberg, A. A., Watson, R. and Zeller, D., 2009,'Rebuilding global fisheries', *Science* **325**: 578-585.

Appendix

Table A: Parasite species found in *Trachurus trachurus* Linnaeus, 1758 from the 38 localities of the HOMSIR project together with earlier records from various literature sources, Kovaleva (1970) and Gaevskaya and Kovaleva (1979, 1980abc, 1982) (adapted from MacKenzie et al. (2004)). *Denotes new host records from the HOMSIR study.

Class	**Parasite species and author**	**Site of infection**
Apicomplexa	*Goussia cruciata* Thelohan, 1892	Liver
Myxosporea	*Alataspora serenum* Gaevskaya and Kovaleva, 1979	Gall bladder
	Alataspora solomoni Yurakhno, 1988	Gall bladder
	Kudoa nova Naidenova, 1975	Musculature
	Kudoa quadratum Thelohan, 1895	Musculature
	**Kudoa* sp.	Gall bladder
	**Myxobolus* sp.	Liver
Monogenea	*Cemocotyle trachuri* Dillon and Hargis, 1965	Gills
	Gastrocotyle trachuri van Beneden and Hesse, 1863	Gills
	Heteraxinoide satlanticus Gaevskaya and Kovaleva, 1979	Gills
	Pseudaxine trachuri Parona and Perugia, 1889	Gills
	*Unidentified *polyopisthocotylean*	Gills
	Paradiplectanotrema trachuri Kovaleva, 1970	Stomach, oesophagus
Digenea	*Lasiotocus typicum* Nicoll, 1912	Intestine
	Aphanurus stossichi Monticelli, 1891	Stomach
	**Bathycreadium elongatum* Mailard, 1891	Intestine
	Lasiotocus tropicus Manter, 1940	Intestine
	Derogenes varicus Muller, 1784	Stomach
	Ectenurus lepidus Looss, 1907	Stomach
	Ectenurus virgulus Looss, 1910	Stomach
	Helicometra pulchella Rudolphi, 1819	Intestine
	Hemiurus communis Odhner, 1905	Stomach
	Hemiurus luehei Odhner, 1905	Stomach
	Lecithaster confusus Odhner, 1905	Intestine
	Lecithaster gibbosus Rudolphi, 1802	Intestine
	Lecithocladium excisum Rudolphi, 1819	Pyloric caeca
	Monascus filiformis Rudolphi, 1819	Pyloric caeca, intestine

	Opechona pyriforme Linton, 1900	Intestine
	Opechona bacillaris Molin, 1859	Intestine
	Pseudopecoeloide schloroscombri Fischal and Thomas, 1970	Intestine
	Prodistomum polonii Molin, 1859	Intestine
	Prodistomum orientalis Layman, 1930	Intestine
	Pseudopecoeloide scarangis Yamaguti, 1938	Intestine
	Stephanostomum sp. Gritli et al., 1989	Intestine
	Lecithochirium musculus Looss, 1907	Stomach
	Tergestia laticollis Rudolphi, 1819	Intestine
	Zoogonus rubellus Olsson, 1868	Intestine
Cestoda (all post larvae)	*Anthobothrium cornucopia* van Beneden, 1850	Intestine
	Callitetrarhynchus gracilis Rudolphi, 1819	Visceral cavity
	Christianella minuta van Beneden, 1849	Visceral cavity
	Grillotia bothridiopunctata Dollfus, 1969	Visceral cavity
	Grillotia erinaceus van Beneden, 1858	Visceral cavity
	Lacistorhynchus tenuis van Beneden, 1858	Visceral cavity
	Nybelinia sp. Kovaleva, 1970	Visceral cavity
	Nybelinia lingualis Cuvier, 1817	Visceral cavity
	Scolex pleuronectis Muller, 1788	Intestine
	**Pseudophyllidean plerocercoids*	Visceral cavity
Acanthocephala	**Corynosoma strumosum* (juveniles) Rudolphi, 1802	Visceral cavity
	**Corynosoma wegeneri* (juveniles) Heinze, 1934	Visceral cavity
	Rhadinorhynchus cadenati Golvan and Houin, 1964	Intestine
Nematoda	*Anisakis simplex* (larvae) Rudolphi, 1809	Visceral cavity
	Anisakis pegreffii (larvae) Campana-Rouget and Biocca, 1955	Visceral cavity
	Anisakis physeteris (larvae) Baylis, 1923	Visceral cavity
	Contracaecum sp. (larvae) Rego, 1987	Intestine, visceral cavity
	Cosmocephalusobvelatus (larvae) Creplin, 1825	Visceral cavity
	Hysterothylacium aduncum (adults) Rudolphi, 1802	Stomach, intestine
	Hysterothylacium aduncum (larvae) Rudolphi, 1802	Visceral cavity
	Paracuaria tridentata (larvae) Linstow, 1877	Visceral cavity
	**Pseudanisakis* sp. (larvae)	Visceral cavity
	**Pseudo terranova decipiens* (larvae)	Musculature
	Raphidascaris sp. (larvae) Rego, 1987	Intestine, visceral cavity
Crustacea	*Caligus diaphanus* Nordmann, 1832	Skin
	Caligus elongatus Nordmann, 1832	Skin
	Caligus pelamydis Kroyer, 1863	Mouth
	Peniculus fistula Nordmann, 1832	Fins
	Lernanthropus trachuri Brian, 1903	Gills
	Ceratothoa oestroides Risso, 1826	Mouth
	**Pranizagnathiid isopod* (larvae)	Skin
	**Argulus purpureus* Risso, 1826	Skin