A review of parasite studies of commercially important marine fishes in sub-Saharan Africa

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SUMMARY

Scattered records of parasitic species infecting commercially important marine fishes in sub-Saharan Africa are known from just a few countries where concerted efforts have been made by local parasitologists (e.g. Senegal, Nigeria, South Africa). Most of these consist of taxonomic records or general surveys of parasite faunas associated with marine hosts, which may or may not have been of commercial value. Little to no multi-disciplinary research is conducted in most parts of sub-Saharan Africa and hence parasitological data are not commonly used to advise fisheries management procedures. This review summarizes current knowledge on all parasitological research associated with commercially important marine fish species in sub-Saharan Africa.

Key words: Africa, marine, parasites, fisheries, aquaculture.

INTRODUCTION

The study of parasitic species associated with economically valuable fishes is an important area of research that contributes to successful and sustainable management of fisheries and aquaculture systems throughout the world. Whether wild-caught or reared in captivity, harvested species inevitably become affected by associated environmental stressors that in turn raise the impacts of pathogenic parasites. This review documents the efforts of marine parasitologists throughout the sub-Saharan Africa region and aims to provide a useful synopsis of publications that may be used by researchers when identifying gaps in knowledge or future research planning.

In most of sub-Saharan Africa it is commonly acknowledged that fundamental research on parasites and their associated fish hosts (both commercial and not) requires more specific attention, especially in recognition of the substantial aquaculture and wild-caught fisheries that exist throughout the continent. During the 1980s, when inland aquaculture facilities were being rapidly established throughout sub-Saharan Africa, Hecht and Endemann (1998) published a review that identified parasites and diseases that may impact on the development of aquaculture in this region. Their listings included mostly freshwater species and they identified ectoparasites as being the most important group of pathogenic organisms that had the capacity to cause large-scale mortalities in fish farms.

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Hardly any mention was made of parasite species that may be problematic for marine aquaculture systems in sub-Saharan Africa. Hecht and Endemann (1998) mentioned only two important marine polychaete ectoparasites: the mud blister worm, *Polydora hoplura*, which infects oysters (*Crassostrea gigas*) in Namibia and South Africa, and indigenous South African sabellid polychaetes that have become problematic in abalone (*Haliotus midae*) farms in South Africa. *Polydora hoplura* is known to form blisters in the nacre of oysters that, when punctured, release a pungent smell that affects product quality. Although infection by *P. hoplura* does not cause severe mortalities, the oysters do expend excessive energy secreting nacre and concholin during mud blister formation, which leads to a reduction in the oyster quality and growth rate (Nel *et al*. 1996). Other sabellid polychaete worms (*Dipolydora capensis* and *Boccardia* sp.) as well as *P. hoplura* are also known to attach themselves to the growing edge of abalone, where they embed and ultimately deform the shells (Hecht and Endemann, 1998). Several parasite species have been recorded from abalone and oysters in South Africa and numerous studies have examined treatments and prevention of these infections (Nel *et al*. 1996; Botes, 1999; Simon *et al*. 2006; Mouton and Gummow, 2011) (Table 1). Above all, the major concern associated with the importation of oysters and abalone is the constant threat of new introductions of pathogenic species that have as yet not been detected (Haupt *et al*. 2009).

In wild-caught marine fisheries, knowledge of associated parasite species is equally important. The potential of certain parasites to, for example, devastate stocks by impairing spawning (e.g. *Eimeria sardinae*

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Table 1. Parasite species known to infect abalone (*Haliotus midae*) and oysters (*Crassostrea gigas*) in southern Africa

Host	Parasites	References
Haliotus midae (abalone)	Gut protozoa, digestive gland protozoa and rickettsia like prokaryotes	Mouton and Gummow (2011)
	Sessile ciliate: *Mantoscyphidia midae*	Botes (1999)
	Polychaete worms: *Dipolydora capensis, Polydora hoplura, Boccardia* sp.	Simon *et al*. (2006)
Crassostrea gigas (oyster)	Polychaete worm: *P. hoplura, Boccardia proboscidea*	Nel *et al*. (1996); Haupt *et al*. (2009)

in Portuguese sardine; Pinto, 1956); influence product quality through myoliquefaction (e.g. *Kudoa thyrsites*); have effects on human health such as inducing allergies (Kirstein *et al*. 2010) or through accidental infections by notorious species (e.g. *Anisakis* sp.) are well known (Lima dos Santos and Howgate, 2011). Perhaps what is less obvious is the usefulness of such parasite data in ecosystem-based fisheries studies where understanding host–parasite relationships can help to predict changes in environmental conditions (such as acting as sensitive indicators of pollution and heavy metal accumulation; Sures, 2004) or where they may be used in applied research (such as the use of parasites as biological tags for fish stock discrimination studies; Baldwin *et al*. 2012), ultimately enhancing sustainable fisheries management practices.

Fishing has clearly stressed wild populations of many commercially valuable species across the globe (Jennings and Kaiser, 1998; Jackson *et al*. 2001). The coastal region of sub-Saharan Africa is no exception. Stretching from Mauritania in the west to Eritrea in the east and covering ±48 000 km of coastline, it includes five of the world's most productive large ocean currents (Fig. 1). This extensive stretch of coastline harbours an intensive fishing culture ranging from small subsistence and artisanal fisherman to large commercial industries. Marine aquaculture and fisheries production in this area amounted to 4 220 412 t (for fish, crustaceans and molluscs) in 2010 (FAO, 2010), an amount far less than the global production total of 148 476 426 t for the same commodities in that year, but still significant enough to have potential effects on wild fish populations.

Despite the importance of fishery resources throughout this region, very little research has been conducted on the effects of parasitic species associated with commercially harvested hosts, and even less work has been done using parasite data in applied studies to enhance fisheries management. Most parasitological research outputs stem from just a few countries (Senegal, Nigeria, Namibia, South Africa and Kenya) where mostly taxonomists have made concerted efforts to document parasitic species associated with hosts of both commercial and non-commercial importance.

WEST COAST OF SUB-SAHARAN AFRICA

Environmental conditions along the western coast of sub-Saharan Africa are driven by two major ocean currents (Gyory *et al*. 2005). The Canary Current (off the coasts of Mauritania, Senegal, the Gambia, Guinea Bissau and Guinea) is a wind-driven cold-water surface current that forms part of the North Atlantic Gyre and flows in a south-westerly direction (Fig. 1), and the Guinea Current (off the coasts of Sierra Leone, Liberia, Cote d' Ivoire, Ghana, Benin, Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo and Democratic Republic of Congo) is fed by the North Equatorial Counter-Current and flows in an easterly direction (Fig. 1). The most abundant commercial species in these regions are the clupeids (*Sardina pilchardus*), jack mackerel (*Trachurus* spp.) and chub mackerel (*Scomber japonicus*), as well as several large pelagic (*Thunnus* spp.) and demersal species.

Research on parasite species associated with marine fishes in this region includes mostly surveys of parasite faunas and descriptions of new species. Parasitologists in Senegal, in particular, have made a tremendous contribution to the known diversity of certain parasitic taxa (esp. Myxozoa, Coccidia and Microsporidia) in both commercial and non-commercial marine fishes (Table 2). Nearly 100 parasite species from these groups have been recorded or described from marine fishes in Senegal since the 1990s. Similarly parasitologists in Nigeria have made a substantial contribution to the known diversity of parasite species infecting specifically commercially important marine and estuarine fishes (Table 3).

Studies on parasites infecting commercially important marine fishes are thus scattered throughout this region, several of which comprise surveys of entire parasite faunas of hosts of commercial value (Table 3). Gaevskaya and Kovaleva (1980, 1985) surveyed the parasites of jack mackerel (*Trachurus* spp.) off the coast of West Africa, emphasizing the importance of using parasites in population studies and the use of parasites to distinguish subpopulations of the *Trachurus* spp. they studied. Shukhgalter (2004) surveyed parasites of chub mackerel (*S. japonicus*) in the same region, showing

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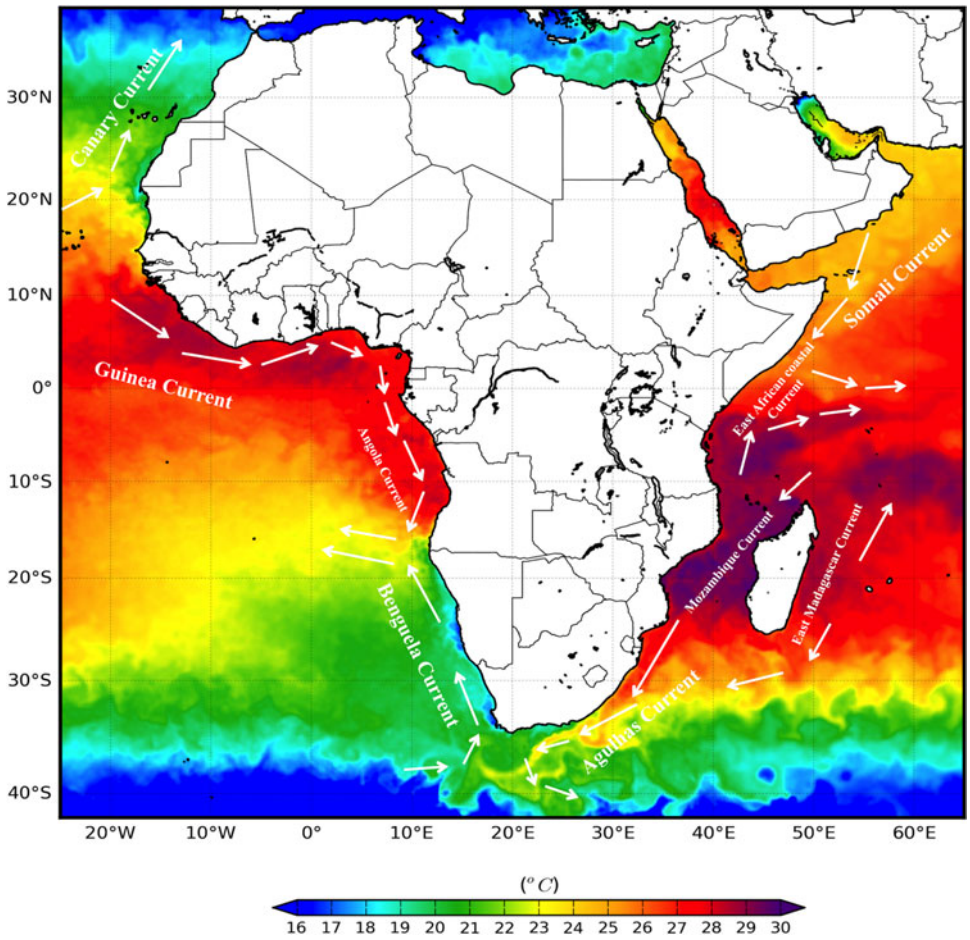

Fig. 1. Sea surface temperature composite map showing the major ocean currents around Africa (Global Odyssea SST at 0.1 degree resolution derived by the CERSAT. Data from http://www.ifremer.fr/cersat1/exp/productscatalogdetails/)?id=CER-SST-GLO-1D-010-ODY-MGD).

the occurrence of differences in parasite assemblages infecting these fish off the coasts of Morocco and Mauritania, and thus the possible existence of two sub-populations of this fish species in those regions. The presence of *Kudoa histolytica* in the musculature of *S. japonicus* was shown to have negative effects on the commercial value of this species. Several parasites that were of concern for human health were also recorded (larvae of *Bolbosoma* sp. that occurred off the Azores Archipelago bank; *Anisakis simplex* and *Contracaecum* sp. that occurred in all the areas sampled). Kijewska *et al*. (2009) surveyed the anisakid parasites of six commercially important fish species caught over the West African Shelf (Table 3).

In an extensive study by Spanish parasitologists, Castro-Pampillón *et al*. (2002*a*, *b*) surveyed the parasites of swordfish (*Xiphias gladius*) in the Gulf of Guinea for the purposes of identifying species that may act as suitable biological tags (Table 3). Subsequently, Garcia *et al*. (2011) compared the metazoan parasite faunas of *X. gladius* from four regions in the Atlantic, finding that certain parasite taxa showed varying levels of infection from these different regions. *Hysterothylacium corrugatum* (s.l.) and *Rhadinorhynchus pristis* were more abundant in fish caught in the northwest, and *Anisakis paggiae* and *Hysterothylacium incurvum* in fish caught in the southern areas, while *A. simplex* (s.s.) was common in fish from all northern localities. The results of this study supported the existence of at least two distinct sub-populations of *X. gladius* in the Atlantic, which corresponds to the results of genetic stock structure of this species.

In Nigeria, efforts to document parasites infecting fishes of commercial value has led to numerous publications on surveys of parasite faunas (Table 3). Anyanwu (1983) described the nematode *Philometra translucida* from the ovaries of commercially harvested croaker species (*Pseudotolithus senegalensis*, *P. typus* and *P. elongatus*), and Obiekezie (1986) described a coccidian, *Goussia ethmalotis*, from west African shad, *Ethmalosa fimbriata*. Obiekezie *et al*. (1988) published data on parasitic infections and gross external lesions of commercially harvested bagrid catfish, *Chrysichthys nigrodigitatus* from the Cross River Estuary and Obiekezie *et al*. (1992) conducted a large-scale survey of parasites infecting commercial fishes from inshore off Nigeria. A large-scale survey of

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Table 2. Some of the major taxonomic contributors to marine parasitology in west and central sub-Saharan Africa

Group	References
Protozoa, Myxozoa	*Benin*: Sakiti (1997); *Nigeria*: Obiekezie (1986); *Senegal*: Toguebaye *et al*. (1989); Faye *et al*. (1990, 1991, 1994, 1995, 1996, 1997, 1998, 1999, 2004); Diouf and Toguebaye (1993, 1994*a*, *b*, 1996, 2003, 2013); Faye and Toguebaye (2005); Kostoïngue and Toguebaye (1994); Kpatcha *et al*. (1996*a*, *b*, 1997*a*, *b*, 1999); Fall *et al*. (1997, 2000); Kostoïngue *et al*. (1998, 1999, 2001); Diebakate *et al*. (1999); Levron *et al*. (2004*a*, *b*); Faye and Toguebaye (2005); Diamanka *et al*. (2008, 2010).
Monogenea	*Benin*: Doussou (1985)
Digenea	*Ghana*: Fischthal and Thomas (1968). *Nigeria*: Oribhabor *et al*. (2012)
Nematodes	*Nigeria*: Anyanwu (1983), Obiekezie (1987); *Senegal*: Vassiliades (1975)
Copepoda	*Benin*: Aladetohun *et al*. (2013); *Nigeria*: Harding (1964) *Senegal*: Diebakate and Raibaut (1996)
Isopoda	*Senegal*: Daguerre de Hereux (1971); Trilles (1986); Bruce and Bowman (1989)
Acanthocephala	*Senegal*: Golvan (1956); Marchand (1984); *Nigeria*: Farooqi (1981)
Cestoda	*Senegal*: Campbell and Beveridge (1997); *Broad Atlantic*: Palm (1992), Palm *et al*. (1997)
General	*Burkina Faso*: Kabre (1997)

Table 3. Studies of parasites infecting commercial marine fishes in west and central sub-Saharan Africa ('Numerous' = more than five fish hosts examined)

Reference	Host	Region	Purpose
Golvan (1956)	Numerous	Senegal	Species descriptions
Bane (1969)	*Thunnus albacare*	Atlantic West Africa	Survey
Bussieras and Aldrin (1965)	*Thunnus thunnus*	Gulf of Guinea	Species description
Baudin-Laurencin (1971)	*Thunnus albacare*	Gulf of Guinea	Parasite survey, including information on stock structure
Szuks *et al*. (1975)	*Brama raii*	Northwest African coast	Survey
Gaevskaya and Kovaleva (1980, 1985)	*Trachurus* sp., *Trachurus pictuarus*	Atlantic West Africa	Parasite surveys and use of parasites in host population studies
Anyanwu (1983)	*Pseudotolithus senegalensis*, *P. typus*, *P. elongatus*	Nigeria	Taxonomic survey, new species description, basic biological data on infections
Obiekezie (1986)	*Ethmalosa fimbriata*	Nigeria – Cross River Estuary	Taxonomic, new species descriptions
Obiekezie *et al*. (1988)	*Chrysichthys nigrodigitatus*	Nigeria – Cross River Estuary	Survey
Obiekezie *et al*. (1992)	Numerous	Nigerian inshore waters	Parasite and disease survey
Palm *et al*. (1994)	Numerous	Nigeria	Survey of trypanorynchid cestodes
Castro-Pampillón *et al*. (2002*a*)	*Xiphias gladius*	Gulf of Guinea	Survey
Shukhgalter (2004)	*Scomber japonicus*	Morocco, Mauritania, Azores	Survey
Kijewska *et al*. (2009)	Numerous	West African Shelf	Survey of anisakid species
Abowei and Ezekiel (2011)	Numerous, mostly freshwater species	Nigeria	Review
Garcia *et al*. (2008, 2011)	*Xiphias gladius*	Atlantic Ocean	Population studies using parasites as indicators of sub-populations
Oribhabor *et al*. (2012)	*Polydactylus quadrifilis*	Nigeria	Survey of helminths
Noor El- Deen *et al*. (2012)	*Mugil cephalus*	Benin	Survey of Caligus disease
Aladetohun *et al*. (2013)	*Mugil cephalus, Liza palcipinnus*	Benin	Survey of copepod parasites
Caira *et al*. (2013*b*)	*Raja cf. miraletus*	Senegal	Taxonomic, biogeographical

trypanorhynchid cestodes infecting commercial inshore fishes off the Nigerian west African coast was conducted by Palm *et al*. (1994) recording nine species and reporting that the low incidence of infection of all species did not pose a threat to the marketability of commercial fishes in this region.

SOUTHERN AFRICA (ANGOLA, NAMIBIA, SOUTH AFRICA, MOZAMBIQUE, MADAGASCAR)

There are several ocean currents that drive environmental conditions around the coast of southern Africa (Fig. 1). On the west coast, cold, nutrient-rich

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water is carried to the surface by the wind-driven Benguela current that originates to the west of the South Atlantic current and transports this water northwards past the west coast of South Africa and the coasts of Namibia and Angola. The Benguela Current is one of four major upwelling systems in the world, but unlike other upwelling systems, the Benguela is flanked on either side (north and south; 19–34°S) by two stratified sub-tropical or warm-temperate boundary regions (Hutchings *et al*. 2009) and is itself divided into the northern and southern Benguela by the powerful Lüdertiz upwelling cell, which is present at 26°S (Fig. 1). This wind-driven upwelling system supports an intensive fishing industry dominated by small pelagic species such as sardine (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*) and horse mackerel (*Trachurus capensis*) as well as larger pelagics such as the Cape hakes (*Merluccius capensis* and *Merluccius paradoxus*).

On the eastern coast of southern Africa, conditions are entirely different. Here the warm Agulhas Current, fed by the Mozambique and East Madagascar Currents (Fig. 1), transports sub-tropical water from the equator southwards past Madagascar, Mozambique and the eastern shores of South Africa, eventually forming a retroflection to re-join the Indian Ocean Gyre near Cape Agulhas (Fig. 1) (Heileman *et al*. 2009). Warmer waters, lower nutrient levels and high species diversity dominate the eastern shores of southern Africa. The existence of these very different environmental conditions around the coast of southern Africa makes this, the southern tip of the African continent, one of the most species-rich marine regions in the world.

Large-scale marine fisheries in Namibia and South Africa are well developed and in both these countries, demersal Cape hake (*Merluccius capenis* and *M. paradoxus*) fisheries are the most valuable. In Namibia, the second most important fishery is that for horse mackerel (*Trachurus capenis* and *Trachurus trecae*), followed by small pelagic species such as sardine (*S. sagax*). In South Africa, the largest fishery in terms of annual tonnage landed is that for small pelagics (sardine, *S. sagax*; anchovy, *E. encrasicolus*; round herring, *Etrumeus whiteheadi*), followed by the fishery for horse mackerel (*T. capensis*). Other important fisheries off Namibia and South Africa include the line fish, netfish such as *Liza richardsonii* (South African mullet; harder) and *Callorhynchus capensis* (St Joseph shark) as well as several species of shark (DAFF, 2012).

In Mozambique, small-scale artisanal fishermen dominate the fishing industry and contribute around 80% of the annual catch landings which are on average about 120 000 t (FAO, 2007). Unlike other coastal African countries, the most important marine species harvested in Mozambique are crustaceans (especially prawns, deepwater shrimp, crayfish, lobsters and crabs). Marine finfish (demersal) and pelagic species such as grouper (Serranidae), snapper (Lutjanidae), emperor (Pomacanthidae) and sea bream (Sparidae), migratory tuna species (*Thunnus alalunga, Thunnus albacares, Thunnus obesus*), swordfish (*X. gladius*) and shark are amongst the harvested species (FAO, 2007). An extensive aquaculture industry has recently been established (in both freshwater and marine environments). The main marine species farmed in Mozambique include black tiger prawn (*Penaeus monodon*), Indian white prawn (*Fenneropenaeus indicus, F. japonicus*), pink prawn (*Macrobrachium monocerosi*), kuruma prawn (*Modiolus philippinarum*), bivalves (*Perna perna, Meretrix meretris, Modiolous philippinarum, Eumarcia pauperculata, Sacrostrea cucullata, Cassostrea gigas* and *Venerupis japonica*) and mud crab (*Scylla serrata*).

Research on marine parasitic species in southern Africa is probably the best documented out of the entire sub-Saharan African region. Taxonomic studies outnumber applied research by far because of the concerted efforts by taxonomists dating back to the early 1900s. Some of the earliest records of parasite species described from marine fishes in southern Africa were by naturalists such as K.H. Barnard, H.B. Fantham and J.D. Gilchrist who described large numbers of new species of parasites from marine fishes during general surveys of marine life in South Africa during the early 1900s. Subsequently specialist taxonomists, in South Africa in particular, have made tremendous progress in describing new parasitic species and recording new host records (Table 4). Although some parasite taxa have received more attention than others, all groups have been investigated in some way by passionate taxonomists.

Recently, attention has turned to parasites of commercially important species in southern Africa. Current research by scientists from South Africa's Department of Agriculture, Forestry and Fisheries and the University of Cape Town aims to include the use of parasite data in fisheries research for the purposes of improving management strategies for target species. Some of these target species currently being investigated are discussed below, while other studies relating to parasite faunas of commercially valuable fishes in southern Africa are listed in Table 5.

Sardine (*S. sagax*) are the target species caught in Namibian and South African pelagic purse-seine fisheries and are the subjects of the first biological tagging project to be attempted in southern Africa. These fish are distributed around the southern African coastline from southern Namibia in the west to Richards Bay in the east (Coetzee *et al*. 2008). Within this distribution range, the Lüderitz upwelling cell (26°S) off Namibia acts as a powerful environmental barrier for sardine movement, hence it is accepted that a separate sub-population of *S. sagax* exists off the Namibian coast. In South Africa, the sardine specific fishery is managed as a single

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Table 4. Some of the major taxonomic contributors to marine parasitology in southern Africa (see reference list for details of these studies).

Group	References
Protozoa	*South Africa: Haemogregarines and trypanosomes*: Davies and Smit (2001); Davies *et al*. (2003, 2004); Ferreira *et al*. (2012); Hayes *et al*. (2006, 2007); Smit and Davies (1999, 2001, 2005, 2006); Smit *et al*. (2002, 2003, 2005); Yeld and Smit (2006); *Ciliates*: Botes (1999)
Myxozoa	*South Africa*: Fantham (1918, 1919, 1930, 1938); Fantham and Porter (1914); Gilchrist (1918, 1924); Dubina and Isakov (1976); Gaevskaya and Kovaleva (1979); Schulman *et al*. (1979); Ali (2000); Reed *et al*. (2007, 2009)
Monogenea	*South Africa*: Bullard *et al*. (2004); Vaughan *et al*. (2008, 2010); Vaughan and Chisholm (2010*a*, *b*, 2011); Vaughan and Christison (2010, 2012)
Digenea and Cestoda	*South Africa: Digeneans*: Prudhoe (1956); Solonchenko (1968); Gaevskaya and Kovaleva (1980); Aleshkina and Gaevskaya (1985); Bray (1984, 1985, 1986, 1987); Gaevskaya (1990). *Cestodes*: Linton (1924); Botha (1986); Palm *et al*. (1994, 1997); Payne (1986), Reimer (1984, 1989); Schramm (1989, 1991); Rodriguez *et al*. (2011); Caira *et al*. (2013*a*, *b*). *Mozambique: Nematodes*: Moravec *et al*. (2000, 2002, 2012); Taraschewski *et al*. (2005). *Acanthocephalans*: Bray (1974); Bray *et al*. (1988); Bray and Reimer (2004); Amin and Christison (2005)
Copepoda	*South Africa*: Wilson (1923); Kabata (1963); Barnard (1948, 1955*a*, *b*); Kensley (1970); Ho (1975); Kensley and Grindley (1973); Jones and Hine (1978); Oldewage and Van As (1988); Dojiri (1989); Oldewage (1992, 1993*a*, *b*); Avenant-Oldewage (1994); Kruger and Oldewage (1997); Van As *et al*. (1999); Van As and Van As (2001); Grobler *et al*. (2002, 2003*a*, *b*, 2004); Smit *et al*. (2005). *On sharks*: Dippenaar (2005); Dippenaar and Olivier (1999), Dipenaar and Jordaan (2006, 2007); Dippenaar *et al*. (2000, 2001, 2004, 2009, 2010); Olivier *et al*. (2000)
Isopoda	*Madagascar*: Barnard (1960); Kensley *et al*. (2009); *South Africa*: Barnard (1914*a*, *b*, 1920, 1925, 1926, 1940, 1957, 1960); Trilles (1979); Kensley (1978, 2001); Smit *et al*. (1999); Smit and Van As (2000), Smit and Basson (2002), Wright *et al*. (2001); Smit and Davies (2004); Hadfield and Smit (2008); Hadfield *et al*. (2008, 2009, 2010, 2011, 2013); Hayes *et al*. (2007)

population around the entire coastline. There are however several indications that the sardine population in South Africa could be separated into two or even three sub-populations (van der Lingen *et al*. 2014). A survey of parasite species infecting *S. sagax* by Reed *et al*. (2012) identified seven parasite taxa (Table 5), two of which (a digenean 'tetracotyle'-type metacercariae infecting the eyes and a coccidian, *E. sardinae* infecting the testes) met the criteria for suitable biological tags as set out by MacKenzie and Abaunza (2013). Subsequent studies (Ssempa, 2013; Weston, 2013) have further supported the existence of multiple sub-populations of *S. Sagax* around the coast of southern Africa (van der Lingen *et al*. 2014).

Amongst the medium-sized pelagics, Cape horse mackerel (*T. capensis*) is an important mid-water species found around the coast of southern Africa from northern Namibia/southern Angola to the east coast of South Africa, where they shoal over the continental shelf (DAFF, 2012). A second species, Cunene horse mackerel (*Trachurus trecae*) occurs off the north coast of Namibia and Angola. Despite the economic importance of these species in both South Africa and Namibia, only a few studies on parasites infecting *T. capensis* have been documented (Table 5). Some of these are incidental accounts of infection such as Hecht (1976) who, whilst investigating the biology of six trawl species in the southern Benguela, noted that the testes and liver of *T. capenis* harboured an unusually high intensity of infection by a nematode from the genus *Anisakis*. This infection was present throughout the year, with highest intensities peaking from December to April, a time that corresponded with the gonads being in early stages of seasonal development. During this peak level of infection intensity the *Anisakis* sp. contributed up to 65·8% of the total gonad mass of *T. capensis* (Hecht, 1976, 1990), raising concern of parasitic castration. No further research took place following these observations. Several years later Gaevskaya and Kovaleva (1980) conducted a full parasitological survey of *T. capensis* specimens collected off the coast of Namibia. These authors recorded numerous species of helminths and two species of protozoan parasites infecting *T. capensis* off Namibia (Table 5).

Recently Le Roux (2013) investigated parasite assemblages of two sub-populations of *T. capensis* from the northern (Namibian) and southern (South African) Benguela ecosystem, respectively (Table 5). These two sub-populations are believed to be divided by the powerful Lüderitz upwelling cell. Some uncertainty exists regarding the degree of mixing that may occur between these northern and southern Benguela sub-populations of *T. capensis*. Le Roux (2013) found that fish from the northern and southern Benguela sub-populations hosted very similar parasite assemblages, but showed significant differences in infection intensity, prevalence and abundance of four parasite species in particular (the liver coccidian, *Goussia cruciata*, the gill monogenean *Gastrocotyle trachuri*, a visceral nematode, *Anisakis* sp., and a gill copepod *Lernanthropus trachuri*), reflecting the distribution of these two sub-populations. In a first ever survey of parasites of *T. trecae*

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collected off the northern coast of Namibia and southern Angola, Bowker (2013) recorded six parasite taxa of which four were identifiable to species, two to genus and one to class level (Table 5). The parasite assemblages recorded by Bowker (2013) were very similar to those for *T. capensis* (Le Roux, 2013), yet significant interspecific differences were seen in *Anisakis* sp. and *G. cruciata* intensity of infection between these two hosts.

Amongst commercial species in southern Africa, the Cape hakes have been the best studied in terms of their parasite faunas, most likely driven by the tremendous value of these species in this region (Table 5). Two species of Cape hake, *M. capensis* and *M. paradoxus* are commercially harvested off the coasts of Namibia and South Africa (Kainge *et al*. 2007). Both species are distributed around the southern African coastline from roughly southern Angola in the west to southern Mozambique in the east, varying only in average distribution with depth and distance from the coast. Within South African waters it is assumed that a single population of each species persists, but the number of populations within the entire Benguela Ecosystem is not entirely confirmed. Several indications are that *M. paradoxus* may comprise a single stock, shared by South Africa and Namibia, while *M. capensis* appears to consist of two stocks separated by the powerful Lüderitz upwelling cell at 26°S. Studies have shown that *M. paradoxus* spawns in both Namibian and South African waters, while *M. capensis* spawns only in South African waters (Burmeister, 2005; Kainge *et al*. 2007). Furthermore, *M. capensis* show morphological variation (colour of the anal fin and iris) between these two regions (Durholtz *et al*. 2014). Yet, recent genetic analyses (von der Heyden *et al*. 2007, 2010) have not successfully clarified the current perceptions of stock structure of these fishes by showing no differences in mitochondrial DNA between *M. capensis* from Namibia and South Africa, but showing significant genetic differentiation between adult *M. paradoxus* from these two regions. Currently both species are managed separately in South Africa and Namibia (Durholtz *et al*. 2014), but were it the case that the *M. paradoxus* population is shared between these countries, serious re-evaluation of management strategies should be considered.

Parasite studies of these fishes date back to Davies and Beyers (1947) who recorded a high incidence of the myxozoan *K. thyrsites* (previously *Chloromyxum*) in *M. capensis* and *M. paradoxus*. Barnard (1955*a*) described two ectoparasitic copepods from the buccal cavity of these fish (*Chondracanthus merluccii* and *Parabrachiella australis*). A further three helminth parasites were identified by Meyer-Rochow (1972): *Dibothriorhynchus grossum, Tetrarhynchus* sp. and *Livoneca reynaudii*. Krzeptowski (1980) recorded larval *A. simplex* and *Hepatoxylon trichiuri* in the body cavities of both species collected off Namibia. Aleshkina (1982) surveyed the parasite fauna of both *M. capensis* and *M. paradoxus* off Namibia and determined that the parasitic species composition was dependent on the age of the hosts. Subsequently Botha (1986) examined the major endoparasites of both *M. capensis* and *M. paradoxus*. Botha (1986) compared the dominant helminth fauna between the two species, while Reimer (1993) showed that the parasite fauna of both species differed remarkably above and below the 25°30′S latitude, suggesting that fish from each of these regions could originate from separate sub-populations. This study was not a dedicated biological tagging project, but provided some insight into possible differences in these fish populations based on parasite assemblages. Most recently, parasitic species infecting Cape hakes, *M. paradoxus* and *M. capensis*, from South African waters were examined (Reed *et al*. unpublished data) revealing the regular occurrence of nine different parasite taxa (Table 5). This study aims to specifically collect parasite data for use as biological tags to contribute to understanding the number of Cape hake sub-populations in southern Africa.

Cape 'snoek', *Thyrsites atun*, is a valuable large pelagic commercial species that occurs predominantly in the Benguela Ecosystem from the Cunene River mouth in Namibia to Cape Agulhas in South Africa. This species is an important predator of small pelagics in the Benguela (Griffiths, 2002) and is also traditionally one of the most valued food species caught by local fisherman in the Western Cape Province of South Africa. One of the oldest and most significant records of a parasitic species from South Africa is the original description of the myxozoan *K. thyrsites* from *T. atun*. Gilchrist (1924) described *Kudoa* (*Chloromyxum*) *thyristes* from the muscles of Cape 'snoek', reporting that the flesh of those fish infected with this myxozoan became soft and liquid after death. Several studies subsequently recorded the presence of this parasite in fish musculature from this region (Davies and Beyers, 1947; Dubina and Isakov, 1976, Gaevskaya and Kovaleva, 1979; Schulman *et al*. 1979) and *K. thyrsites* is today known as a notorious cosmopolitan species negatively affecting the quality of fish fillets in many parts of the world.

The widespread occurence of this parasite in other commercially valuable fish species in South Africa, such as *S. sagax*, led to several studies examining aspects of its infection by scientists at South Africa's Department of Agriculture, Forestry and Fisheries (Lamprecht *et al*. 1989; Avery *et al*. 1990; Webb, 1990, 1993; Matta and Cloete, 1992). In acknowledgement of the economic concerns of *K. thyrsites* infections, Henning *et al*. (2013) reviewed the occurrence of *Kudoa*-induced myoliquefaction in South Africa and other parts of the world. These authors recognized the need for an early detection

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Table 5. Studies of parasites infecting commercial marine fishes in southern Africa ('Numerous' = more than five)

Reference	Hosts	Parasites	Region	Purpose
Small pelagics (*sardine and anchovy*)				
Hennig (1974)	*Engraulis encrasicolus*	*Anisakis* sp.	South Africa	Effects of infection
Reed *et al*. (2012)	*Sardinops sagax*	Numerous	South Africa	Survey and identification of potential biological tag
Horse mackerel				
Solonchenko (1968)	*Scomber colias*	Numerous	SW Atlantic	Survey
Hecht (1976)	*Trachurus capensis*	*Anisakis* sp. (nematode); *Nybelina* sp. (digenean)	South Africa	Part of general biology study of host
Gaevskaya and Kovaleva (1980)	*T. capensis*	Numerous	Namibia	Survey
Le Roux (2013)	*T. capensis*	Numerous	South Africa, Namibia	Survey of two populations in Benguela
Bowker (2013)	*T. trecae*	Numerous	Angola, Namibia	Survey of two populations in northern Benguela
Cape hakes				
Davies and Beyers (1947)	*Merluccius capensis, M. paradoxus*	*Kudoa thyrsites* (myxozoan)	South Africa	Survey
Barnard (1955*a*)	*M. capensis, M. paradoxus*	*Chondracanthus merluccii, Parabrachiella australis* (copepods)	South Africa	Survey
Priebe (1967)	*M. capensis*	Myxozoan species	SW Atlantic	Survey
Meyer-Rochow (1972)	*M. capensis, M. paradoxus*	*Dibothriorhynchus grossum, Tetrarhynchus* sp., *Livoneca reynaudii* (helminths)	Namibia	Survey
Krzeptowski (1980)	*M. capensis*	*Anisakis simplex* (nematode); *Hepatoxylon trichiuri* (trypanorynch)	Namibia	Survey
Aleshkina (1982)	*M. capensis, M. paradoxus*	Numerous	Namibia	Survey and faunal comparison
Rokicki (1983)	*M. capensis, M. paradoxus*	Numerous	South African	Aid to host systematics
Botha (1986)	*M. capensis, M. paradoxus*	*Anisakis simplex* (nematode); *Hepatoxalyn trichiuri* (trypanorynch)	South Africa	Survey
Reimer (1993)	*M. capensis, M. paradoxus*	Numerous	Namibia	Faunal comparison above and below 25°30′S
Reed *et al*. (unpublished data)	*M. capensis, M. paradoxus*	Numerous	South Africa	Survey and faunal comparison
Reed *et al*. (unpublished data)	*M. paradoxus* only	*Chondracanthus* sp. (copepod); *Capillaria* sp. (digenean); *Clestobothrium crassiceps* (cestode)	South Africa	Survey aimed at identifying suitable biological tags
Snoek				
Gilchrist (1924)	*Thyrsites atun*	*Kudoa thyrsites* (myxozoan)	South Africa	Species description
Lamprecht *et al*. (1989)	*T. atun* (also *S. sagax*)	*Kudoa thyrsites* (myxozoan)	South Africa	Product quality
Avery *et al*. (1990)	*T. atun* (also *S. sagax*)	*Kudoa thyrsites* (myxozoan)	South Africa	Product quality
Webb (1990)	*T. atun* (also *S. sagax*)	*Kudoa thyrsites* (myxozoan)	South Africa	Product quality
Matta and Cloete (1992)	*T. atun* (also *S. sagax*)	*Kudoa thyrsites* (myxozoan)	South Africa	Product quality
Kingklip				
Payne (1986)	*Genypterus capensis*	Numerous	South Africa	Survey of conspicuous parasites

Hottentot				
Wright *et al.* (2001)	*Pachymetopon blochii*	*Anilocra capensis*	South Africa	Aspects of infection
Mullet				
Oldewage and van As (1988)	*Mugil cephalus*	*Dermoergasilus mugilis*	South Africa	Species description
Schramm (1991)	Numerous	*Grillotia perelica*	South Africa, Wild Coast	Survey of mullet species
Kruger and Avenant-Oldewage (1997)	Numerous	*Mugilicola smithae*	South Africa	Ecological observations
Smit *et al.* (2002)	*Mugil cephalus*	*Desseria* sp.	South Africa	Species record
Commercial sharks				
Linton (1924)	*Callorhynchus capensis*	*Gyrocotyle plana* (cestode)	South Africa	Species description
Manter (1955)	*Callorhynchus capensis*	*Callorhynchicola multitesticulatus* (monogenean)	South Africa	Species description
Beverly-Burton *et al.* (1993)	*Callorhynchus capensis*	*Callorhynchocotyle callorhynchi* (monogenean)	South Africa	Species record
Oldewage and Smale (1993)	Numerous	10 species of parasitic Copepoda	South Africa	Survey and species records
Dippenaar *et al.* (2000)	*Carcharhinus brevipinna*	*Kroyeria deetsi* (copepod)	South Africa	Species description
Dippenaar *et al.* (2001)	*Sphyrna lewini*	*Kroyeria sphyrnae* (copepod)	South Africa	New host and locality record
Bih-Awa (2012)	*Callorhynchus capensis*	Numerous	South Africa	Survey
Dippenaar and Lebepe (2013)	*Mobula kuhlii* and *M. eregoodootenkee*	*Pupulina cliffi.* and *P. merira* (copepods)	South Africa	New species descriptions

mechanism for *Kudoa* infection in commercially harvested hosts, such as *T. atun*, and suggest the use of technologies such as ionizing irradiation of fish fillets to prevent the effects of myoliquefaction. These technologies still need to be developed in South Africa, and hence an opportunity exists for food scientists such as the authors of Henning *et al.* (2013) to make significant contributions towards reducing potential food wastage.

Recent medical research involving parasites of *T. atun* (and other species such as *M. capensis* and *M. paradoxus*) from South Africa includes that of Nieuwenhuizen *et al.* (2006, 2009, 2013), Kirstein *et al.* (2010) and Nieuwenhuizen and Lapata (2013) who examined, amongst other things, the effects of exposure of fish workers to anisakid nematodes and the associated upper respiratory tract allergies that are manifested in these fish workers who handle species such as *T. atun* in fish factories in the Western Cape Province of South Africa. A current project (Nunkoo, unpublished data) is investigating temporal and spatial variation in parasite assemblages of *T. atun* off the coast of South Africa.

More than 180 species of sharks, skates, rays and chimaeras are known to live in coastal inshore waters of southern Africa, 98 of which are harvested commercially (DAFF, 2012). Limited, and again mostly taxonomic research has been conducted on the parasite species associated with numerous shark species off southern Africa, with parasitic Copepoda being extremely well documented (Tables 4 and 5). Some studies, such as that of Yeld (2006), examined whole parasite assemblages of endemic shyshark species on the west and south coasts of South Africa. Amongst the commercially harvested sharks, the small chondrichthyan, *Callorhinchus capensis*, which is caught in the demersal longline and trawl fisheries off the west and south coasts of South Africa has received more general parasitological attention than others. This species is known to harbour a unique lineage of cestodes from the genus *Gyrocotyle*. Linton (1924) was the first to describe *Gyrocotyle plana* from *C. capensis* in False Bay. Subsequently a species of monogenean (*Callorhynchicola multitesticulatus*) was described from the gills by Manter (1955) and later recorded once more by Beverly-Burton *et al.* (1993). Recently, Bih-Awa (2012) conducted a survey of parasites infecting this species on the west coast of South Africa recording five species, including the two previously mentioned (Table 5). A current project (Morris, unpublished data) is investigating the accumulation of heavy metals in parasites of *C. capensis* off the coast of South Africa.

Several taxonomic studies have recorded parasitic species infecting fishes, cephalopods and crustaceans off the coasts of Mozambique and Madagascar. Important contributions include the works of Reimer (1984, 1989) who recorded parasites associated with prawns, fishes and cephalopods in Mozambique,

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Table 6. Studies of parasitic species infecting commercial marine fishes in east Africa. ('Numerous' = more than five fish hosts examined)

Reference	Host	Parasites	Region	Purpose
Martens and Meons (1995)	*Siganus sutor*	*Tetrancistrum sigani*; *Microcotyle mouwoi*; *Pseudohaliotrema* sp. 1 and sp. 2, and an unidentified Microcotylidae species (monogeneans); *Caligus* sp. and *Hatschekia* sp. (copepods); Gnathiidae species (isopod); *Opisthogonoporoides* cf. *hanumanthai*; *Gyliauchen papillatus*; *Hexangium sigani*; and three other unidentified digeneans; *Sclerocollum rubrimaris* (acanthocephalan); *Procamallanus sigani* (nematode)	Kenya	Survey
Aloo *et al.* (2004)	*Siganus sutor*	*Procamallanus* (nematode); Cestode (unidentified); Opisthogonoporoides (trematode)	Kenya	Survey
	Numerous species	*Camallanus* (nematode)		
	Thunnus sp.	*Camallanus* sp.		
	Leptoscarus vagiensis, *Sardinella gibbosa* *Hemiramphus far*	*Aega* sp., *Nerocila* sp. (isopods)		

Palm *et al.* (1997) who recorded numerous species from the trypanorynch (Cestoda) genus *Nybelinia* and Kensley *et al.* (2009) who recorded 12 new species of parasitic isopods from the family Gnathiidae (Tables 4 and 5).

EAST COAST OF SUB-SAHARAN AFRICA

Environmental conditions off the east African coastal countries of Tanzania, Kenya, Somalia and Comores are driven by the southwards flowing Somali Coastal Current and the northwards flowing East African Coastal Current that meet and then diverge off the coast of Kenya (Fig. 1). This region boasts a rich diversity of important habitats such as mangroves, coral reefs, seagrass beds and estuaries, even including the presence of several endangered marine turtle and whale species, dugong and the CITES-listed coelacanth, *Latimeria chalumnae*. The majority of fisheries along this coastline consist of subsistence and artisanal fisheries that are confined to inshore areas due to the ease of access and lack of technology to fish in offshore waters. More than 96% of marine fisheries in Tanzania and 80% in Kenya are due to small-scale artisanal fishers. In Somalia, a larger industrial fishing sector exists that contributes about 40% to the annual landings, with an artisanal sector operating in inshore areas and accounting for most of the landings (60%). More than 500 species of fish are caught for food in this region, with reef fishes being the most important category including emperors (Lethrinidae), snappers (Lutjanidae), sweetlips (*Plectorhinchus* sp.), parrotfish (Scaridae), surgeonfish (Acanthuridae), rabbitfish (Siganidae), groupers (Serranidae) and goatfish (Mulidae) (Jiddawi and Ohman, 2002). Off shore fisheries are dominated by distant fleets from Europe and East Asia.

Several taxonomic reports (such as Bassett-Smith, 1903; Parukhin, 1976*a*, *b*, 1978; Moravec *et al.* 1988; Bruce and Bowman, 1989; Hadfield *et al.* 2011) are known from this region as well as a few studies that describe the parasite assemblages associated with single host species, such as Martens and Meons (1995) who described the ecto- and endo-parasites infecting rabbitfish, *Siganus sutor* off the Kenyan Coast (Table 6) and Aloo *et al.* (2004) who conducted a survey of parasitic species infecting commercially important marine fishes in Kenya (Table 6).

Some studies from this region of particular interest include that of Kamegai (1971) who described a new genus and species of monogenea (*Dactylodiscus latimeris*) from the gills of *L. chalumnae* caught off Anjouan Island, Comoros. Two larval helminths, *Tentacularia* sp. (Cestoda) and *Anisakis* sp. (Nematoda), were also recorded from this specimen of coelacanth. Thoney and Hargis (1991) subsequently recorded juvenile anisakid nematodes from two coelacanths captured in waters off the Comoros Islands. Eight third-stage anisakines of the genus *Terranova* or *Pulchrascaris* were collected from the spiral valve and rectum of the two coelacanths examined. Anderson (1993) also reported on 3rd stage larval anisakids coiled in the mesenteries of a female coelacanth examined at Guelf.

FUTURE PROSPECTS FOR APPLIED MARINE PARASITOLOGY RESEARCH IN SUB-SAHARAN AFRICA

Despite the lack of applied parasitological studies relating directly to marine fisheries management in sub-Saharan Africa, there exists a tremendous amount of information on parasitic species infecting certain fishes of commercial value due to the efforts of taxonomists. The availability of these data provides a foundation for future applied parasitological studies of economically important fishes that could aid in sustainable management strategies and will provide

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an added biological understanding of these important natural resources in this region. Aquatic parasitologists (marine and freshwater) in Africa have a tremendous opportunity to rapidly advance this field of research by documenting new species and also recording species assemblages associated with certain hosts in different regions. There is also an urgency to begin collecting long-term datasets on key commercial species. Inferring information from single-year datasets is not ideal in a constantly changing environment influenced by El Niño, La Niña and numerous other anthropogenic pressures such as over-fishing and global climate change.

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