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Parasite community structure as a predictor of host population structure: An example using *Callorhinchus capensis*

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ABSTRACT

This paper describes the parasite community structure of the Cape elephant fish or St Joseph shark (*Callorhinchus capensis*) caught off the West and South Coast of South Africa between 2010 and 2015. These data were used to build species accumulation curves (SAC) and calculate biodiversity indices including rarefied species richness, Shannon Weiner's diversity index, Simpson's index and Pielou's J index. The biodiversity indices were correlated with the host's biological data to determine how these affected the parasite community structure and provide insight into the host's population structure. The parasites identified in *C. capensis* ($n = 259$) include a cestode (*Gyrocotyle plana*), two monogeneans (*Callorhynchicotyle callorhynchi* and *Callorhinchicola multitesticulatus*), an isopod (*Anilocra capensis*) and a leech (*Branchellion* sp.). *Gyrocotyle plana* was the most prevalent at 71.43% and the monogenean *C. callorhynchi* had the highest mean abundance (1.55 ± 0.45 parasites.fish^{-1}) and the highest mean infection intensity (4.79 ± 0.66 parasites.infected fish^{-1}). The SAC and biodiversity measures indicate a uniform parasite community across the sampled host population, suggesting a highly interactive shark community with no evidence for population structure. These results show that parasite community structure can be used to infer their host's population structure.

1. Introduction

Marcogliese (2004) highlighted the importance of including parasites in our studies of ecosystem diversity and functioning. Parasites often exhibit complex life cycles and a resulting multi-host nature which enables them to integrate themselves at all levels of a functioning ecosystem. As a result, parasite studies can provide vital contributions to marine science in the form of information on host population structure, environmental stressors such as heavy metal or hydrocarbon pollution, as well as general biodiversity (Dove and Cribb, 2006; Nachev and Sures, 2016; Palm, 2011; Rohde, 2016).

Species richness is a measurement central to the understanding of community and regional diversity (Gotelli and Colwell, 2001). It allows us to place a quantitative measurement on the comparisons between different sites within an ecosystem, and it is these comparisons that form the basis for community and conservation ecology. Studies of parasite diversity can and have benefitted from the application of species richness measurements, as they provide information on the unseen biodiversity that organisms may be hiding (Dove and Cribb, 2006).

To gain insight into this covert world of parasite richness, Dove and Cribb (2006) recommend utilizing Species Accumulation Curves (SAC's). SAC's are useful in providing an estimate of the total number of species for a given host population and provides a measure of sampling effort. Properties of SAC's are also incredibly informative of community patterns and the structure of parasitic and host diversity. Dove and Cribb (2006) warn that knowledge of the true distribution of parasite richness over multiple host-derived and spatial scales is far from complete, but SACs can improve the understanding of diversity patterns in parasite and host assemblages.

Species of the genus *Callorhinchus* are small chondrichthyans of the subclass Holocephali, a primitive group of shark which made an appearance early in the fossil record (Carroll, 1988). The genus is restricted to shallow temperate waters in the southern hemisphere (Smith and Heemstra, 1986). The three recognised plough-nosed chimaeras are the southern African species *Callorhinchus capensis*, the New Zealand/Australian species *C. milii* and the southern South American species *C. callorhynchus* (Didier et al., 2012).

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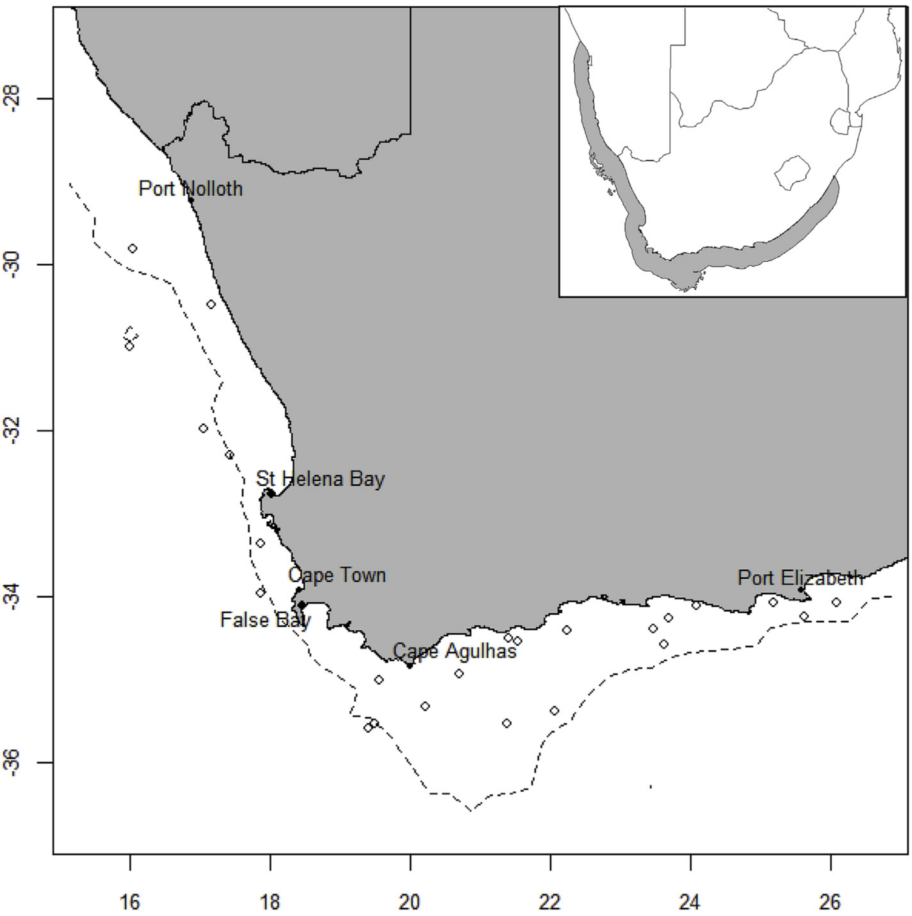


Fig. 1. Map showing sample locations (St Helena Bay, False Bay and trawl locations shown by diamond symbols) in which *Callorhinchus capensis* were caught (dashed line indicates 200 m depth contour). The inset shows the distribution range of *Callorhinchus capensis* (IUCN, 2012).

Callorhinchus capensis (locally known as St Joseph or Cape elephant fish) is primarily found off the Namibian and South African West and South coasts, with very few records off the East Coast (Mann, 2013) (Fig. 1 - inset). This species is caught by directed gillnet and beach seine fisheries off the South African West Coast and in False Bay (Fig. 1). This species contributes around 10% of total reported landings from these two fisheries combined, although there is substantial under-reporting (Lamberth et al., 1997). In addition, *C. capensis* is also taken as by-catch in the South African demersal trawl fishery, mostly off the South Coast, and annual reported catches of this species (gillnet, beach seine and demersal trawl sectors combined) have ranged between 500 and 1 000t over the past decade (Fairweather and Durholtz, 2017). Abundance estimates for St Joseph shark derived from demersal research surveys and using the swept-area approach show no trends and roughly equal biomass levels off both the West and South coasts of between 10 000 and 20 000t since 2010 (Fairweather and Durholtz, 2017). Chimeroid research is a high priority, especially given that many species have restricted distributions and fishing pressures may increase (Mann, 2013).

Here we collate previously unpublished information (Bih Awa, 2012; Morris, 2015; Van der Ploeg, 2015) on the metazoan parasites found to infect the chondrichthyan *Callorhinchus capensis* off the West and South Coast of South Africa. Parasite infection indices are used to derive individual-based parasite species accumulation curves and biodiversity indices in order to provide insight into the parasitic community structure present in *C. capensis* and assess whether this can be used to infer host population structure. We also compare parasite infection indices with host condition factor to determine whether there are any physiological impacts arising from infection.

2. Materials and methods

2.1. *Callorhinchus spp. parasite literature survey*

Apps.webofknowledge.com was searched for publications containing any combination of the terms *callorhinchus* and *parasit**, published before January 2018. The World Register of Marine Species (www.marinespecies.org) was used to find synonymised and misspelled genus names (e.g.: *Callorhynchus*). This initial survey yielded eleven publications. Of these, only nine publications were relevant to *Callorhinchus spp.* and their parasitic species (Amato and Pereira, 1995; Beverley-Burton et al., 1993; Llewellyn and Simmons, 1984; Luque and Iannacone, 1991; Morris et al., 2016; Larisa G Poddubnaya et al., 2015a, b; Larisa G. Poddubnaya et al., 2015a, b; Poddubnaya et al., 2017; Simmons et al., 1972). These search terms were also searched for in Google Scholar. Excluding the references found on Web of Science, a further nine relevant papers and unpublished works were recorded (Boeger and Kritsky, 1989; Freer and Griffiths, 1993; Linton, 1924; Manter, 1954, 1953; 1951; Larisa G. Poddubnaya et al., 2015a, b; Richardson, 1949; Szidat, 1972). Along with the research conducted by students Bih Awa (2012); Morris (2015) and Van der Ploeg (2015), results have been summarized in Table 6.

2.2. *Sample collection and dissection protocol*

Samples of *Callorhinchus capensis* (n = 259) were collected on four separate occasions between 2010 and 2015, using various methods and across various locations off the West and South Coasts of South Africa (Table 1; Fig. 1). Sharks were removed deceased from the nets, placed

Table 1
Collection details of samples of *Callorhinchus capensis* caught off the West and South Coast of South Africa (2010–2015).

Year	Method of capture, Location	Sample size (n)	Size Range (TL; mm)
2010	Commercial gill nets, St Helena Bay	163	361–852
2013	Commercial beach seine nets, False Bay	19	311–817
2015	Demersal trawl survey, West Coast	40	459–859
2015	Demersal trawl survey, South Coast	37	410–876

in labelled plastic bags and frozen until processing at the Department of Biological Sciences, University of Cape Town.

Prior to processing, sharks were thawed individually at room temperature, had their sex determined, and were then weighed to the nearest gram (g) and measured for total length (TL) and standard/caudal length (SL; base of tail) to the nearest millimeter (mm). Length measurements were done with the proboscis bent up against the base plate of the measuring board, as recommended by Coakley (1973). Relative condition factor (CF) was calculated according to the following equations (Froese, 2006; Le Cren, 1951):

$$CF = W/aL^b \tag{1}$$

where W = weight (g), L = total length (cm). The values *a* and *b* are derived from the length–mass relationship which is described by:

$$W = aL^b \tag{2}$$

A survey of the parasitic fauna of each individual shark was conducted, as recommended by MacKenzie and Abaunza (2005). After an external examination for macroparasites, sharks were eviscerated and their organs separated. The abdominal cavity, eyes, gills and interior of the alimentary canal were examined for macroparasites using a dissecting microscope at 10× magnification (Leica EZ4), whereas kidney, liver, muscle, gallbladder, and gonad tissue samples were smeared under a coverslip and examined at 40× magnification (Leica ICC50, DM750) for microscopic parasites. Parasites were identified as far as possible using local expertise and literature (Beverley-Burton et al., 1993; Freer and Griffiths, 1993; Linton, 1924) and were then counted and preserved in 10% formalin.

2.3. Statistical analyses

Basic infection statistics including infection prevalence, mean infection intensity and mean parasite abundance were collected following the methods of Bush et al. (1997) for each parasite taxon collected (see Table 2). Rarefied species richness, Shannon Weiner diversity index (H), Simpson index (λ) and Pielou's J (J) index were calculated across the sampled population. Species accumulation curves were used to validate richness comparisons and infer host population structure (Dove and Cribb, 2006). Rarefaction curves are produced by randomly sampling and resampling the existing dataset to predict species richness (Gotelli and Colwell, 2001). These sample-based rarefaction curves depend on the spatial distribution of individuals as well as the size and placement of samples (Gotelli and Colwell, 2001). Rarefaction curves produce smoother lines than traditional species accumulation curves and allows for meaningful standardization and comparison of datasets. It also randomizes data and prevents the impact of the "host effect"; differences in host traits that could affect parasite species infection (Dove and Cribb, 2006).

Correlations between biological measures (length, weight and CF) and diversity indices were attempted with the use of Spearman's rank order correlation index to confirm statistical significance at 95% ($p < 0.05$). Chi-squared ($\chi 2$) and Mann Whitney U statistical analyses were used to test whether sex may have a significant effect on the prevalence and abundance of parasitic infection. All analyses were conducted in either Microsoft Excel (2013) or R 2.15.1 (R Core Team, 2013), with the use of R packages Vegan (Oksanen et al., 2012) for rarefaction and calculation of biodiversity indices.

3. Results

3.1. Summary statistics

Five parasitic taxa were found infecting a total of 259 specimens of *Callorhinchus capensis*, including a cestode (*Gyrocotyle plana*), two monogeneans (*Callorhynchicotyle callorhynchi* and *Callorhinchicola multitesticulatus*), an isopod (*Anilocra capensis*) and a leech (*Branchellion* sp.). *Gyrocotyle plana* was the most prevalent at 71.43%, with the monogenean *C. callorhynchi* having the highest mean abundance (1.55 ± 0.45 parasites.fish^{-1}) and the highest mean infection intensity (4.79 ± 0.66 parasites.infected fish^{-1}) (Table 3; Fig. 2).

3.2. Parasite abundance correlations

Normality tests indicated that data were not normally distributed, as expected with parasite count data. Only *Callorhynchicotyle callorhynchi* abundance was significantly correlated to host total length, weight and condition factor, with all variables showing a positive relationship with parasite abundance (Table 3). *Gyrocotyle plana* abundance also had a significant, positive relationship with the weight of *Callorhinchus capensis* but not length or condition factor, and abundance of the remaining three parasites was not significantly correlated with host measurements.

3.3. Species richness estimation

A randomized, individual-based species accumulation curve (SAC) for parasites infecting *C. capensis* reached an asymptote of 5 species at 200 examined hosts (Fig. 3). SAC, Chao2, and Jackknife1 richness algorithms all estimated a total species richness of 5 parasitic species.

Table 2
Summary statistics for parasites found infecting *Callorhinchus capensis* (n = 259) caught off the West Coast of South Africa between 2010 and 2015.

Parasite Class	Parasite Species	Site of Infection	Prevalence (%)	Mean (± SE) Parasite Abundance (parasites.fish^{-1})	Mean (± SE) Parasite Infection Intensity (parasites. infected fish^{-1})
Cestoda	*Gyrocotyle plana*	Spiral valve	71.43	1.27 (0.07)	1.78 (0.04)
Monogenea	*Callorhynchicotyle callorhynchi*	Gill	32.43	1.55 (0.45)	4.79 (0.66)
Monogenea	*Callorhinchicola multitesticulatus*	Gill	21.24	0.53 (0.23)	2.49 (0.41)
Isopoda	*Anilocra capensis*	External	2.70	0.03 (0.08)	1.29 (0.18)
Hirudinia	*Branchellion* sp.	External	0.77	0.01 (0.06)	1.00 (0.00)

Table 3

Correlation coefficients (r_s) of parasite abundance as a function of total length, weight, and condition factor of host *Callorhinchus capensis* caught off the West and South Coasts of South Africa between 2010 and 2015 (n = 259). * indicates significance at $p < 0.05$.

Parasite Species	Total Length		Weight		Condition Factor	
	r_s	p	r_s	p	r_s	p
Gyrocotyle plana	0.09	0.158	0.13	0.034*	0.11	0.084
Callorhynchicotyle callorhynchi	0.21	0.001*	0.23	0.0002*	0.18	0.003*
Callorhinchicola multitesticulatus	0.03	0.620	0.02	0.771	−0.05	0.408
Anilocra capensis	−0.11	0.080	−0.11	0.080	0.07	0.272
Branchellion sp.	0.00	0.939	−0.02	0.747	−0.05	0.414

3.4. Parasite biodiversity values and correlations

Species richness, Shannon Weiner diversity index (H = 0.254 ± 0.02), and Pielou's J index (J = 0.608 ± 0.03) values all showed a significant, positive correlations with shark total length, weight and condition factor, with significant correlations having slopes (r_s) of ± 0.20 (Table 4). Simpsons index (λ = 0.335 ± 0.02) was not correlated with any host measurement.

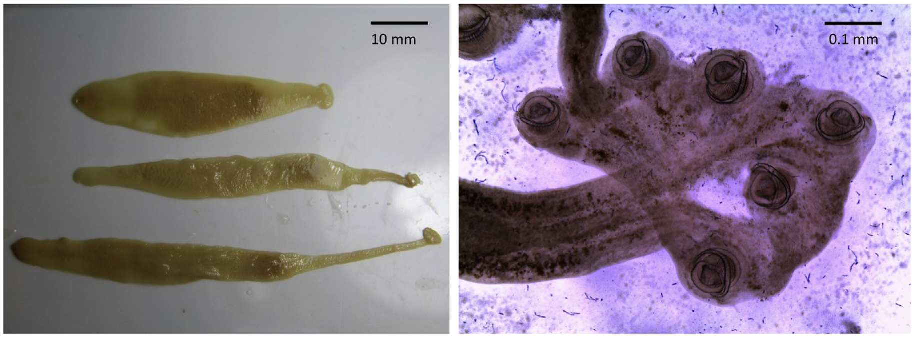
3.5. Sex as a determinant of parasite abundance and prevalence

Parasite species prevalence did not indicate a dependency with sex of *C. capensis* (Table 5). However, *G. plana* abundance was significantly higher in males than females (W = 7008, p = 0.019, female n = 142, male n = 117).

4. Discussion

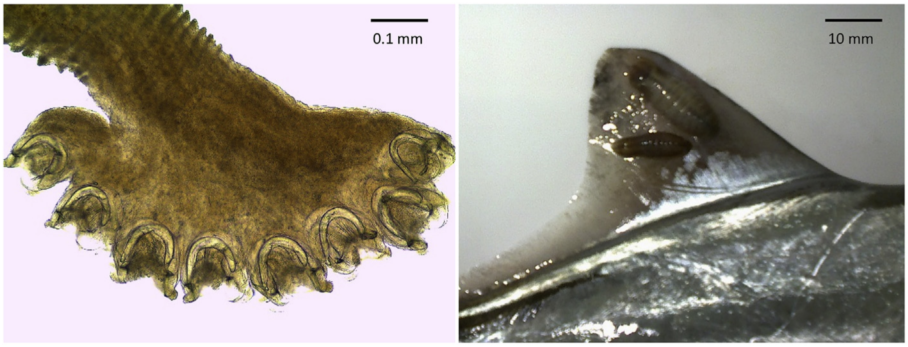
Reed (2015) highlighted the need for more fundamental research on parasites and their associated fish hosts (both those with commercial value and those without) specifically within sub-Saharan Africa. By increasing the knowledge we have on parasite loads and infection patterns, and expanding the sampled species and areas, we can make more informed management decisions regarding commercially important fish species. For example; Reed et al. (2012), MacKenzie and Abaunza 2005 and van der Lingen et al. (2015) documented the parasite assemblage of South African sardine *Sardinops sagax* and identified a digenean parasite biotag which subsequent studies have shown to provide strong evidence for multiple sardine stocks (van der Lingen et al., 2015; Weston et al., 2015). Stock-specific sardine assessment models that incorporate these parasite data have been developed (De Moor et al., 2017) and are now used in management of the sardine fishery. Similarly, increasing knowledge will allow the documenting of previously undiscovered parasitic species and, when integrated with biodiversity indices, can provide information on parasite dynamics within a population and the impact of parasites within important ecosystems (Poulin and Morand, 2004).

This study documented a total of five parasite taxa for *C. capensis* off the South African West and South Coasts, bringing the total number of parasite taxa reported for this species to seven. Several parasites are known to infect holocephalan species (Table 6), with the most prevalent being the gyrocotylideans, a group of Platyhelminthes comprised of only a dozen known species. Nearly every holocephalan species examined to date is said to be parasitized by either one very common or one rare species of the genus *Gyrocotyle* (Simmons et al., 1972; Williams et al., 2009), with most authors who have recognised two sympatric species noting that mixed infection never, or very rarely, occurs (Simmons and Laurie, 1972). Little is known about their lifecycle as



a. Gyrocotyle plana

b. Haptor of *Callorhynchicotyle callorhynchi* (40X)



c. Haptor of *Callorhinchicola multitesticulatus* (40X)

d. Anilocra capensis

Fig. 2. a–d: Four metazoan parasites found infecting *Callorhinchus capensis* caught in False Bay, South Africa in 2013. Photos taken by T. Morris.

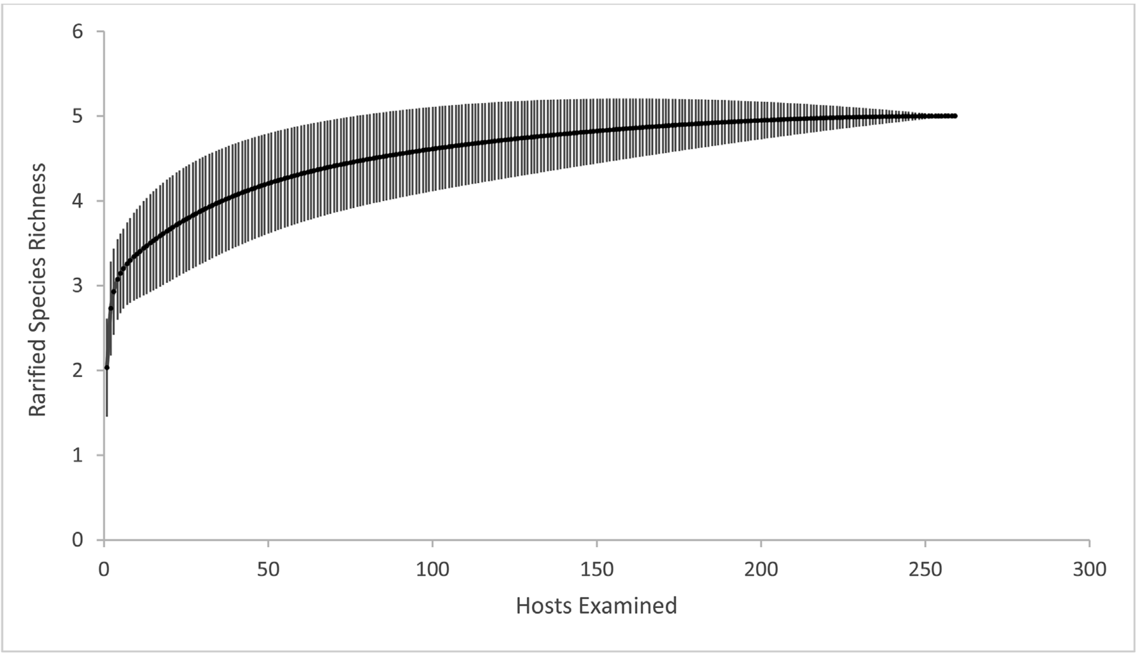


Fig. 3. Randomized individual-based species accumulation curve of parasites infecting *Callorhinchus capensis* (n = 259) caught off the West and South Coasts of South Africa between 2010 and 2015.

Table 4
Parasite Species richness, Shannon Weiner diversity index (H), Simpsons Index (λ) and Pielou's J (J) Index as a function of total length, weight and condition factor of *Callorhinchus capensis* caught off the West and South Coasts of South Africa between 2010 and 2015 (n = 259). * indicates significance at $p < 0.05$.

Biodiversity Indices	Total Length		Weight		Condition Factor	
	r_s	p	r_s	p	r_s	p
Species richness	0.18	0.004*	0.22	0.0004*	0.17	0.007*
H	0.19	0.003*	0.21	0.001*	0.16	0.011*
λ	0.05	0.425	0.03	0.630	0.00	0.948
J	0.27	0.001*	0.34	0.00006*	0.23	0.007*

Table 5
Summary of parasite prevalence (%) and abundance dependence on sex of *Callorhinchus capensis* caught off the West and South Coasts of South Africa between 2010 and 2015 (χ^2 = Chi-Squared statistic, U = Mann Whitney U statistic). * indicates significance at $p < 0.05$.

Parasite Species	Prevalence			Abundance		
	χ^2	df	p	U	df	p
Gyrocotyle plana	1.18	1	0.278	7008.0	258	0.019*
Callorhynchicotyle callorhynchi	0.15	1	0.700	8832.0	258	0.292
Callorhinchicola multitesticulatus	2.66	1	0.107	9058.0	258	0.079
Anilocra capensis	0.07	1	0.795	8199.0	258	0.522
Branchellion sp.	0.00	1	0.990	8294.5	258	0.891

these parasites have not been observed outside their chimeroid host but there are arguments presented by Xylander (1989) to suggest a complex life cycle.

Callorhinchus spp. have a predictable parasite community with 5–7 parasitic species known to infect these hosts. Apart from the *Gyrocotyle* spp. that are incredibly prevalent in this genus, the literature indicates strong infection from monogenean species. Monogenea are highly host specific and the structuring of their communities are related to both ecological and historical constraints (Morand et al., 2002). Having evolved quite early in the fossil record, the relationship between the *Callorhinchus* hosts and their monogenean species have established a long phylogenetic history, as shown by the same monogenean species infecting multiple *Callorhinchus* species (Table 6).

Within South Africa, only recently has there been a concerted effort in studying these unique sharks and their parasites. As early as 1924, Linton described a species of *Gyrocotyle* from the spiral valve of *C. capensis*. It was only after 80 years that *G. plana* was mentioned again by Freer and Griffiths (1993), who conducted research on the general biology and fishery for *C. capensis*. Other parasitic studies concerning *C. capensis* are opportunistic taxonomic surveys of species from general trawls off the west coast of South Africa (Beverley-Burton et al., 1993; Manter, 1955). Since 2015, four papers have been published focussing on the unique parasites that infect this species; three of them focussed on structural characteristics of the hexabothriid monogenean *Callorhynchicotyle callorhynchi* (Larisa G Poddubnaya et al., 2015a, b; Larisa G. Poddubnaya et al., 2015a, b; Poddubnaya et al., 2017) and the fourth which measured the possibility of *Gyrocotyle plana* as an indicator for heavy metal bioaccumulation (Morris et al., 2016).

Gyrocotyle plana was the most prevalent parasite found infecting *C. capensis* and correlated significantly with fish weight in this study. However, with a range of infection from zero to three parasites, these results may be circumstantial. Larval encysted parasites have been shown to correlate significantly with fish size (e.g. Lo et al., 1998), which has been attributed to larger hosts requiring more food to satisfy metabolic demands and hence ingesting more parasitic larva from intermediate hosts. Therefore, the significant relationship could be due to an accumulation of parasites with age. *Gyrocotyle plana* abundance was also significantly higher in males than females. However, there was no significant difference in size between males and females examined in this study therefore this result could be a product of the low range of observed infection or due to some other reason.

Gyrocotyle as a genus has very close evolutionary ties to holocephalan sharks around the world (Williams et al., 2009), yet there is little known about the transmission of these parasites. Xylander (1989) suggested a transmission method that involves intermediate hosts due to smaller/younger sharks having a lower parasite abundance compared to larger/older sharks, as seen in this study. Freer and Griffiths (1993) also suggested an intermediate host and concluded that it could be a common dietary item due to the high prevalence of *G. plana*

Table 6
Parasite records for all plough-nosed chimeroids (*Callorhinchus* spp.). The table includes the location of studies conducted, parasite species, site of infection (SOI), parasite class, and the associated references.

Parasite Species	Parasite Class	SOI	Reference
Callorhinchus capensis (Southern Africa)			
Gyrocotyle plana	Cestoda	Spiral valve	(Bih Awa, 2012; Freer and Griffiths, 1993; Linton, 1924; Morris et al., 2016; Morris, 2015; Van der Ploeg, 2015)
Unidentified copepod	Copepoda	External	Freer and Griffiths (1993)
Anilocra capensis	Isopoda	External	(Bih Awa, 2012; Morris, 2015)
Branchellion sp.	Hirudinea	External	Bih Awa (2012)
Callorhynchicola branchialis	Monogenea	Gills	Beverley-Burton et al. (1993)
Callorhynchicotyle callorhynchi	Monogenea	Gills	(Bih Awa, 2012; Morris, 2015; Larisa G Poddubnaya et al., 2015a,b; Larisa G. Poddubnaya et al., 2015a,b; Poddubnaya et al., 2017; Van der Ploeg, 2015)
Callorhynchicola multitesticulatus	Monogenea	Gills	(Beverley-Burton et al., 1993; Bih Awa, 2012; Manter, 1955; Morris, 2015; Van der Ploeg, 2015)
Callorhinchus callorhynchus (Southern South America)			
Rugogaster hydrolagi	Aspidogastrea	Rectal Glands	Amato and Pereira (1995)
Rugogaster callorhinchi	Aspidogastrea	Rectal Glands	Amato and Pereira (1995)
Branchellion sp.	Hirudinea	External	Szidat (1972)
Callorhynchicola branchialis	Monogenea	Gills	Beverley-Burton et al. (1993)
Callorhynchocotyle marplatensis	Monogenea	Gills	Luque and Iannacone (1991)
Callorhinchus milii (Southern Australia and New Zealand)			
Macraspis elegans	Aspidogastrea	Gall bladder	Manter (1954)
Gyrocotyle maxima	Cestoda	Not specified	Simmons et al. (1972)
Gyrocotyle rugosa	Cestoda	Spiral valve	(Manter, 1953, 1951)
Gyrocotyle urna	Cestoda	Spiral valve	(Manter, 1953, 1951)
Branchellion parkeri	Hirudinea	Not Specified	Richardson (1949)
Callorhynchicola multitesticulatus	Monogenea	Gills	(Beverley-Burton et al., 1993; Llewellyn and Simmons, 1984)
Callorhynchocotyle amatoi	Monogenea	Gills	Boeger and Kritsky (1989)

infection. That the life cycle of the genus *Gyrocotyle* has still not been described precludes definitive conclusions.

With respect to the ectoparasites, both monogenean parasite species show low to moderate prevalence (> 20%) levels, with *C. callorhynchi* abundance correlating significantly with host length, weight and condition factor. Ectoparasites, particularly monogeneans, have been shown to accumulate on large-bodied fishes living in groups and/or on fishes with high population densities (Morand et al., 2002). *Anilocra capensis* and the *Branchellion sp.* are opportunistic in nature (Kearn, 2004) and may have infected host individuals as generalist parasites, explaining their relatively low prevalence (Rohde, 2005). The isopod, *A. capensis* is a common ectoparasite that occurs in False Bay, particularly on the Sparid *Pachymetopon blochii* (Wright et al., 2001). Leeches belonging to the genus *Branchellion* are common parasites of cartilaginous fish species (Rohde, 2005) and members of this genus have been reported from individuals of *C. callorhynchus* (Szidat, 1972) and *C. milii* (Richardson, 1949) (Table 6).

4.1. Species community structure

The species accumulation curve, with its steep slope and early asymptote, suggests the parasitic community structure of *C. capensis* is interactive. Parasitic infracommunities are the sub-populations of parasites living on or within individual hosts (Poulin, 2001), and interactive infracommunities are considered to be composed of species with high transmission rates and engaged in strong interspecific interactions, leading to predictable infracommunity structure and high similarity among infracommunities (Dove and Cribb, 2006). With three of the five parasites documented here for *C. capensis* showing prevalence values of > 20%, the infracommunities seem to be easily predictable and highly similar across the population.

All biodiversity indices complement this finding with species richness, Shannon Weiner's diversity index and Simpson's index displaying low diversity values. Pielou's J evenness also supports the interactivity of the sample with a value closer to 1, indicating an evenly-distributed species diversity across the sampled specimens. The interactive parasite infracommunity also suggests the dynamics with which the host population is being controlled. If the parasitic communities are even across individual hosts, it suggests a host population that is also interactive and shows no community or population structuring off South Africa's coast.

There is a lack of biological data for the majority of shark species, including *C. capensis*, which makes the development of a management plan for fishery purposes a priority (Mann, 2013). By understanding the interactive nature of this species, we can better understand how different fishing pressures may affect it. Whereas reproductive activity occurs throughout the year it peaks in summer, when mature fish move inshore to breed and lay eggs before dispersing to deeper waters, and immature fish are only found inshore (Freer and Griffiths, 1993). That sex was not a determinant of parasite abundance, except for *Gyrocotyle plana*, supports the interactivity of the host population.

4.2. Future suggestions and conclusions

There is still much work that needs to be conducted on *Callorhinchus* spp. and the interaction with its parasites. These topics include an up-to-date description of *Gyrocotyle plana*, as other holocephalan studies have frequently found two species from the genus *Gyrocotyle*. Whereas we recorded only one species of the genus *Gyrocotyle* from *C. capensis*, the use of up-to-date (e.g. molecular) taxonomic methods may discover a new parasitic species. Additionally, a more holistic project should be established to understand the movement patterns of *C. capensis* throughout its distribution range, particularly the East Coast of South Africa and Namibia. The East Coast of South Africa is strongly influenced by the warm Agulhas Current and is considered a different bioregion to the cold West Coast which is influenced by the Benguela Current (Teske et al., 2011). The Luderitz upwelling cell in southern Namibia is known to form a partial barrier to many pelagic fish species (Hutchings et al., 2009) and has not been studied for *C. capensis*. There is much literature suggesting that parasite community structure is influenced by temperature (e.g. Lo et al., 1998) and this appears to play a role in host community and population structure of some of Southern Africa's commercially exploited fish species. Therefore, there is precedent to assume separate discreet stocks in Namibia and the East Coast of South Africa respectively. This will have implications for the commercial fishing industry as it could inform fisheries management on the population structure of *C. capensis*.

In conclusion, *C. capensis* has a community of parasites that remain quite stable throughout the sampled population, with relatively low infection rates and a highly interactive parasite community. This study shows that by investigating the parasitic community, and using various biodiversity measures, we can infer the community/population structure of their hosts.

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