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Co-introduction of ancyrocephalid monogeneans on their invasive host, the largemouth bass, *Micropterus salmoides* (Lacepède, 1802) in South Africa

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ABSTRACT

Largemouth bass, *Micropterus salmoides* (Lacepède, 1802) were sampled from three provinces (Eastern Cape EC, North West NWP and KwaZulu-Natal KZN) in South Africa to assess for parasite diversity and community composition. Morphological evaluation of the sampled parasite specimens provided evidence for the first record of five monogeneans from the family Ancyrocephalidae: *Clavunculus bursatus* (Mueller, 1963), *Onchocleidus dispar* (Mueller, 1936), *Onchocleidus furcatus* (Mueller, 1937), *Onchocleidus principalis* (Mizelle, 1936) and *Synleithrium fusiformis* (Mueller, 1934) from the African continent. Community composition differed between localities. *Clavunculus bursatus* were only sampled from the EC and KZN, *O. dispar* and *O. principalis* were only sampled from the EC, *O. furcatus* was only sampled from the NWP and KZN localities and *S. fusiformis* only from KZN. Prevalence was 100% at all localities. Data from this study support the enemy release hypothesis as many of the parasites reported from the native range of *M. salmoides* were not collected.

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1. Introduction

With the introduction of a species into a new environment, introduction of its symbionts and parasites can also occur (Taraschewski, 2006) if the parasites are able to overcome the barriers to introduction, establishment and spread (*sensu* Blackburn et al., 2011). With regard to fish parasites, the movement and introduction of their fish hosts typically results in four possible scenarios: enemy release, dilution, spillback and spill-over (Sheath et al., 2015). Enemy release is attained when, upon introduction into a new environment, the alien host loses some of its natural parasites. The result is that in some cases, introduced fishes may host fewer parasite species than in their native range (Pettersen et al., 2016; Grendron et al., 2012; Roche et al., 2010; Torchin et al., 2003). Spillback occurs when parasites from native hosts transfer to the introduced alien host and there is increase in infection (Kelly et al., 2009). In some cases, spillback may result in dilution, when there is a decrease in the infection of the native hosts as aliens reduce transmission of parasites (Poulin et al., 2011; Keesing et al., 2006). Finally, spill-over, also called pathogen pollution, might occur when an alien host introduces new parasites which then parasitise novel hosts in the new range (Taraschewski, 2006; Daszek et al., 2000).

Parasites introduced with their host are known as co-introduced, while those introduced into a new environment with their alien host and then spill over to native hosts are known as co-invaders (Lymbery et al., 2014). Examples of co-introduced parasites of fishes are that of the monogeneans *Onchocleidus dispar* (Mueller, 1936) with the pumpkinseed fish *Lepomis gibbosus* (Linnaeus, 1758) into Norway (Sterud and Jørgensen, 2006) and Britain (Hockley et al., 2011); and *Onchocleidus principalis* (Mizelle, 1936) with largemouth bass into the British Isles (Maitland and Price, 1969). Examples of co-invader spill-over includes the copepod *Lernaea cyprinacea* Linnaeus, 1758 which was introduced with *Cyprinus carpio* Linnaeus, 1758 and *Carassius auratus* (Linnaeus, 1758) into the Kor River Basin, Iran where it now infests native cyprinids (Sayyadzahed et al., 2016).

In South Africa, fishes have been introduced since the 18th century for angling, aquaculture, biocontrol and as pets, and there are several examples of parasite co-introductions (Ellender and Weyl, 2014). Co-introductions are best described for cyprinid species such as *C. caprio* which are thought to have resulted in the co-introduction of *Ichthyobodo necator* Henneguy 1883, *Chilodonella cyprini* (Moroff, 1902), *C. hexasticha* (Kiernik, 1909), *Apiosoma piscicola* (Blanchard, 1885), *Trichodina acuta* Lom, 1961, *T. nigra* Lom, 1960 and *Trichodinella epizootica* (Raabe, 1950). The grass carp, *Ctenopharyngodon idella* (Valenciennes, 1844), are thought to be responsible for the introduction of the Asian tapeworm, *Schyzocotyle (Bothriocephalus) acheilognathi* (Yamaguti, 1934), and the Japanese fishlouse, *Argulus japonicus* Thiele, 1900 was most likely introduced in association with fishes in the pet trade (reviewed by Ellender and Weyl, 2014). Spill-over to native fishes, with conparthenogenic effects have been observed for five of these species *C. hexasticha*, *I. multifiliis*, *A. japonicus*, *S. acheilognathi*, *T. acuta* (Bruton and van As, 1986).

Largemouth bass *Micropterus salmoides* (Lacepède, 1802) were first introduced into South Africa in 1928 when 45 largemouth bass fingerlings were imported into the Jonkershoek Inland Fish Hatchery, Western Cape and an unknown number to the Pirie Hatchery in the Eastern Cape from the Surrey Trout Farm, England (Harrison, 1936). This was followed by the introduction of four other centrarchid species: smallmouth bass *Micropterus dolomieu* (Lacepède, 1802) in 1937; bluegill *Lepomis macrochirus* Rafinesque, 1819 in 1939; spotted bass *Micropterus punctulatus* (Rafinesque, 1819) in 1940 and Florida bass *Micropterus floridanus* (Lesueur,

1822) in 1984 (Ellender and Weyl, 2014). Following their introduction, *M. salmoides* and the other centrarchid species were widely distributed for sport angling and populations have established throughout South Africa (Ellender et al., 2014; Hargrove et al., 2015). While the impacts of largemouth bass predation on native invertebrates and fishes are well documented (e.g., Weyl et al., 2010; Ellender et al., 2011; Kimberg et al., 2014), their parasite communities have not received much attention (see Ellender and Weyl, 2014).

The parasite diversity of largemouth bass in its native range has been extensively documented (Beverley-Burton, 1984; Hoffman, 1999). On the African continent only a few records of Nematoda and Acantocephala parasitising the introduced largemouth bass exist and mainly from Kenya (Schmidt and Canaris, 1967, 1968; Amin and Dezfuli, 1995; Khalil and Polling, 1997; Aloo and Dezfuli, 1997, Aloo, 1999). In South Africa, current knowledge is limited to the report of the presence of the monogenean parasite *Acolpenteron ureterocoetes* Fischthal and Allison, 1940 from the ureter of largemouth bass in the Jonkershoek hatchery in the western Cape Province (Du Plessis, 1948) and the sampling of *Contracaecum* spp. larvae in specimens collected in the Limpopo and Mpumalanga provinces of South Africa by Tavakol et al. (2015). As a result, the main objective of the current paper was to investigate the parasite communities on *M. salmoides* almost 90 years after their initial introduction and to assess for the potential of enemy release, parasite dilution, spillback and spill-over.

2. Material and methods

2.1. Host and specimen collection

Micropterus salmoides were collected by angling from the Mooi River (26°41'3.60" S; 27°5'59.65" E) and Potchefstroom Dam (26°40'14.20" S; 27°05'46.94" E) in the North West Province (NWP) in October 2015; from Howison's Poort Dam (33°23'10.07" S; 26°29'4.00" E) and Settlers Dam (33°24'41.67" S; 26°30'11.73" E) in the Eastern Cape (EC) in February 2016 and from Friedrichskrön Dam (29°26'46.66" S; 30°33'38.67" E) in KwaZulu-Natal (KZN) in March 2016 (Fig. 1). Water temperature during sampling period ranged from 19.5 °C to 23.1 °C, with lowest values in KZN and highest in NWP.

Fish were kept alive in keep-nets or aerated containers until euthanasia by percussive stunning and cervical vertebrae dislocation was performed. All fish were measured for standard length (SL) in mm and weighed (W) to the nearest in gram. A full parasitological screening was performed following the techniques described by Truter et al. (2016) and McHugh et al. (2016) and parasite specimens were removed from the fins, gills and body cavity and the total number of all gill parasites was counted. This study received the relevant ethical approval (North-West University ethics approval no: NWU-00439-16-S5).

2.2. Specimen preparation and morphological analysis

All monogenean specimens collected were mounted on a microscope slide and fixed in glycerine ammonium picrate for morphological analysis (Malmberg, 1970). Parasites were examined (under 40×, 60× and 100× oil immersion magnification) using a Nikon Eclipse 80i compound microscope. Morphometrics and images were obtained using a Nikon DS-Fi1 camera mounted on the compound microscope and NIS-Element v4 software. Identification of individual specimens was done comparing morphology and measurements of taxonomic important structures, hamuli and male copulatory organ (MCO), to literature (Beverley-Burton and Suriano, 1980; Beverley-Burton, 1986; Wheeler and Beverley-

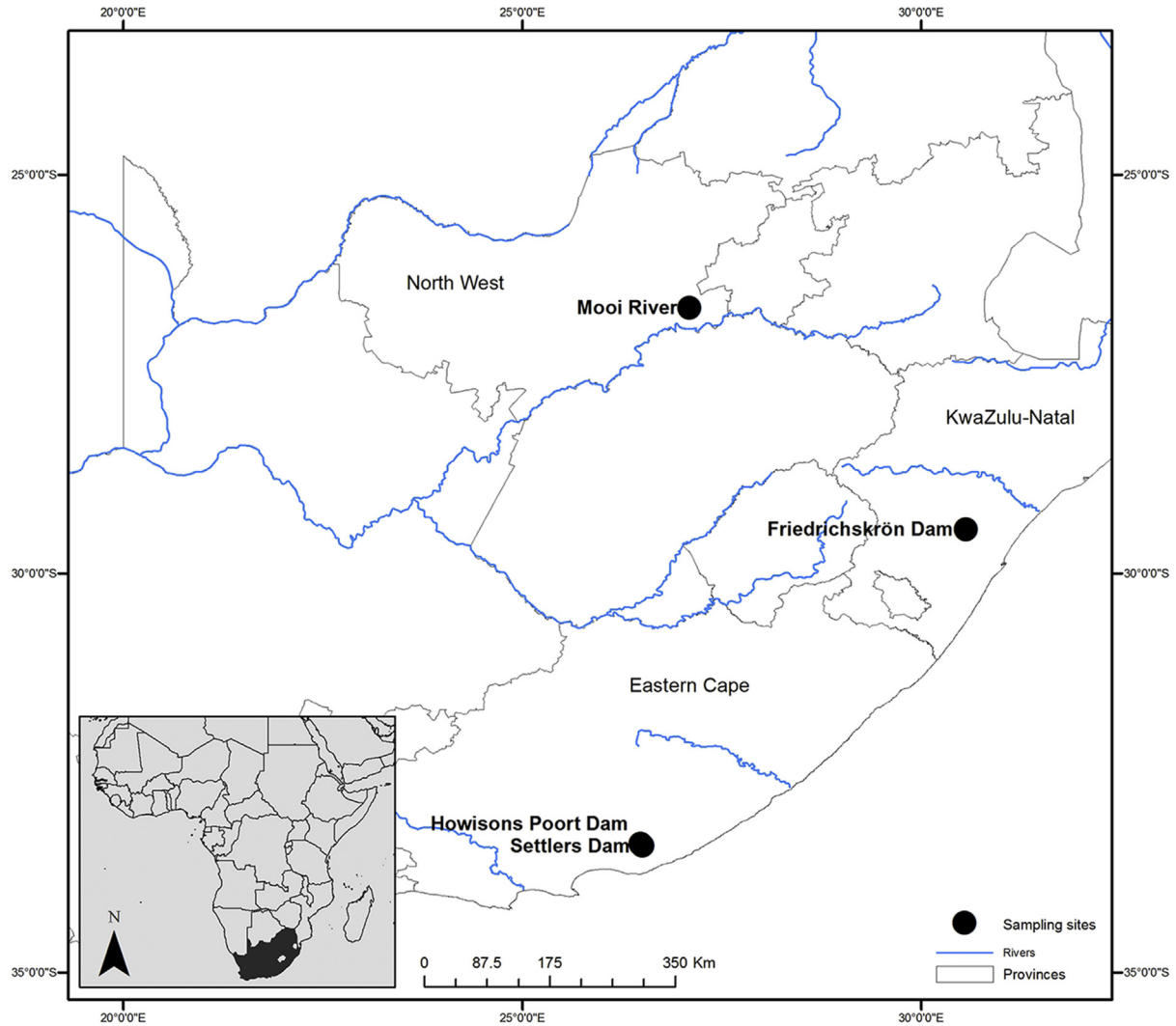


Fig. 1. Map of the sampling localities in the Eastern Cape, Kwazulu-Natal and North West Provinces of South Africa.

Burton, 1989). Marginal hook arrangement for *Onchocleidus* spp. follows that of Wheeler and Beverley-Burton (1989) and *Clavunculus* and *Synclathrium* that of Mizelle (1940). Mean and range are given in micrometers for all structures measured, unless otherwise indicated.

2.3. Statistical analysis

Prevalence, mean intensity and intensity of infection were calculated according to Bush et al. (1997). GraphPad Prism 5 software was used to perform statistical analysis and comparisons of data collected from each locality. The D'Agostino & Pearson omnibus normality test was used to test for normality of fish size (SL) and intensity of parasite infection of each locality in relation to one another. One-way analysis of variance (ANOVA) was performed with Tukey's multiple comparison test as a post test, if data were parametrically distributed. For non-parametric data sets, the Kruskal-Wallis test was performed with Dunn's multiple comparison test as a post-hoc test. A $p < 0.05$ was considered as significant. Spearman's rank correlation analysis was used to determine if there was a correlation between fish size and parasite load.

3. Results

3.1. General

The gills of all host specimens were infected with monogeneans. Table 1 summarizes size of fish and monogenean ecological parameters. Intensity of infection from hosts in the NWP was significantly lower from those in the EC and in KZN ($p < 0.0001$).

The size of hosts examined from KZN was significantly larger ($p < 0.05$) than those collected from the EC and NWP. A strong correlation was found between log-transformed data of fish size and intensity of parasite infection for NWP ($r = 0.81$), intensity of infection increases with fish size. Fish from KZN ($r = 0.06387$) and

Table 1 Summary of fish biometrics and ecological parameters of monogenean parasites load. n – number of fish studied; Mean SL – mean standard length; Mean IF – mean intensity of infection.

	n	Mean SL ±SD	Prevalence (%)	Mean IF
North West	13	165.8 ± 79.24	100	32 (1–86)
Eastern Cape	30	228.1 ± 39.74	100	448 (194–1668)
KwaZulu-Natal	15	260.2 ± 34.66	100	399 (60–736)

EC ($r = 0.01876$) had a weak correlation between log-transformed data for fish size and intensity of parasite infection, thus the size of the fish did not affect the intensity of infection.

3.2. Parasite community

Parasites of two nematode, one protozoan and five monogenean parasite species were sampled. The nematodes comprised larval *Contracaecum* sp. present in low numbers on specimens in the EC ($n = 4$) and KZN ($n = 2$) populations and a larval *Spinitectus* sp. from the NWP ($n = 1$). Seven *Trichodina* sp. specimens were also sampled from the EC populations. Of the 19 863 monogenean parasites counted, a sub-sample of 816 specimens was collected. These were identified as five species belonging to three different genera of Ancyrocephalidae: *Clavunculus bursatus* (Mueller, 1936) (Fig. 2A–B), *Onchocleidus dispar* (Mueller, 1936) (Fig. 2C–D), *Onchocleidus furcatus* (Mueller, 1937) (Fig. 2E–H), *Onchocleidus principalis* (Mizelle, 1936) (Fig. 3A–C) and *Synclathrium fusiformis* (Mueller, 1934) (Fig. 3D–E). Overall monogenean species richness was higher in KZN (3 species) and the EC (3 species) than in the NWP (1 species). As the nematode and protozoan parasites could not be identified to species level, they were elided for subsequent analyses.

Monogenean parasite community composition and abundance, in percentage, of the parasite species at each locality is presented in Fig. 4. *Synclathrium fusiformis* (8%) from KZN were the least abundant species, followed by *C. bursatus* 3% (KZN) and 4% (EC) and *O. dispar* 9% (EC). *Onchocleidus furcatus* 100% (NWP) and 89% (KZN) and *O. principalis* 86% (EC) were the most abundant species and were not found in association with each other, but dominating in their respective geographic region in South Africa.

3.3. Morphology

Family Ancyrocephalidae Bychowsky and Nagibina, 1978.

Genus *Clavunculus* Mizelle, Stokely, Jaskoski, Seamster and Monaco, 1956.

Clavunculus bursatus (Mueller, 1936) (Fig. 3A–B).

Type host: *Micropterus salmoides*.

Other hosts: *Lepomis macrochirus*; *M. dolomieu*; *M. punctulatus*.

Type locality: London, Ohio, USA.

Material examined: Eleven specimens collected from *M. salmoides* caught in the Howison's Poort Dam (33°23'10.07" S; 26°29'4.00" E), four specimens collected from *M. salmoides* caught in the Settlers Dam (33°24'41.67" S; 26°30'11.73" E) and four from *M. salmoides* caught in the Friedrichskrön Dam (29°26'46.66" S; 30°33'38.76" E) were studied. Voucher material (acc. no. NMB P 442) are deposited in the parasite collection of the National Museum, Bloemfontein (NMB).

Description: Large gyroductylid with characters of genus. Umbrella-like haptor with typical marginal indentations each accommodating a larval hook (pairs III – VII), pair I directly anterior to ventral bar, pair V situated between the two pairs of anchors. Marginal hooks similar in shape and size (Fig. 2A), with bulbous base, elongate shaft and hook. Hamuli and bars small relative to haptor, in central region of haptor. Hamuli similar in size and shape, with short robust blade and distinctive outer root notch. Transverse bars articulate with each other, dorsal bar with median suture appearing bipartite, ventral bar V-shaped. Male copulatory complex (Fig. 2B) well sclerotized tubular penis with distinctive shaft with inflated sclerotized base, accessory piece well sclerotized with fenestrated base attached to proximal region of penis shaft and sharp distal point.

Remarks: Morphometrics of specimens from South African were within the same ranges as those parasitising *M. punctulatus* and

M. salmoides from native regions reported by Mizelle (1940) and Beverley-Burton (1986), except in that the male copulatory complex of the South African specimens are larger in size (see Table 3).

Genus *Onchocleidus* (Mueller, 1936).

Onchocleidus dispar (Mueller, 1936) (Fig. 2C–D).

Type host: *Lepomis gibbosus*.

Other hosts: *Archoplites interruptus*; *Lepomis auritus*; *L. cyanellus*; *L. gulosus*; *L. humulis*; *L. macrochirus*; *L. megalotis*; *Micropterus dolomieu*; *M. salmoides*.

Type locality: Constantia, New York, USA.

Material examined: Three specimens collected from *M. salmoides* caught in the Howison's Poort Dam (33°23'10.07" S; 26°29'4.00" E) and four specimens from *M. salmoides* caught in the Settlers Dam (33°24'41.67" S; 26°30'11.73" E). Voucher material (acc. no. NMB P 443) are deposited in the parasite collection of the National Museum, Bloemfontein.

Description: Two pairs of hamuli, dissimilar in shape and size (Fig. 2C); dorsal bar straight with knobbed ends, ventral bar bow shaped. Marginal hooks with ovate elliptical base, slender shaft and sickle shaped hook, similar in shape, pairs I – II similar in size, pairs III – VII slightly longer, distributed along anterolateral margins of haptor. Male copulatory complex (Fig. 2D) comprise of sclerotized straight penis, thick at base, sclerotized accessory piece with elongate handle and distal ring through which penis passes. Vagina not observed.

Remarks: Compared to *O. dispar* populations from native regions, individuals from non-native region (present study) has shorter ventral bar length and smaller marginal hooks than those reported by Beverley-Burton and Suranio (1980). All other characters were within range of measurements given from the different hosts (see Table 2).

Onchocleidus furcatus (Mueller, 1937) (Fig. 2E–H).

Type host: *Micropterus salmoides*.

Other hosts: *Lepomis cyanellus*; *L. macrochirus*; *L. marginatus*; *L. megalotis*; *L. microlophus*; *Micropterus dolomieu*; *M. punctulatus*.

Type locality: Florida, USA.

Material examined: Fifteen specimens collected from *M. salmoides* caught in the Mooi River (26°41'3.60" S; 27°5'59.65" E) and Potchefstroom Dam (26°40'14.20" S; 27°5'46.94" E) and three specimens collected from *M. salmoides* in the Friedrichskrön Dam (29°26'46.66" S; 30°33'38.76" E) were studied. Voucher material (acc. no. NMB P 444) are deposited in the parasite collection of the National Museum, Bloemfontein.

Description: Two pairs of hamuli dissimilar in shape and size (Fig. 2E); dorsal bar straight with knobbed ends, ventral bar slightly bowed with or without membrane (Fig. 2F). Marginal hooks similar in shape with ovate elliptical base, slender shaft and sickle shaped hook with, pair I – II similar in size, positioned directly posterior to dorsal hamuli and anterior to ventral hamuli, respectively, pairs III – VII longer, distributed along lateral margins of haptor, male copulatory complex, larger than *O. dispar*, comprise of sclerotized straight to slightly curved penis, sclerotized accessory piece with elongate handle and distal ring through which penis passes. Spiral filament 8–9 turns. Vagina unsclerotized (Fig. 2H).

Remarks: *Onchocleidus furcatus* collected during the present study has shorter hamuli and marginal hooks, but all other measurements fall within ranges reported for this species (Mizelle, 1940; Wheeler and Beverley-Burton, 1989). A ventral bar is present with membrane absent or present (Fig. 2F), which has not been reported from previous studies. Penis is shorter than previously reported and accessory piece (Fig. 2G) has a closed distal ring (see Table 2).

Onchocleidus principalis (Mizelle, 1936) (Fig. 3A–C).

Type host: *Micropterus punctulatus*.

Other hosts: *Lepomis cyanellus*; *L. macrochirus*; *Micropterus*

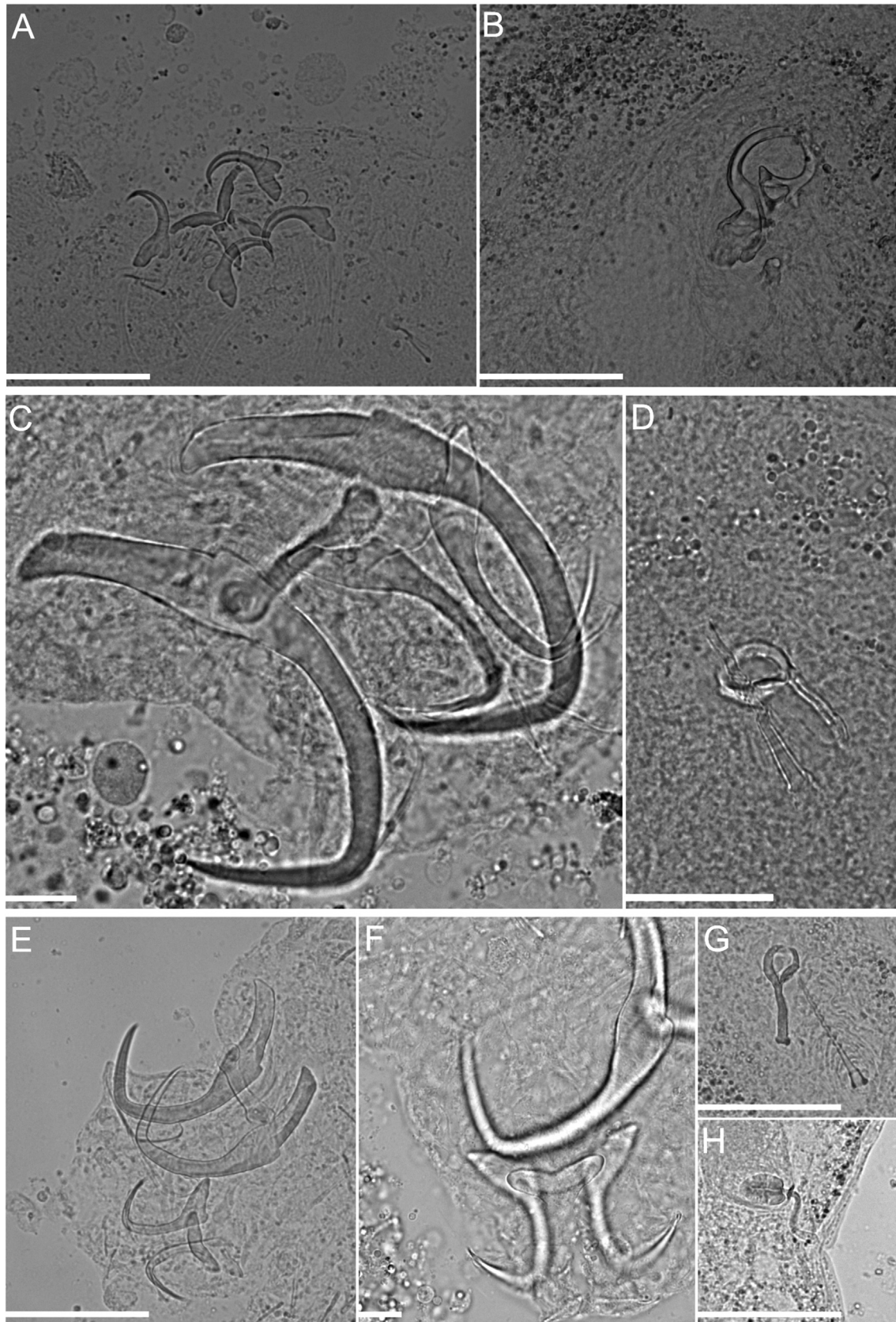


Fig. 2. *Clavunculus bursatus* (Mueller, 1936) haptoral hooks (A), male copulatory organ (B); *Onchocleoides dispar* (Mueller, 1936) haptoral hooks (C); male copulatory organ (D); *Onchocleoides furcatus* (Mueller, 1937) haptoral hooks (E); male membrane on ventral bar (F), copulatory organ (G), vagina (H). Scale: A–E, G–H: 50 μm; F: 10 μm.

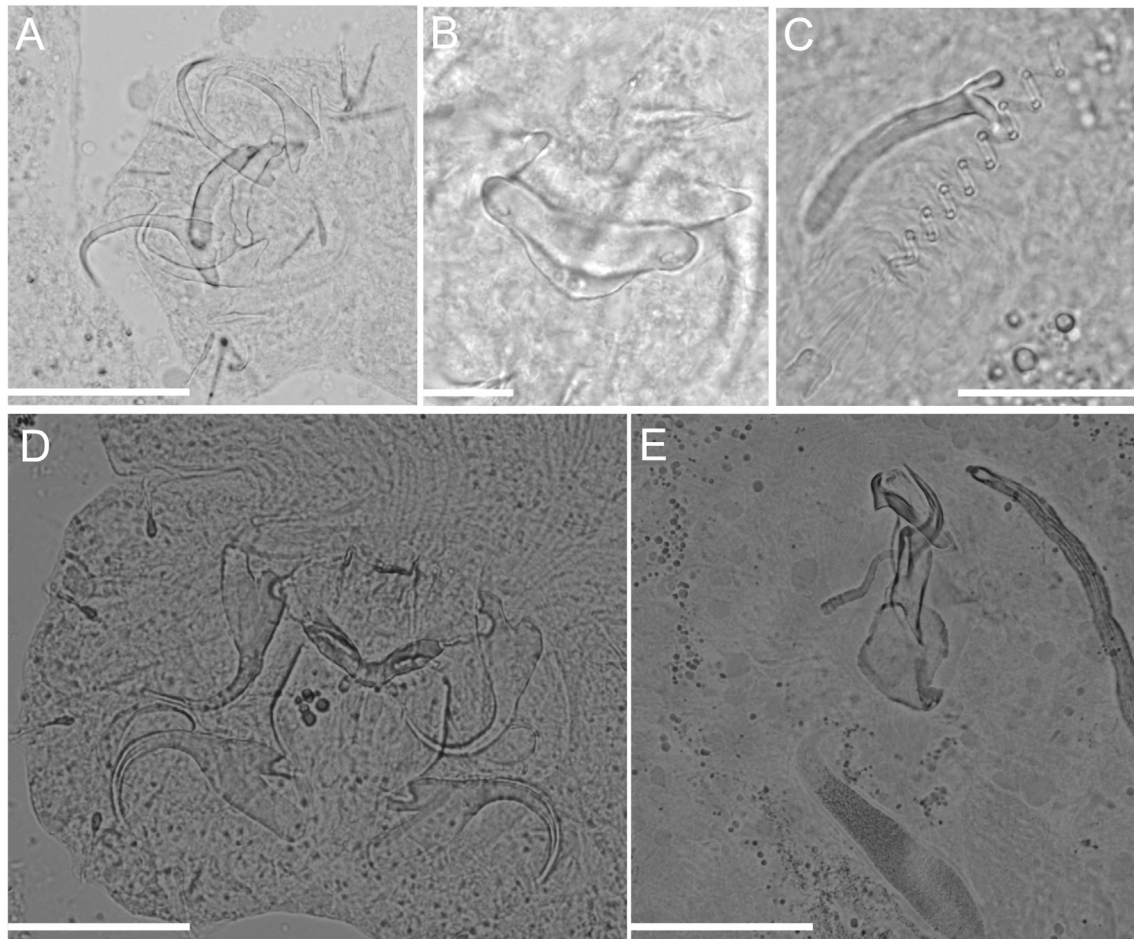


Fig. 3. *Oncholeiidus principalis* (Mizelle, 1936) haptor hooks (A), membrane on ventral bar (B); male copulatory organ (C); *Synclathrium fusiformis* (Mueller, 1934) haptor hooks (D) male copulatory organ (E). Scale: A, C–E: 50 μ m; B: 10 μ m.

dolomieui; *M. salmoides*.

Type locality: Salt Fork of the Big Vermillion River, Homer, Illinois, USA.

Material examined: Fifteen specimens collected from *M. salmoides* caught in the Settlers Dam (33°24'41.67" S; 26°30'11.73" E) were studied. Voucher material (acc. no. NMB P 445) are deposited in the parasite collection of the National Museum, Bloemfontein.

Description: Two pairs of hamuli similar in shape and size (Fig. 3A); dorsal bar curved with knobbed ends, ventral bar slightly curved with membrane present or absent (Fig. 3B). Marginal hooks similar in shape, pairs I – II similar in size, positioned directly posterior to dorsal hamuli and anterior to ventral hamuli, respectively, pairs III – VII slightly longer, distributed along anterolateral margins of haptor. Male copulatory complex comprise of sclerotized helical with 6–9 turns, sclerotized accessory piece with elongate handle, bifid distally (Fig. 3C). Vagina unsclerotized.

Remarks: *Oncholeiidus principalis* found in present study is morphometrical and morphological similar to previously descriptions of this species (see Table 2), except that in the South African population a membrane on the ventral bar can be present or absent (Fig. 3B) where previously no mention was made of a membrane (Wheeler and Beverley-Burton, 1989).

Genus *Synclathrium* Price, 1967.

Synclathrium fusiformis (Mueller, 1934) Price, 1967 (Fig. 3D–E).

Type host: *Micropterus dolomieui*.

Other hosts: *Lepomis cyanellus*; *L. gulosus*; *L. macrochirus*; *L. megalotis*; *M. punctulatus*; *M. salmoides*.

Type locality: Syracuse, New York; London, Ohio, USA.

Material examined: Seventeen specimens collected from *M. salmoides* caught in the Friedrichskrön Dam (29°26'46.66" S; 30°33'38.76" E) were studied. Voucher material (acc. no. NMB P 446) are deposited in the parasite collection of the National Museum, Bloemfontein.

Description: Large gyroductylid with characters of genus. Haptor not wider than body. Marginal hooks distributed in typical ancyrocephalid pattern, as described above. Marginal hooks similar in shape, with base, elongate shaft and hook, slightly dissimilar in size. Hamuli and bars in central region of haptor ventral and dorsal bars projecting laterally beyond haptor margin (Fig. 3D). Hamuli robust, distinguishable – dorsal hamuli long inner root, compared to that of ventral hamuli. Transverse bars articulate with each other forming single supporting plate for hamuli. Ventral bar centrally horizontal, V-shaped, with oblique distal struts, dorsal bar a solid, shield-like plate, wider than long, central portion may be absent. Male copulatory complex (Fig. 3E) comprising of well sclerotized penis with shaft and curved distal point and a lightly sclerotized base, accessory piece sclerotized with distal limb characterized by bifid tip which guides distal extremity of penis. Accessory piece attached to penis by strands of muscle. Vagina sclerotized, submarginal, left side of body.

Remarks: The *Synclathrium fusiformis* collected from South

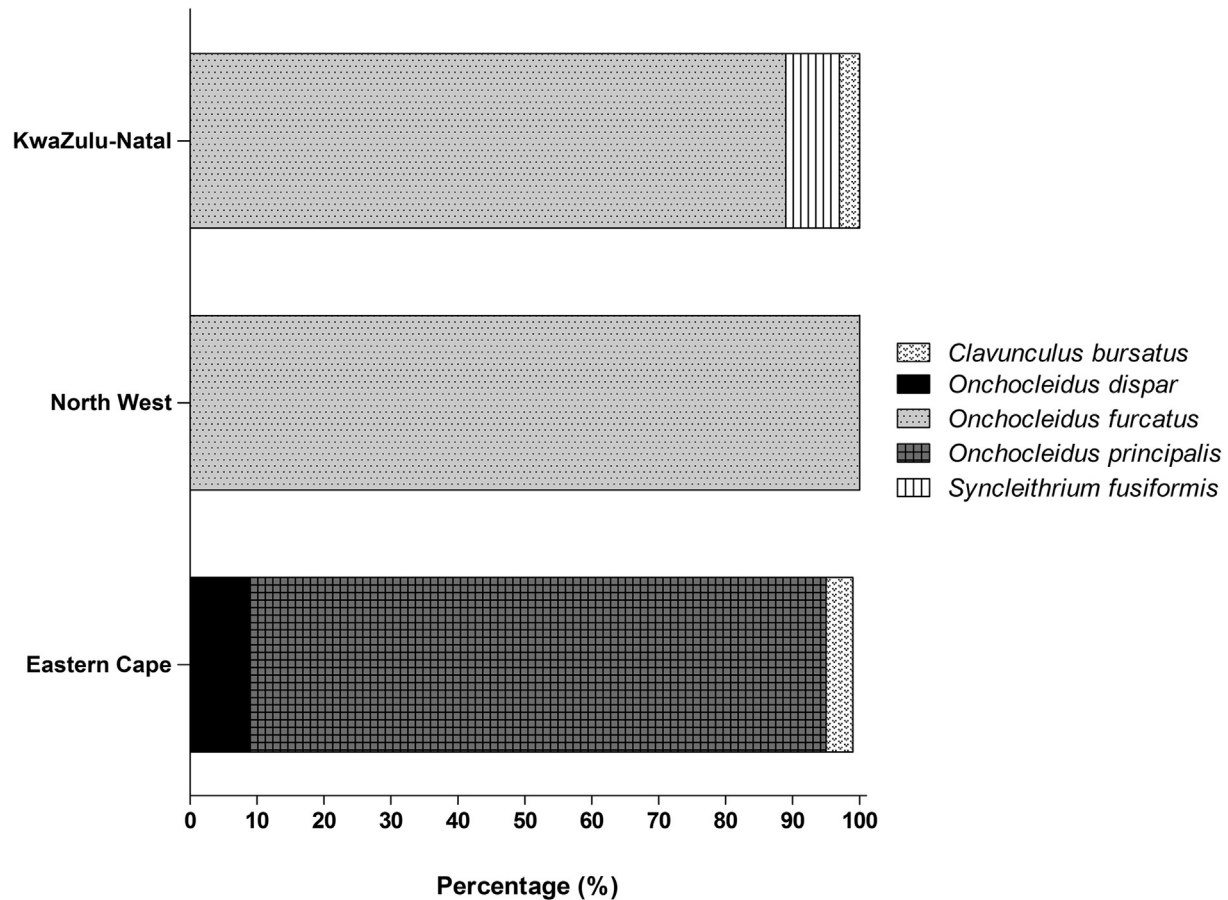


Fig. 4. Composition and abundance of monogenean species at each sampling locality.

Africa is morphological and morphometrically similar to those previously described (see Table 3).

4. Discussion

Until recently seven Ancyrocephalid species: *Actinocleidus fergusonii* Mizelle, 1938, *C. bursatus*, *O. dispar*, *O. furcatus*, *O. helcis* Mueller, 1936 *O. principalis* and *S. fusiformis* were known to parasitise *M. salmoides* in their native range (Mizelle and Cronan, 1943; Mueller, 1937; Mizelle and Crane, 1964; Hargis, 1953; Rawson and Rogers, 1972; Molnar et al., 1974; Joy, 1984; Hoffman, 1999). Galaviz-Silva et al. (2016) commutated this to eight, when reporting *M. salmoides* as a new host of *Clavunculus bifurcatus* (Mizelle, 1941). Five of these eight ancyrocephalid species were sampled from *M. salmoides* in South Africa during the present study. As these parasites are common in centrarchid fishes in their native range, they were most likely co-introduced with *M. salmoides* or the other centrarchid fishes that were introduced into South Africa between 1928 and 1980. Interestingly, the results of the current study (Fig. 4) also correspond to Mizelle and Crane (1964) observations that no more than four of the seven known species occur at any one locality.

Studies yielding similar results in parasite community structure reported here, include that of Joy (1984) reporting four ancyrocephalids with a low frequency of *C. bursatus* and *S. fusiformis* with *O. furcatus* and *O. helcis* as the dominant species from *M. salmoides* collected in Beech Fork Lake, West Virginia. Mizelle and Crane (1964) and Rawson and Rogers (1972) reported a parasite community comprising of all species present in this study with the

exclusion of *O. dispar*. The former reported fluctuation in proportions of species in parasite population between summer and autumn, respectively, from the California pond: *C. bursatus* (50% and absent), *O. furcatus* (23% and 32%), *O. principalis* (60% both seasons) and *S. fusiformis* (3% and 7%). Similarly, the latter reported *O. furcatus* and *O. principalis* dominating on the same host in association with low numbers of *C. bursatus* and *S. fusiformis* from the Walter F. George Reservoir, Alabama, USA. Cloutman (1975) also reported the same four monogenean species (excluding *O. dispar*) and *A. ureterocoetes* parasitising *M. salmoides* from Lake Fort Smith, Arkansas. All of the aforementioned literature reflects seasonal differences in the abundance of parasite community from a single location studied. In the study of Galaviz-Silva et al. (2016) the parasite community of *M. salmoides* from five localities were investigated. Of the six monogenean species found to parasitise *M. salmoides*, the presence of four ancyrocephalids correspond with the present study. *Clavunculus bursatus* were found to parasitise between 60% and 86.6% of hosts at all studied locations in relative high abundances *Onchocleidus furcatus*, *O. principalis* and *S. fusiformis* occurred only on a few hosts from one locality in relative low numbers. From above mentioned studies, it is clear that changes in season, (reflected in the changes of water temperature, have an influence on the abundance or reproduction of these ancyrocephalids. Predominantly parasite community structure, in terms of abundance and not richness, changed. Although investigation of parasite fauna for the selected localities in the present study were not performed throughout all seasons, it is interesting that such distinct community structures were found from each locality despite the relevantly low fluctuation in water temperature. This

Table 2
Morphometrics of *Onchocleidus dispar*, *O. furcatus* and *O. principalis*, from gills of *Micropterus salmoides* in South Africa.

	<i>Onchocleidus dispar</i>				<i>Onchocleidus furcatus</i>			<i>Onchocleidus principalis</i>		
	Mizelle and Cronan, 1943 (n = 1) ^a	Hanek and Fernando, 1972 (n = 10) ^a	Beverly-Burton & Suranio, 1980 (n = 20)	Present study (n = 6) ^a	Mizelle, 1940 (n = 9) ^a	Wheeler and Beverley-Burton, 1989 (n = 13) ^a	Present study (n = 18) ^b	Mizelle, 1940 (n = 4)	Wheeler and Beverley-Burton, 1989 (n = 10)	Present study (n = 15)
Body length	650	540–732	410 (320–512)	596 (420–785)	352 (238–495)	424 (403–451)	800 (715–885)	237 (207–289)	411 (342–510)	395 (347–443)
Body width	86	84–108	100 (90–150)	111 (68–126)	107 (81–135)	128 (100–146)	146 (117–175)	97 (83–117)	88 (54–119)	99 (80–118)
Haptor length	57	72–86	75 (50–100)	–	67 (58–82)	64 (46–77)	–	47 (37–58)	65 (60–75)	–
Haptor width	71	116–132	125 (100–150)	–	82 (68–86)	69 (58–77)	–	71 (67–73)	85 (66–104)	–
Pharynx	43	40–44	30 (28–40)	–	25 (22–30)	39	–	20 (19–22)	24 (18–33)	–
Dorsal hamuli Anchor length	69	51–54	71 (60–85)	70 (64–75)	74 (43–81)	79 (77–80)	67 (63–70)	38 (32–41)	34 (29–41)	35 (33–37)
Point length	–	–	–	26 (21–29)	–	32 (28–34)	29 (27–31)	–	13 (8–16)	13 (12–14)
Shaft length	–	–	–	53 (48–57)	–	61 (59–63)	50 (46–55)	–	32 (29–36)	31 (30–33)
Inner root length	–	–	–	24 (23–26)	–	26 (23–29)	27 (25–30)	–	9 (8–10)	11 (9–12)
Outer root length	–	–	–	1 (1–2)	–	–	2 (1–3)	–	–	2 (2–3)
Aperture length	–	–	–	34 (31–35)	–	–	34 (31–38)	–	–	21 (20–23)
Dorsal bar length	23	25–27	30 (28–35)	28 (26–28)	30 (20–37)	36 (33–39)	31 (29–34)	36 (32–38)	31 (26–36)	32 (30–33)
Dorsal bar median width	–	5–6	4 (3–5)	4 (3–4)	–	5 (4–6)	5 (4–7)	–	5 (4–6)	5 (4–6)
Ventral hamuli Anchor length	36	32–34	40 (35–45)	36 (34–39)	35 (25–38)	36 (31–40)	33 (31–34)	42 (38–46)	37 (32–45)	35 (33–37)
Point length	–	–	–	17 (16–21)	–	17 (14–19)	17 (16–19)	–	14 (12–16)	13 (12–14)
Shaft length	–	–	–	30 (27–32)	–	31 (28–33)	27 (25–30)	–	33 (28–41)	31 (30–33)
Inner root length	–	–	–	10 (8–12)	–	12 (9–16)	11 (9–14)	–	11 (8–14)	11 (9–12)
Outer root length	–	–	–	–	–	–	–	–	–	2 (2–3)
Aperture	–	–	–	16 (15–18)	–	–	16 (15–18)	–	–	21 (20–23)
Ventral bar length	14	16–18	21 (17–25)	17 (16–19)	28 (25–32)	–	22 (19–24)	33 (27–40)	31 (26–36)	33 (31–36)
Ventral bar median width	–	4–5	6 (5–7)	4 (3–6)	–	–	5 (4–7)	–	5 (4–6)	6 (5–8)
Marginal hooks					11–26			12–24		
Pair I	14–17	14–20	16 (15–20)	14 (13–16)	–	19 (18–21)	16 (13–18)	–	15 (12–19)	17 (14–19)
Pair II	14–17	14–15	18 (15–20)	14 (13–16)	–	17 (16–18)	16 (12–19)	–	13 (10–16)	14 (12–17)
Pair III – VII	“shorter than the rest”	14–20	16 (15–20)	18 (16–20)	–	20 (18–24)	20 (17–22)	–	17 (13–20)	19 (17–22)
Male copulatory complex										
Penis length	26	26–29	31 (26–35)	29 (26–38)	64 (62–66)	71 (62–80)	53 (46–60)	41 (37–45)	44 (38–48)	46 (44–49)
Accessory piece	–	20–23	20 (17–25)	21 (20–22)	32 (20–38)	36 (30–40)	31 (22–39)	23 (19–26)	24 (19–31)	23 (21–26)
Spiral filament turns	–	–	–	3–5	–	9–10	8–9	–	7–9	6–9
Host(s)	<i>M. salmoides</i>	<i>M. dolomieu</i>	<i>L. gibbosus</i>	<i>M. salmoides</i>	<i>M. salmoides</i>	–	<i>M. salmoides</i>	<i>M. salmoides</i>	–	<i>M. salmoides</i>
Geographic locality	Tennessee, USA	Ontario, Canada	Ontario, Canada	South Africa	Tennessee, USA	–	South Africa	Tennessee, USA	–	South Africa

^a Average, minima and maxima is given.^b 15 specimens from North West and 3 from KwaZulu-Natal were examined.

might be an example of interspecific competition between species for a specific niche on the host in the novel environment (Cloutman, 1975). Further investigation is needed. Species richness for monogeneans in general was lower in South Africa (n = 5) than

in North American *M. salmoides* populations with a total of 13 monogenean species reported from its native range (Hoffman, 1999; Galaviz-Silva et al., 2016). The lower abundance and species richness in South Africa therefore supports the enemy release

Table 3
Morphometrics of *Clavunculus bursatus* and *Synclathrium fusiformis* from gills of *Micropterus salmoides* in South Africa.

	<i>Clavunculus bursatus</i>			<i>Synclathrium fusiformis</i>			
	Mizelle, 1940 (n = 10) ^a	Beverley-Burton, 1986 (n = 3) ^a	Present study (n = 19)	Mizelle, 1940 (n = 4) ^a	Hanek and Fernando, 1972 (n = 15)	Beverley- Burton, 1986	Present study (n = 17) ^b
Body length	820 (646–1006)	1086 (725–1431)	1668 (639–2835) ^a	483 (270–910)	1224–1692	437 (283–717)	1053 (756–1443) ^a
Body width	328 (172–405)	342 (205–450)	314 (203–425)	132 (68–180)	146–168	136 (83–183)	188 (147–229)
Haptor length	216 (144–270)	169 (98–257)	174 (85–282) ^a	89 (85–97)	168–180	78 (67–93)	136 (98–232) ^a
Haptor width	242 (134–294)	275 (197–325)	308 (85–457) ^a	–	216–240	98 73 110	178 (83–178) ^a
Pharynx length	111 (61–130)	–	137 (76–197)	35 (29–43)	96–108	–	76 (59–93)
Pharynx width	–	–	146 (91–202)	–	120–132	–	83 (64–103)
Dorsal hamuli							
Anchor length	27 (22–30)	25 (24–28)	26 (25–27)	51 (44–51)	49–52	40 (34–45)	54 (37–59) ^a
Point length	–	–	7 (6–9)	–	26–27	–	15 (12–18) ^a
Shaft length	–	–	24 (23–28)	–	–	–	40 (31–44) ^a
Inner root length	–	–	6 (4–7)	–	17–19	–	20 (16–24) ^a
Outer root length	–	–	2 (1–3)	–	6–10	–	8 (4–12) ^a
Aperture length	–	–	14 (13–15)	–	–	–	26 (24–31) ^a
Dorsal bar length	19 (15–22)	10 (6–13)	16 (14–18)	46 (45–47)	38–42	33 (30–36)	41 (38–45) ^a
Dorsal bar median width	–	–	5 (4–6)	–	42–44	–	49 (45–55) ^a
Ventral hamuli							
Anchor length	27 (25–28)	26 (24–27)	26 (25–27)	42 (40–43)	43–45	39 (35–45)	47 (41–55) ^a
Point length	–	–	6 (6–7)	–	27–28	–	14 (12–18) ^a
Shaft length	–	–	23 (23–25)	–	–	–	39 (36–46) ^a
Inner root length	–	–	7 (6–8)	–	13–15	–	14 (9–20) ^a
Outer root length	–	–	2 (1–3)	–	8–9	–	6 (4–11) ^a
Aperture length	–	–	14 (11–16)	–	–	–	24 (21–30) ^a
Ventral bar length	31 (26–36)	30 (27–33)	18 (17–20)	64 (59–68)	69–72	46 (36–57)	65 (57–71) ^a
Ventral bar median width	–	–	4 (4–6)	–	9–10	–	7 (3–10) ^a
Marginal hooks							
Pair I	14–21	11–18	16 (15–18)	11–18	17–18	17–21	19 (17–22) ^a
Pair V	–	–	16 (15–17)	–	16–17	–	16 (12–20) ^a
Pair II - VII	–	–	17 (17–19)	–	18–21	–	19 (16–22) ^a
Male copulatory complex							
Vagina length	–	–	–	–	–	–	27 (21–36) ^a
Vagina width	–	–	–	–	–	–	15 (13–19) ^a
Penis length	41 (39–46)	55 (51–63)	69 (58–80)	49 (38–55)	37–41	61 (48–70)	69 (64–73)
Accessory piece	27 (25–28)	23 (19–27)	31 (27–34)	–	24–26	41 (29–46)	65 (59–71)
Host (s)	<i>M. punctulatus</i>	<i>M. salmoides</i>	<i>M. salmoides</i>	<i>M. salmoides</i>	<i>M. salmoides</i>	–	<i>M. salmoides</i>
Geographic locality	Tennessee, USA	–	South Africa	Tennessee, USA	Ontario, Canada	–	South Africa

^a Average, minima and maxima is given.

^b Only 12 haptors and complete specimens could be studied.

hypothesis (Sheath et al., 2015). With regard to the ancyrocephalid communities in particular, the species composition on the *M. salmoides* host populations is also less diverse (50%) than in North American populations (n = 10) and is comprised of those species capable of overcoming barriers set by introduction into a novel environment, supporting enemy release (Lymbery et al., 2014).

Differences between studied localities in South Africa could also be a consequence of the introduction from populations which might simply reflect the parasite community structure in the native region from where they were sourced (Mizelle and Crane, 1964). Although evidence is scant, the possibility of multiple *M. salmoides* or cross-infection from other centrarchid species introductions cannot be ignored. Although *C. bursatus*, *O. principalis* and *S. fusiformis* are extremely host specific, only parasitising *M. salmoides* even in the presence of other potential centrarchid hosts, *O. dispar* and *O. furcatus* are less host specific, having been reported to also parasitise *Lepomis cyanellus* Rafinesque, 1819, *L. macrochirus* and *Pomoxis nigromaculatus* (Collins and Janovy, 2003). As a result, the potential for spill-over to native fishes and the spill-back to other introduced centrarchids requires further investigation.

In conclusion, this study presents the first report of *C. bursatus*, *O. dispar*, *O. furcatus*, *O. principalis*, *S. fusiformis* from introduced alien *M. salmoides* on the African continent. Furthermore, these parasites are all considered as co-introduced with largemouth bass. In revisiting invasion hypotheses, our results support the enemy

release hypothesis in that the invasive largemouth bass have lost some of its natural parasites, but due to the paucity of our knowledge on the parasites of the native fishes from the regions studied it is not clear whether spillback, dilution or spill-over have occurred.

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