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Spatio-temporal variation in length-frequency and salinity tolerance of dominant fishes utilizing the Orange River-Estuary Continuum

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Abstract

The length-frequency distribution of the dominant species of euryhaline marine *Chelon richardsonii*, estuarine *Gilchristella aestuaria* and freshwater species *Labeobarbus aeneus, Mesobola brevianalis* and *Pseudocrenilabrus philander* were investigated seasonally along the Orange River Estuary Continuum (OREC) during high-flow and low-flow periods, conducted in eight years, within 15 years (2004-2018). We sampled fish using a seine net at 18 sites spanning from the mouth of the estuary up to 35 km upstream. The length-frequency distributions of all species did not differ between the high-flow and low-flow season. Spatial differentiation in size-frequency distribution of all freshwater taxon was recorded along the river-estuarine continuum but not for *C. richardsonii* and *G. aestuaria*. Total catch-per-unit-effort (CPUE) was low for both *M. brevianalis* and *P. philander,* and their abundance declined downstream into the estuarine region as expected for these two freshwater species. A positive correlation between salinity and fish length of all five species was found, demonstrating that juvenile fishes, in particular, freshwater species are less salt-tolerant than the adults. It is concluded that the lower OREC provides a vital fish nursery habitat suitable for growth and development, particularly for marine *C. richardsonii* and estuarine *G. aestuaria*.

Keywords: Catch-per-unit-effort, distribution, euryhaline, salinity, stenohaline.

1.Introduction

Length-frequency distribution measurements are fundamental to many aspects of fisheries science as they aid in understanding the state of the fish population (Pope et al., 2010). Investigating the length-frequency distributions (LFDs) of fish species is the first step to evaluating gear selectivity on catches (Andem et al., 2013). Body size is one of the fundamental traits of an organism (White et al., 2007) and it is a significant determinant of both the occurrence and magnitude of species interactions (Woodward et al., 2006; Stevenson et al., 2016). The body size is related to many aspects of species ecology, including its abundance, lifespan, the spatial scale of resource use and its competitive relationships with other members of the food web (Woodward et al., 2006; White et al., 2007).

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Environmental factors across gradient may further govern the length-frequency distribution of species as it correlates strongly with aspects of physiology (Zhang & Payne, 2012). For example, juveniles of most fish species are less salt-tolerant than adults (Chervinski, 1984; Lisboa et al., 2015; Sallam et al., 2017), this is because early life stages in fish are sensitive to environmental challenges, both natural and anthropogenic and if disrupted can lead to mortality (McCormick et al., 2013). With many exceptions, several species exhibit spatial variation in body size within and among species across large-scale environmental gradient (Roy & Martien, 2001) such as salinity, which influences growth and perturb body water and salt homeostasis (i.e. osmoregulation) (Kültz, 2015; Anni et al., 2016). Many freshwater species are stenohaline and can tolerate very narrow ranges of salinity. Euryhaline fish, by contrast, tolerate a wide range of salinity at some phase in their life cycle (Whitfield, 1998; Kültz, 2015) and this is due to their abilities to synthesize new salt-transporting proteins as they move from salt to freshwater and vice versa (Kidder III et al., 2006). Euryhaline ability benefits the fish in an environment with fluctuating salinity by reducing competition, whereas for non-tolerant species they are a stressor (Smyth & Elliott, 2016). Salinity preferences and tolerances of fishes play an important role in structuring fish assemblages within estuaries (Whitfield, 1999; Harrison & Whitfield, 2006).

Consequently, understanding spatial patterns of fishes in an aquatic environment can provide useful information on how these patterns are controlled by aspects of the physical environment versus ecological interactions among species. These and other environmental variables can be regarded as potential factors tapering length-frequency distribution of species in an estuarine environment. From a fisheries perspective, the Orange River provides a perfect geographic space to study the size structure and interactions of fishes of different origin along a gradient in the estuarine environment.

The Orange River is among the most regulated rivers in the world with several impoundments and inter-basin transfer schemes (Davies et al., 1993; Snaddon et al., 1999). These anthropogenic impacts, together with mining, agriculture and development along the lower part of the river and estuary have modified the flow regime downstream (DWAF, 1999). Flow modification has contributed to “seasonal reversals’’ in flow and less than 20% of historical MAR (million m^3/annum) reaching the estuary (Lamberth, 2003; van Niekerk & Turpie, 2012). Despite the threats, the lower Orange River and estuary remain ecologically crucial to a variety of aquatic species and provide seasonal nursery habitat and feeding grounds for many fish species of marine and freshwater origin (Lamberth, 2003; van Niekerk & Turpie, 2012). Consequently, altered flows would have confused behavioural cues for recruitment or emigration and can cause changes in catch composition and resource base (ORASECOM, 2013).

The Orange Estuary presents both horizontal and vertical (stratification) salinity gradients with various degrees of mixing between the outward-flowing surface layer of fresh water and the inward-flowing bottom layer of saline water (Seaman & van As, 1998). However, the Orange River Estuary Continuum (OREC) remains freshwater dominated with the fish assemblages comprising species tolerant of low salinity (Lamberth, 2003). This study investigated the spatial and temporal variation in the LFDs of the five dominant fish species in the OREC. These species include the southern mullet *Chelon richardsonii*, estuarine roundherring *Gilchristella aestuaria*, smallmouth yellowfish *Labeobarbus aeneus*, southern mouthbrooder *Pseudocrenilabrus philander* and the river sardine *Mesobola brevianalis*. The primary objectives of this study are (i) to determine the influence of salinity on the distribution of fishes along the river-estuarine continuum, and (ii) to determine the relationship between changes in fish growth and salinity tolerance.

2. Materials and methods

Study area

The lower section of the Vaal-Orange system forms part of the international border between South Africa and Namibia. The study area is situated between latitude 28°28'19"S and longitude 16°26'56"E seawards (Fig. 1). The study area covered a distance of about 35 km from the mouth of the estuary (site 1) to the lower reaches of the river (Site 18, Fig. 1). Within the estuary region, mixing of freshwater from rivers and saltwater from the sea were apparent. After that, the system becomes riverine, reflecting a progression from marine to estuarine and freshwater influences forming a river-estuary continuum. The Vaal-Orange River basin originates in the highlands of Lesotho from which the river flows across central and western South Africa and discharges into the Atlantic Ocean at Alexander Bay (Næsje et al., 2007; Ramollo, 2011).

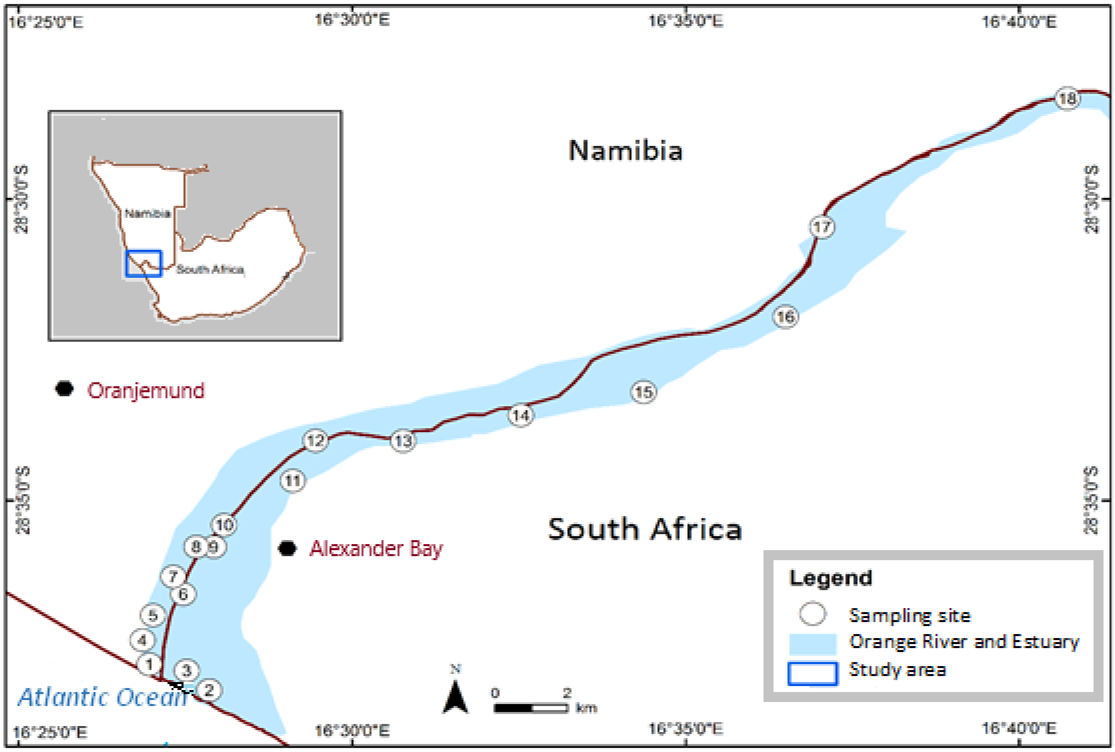


Figure 1. Map showing the extends of the Orange River from the mouth. The Orange Estuary extends from site 1 to 11, whilst the river section extent from site 12 to 18.

At the mouth of the estuary, there is a Ramsar site which extends up to 10 km upstream (Williams, 1986). Water flows from the upper Orange River remain the largest source of water supplying the lower Orange River and its Estuary (Basson & Rossouw, 2003). The surface water area of the estuary is estimated at 600 ha, whereas the entire wetland area, including salt marsh and floodplain, is approximately 2 000 ha (van Niekerk et al., 2003).

Field sampling

Sampling was conducted biannually, during December - March high-flow season (high-flow from the catchment contrasts with the estuary falls within the winter rainfall zone) and August - October low-flow season (van Langenhove et al., 1998) for a period of eight years within 15 years (2004 to 2018).

A 30 x 2 m beach-seine net with 10 mm stretched mesh size in the centre including the cod-end (bag), and 10 m of 15 mm stretched mesh size in each of the wings were used for sampling at 18 fixed sampling sites along the OREC. Fish caught at each site were counted, identified to species level (Smith & Heemstra, 1986; Skelton, 2001) and measured to the nearest mm in total length (TL). Subsequently, fish were released alive into the water where possible. The minimum and maximum TL of fishes were determined. Length measurements were grouped into length categories of 10 mm interval. The length at maturity in standard length (SL) of selected fish species was obtained from the literature (Skelton, 2001; Næsje et al., 2007; Froese & Pauly, 2018) and where possible converted to total length (TL) using the length-length table in FishBase (Froese & Pauly, 2018).

Table 1. The length at maturity of dominant species collected in the lower Orange River and estuary during the study period.

Species	Estuary association	Length at maturity (mm)		Source
		TL	SL	
Chelon richardsonii	Marine estuarine-opportunist	244.1	180	Froese & Pauly, 2018
Labeobarbus aeneus	Freshwater straggler	~244.2	M: 200; F: 240	Næsje et al., 2007
Pseudocrenilabrus philander	Freshwater estuarine-opportunist	30.9	25	Froese & Pauly, 2018
Mesobola brevianalis	Freshwater straggler	31.2	30 FL	Næsje et al., 2007
Gilchristella aestuaria	Solely estuarine	35.8	30	Froese & Pauly, 2018

M = Male, F = Female, FL = Fork Length

Salinity (expressed as practical salinity units) was measured at each site, from the middle of the water column; the zone between near-surface and near the bottom, using a YSI *v6920/EXO* 1 multi-parameter probe. Sampling sites were categorized into salinity zones based on an adaptation of the Venice system for the classification of South African salinity zones in estuaries (Strydom et al., 2003). The following salinity zones and salinity ranges in practical salinity units: freshwater = 0–0.49; oligohaline = 0.5–4.9; mesohaline = 5.0–17.9; polyhaline = 18.0–29.9; euhaline = 30.0–35.9; hypersaline ≥40.

Data analyses

Assumptions for normality and homogeneity of variance were violated by length-frequency distribution data observed along the salinity gradient over the years. As a result, non-parametric statistical tests were used. The Mann-Whitney *U*-test was performed to investigate the differences in mean length of fish on a seasonal basis (high-flow and low-flow season). The LFDs of species among salinity zones were investigated for each species separately using the non-parametric Kruskal-Wallis test using SPSS *v23* software. Catches were expressed as catch-per-unit-effort (CPUE) and calculated as the number of fishes that were collected per net haul. Spearman's rank correlation analysis was performed to investigate the influence of salinity ranges on body size of each species. Graphs of bar charts were plotted using Microsoft Excel to show the variation of the length-frequency distribution of species throughout the study period. All statistical tests were carried out at the 0.05 alpha level.

3. Results

The marine estuarine-opportunist *C. richardsonii* made up the most significant portion of the catch (70%) while freshwater stragglers *M. brevianalis* was the lowest (2%), Table 2.

Table 2. The number of fish species, mean total length with minimum and maximum length values of fish species caught in the Orange River Estuary Continuum, 2004 - 2018.

Common name	Scientific name	N	Mean	CPUE (mean)	Min. TL (mm)	Max. TL (mm)
Southern mullet	*Chelon richardsonii*	16 374	33.13	79.01	11	490
Estuarine roundherring	*Gilchristella aestuaria*	3 566	57.39	17.63	22	95
Smallmouth yellowfish	*Labeobarbus aeneus*	1 913	118.29	9.24	13	520
River sardine	*Mesobola brevianalis*	475	46.14	2.29	19	66
Southern mouthbrooder	*Pseudocrenilabrus philander*	1 035	44.29	5.00	11	140

The majority of fishes caught were mature except for *C. richardsonii* and *L. aeneus*. Approximately 99% of the total catch of *C. richardsonii* had an estimated length below the maturity level (~244.08 mm TL; Table 1). About 88% of *L. aeneus* caught during the study period were juveniles (~244.20 mm TL; Table 1). More than 87% of *G. aestuaria, M. brevianalis* and *P. philander* species showed sexual maturity while less than 13% did not show sexual maturity. No records of fishes with body size under 10 mm were caught in the OREC. Fishes with body size below 10 mm are larvae, and the gear used 10 mm stretched mesh misses them. The same holds for all other fish species under 10 mm.

Seasonal and spatial variation in the length-frequency distribution of fishes

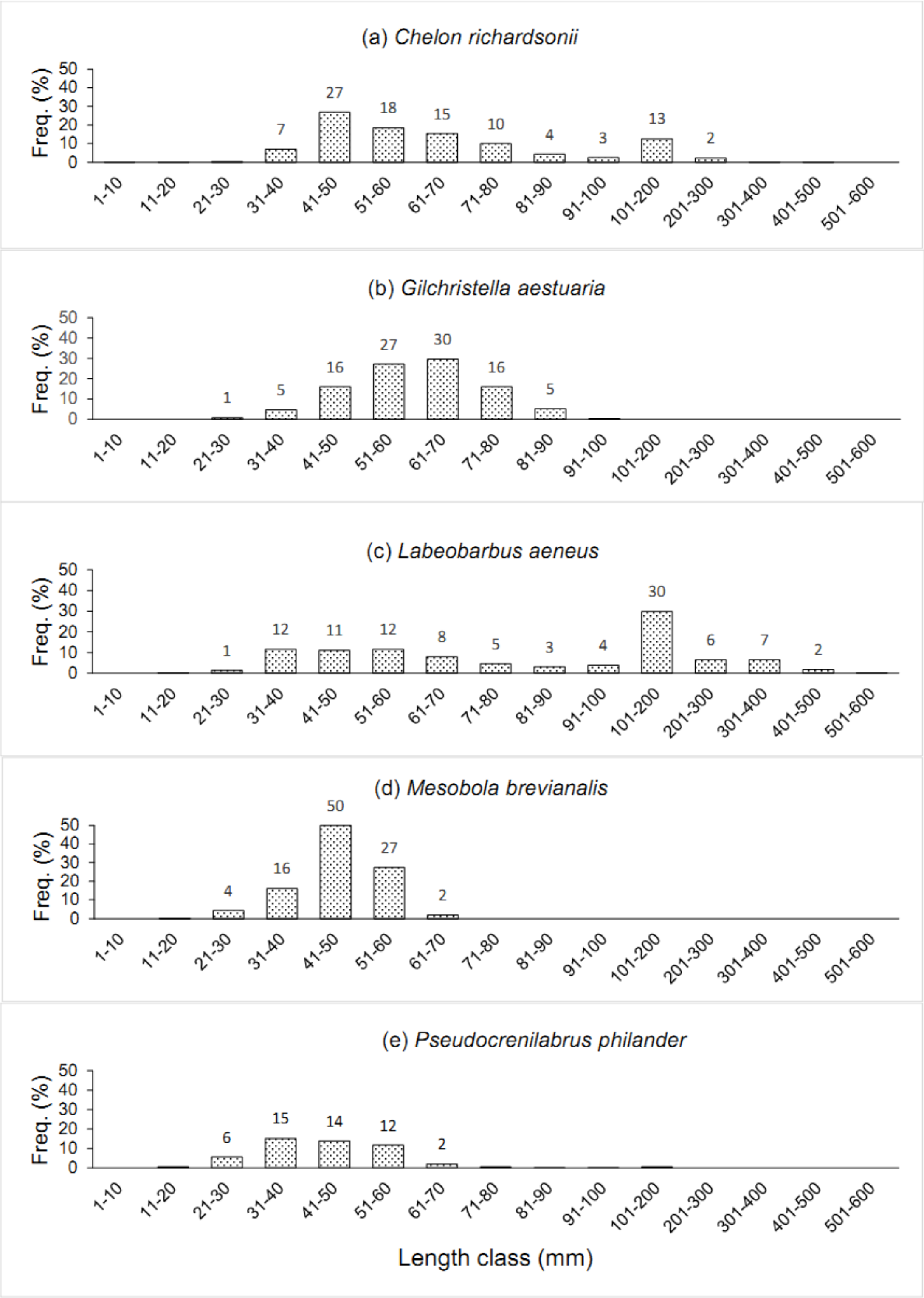
The length-frequency distributions (LFDs) of all five species did not vary significantly seasonally (high-flow and low-flow) ($p > 0.05$). As a result, the length-frequency distributions of specific species were grouped. The percentage LFDs of all freshwater species differs significantly along the OREC ($p < 0.05$) but not for the marine and estuarine species ($p > 0.05$). The marine *C. richardsonii* and estuarine *G. aestuaria* were widely distributed along the entire OREC (Fig. 1). The percentage length-frequency curvesof *C. richardsonii*, *G. aestuaria*, *P. philander* and *M. brevianalis* are classical bell-shape except for *L. aeneus* which indicates a bimodal shape with two cohorts (Fig. 2a, Fig. 2b, Fig. 2c, Fig. 2d, & Fig. 2e).

The distribution of *C. richardsonii* varied between length classes (H = 144.37, d.f. = 13, $p < 0.001$), but not along the OREC (H = 2.12, d.f. = 5, $p > 0.001$). The LFDs showed that the fishes of 41 - 50 mm length category occurred in the highest percentage in the OREC (Fig. 2a). Similarly, the distribution of *G. aestuaria* varied amongst the different length classes (H = 73.29, d.f. = 9, $p < 0.001$) but not along the length of the river (i.e. salinity gradient; Fig. 3) (H = 4.35, d.f. = 5, $p > 0.50$).

The distribution of *L. aeneus* differs significantly amongst the different length classes (H = 85.13, d.f. = 14, $p < 0.001$) and along the OREC (H = 23.44, d.f. = 5, $p < 0.001$). Observed trends in the distribution of

L. aeneus amongst length classes showed that fishes of 101 to 200 mm were commonly recorded in highest percentage, followed by length classes of 31 - 60 mm (Fig. 2). A few adults were caught in the lower reaches of the estuary (i.e. mesohaline waters; Fig. 3), whilst juveniles showed an upstream shift into the river (Fig. 3).

The percentage length-frequency distribution of *M. brevianalis* (H = 43.05, d.f. = 7, $p < 0.001$) and *P. philander* (H = 59.79, d.f. = 10, $p < 0.001$) differ significantly between length classes and along the OREC (H = 11.51, d.f. = 5, $p < 0.001$); (H = 14.99, d.f. = 5, $p < 0.001$), respectively. The two freshwater species also showed an upstream shift into the freshwater (Fig. 3). For *M. brevianalis* the highest percentage of length-frequency distribution was recorded at 41 - 50 mm length class, followed by 51 - 60 mm and 31 - 40 mm, respectively (Fig. 2d).



(a) *Chelon richardsonii*

(b) *Gilchristella aestuaria*

(c) *Labeobarbus aeneus*

(d) *Mesobola brevianalis*

(e) *Pseudocrenilabrus philander*

Figure 2. The percentage distribution of individual fish species amongst different length classes recorded in the Orange River Estuary Continuum, 2004-2018.

The percentage LFDs of *P. philander* was recorded the highest in fishes of 31 - 40 mm, 41 - 50 mm and 51 - 60 mm length classless, respectively (Fig. 2). The two freshwater species were relatively abundant towards the freshwater reaches of the river, and only a few numbers of fish was caught in the estuary, especially for *M. brevianalis*. *Mesobola brevianalis* and *P. philander* were not recorded at the mouth of the estuary in polyhaline waters (Fig. 3).

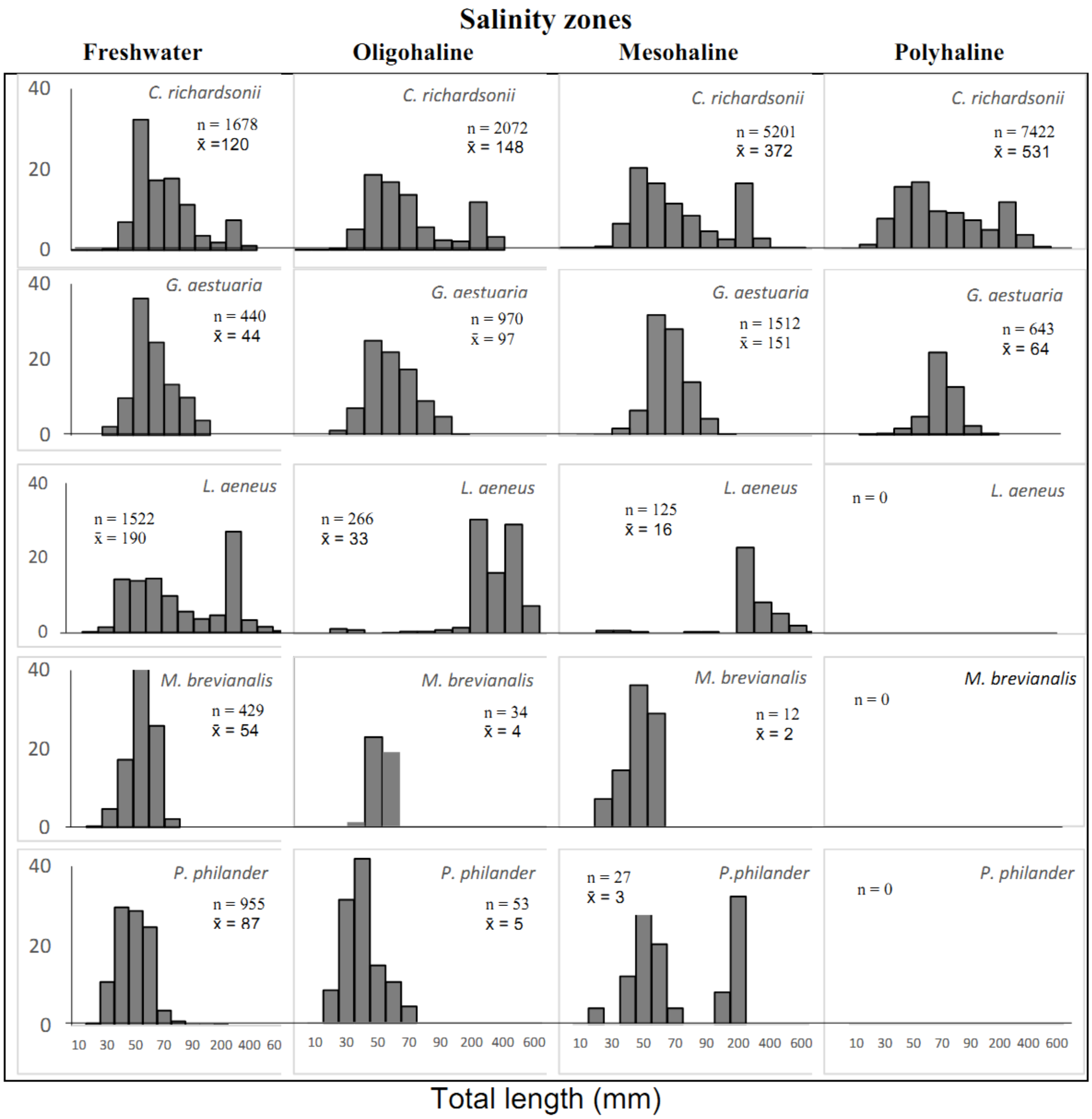


Figure 3. The percentage length-frequency distribution of fish species recorded at different salinity zones in the Orange River Estuary Continuum, 2004 - 2018.

Sampling sites (Fig. 1) were categorized into salinity zones: freshwater: site 10-18; oligohaline: site 8-9; mesohaline: site 3-7; polyhaline: site 1-2 (Fig. 3). All five species showed a significant positive correlation between salinity and length (Table 3).

Table 3. Spearman's rank correlation between changes in salinity ranges and body size (total length; TL, mm) of each species.

Species	Salinity ranges vs TL	
	r	*p-value*
Chelon richardsonii	0.254	0.000***
Gilchristella aestuaria	0.304	0.000***
Labeobarbus aeneus	0.576	0.000***
Pseudocrenilabrus philander	0.453	0.000***
Mesobola brevianalis	0.313	0.018**

*, **, significant at $P < 0.05$ and < 0.01.

4. Discussion

Length-frequency distribution analysis plays a significant role in understanding the size structure of fish populations (Johnson & Tamatamah, 2013). It is fundamental in estimating growth, recruitment, geographical isolation, reproduction and strength of species interactions among fish populations (Begg, 2005; Johnson & Tamatamah, 2013; Stevenson et al., 2016). *Chelon richardsonii* and *G. aestuaria* are planktivores, but the latter is also detritivore with a high detritus, benthic diatom intake (Pillay et al., 2012), hence their abundance (numerically) in the OREC can be partly related to the availability of planktonic food resources associated with chlorophyll-*a* productivity (Snow, 2013).

The euryhaline *C. richardsonii* and estuarine *G. aestuaria* were the two dominant species found widely distributed in all salinity zones. *Chelon richardsonii* can live or survive in wide ranges of salinities (0 – 44), varying from fresh to brackish and marine waters (Whitfield et al., 1981; Seaman & van As 1998). The dominance of the juvenile component of *C. richardsonii* present in the OREC indicates that the study area is probably providing suitable conditions (i.e. physiological and food resources) for all the stages in the life cycle of the species.

The LFDs of *G. aestuaria* was bell-shaped and symmetrical, with the number of individuals decreasing towards the smallest and the largest body size classes (Fig. 2). This observation is typical in most animal taxa (Gaston & Blackburn, 2000). *Gilchristella aestuaria* lives and breeds in estuaries throughout the year with a peak in spring and early summer (Haigh & Whitfield, 1993; Skelton, 2001). They are also known to breed in freshwater (Skelton, 2001).

The wide distribution of *G. aestuaria* along the river-estuarine continuum might be attributed to preferred salinity range in estuaries which is the River Estuarine Interface (REI zone) of 0 - 10 (Lamberth et al., 2008). The REI region is defined as that part of an estuary where the river and estuarine waters mix, and where the vertically integrated salinity is usually less than 10 (Whitfield & Wood, 2002). Although *G. aestuaria* is not limited by salinity except for hyper-salinity above 40, its length-distribution was positively.correlated with salinity in the OREC, demonstrating that juveniles fishes were less salt-tolerant to high salinity level.

Freshwater species were numerically abundant in fresh and oligohaline water but poorly represented in salinity above mesohaline. Most freshwater species are known to avoid salinity above mesohaline waters due to their inability to develop chloride cells in gill filament epithelia and lack of other osmoregulatory adaptation present in euryhaline fishes (Whitfield, 2015). The majority of *M. brevianalis* and *P. philander* species captured in this study were mature adults from the length category 41 - 50 mm and 31 – 60 mm, respectively, this is partly a function of mesh selectivity. There were fewer fishes captured in the lower reaches of the estuary compared to those recorded upstream in the river reach. A considerable decline in the abundance of *M. brevianalis* and *P. philander* downstream into the estuarine region indicates that the estuarine environment is not preferred habitat for these two freshwater species.

The absence of small size length (<10 mm) of *L. aeneus* captured in the OREC is due to mesh selectivity; hence there is ample spawning habitat (gravel beds) in the upper reaches of the river from site 10 - 18 (~10 - 35 km; Fig. 1). When *L. aeneus* are ready to spawn, they migrate upstream to the spawning sites, where there is running water over the gravel (Jubb, 1962), but has also been observed in still waters over gravel beds in Hardap dam, Namibia (Groenewald, 1951 as cited in Gaigher, 1976). Breeding fish make hollows in gravel with their snouts and tail fins, into which the eggs are deposited (Groenewald, 1951). Fishes with length categories between 101 to 200 mm were commonly recorded, followed by length classes of 31 – 60 mm (possibly spawned in the last month or two before sampling). Altered flow regime associated with inadequate water management of the river system may be impacting the fish species abundance in the OREC.

No records of *L. aeneus* were captured at the proximity of the estuary mouth, particularly in polyhaline and euhaline waters (Fig. 3). *Labeobarbus aeneus* predominantly inhabits shallow (< 1 m) fast-flowing habitats (Eccles, 1986) and its distribution is restricted by water temperature (De Villiers & Ellender, 2007). Its CPUE amplified upstream into the river where their catches remained relatively the same. Therefore, during low-flow, its distribution is governed by the intrusion of cold seawater at the mouth of the estuary. Also, *L. aeneus* penetration into estuaries from the rivers is based on their salinity tolerance (Whitfield, 1998), hence this can be another reason for the absence of species (i.e. mostly juveniles) close to the mouth of the estuary. However, during high-flow periods, *L. aeneus* has been recorded at the mouth and occasionally caught by anglers fishing the surf for kob (*Argyrosomus inodorus*), the surf is often low salinity at those times (S.J Lamberth, personal communication, August 11, 2019).

This study supports evidence from other studies (e.g. Chervinski, 1984; Lisboa et al., 2015; Sallam et al., 2017) confirming a positive correlation between salinity and fish length, demonstrating that juvenile fishes are less salt-tolerant than the adults (Table 3). This is because juvenile fish are sensitive to environmental challenges, resulting in physiological limitations (McCormick et al., 2013). Salinity is regarded as a critical environmental factor for all aquatic organisms (Whitfield, 1999; Harrison & Whitfield, 2006; Smyth & Elliot, 2016), responsible for causing salinity stress to fishes and, if not compensated for, it interferes with physiological homeostasis and routine biological processes (Kültz, 2015). As a result, most stenohaline fishes are limited to environments of stable salinity while euryhaline fishes inhabit environments with variable salinity (Wurts, 1998; Kültz, 2015)

Moreover, salinity can act synergistically or antagonistically with other environmental stressors, producing a dynamic and changing environment (Smyth & Elliott, 2016). For example, in most South African estuaries, temperature and salinity both play a substantial role in determining the biogeographical distribution of fishes (Harrison & Whitfield, 2006) and structuring fish communities (Whitfield, 1999).

Overall declining or limited individuals with body sizes below 10 mm caught in the OREC may be influenced by the mesh size, which determines the size of fish seined. The bag (cod-end) and stretched mesh of seine net used were 10 mm. Another influential factor is predation which is the principal cause of mortality (Stevenson et al., 2016). As with most teleost's, the mortality rate is high and variable during the early life stage of the species (Olafsson et al., 1994; Houde, 2002) and after that, the relative strength of the size class is more or less set, it then decreases through a relatively constant natural mortality, but does not change dramatically. The size of the prey is fundamental to predation risk, and most predators can only ingest prey up to a specific maximum size (Kerfoot & Sih, 1987; Nilsson & Brönmark, 2000). These and other dynamics may explain the observed length-frequency distribution patterns of species in the OREC. Overlapping length-frequency distribution observed among the dominant species in the OREC may suggest possible resource partitioning. Feeding ecology study using stable isotope analysis revealed overlap in the feeding behaviour of these species (Nashima et al., 2020), with possibilities that these species are exploiting food resources which may be derived from the same or similar food sources.

This study precluded cohort analysis and precise estimates of spawning times or migration of these populations due to low sampling frequency (twice annually). For the entire study period, there was no high-flow event during any of the sampling trips. This and other factors could explain the non-significant observation in the length-frequency distribution of fishes between seasons. At least part of this can be attributed to regulation of the river system, in particular, the Gariep and Vanderkloof dams (Anderson et al., 2003) which significantly reduced the amount of water flowing downstream to the estuary.

5. Conclusion

This study highlighted that marine *C. richardsonii* and estuarine *G. aestuaria* can secure refuge in the lower OREC. This capacity is, however, limited to freshwater taxa which were abundant in the upper reaches of the river. The movement of freshwater species into the lower reaches of the estuary is likely to have been influenced by the inability to tolerate high salinity. There is no seasonal variation in the length-frequency distribution of any of the species considered. This could be attributed to the regulation of the river system, which significantly reduced the amount of water flowing downstream to the estuary. Spatial differentiation in size-frequency distribution varied for all freshwater species (i.e. *L. aeneus*, *M. brevianalis* and *P. philander*) but not for the marine *C. richardsonii* and estuarine *G. aestuaria* species along the river-estuarine continuum. Findings of this study confirmed a positive correlation between salinity and fish length, demonstrating that juveniles of selected fish, in particular, freshwater species are less salt-tolerant to high salinity level. Small-sized individuals of < 10 mm of all species in the OREC were under-represented but most likely due to gear selectivity, not predation. Future research should categorise the length-frequency distribution of fishes based on sexes as species may have different maturity sizes.

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Disclosure of conflict of interest

The author declares no conflict of interest

References

Andem, A. B., George, U. U., & Eyo, V. O. (2013). Length Frequency Distribution of (*Chrysichthys nigrodigitatus*) (Lecepede, 1803) (Chrysichthys, Bagridae) from Itu Head Brigde, in Akwa Ibom State, Nigeria. *International Journal of Science and Research*, *2*(9), 2319–7064.

Anderson, M. D., Kolberg, H., Anderso, P. C., Dini, J., & Abrahams, A. (2003). Water bird populations at the Orange River mouth from 1980–2001: a re-assessment of its Ramsar status. *Ostrich*, *74*(3–4), 159–172.

Anni, I. S. A., Bianchini, A., Barcarolli, I. F., Junior, A. S. V., Robaldo, R. B., Tesser, M. B., & Sampaio, L. A. (2016). Salinity influence on growth, osmoregulation and energy turnover in juvenile pompano *Trachinotus marginatus* Cuvier 1832. *Aquaculture*, *455*, 63-72.

Basson, M. S., & Rossouw, J. D. (2003). *Lower Orange Water Management Area: overview of water resources availability and utilisation*. DWAF Report No: P WMA 141000/0010203. Pretoria, South Africa.

Begg, G. A. (2005). Life History Parameters. In S. X. Cadrin, K. D. Friedland & J. R. Waldman (Eds.), *Stock Identification Methods, Applications in Fishery Science* (pp. 119–150). San Diego: Academic Press.

Chervinski, J. (1984). Salinity tolerance of young catfish, *Clarias lazera* (Burchell). *Journal of fish biology*, *25*(2), 147-149.

Davies, B. R., O'Keefe, J. H., & Snaddon, C. D. (1993). *A synthesis of the ecological functioning, conservation and management of South African river ecosystems.* Pretoria: Water Research Commission Report No. TT 62/93.

De Villiers, P., & Ellender, B. (2007). Status of the Orange-Vaal Smallmouth Yellowfish *Labeobarbus aeneus* (Burchell, 1822). In D. N. Impson, I. R. Bills & L. Wolhuter (Eds.), *Technical Report on the state of yellowfishes in South Africa 2007* (pp. 77–92). WRC Report No. KV 212/08.

DWAF (Department of Water Affairs and Forestry). (1999). *Orange River Re-planning Study.* Report Number: PD 00/00/5295. Pretoria: Government Printers.

Eccles, D. H. (1986). Diet of the cyprinid fish *Barbus aeneus* (Burchell) in the P.K. le Roux Dam, South Africa, with special reference to the effect of turbidity on zooplanktivory. *South African Journal of Zoology, 21*(3), 257–263.

Froese, R., & Pauly, D. (2018). FishBase. Retrieved 18 July 2018, from www.fishbase.org

Gaigher, I. G. (1976). The Reproduction of *Barbus Cf. Kimberleyensis* (Pisces, Cyprinidae) in the Hardap Dam, South West Africa. *Zoologica Africana*, *11*(1), 97–110.

Gaston, K. J., & Blackburn, T. M. (2000). *Pattern and Process in Macroecology*. Oxford: Blackwell Science.

Groenewald, A. A. V. J. (1951). The Vaal River yellowfish (*Barbus aeneus*). *Fauna Flora, Pretoria*, *2*, 16–23.

Haigh, E. H., & Whitfield, A. K. (1993). Larval development of *Gilchristella aestuaria* (Gilchrist, 1914) (Pisces: Clupeidae) from southern Africa. *South African Journal of Zoology*, *28*(4), 168–172.

Harrison, T. D., & Whitfield, A. K. (2006). Temperature and salinity as primary determinants influencing the biogeography of fishes in South African estuaries. *Estuarine, Coastal and Shelf Science*, *66*(1–2), 335–345.

Houde, E. D. (2002). Chapter 3. Mortality. In: Fuiman, L. A. and R. G. Werner (eds.), *Fishery science: The unique contribution of early life stages*. Blackwell Scientific Publishing, Oxford.

Johnson, M. G., & Tamatamah, A. R. (2013). Length frequency distribution, mortality rate and reproductive biology of Kawakawa (*Euthynnus affinis-cantor*, 1849) in the coastal waters of Tanzania. *Pakistan Journal of Biological Sciences*, *16*(21), 1270–1278.

Jubb, R. A. (1962). Yellowfishes of the Orange–Vaal River system. *Piscator*, *53*, 107–109.

Kerfoot, W. C., & Sih, A. (1987). *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover and London.Kidder III, G. W., Petersen. C. W., & Preston, R. L. (2006). Energetics of osmoregulation: II. Water flux and osmoregulatory work in the euryhaline fish, *Fundulus heteroclitus*. *Journal of Experimental Zoology*, *Part A: Comparative Experimental Biology*, *305*(4), 318-327.

Kültz, D. (2015). Physiological mechanisms used by fish to cope with salinity stress. *Journal of Experimental Biology*, *218*(12), 1907-1914.

Lamberth, S. J. (2003). *Draft specialist report on the fish of the Orange River estuary. Orange River Estuary Rapid Ecological Reserve*. Final Draft. Unpublished. 12pp.

Lamberth, S. J., van Niekerk, L., & Hutchings, K. (2008). Comparison of, and the effects of altered freshwater inflow on, fish assemblages of two contrasting South African estuaries: the cool-temperate Olifants and the warm-temperate Breede. *African Journal of Marine Science*, 30(2), 311-336.

Lisboa, V., Barcarolli, I. F., Sampaio, L. A., & Bianchini, A. (2015). Effect of salinity on survival, growth and biochemical parameters in juvenile Lebranch mullet *Mugil liza* (Perciformes: Mugilidae). *Neotropical Ichthyology*, *13*(2), 447-452.

McCormick, S. D., Farrell, A. P., & Brauner, C. J. (Eds.). (2013). *Fish physiology: euryhaline fishes*. Oxford: Academic Press.

Nashima, F. P., Strydom, N. A., Connan, M., & Lamberth, S. J. (2020). Stable isotopes reveal linkages among fish species utilizing the Orange River Estuary Continuum. *Food Webs*. e00145.

Næsje, T. F., Hay, C. J., Nickanor, N., Koekemoer, J., Strand, R., & Thorstad, E. B. (2007). *Fish populations, gill net catches and gill net selectivity in the Lower Orange River, Namibia, from 1995 to 2001*. NINA Report 231.

Nilsson, P. A., & Brönmark, C. (2000). Prey vulnerability to a gape-size limited predator: Behavioural and morphological impacts on northern pike piscivory. *Oikos*, *88*(3), 539–546.

Olafsson, E. B., Peterson, C. H., & Ambrose, W. G. (1994). Does recruitment limitation structure populations and communities of macroinvertebrates in marine soft sediments - the relative significance of presettlement and postsettlement processes. *Oceanography and Marine Biology Annual Review*, *32*, 65–109.

ORASECOM (Orange–Senqu River Commission). (2013). *Estuary and Marine EFR assessment, Volume 2: Orange Estuary EFR:* Supporting Information. *Research Project on Environmental Flow Requirements of the Fish River and the Orange-Senqu River Mouth*. UNDP-GEF: Orange-Senqu Strategic Action Programme, Technical Report No. 33.

Pillay, D., Williams, C., & Whitfield, A.K. (2012). Indirect effects of bioturbation by the burrowing sandprawn *Callichirus kraussi* on a benthic foraging fish, *Liza richardsonii*. *Marine Ecology Progress Series*, *453*, 151-158.

Pope, K. L., Lochmann, S. E., & Young, M. K. (2010). Methods for assessing fish populations. In W. A. Hubert & M. C. Quist (Eds.), *Inland Fisheries Management in North America*, (3rd ed., pp. 325–351). Bethesda, Maryland: American Fisheries Society.

Ramollo, P. P. (2011). Freshwater fish abundance and distribution in the Orange River South Africa. *Journal of Fisheries International*, *6*(1), 13–17.

Roy, K., & Martien, K. K. (2001). Latitudinal distribution of body size in north-eastern Pacific marine bivalves. *Journal of Biogeography*, *28*(4), 485–493.

Sallam, G. R., Fayed, W. A, El-Absawy, M. A, Aly, H. A. & El-Greisy, Z. A. (2017). Red tilapia broodstocks and larval production under different water salinities without acclimation. *Journal of Aquaculture Research Development*, *8*, 476.

Seaman, M. T., & van As, J. G. (1998). *The environmental River mouth as reflected by the fish community*. WRC Report No. 505/1/98, South Africa. 73pp.

Skelton, P. H. (2001). *A Complete Guide to the Freshwater Fishes of Southern Africa*. Pretoria: Struik Publishers.

Smith, M. M., & Heemstra, P. C. (1986). *Smith's sea fishes*. Berlin: Springer-Verlag.

Snaddon, C. D., Davies, B. R., & Wishart, M. J. (1999). *A global overview of inter-basin water transfer schemes, with an appraisal of their ecological, socio-economic and socio-political implications and recommendations for their management*. Pretoria: Water Research Commission Report No: TT 120/00. 114pp.

Snow, G. (2013). Chapter 3: Estuarine Microalgae Report. In *Volume 2: Orange Estuary Supporting Information. Orange-Senqu River Commission Research Project on Environmental Flow Requirements of the Fish River and the Orange-Senqu River Mouth. Technical Report 33. Ver. 1, 1 May 2013.* UNDP-GEF Orange-Senqu Strategic.

Stevenson, C. F., Demes, K. W., & Salomon, A. K. (2016). Accounting for size-specific predation improves our ability to predict the strength of a trophic cascade. *Ecology and Evolution*, *6*(4), 1041–1053.Strydom, N. A., Whitfield, A. K., & Wooldridge, T. H. (2003). The role of estuarine type in characterizing early stage fish assemblages in warm temperate estuaries, South Africa. *African Zoology*, *38*(1), 29–43.

Smyth, K., & Elliott, M. (2016). Effects of changing salinity on the ecology of the marine environment. In M. Solan, & N. Whiteley (Eds.), *Stressors in the Marine Environment: Physiological and ecological responses; societal implications*, 161-174. Oxford: Oxford University Press.

van Langenhove, G., Amakali, M., & De Bruine, B. (1998). Variability of flow regimes in Namibian rivers: natural and human induced causes. *IAHS Publication*, 252, 455-462.

van Niekerk, L., & Turpie, J. K. (2012). *South African National Biodiversity Assessment 2011*. Stellenbosch: Estuary Component. CSIR Report Number CSIR/NRE/ECOS/. Council for Scientific and Industrial Research.

van Niekerk, L., Huizinga, P., Aljaard, S., & Theron, A. (2003). *Orange Estuary abiotic specialist report: hydrodynamics, water quality and sediment dynamics*. CSIR Report ENV-S-C2003-114.

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, *22*(6), 323–330.

Whitfield, A. K, Blaber, S. J. M. & Cyrus, D. P. (1981). Salinity ranges of some southern African fish species occurring in estuaries. *South African Journal of Zoology*, *16*(3), 151–155.

Whitfield, A. K. (1998). *Biology and Ecology of Fishes in Southern Africa Estuaries* (Vol. 2). Grahamstown, South Africa: Ichthyological Monographs of the J.L.B. Smith Institute of Ichthyology.

Whitfield, A. K. (1999). Ichthyofaunal assemblages in estuaries: A South African case study. *Reviews in Fish Biology and Fisheries*, *9*(2), 151–186.

Whitfield, A. K. (2015). Why are there so few freshwater fish species in most estuaries? *Journal of Fish Biology*, *86*(4), 1227–1250.

Whitfield, A. K., & Wood, A. D. (eds.) (2002). *Studies on the River-Estuary Interface Region of Selected Eastern Cape Estuaries*. Water Research Commission Report No 756/2/02. 314pp.

Williams, A. J. (1986). Wetland birds at the Orange River mouth and their conservation significance. *Bontebok*, *5*, 17-23.

Woodward, G., Ebenman, B., Emmerson, M. C., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2006). Body Size Determinants of the Structure and Dynamics of Ecological Networks: Scaling from the Individual to the Ecosystem. In *Dynamic Food Webs*. Food Web Symposium 2003, London: Elsevier.

Wurts, W. A. (1998). Why can some fish live in freshwater, some in salt water, and some in both. *World Aquaculture*, *29*(1), 65.

Zhang, Y., & Payne, J. L. (2012). Size-frequency distributions along a latitudinal gradient in Middle Permian Fusulinoideans. *PLoS ONE*, *7*(6), e386.