

fishes. This study also suggested that grazing may have been important in determining the temporal variation observed in epiphyte biomass. Experimental exclosures and enclosures have shown that invertebrate biomass was the main factor influencing epiphyte biomass, with an increase in epiphyte biomass being linked to a decrease in invertebrate grazers and vice versa (Cattaneo 1983; Schanz et al. 2002). Epiphyte biomass was significantly greater in winter than in spring in this study (Chapter 4), which may be indicative of decreased grazing occurring during this season. In Chapter 5 of this study, it was observed that the polychaete *Spirorbis* sp. was significantly greater in summer than in winter and spring, with it being completely absent from seagrass blades during winter. The highest epiphyte biomass was observed in winter, which corresponds to the decrease in *Spirorbis* sp. on seagrass blades during this season. In Chapter 5, it was also observed that the percentage cover of epibionts on seagrass blades, was significantly greater in spring and summer than in winter. In Chapter 4, the species richness of epiphytic diatom taxa, was the lowest during summer (5 species), this could be explained by the high density of *Spirorbis* sp. during summer in addition to the greater percentage cover of epibionts on seagrass blades during this season.

The seagrass habitat has been identified as a core nursery area for *R. holubi* as it provides an abundance of food resources and protection from predators, which allows high specific growth rates and survival of juveniles respectively (Leslie et al. 2017; James et al. 2019). The significantly higher relative abundance of *R. holubi* observed in *Z. capensis* seagrass compared to *Spartina maritima* salt marsh and sand flats by Leslie et al. (2017) in the Bushmans Estuary, suggests that seagrass supports more *R. holubi* juvenile recruits to adult populations. This is due to relative abundance being related to density and studies using higher densities of juvenile fish as important indicators of emigration and recruitment (Minello 1999; Heck et al. 2003). Estuarine habitats may provide resources for juvenile fish without being considered a nursery habitat. This was observed in the sand flats habitat of the Bushmans Estuary by James et al. (2019), that provided invertebrate food resources for *R. holubi*, however, the low abundance of fish observed in this habitat, suggested that it was of limited value as a nursery for *R. holubi*. Refugia from predation likely diminishes the nursery potential of sand flats rather than food resource availability. The value of a critical estuarine nursery habitat depends on submerged aquatic vegetation providing optimum feeding and refuge opportunities, whilst also supporting a great diversity and abundance of fish and invertebrate species (Edworthy and Strydom 2016). Seagrass ecosystems are experiencing a global decline due to direct (mechanical damage, eutrophication and coastal development) and indirect (negative impacts of climate change

including erosion by sea-level rise and increased storms) anthropogenic disturbances, with the loss of these habitats leading to a decline in the abundance and diversity of juvenile fish that depend on these areas as nurseries (Duarte 2002). Sea-level rise is predicted to be a significant cause of seagrass decline (Hemminga and Duarte 2000). Erosion associated with sea-level rise and an increase in storm surges and high intensity rainfall events, will likely remove seagrass beds through uprooting (Duarte 2002). Sea-level rise will also affect the distribution of seagrass beds in estuaries due to changes in water depth and seawater intrusion (Short and Neckles 1999). Changes in the occurrence, spatial extent and functioning of estuarine macrophyte habitats in response to potential sea-level rise, therefore, needs to be documented in order to properly assess how sea-level rise will impact fish nursery areas (Whitfield 2017).

The evaluation of estuarine habitats as fish nursery areas has received significant attention in recent years, with the majority of studies suggesting that a habitat is a nursery due to supporting a higher density of juveniles relative to other habitats (Sogard and Able 1991; Rozas and Minello 1997; Bloomfield and Gillanders 2005). However, Beck et al. (2001), suggests that it is insufficient to use these single factors such as density, proof of feeding or protection from predators in isolation as proof of nursery provision and that multi-method approaches would provide better insight. Multi-method approaches quantifying growth, survival of juveniles and recruitment of sub-adults to adult populations are, however, rare due to the difficulty implementing them in a wide range of estuarine habitats. It is, therefore, necessary to develop more practical approaches to assess juvenile nursery habitats in estuaries. Future studies should focus on the nursery value of multiple habitat types in South African estuaries for *R. holubi* and other estuarine-dependent fish species. Studies should also focus on the nursery role of other submerged aquatic macrophyte species including *Potamogeton pectinatus* and *Ruppia cirrhosa*, occurring along the southern and eastern Cape coast of South Africa in addition to mangrove forests occurring along the east coast of South Africa northwards of the Nahoon Estuary, as little is known about the nursery value of these habitat types (Leslie 2016).

Estuaries are considered to be one of the most valuable aquatic ecosystems in the coastal zone attributed to their wide range of ecosystem services. Despite this, they are also one of the most degraded environments on earth due to being the focal points for human colonisation (Edgar et al. 2000). There is, therefore, widespread interest in the conservation and management of these coastal waters. Studies evaluating the nursery role of estuarine habitats, will provide insight on the nursery value of different habitat types, which will inform ecosystem management and conservation plans (Beck et al. 2001). The link between threatened estuarine habitats such as

seagrasses and the communities that depend on them, also highlights the need for an ecosystem-based management approach that incorporates interdependencies and facilitation between species (Hughes et al. 2009), which is essential for effective conservation.

An assessment of the epiphytic diatoms and macrofauna associated with *Z. capensis* beds in the middle reaches of the Swartkops Estuary in this study, would have been useful in identifying additional taxa that were not represented in the lower reaches. The composition of the epiphytic diatom and macrofauna communities were similar across all sites based on their location in the lower reaches of the estuary, so a broader study area (not confined to the lower reaches) would have incorporated a wider range of epiphytic diatom and macrofauna taxa. To further improve this study, an assessment of food availability during autumn would have been beneficial in a comparison of the temporal variation in the abundance and diversity of epiphytic diatom and macrofauna species, however, this was not possible due to the COVID-19 pandemic. Future studies should expand on the diatom assemblages associated with filamentous algae, which is abundant in the lower reaches of the Swartkops Estuary, as de Wet and Marais (1990), found that *Z. capensis* together with filamentous algae, comprised the major proportion of the seasonal dietary pattern of *R. holubi* juveniles in the Swartkops Estuary. Future studies should also assess the nursery value of the seagrass habitat for other estuarine-associated fishes including Cape silverside *Atherina breviceps*, estuarine round-herring *Gilchristella aestuaria* in addition to white seabream *Diplodus sargus*, that dominate this habitat in the Swartkops Estuary.

This study showed the importance of *Z. capensis* seagrass beds in providing an abundance of food resources for juvenile fish, with the loss of this habitat, further influencing the communities that depend on them. Human disturbances such as boating and bait digging have reduced *Z. capensis* area cover and biomass in South African estuaries. Boating can reduce seagrass cover through physical removal by propellers in addition to bank erosion and by increasing turbidity (Adams 2016). Trampling as a result of bait digging and pumping for mud and sandprawns, have caused localised extinction of *Z. capensis* in Langebaan Lagoon (Pillay et al. 2010). Trampling, sand excavation and scouring due to bivalve collection in addition to fishing gear, has also significantly reduced the extent of *Z. capensis* beds in Maputo Bay (Bandeira and Gell 2003). Swartkops Estuary has one of the largest subpopulations of *Z. capensis* in South Africa and, therefore, it is essential that this habitat is properly managed due to the important resources that it provides for juvenile marine fish, which is integral for their survival and recruitment to adult populations.

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Appendix

Appendix Table 1: Abundance (n cm⁻²) of epibiont taxa per site per season

Season	Site	Species Abundance (n cm ⁻²)		
		<i>Hiatula</i> sp.	<i>Assimineea ovata</i>	<i>Spirorbis</i> sp.
Winter	1	0	0	0
Winter	1	0	2	0
Winter	1	0	0	0
Winter	3	0	0	0
Winter	3	0	0	0
Winter	3	0	0	0
Winter	5	2	0	0
Winter	5	0	0	0
Winter	5	0	0	0
Spring	1	0	0	81
Spring	1	0	3	0
Spring	1	0	0	0
Spring	3	0	0	0
Spring	3	0	1	0
Spring	3	0	5	0
Spring	5	0	0	0
Spring	5	0	0	0
Spring	5	0	0	0
Summer	1	0	0	656
Summer	1	0	0	44
Summer	1	0	3	622
Summer	3	0	1	220
Summer	3	0	0	160
Summer	3	0	2	102
Summer	5	0	0	125
Summer	5	0	2	15
Summer	5	0	2	2

Appendix Table 2: Abundance (n cm⁻²) of mobile epifaunal taxa per site per season

		Species Abundance (n cm ⁻²)					
Season	Site	<i>Palaemon peringueyi</i>	<i>Nassarius kraussianus</i>	<i>Hymenosoma orbiculare</i>	Unid. mollusc 1	<i>Assimineea ovata</i>	<i>Paridotea ungulata</i>
Winter	1	0	0	0	0	10	0
Winter	1	0	0	0	0	0	0
Winter	1	0	0	0	0	0	0
Winter	3	7	0	0	0	0	0
Winter	3	0	0	0	0	0	0
Winter	3	0	0	0	0	0	0
Winter	5	0	0	0	18	0	0
Winter	5	0	0	0	0	0	0
Winter	5	0	0	0	0	0	0
Spring	1	0	0	0	0	8	0
Spring	1	0	0	0	0	5	5
Spring	1	0	0	0	0	0	0
Spring	3	0	0	0	0	0	0
Spring	3	0	0	0	6	0	0
Spring	3	0	6	0	0	0	0
Spring	5	0	0	0	0	0	0
Spring	5	0	0	0	0	0	0
Spring	5	0	0	0	0	0	10
Summer	1	0	0	0	0	0	0
Summer	1	0	0	0	0	0	0
Summer	1	0	0	0	0	0	0
Summer	3	0	7	0	0	0	0
Summer	3	0	6	0	0	0	0
Summer	3	0	0	0	0	0	0
Summer	5	8	0	0	0	0	0
Summer	5	0	0	10	10	0	0
Summer	5	0	8	0	0	0	0