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Habitat partitioning by juvenile fishes in a temperate estuarine nursery, South Africa

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Summary: Multiple habitats were investigated in a known fish nursery area to further understand habitat partitioning among juveniles in the lower reaches of the warm temperate, permanently open Swartkops Estuary, South Africa. Fishes were collected using a 30-m seine net with a mesh size of 10 mm in sand, mud, creek and vegetated habitat types. Each habitat type was sampled in two locations twice per season from February 2013 to January 2014. Shallow-water creeks and vegetated habitats with coverage of *Zostera capensis* and *Spartina maritima* were found to be important use areas for numerous solely estuarine and marine estuarine-dependent species. This was evidenced by the high species diversity, abundance and size range per species occurring in these habitats. Seasonal trends were similar to those in previous studies worldwide, where higher abundances of juveniles of marine estuarine-dependent species coincided with summer recruitment into estuarine nurseries. However, recruitment appears to begin as early as late winter in some species, a phenomenon probably linked to a warming climate. Both resident species and those utilizing the area as a nursery area show a large degree of plasticity in habitat use in the lower reaches of the estuary, which became apparent when multiple habitats were compared. The drivers of these patterns involve a complex interaction of species, habitat type, behaviour, feeding, predator avoidance and physico-chemical factors occurring in the estuary.

Keywords: Ichthyofauna; nursery grounds; community composition; estuary association; recruitment.

Segregación de hábitat en juveniles de peces en una región de cría de un estuario templado, Sudáfrica

Resumen: Con objeto de entender mejor la segregación de hábitats en juveniles de peces se investigaron múltiples hábitats en una zona de cría en la parte baja del estuario del Swartkops (Sudáfrica) (de tipo templado-cálido y abierto permanentemente). Los peces fueron recolectados con una red de cerco de 30 m, con malla de 10 mm de abertura, sobre fondos de arena, barro, arroyos y hábitats con vegetación. Cada tipo de hábitat se muestreó en dos lugares, dos veces por estación, de febrero 2013 a enero 2014. Se observó que los arroyos de aguas poco profundas y los hábitats con cobertura de *Zostera capensis* y *Spartina maritima* eran áreas importantes para numerosas especies exclusivamente estuáricas y para especies marinas dependientes de los estuarios. Esto se evidenció por la gran diversidad de especies, abundancia y rango de tallas de las especies que aparecieron. Las tendencias estacionales fueron similares a los de estudios anteriores en todo el mundo, donde las más altas abundancias de juveniles de las especies marinas que dependen de los estuarios coincidieron con el reclutamiento de verano dentro del estuario. Sin embargo, en algunas especies el reclutamiento parece comenzar más pronto, a finales del invierno, un fenómeno probablemente ligado al calentamiento climático. Tanto las especies residentes en el estuario como las que lo utilizan como área de cría muestran un alto grado de plasticidad en el uso del hábitat en la parte baja del estuario, que resulta evidente cuando se compararon varios hábitats. Los mecanismos impulsores de estos patrones implican una compleja interacción de especies, tipo de hábitat, comportamiento, alimentación, evasión de depredadores, y los factores físico-químicos del estuario.

Palabras clave: ictiofauna; áreas de cría; composición de la comunidad; asociación estuárica; reclutamiento.

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INTRODUCTION

Estuaries are highly successful nursery areas worldwide in an otherwise competitive environment where

refuge and food are premium (Whitfield 1999, Potter et al. 2015). Since multiple species co-exist in estuarine nursery areas, this presents clear evidence of successful niche differentiation and some level of successful

community co-existence. Co-existing species can differentiate niches through habitat partitioning for a multitude of reasons (Felley and Felley 1986, Welsh and Perry 1998) but this is seldom explored across a range of habitat types in estuarine ecosystems. This work examined a well-known estuarine fish nursery in warm temperate South Africa in order to further understand habitat partitioning among juvenile fishes. Early stage marine fishes recruit into estuarine nurseries typically in spring and summer to utilize the mosaic of available habitats in these systems (França et al. 2009) during certain life stages (Strydom 2015, Potter et al. 2015). Specific habitat preferences within these systems remain an area of interest for fish conservation worldwide (Beck et al. 2001, Able 2005, Strydom 2015). Fishes are likely to select those habitats, or a combination of habitats, that meet their physico-chemical requirements as well as provide abundant food resources and protection from larger predatory fishes (Courrat et al. 2009, França et al. 2009, Sheppard et al. 2011).

Much research has focussed on the value of refugia in estuaries, specifically mangroves (Nanjo et al. 2014) and eelgrass and/or seagrass habitats in both South Africa (Whitfield et al. 1989, Paterson and Whitfield 2000, Strydom 2003) and other estuarine zones around the world (França et al. 2009, Baillie et al. 2015). This work has also been supplemented with the inclusion of saltmarsh creeks as important refugia for juvenile fishes in estuaries (Le Quesne 2000, Paterson and Whitfield 2000, Jin et al. 2007). However, most studies involving habitat evaluation have only considered two habitats simultaneously (Weinstein and Brooks 1983, Sogard and Able 1991, Paterson and Whitfield 2000), sometimes with conflicting results on the value of certain habitat types for different species. Moreover, there is a paucity of work involving multiple habitat comparisons, including other substrata such as sand and mud (Sogard and Able 1991, Baillie et al. 2015).

In temperate South Africa, halophytic plant species such as seagrass (*Zostera capensis*) (Talbot and Bate 1987) and ricegrass (*Spartina maritima*) are widely distributed (Colloty et al. 2000) in the lower reaches of permanently open estuaries. Despite the known importance of these habitats, which support a high abundance and diversity of juvenile fishes due to their high productivity and structural complexity (Ter Morshuizen and Whitfield 1994, Martino and Able 2003, Sheppard et al. 2012), the value of vegetated areas relative to other adjacent habitat types on offer in estuarine nurseries leaves room for further enquiry.

Habitat use and preferences in young fishes utilizing estuarine nurseries is important for the elucidation of critical habitats for species and for conservation planning in estuaries worldwide (Beck et al. 2001). However, given conflicts in the literature, more information is needed to fully understand use patterns within estuarine nurseries.

The permanently open Swartkops Estuary on the warm temperate coast of South Africa provided an ideal study system for assessing habitat partitioning among juveniles fishes across a range of common habitat types that are typical in estuaries worldwide

and could serve as nurseries. The ecology of Swartkops Estuary fish fauna is well studied, with research on adults (Marais and Baird 1980), juveniles (Winter 1979, Beckley 1983) and larval stages (Strydom 2003, Strydom 2015) already undertaken.

The aim of this study was to assess the habitat partitioning in juvenile fishes in four abundant and well-defined habitat types, namely eelgrass/ricegrass vegetation stands, saltmarsh creeks, muddy substrata and sand substrata within the lower reaches of the estuary. It was hypothesized that species, particularly in the marine estuarine-dependent group that rely on estuaries as nurseries, will favour vegetated habitats, exhibiting a higher abundance and diversity of species, while lesser studied sand and mud substrata will show species-specific preferences (Connolly 1994, Gray et al. 1996). It is also hypothesized that the physico-chemical conditions within each habitat type will be distinct and that fishes will be associated with specific environmental conditions, particularly warmer temperatures.

MATERIALS AND METHODS

Study area

The study area was located in the lower reaches of the Swartkops Estuary (33°52'S; 25°38'E), on the warm temperate coastline of South Africa (Fig. 1). The permanently open estuary is approximately 16 km in length with a tidal range of <1.5 metres (Beckley 1983). The area experiences bimodal rainfall with peaks in autumn and spring (Whitfield 1998). The lower reaches of the estuary are characterized by extensive mudflats, salt marshes and large stands of submerged aquatic vegetation dominated by halophytic eelgrass *Zostera capensis* and ricegrass *Spartina maritima* (Talbot and Bate 1987, Colloty et al. 2000). The Tipper's Creek arm of the lower estuary (Fig. 1) supports the highest percentage (59%) of this vegetation (Talbot and Bate 1987).

Field sampling and laboratory analysis

Juvenile fishes were sampled in the lower reaches of the Swartkops Estuary in consecutive months, twice per season for a period of one year, spanning a total of eight sampling trips between March 2013 and January 2014. Fishes were collected in four habitat types, and each habitat type was sampled in two separate locations in the lower estuary. Each sampling trip was conducted on an incoming tide during the day. Fishes were sampled using a 30×1.5 m seine net (mesh size=10 mm) at eight sites accessed by boat in the lower 3 km of the estuary. Two replicate sites were selected to represent four predetermined habitat types: sand flats (S), mud flats (M), vegetated areas (V) and shallow estuarine creeks (C) (Fig. 1). The sand and mud habitat types were selected based on a consistent substrate of either sand or mud, respectively, with no vegetation cover. Estuarine creek habitats were characterized by shallow, unvegetated drainage channels that were permanently supratidal and surrounded by an adjacent *Sarcocornia* spp. saltmarsh

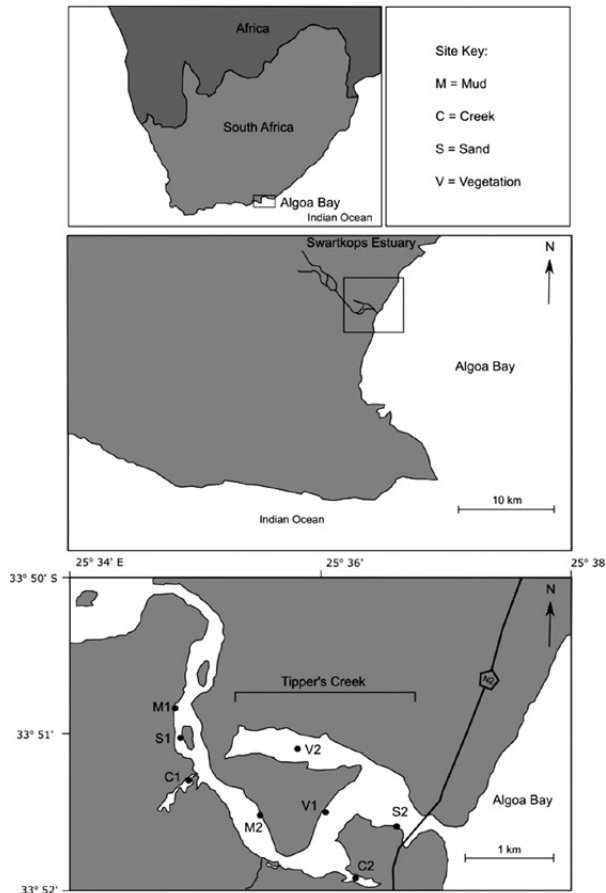


Fig. 1. – Geographic location of the Swartkops Estuary, South Africa, showing the location of the sampling sites in the lower 3 km of the estuary.

with a muddy substrate. The creek habitats differed from the mud habitats as they were not situated in the main channel but maintained tidal connectivity with the main channel. Vegetated habitats were selected in areas where there was consistent and dense coverage of submerged *Zostera capensis* and/or *Spartina maritima* ranging in cover from 90% to 100%. It was impossible to separate *Spartina maritima* and *Zostera capensis* vegetation as they co-occurred along the margins. Sampling of vegetated areas involved dragging a seine net directly through the vegetated areas. Sites were selected to ensure no overlap in habitat types and habitats were replicated to ensure that species occurrence patterns were persistent with habitat type, if applicable, and were treated as separate samples for analyses. Water sampling depth for fishes and physico-chemical variables at each site did not exceed 1.2 m on all sampling occasions. On each sampling occasion, temperature ($^{\circ}\text{C}$), total dissolved solids (TDS), salinity, pH, turbidity (NTU) and conductivity ($\mu\text{S}/\text{cm}$) were measured at each site 20 cm below the water surface using a YSI multi-parameter meter (660 V).

A single seine net haul was conducted at each site on each occasion. The seine net was manually operated by two to four people in a semi-circle over the selected habitat area and pulled perpendicular to the shoreline. Each fish was identified to the lowest possible taxon (Van der Elst and Wallace 1976, Smith and Heemstra

1995) and was measured to the nearest 1.0 mm total length (TL) in the field. All catches were expressed as catch per unit effort (CPUE) referring to the number of fishes per seine haul. All fish were released except for individuals that could not be positively identified. These were fixed in 10% formalin for later laboratory identification and measurement. All positively identified fishes were categorized into estuary association categories based on guild according to Potter et al. (2015). The categories applicable to this study include, in the marine category, the marine straggler group, the marine estuarine-opportunist group and the marine estuarine-dependent group. Within the estuarine category, the relevant groups include the solely estuarine group, the estuarine and marine group and the estuarine migrant group. Finally, catadromous species and freshwater estuarine-opportunist species also feature (Potter et al. 2015).

Statistical analyses

Descriptive and inferential statistics for both the physico-chemical and biological data were generated using the Statistica software package version 11, 2012. Data were assessed for normality using a visual normal probability plot and the Shapiro-Wilk test and homogeneity of variance was tested using Levene's test following square root and log transformations. All biological and physico-chemical data did not conform to parametric assumptions and therefore only non-parametric tests were used. Multivariate and diversity analyses were done using the Primer statistical package version 6.1 (2001) (Clarke and Gorley 2001).

Spatial and seasonal variability in temperature ($^{\circ}\text{C}$), TDS, salinity, pH, turbidity (NTU) and conductivity ($\mu\text{S}/\text{cm}$) were assessed using a Kruskal-Wallis test by rank. A Kruskal-Wallis test was also used to test for differences in fish abundance among habitats and seasons. Species included in these analyses (dominant species) were identified as those that showed a total catch of more than 40 individuals throughout the study period in order to allow for a large enough sample size. Species showing significant habitat partitioning were explored for relationships with environmental variables also showing a significant difference between habitats using multiple linear regression. Shannon-Wiener diversity indices (H') were compared among habitats and seasons using a non-parametric Kruskal-Wallis test.

For community analysis, abundance data were transformed by $\log(x+1)$ and grouped by both habitat type and season for the multivariate analyses. This transformation was used to reduce the contribution of highly abundant species. Abundance data were grouped into a similarity matrix using the Bray-Curtis similarity measure. A 3-D non-metric multidimensional scaling (nMDS) plot of abundance in each habitat type was generated. Species that were not frequently caught during the study period (caught on less than three occasions) and sites that showed zero catch during the study period were excluded from the nMDS so that clear community trends could be observed. A two-way crossed ANOSIM analysis was conducted to

Table 1. – Summary statistics of physico-chemical variability among the four habitat types and seasons in the Swartkops Estuary, February 2013 - January 2014. Statistics represented as mean; range (minimum - maximum).

	Creek	Mud	Sand	Vegetation
Autumn				
Temperature	20.17 (17.25-23.28)	20.67 (18.60-22.74)	20.70 (17.31-23.75)	20.29 (17.25-23.78)
TDS	26.91 (11.85-34.95)	28.10 (22.90-33.98)	29.56 (20.78-35.22)	33.63 (32.03-34.9)
Salinity	26.85 (10.82-35.56)	27.94 (22.40-34.46)	29.39 (19.90-35.64)	33.82 (32.05-35.50)
pH	8.29 (8.03-8.47)	8.10 (8.06-8.17)	8.22 (8.05-8.45)	8.39 (8.17-8.58)
Turbidity	9.70 (3.50-20.40)	13.70 (11.00-52.26)	6.05 (2.20-15.20)	4.35 (0.40-9.50)
Conductivity	41.42 (18.80-53.76)	43.26 (35.28-52.26)	45.37 (31.94-53.87)	51.69 (49.85-53.69)
Winter				
Temperature	15.81 (14.36-17.67)	14.34 (13.21-15.42)	16.09 (13.57-18.20)	17.11 (16.08-18.13)
TDS	26.01 (19.74-32.63)	23.36 (21.06-25.5)	26.98 (19.78-32.76)	30.45 (27.40-32.44)
Salinity	25.68 (18.83-33.1)	22.74 (20.31-25.04)	26.60 (18.93-32.23)	30.48 (27.09-32.73)
pH	7.76 (7.32-8.27)	7.78 (7.60-7.95)	7.66 (6.98-8.05)	7.79 (7.14-8.10)
Turbidity	8.20 (1.70-14.00)	6.90 (0.00-21.00)	1.05 (0.00-2.40)	2.72 (0.00-6.10)
Conductivity	39.74 (29.86-49.67)	32.56 (18.57-39.15)	41.59 (30.43-49.60)	42.55 (27.52-50.33)
Spring				
Temperature	18.95 (16.72-20.82)	18.78 (15.81-21.91)	18.58 (15.16-21.62)	19.05 (16.59-21.34)
TDS	29.93 (24.46-35.32)	27.66 (22.87-30.33)	29.89 (24.03-35.35)	33.78 (31.80-25.36)
Salinity	29.98 (23.91-36.00)	27.48 (22.2-30.37)	29.85 (14.93-35.52)	34.35 (32.50-36.01)
pH	6.67 (6.45-7.54)	6.06 (6.20-7.30)	6.79 (5.45-6.92)	6.55 (5.80-7.20)
Turbidity	16.65 (0.30-39.5)	9.00 (1.60-21.00)	0.70 (0.80-4.30)	5.60 (1.50-10.10)
Conductivity	45.96 (37.64-54.32)	37.40 (24.9-46.67)	46.38 (24.44-53.51)	51.95 (48.90-54.36)
Summer				
Temperature	25.01 (21.47-27.86)	25.32 (22.65-27.81)	24.95 (22.37-28.31)	25.26 (22.37-27.86)
TDS	24.67 (14.09-34.85)	21.99 (12.39-27.77)	27.00 (15.99-34.87)	33.22 (30.32-24.44)
Salinity	24.73 (13.04-35.47)	21.39 (11.42-27.59)	26.82 (35.53-14.93)	33.39 (30.12-35.06)
pH	6.50 (6.19-6.69)	6.57 (5.69-7.57)	6.14 (5.45-6.92)	6.68 (5.72-7.35)
Turbidity	9.65 (1.20-18.80)	7.47 (2.70-16.20)	2.70 (0.80-4.30)	6.22 (1.10-11.50)
Conductivity	38.69 (21.76-53.65)	33.83 (19.07-42.93)	41.43 (24.44-53.51)	50.89 (46.53-53.00)

assess habitat and seasonal similarities in community composition and a two-way crossed SIMPER analysis by Bray-Curtis similarity was used to assess individual species contributions to the similarity attributes among these groups.

RESULTS

Environmental variability

Of the six physico-chemical parameters measured during the study, TDS ($H=14.89$; $n=64$; $P<0.01$), salinity ($H=14.91$; $n=64$; $P<0.01$) and conductivity ($H=14.40$; $n=64$; $P<0.01$) showed a significant difference between the four habitat types ($df=3$). Temperature, turbidity and pH showed no significant variation between habitats, but temperature and pH varied significantly between seasons (temperature $H=42.64$, $n=64$, $P<0.01$; pH $H=49.38$, $n=64$, $P<0.01$; $df=3$). As expected, the highest water temperatures occurred in summer (mean= 25.32°C) and the lowest in winter (mean= 14.34°C), with spring (mean= 19.05°C) and autumn (mean= 20.67°C) showing moderate temperatures. The ranges of environmental variables recorded in each habitat are shown in Table 1. During the summer sampling period, the highest temperatures were recorded in the shallow creek sites, but vegetated sites showed the highest temperatures in winter and spring. The lowest temperatures were generally recorded at the sand sites (Table 1). The range of temperatures recorded was fairly consistent among the different habitat types. TDS was variable among the different habitat types but consistent throughout the seasons and also showed a large range of values within specific habitat types, exceeding 20 TDS units in some cases, particularly in

the creek habitats (Table 1). The highest salinity and conductivity values recorded were in the vegetated habitats, which maintained stable salinities throughout the seasons. The most variable salinities were recorded in the creek and sand habitats (Table 1). pH was fairly stable throughout the different habitat types (range not exceeding 1.0 unit), but changes >1 unit were observed between seasons, with the lowest average pH in the system recorded in spring and summer and the highest pH in the colder seasons (Table 1). Turbidity was highly variable throughout the habitat types and seasons but this variability was not significant.

Habitat occurrence

Species composition

A total of 11537 fishes were sampled belonging to 18 families and 35 species (Table 2). The dominant species caught were the solely estuarine *Gilchristella aestuaria* and estuarine and marine *Atherina breviceps*, which contributed 27.10% and 25.80%, respectively, to the total catch. The marine estuarine-dependent sparid, *Rhabdosargus holubi*, was the third most abundant species, contributing 11.50% to the total catch. Other families that contributed notably to the catch were the Mugilidae and Gobiidae, while all the remaining families contributed less ($<1\%$) to the total catch. In terms of estuarine dependence, solely estuarine and estuarine and marine species dominated the catches, comprising 64.18%, followed by the marine estuarine-dependent species with 23.14%. Mugilidae individuals <30 mm TL, which could not be identified, contributed 6.70% of the total catch and probably belonged to the marine estuarine-opportunist category, as is typical for the

Table 2. – Species composition, total catch (N), total length summary statistics (mean, min., max.) and estuary association (according to Potter et al. 2015) of juveniles caught in each habitat type throughout the sampling period in the Swartkops Estuary. SE, solely estuarine species; E&M, estuarine and marine species; MEO, marine migrant estuarine opportunists; MED, marine migrant estuarine dependent; MS, marine stragglers; CA, catadromous; FEO, freshwater estuarine opportunists; ?, unknown.

Family	Species	Creek			Mud			Sand			Vegetated			Estuary association
		N	Mean	Max.	N	Mean	Max.	N	Mean	Max.	N	Mean	Max.	
Ambassidae	<i>Ambassis natalensis</i>	11	27.04	32.41	0	-	-	0	-	-	0	-	-	E&M
Ariidae	<i>Galeichthys feliceps</i>	6	67.83	71.00	0	-	-	0	-	-	0	-	-	MEO
Atherinidae	<i>Atherina breviceps</i>	5	57.00	61.00	110	55.46	69.00	85	60.96	75.00	113	53.47	73.00	E&M
Bleenniidae	<i>Omobranchius woodii</i>	1	40.74	40.74	0	-	-	0	-	-	0	-	-	SE
Carangidae	<i>Caranx sexfasciatus</i>	0	-	-	2	78.00	80.00	0	-	-	0	-	-	MEO
Carangidae	<i>Lichia amia</i>	1	305.00	305.00	0	-	-	0	-	-	0	-	-	MED
Cichlidae	<i>Oreochromis mossambicus</i>	10	110.60	139.00	0	-	-	0	-	-	3	38.79	46.92	FEO
Clinidae	<i>Clinus superciliosus</i>	0	-	-	0	-	-	0	-	-	3	38.79	46.92	E&M
Clinidae	<i>Gilchristella aestuaria</i>	383	44.81	96.00	138	52.16	67.00	81	49.78	71.00	68	41.13	55.00	SE
Elopidae	<i>Elops machnata</i>	3	150.33	157.00	0	-	-	0	-	-	0	-	-	MED
Gobiidae	<i>Caffrogobius gilchristi</i>	197	36.76	65.00	102	38.07	64.00	1	33.00	33.00	57	43.39	86.98	E&M
Gobiidae	<i>Caffrogobius nudiceps</i>	136	42.53	75.00	80	41.87	77.00	2	56.00	59.00	108	48.21	90.00	E&M
Gobiidae	<i>Glossogobius callidus</i>	69	36.12	65.40	35	37.87	58.00	0	-	-	2	33.00	35.00	E&M
Gobiidae	Gobiidae species 1	0	-	-	0	-	-	0	-	-	16	62.38	81.00	?
Gobiidae	<i>Psammogobius kryssnaensis</i>	91	39.83	58.00	76	38.07	60.00	135	37.74	60.00	19	45.47	64.00	E&M
Monodactylidae	<i>Monodactylus falciformis</i>	0	-	-	2	67.50	68.00	0	-	-	0	-	-	MED
Mugilidae	<i>Liza dumerilii</i>	48	85.73	205.00	22	104.90	192.00	1	30.77	30.77	17	191.37	267.00	MEO
Mugilidae	<i>Liza species (>30mm)</i>	124	35.62	51.38	22	42.22	20.63	8	31.67	27.50	18	35.74	47.53	?
Mugilidae	<i>Liza macrolepis</i>	45	57.91	102.11	19	59.04	93.12	1	42.83	42.83	2	52.68	52.76	MED
Mugilidae	<i>Liza richardsonii</i>	39	63.03	211.00	8	72.08	184.00	8	93.82	59.49	2	242.50	236.00	MEO
Mugilidae	<i>Liza tricuspidens</i>	1	175.00	175.00	4	57.36	67.68	5	59.57	55.41	9	68.21	215.00	MEO
Mugilidae	<i>Mugil cephalus</i>	127	52.75	16.38	84	68.00	30.86	39	61.27	26.69	8	140.77	295.00	MED
Mugilidae	<i>Myxus capensis</i>	5	41.40	27.00	0	-	-	5	42.04	21.18	0	-	-	CA
Mugilidae	Mugilidae (<30 mm)	163	25.95	11.64	46	28.73	23.14	71	27.67	14.99	60	28.67	40.49	?
Mugilidae	<i>Valimugil robustus</i>	57	40.09	20.52	1	29.58	29.58	0	-	-	2	45.96	54.73	MED
Pomatomidae	<i>Pomatomus saltatrix</i>	1	142.00	142.00	0	-	-	0	-	-	0	-	-	MS
Sillaginidae	<i>Sillago sihama</i>	0	-	-	2	54.43	55.45	0	-	-	0	-	-	MS
Soleidae	<i>Heteromyceteris capensis</i>	1	42.00	42.00	38	38.20	25.00	91	43.23	21.00	1	28.00	28.00	MEO
Soleidae	<i>Solea turbynei</i>	13	44.15	20.00	12	41.24	30.00	5	50.40	35.00	3	120.00	181.00	MEO
Sparidae	<i>Diplodus capensis</i>	4	30.75	24.00	67	32.58	20.00	0	-	-	268	30.82	2.00	MEO
Sparidae	<i>Rhabdosargus globiceps</i>	209	43.39	24.00	47	32.83	19.00	26	40.42	21.00	35	36.56	19.45	MEO
Sparidae	<i>Rhabdosargus holubi</i>	252	55.45	15.93	197	67.27	22.00	1	26.00	26.00	271	50.08	17.36	MEO
Sparidae	<i>Sarpa salpa</i>	1	41.59	41.59	11	37.97	30.56	0	-	-	0	-	-	MED
Syngnathidae	<i>Syngnathus temminckii</i>	0	-	-	1	190.00	190.00	0	-	-	1	190.00	190.00	E&M
Tetraodontidae	<i>Amblyrhynchotes honckenii</i>	0	-	-	0	-	-	0	-	-	1	46.00	46.00	MS

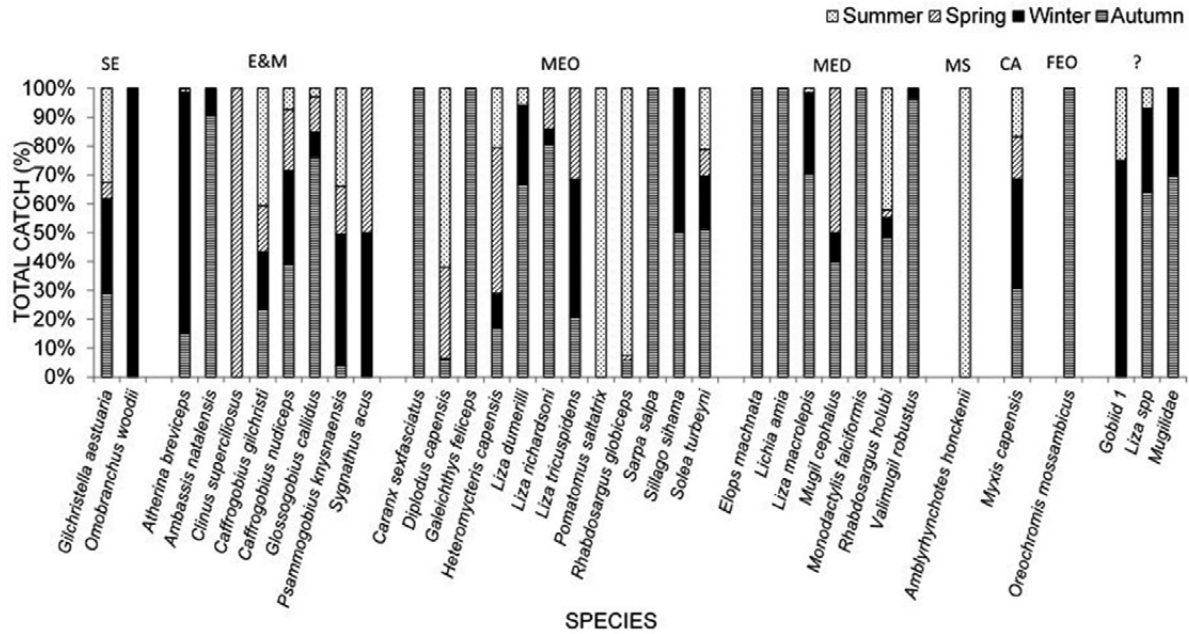


Fig. 2. – Percentage contribution of each season to total catch by the large-mesh seine net for each species grouped by estuarine association (Potter et al. 2015) in the Swartkops Estuary (February 2013 - January 2014). SE, solely estuarine species; E&M, estuarine and marine species; MEO, marine migrant estuarine opportunists; MED, marine migrant estuarine dependent; MS, marine stragglers; CA, catadromous; FEO, freshwater estuarine opportunists; ?, unknown.

most commonly occurring Mugilidae in warm temperate South African estuaries.

Temporal trends

Five of the dominant species showed a significant difference in catch among seasons (df=3) (Fig. 2). These were all marine species including *Diplodus capensis* (H=17.68; n=13; P<0.01), *Liza dumerilii*

(H=14.73; n=17; P<0.01), *L. macrolepis* (H=11.03; n=12; P<0.01), *R. globiceps* (H=20.51; n=16; P<0.01) and *R. holubi* (H=14.93; n=35; P<0.01). The highest catches were in winter (CPUE=280.62) and autumn (CPUE=218.38), followed by summer (CPUE=176.12) and spring (CPUE=45.81). The unusually high catches in winter were attributed exclusively to large catches of the solely estuarine and estuarine and marine *G. aestuaria* and *A. breviceps*, respectively. When these two

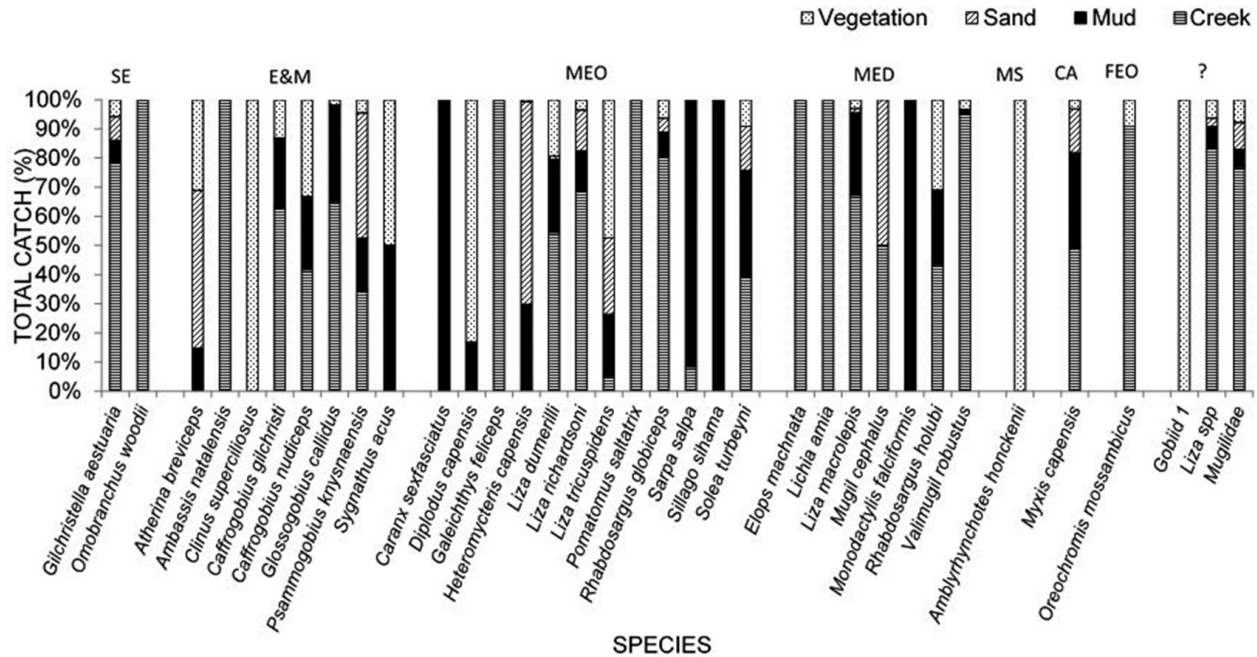


Fig. 3. – Percentage contribution of each habitat to total catch by the large-mesh seine net for each species grouped by estuarine association (Potter et al. 2015) in the Swartkops Estuary (February 2013 - January 2014). SE, solely estuarine species; E&M, estuarine and marine species; MEO, marine migrant estuarine opportunists; MED, marine migrant estuarine dependent; MS, marine stragglers; CA, catadromous; FEO, freshwater estuarine opportunists; ?, unknown.

species were excluded from the analyses, the winter season showed the lowest fish abundance. The largest contribution of marine species to total catch occurred in autumn and spring, whereas the estuarine species showed greater variability in abundance throughout the year (Fig. 2).

Diversity peaked in autumn ($H' = 1.17$) and summer ($H' = 1.11$), with lower diversity occurring in spring ($H' = 0.98$) and winter ($H' = 0.96$), but diversity did not vary significantly between seasons ($P > 0.05$).

TLs of dominant species caught were compared between seasons. Seasonal variation in TL occurred in estuarine resident species, namely *A. breviceps* ($H = 44.48$; $n = 313$; $P < 0.01$), *Glossogobius callidus* ($H = 14.88$; $n = 357$; $P < 0.01$), *Caffrogobius nudiceps* ($H = 47.97$; $n = 326$; $P < 0.01$), *G. aestuaria* ($H = 180.11$; $n = 670$; $P < 0.01$), *Psammogobius knysnaensis* ($H = 24.78$; $n = 321$; $P < 0.01$), and in marine estuarine migrant species, namely *Heteromycteris capensis* ($H = 45.84$; $n = 131$; $P < 0.01$), *Myxus capensis* ($H = 38.30$; $n = 258$; $P < 0.01$), *R. holubi* ($H = 33.06$; $n = 721$; $P < 0.01$) and *Solea turbynei* ($H = 8.36$; $n = 32$; $P < 0.05$).

Spatial trends

The abundance of fishes was compared between four habitat types at the species level and 8 of the 15 dominant species showed a significant difference in abundance between the four habitat types. These included the solely estuarine *Gilchristella aestuaria* ($H = 9.54$; $n = 64$; $P < 0.05$), three estuarine and marine species, *Caffrogobius gilchristi* ($H = 20.36$; $n = 64$; $P < 0.01$), *Caffrogobius nudiceps* ($H = 15.98$, $n = 64$, $P < 0.01$) and *Glossogobius callidus* ($H = 10.38$, $n = 64$, $P < 0.01$), two marine estuarine opportunists, *Diplodus capensis* ($H = 11.64$; $n = 13$; $P < 0.01$) and *Heteromycteris capensis* ($H = 21.73$; $n = 21$; $P < 0.01$), the marine estuarine-dependent *Rhabdosargus holubi* ($H = 19.13$; $n = 35$; $P < 0.01$) and finally the catadromous *Myxus capensis* ($H = 10.66$; $n = 29$; $P < 0.01$).

Of these species, the commonly estuarine families, including the Gobiidae (>50.00%) and the Clupeidae (*G. aestuaria*) (78.00%), showed the highest proportions of catches in the creek sites, whereas the Sparidae (*D. capensis*) (83.00%) showed the highest proportion of catches in the vegetated sites (Fig. 3). Although the highest proportion of *R. holubi* was caught in the creek habitat (45.00%), the vegetated habitat also yielded a large proportion of the total catch (31.00%) of this species (Fig. 3). Overall, CPUE (including all species) was highest in the creek sites (CPUE=331.38) followed by the sand sites (CPUE=144.56) with the lowest CPUE occurring in the vegetated (CPUE=139.31) and mud sites (CPUE=105.94). However, the largest contributor to catch in the sand sites, *A. breviceps*, was caught in high numbers on a single sampling occasion. If this species is excluded from calculations, the average CPUE for sand habitats is reduced (CPUE=45.88), making it the site with the lowest CPUE. Despite differences in species catch among habitats and the variability of salinity, TDS and conductivity between habitats, no significant relationships were observed between partition-

ing species and the environmental variables measured in these habitats in the lower estuary.

Species diversity (H') was highest in the mud ($H' = 1.24$) and vegetated ($H' = 1.02$) habitats, followed by the sand ($H' = 0.79$) and creek ($H' = 0.44$) habitats. These differences were, however, not significantly different among the four habitat types ($P > 0.05$).

Of the dominant species caught, *A. breviceps* ($H = 42.91$; $n = 313$; $P < 0.01$), *C. gilchristi* ($H = 11.22$; $n = 357$, $P < 0.01$), *C. nudiceps* ($H = 20.68$; $n = 326$, $P < 0.01$), *G. aestuaria* ($H = 182.02$; $n = 670$; $P < 0.01$), *Heteromycteris capensis* ($H = 10.06$; $n = 131$; $P < 0.05$), *L. dumerilli* ($H = 32.40$; $n = 88$; $P < 0.01$), *M. capensis* ($H = 9.75$; $n = 258$; $P < 0.01$), *P. knysnaensis* ($H = 10.41$; $n = 321$; $P < 0.01$), *R. globiceps* ($H = 57.87$; $n = 317$; $P < 0.01$) and *R. holubi* ($H = 76.76$ $n = 721$; $P < 0.01$) showed a significant difference in TL among the four habitat types. The largest *R. holubi* (mean TL=50.08) and *L. dumerilli* (mean TL=191.37) individuals were caught in the vegetated habitats and the smallest in the sand habitats (mean TL=26.00 and 30.77, respectively), whereas *R. globiceps* were largest in the creek habitats and smallest in the mud habitats (mean TL=43.39 and 32.83, respectively) (Table 2). *Diplodus capensis*, *G. callidus*, *L. macrolepis* and *S. turbynei* were dominant species in the community in the lower reaches and showed no significant differences in TL between the four habitat types sampled.

Fish community trends

A two-way crossed ANOSIM also revealed a significant difference between seasonal groups (Global $R = 0.21$; significance level (SL)=0.10%, averaged across habitat). Pairwise tests showed that the seasons that differed significantly included autumn and spring (R statistic=0.26; SL=1.60%), autumn and summer (R statistic=0.28; SL=0.70%), winter and summer (R statistic=0.36; SL=0.10%) and spring and summer (R statistic=0.31; SL=0.20%) combinations. Comparisons between autumn and winter and winter and spring showed no significant differences. SIMPER analysis showed that the summer season differed significantly from the other seasons due to high catches of the marine estuarine-dependent Sparidae *Rhabdosargus holubi* (26.66%) and marine estuarine opportunists *Diplodus capensis* (21.87%) and *Rhabdosargus globiceps* (15.46%) (Table 3). The winter and spring seasons were characterized by higher catches of estuarine resident Gobiidae species compared with other seasons (Table 3).

A two-way crossed ANOSIM revealed that there was a significant difference between habitat groups (Global $R = 0.27$; significance=0.10%, averaged across season). Pairwise tests comparing habitats showed that the habitats that differed the most were the creek and sand habitats (R statistic=0.39; SL=0.10%), the sand and vegetated habitats (R statistic=0.53; SL=0.10%) and the mud and vegetated habitats (R statistic=0.27; SL=0.40%). The comparison of creek and mud habitats as well as mud and sand habitats showed no significant differences. Abundance data in a 3-D nMDS analysis showed a distinct grouping of sites by habitat

Table 3. – SIMPER test results for each habitat and season. The three species from the estuarine groups (SE and E&M) and marine species groups (MEO, MED, MS) (Potter et al. 2015) that contribute the highest percentages to catch in each habitat.

Habitat	Estuarine species (% contribution)	Marine species (% contribution)
Creek	<i>G. aestuaria</i> (18.90%) <i>C. gilchristi</i> (13.67%) <i>C. nudiceps</i> (12.52%)	<i>R. holubi</i> (13.15%) <i>R. globiceps</i> (6.14%) Mugilidae (5.85%)
Mud	<i>P. knysnaensis</i> (18.53%) <i>C. gilchristi</i> (15.31%) <i>G. aestuaria</i> (5.5%)	<i>R. holubi</i> (23.71%) <i>H. capensis</i> (6.45%) <i>D. capensis</i> (4.90%)
Sand	<i>P. knysnaensis</i> (37.41%)	<i>H. capensis</i> (31.34%) <i>R. globiceps</i> (12.27%) Mugilidae (5.22%)
Vegetated	<i>C. nudiceps</i> (22.86%) <i>C. gilchristi</i> (13.39%) <i>A. breviceps</i> (3.60%)	<i>R. holubi</i> (28.46%) <i>D. capensis</i> (20.49%) <i>R. globiceps</i> (3.88%)
Season		
Autumn	<i>G. aestuaria</i> (10.96%) <i>C. gilchristi</i> (7.86%) <i>P. knysnaensis</i> (6.01%)	<i>R. holubi</i> (28.99%) <i>L. dumerilli</i> (6.92%) <i>H. capensis</i> (6.22%)
Winter	<i>P. knysnaensis</i> (20.97%) <i>C. nudiceps</i> (16.08%) <i>C. gilchristi</i> (13.78%)	Mugilidae (9.61%) <i>R. holubi</i> (8.31%)
Spring	<i>P. knysnaensis</i> (31.77%) <i>C. nudiceps</i> (26.39%) <i>C. gilchristi</i> (18.49%)	<i>H. capensis</i> (11.96%) <i>R. holubi</i> (4.4%)
Summer	<i>C. gilchristi</i> (9.8%) <i>P. knysnaensis</i> (4.85%)	<i>R. holubi</i> (26.66%) <i>D. capensis</i> (21.87%) <i>R. globiceps</i> (15.46%)

based on similarities in species abundance (Fig. 4). Although habitat groupings based on dissimilarity are not distinct, there is subtle grouping of sand, creek and vegetated habitats with mud habitats tending to fall in between these groups.

SIMPER analysis of habitat types showed that sand habitats were characterized by sand-associated species such as *Psammogobius knysnaensis* (37.41%) and *Heteromycteris capensis* (31.34%), whereas these species did not contribute significantly to catches in the other habitats (Table 3). The mud habitats showed high

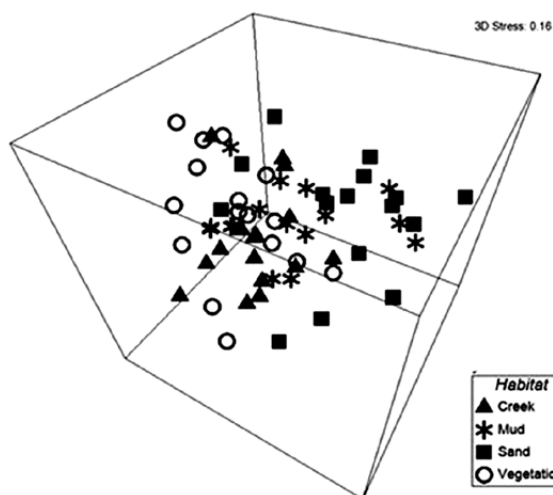


Fig. 4. – A three-dimensional nMDS plot of similarity of species abundance among habitat types in the Swartkops Estuary (February 2013 - January 2014)

catches of the estuarine resident Gobiidae as well as *Rhabdosargus holubi* (23.71%) (Table 3). However, the highest catches of marine Sparidae were in the vegetated habitats separating this habitat type from the others in terms of species catch composition (Table 3). The creek habitats differed from other habitats in the high abundance of the estuarine species *Gilchristella aestuaria* (18.90%), in addition to the moderate abundance of some marine Sparidae (Table 3). Other predatory piscivorous fishes were found only in the creek habitats in low numbers.

DISCUSSION

Distinct species suites were recognized across all four habitat types typifying the lower reaches nursery area within the Swartkops Estuary. The importance of submerged aquatic vegetation for young fishes in the Swartkops Estuary supports previous findings on habitat use at the species level within eelgrass beds (Orth et al. 1984, Sheppard et al. 2011) in studies comparing seagrasses and adjacent unvegetated areas (Beckley 1983, Connolly 1994, Jenkins and Wheatley 1998) as well as in studies comparing multiple habitat types in nursery areas (Sogard and Able 1991, Guidetti 2000, França et al. 2009). However, in the present study, shallow-water creeks yielded the highest catches, supporting findings in a Northern Hemisphere study (Sogard and Able 1991) and contrary to findings in the Kariega Estuary situated 130 km to the east of the study system (Paterson and Whitfield 2000), where vegetated areas showed higher fish abundance and more selective species occurrence among habitats.

Use of vegetated habitats by fish has been attributed to a number of driving forces, including the protective function as a result of structural complexity as well as their provision of food for growing larvae and juveniles (Orth et al. 1984, Paterson and Whitfield 2000, Nanjo et al. 2014). This would suggest that the more structurally complex vegetated areas should support more fishes, but in this study shallow, warm creeks were also important use area for numerous species. All habitats sampled showed unique species suites as well as a level of plasticity within species in terms of occurrence across habitats. Use of habitats was also found to vary seasonally within the estuary, coinciding with peak juvenile fish recruitment into estuaries during warmer spring and summer months.

Temporal trends

Seasonal use of temperate estuaries where abundance of juveniles increases in spring and peaks in summer, with numbers declining in autumn, after which abundance and diversity declines markedly as the water temperature cools, is a worldwide phenomenon coupled to recruitment from the ocean and productivity maxima within the estuary, typically linked to rainfall patterns and therefore food availability (Whitfield 1999, Ramos et al. 2006, Strydom 2015). This phenomenon was particularly evident for juveniles of marine spawned Mugilidae, Soleidae and Sparidae utilizing

the estuary as a nursery. Schooling adults of resident pelagic Atherinidae and Clupeidae species within the estuary, however, compounded catches in the winter months in the Swartkops. *Atherina breviceps* breeds in spring and summer in the estuary and juveniles can be found in high abundances in autumn and winter (Neira et al. 1988, Whitfield 1998). Using the guild approach as described by Potter et al. (2015) to categorize fish prior to analysis allows better elucidation of use patterns without the compounding effects of resident species on seasonal catches of marine recruits.

Spatial trends

There was clear evidence of partitioning among juvenile fishes within the four habitat types common to the lower reaches of the Swartkops Estuary. Eight species showed significantly higher abundance in particular types of habitat and included species of both estuarine and marine origin. The highest catches throughout the study period occurred at shallow creek sites, as is supported by habitat use observations in an Atlantic estuary (Sogard and Able 1991) but has not yet been described locally. The shoaling estuarine resident *Gilchristella aestuaria* often occurred in high numbers in creeks. It has been suggested that species also select habitats based on the degree of protection afforded by either the habitat directly (vegetation) or the behaviour of the species to avoid predation (Weinstein and Brooks 1983, Orth et al. 1984). In the case of resident *G. aestuaria*, this species is able to limit predation by shoaling in shallow creeks (Paterson and Whitfield 2000). However, creeks were also important areas for other species, evidenced by the high species diversity and the larger size range within species in creek habitats, particularly in the resident Gobiidae and the marine estuarine-dependent Sparidae and Mugilidae. The mixed community within creeks is contrary to findings by Paterson and Whitfield (2000), who found saltmarsh creeks dominated by taxa mainly of marine origin as well as to findings by Sogard and Able (1991) and Weinstein and Brooks (1983), who both found that although density of fish in creeks was high, catches were dominated by only a few species and that these habitats showed a lower diversity of species when compared with vegetated sites.

Zostera capensis and *Spartina maritima* rich vegetated habitats also supported high abundances of juveniles, although the abundance was species-specific. All estuary guilds (Potter et al. 2015) were recorded in vegetated areas, and these habitats appear to be very important for juvenile marine species, especially the marine estuarine-dependent sparid *Rhabdosargus holubi* and the marine estuarine opportunist *Diplodus capensis*, a finding also supported by Paterson and Whitfield (2000) in the nearby Kariega Estuary. Aside from the solely estuarine resident species, these Sparidae contributed the most to catches in these areas containing submerged vegetation, which was also reported by Beckley (1983). However, vegetated habitats are seemingly less important for other marine estuarine opportunist species such as the sparid *Rhabdosargus globiceps*, which tends to occur more often in creek habitats.

Mud habitats also showed a higher diversity of juvenile fish species. In contrast to creek and vegetated habitats, sand habitats appeared to support the lowest abundance (excluding the large catch of shoaling marine and estuarine *Atherina breviceps* on a single occasion) and diversity of species. Sand habitats are the most uniform in terms of complexity and typically only support specialist sand species, namely the sand goby *Psammogobius knysnaensis* and the Soleidae. Based on these characteristics, vegetated and mud habitats tend to fall in between these extremes. This was evident in the study by Hanekom and Baird (1984) in the Kromme Estuary, in which they compared *Zostera* beds with adjacent non-*Zostera* areas of muddy substrate. They found no significant differences in fish community. These habitats often share species composition and it could be that fish move between the two for feeding and refuge. Diet studies on species utilizing both habitat types will provide much insight into microhabitat use and habitat partitioning.

Habitat partitioning with ontogeny showed that species use of habitats varied depending on their estuary association category. The solely estuarine and estuarine migrants, such as the Gobiidae, Atherinidae (namely *A. breviceps*) and Clupeidae (namely *G. aestuaria*), were frequently sampled in all habitats in both juvenile and adult stages, suggesting less segregation based on size. Mugilidae, many of which are dependent on estuaries as juveniles, were also commonly caught in all habitats in sizes ranging from recently transformed juveniles to older juvenile stages, with some adults also recorded in catches.

In contrast, the marine estuarine-opportunist and dependent Sparidae species occurred mostly as small juveniles: no adults were caught (>190 mm TL) across habitats and larger specimens were mostly associated with vegetated and creek habitats. The average size of *D. capensis* is less than the average size of *R. holubi* and *R. globiceps*. This suggests that the marine estuarine-opportunist *D. capensis* may utilize estuarine nurseries for a shorter period of time during their juvenile phase when compared with the other two estuarine-dependent sparid species co-occurring in the nursery area due to their reliance on estuaries. This probably also contributes to the success of sharing habitats as diet and gape size will vary. *Diplodus capensis* is not wholly dependent on estuaries, often moving into tide pools and gullies in the ocean at larger sizes (Strydom et al. 2014), whereas *R. holubi* has a fully dependent estuarine phase in its early life history. Sparidae typically also show ontogenetic shifts in habitat that are critical to survival as these species recruit into estuaries as postflexion larvae (Strydom 2015). Smaller-sized individuals were recorded in the open water areas at sand and mud sites. Strydom (2003) proposed that the high numbers of recruiting postflexion Sparidae in open water areas as opposed to *Zostera* beds was a predation avoidance mechanism as transparent larvae are less visible in open water than against the darker background of the *Zostera* beds, which are already rich with juvenile predators. Upon completion of settlement, the Sparidae move into vegetated and creek habitats, where

they occur mostly as larger juveniles, as was observed in this study. Open shallow water over sand and muddy substrata therefore becomes a transient habitat during ontogeny for marine species recruiting as larvae into estuaries (Strydom 2003), after which they filter into vegetated or creek areas as juveniles, thereby utilizing multiple habitats throughout their early development following an ocean-estuarine habitat continuum (Able 2005, Baillie et al. 2015, Strydom 2015).

Drivers of spatial and temporal trends

Surprisingly, temperature was not found to be an important driver of habitat use. This is likely because all habitats were shallow and located in the lower reaches of the estuary, so they were subject to similar tidal and solar radiation effects and therefore had similar temperatures. Despite there being no significant difference in temperature among habitat types, the highest temperatures were recorded in creek and vegetated habitats, which also yielded the highest catches. As the Sparidae contributed substantially to catches in these two habitats, it is likely that this is a reflection of the temperature sensitivity in growth for these species (Strydom et al. 2014) and these species also select these habitats based on subtly higher temperatures. The value of generally warmer estuarine nursery areas compared with the neighbouring ocean must be emphasized in species with temperature-dependent growth. These conditions are generally more suitable for the faster growth of larvae and juveniles using shallow-water nurseries such as estuaries and shallow embayments, thereby enhancing chances of survival (Strydom et al. 2014, Baillie et al. 2015). Temperature most probably plays a more significant seasonal role rather than being a contributor to habitat occurrence on a fine scale, as in this study, which focuses on the lower estuary within the nursery area. Higher turbidity in creek sites, subject to tidal drainage of the salt marsh, may also provide additional protective isolation for young fishes from visual predators, lending to the value of creeks along with vegetated areas for refuge, but this value is not statistically measureable on such fine scales. Since environmental variables such as salinity, conductivity and TDS, which were significantly different among habitats, also showed no clear trends in structuring fishes in these areas, it is highly likely that other factors such as behaviour, linked to predator avoidance and coupled with feeding, are significant drivers of use in these habitats. Behaviour and feeding need to be considered in future studies focussed on fine-scale habitat partitioning.

CONCLUSION

Although vegetated habitats have received worldwide attention and therefore show value in terms of their nursery role in estuaries, this work provides evidence for the importance of multiple habitat types among and within species and with ontogeny in temperate estuarine nurseries. Coupled with vegetated areas, shallow-water estuarine creeks also play an important

role in the nursery function of estuaries in temperate South Africa given the high density of juvenile fishes concentrating in these areas. The value of an estuarine nursery is therefore likely to increase with increased submerged aquatic vegetation and shallow-water creek availability, essentially increasing refuge opportunities, assuming food availability is optimal. Large-scale and small scale environmental variability in estuaries probably shift in priority on a temporal and spatial scale in nursery areas. Temperature and olfactory cues provide the critical drivers of recruitment of larvae and juveniles into estuaries but upon arrival, a suite of factors probably underpin the success of the nursery, including habitat availability, physico-chemical factors, food availability and fish behaviour relative to competitors and predators. The ubiquity of various sizes across the four habitats in certain fish groups suggests greater habitat plasticity than was previously thought. This is seen in both resident and marine migrant fishes and therefore less partitioning exists among species than was previously hypothesized. This explains the conflicting findings of habitat use in previous studies, especially those using vegetated areas as a variable. Many studies have failed to identify plasticity in habitat use (Sogard and Able 1991, this study) because, most often, only two habitat types were compared at a time and with little separation of fishes into guilds prior to analysis to remove confounding effects from different use groups. Multiple habitat comparisons are required in future studies coupled with diet and ontogenetic shifts to fully understand how and whether nursery habitat use is as plastic as it appears to be among some species, particular estuary specialists. The subject is bound to remain complex and multidimensional as species may be partitioning habitats on finer scales than those currently being measured and these are as yet unexplored. Resilience appears to be a hallmark characteristic of fishes regularly using estuaries as nursery areas and success may well be embedded in behavioural and feeding plasticity rather than specialization.

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