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Spatial habitat partitioning enables coexistence of three Gobiidae species in estuarine environments

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Abstract

This study examines resource partitioning (feeding morphology, diet and habitat partitioning) among three gobiid species, the Knysna sandgoby *Psammogobius knysnaensis*, the prison goby *Caffrogobius gilchristi* and the river goby *Glossogobius callidus*, within an estuarine environment. The findings revealed distinct habitat preferences: *P. knysnaensis* predominantly occupied the sandy mouth of the estuary, *C. gilchristi* favoured the lower reaches and *G. callidus* was abundant in the upper reaches. Principal component analysis of feeding morphological traits indicated significant overlap between the feeding morphology of *C. gilchristi* and *G. callidus*. Although the two species showed overlapping morphological traits, they exhibited distinct diets, influenced by differences in prey availability within their feeding environments. Cyclopoids, which were widespread throughout the estuary, were a common dietary item for both species. *Psammogobius knysnaensis* and *C. gilchristi* had overlapping diets, but each species appeared to dominate in different habitats. This study highlights that habitat partitioning drives resource partitioning among the three species, enabling their coexistence in a dynamic estuarine ecosystem.

KEYWORDS
ecomorphology, estuarine environment, feeding morphology, predation, resource partitioning

1 | INTRODUCTION

Gobies occur in high numbers and are a dominant component of the demersal fish assemblage in South African estuaries (Bailey & James, 2013; Nodo et al., 2018; Richardson et al., 2006). They are one of only two fish families (the other being Mugilidae) that are well represented in cool-temperate, warm-temperate and subtropical estuaries (Whitfield, 2019). Estuaries are fluctuating aquatic environments and as a result few species are able to complete their entire life cycle in estuaries (Whitfield & Harrison, 2020). Of the 172 fish species that occur in South Africa's 290 estuaries, only 43 species are able to breed in estuaries, with 25 from the Gobiidae family (Whitfield, 2019). Although gobies are an important component of the fish community in estuaries, very few studies have focused on the biology and mechanisms enabling the coexistence of gobies in South African estuaries.

When species are functionally similar and coexist in a closed water body or an area with restricted movement, they are able to persist in sympatry through resource partitioning by evolving traits which facilitate differential consumption of resources or by responding differently to environmental heterogeneity (i.e. habitat partitioning),

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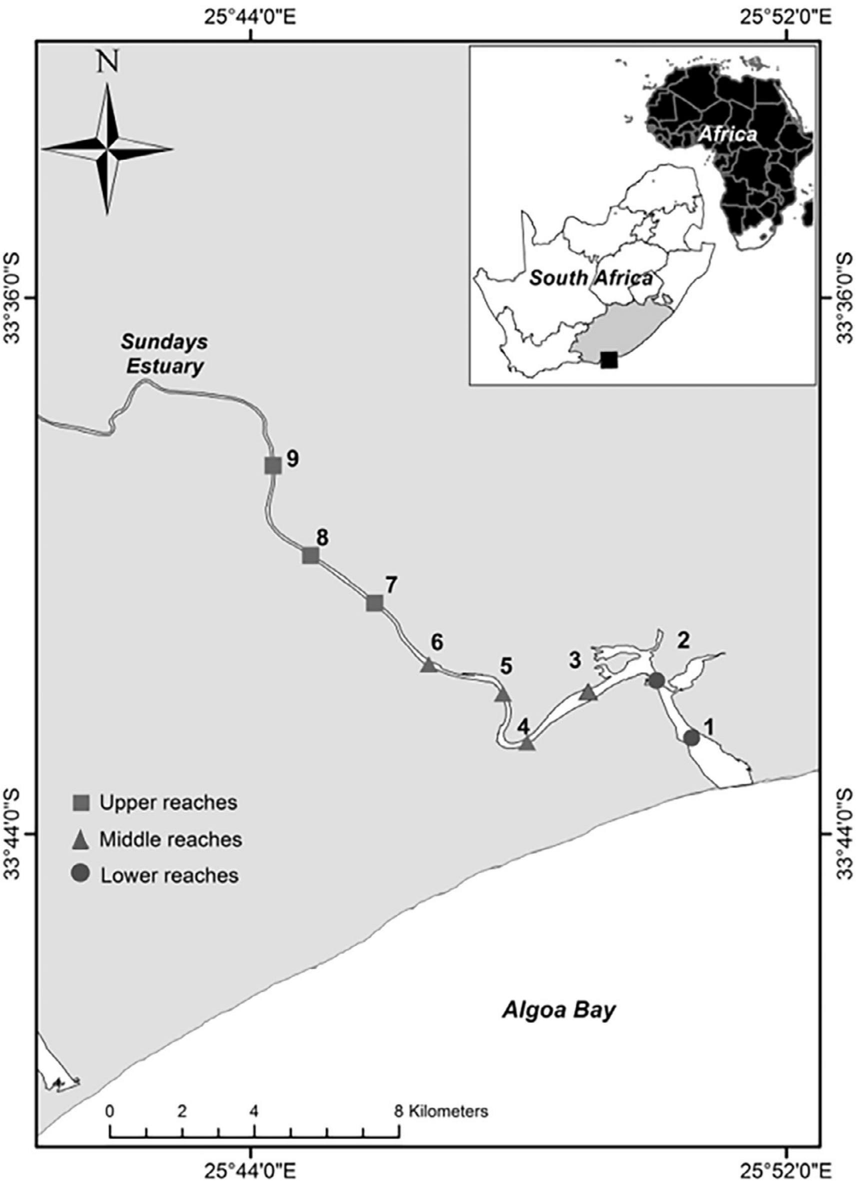

FIGURE 1 Sampling sites within the Sundays Estuary, Eastern Cape and South Africa.

which then drives spatially explicit abundance patterns (Bolnick et al., 2007; Leibold & McPeek, 2006). Specialisation in resource use minimises competition, thereby enabling stable coexistence between similar species in aquatic systems (Guo et al., 2014).

Trophic niche differentiation can be promoted by diversification of morphological structures responsible for feeding (Porreca et al., 2017). An organism's morphology influences its capacity to locate, chase, capture and process a prey. As such, functional morphological traits have been used to predict resource partitioning in a wide variety of fishes (e.g. Burress, 2016; Mittelheiser et al., 2022; Sibbing & Nagelkerke, 2001; Wainwright & Richard, 1995). For example, in a large-scale study of 367 species from 20 orders from the Nearctic, Neotropical and Afrotropical regions, Keppeler et al. (2020) showed that gut length, tooth shape, mouth width, mouth orientation and body depth are strong predictors of trophic level.

Some species mitigate interspecific food competition by consuming similar food resources but from different habitats (Sone et al., 2001), with habitat partitioning promoting resource partitioning among coexisting species. For example, in the Western Bug River, Poland, three species, the monkey goby (*Neogobius fluviatilis* Pallas, 1814), the racer goby (*Babka gymnotrachelus* Kessler, 1857) and the Eurasian perch (*Perca fluviatilis* Linnaeus, 1758), separated their food resources by foraging in different habitats (Grabowska et al., 2024). Gobies primarily fed on benthic prey of muddy, stagnant environments, while perch favoured epibenthic prey occurring in clear water habitats (Grabowska et al., 2024). Realised foraging niche is also mediated by prey abundance within habitats, where generalists tend to shift to the most available prey in a given environment (Coblentz, 2019; Sheaves et al., 2014).

The Gobiidae family provides excellent subjects to study trait-based mechanisms of resource partitioning. The three most abundant goby species in temperate South African estuaries, the Knysna sand goby *Psammogobius knysnaensis* (Smith, 1935), the prison goby *Caffrogobius gilchristi* (Boulenger, 1898) and the river goby *Glossogobius*

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callidus (Smith, 1937), are functionally similar and represent estuarine resident and zoobenthivorous functional groups. Here, we used a three-pronged investigation to explain their coexistence and abundance in South African estuaries, assessing interspecific differences in feeding morphology, feeding ecology and habitat partitioning. We predicted that each species would exhibit spatial and trophic niche differentiation, which would be reflected by morphological specialisations suited to particular habitat and feeding types.

2 | MATERIALS AND METHODS

2.1 | Study area

The Sundays Estuary is one of two predominantly open estuaries in warm-temperate Algoa Bay, South Africa. The estuary flows into the Indian Ocean at 33°43′14.5″ S, 25°51′10.4″ E, and is approximately 21 km long with a catchment area of 20,792 km^2 (Figure 1). The lower reaches extend for 6 km, the middle reaches for 10 km and the upper reaches for 19 km (Nodo et al., 2024). Salinity decreases from an average of 30 in the mouth to 1 in the upper reaches (Nodo et al., 2023). As a result of agricultural activities in the catchment, the estuary is permanently eutrophic (Lemley et al., 2018).

2.2 | Study species

Psammogobius knysnaensis is endemic to southern African estuaries, ranging from Port Nolloth to KwaZulu-Natal (Whitfield, 2019) and is abundant in the sandy lower reaches of South African estuaries (Bailey & James, 2013; Nodo et al., 2018; Richardson et al., 2006). Prey items present in its diet include amphipods, polychaetes, insect larvae, isopods, copepods, cumacea, decapods and ostracods (Bennett, 1989; Whitfield, 1988). *Psammogobius knysnaensis* comprises 11% of the demersal catch in the channel of the Sundays Estuary (Nodo et al., 2024). *Caffrogobius gilchristi* is also endemic to South African estuaries, occurring from the Olifants system on the west coast to Durban Bay (Whitfield, 2019). The species is associated with muddy habitats located in the middle and lower reaches of estuaries (McGregor & Strydom, 2018; Nodo et al., 2018). Prey items present in their diet include copepods, mysids, crabs, gastropods, amphipods, chironomid larvae, anomurans, polychaetes, macrurans and small fishes (Bennett & Branch, 1990; Whitfield, 1988). *Caffrogobius gilchristi* is the dominant goby in the Sundays Estuary, comprising 15% of the demersal catch in the channel of the estuary (Nodo et al., 2024).

Glossogobius callidus is endemic to coastal rivers and estuaries of southern Africa (Whitfield, 2019). The distribution of this species ranges from Mozambique to the Swartvlei region of the Western Cape (Whitfield, 2019). In estuaries, *G. callidus* are mostly recorded in the low saline upper and middle reaches (Ter Morshuizen & Whitfield, 1994). Amphipods, cyclopoids and chironomid larvae dominate the diet of this species in the early life stages (Vumazonke et al., 2008; Wasserman, 2012). *Glossogobius callidus* comprises 10% of the demersal catch in the channel of the Sundays Estuary (Nodo et al., 2024). All three species reproduce in spring and summer and reach 50% maturity at approximately 40 mm total length (TL) (Ndaleni et al., 2024).

2.3 | Habitat partitioning

To determine spatial and temporal trends in the abundance of the three species in the estuary, fish were sampled in the channel of the estuary at nine sampling sites using a 3-m long shoeless beam-trawl with a body made from 14-mm mesh and a 1 m long × 0.5 m wide cod end made from 6 mm mesh. Fish were collected from February 2018 to September 2019 for a total of 12 sampling occasions. Fish were sampled as part of a larger study on the demersal fish assemblages of the Sundays and Swartkops estuaries and adjacent nearshore (see Nodo et al., 2023, 2024 for sampling details). Sites were 2 km apart, with the first two sampling sites, site 1 (2 km from the mouth) and site 2 (4 km from the mouth), representing the lower reaches. Sites 3–6 represented the middle reaches and sites 7–9 the upper reaches (Figure 1). At each sampling site the net was towed 20 m behind the boat at a constant towing speed of approximately 2 knots for 3 min. One trawl haul was done at each site, covering a distance of approximately 200 m. Fish were identified and measured to the nearest millimetre TL and then released alive. Catch-per-unit-effort (CPUE) was calculated as the index of fish abundance (number of fish per 1000 m^2).

As part of the larger study, bottom-water physicochemical parameters (temperature, pH, salinity, depth, turbidity and dissolved oxygen) were recorded at each site using a YSI (6290) multi-parameter probe. Sediment samples were also collected using a cone dredge for particle size and sediment organic content analysis (detailed in Nodo et al., 2024). The mean, median and the range for each variable (salinity, turbidity [NTU], temperature [°C], dissolved oxygen [mg/l], organic content [%] and silt [%]) were calculated and these were visually presented using boxplot graphs. Spearman rank correlation coefficients were used to explore significant relationships between environmental variables and the CPUE of the three species. Correlations were considered significant at a level of $p < 0.05$. Analysis was performed in R 4.4.0 (R Core Team, 2024).

2.4 | Feeding morphology

For feeding morphology analysis, a total of 54, 60 and 48 *P. knysnaensis*, *C. gilchristi* and *G. callidus*, respectively, were collected in July 2018 using a small mesh seine net (30 × 2 m) with a 5-mm bar mesh. Sampling was conducted throughout the estuary. After capture, bycatch species were released back to the water alive and the three study species were placed in a bucket containing water with 40 mg/L clove oil for humane euthanasia and transported on ice for laboratory analysis (Rhodes University ethical clearance number 2019-0543-750).

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In the laboratory, a total of 34 feeding traits were measured in each individual fish using digital callipers, and a Zeiss Stemi 508 microscope was used for measurements of less than 2 mm (Tables S1 and S2). Measurements followed those detailed in Nagelkerke et al. (2018) and Sibbing and Nagelkerke (2001) for cyprinids. Functional morphological traits measured include those responsible for prey location, chasing, capturing, mastication and digestion (Table S1 and Figure S1).

Metric variables were expressed as a proportion of standard length (SL) and data were then standardised by subtracting the mean value (per variable) and dividing by the standard deviation. Correlations of variables were calculated for each species to avoid collinearity and variables excluded based on this.

A principal component analysis (PCA) was then performed on the standardised data to visualise the overall trophic morphology of each fish specimen using the factoextra R-package (Kassambara & Mundt, 2020). The distance of the species to others represents the level of similarity in their trophic morphology. The potential food niches of each species were then predicted using the procedures outlined in Nagelkerke et al. (2018). To compare the overall capacity to feed on different aquatic food types a PCA was performed on the trophic profiles (TPs). Trophic profiles represent the capacity of each individual fish to utilise each of the tested food types in the wild (Sibbing & Nagelkerke, 2001). To compare feeding capacity between species and by food type, to observe which species were most likely to differ, mean TPs were calculated and clustered using the pvclust package in R (Suzuki & Shimodaira, 2006), 10,000 bootstrap replicates and the wardD2 option.

2.5 | Diet

For foregut content analysis fish were collected twice, in spring (September/October 2018) and in winter (August 2019). Fish samples were collected by beam trawling at the nine sampling sites in the channel of the estuary (as for habitat partitioning) and supplemented by seine netting (30 × 2 m with a 5-mm bar mesh) in the littoral zone (as for feeding morphology). This sampling was conducted independently from the habitat partitioning sampling. A total number of 106 *P. knysnaensis*, 103 *C. gilchristi* and 67 *G. callidus* were collected in September/October 2018 and 170 *P. knysnaensis*, 49 *C. gilchristi* and 81 *G. callidus* in August 2019. *Psammogobius knysnaensis* were mostly collected at sites 2, 4, 8 and 21 km from the mouth. *Caffrogobius gilchristi* were mostly collected at sites 4 and 6 km from the mouth, while *G. callidus* were mostly collected at sites 16 and 21 km from the mouth.

In the laboratory, each fish was measured to the nearest mm total length (mm TL) and the foregut of the fish then removed via dissection. Fish were divided into length classes of <20 mm, 20–29 mm, 30–39 mm, 40–49 mm, 50–59 mm, 60–69 mm and >70 mm. Prey abundance (%*N*), frequency of occurrence (%*F*) and percentage volume (%*V*) were calculated for each dietary prey in each fish species following the procedures of Wasserman (2012). For digested prey, head counts were conducted. The relative importance of prey items were assessed using the index of relative importance ($\text{IRI} = [\%N + \%V] \times \%F$).

For comparative purposes, the IRI value for each group was expressed as a proportion of the sum of IRI values calculated for all prey items (%IRI).

Levins niche breadth was compared using %IRI values:

$$B = \frac{1}{\Sigma Pi^2}$$

where B is the niche breadth and Pi is the relative frequency for prey item i in the diet of predator P (Levins, 1968).

The results were then standardised to the scale of 0–1:

$$B_a = (B-1)(n-1)$$

where B_a is the standardised niche breadth and n is the summation number of all the prey items.

PRIMER (version 7) was used to assess dietary similarities among the study species. The percentage volume (%*V*) of prey items per size class per species was fourth root transformed and a Bray–Curtis similarity matrix calculated. A cluster analysis was applied to the Bray–Curtis similarity matrix and the significance of branches/groupings tested using the similarity profile routine (SIMPROF, $p < 0.05$). Significantly different groups based on diet were visualised using a non-metric multidimensional scaling (nMDS) ordination and a shade plot.

2.6 | Prey resources

Putative prey resource abundance in the environment was sampled once (one replicate) during the day (28 August 2019) to complement the dietary analysis. Mesozooplankton communities were sampled using an epibenthic sled at the nine beam trawl sampling sites. The epibenthic sled was fitted with 200 μm mesh, with a semicircular mouth with a radius of 18.5 cm. The net was mounted on a sled, so that the net was raised 7.5 cm above the sediment surface. The net was deployed from a boat in the channel of the estuary and towed for 35 m. After sampling, the sample was rinsed in a 1-L bottle and preserved with 4% formalin. In the laboratory, samples were suspended in 2 L of distilled water and stirred so that the organisms remained in a homogeneous suspension and the entire sample analysed. Zooplankton were identified to the lowest possible taxon and counted using a Zeiss Stemi 508 dissecting microscope with magnification dependent on prey size. Abundances were converted to densities ($\text{ind}\cdot\text{m}^{-3}$). To calculate the volume of filtered water ($1.925\ \text{m}^{-3}$), the area of the sled mouth ($0.055\ \text{m}^{-2}$) was multiplied by distance trawled (35 m).

Following mesozooplankton sampling, macrozoobenthic communities were sampled by taking three replicate sediment samples at each of the nine sampling sites using a Van Veen grab. The grab collected approximately $0.09\ \text{m}^2$ of sediment. Each sample was then rinsed through a 500-μm mesh sieve to collect the macrozoobenthos. Samples were then placed in a 1-L bottle with 7% magnesium chloride

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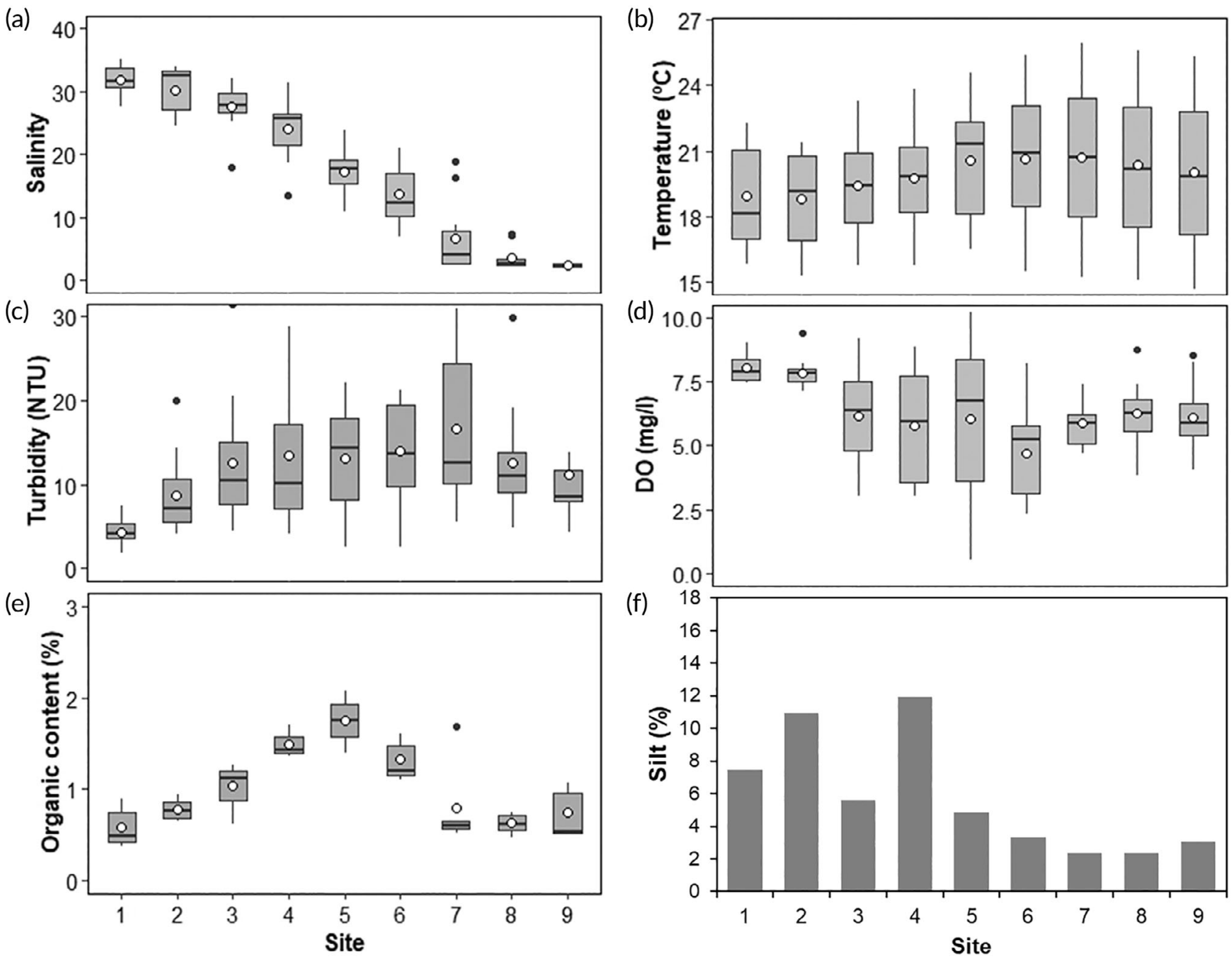

FIGURE 2 Box plot and bar plots showing environmental variables (a–f) recorded in the Sundays Estuary. Boxes represent the upper and lower limits of the third and first quartiles, whiskers represent the range, and thick solid lines represent the median. Black dots represent outliers and white circles represent the mean.

to anaesthetise the animals. To rinse the magnesium chloride from the sample, a smaller size mesh (200 μm) was used. The samples were then later fixed in 4% formalin and stained using Rose Bengal. Sorting and processing were done under a Zeiss Stemi 508 dissecting microscope. Organisms were sorted based on their taxonomic groups (polychaetes, gastropods, bivalves) and then identified to the lowest possible taxon level and counted. The mean macrozoobenthic density was calculated (ind·m^{-2}). To obtain mean density, an average of the three samples was taken per sampling site.

3 | RESULTS

3.1 | Habitat partitioning

Euhaline salinity conditions (30.0–39.9) were confined to the lower reaches, specifically at sites 1 and 2. Polyhaline conditions (18.0–29.9) extended from sites 3 to 6, while mesohaline conditions (5.0–17.9) were observed at sites 7 and 8. Oligohaline conditions (0.5–4.9) were limited to site 9 (Figure 2a). Mean bottom water temperatures increased from 18.9°C at site 1 near the mouth to 20.7°C at site 7 in the upper reaches (Figure 2b). The highest turbidity levels (13.1–16.6 NTU) were recorded in the middle reaches (sites 5 and 6) compared to other sites, which ranged from 4.3 to 12.6 NTU (Figure 2c). Dissolved oxygen levels were notably low at site 6 in the middle reaches, with a mean of 4.7 mg/L (Figure 2d). Organic content was highest in the middle reaches (sites 4–6), ranging between 1.3% and 1.7% (Figure 2e). The lower reaches had the highest silt content, varying from 5.6% at site 3 to 11% at site 4 (Figure 2f).

A total of 541 *C. gilchristi* (27.3 fish 1000 m^{-2}), 421 *P. knysnaensis* (21.3 fish 1000 m^{-2}) and 367 *G. callidus* (18.5 fish 1000 m^{-2}) were caught from July 2017 to September 2019. The three species exhibited habitat partitioning in spring, summer and autumn (Figure 3). Juvenile (<40 mm TL) and adult (>40 mm TL) *P. knysnaensis* were primarily found at site 1 near the estuary mouth, with adult individuals also occurring in the upper reaches, except during summer. Juvenile

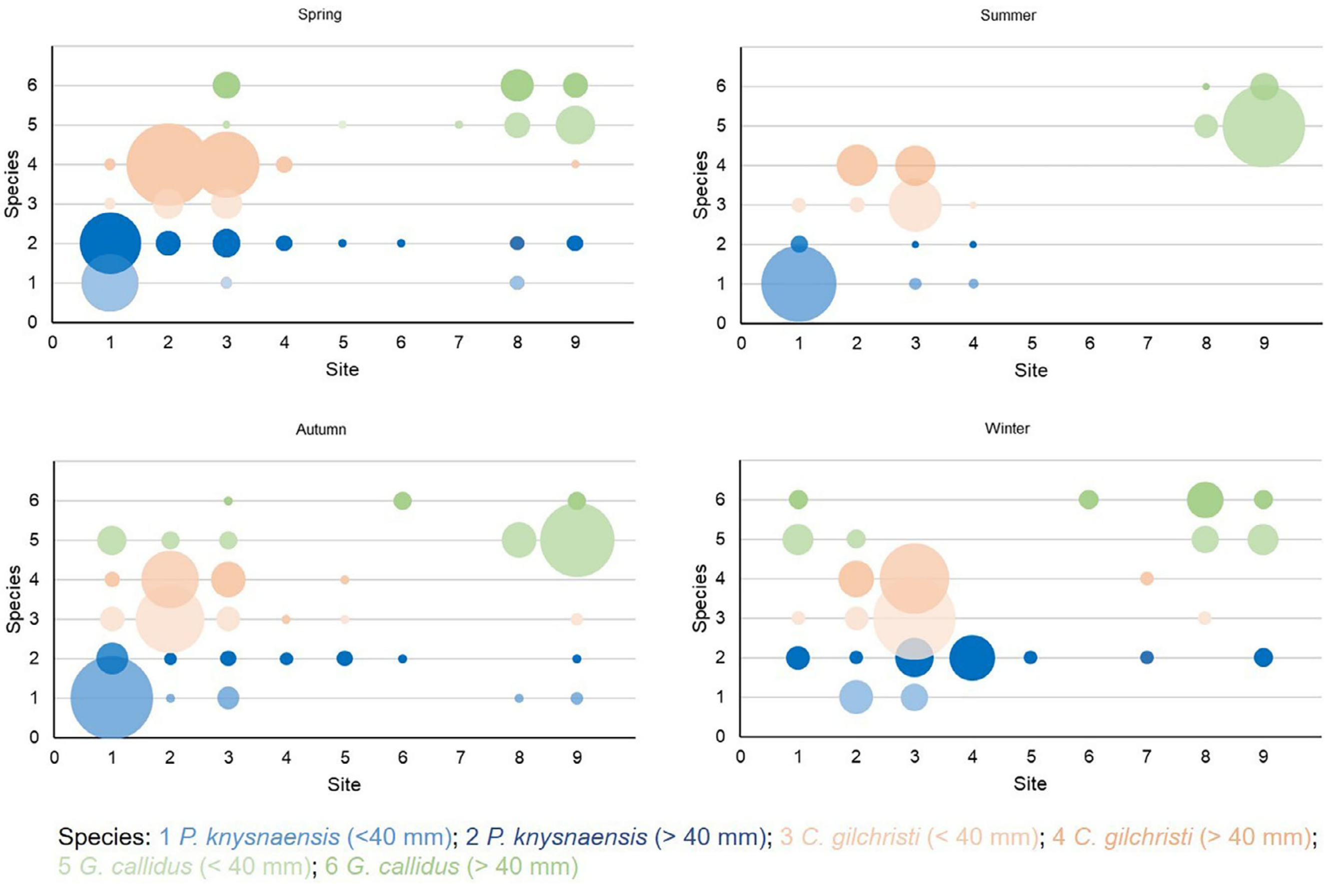

FIGURE 3 Bubble plots showing the catch-per-unit-effort (CPUE) (fish 1000 m^{-2}) of juvenile (<40 mm TL) and adult (>40 mm TL) *P. knysnaensis*, *C. gilchristi* and *G. callidus* in the Sundays Estuary.

TABLE 1 Spearman rank correlation coefficient of *Psammogobius knysnaensis*, *Caffrogobius gilchristi* and *Glossogobius callidus* and environmental variables.

Species	*n*	Salinity	Turbidity	Temp	DO	Organic content	Silt
P. knysnaensis	421	0.34**	−0.25*	−0.07	0.27**	−0.21*	0.15
C. gilchristi	541	0.32**	−0.10	−0.09	0.23*	−0.06	0.29**
G. callidus	367	−0.36**	−0.02	0.18	−0.09	−0.25*	−0.25*

Abbreviations: DO, dissolved oxygen; *n*, number of individuals; Temp, temperature.
*$p < 0.05$.**$p < 0.001$.

(<40 mm TL) and adult (>40 mm TL) *C. gilchristi* were mainly found at sites 2 and 3 in the lower reaches, while *G. callidus* juveniles (<40 mm TL) and adults (>40 mm TL) were concentrated at sites 8 and 9 in the upper reaches. In winter, *P. knysnaensis* and *G. callidus* were distributed throughout the estuary, with only *C. gilchristi* being abundant at sites 2 and 3.

The distribution and abundance of *P. knysnaensis* were significantly positively correlated with salinity and dissolved oxygen, and negatively correlated with turbidity and organic content (Table 1). *Caffrogobius gilchristi* was positively correlated to salinity, silt and dissolved oxygen. The species was negatively correlated with turbidity and organic content. *Glossogobius callidus* dominated the upper reaches of the Sundays Estuary and showed a significant negative correlation with salinity, organic content and silt (Table 1).

3.2 | Feeding morphology

The first three dimensions of the PCA ordination of the functional feeding traits of the three species represented 17.0%, 13.8% and 9.4% of the total variation (Figure 4a,c). The feeding morphology of *P. knysnaensis* separated from the other two species, mostly through larger gill arch resistance, anal fin area and gut length. *Glossogobius callidus* and *C. gilchristi* overlapped, and were characterised by higher body roundness, body depth and caudal peduncle depth than *P. knysnaensis* (Figure 4a,c). Some individuals of *G. callidus* separated out and were characterised by larger opercular volume capacity.

The first three dimensions of the PCA ordination of the trophic profiles represented 37.2%, 28.3% and 14.6% of the total variation (Figure 4b,d). The trophic profile of *C. gilchristi* overlapped completely with *P. knysnaensis* and *G. callidus*, with this species potentially a

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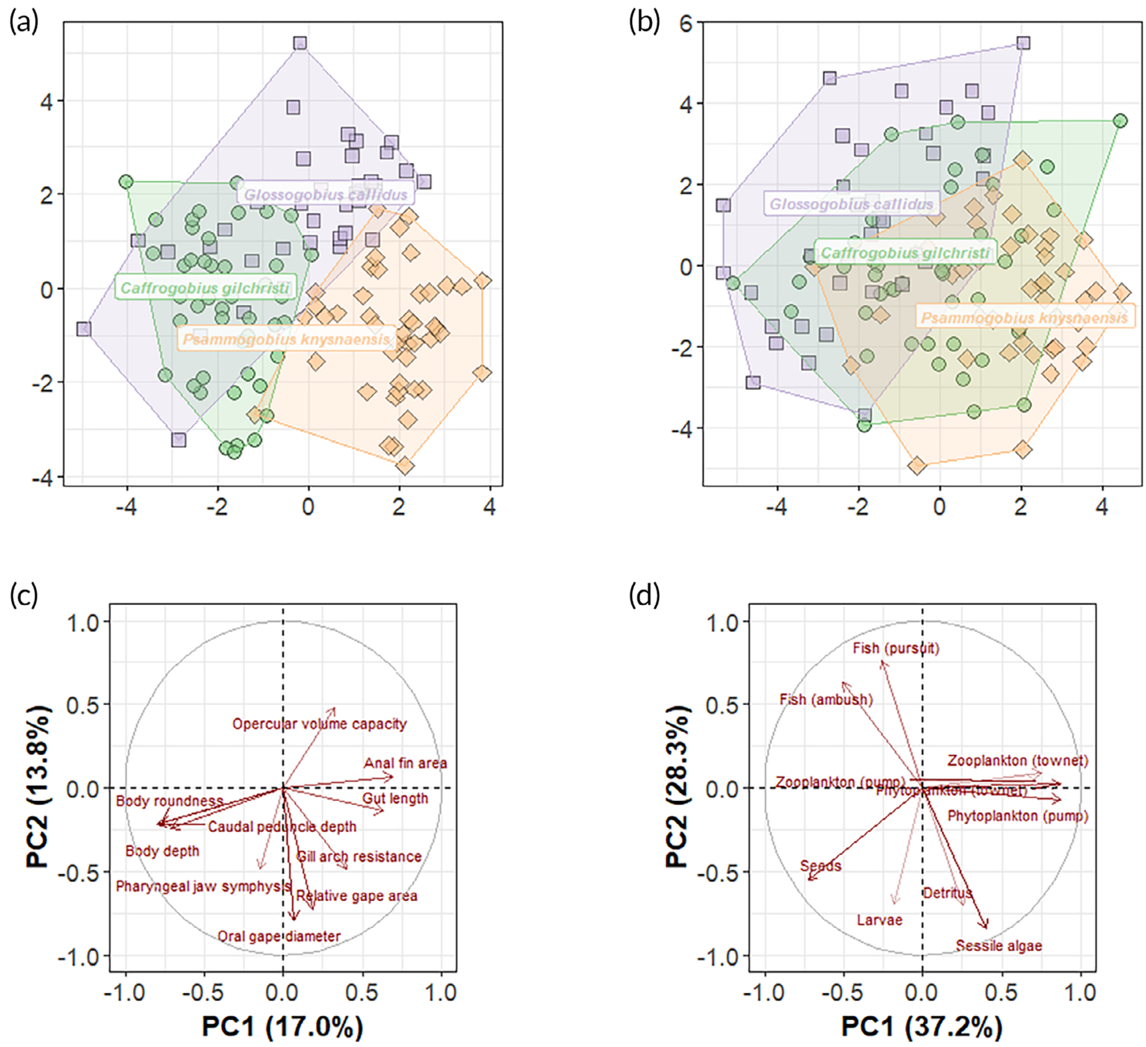

FIGURE 4 Principal component analysis of (a, c) the 32 measured functional feeding traits and (b, d) trophic profiles of *Psammogobius knysnaensis*, *Caffrogobius gilchristi* and *Glossogobius callidus* collected from the Sunday Estuary.

generalist (Figure 4b). *Glossogobius callidus* is predicted to be better at preying on larger prey (such as fish). *Psammogobius knysnaensis* is predicted to be better at preying on small prey (phytoplankton and zooplankton), sessile algae and detritus (Figure 4d).

3.3 | Diet

In total, 276 foreguts were examined for *P. knysnaensis*. Of the foreguts analysed only two were empty. A total of 13 prey taxa represented the diet of this species, with ostracods and cyclopoids dominating the diet of this species both in %IRI and %*N* (Table 2). Diet composition significantly changed ($\chi^2 = 377.8$, $df = 48$, $p < 0.05$) with fish size (Figure 5), with an ontogenetic shift in diet occurring from 30 to 39 mm TL, with ostracods and cyclopoids together comprising less than 50% of the diet in larger individuals (<50% IRI) (Table S2). In individuals of 40–49 mm TL, bivalves contributed 52.9% IRI. This prey item was only recorded in the foregut of individuals larger than 30 mm. Amphipod consumption increased with fish size, with amphipods recorded in the largest numbers in the largest size class (50–59 mm TL) (%IRI = 31.26%). Chironomids (%IRI = 3.08%) were also most prevalent in the diet of the largest size class (Table S2).

A total of 154 foreguts of *C. gilchristi* were analysed. Of all the foreguts analysed, only one was empty. A total of 12 prey taxa were identified in the diet of *C. gilchristi*, with Cyclopoida having the highest contribution (20–49 mm = >70%, >49 mm = >20%) to this species' diet both in terms of %IRI and %*N* (Table 2). Prey consumption changed significantly with fish size ($\chi^2 = 165.4$, $df = 33$, $p < 0.05$). An ontogenetic shift in diet occurred from 50 mm TL, when cyclopods comprised less than 50% of the diet (<50% IRI) (Tables 2 and S3). Gastropoda were only recorded in the foregut of individuals greater than 30 mm TL, and their proportion in the diet increased with fish size. Brachyura, although consumed by all size classes, were recorded in the greatest numbers in the smallest (20–29 mm TL) (IRI = 3.79%) and largest (50–59 mm TL) (IRI = 7.28%) size classes. Ostracods, although also consumed by all size classes, comprised a relatively

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TABLE 2 Foregut contents of *Psammogobius knysnaensis*, *Caffrogobius gilchristi* and *Glossogobius callidus* sampled in the Sundays Estuary.

	P. knysnaensis				***C. gilchristi***				***G. callidus***			
	(*n* = 276; 17.1–62.2 mm TL)				**(*n* = 154; 20.5–94 mm TL)**				**(*n* = 146; 19.1–83.4 mm TL)**			
Prey taxa	**%*N***	**%*F***	**%*V***	**%IRI**	**%*N***	**%*F***	**%*V***	**%IRI**	**%*N***	**%*F***	**%*V***	**%IRI**
Ostracoda	37.1	26.9	5.8	**30.1**	7.7	14.7	<0.1	**2.4**	2.3	2.7	0.3	0.1
Cyclopoida	36.5	38.0	13.5	**49.6**	67.4	63.5	0.2	**92.3**	47.0	45.3	16.3	**42.8**
Chironomidae	1.0	8.2	1.2	0.5	1.2	5.1	<0.1	0.1	17.1	50.7	7.9	**18.9**
Amphipoda	5.0	15.4	3.7	**3.5**	7.9	12.2	<0.1	**2.1**	25.4	57.4	14.6	**34.3**
Cyclopoid eggs	2.3	1.7	0.1	0.1	–	–	–	–	–	–	–	–
Mysidae	1.2	9.0	5.2	1.5	2.9	15.4	0.1	1.0	0.4	2.0	1.5	0.1
Baetidae	0.2	2.2	0.2	<0.1	–	–	–	–	5.7	20.9	5.9	**3.6**
Brachyura	0.7	6.5	1.6	0.4	1.8	13.5	<0.1	0.5	0.2	1.4	0.1	<0.1
Fish eggs	–	–	–	–	3.6	1.3	<0.1	0.1	–	–	–	–
Bivalve	13.0	21.5	10.7	**13.3**	0.1	0.6	<0.1	<0.1	–	–	–	–
Cumacea: Bodotriidae	1.1	10.4	1.1	0.6	0.2	2.0	<0.1	<0.1	–	–	–	–
Gastropoda	1.1	7.5	0.7	0.4	6.6	9.6	<0.1	**1.4**	1.1	2.0	0.9	0.1
Fish larvae	0.1	0.7	0.2	<0.1	–	–	–	–	0.1	0.7	0.3	<0.1
Polychaeta	0.5	1.8	0.6	0.1	0.1	0.6	<0.1	<0.1	–	–	–	–
Glyceridae	–	–	–	–	0.4	3.2	<0.1	<0.1	–	–	–	–
Calanoid	0.3	0.4	0.4	<0.1	–	–	–	–	0.8	3.4	0.1	<0.1

Note: %*N* is the number of individuals as a proportion of all prey items and %IRI is the index of relative importance as a proportion of the total IRI of all species sampled. Bold values indicate high %IRI contribution.
Abbreviations: %*F*, frequency of occurrence; %*N*, prey abundance; %*V*, percentage volume; IRI, index of relative importance; TL, total length.

small proportion of the diet in all size classes (0.63–5.56 %IRI) (Table S2).

A total of 146 foregut of *G. callidus* were analysed. Of the foreguts analysed only one was empty. A total of 10 prey taxa were identified in the diet of this species (Tables 2 and S2), with amphipods, chironomids and cyclopoids being dominant in the diet of this species. An ontogenetic dietary shift was observed at 40 mm, as above this length the consumption of cyclopoids was less than 50% IRI, with amphipod, chironomids and baetidae increasing in importance. Calanoid (IRI = 1.23%) and mysid (IRI = 8.74%) consumption was only noticeable in the diet of the largest size class (>69 mm).

Niche breadth was highest for *G. callidus* (0.35) followed by *P. knysnaensis* (0.30) and *C. gilchristi* (0.27).

Both the cluster analysis and nMDS analyses showed two statistically significant clusters at a similarity of 62.7% (SIMPROF, $p < 0.05$). All *G. callidus* grouped along with *P. knysnaensis* less than 20 mm. This group is characterised by cyclopoida, chironomidae, amphipoda and baetidae. *Psammogobius knysnaensis* (20–50 mm) grouped together with all size classes of *C. gilchristi* characterised by ostracoda, cyclopoida and amphipoda (Figure 5).

3.4 | Prey resources

Mesozooplankton comprised nine different taxa (Table 3), with 15 macrozoobenthic taxa identified in total (Table 4). In terms of taxa important in the diet, cyclopoids were important in the diet of all three species and were found at sites 1, 6 and 8 (Table 3). Ostracods, which dominated the diet of *P. knysnaesis*, were most abundant at sites 1 and 3 (Tables 3 and 4). Bivalves, which were only recorded in the diet of large *P. knysnaensis*, were most abundant at site 1 (Table 4).

Brachyura, which were important in the diet of small *C. gilchristi*, were only recorded at sites 1 and 3 (Table 4). Gastropods, which were important in the diet of *C. gilchristi* larger than 50 mm, were most abundant at site 3 (Table 3). Amphipods, which were important in the diet of *G. callidus* were most abundant at site 9 (Table 4), while chironomids, which were also important in the diet of *G. Callidus*, were most abundant in the upper reaches (Tables 3 and 4). Baetidae, important in the diet of larger *G. callidus*, were most abundant at sites 6, 8 and 9 (Tables 3 and 4).

4 | DISCUSSION

Although there was high morphological overlap between *C. gilchristi* and *G. callidus*, suggesting the potential to compete for food resources, in the Sundays Estuary these two species occurred in different habitats, with *C. gilchristi* dominant in the lower reaches and *G. callidus* in the upper reaches. Despite similarity in feeding traits, the diets of these two species were also significantly different. Although cyclopoids were important in the diet of both species, chironomids

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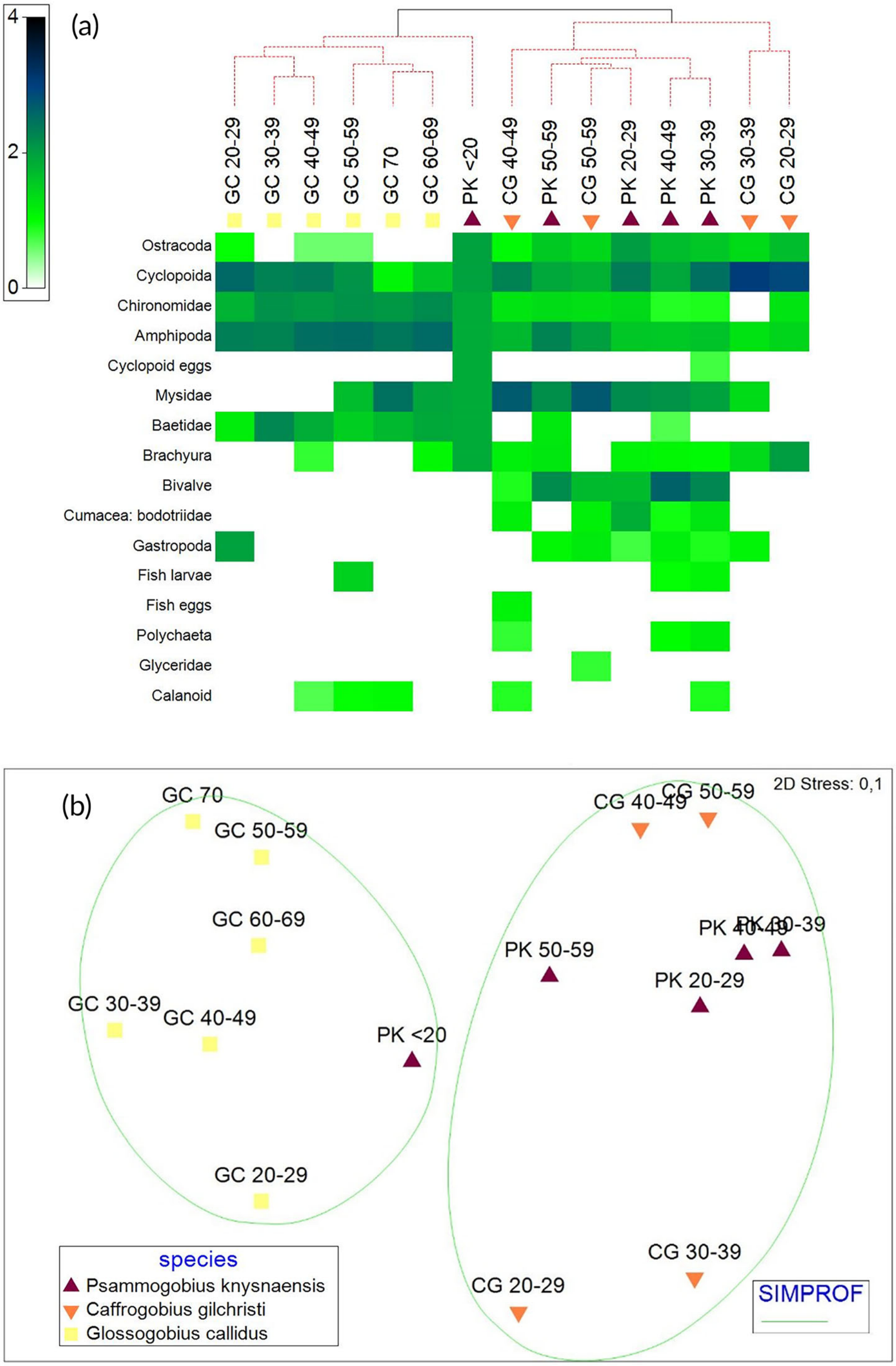

FIGURE 5 Cluster ordination, similarity profile routine (SIMPROF) groupings and shade plot (a) and non-metric multidimensional scaling (nMDS) and SIMPROF groupings (b) of fourth-root transformed dietary similarities (% V) of *Psammogobius knysnaensis*, *Caffrogobius gilchristi* and *Glossogobius callidus* sampled in September/October 2018 and August 2019 from the Sundays Estuary.

and amphipods, which were abundant in the upper reaches, were important in the diet of *G. callidus*, while ostracods, which were abundant at sites 1 and 3, were important in the diet of *C. gilchristi*. The dominance of cyclopoids in the diet of gobies is a common phenomenon within this family (Mesa et al., 2008; St. John et al., 1989) and this may be due to their high abundance. Although there were differences in the feeding morphology of *P. knysnaensis* and *C. gilchristi*, suggesting differences in feeding preferences, the diets of these two species overlapped. This suggests that habitat partitioning in the lower reaches, with *P. knysnaensis* occurring nearer the mouth (site 1), enables the two species to coexist in this reach while feeding on similar prey. As both species require the marine environment to complete their life cycle, this could also explain why they dominated in the high saline region (Whitfield, 2024).

To reduce competition for food and promote coexistence, *C. gilchristi* dominated in habitats with high silt, while *P. knysnaensis* dominated in the sandy site near the mouth. Gastropods, which were only consumed in high numbers by *C. gilchristi*, were abundant in sites 2 and 3 (silty sites), while bivalves and ostracods, which were important in the diet of *P. knysnaensis*, were abundant at site 1 (sand site)

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TABLE 3 Density of winter (28 August) 2019 mesozooplankton taxa recorded in the Sundays Estuary.

	Sampling site								
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Branchiopoda					0.5		1.0	31.7	25.5
Calanoida		4281.6		265.5	231.2	1359.5	5.2	22.3	13.0
Cyclopoida	0.5					13.0		1.0	
Decapoda					5.2	22.9	10.9	43.6	1.0
Gastropoda	95.1	57.1	385.5						
Insecta: Baetidae					0.5		0.5	1.6	1.6
Insecta: Chironomidae	3.6					0.5	0.5	13.5	3.1
Mysidae	215.1	164.7	578.7	51.4	560.5	120.5	248.3		
Ostracoda	34.3	7.8	29.1			2.6	8.3	14.0	

Note: Taxa present in the diet of the three goby species are shaded in grey.

TABLE 4 Density of winter (28 August) 2019 macrozoobenthos taxa recorded in the Sundays Estuary.

	Sampling site								
Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Amphipoda						14.8	51.9	25.9	185.2
Bivalvia	177.8		3.7						14.8
Calanoida	3.7	3.7			3.7				
Cypridopina		14.8						85.2	463.0
Decapoda: Brachyura	7.41		7.41						
Decapoda: *Paratylodiplax* spp	11.1	255.6							
Decapoda: *Upogebia africana*			3.7						
Gastropoda	207.4	1125.9	4644.5	677.8	18.5	18.5	148.1	129.6	307.4
Insecta: Baetidae	3.7					3.7		3.7	
Insecta: Chirinomidae			3.7	29.6	7.4	88.9	296.3	25.9	29.6
Isopoda							3.7	103.7	48.2
Malacostraca	7.4								
Mysidae	0.0		3.7		3.7	18.5			3.7
Ostracoda	48.2	7.4							
Polychaeta	318.5	348.2	88.9	333.3	166.7	525.9	1044.5	170.4	1000.0

Note: Taxa present in the diet of the three goby species are shaded in grey.

near the mouth. The consumption of crabs and gastropods by *C. gilchristi* is promoted by a large oral gape and by a relatively large pharyngeal jaw symphysis, which enables a high pharyngeal crushing force (Sibbing & Nagelkerke, 2001).

Glossogobius callidus is a freshwater and estuarine species, and although this species preferred the low salinity upper reaches it can tolerate high saline environments (Nodo et al., 2018). The preference for the upper reaches is likely due to prey availability, with chironomids and amphipods most abundant in this reach, high turbidity and nesting sites, as high abundances of larval fish have been recorded in the upper reaches of estuaries (Wasserman, 2012). This distribution pattern was also evident in the St Lucia Estuary, where *G. callidus* was mostly recorded in the upper reaches (Harris & Cyrus, 2000). Similarly, in the Kariega Estuary, *G. callidus* was mostly recorded in the upper reaches (Nodo et al., 2018), with a high dominance of juvenile fishes recorded during summer months (Ter Morshuizen & Whitfield, 1994).

We expected the focal species to have morphological traits which related to their diet preferences but found that despite differing morphologies their diet was largely similar. Thus, spatial niche partitioning is acting to reduce competition between the species at the moment. Functionally analogous species often exhibit both spatial and trophic partitioning to reduce competition, based on prey availability, foraging characteristics and habitat characteristics (Říha et al., 2025; Werner & Hall, 1979). Lack of difference in diet, despite ecomorphological dissimilarities, could be driven by Liem's paradox, whereby fish with morphological specialisations often exhibit generalist feeding tendencies, so long as resources are abundant (Binning et al., 2009; Liem, 1980, 1991).

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Many fish species change their diet from feeding on small prey with less energy gain to large prey with high energy gain as they develop (Choi & Suk, 2012; Gaughan & Potter, 1997; Guo et al., 2014). This was true in our study, where cyclopoids and ostracods were common in the diet of small individuals of the study species, with the exception of *G. callidus*, which did not prey on ostracods. Bivalves, amphipods, chironomids, baetidae, mysids and gastropods were common in the diet of large individuals. Bennett (1989) also found that juvenile *P. knysnaensis* specialised in consuming ostracods and copepods, while adults specialised in the consumption of amphipods and decapods. Similarly, specialising in cyclopoids during juvenile stages is common in the *Caffrogobius* species. For example, in the Palmiet Estuary, juvenile *Caffrogobius gilchristi* were found to be specialist feeders on cyclopoids (Bennett, 1989). In other related species, such as *Caffrogobius caffer*, copepods were recorded in the diet of juvenile fish, with molluscs only recorded in the diet of adults (Butler, 1980). The diet richness (number of prey taxa) also increased with size for *P. knysnaensis* and *C. gilchristi*.

Our results suggest that prey availability had more influence on realised foraging niche than feeding morphology. This is highlighted in the dominance of cyclopoids across all species stomach contents and within the estuary. Similar results have been recorded in Darter Goby *Gobionellus boleosoma* (Jordan and Gilbert, 1882) and Isaza *Gymnogobius isaza* (Tanaka, 1916) whereby their diet reflects the relative abundance of prey (Briones et al., 2012; Carle & Hastings, 1982). Many species exhibit prey switching and select for the most abundant resources as an evolutionarily stable strategy to reduce pressure on diminishing resources and reduce the costs of foraging for scarce prey (Hughes & Croy, 1993; McCard et al., 2021; Murdoch et al., 1975). However, this is only possible in generalist feeders, which are able to flexibly switch between resources.

The greatest potential for competition between the three species is in the middle reaches of estuaries, where the distribution of *G. callidus* and *C. gilchristi* normally overlaps (e.g. Nodo et al., 2018, 2024; Ter Morshuizen & Whitfield, 1994). For example, in the Kariega Estuary the abundance of these two species is highest in the middle reaches (Nodo et al., 2018). In our study, despite the availability of key prey items, such as amphipods, chironmoids, cyclopods and ostracods, in the middle reaches (sites 6–7) the abundance of all species was very low (0.3–1.7 fish 1000 m^{-2}) in this region, particularly in spring and summer. The Sundays Estuary is surrounded by agricultural activities, with the middle reaches permanently eutrophic (Lemley et al., 2018). The lowest dissolved oxygen concentrations are consistently recorded in the middle reaches of the estuary, with hypoxic (<2 mg/L) conditions indicative of harmful algal blooms recorded during summer and spring (Adams et al., 2020; Lemley et al., 2018; Nodo et al., 2024). Hypoxic conditions can cause habitat squeeze by reducing habitat available for benthic fishes by concentrating populations into smaller geographic areas (Craig & Crowder, 2005; Switzer et al., 2009). In the Sundays Estuary during hypoxic events (<2 mg/L) no demersal fish species are recorded in affected sites, while in the nearby Swartkops Estuary, *C. gilchristi* is one of only two demersal species which is also affected during moderately low dissolved oxygen (2–4 mg/L) events (Nodo et al., 2024). Our study highlights that low dissolved oxygen in the middle reaches consistently reduces the habitat available for coexisting species, particularly in spring and summer.

5 | CONCLUSIONS

The gobiids of the Sundays estuary coexist in sympatry through habitat differentiation and subsequently consuming the most available resources within those habitats. Future perturbations within the estuary may degrade or reduce trophic resources within a given habitat and cause increased habitat overlap and resource competition between the species. In particular, the combined pressures from agriculture and climate change could cause seasonal habitat restriction, with *C. gilchristi* most at risk from physiological stress. This may disrupt interspecific interactions as *C. gilchristi* is functionally more competitive than *G. callidus* and *P. knysnaensis*. Currently, resource abundance is sufficient to support the foodweb of the Sundays Estuary without exacerbating any adverse competitive interactions between the focal species. Endeavouring to maintain habitat integrity with water parameters at ecologically suitable levels will support all trophic levels in persistence.

AUTHOR CONTRIBUTIONS

All authors contributed to the data collection, analysis, writing and editing the manuscript, but J. South, L.A.J. Nagelkerke, O.L.F. Weyl could not assist with data collection as their offices are not located in Gqeberha where the study was conducted.

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SUPPORTING INFORMATION

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