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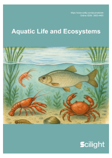

Article

Growth Performance of Three Forage Fish in a Hyper-Saline Lagoon: The Coorong, South Australia

Md. Afzal Hossain [1,2,]*, Shefali Aktar [3], Deevesh A. Hemraj [4], Qifeng Ye [5] and Sophie Leterme [1]

[1] College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia
[2] Department of Fisheries Management, Hajee Mohammad Danesh Science and Technology University (HSTU), Dinajpur 5200, Bangladesh
[3] Department of Biochemistry and Molecular Biology, Hajee Mohammad Danesh Science and Technology University (HSTU), Dinajpur 5200, Bangladesh
[4] Department of Ecoscience, Aarhus University, 399 Frederiksberg, Risø, DK 4000 Roskilde, Denmark
[5] South Australian Research and Development Institute, Aquatic Sciences, 2 Hamra Avenue, West Beach, SA 5024, Australia
* Correspondence: afzal@hstu.ac.bd

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Abstract: The present study investigates environmental impacts on the growth performance of three forage fish: small-mouthed hardyhead (*Atherinosoma microstoma*), Tamar goby (*Afurcagobius tamarensis*), and sandy sprat (*Hyperlophus vittatus*) in the Murray Estuary and Coorong. Fish were sampled using a seine net and fish age was estimated using the daily increment of sagittal otoliths to determine growth patterns of these three forage fishes. The estimated growth rates were 0.019 day^{-1} ($r^2 = 0.98$) for small-mouthed hardyhead, 0.038 day^{-1} ($r^2 = 0.95$) for Tamar goby and 0.016 day^{-1} ($r^2 = 0.94$) for sandy sprat. The length-weight relationship indicated the slope ($b = 2.96$; $r^2 = 0.97$) in small-mouthed hardyhead, ($b = 3.06$; $r^2 = 0.98$) in Tamar goby and ($b = 3.1$; $r^2 = 0.88$) in sandy sprat. Spatiotemporal variation in the condition factor was observed in all three-forage fish across the salinity gradients. Chlorophyll-*a*, water transparency, salinity, and to a lesser extent temperature and oxygen predominantly influenced the growth of forage fish. This study indicates that environmental factors can greatly influence the growth parameters of forage fish. The findings offer new insights into the growth variations of small-bodied forage fish in a reserve estuary with a broad salinity gradient.

Keywords: salinity; chlorophyll; estuary; growth; forage fish

1. Introduction

Estuaries are naturally dynamic environments with varying salinity, high nutrient input from runoff, and high biological productivity. Estuaries support a large biological assemblage of multi-species including fish, waterbirds and invertebrates [1,2]. Globally, estuaries are often subjected to the impacts of anthropogenic development, resource exploitation and river regulation [3]. In estuaries, environmental factors frequently vary and can influence the overall biological productivity [4]. Therefore, the growth and development of estuarine organisms are likely to be affected by salinity change, hydrological alterations and temperature variation [4–6]. Salinity, temperature and food availability are key limiting factors for the growth and development of fish [7–11]. Thus, the ontogeny and life history traits of fish and other organisms can be influenced by natural variability of environmental factors in an estuarine system [12].

The Murray Estuary and Coorong are an inverse estuary and lagoon located at the terminus of Australia's largest river system, i.e., the Murray–Darling Basin. The Murray Estuary and Coorong are important habitats for large-bodied commercial and recreational fishes and small-bodied forage fish species [13]. In the 1940s, a series of dams were built across the Murray Mouth at the Murray Estuary to avoid saline water incursion into the Murray River and the lower Lakes. From 2001 to 2010 the Murray Estuary and Coorong experienced the worst drought in history and low freshwater inflow from up streams [14]. As a result, water salinity has increased throughout the system, generally with marine conditions in the Murray Estuary, marine to hyper-saline at North Lagoon and extremely hyper-saline (>100) at South Lagoon in the Coorong. Hyper-salinity is typical in the Coorong and persists even during the period of high freshwater flow into the Murray Estuary [15]. During drought and low freshwater inflows, hyper-salinity conditions were exacerbated, and the extent increased in the Coorong. Consequently, the ecological condition further degraded throughout the system [14,16]. Salinity is widely considered as key factor driving the ecological and physiological adaptation of fish and other organisms in the Murray Estuary and Coorong [17,18]. Hyper-salinity has adversely impacted the abundance and distribution of vertebrates and invertebrates in the Coorong [19,20]. Salinity influences the abundance of food resources such as phytoplankton [21], picophytoplankton [22] and zooplankton [23] in the Coorong. Therefore, hyper-salinity associated with low freshwater flow can influence the growth and development of estuarine resident and migratory fish species in the Coorong [24].

Forage fish are small-bodied species and commonly fed on by piscivorous fish, birds and mammals in the aquatic ecosystem [25]. Typically, forage fish play an important role by transferring energy from low to high trophic levels (e.g., seabirds, marine mammals and carnivorous fishes) in estuarine and marine food webs [26]. In the Coorong, small-mouthed hardyhead (*Atherinosoma microstoma*), sandy sprat (*Hyperlophus vittatus)* and Tamar goby (*Afurcagobius tamarensis*) are small-bodied fish that are important prey for piscivorous fish and birds [27,28]. Thus, these forage fish are significant players in food webs and are ecologically important to the Coorong commercial fishery [13]. Small-mouthed hardyhead are widespread in temperate streams, inland lakes, estuaries, and adjacent marine areas in south-eastern Australia, Tasmania, Victoria, and the Coorong lagoon in South Australia [29]. In the Coorong, this species is dominant in the South Lagoon and found in the North Lagoon and the Murray Estuary [18,19,30]. Tamar goby is commonly found in Victoria, New South Wales, eastern South Australia and northern Tasmania in Australia [31]. However, the Tamar goby is mainly distributed in the Murray Estuary and part of North Lagoon in the Coorong [18,32]. On the other hand, sandy sprat is common in estuaries and inshore waters in South Australia and is distributed from southern Queensland to southern Western Australia [33]. Sandy sprat moves from sea to the Murray Estuary and, North Lagoon of the Coorong. However, Tamar goby and sandy sprats are completely absent at the South Lagoon in the Coorong [18].

Fluctuation of environmental factors can affect fish growth, development and reproduction in estuaries [5]. At the Bemm River estuary in Australia, freshwater inflow can influence the growth and spawning of the estuary perch *Percalates colonorum* [34]. At the Mundau lagoon in Brazil, salinity has impacted the growth and ontogeny of mullets *Mugil liza* [35]. In the Coorong, the elevated salinity and low freshwater flow have caused spatial and temporal variation in abundance, distribution and assemblage of forage fish [18] and reduced the fish species diversity [36]. The growth rate of sandy sprat larvae is reduced by salinity variation due to irregular freshwater flow in the lower reaches of the Murray River in the Coorong [12]. The changes in life history and reproductive ecology of small-mouthed hardyhead are attributed to food variability associated with salinity change [37]. However, our knowledge on growth performance of small forage fish species under extreme environmental conditions (e.g., salinity) is still limited.

Hyper-salinity usually occurs in the Coorong in dry summer when freshwater flow from the Murray River is low. This study covered the dry season from November to March, when forage fish would experience high salinity stress in Coorong. This study aimed to determine the age-dependent growth pattern of three forage fish that have different habitat preference. We hypothesised that forage fish would display different growth patterns in response to environmental variability. The results of this study would improve our understanding on the impact of salinity and other environmental factors on the growth and body condition of small-bodied fishes that greatly contribute to the forage of commercially important fishes.

2. Materials and Methods

2.1. Study Area

The Murray Estuary and Coorong are an inverse saline lagoon located 70 km south of Adelaide, South Australia (Figure 1). The Murray Estuary is the terminal of the Murray River and connects the estuary and Coorong lagoon with the Southern Ocean by a narrow channel at the Murray Mouth. The Coorong is stretched by >100 km in length, ≈2 m mean depth and <4 km width and separated from the Southern Ocean by a narrow strip of peninsular sand-dune. Typically, the Murray Estuary and Coorong split into three distinct regions: Murray Estuary in the vicinity of the Murray River mouth (salinity 7–21), North Lagoon (salinity 20–76) and the South Lagoon (salinity 76–79) [38]. The Coorong is divided into two main lagoons, the North Lagoon and the South Lagoon. The North Lagoon is separated from the South Lagoon by a narrow and shallow channel at Parnka Point in the Coorong. Overall, the

Murray Estuary and Coorong exhibit an inverse estuarine system with a north-south gradient of increasing salinity from 2 to ~80.

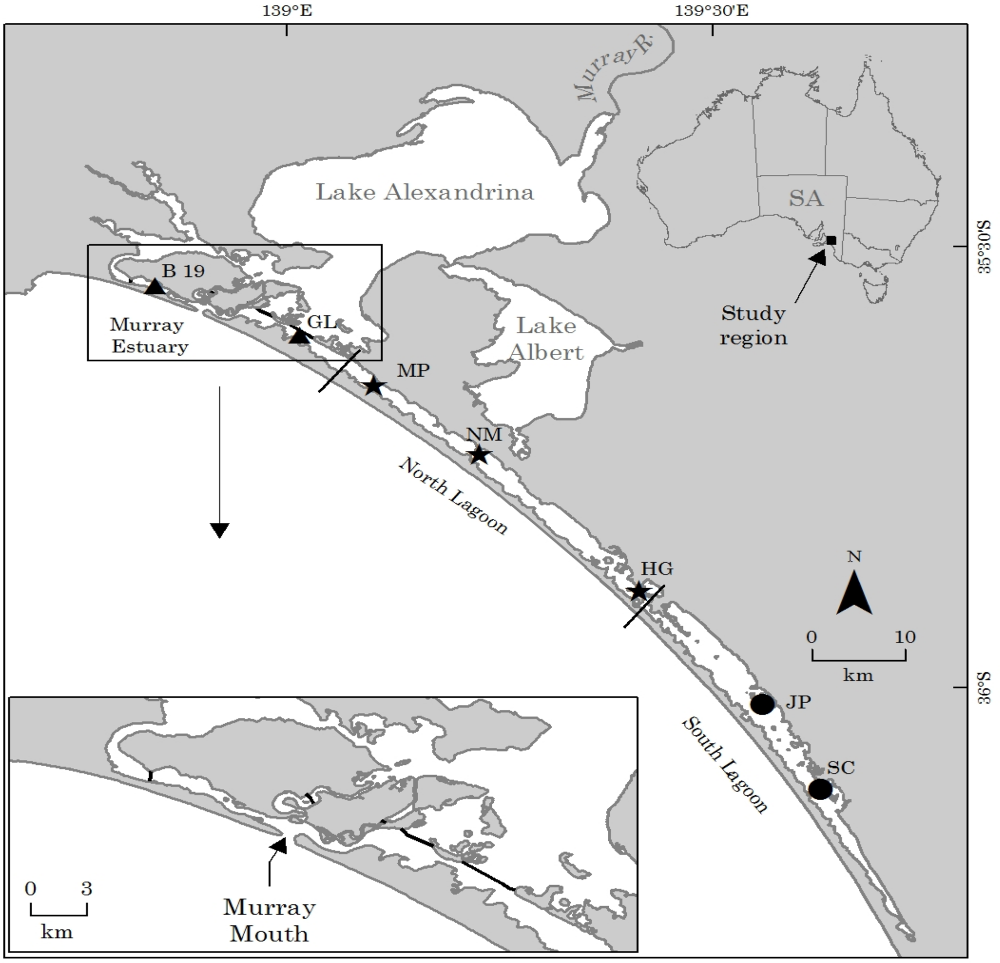


Figure 1. Map of Murray Estuary, North Lagoon and South Lagoon showing the sampling sites; Beacon 19 (B19), Godfry's landing (GL), Mark point (MP), Noonameena (NM), Hells Gate (HG), Jack point (JP) and Salt Creek (SL) in the Coorong, South Australia.

2.2. Data Collection

Sampling was performed at three regions: the Murray Estuary, the North Lagoon and the South Lagoon. Two sites in the Murray Estuary, three sites in the North Lagoon and two sites in the South Lagoon were selected for sampling to cover the existing typical broad salinity gradient in the Coorong. Fish were sampled using a seine net of 61 m long, 29 m wing length (22 mm mesh) and 3 m bunt length (8 mm mesh) at each site. Sampling was conducted every month from November 2013 to March 2014 in a low flow year. The seine net was arrayed in a semi-circle and covered an area of ~ 600 m^2 to a maximum depth of 2 m at each site in the Murray Estuary and Coorong. Of the collected fish at each site, 20 individuals of each species of sandy sprat, Tamar goby and small-mouthed hardyhead were transferred to an aerated holding tank and euthanized using AQUI–S^{TM} (40 mg L^{-1}). The euthanized forage fish were preserved in 10% formalin for otolith collection in the laboratory. The length and weight of each fish species were recorded to the nearest millimeter (mm) for total length (TL) and weighed to the nearest 0.1 gram (g) for wet weight (WW). Zooplankton samples were collected from the fish sampling sites using a modified 35-L Schindler-Patalas plankton trap with a 50-micron mesh. The zooplankton gathered in the cod-end were stored in a 250-milliliter plastic container and fixed in 5% formalin for identification and counting. Additionally, water samples were collected and filtered to measure chlorophyll a concentration using a Turner 450 Fluorometer.

At each sampling site, three replicates of physicochemical variables—including salinity, temperature, dissolved oxygen (DO), and pH—were recorded at 30 cm below the water surface using a water quality meter (TPS 90-FLT Field Lab Water Quality Analyser, Brendale, Australia) around midday. Water transparency was assessed using a Secchi disk at each site on every sampling day. All samples were collected from a boat in the Murray Estuary and North Lagoon, as well as from the shore in the South Lagoon.

2.3. Laboratory Analysis

2.3.1. Zooplankton Identification

Zooplankton samples were poured onto a gridded Greiner square Petri dish (12 × 12 cm^2 (Greiner Bio-One, Kremsmünster, Austria) for identification and quantification. Using an inverted microscope (Nikon Eclipse TS100F, Tokyo, Japan), the zooplankton individuals were identified and counted to the lowest possible taxonomic level, following established identification keys [39–43].

2.3.2. Otolith Preparation

Sagittal otoliths were extracted from the small-mouthed hardyhead (n = 135), Tamar goby (n = 60) and sandy sprat (n = 95) using a pair of fine forceps (Dumont AA-Epoxy coated Forceps, Dumont, Montignez, Switzerland) on a dissecting microscope (Olympus SZ30, Olympus Corporation, Tokyo, Japan) in the laboratory. Otoliths were then cleaned, dried, labelled and stored in plastic vials. As the otoliths of forage fish are very small in size, the grinding and polishing technique was used to obtain a thin transverse section [44,45]. Otolith was mounted on a glass slide using thermoplastic resin (Crystalbond 509, SPI Supplies, West Chester, PA, USA) in a manner that the anterior half of the otolith extended beyond the edge of the slide. Holding the slide to adjust otolith orientation, the anterior half was hand-ground away using 600 grit wet/dry sand paper. Then the ground face of the otolith was finely polished using three different grades of imperial lapping film (15 µm, 9 µm and 3 µm; Saint-Gobain Abrasives, Lake Forest, IL, USA) based on the otolith's primordium. The slide was then heated, and the remaining half of the otolith was removed and remounted in the center on another glass slide with its polished face down. The posterior half of the otolith was ground and polished until a transverse section of otolith was 250 µm thick and contained the otolith primordium. Immersion oil was used during the reading of the irregular surface for clear visualisation.

2.3.3. Age Determination

The polished otolith mounted on a slide was read and counted for the opaque rings on a compound microscope (Olympus CX40, Tokyo, Japan) for daily age determination (Figure 2). To assess ageing precision, three independent counts of daily increments for each otolith were performed without the prior knowledge of fish length or other data. The average of three readings was considered the age of the fish. In addition, the average percent of error (APE) was used to measure the precision of the estimated age. The otoliths that showed >5% APE were rejected for age estimation [46].

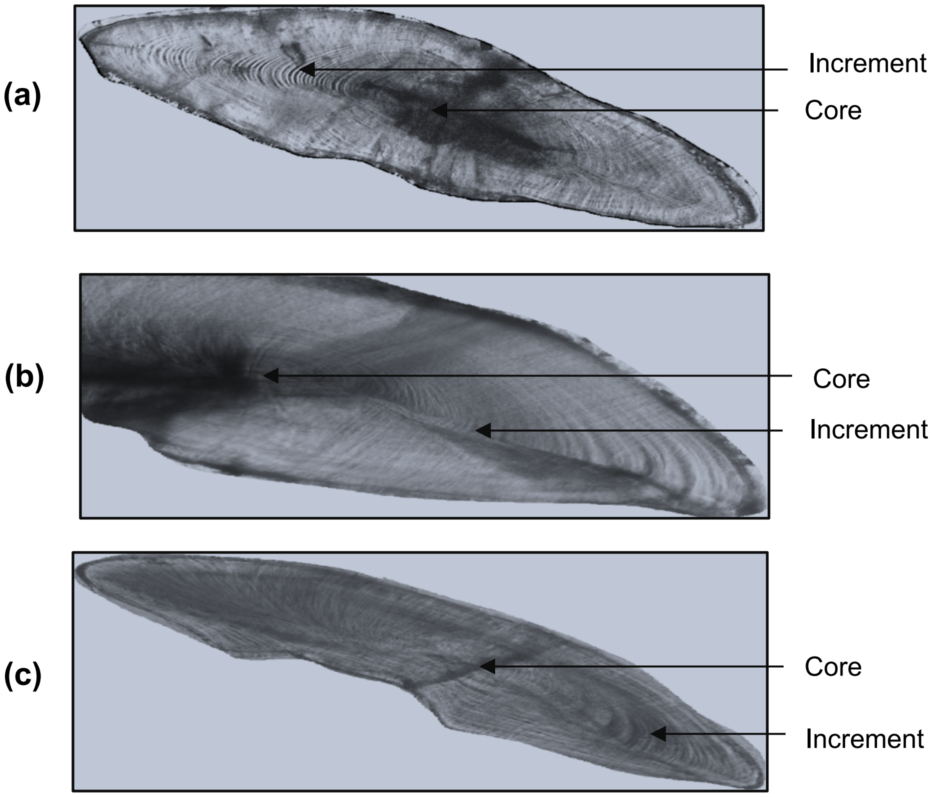


Figure 2. Polished sections of sagittal otoliths of (**a**) small-mouthed hardyhead; (**b**) Tamar goby; and (**c**) sandy sprat displaying daily growth increments (opaque zones; scale bar = 100 µm) from the Murray Estuary and Coorong.

2.3.4. Data Analysis

The average percent error (APE) of counts was calculated using the following formula:

$$APE_j = 100 \times \frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_j}$$

where R represents the number of times the fish are aged, X_{ij} is the ith age determination of the jth fish, and Xj is the mean age estimate for the jth fish [47].

Growth parameters were estimated by fitting the estimated age-at-lengths to the von Bertalanffy growth equation: $L_t = L_\infty\ [1 - e^{K(t-to)}]$, where L_t is total length (TL) at age t, L_∞ is the theoretical asymptotic length, k is the body growth coefficient and t_0 is the theoretical age when fish length is equal to 0. The length-weight relationship of fish was calculated for each forage fish population using the power equation $W = qL^b$, where W is the total weight of the fish (g); L is the total length of fish (cm); q and b are the regression parameters. The 95% confidence limits of b were calculated to estimate differences between the individuals of each forage fish collected at different regions in the Murray Estuary and Coorong [48,49]. The condition factor of each forage fish was estimated to determine the growth performance of each species at different regions in the Murray Estuary and Coorong during the study period. The condition factor (q) of an individual was calculated using the transformed power equation $q = W/L^b$ [50]. The estimated b value from the power equation $W = qL^b$ was applied in the estimation of the condition factor.

2.3.5. Statistical Analysis

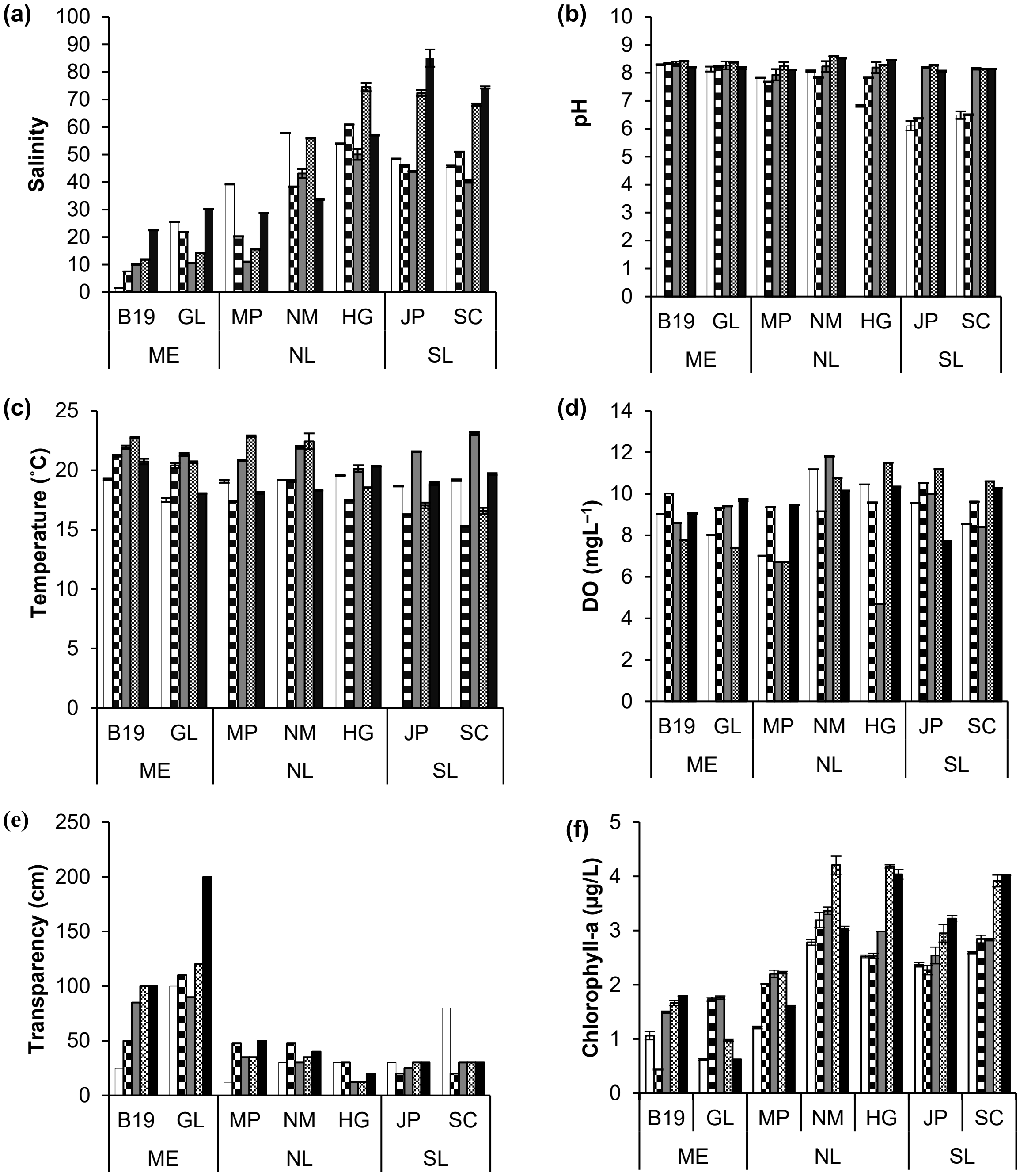
The fourth root transformation of the condition factor data of all three-forage fish was performed before analysis. The fourth root transformed data of the condition factor were used to construct a Bray-Curtis resemblance matrix [51]. The environmental variables were normalised and used to construct a Euclidean distance resemblance matrix. Permutational analysis of variance (PERMANOVA; pseudo-$p > 0.05$) was used to test the univariate non-parametric data. PERMANOVA was run using the resemblance matrices to test the difference of each environmental variable (univariate) and growth performance of all three-forage fish among months and regions in the Murray Estuary and Coorong [52]. In case of growth performance analysis, the model was designed with two factors, including five sampling months as random five levels and three sampling regions as fixed three levels. For analysis of environmental variables, the design consisted of three factors, including months (random, 5 levels), regions (fixed, 3 levels) and sites nested within the region (random, 7 levels). Pairwise post-hoc comparisons using the multivariate analog of the t-test (pseudo-t) were performed at each level to identify significant differences. Unrestricted permutation was performed for each factor and interaction with 999 permutations to detect differences at $\alpha = 0.05$ [53]. A distance-based linear model (DistLM) was performed to identify the effect of environmental and biological variables on condition factor of forage fish. Normalised environmental data, Shannon-Weaver index (H') of zooplankton diversity and fourth root transformed condition factors of forage fish were used in DistLM analysis [51]. A distance-based redundancy analysis (dbRDA) was then plotted during DistLM analysis to give a visual representation of the influence of environmental variables on the variation of condition factors. All tests were performed using PRIMER v6 with the PERMANOVA+ add–on [51].

3. Results

3.1. Environmental Variables

Salinity was significantly different among months ($p = 0.04$) and regions ($p = 0.003$, Figure 3a). In particular, a north-south increasing trend in salinity gradient was observed in the Coorong lagoon. Salinity was highly variable during the study period and ranged 2–30 in Murray Estuary, 11–75 in North Lagoon, and 40–85 in South Lagoon. In the Murray Estuary region, the highest salinity (~31) was measured at Godfrey's landing site in March 2014 while the Beacon 19 site showed the lowest salinity (~2) in November 2013 (Figure 3a). There was a remarkable variation in salinity in the North Lagoon with the highest salinity (~75) at the Hells Gate site in February 2014 and lowest salinity (11) at the Mark Point in January 2014 (Figure 3a). Similarly, the highest salinity (~85) at the Jack Point in March 2014 and the lowest (~40) at the Salt Creek site in January 2014 were measured in the South Lagoon (Figure 3a). In contrast, pH showed the significant spatiotemporal variation among months ($p = 0.001$) and regions ($p = 0.036$, Figure 3b). The pH ranged 8.13–8.42 at Murray Estuary; 6.82–8.59 at North Lagoon and 6.11–8.27 at South Lagoon during the study period (Figure 3b). The highest pH (8.59) was recorded at the Noonameena site in the North Lagoon in February 2014 and the lowest (6.11) was observed at the Jack Point in the South Lagoon in November 2013 (Figure 3b). Water temperature showed temporal variation ($p = 0.001$) and ranged 17.50–22.73 °C in the Murray Estuary, 17.37–22.87 °C in the North Lagoon and 15.27–23.07 °C in the

South Lagoon. Water temperatures were higher in January 2014 and February 2014 compared to other sampling months in the Murray Estuary and North Lagoon (Figure 3c). However, sampling in March 2014 demonstrated comparatively high-water temperature in the South Lagoon and at Hells Gate of North Lagoon (Figure 3c). In addition, the water transparency exhibited significant temporal (months; $p = 0.038$) and spatial variations (regions; $p = 0.006$) over the study period. The highest water transparency (200 cm) was measured at Godfrey's landing site in the Murray Estuary region in March 2014 and the lowest (25 cm) was observed at the Beacon 19 site in November 2014. Water transparency exhibited maximum (50 cm) in March 2014 and minimum (12 cm) at the Mark Point site in the North Lagoon in November 2013. In the South Lagoon, the highest water transparency (80 cm) was detected at the Salt Creek site in November 2013 while the lowest water transparency (20 cm) was recorded at Jack point and Salt Creek sites in December 2013 (Figure 3e). Similarly, chlorophyll-a showed significant temporal (months; $p = 0.024$) and spatial (regions; $p = 0.012$) variations and ranged 0.44–1.79 µg/L in the Murray Estuary, 1.21–4.21 µg/L in the North Lagoon and 2.27–4.03 µg/L in the South Lagoon. The highest chlorophyll-a (4.21 µg/L) was recorded at the Noonameena site in the North Lagoon in February 2014 and the lowest (0.44 µg/L) was observed at the Beacon 19 site in the Murray Estuary in December 2013 (Figure 3f). However, DO and zooplankton diversity did not show any spatial and temporal variation during the study period.



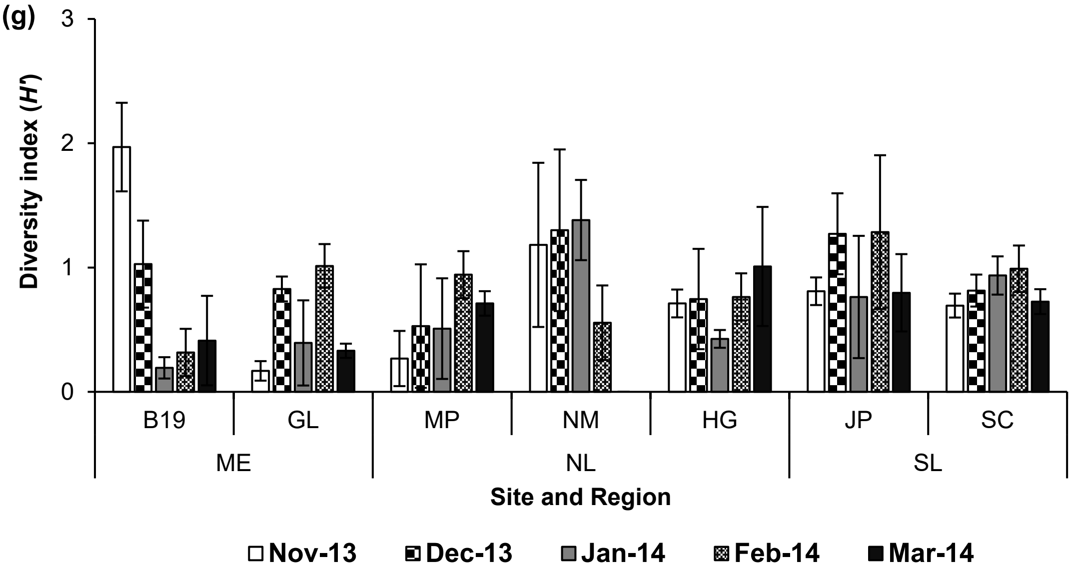
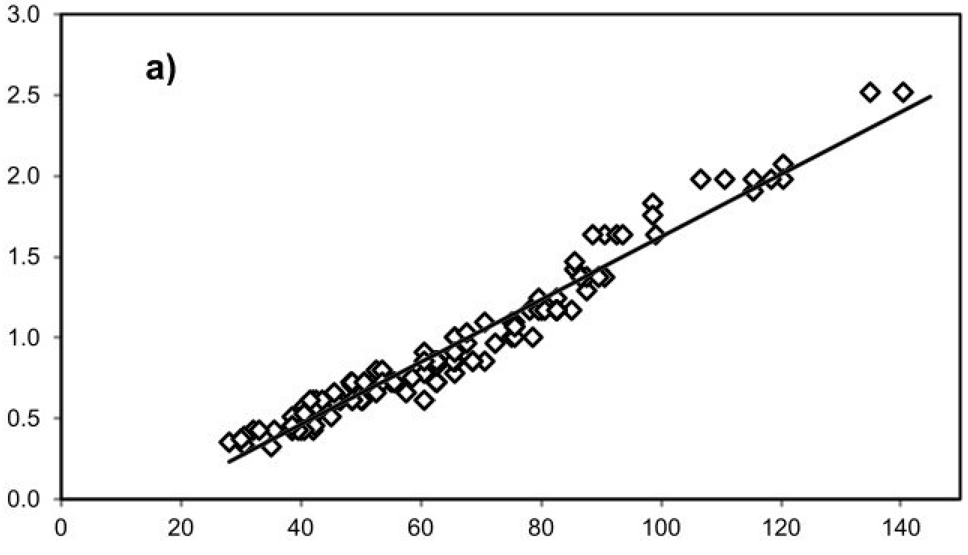


Figure 3. Mean values ± S. E. of (**a**) salinity; (**b**) pH; (**c**) temperature (°C); (**d**) water transparency (cm); (**e**) dissolved oxygen (DO; mgL^{-1}); (**f**) chlorophyll-a (μg/L); (**g**) zooplankton diversity (H') at each site in three regions (ME: Murray Estuary, NL: North Lagoon and SL: South Lagoon) in the Murray Estuary and Coorong form November 2013 to March 2014.

3.2. Growth

Estimated age-at-length data of each individual of each forage fish were fitted to the von Bertalanffy model. In this study, the maximum total length of collected fish (small-mouthed hardyhead = 8.7 cm; Tamar goby = 8.9 cm, and sandy sprat = 7.0 cm) was used as L_α and fitted to the von Bertalanffy model of each forage fish species. The von Bertalanffy model detected the growth rates (K = 0.019 day^{-1}; r^2 = 0.98, Figure 4a) in small-mouthed hardyhead, (K = 0.038 day^{-1}; r^2 = 0.95, Figure 4b) in Tamar goby and (K = 0.016 day^{-1}; r^2 = 0.94, Figure 4c) in sandy sprat in the Murray Estuary and Coorong during the study period. Length-weight relationships were calculated using the data of 512 small-mouthed hardyhead, 226 Tamar goby and 344 sandy sprat. The estimated length and weight relationship were $W = 0.01 \times L^{2.96}$ with r^2 = 0.97 and 95% confidence limits; 2.88–3.04, Figure 4a) in small-mouthed hardyhead. In case of Tamar goby, the relationship showed $W = 0.01 \times L^{3.06}$ (r^2 = 0.98 and 95% confidence limits; 2.88–3.24, Figure 4b). Similarly, the length-weight relationship of sandy sprat was determined as $W = 0.01 \times L^{3.1}$ with 95% confidence limits 2.98–3.22 and r^2 = 0.88 (Figure 4c).



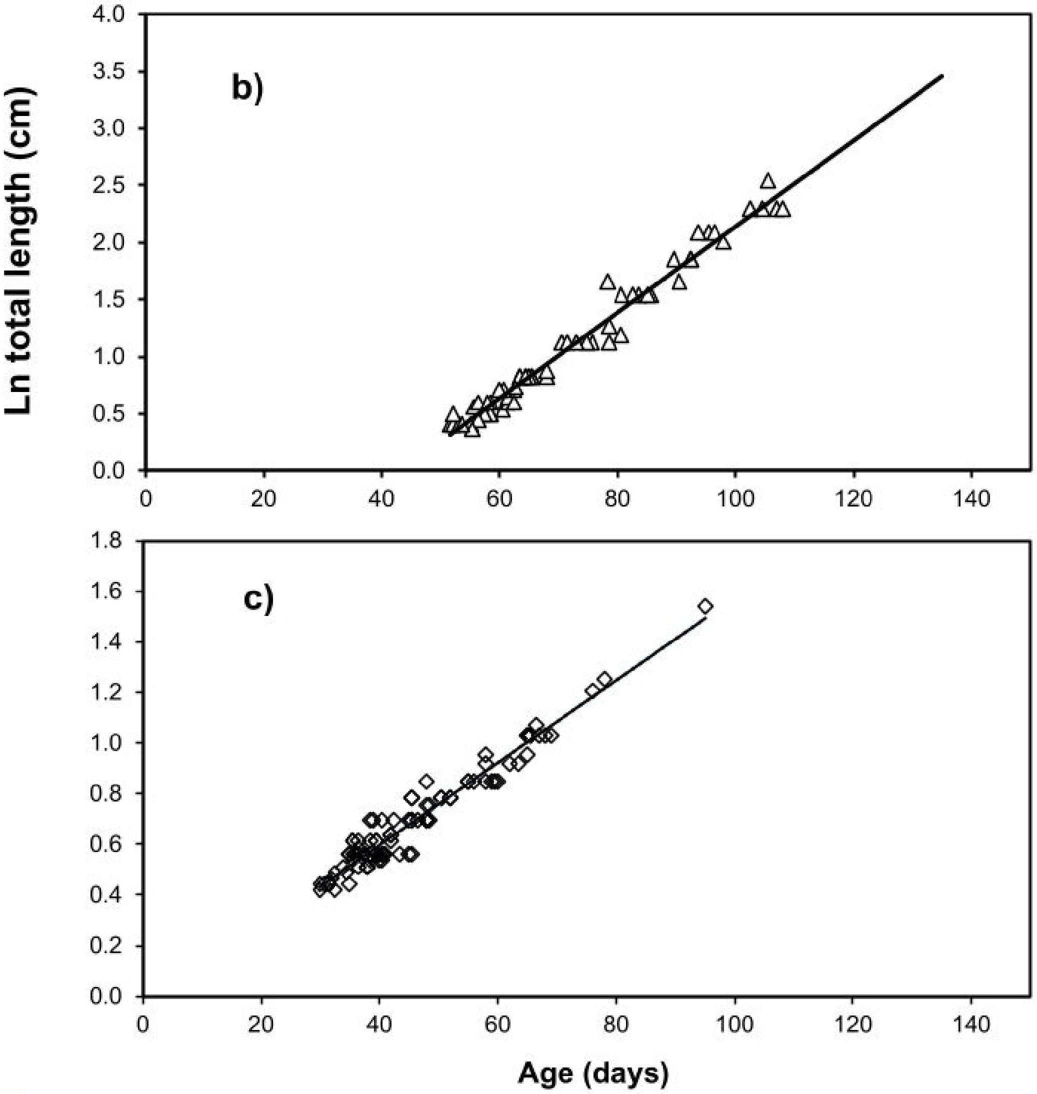


Figure 4. The von Bertalanffy model of (**a**) small-mouthed hardyhead; (**b**) Tamar goby and (**c**) sandy sprat. Natural logarithmic of length at age data were fitted to the model in growth rate estimation of each forage fish species.

3.3. Variation in Condition Factor

PERMANOVA showed a significant spatial (p = 0.004) and temporal (p = 0.001) variation in condition factors of all three-forage fish in the Murray Estuary and Coorong during the study period (Table 1). However, a month-by-region interaction (p = 0.002) was detected in condition factors of all three-forage fish, suggesting that the pattern of variations was not consistent between months and regions. Pairwise test indicated significant differences in condition factors among the months except December 2013 vs. January 2014, December-2013 vs. March 2014 and January-14 vs. March-14 (Table 2). Similarly, condition factors of forage fish were significantly variable among the regions except between the South Lagoon and the North Lagoon of the Coorong.

Table 1. PERMANOVA results of condition factors of all three-forage fish at different regions in the Murray Estuary and Coorong. This PERMANOVA table includes fixed factors contributing to the changes of condition factor during this study. Significant difference was set at $p < 0.05$.

Source	df	SS	MS	Pseudo-F	*P* (Perm)
Month	4	586.22	146.55	10.375	0.001
Region	2	2015.50	1007.80	17.255	0.004
Month × Region	8	468.79	58.60	4.148	0.002
Residuals	1099	15524	14.136		

Table 2. PERMANOVA results of pair-wise comparison between the months and regions of condition factor of all three forage fish species in the Murray Estuary and Coorong.

Groups	Pseudo-*t*	*P* (Perm)
13 November vs. 13 December	5.216	0.001
13 November vs. 14 January	4.771	0.001
13 November vs. 14 February	3.626	0.002
13 November vs. 14 March	5.632	0.001
13 December vs. 14 January	0.228	0.929
13 December vs. 14 February	2.592	0.003
13 December vs. 14 March	0.326	0.755
14 January vs. 14 February	2.468	0.013
14 January vs. 14 March	0.514	0.636
14 February vs. 14 March	2.586	0.014
South Lagoon vs. North Lagoon	1.710	0.164
South Lagoon vs. Murray Estuary	3.968	0.036
North Lagoon vs. Murray Estuary	5.694	0.005

3.4. Environmental Effects on Growth Performance

Salinity (DistLM, $p = 0.001$), water transparency (DistLM, $p = 0.001$) and chlorophyll-a (DistLM, $p = 0.001$) were the most influential variables to predict the spatial and temporal variations in condition factor of all three-forage fish in the Murray Estuary and Coorong (Table 3). These three variables were the best combination of predictors on the variation in condition factor, which together contributed 36% (proportion: 0.36) to the variation. However, water temperature and DO were also significant in the model (DistLM, $p < 0.05$), but these variables together explained only 0.8% (proportion: 0.008) variation of condition factor (Table 3). Similarly, in the dbRDA analysis, the first two axes (i.e., dbRDA1 and dbRDA2) explained 100% of the variability in forage fish condition factor. At the same time, chlorophyll-a, salinity and water transparency were the main driving factors of that variability (Figure 6).

Table 3. DistLM sequential results of environmental and biological variables on the condition factor of all three forage fish species at different regions in the Murray Estuary and Coorong over the study period (SS=Sum of Square; Prop = Proportion of the variation; Cumul = Cumulative variation).

Variable	SS (trace)	Pseudo-F	DistLM *p*	Prop.	Cumul.
Salinity	1109.70	70.56	0.001	0.060	0.060
pH	27.42	1.74	0.180	0.001	0.061
Temperature	97.93	6.26	0.008	0.005	0.066
Dissolved oxygen (DO)	54.91	3.52	0.049	0.003	0.069
Water transparency	1373.00	95.47	0.001	0.074	0.143
Chlorophyll-a	4241.40	401.50	0.001	0.228	0.371
Zooplankton diversity	4.21	0.40	0.562	0.001	0.371

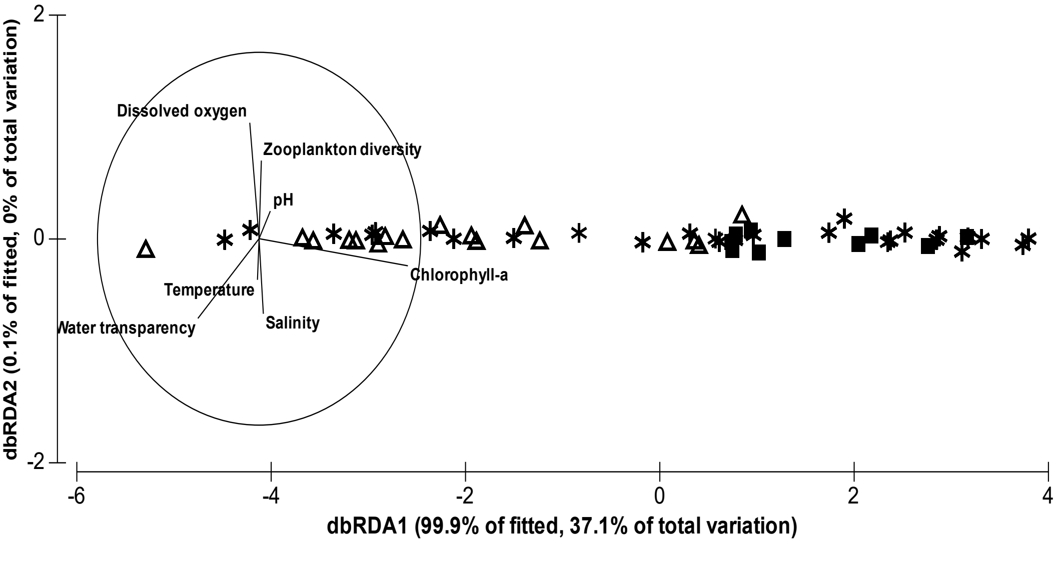


Figure 6. Shows a dbRDA ordination of the fourth root transformed condition factor of forage fish across three regions in the Murray Estuary and Coorong. This ordination is compared against various predictor variables: chlorophyll-a, water transparency, salinity, pH, water temperature, dissolved oxygen (DO), and zooplankton diversity. The data points are represented with different symbols: triangles for the Murray Estuary, asterisks for the North Lagoon, and squares for the South Lagoon.

4. Discussion

The growth coefficient and L_∞ derived from the von Bertalanffy model indicate rapid growth of small-mouthed hardyhead and Tamar goby. In the current study, the estimated growth rate was 0.019 mm day^{-1} and L_∞ = 8.7 cm for small-mouthed hardyhead. Previous studies presented similar growth pattern of small-mouthed hardyhead found the Coorong [37,54,55]. Small-mouthed hardyhead is a multiple spawner with a protracted breeding season from September to December in the Coorong and exhibits post-breeding mortality at the end of the first-year spawning [37,55]. In October, fish larvae usually start to recruit to the spawning population, and most adults die in November/December after spawning [37]. It is therefore likely that the fast growth is an adaptation for early recruiting to the spawning population.

Likewise, the Tamar goby has a short lifespan of 1–2 years [31]. The Tamar goby is a ubiquitous spawner and spawns mainly during spring (October–December), but spawning lasts over 5 months [56]. In the current study, the growth rate of Tamar goby was 0.38 mm day^{-1} with the largest size of 8.9 cm in the Coorong. Of the goby species, the Tamar goby is usually most abundant in the lower reaches of the Murray River Estuary and the North Lagoon in the Coorong [19]. The extended spawning season with greater recruitment of Tamar goby is usually accomplished during spring and summer in the Coorong [56]. Therefore, current growth pattern of Tamar goby coincided with the recruitment of the young in the dry season.

In the present study, sandy sprat showed the growth rate 0.16 mm day^{-1} with L_∞ = 7 cm in the Murray Estuary and Coorong. Other study reported the average growth rate of 0.12 mm day^{-1} for the 20.1–27.6 mm length sandy sprat in the Coorong [12]. Despite the slow growth of sandy sprat in previous studies in the Coorong [12] and on the coast of south-western Australia [57], this species showed more rapid development in the Murray Estuary and Coorong in this study. In particular, the growth and abundance of sandy sprat are strongly related to the freshwater inflow and salinity regime in the Coorong [13]. Sandy prat requires marine conditions for spawning, though this species uses estuaries as feeding and nursery habitats [57]. In this study, marine salinity at the Murray Estuary and the North Lagoon might stimulate the spawning of sandy sprat during the study period, and the rapid growth of new recruits could potentially be mediated by the increased productivity associated with freshwater inflows to the Murray Estuary.

Length-weight relationship indicates a positive isometric growth (slope b = 3.04) for small-mouthed hardyhead in the Coorong. Our finding is similar to the growth (b = 2.79–3.13) of this species in the Coorong two decades ago [37] and other atherinids such as sand smelt *Atherina boyeri* (b = 3.33) at Mellah Lagoon in Eastern Algeria [58]. Growth variation (*b* values) in fish can be influenced by environmental variables, including salinity and temperature in the estuary [59]. Particularly, salinity variation is an overwhelming factor influencing fish growth through extra energy spent on osmoregulation in the estuary [7]. Small-mouthed hardyhead is a euryhaline estuarine fish and tolerates a wide range of salinity fluctuation (LD_{50}: 3.3–108 g L^{-1} both in the laboratory and field [60]. The ability of salinity tolerance enables the wide distribution of small-mouthed hardyhead across different regions in the Coorong [32]. In this study, the fast growth of small-mouthed hardyhead is most likely attributed to its wide salinity tolerance that allows this species to explore abundant food resources in the Coorong.

Tamar goby (slope b = 3.06) also showed positive allometric growth in the Coorong. The growth of Tamar goby is similar to other gobids where the rock goby *Gobius paganellus* shows allometric growth (b = 3.163) in Azores, Portugal [61]. Tamar goby in the Coorong shows LC_{50} salinity tolerance of 73.2 at 14 °C (winter) and 71.4 at 23 °C (summer) in the laboratory conditions [62]. Despite the hyper-marine salinity tolerance of Tamar goby, this species is completely absent in the South lagoon (salinity 40–85) in the Coorong [18,63]. The spawning and recruitment success of the Tamar goby is inhibited by the varying salinity regime associated with low freshwater flow into the Coorong [64]. Thus, the wide salinity variation in the Coorong contributes to the discrepant growth of Tamar goby across the salinity gradient in the Coorong.

Similarly, sandy sprat exhibited positive allometric growth (slope b = 3.1) in the Coorong. The length-weight relationship of sandy sprat in the present study is similar to other clupeoid species such as the anchovy *Engraulis encrasicolus* (slope b = 3.134) in the Black Sea [65]. Usually, the length-weight relationship in fish is age-specific and varies with sex, gonad maturity, and the spawning period [66]. The marine sandy sprat frequently moves to the nearby estuaries and wetlands for breeding and larval nursing [12,67]. The presence of marine salinity in the Coorong makes it is possible that the sandy sprat would moves to the Coorong for breeding and feeding during the study period. In the Coorong, the spawning of this species occurs from October to February (spring and summer) and peaks in November [12].

The condition factor of fish depends on gonadal development, food availability and environmental variability in the estuarine system [34,68]. The growth performance of barramundi (*Lates calcarifer*) is better in Lake Tinaroo where the prey was more abundant than in the Johnstone River in Australia [69]. In the current study, the spatiotemporal variation in forage fish is possibly related to the preferred food resources in the Coorong. Among forage fishes, small-mouthed hardyhead and sandy sprat feed on planktonic and epi-benthic prey in estuaries [70,71], while Tamar goby is an epibenthic feeder [71]. Low freshwater flow during the drought period reduces the diversity of zooplankton [23] and benthic organisms in the Coorong [20]. Thus, the ultimate low food variability leads to variation of condition factors of these three forage fish species in the Coorong.

Growth performance of all three forage fishes is related to the changes in chlorophyll-a, water transparency and salinity. This result is supported by other studies where high chlorophyll-a and transparency are positively related to the growth of tilapia (*Oreochromis leucostictus*) in Ugandan crater lakes [72]. In this study, chlorophyll-a and transparency together explained ~30% variation of the condition factor. Previous study reported a major shift of phytoplankton community from chlorophytes at Murray Estuary to diatoms and picophytoplankton at North Lagoon and South Lagoon, indicating variation in primary productivity across different salinity regions in the Murray Estuary and Coorong [16]. It is likely therefore, the diversity and abundance of prey organisms (zooplankton and benthos) can be influenced by the variability of primary production that ultimately impacts the fish growth in the Coorong.

In addition to chlorophyll-a, water transparency significantly influenced the growth of forage fish in the present study. Water transparency usually regulates productivity by influencing primary productivity through photosynthesis [73]. The impact of water transparency on abundance, distribution and growth of fish and other organisms is widely reported in wetlands and estuaries [74,75]. The growth performance of yellow perch (*Perca flavescens*) is impacted by water transparency in Lake Erie, USA [74]. Abundances of *Cnesterodon decemmaculatus*, *Jenynsia multidentata*, *Corydoras paleatus*, *Pimelodella laticeps* and *Odontesthes bonariensis* are significantly affected by water clarity at Mar Chiquita, Gómez, Carpincho and Rocha Lakes in Argentina [75]. In addition, water transparency can affect fish growth by interfering with the feeding process of visual feeders [76]. Thus, the difference in growth performance of forage fish among regions could be attributed to food availability and water transparency in the Murray Estuary and Coorong.

Hyper-salinity is an overwhelming stressor regulating the growth and productivity in estuaries [7,77]. In the present study, salinity explained 6% of the fish condition factor. Salinity can be an ecological factor and physiological barrier limiting the function of aquatic organisms [78]. In particular, the growth of estuarine fishes is often affected by salinity tolerance because most energy is utilised in osmoregulation instead of growth [8,79]. Hyper-salinity (>60 psu) affects the growth performance and reduces the size-at-maturity of Bonga shad *Ethmalosa fimbriata* at the inverse Saloum estuary in West Africa [8]. In the Coorong, salinity variation is likely to influence growth through energy reallocation to osmoregulation between geographic regions.

Water temperature and DO only explained <1% of fish condition in forage fishes in the Coorong. Although temperature can influence the growth of estuarine fish species such as black bream (*Acanthopagrus butcheri*) in the Murray River estuary, the impact of temperature on the growth performance of forage fish was not detected in this study. The possible reason is that the temperature range (15.27–23.07 °C) during the study period is suitable for the growth of these forage fish species in the Coorong. Hypoxia can potentially impact the growth and ontogeny of estuarine fishes [80]. However, estuarine hypoxia generally occurs due to water stratification and a lack of water exchange between surface and bottom habitats [81]. In this study, the oxygen level ranged from 4.70 to 11.80 mg/L, which is much higher than the hypoxia level and is unlikely to affect the growth of forage fish in the Coorong [82].

5. Conclusions

In summary, the von Bertalanffy model and length-weight relationship suggest a trend of fast growth of all three-forage fish in the early life history. Still, fish growth performance varied among regions in the Coorong. Chlorophyll a is the most important single variable that explained ~23% of growth variation. Chlorophyll *a,* water transparency and salinity together explained ~36% of growth variations. However, temperature, dissolved oxygen and pH contributed 0.9% towards growth variation. These results of this study improve our understanding on how environmental factors could contribute to the variation of growth performance of forage fishes in an estuarine-hypersaline lagoonal system. Such knowledge is useful to improve management and conservation of small forage fish in estuarine systems.

Author Contributions

M.A.H.: writing—original draft preparation, investigation data curation; S.A.: writing—reviewing and editing; D.H.: data curation, investigation, visualization; Q.Y.: conceptualization, methodology, supervision; S.L: writing—reviewing and editing, supervision. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement

The study was conducted according to the guidelines approved by the Animal Welfare Committee of Flinders University and the Southern Adelaide Local Health Network (Approval E394, Date: 1 April 2014).

Informed Consent Statement

Not applicable.

Data Availability Statement

The data of this study are archived in the College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide, SA 5001, Australia.

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Conflicts of Interest

The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

No AI tools were utilized for this paper.

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