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Influence of tidal and diurnal rhythms on fish assemblages in the surf zone of sandy beaches

Wentong Xia | **Zhongbo Miao** | **Sai Wang** | **Kai Chen** | **Yinglong Liu** | **Songguang Xie**

State Key Laboratory of Marine Resource Utilization in South China Sea, Hainan University, Haikou 570228, China

Correspondence
Songguang Xie, State Key Laboratory of Marine Resource Utilization in South China Sea, Hainan University, Haikou 570228, Hainan, China.
Email: xiesg@hainanu.edu.cn

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Abstract

The surf zones are significantly affected by tides, however, several gaps still in knowledge of fish assemblages in surf zones response to spring-neap and daily tidal cycles. We investigated fish assemblages in a surf zone of Gaolong Bay in China. The dynamics of fish assemblages were examined during the neap tide and the spring tide to test the hypotheses that (1) fish assemblages reflect a combination of species from around coastal habitats, and (2) dynamics of the fish assemblages were determined by both the spring-neap cycles and diel rhythms of fish species. We collected 46 fish species comprising 16 coral reef-seagrass species, 24 mangrove-estuarine species, and 6 common coastal species. Fish abundance and richness were significantly higher during the neap tide than during the spring tide. Furthermore, during the neap tide, fish assemblages were mostly carnivorous coral reef-seagrass species at night and were mostly omnivorous and planktivorous species during the daytime. However, no clear diel patterns were observed during the spring tide. We suggested that dynamics of the fish assemblages were mainly shaped by the diurnal rhythms of fish during the neap tide and by the tidal cycle during the spring tide. Our results support the notion that surveys of fish assemblages during the neap tide could collect more abundance and rich species of multiple ecotypes of fish to evaluate fish resource status in the around coastal habitats. Consequently, management approaches around surf zones with heterogeneous seascapes can lead to positive outcomes for inshore fish resources and ecosystem conservation.

KEYWORDS
coastal seascape, diel activity, ecotypes, fish assemblages, spring-neap tidal cycles, surf zones, temporal patterns

1 | INTRODUCTION

Surf zones (the area of breaking waves abutting ocean beaches) are an integral part of sandy beaches that dominate the world's coastlines (Borland et al., 2017; Olds et al., 2018). As a land-sea interface, surf zones contain abundant food resources due to surface runoff and tides (e.g., drifting algae and seagrass and patches of intense phytoplankton growth) and provide critical feeding habitats for fish (Henderson et al., 2022; Hyndes et al., 2014). Surf zones also have heterogeneous and complex structures, such as offshore bars and nearshore troughs, characterized by wave conditions that provide refuges from predators (Mosman et al., 2020). Hence, surf zones serve

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as nurseries, refuges, foraging areas, and dispersal corridors for organisms, especially marine fishes, in their early life stages (Olds et al., 2018; Pinto et al., 2021).

An increasing number of studies (Olds et al., 2018; Pessanha et al., 2021; Pittman & McAlpine, 2003) have documented that surf zones represent a critical linkage for fish movement in typical coastal seascapes around (e.g., estuaries, mangroves, seagrass meadows, coral, and rocky reefs). Coastal seascape configuration, connectivity, and habitat complexity have a major influence on the assemblage of fishes in surf zones (Mosman et al., 2020; Nagelkerken et al., 2013; Vargas-Fonseca et al., 2016). It has also been suggested that fish assemblages in surf zones could be used as an indicator that reflects the status of fish resources in neighboring typical ecosystems (Henderson et al., 2022; Olds et al., 2016; Sheaves et al., 2012). In addition, surveying and assessing fish assemblages in surf zones is relatively convenient and efficient compared to those in structured coastal habitats (Shah Esmaeili et al., 2021). Thus, studies on fish assemblages in surf zones could be used to promote the conservation and management of fisheries in coastal seascapes (Borland et al., 2017).

Surf zones are highly dynamic areas dominated by tides with "harsh" hydrodynamic conditions such as strong wave energy and high turbidity (Schlacher et al., 2015). Spring and neap tides with different wave energies affect the habitat characteristics of surf zones (Artal et al., 2019). Mounting evidence shows that the degree of wave exposure associated with tides is the primary factor driving fish assemblage structures (Inui et al., 2010; Schultz et al., 2019). For instance, flood tides provide new food resources for fish that feed in surf zones (Hyndes et al., 2014), and many species move toward the sandy beach to capitalize feeding opportunities (Olds et al., 2018). Similarly, diel changes in the water physiochemical parameters (e.g., water temperature [WT] and turbidity) and plankton density in surf zones (Olds et al., 2018; Pittman & McAlpine, 2003), which are triggered by tides, light, or other cues (Lowe & Bray, 2006), could also lead to changes in the fish abundance between day and night (Arndt & Evans, 2022). Therefore, information about fish assemblages as a result of tidal and diel cycles of the surf zones is critical for surveying and assessing the fish resource status in and around coastal seascapes.

Hainan Island, China, has a coastal line of 1944 km, and a major part of it is a sandy beach (Hainan Provincial Bureau of Statistics, http://stats.hainan.gov.cn/). Inshore coastal areas consist of multiple seascapes, such as mangroves, estuaries, seagrass meadows, and coral reefs (Herbeck et al., 2020). Coastal marine biodiversity, specifically fishes, has been dramatically threatened by increasing anthropogenic activities and coastal degradation (Henderson et al., 2020; Herbeck et al., 2013). It is important to investigate the fish assemblages in coastal areas to assess their functions and to identify priority areas for conservation by comparing among multiple coastal waters (da Silva et al., 2022; Henderson et al., 2022). In this study, we investigated the daily fluctuations of fish assemblages during both neap and spring tides in the surf zones of a sandy beach at Wenchang, on the eastern coast of Hainan Island. Our major aims were to (1) determine patterns of fish assemblages in surf zones associated with daily tidal cycles during the neap tide and the spring tide and clarify surf-zone fish assemblages as a combination of fish species from around coastal habitats and (2) identify the key factors influencing fish assemblages in surf zones. We hypothesized that (1) fish assemblages reflect a combination of fish species from nearby coastal habitats, and (2) the dynamics of the fish assemblages are determined by both the tides and diel rhythms of the fish species. By addressing these specific objectives, our study seeks to understand how tides influence fish assemblages in surf zones, which is critically important for designing fish assemblage surveys in surf zones to reflect the fish resource status in coastal seas.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in the surf zones of Gaolong Bay (19.50° N, 110.81° E) at Wenchang, the eastern coast of Hainan Island, a tropical island located in the northern part of the South China Sea (Figure 1). The study area is characterized by a tropical monsoon climate with distinct seasonal inshore currents and wind currents. The Qiongdong coastal upwelling between April and September month brings large amounts of nutrients to the coast, resulting in extremely high primary productivity and biodiversity (Xie et al., 2016). The study area is also subjected to a mixed semi-diurnal tide with a tidal level (TL) of about .5 and 2.0 m at neap tides and spring tides, respectively (Herbeck et al., 2020). The Wenjiao River that originating from Shudetou, Wenchang City flows into the Gaolong Bay, forms an estuary of approximately 40 km^2 in area, which consists of diverse coastal seascapes. For example, large mangrove-covered shorelines form the southern part of the Bay, coral reef fringes can be found ~4 kms from the shore, and seagrass meadows occur in the back-reef areas between the shore and coral reef fringes. The shoreline of the Gaolong Bay consists mainly of sandy beaches extending for approximately 7 km (Figure 1).

2.2 | Fish sampling

Fish were collected from the surf zones using a beach seine net. The net was 1 × 1 mm of mesh size, 4 m in length, 1 m in height, and had a purse-bag of 1 m in length (Inui et al., 2010). When sampling, the net was pulled by two samplers parallel to the shoreline at a depth of approximately 1.0 m. There were a total of four samplers to carry out the sampling who were trained before the formal sampling. During the sampling, one of the two samplers was changed in turn in every 4 h. It ensured that one of the two samplers during a 4-h sampling period had participated in the previous 4-h sampling, thus to minimize the impact of the sampling process on the results.

For each sampling, surveys were conducted at three sites along the beach. The distance between the starts of two adjacent sampling sites was 200 m. At each sampling site, we conducted two spatially

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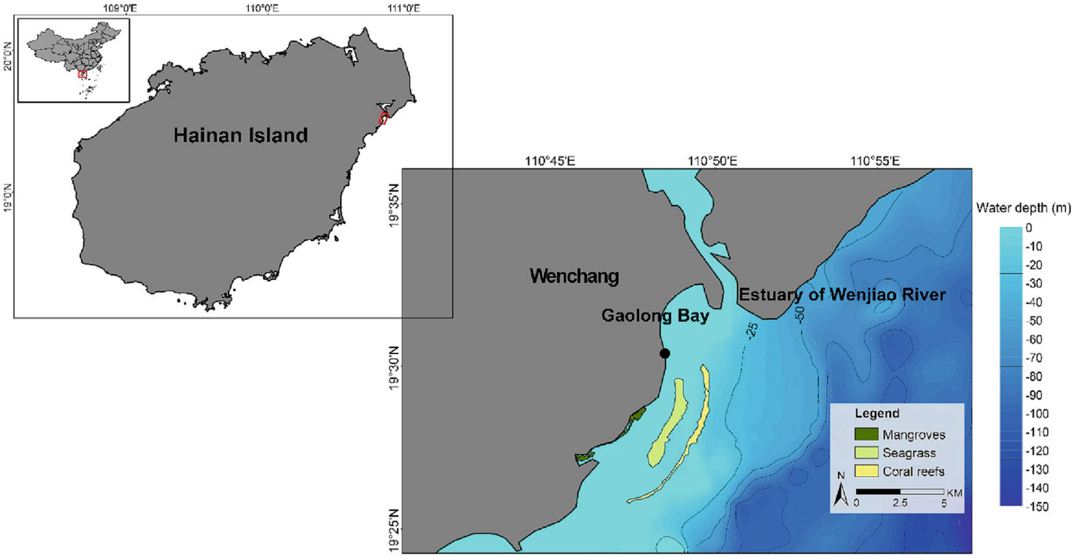

FIGURE 1 Location of sandy beach for fish sampling in Wenchang coast, Hainan Island, China.

continuous 25-m hauls (with a total sampling distance of 50 m). To represent the total abundance of fish, the set of specimens obtained in all sites and samplings was taken into account. Sampling was carried out every 2 h daily and lasted for three successive days in both a neap tide and a spring tide. The neap tide was sampled from 0:00 a.m. on May 19 to 22:00 p.m. on May 21, and the spring tide was sampled from 0:00 a.m. on May 26 to 22:00 p.m. on May 28, 2021. Wind and wave conditions were similar and consistent during the neap tide and spring tide sampling periods. Wind speed ranged 15–32 kph (average ± SD: 24.8 ± 4.7 kph) during the neap tide sampling period and 14–36 kph (average ± SD: 22.6 ± 4.8 kph) during the spring tide sampling period. Wind direction was mainly southerly (National Marine Data Center, http://mds.nmdis.org.cn/). Wave was calm during both sampling periods with the highest wave less than 2 m and the mean wave height (±SD) of 1.0 ± .2 m during the neap tide sampling period and 1.1 ± .1 m during the spring tide sampling period (National Meteorological Data Center, https://data.cma.cn/).

The collected fish (mostly at the juvenile stage) were immediately fixed in a 4% neutral seawater formalin solution for 4 h and then preserved in 75% alcohol. In the laboratory, we enumerated and identified all individual fishes at the species level. Early juvenile individuals were determined through a combination of morphological and molecular analyses (Hou et al., 2018; Song et al., 2019). Fish species in the later juvenile stage were mainly identified by their morphology, but molecular analyses were also used when needed.

We categorized each species into one of the three ecotypes based on their primary habitat: (1) coral reef-seagrass-associated species (CS), which appear mainly in coral reefs and/or seagrass meadows; (2) mangrove-estuarine-associated species (ME), which are common in mangroves and/or estuaries; (3) the common coastal associating species (CO), which are common in coastal waters and large sandy shorelines (Du et al., 2020; Inui et al., 2010; Krumme, 2009; Pessanha et al., 2021; Travers et al., 2010).

2.3 | Environmental variables

Environmental variables were measured .5 m below the water surface at each sampling site. WT (°C), conductivity (μS/cm), dissolved oxygen (DO, mg/L), total dissolved solids (TDS, mg/L), pH, and salinity (‰) were measured using a portable multiparameter water quality meter (YSI Professional Plus, USA). Turbidity was measured using a turbidimeter (HACH 2100Q, USA). TL of the study area was obtained from the National Marine Data Center (http://mds.nmdis.org.cn/).

2.4 | Statistical analyses

We used two-way analyses of variance (ANOVAs) to test the effects of tides (neap tide and spring tide), sampling time (every 2 h around a day), and their interactions on abundance and number of species in fish assemblages. If there was a significant interaction between tide type and sampling time, we conducted one-way ANOVAs and multiple comparison tests separately to test for group differences. Prior to the ANOVAs, all raw data were log $(x + 1)$ transformed. Further, Shapiro–Wilk test and Levene's test showed that the transformed data met the conditions of normality and homogeneity. The two-way ANOVAs were carried out in the R statistics software at a significance level of $p < .05$ (R Core Team, 2019).

The index of relative importance (IRI) during the neap tide and the spring tide was calculated for each species by

$$\mathrm{IRI} = \mathrm{N\%} \times \mathrm{F\%}$$

where N% is the percentage of the number of each species among the total number of fish species and F% is the species frequency per species sampled in percentage. Accordingly, each species was defined

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TABLE 1 Results of two-way ANOVAs testing the effects of tides (neap and spring), sampling times, and their interactions on abundance and number of total species, coral reef-seagrass species (CS), mangrove-estuarine species (ME), and common coastal species (CO). df, degree of freedom; *F*, ratio of variance. Significant *p* values ($p < .05$) were in bold.

		Abundance				Number of species			
		Total	CS	ME	CO	Total	CS	ME	CO
Tide type	df	1	1	1	1	1	1	1	1
	F	23.05	10.71	10.86	22.62	17.24	11.53	24.67	8.88
	p	***<.001***	***.002***	***.002***	***<.001***	***<.001***	***.001***	***<.001***	***.04***
Sampling time	df	11	11	11	11	11	11	11	11
	F	2.07	.82	2.04	2.28	2.15	1.06	2.70	1.69
	p	***.04***	*.62*	***.04***	***.02***	***.03***	*.41*	***.008***	*.10*
Tide type × Sampling time	df	11	11	11	11	11	11	11	11
	F	3.27	.94	1.44	4.17	2.29	.97	1.95	2.65
	p	***.002***	*.51*	*.19*	***<.001***	*.02*	*.49*	*.06*	***.01***

as dominant (IRI ≥ 100), common (100 ≥ IRI ≥ 10), or rare (IRI < 10) (Pinkas et al., 1971; Song et al., 2019).

Permutational multivariate analysis of variance (PERMANOVA) was used to test whether neap/spring tides, and sampling times had distinct fish assemblages (Anderson, 2001). PERMANOVA was performed on species abundance data of the assemblages based on Bray–Curtis dissimilarity. The coefficients of the Adonis model were plotted from the heat maps to visualize the species contributions. PERMANOVA was performed using the "vegan" package in R (R Core Team, 2019).

We also applied the Dufrene–Legendre indicator species analysis to identify species that contribute significantly to differences in fish assemblages (Dufrene & Legendre, 1997). Species with an indicator value >.1 and a significant *p* value (<.05) were determined as indicator species (Mosman et al., 2020). In addition, non-metric multidimensional scaling analysis (nMDS) was used to visualize differences in fish assemblage and the contributions of indicator species (Clarke et al., 2008). Indicator species analysis and nMDS were performed using the "labdsv" and "vegan" packages in R, respectively (Oksanen et al., 2022).

Canonical correspondence analysis (CCA) was applied to analyze the influence of environmental variables on fish assemblages using the "ade4" and "vegan" packages in R (Bougeard & Dray, 2018). Forward selection procedure combined with Monte Carlo randomization tests (999 permutations) was used to identify the significant environmental variables ($p < .05$). Shape and strength of relationships between significant environmental variables, abundance of total species, and most abundant species were assessed with the generalized additive models (GAMs) using the "mgcv" and "MuMIn" packages in R (Barton, 2009; Wood, 2012). We selected the best-fit models using the corrected Akaike's information criterion (AICc) and identified the most "important" factors across all models based on the summed factor importance values for each significant factor within a best-fit model (Gilby et al., 2017). These factor importance values were standardized between 0 and 1. The environmental variables were analyzed of variation inflation factors (VIFs) to check the multi-colinearity before applied to CCA and GAMs. Environmental variables with VIF < 10 were then included in the analyses (Zuur et al., 2010).

3 | RESULTS

3.1 | Patterns of fish assemblages in the surf zones

We collected a total of 7485 fish, belonging to 24 families, 37 genera, and 46 species. Out of all the fish collected, we identified 16 CS, 24 ME, and 6 CO species (Table S1). Both the abundance and number of species were significantly higher during the neap tide than during the spring tide (two-way ANOVAs, $p < .05$; Table 1, Figure 2).

During the neap tide, abundance of total fish, ME, and CO species were significantly affected by the sampling time (one-way ANOVAs, $p < .05$; Table 1, Figure 3). Compared to the low TL period, a significantly higher abundance of fish was observed during the high TL period, which mainly reflects the increase in the abundance of CO species ($p < .05$; Table 1, Figure 3). Significantly higher abundance of ME species was observed when the TL decreased ($p < .05$; Table 1, Figure 3). The total number of species and the number of CS and ME species were significantly affected by the sampling time (one-way ANOVAs, $p < .05$; Table 1, Figure 4). The number of species generally increased with decreasing TLs ($p < .05$; Table 1, Figure 4).

During the spring tide, the abundance of total fish and the CS, ME, and CO species tended to increase when the TL increased, and vice versa. However, temporal fluctuations were not statistically significant ($p > .05$, Figure 3). Fluctuations in the total number of species and in the CS, ME, and CO species showed a similar pattern of abundance. A significantly lower number was observed, for species in total and for ME and CO species when the TL was lowest (Figure 4).

Fish assemblages varied between the neap tide and the spring tide (PERMANOVA, $R^2 = .08$, $p < .01$; Table 2). Most of the CS species, such as Carangidae, Lethrinidae, and Lutjanidae, were collected only during the neap tide (Table S1, Figure 5). Fish assemblages during the neap tide were also highly concentrated, whereas those during

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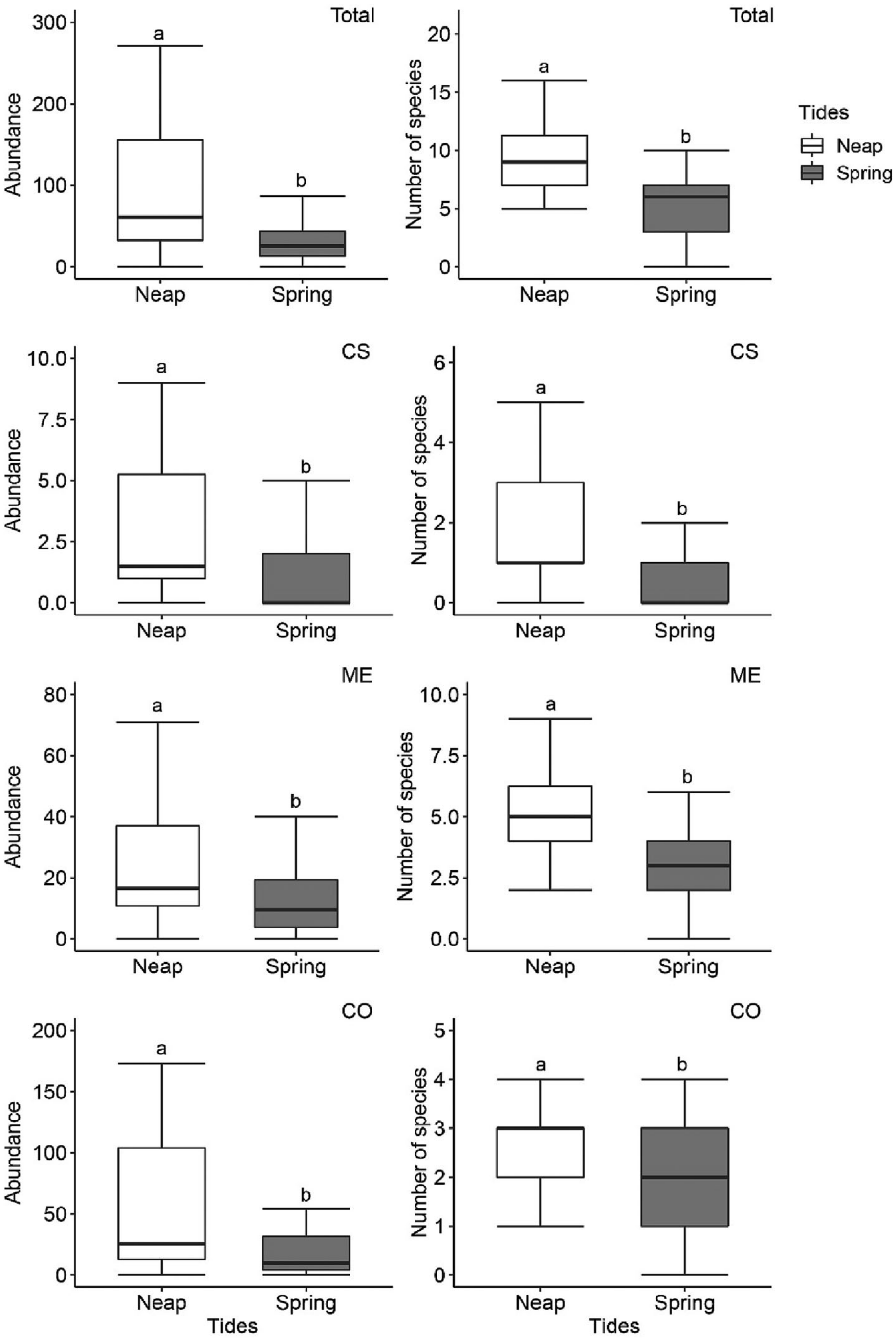

FIGURE 2 Comparisons of abundance and number of fish species in different tide types in surf zones. *Note*: Total, total species; CS, coral reef-seagrass species; ME, mangrove-estuarine species; CO, common coastal species; bars with different lowercase letters indicate statistically significant differences ($p < .05$) between the neap tide and the spring tide.

the spring tide were much dissimilarity (stress value .20, Figure 6). Eight indicator species were identified (Table S2 and Figure 6). *Atherinomorus endrachtensis* was highly contributed to fish assemblages at night (0:00–4:00) and afternoon (14:00) during the spring tide (Table S2, Figure 6). *Sillago aeolus*, *Gerres oyena*, and *Valamugil seheli* were higher at night time during the neap tide, whereas *Elops machnata*, *Leiognathus equulus*, and *Sardinella melanura* were associated with a major part of the assemblages at daytime during the neap tide (Table S2, Figure 6).

3.2 | Relationships between fish assemblages and environmental variables

During the neap tide, fish assemblages were significantly affected by TL, WT, and DO ($p < .05$). The first two CCA axes accounted for 26.4% and 9.2% of the variance in the relationship between fish assemblages and environmental factors, with DO that negatively correlates to the first axis, and TL and WT negatively correlated to the second axis. Fish species were highly scattered in the biplot of the

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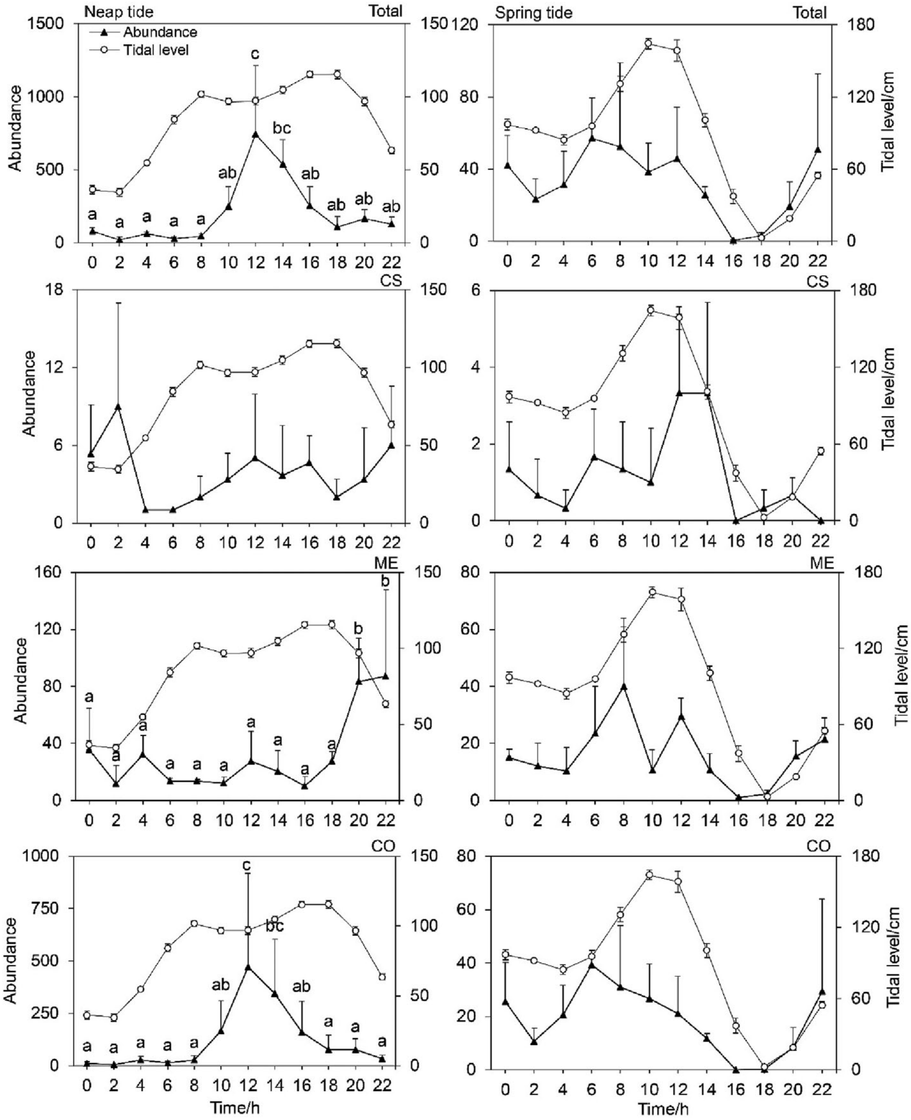

FIGURE 3 Relationships between abundance and tide levels in the surf zones at different tide types. *Note*: Total, total species; CS, coral reef-seagrass species; ME, mangrove-estuarine species; CO, common coastal species; bars with different lowercase letters indicate statistically significant differences ($p < .05$) between different sampling times.

first two CCA axes (Figure 7a). Fish assemblages of the samples in the night and early morning were negatively correlated with lower DO, WT, and TL, while those in the daytime (especially at noon and afternoon) were positively correlated with these environmental variables (Figure 7b). Total fish abundance was positively correlated with both WT and DO (GAMs, $R^2 = .40$, Figure 8a,b), which also reflects the fluctuation of the most abundant species, *S. melanura* (GAMs, $R^2 = .68$, Figure 8c,d).

During the spring tide, fish assemblages were significantly affected by TL and turbidity ($p < .05$). The first two CCA axes accounted for 19.9% and 13.7% of the variance in the assemblage–environment relationship, respectively (Figure 7c,d). Species tended to concentrate in the biplot of the first two CCA axes with a group of species apparently associated with high TL (Figure 7c). Fish assemblages collected in the day time tended to be associated with high TL and low turbidity (Figure 7d). Total fish abundance was positively correlated with TL (GAMs, $R^2 = .48$, Figure 8e), which mainly reflected the relationship between the abundance of *A. endrachtensis* and TL (GAMs, $R^2 = .33$, Figure 8f). However, values of the CCA inertias and the R^2 of the GAM models were all very low, which probably indicated that environmental variables not included in our investigation may influence patterns of fish assemblages in such highly dynamic surf zones.

4 | DISCUSSION

Our results demonstrate that fish assemblages in the surf zones highly fluctuate between neap tide and spring tide and over diel time period. Fish abundance and species richness were significantly higher, with less dissimilar fish assemblages during the neap tide than during the spring tide.

Variations in the temporal patterns of fish assemblages in the surf zones between the neap tide and the spring tide may mainly reflect the effects of variations in fluctuation of TLs on fish species. The classical moderate interference hypothesis states that abundance and

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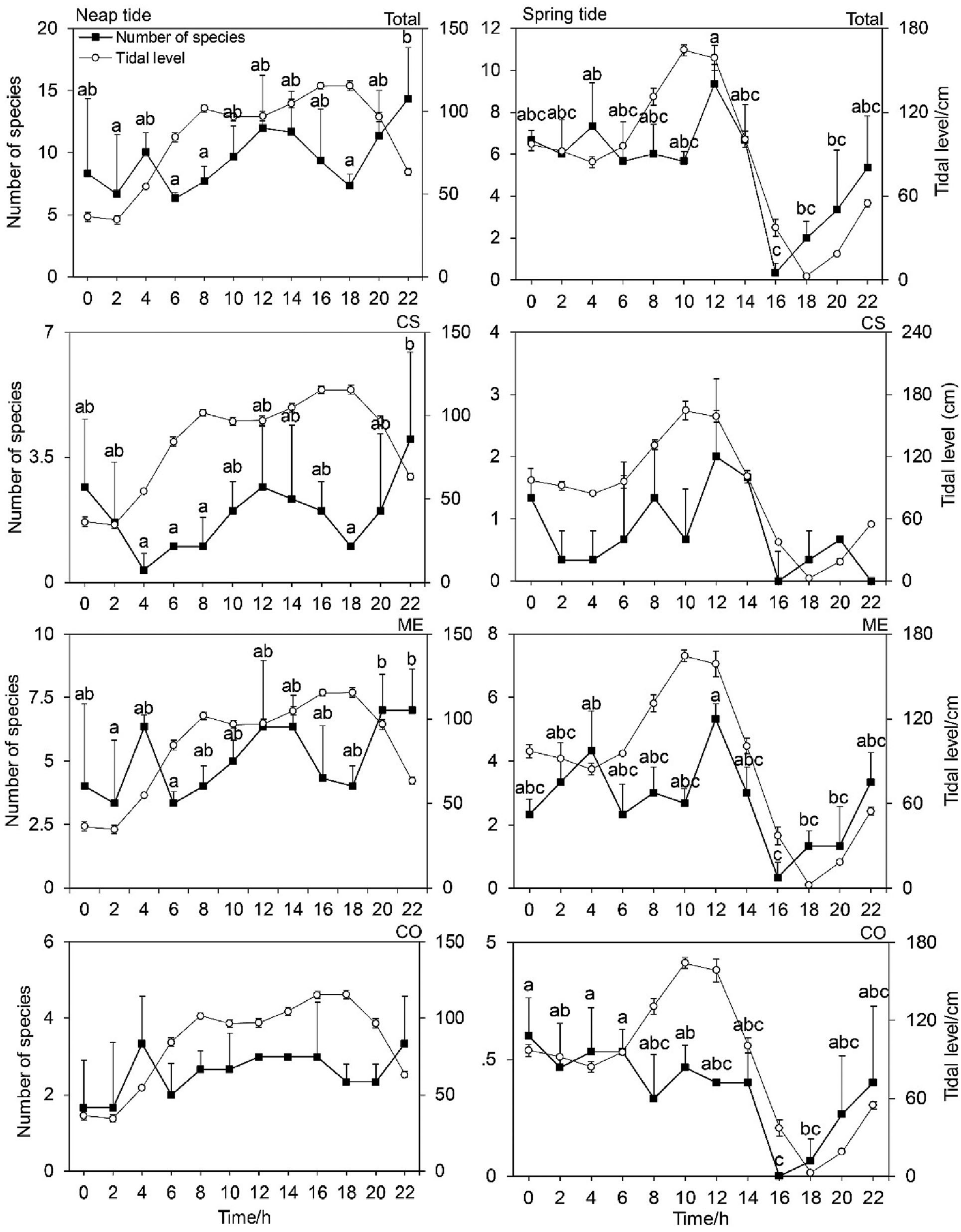

FIGURE 4 Relationships between number of fish species and tide levels in the surf zones at different tide types. *Note*: Total, total species; CS, coral reef-seagrass species; ME, mangrove-estuarine species; CO, common coastal species; bars with different lowercase letters indicate statistically significant differences ($p < .05$) between different sampling times.

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TABLE 2 PERMANOVA on effects of tide types and sampling time on fish community in the surf zones and comparisons for tide type and sampling time. F, ratio of variance; R^2, coefficient of determination. Significant p values ($p < .05$) were in bold.

Parameter	F	R^2	p
Tide type	6.55	.08	**.001**
Sampling time	1.62	.21	**.001**
Tide type × Sampling time	1.57	.20	**.001**

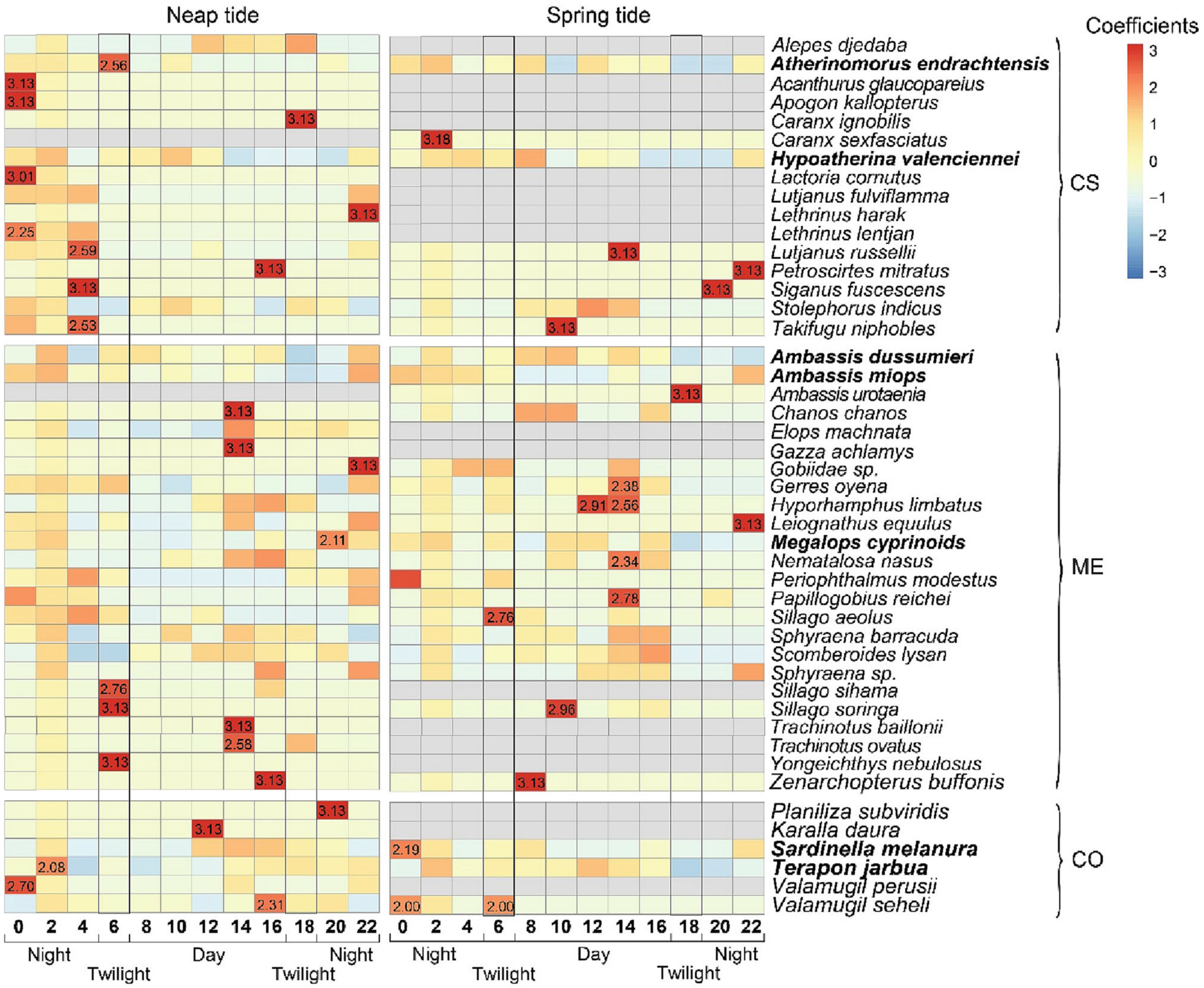

FIGURE 5 Groups-specific contributions to the differences of fish assemblages during diel in surf zones. *Note*: CS, coral reef-seagrass species; ME, mangrove-estuarine species; CO, common coastal species; the dominant species were in bold; numbers indicate the coefficients of fish species of the Adonis model to represent the contributions to the differences of fish communities between the neap tide and the spring tide.

diversity peak at intermediate disturbance and should be low in harsh environments (Clark, 1997; Connell, 1978; Sousa, 1979). Tide is a major factor shaping features of coastal seascape and movement of nearshore fish (Clark, 1997; Pattrick & Strydom, 2014). Compared with the dramatic shifts in TL and strong flow energy in spring tides, neap tides have moderate TL shifts and gentle flow energy (Artal et al., 2019). Thus, higher abundance and richness and more stable assemblage of fish in the surf zones during the neap tide compared to the spring tide observed in this study were in line with the moderate interference hypothesis. Optimal foraging theory predicts that fishes are adapted to invest the lowest energy to obtain abundant food in a stable and safe environment (Lowe & Bray, 2006). With plenty of food resources and relatively stable environments, the surf zones during neap tides provide an optimal environment for fish with different foraging strategies compared with spring tides (Jarrin & Shank, 2010). However, during spring tides, the surf zones are highly dynamic with strong tidal flow, which influences the feeding efficiency of most fishes. Several other studies also reported that harsh environments in the coastal water induced low abundance and species richness of fish (Borland et al., 2017; Clark, 1997; Pattrick & Strydom, 2014).

On the other hand, some fish species, usually opportunistic and planktivorous, have adapted to feed in surf zone during high tide.

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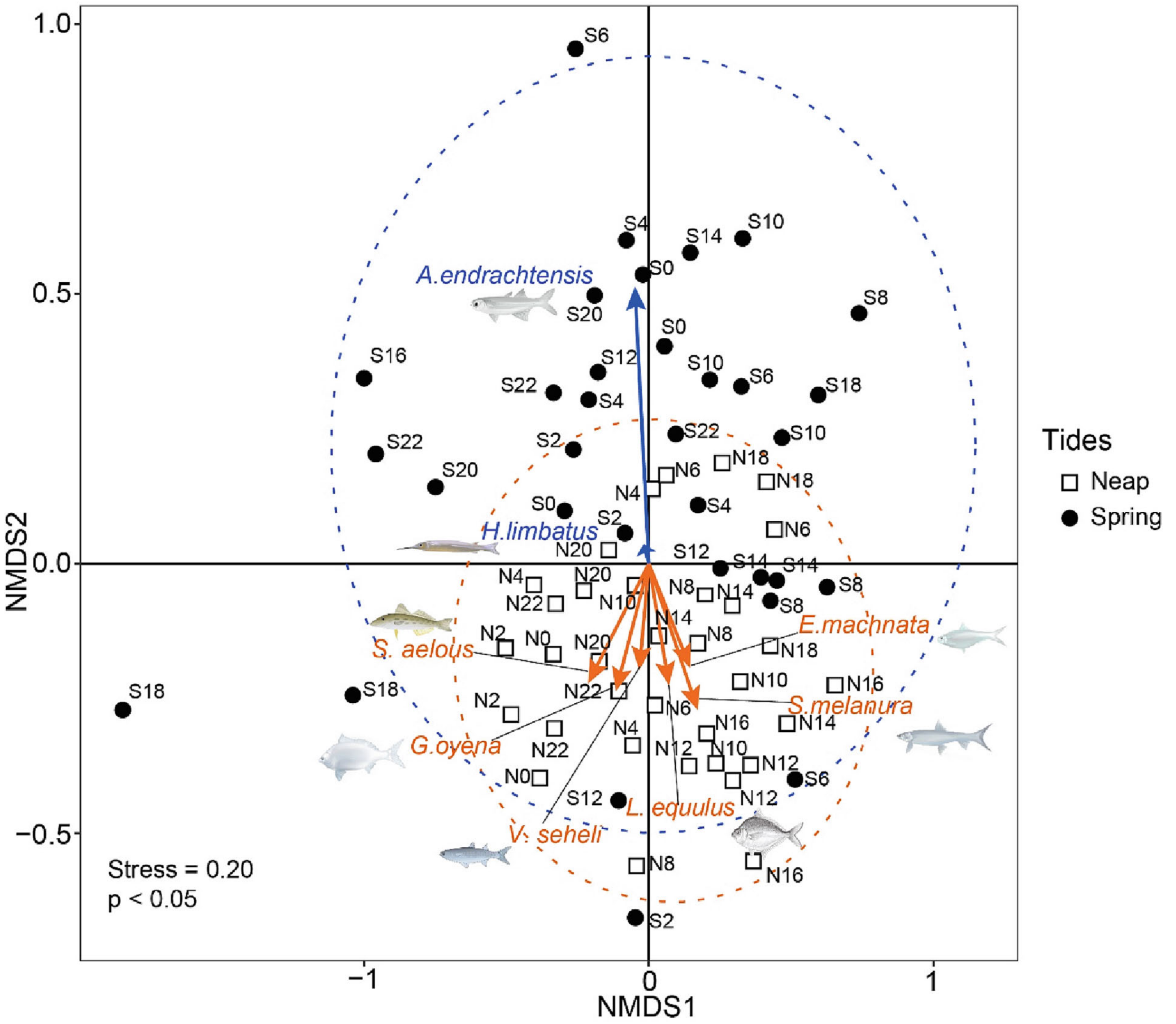

FIGURE 6 Non-metric multidimensional scaling ordination contrasting fish assemblages between the neap tide and the spring tide. Indicator species in the plot were identified by Dufrene–Legendre indicator analysis. Vectors display the strength of species correlations within the ordination space, with longer vectors indicating a greater correlation. In the labels of fish assemblages, "S" is spring tide, "N" is neap tide, and the followed number is the sampling time.

Flood tides bring a large number of zooplanktons to the surf zones, which elevates the feeding efficiency of planktivorous species (Krumme & Liang, 2004). Juveniles of *Lateolabrax japonicus*, a planktivorous species, were reported migrating to the surf zones during flood tides to feed on zooplanktons in the Ariake Bay in Japan (Hibino et al., 2006). In our study, *A. endrachtensis* (a planktivorous species) was the most abundant indicator species during spring tides and was higher during the flood tide period. Our observation was conducted only for one spring tide and one neap tide. The observed patterns need to be further verified in other coastal waters and/or by investigating multiple spring-neap tidal cycles in the future.

Diel fluctuations of fish assemblages in the surf zones varied between the neap tide and the spring tide. During the neap tide, fish assemblages at night mostly included some CS fish, such as *Apogon kallopterus* and *Lethrinus lentjan*, which are mainly carnivorous (Travers et al., 2010). While fish assemblages during the daytime and twilight mainly comprised omnivorous and planktivorous fishes (e.g., *A. endrachtensis* and *Sillago sihama*). These diel patterns, however, were not observed in the surf zones during the spring tide. Numerous fishes have prominent circadian rhythms, which allows them to adapt to periodic events of the external environment (Albrecht, 2012; Arndt & Evans, 2022; Pessanha et al., 2003). The CS fishes, such as species of Apogonidae and Lethrinidae, are usually nocturnal carnivores, which prefer sheltering in complex structured coral reefs throughout the daytime and move to foraging grounds at night (Krumme, 2009; Marnane & Bellwood, 2002). High abundance of CS juveniles in the evening during neap tide indicated critical nursing function of the surf zones for these CS species. Benthic invertebrates (e.g., polychaetes, bivalves, and crabs), which are dominant prey resource of many CS species (ref), are usually abundant in the surf zones (Borland et al., 2017). Thus, the SC juveniles should get improved feeding efficiency from migrating into and feeding in the

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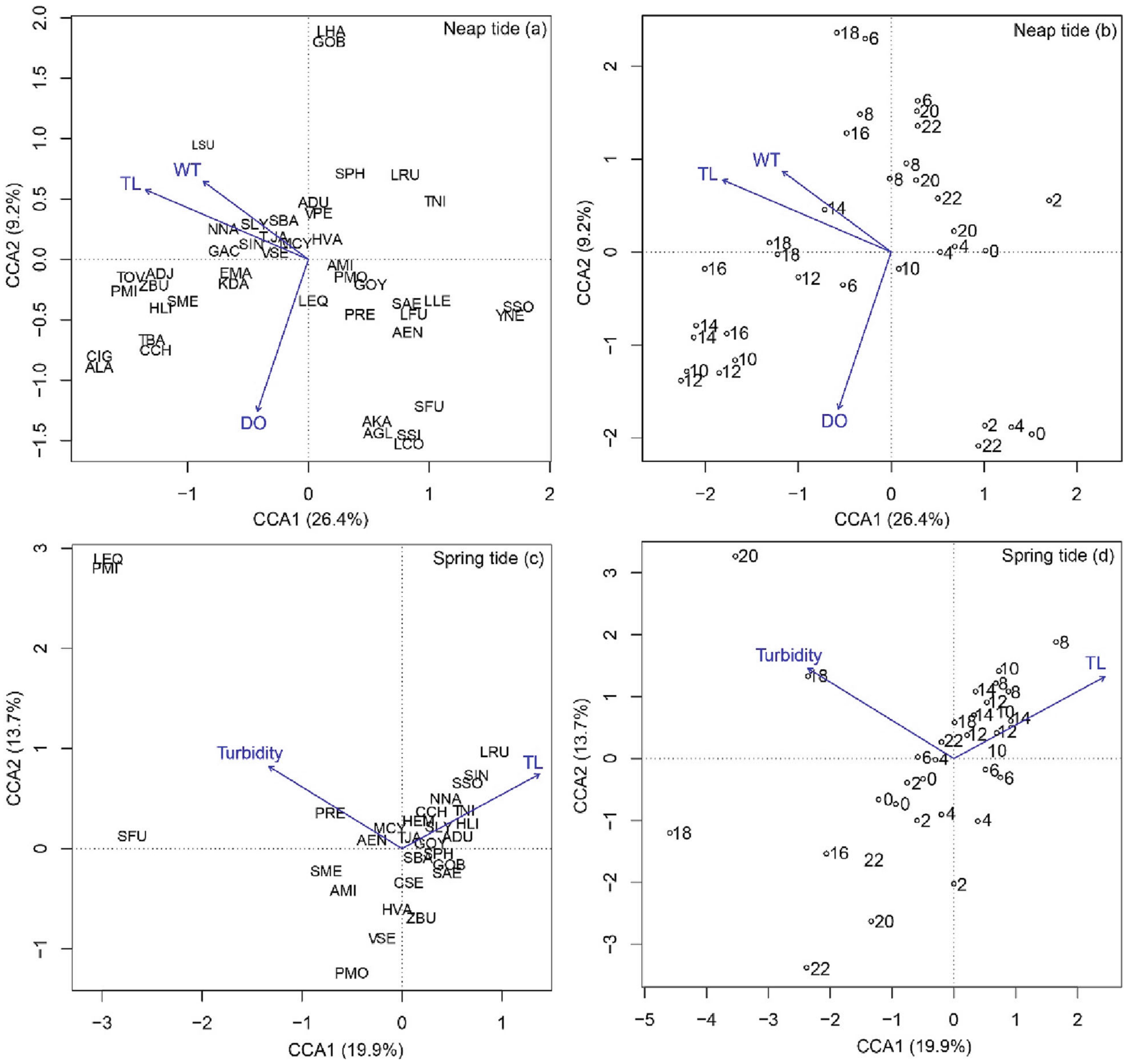

FIGURE 7 Canonical correspondence analysis of fish assemblages (abundance data) related with environmental variables. Only significant environmental variables ($p < .05$) are depicted in the figure; species codes in panels neap tide (a) and spring tide (c) are presented in Table S1; numbers in panels neap tide (b) and spring tide (d) indicate the sampling time.

surf zones, which would benefit recruitment success of the fish populations. In contrast, many omnivorous and planktivorous species such as species of Atherinidae and Sillaginidae are mainly diurnal, which feed in the shallow coastal waters in the daytime and move to adjacent shelters at night (Arndt & Evans, 2022; Krumme, 2009). Thus, circadian rhythms of fish activities may contribute critically to the diel patterns of fish assemblages during neap tides but not during spring tides.

Environmental factors also influenced fluctuations in fish assemblages and differently for the neap tide and the spring tide. During the neap tide, WT and DO were the significant influencing factors for fluctuations in fish abundance. Whereas during the spring tide, the key factor was the TL. Fluctuation ranges of WT and DO were much calmer during the neap tide than the spring tide (Figure S1). Daily fluctuations in WT and DO represent natural circadian rhythms with higher values in the day time and lower values in the night time (Jarrin & Shank, 2010). Thus, diel patterns of fish assemblages during the neap tide should be driven by the circadian rhythms of both the fish activities and water physicochemical parameters (i.e., WT and DO). Instead, during the spring tide, with large fluctuation of TL (Figure S1), TL was the driving factor shaping the diel pattern of the fish assemblage.

Surf zones act as important feeding grounds and nurseries for juvenile fish and as corridors for migration across various coastal habitats (Mosman et al., 2020; Vargas-Fonseca et al., 2016). The coastal waters around Gaolong Bay, our sampling location, consisted

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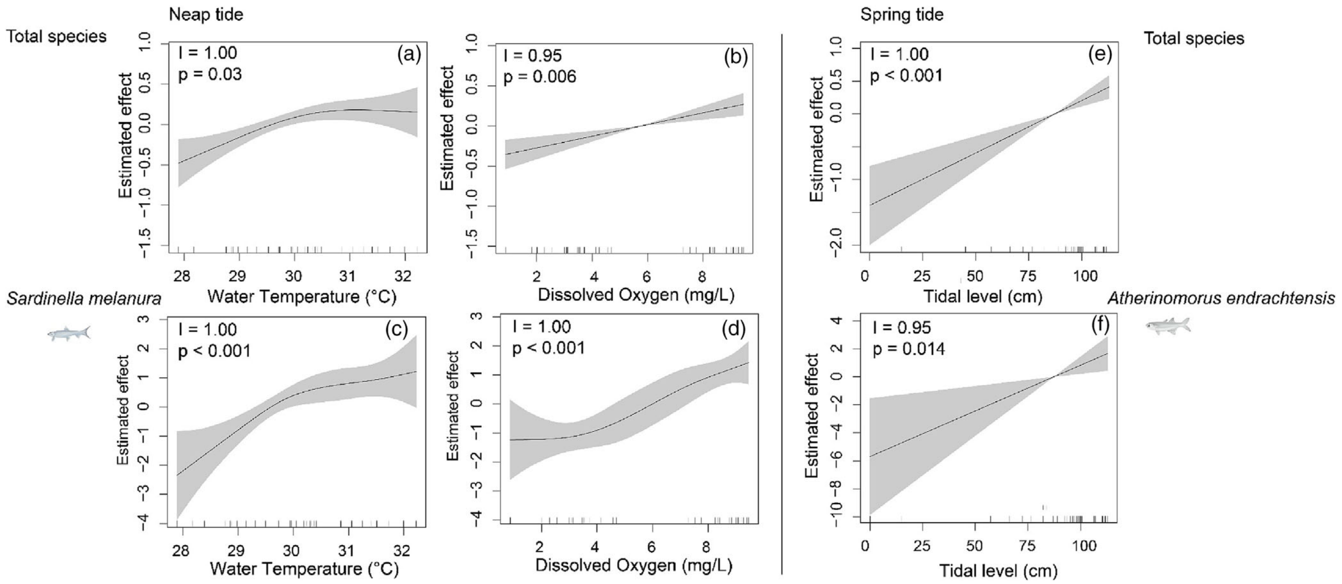

FIGURE 8 Generalized additive models (GAMs) partial plots illustrating relationships between abundance of total species and most abundant indicator species identified by Dufrene–Legendre indicator species analysis and environmental factors in two tide types. Shaded regions indicate 95% confidence intervals.

of multiple habitats, including estuaries, mangroves, seagrass meadows, and coral reefs. We collected a total of 46 species, and the fish assemblages were a combination of species from multiple coastal habitats, including 16 CS, 24 ME, and 6 CO species, with most individuals at the juvenile stage. It indicated essential nursing function of the surf zones, which may contribute critically to recruitment success of fish populations in the adjacent coastal habitats. We suggested that surf zone with multiple adjacent coastal habitats (e.g., mangroves, estuaries, seagrass, and coral reefs) should be set as priority of conservation (da Silva et al., 2022; Ortodossi et al., 2018).

Surveys of fish assemblages in the surf zones of sandy beaches are usually more practical and convenient than in structured coastal habitats, such as coral reefs, mangroves, and seagrass meadows (Olds et al., 2018; Sheaves et al., 2012). Our results demonstrated that fish assemblages in the surf zones could reflect the fish biodiversity status of the adjacent coastal waters. Thus, surveys of fish assemblages in surf zones could be used as a substitution reflecting fish resource status in the adjacent coastal waters (Olds et al., 2016; Schlacher et al., 2015). Comparison of fish assemblages among multiple surf zones may provide fundamental information to identify priority areas of coasts for conservation. Fish assemblages in surf zones are highly dynamic (Pinto et al., 2021) and often influenced by tides (Borland et al., 2017; Pattrick & Strydom, 2014). Our results demonstrated that fish assemblages during the neap tide had higher abundance and number of species and were more stable in assemblage structure than during the spring tide. Thus, surveys of fish assemblages in surf zones should consider the diel dynamics of the assemblages and should be conducted during the neap tide based on our results.

5 | CONCLUSION

With high ecological importance and usually intensive anthropogenic disturbance in the surf zone, biotic communities in the surf zone have been poorly studied compared to other coastal systems. Our results highlight that fish assemblages in the surf zones fluctuate between neap and spring tides and over a diel period. Particularly, fish abundances and richness were significantly higher, and fish assemblage structures were more stable, during the neap tide than during the spring tide. Diel patterns of fish assemblages during the neap tide were driven mainly by the circadian rhythms of both the fish activities and water physicochemical parameters, whereas those during the spring tide were by the tidal cycles. Our study also has significant implications for conservation planning of coastal ecosystems. We suggest that surf zones should be included in activities aimed biodiversity conservation. Furthermore, fish assemblages in the surf zones could reflect fish resource status in the coastal ecosystem and provide essential information for setting priority areas of conservation. We suggested that surveys of fish assemblages in surf zones should consider the diel dynamics of the assemblages and should be conducted during the neap tide. Our observation was conducted only for one spring tide and one neap tide. The observed patterns need to be further verified in other coastal waters and/or by investigating multiple tidal cycles in the future.

AUTHOR CONTRIBUTIONS

All the authors contributed to the conception and design of the study. Material preparation, data collection, and analysis were performed by W.T. Xia, Z.B. Miao, Y.L. Liu, and S.G. Xie. W.T. Xia and S.G. Xie wrote the manuscript with substantial edits from all other authors.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data will be available on reasonable requests to the corresponding author.

ORCID

Wentong Xia https://orcid.org/0000-0002-3839-6755

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