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Research Article

Fish community, seasonal movement and habitat use in a subtropical coastal lagoon

Isadora Jy'asu Moreno-Pérez[1], Juana López-Martínez[1]
Jesús Guadalupe Padilla-Serrato[2,3], Jesús Rodríguez-Romero[4]
Emelio Barjau-González[5] & José Alfredo Arreola-Lizárraga[1]
[1]Centro de Investigaciones Biológicas del Noroeste, S.C., Guaymas, Sonora, México
[2]Facultad de Ecología Marina, Universidad Autónoma de Guerrero, Acapulco, Guerrero, México
[3]Investigadoras e Investigadores por México, Consejo Nacional de Humanidades
Ciencias y Tecnologías (CONAHCYT), Ciudad de México, México
[4]Centro de Investigaciones Biológicas del Noroeste, S.C.
Instituto Politécnico Nacional, La Paz, Baja California Sur, México
[5]Departamento Académico de Ciencias Marinas y Costeras
Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México
Corresponding author: Juana López-Martínez (jlopez04@cibnor.mx)

ABSTRACT. Coastal lagoons are environmentally and naturally dynamic areas crucial for fish reproduction and nursery. Thus, this research aims to evaluate the importance of the species performing their biological processes and development in this ecosystem. For this purpose, a subtropical coastal lagoon in the Gulf of California was taken as a case study, where four sampling seasonal campaigns were performed within the lagoon (internal zones) and the marine environment (external) nearby zones from 2016 to 2017. Diversity, evenness, and dominance indices were determined, and the number of individuals, size, length at first maturity, and reproductive period of each species were analyzed to obtain fish use of the lagoon. This coastal lagoon shows a high abundance of juvenile organisms in the cold season, whereas mature adults were mostly present during the warm season. Environmental variables influencing fish species development and distribution, such as sea surface temperature, salinity, and chlorophyll-*a*, were detected. To conclude, the subtropical coastal lagoon in the Gulf of California is an important nursery area where reproduction occurs mostly near adjacent areas.

Keywords: ichthyofauna; coastal lagoon; nursery; environmental variables; coastal zone

INTRODUCTION

Coastal lagoons are semi-enclosed inland water bodies with connections to the sea. These lagoons have a complex ecological structure related to habitat heterogeneity, close relationship with the marine environment, environmental variability, high primary productivity, and biological diversity (Díaz-Ruiz et al. 2004, Padilla-Serrato et al. 2017). However, these lagoons are environmentally and naturally stressed areas. Thus, species living in these environments must tolerate pressure and adapt (Pérez-Ruzafa et al. 2019). It is greatly important for the communities to carry out their biological processes and development in this ecosystem (Nagelkerken 2009).

In coastal lagoons, fish species are among the most rich and abundant communities (Arceo-Carranza et al. 2010). Temporal variations of community structures and their interactions throughout the year are determined by seasonal changes in environmental variables in coastal lagoons (Lanzoni et al. 2021). These changes cause different fish species to use them permanently or temporarily throughout their life cycle (Díaz-Ruiz et al. 2018), which is ecologically important

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since the marine ichthyofauna perform functions related to energy flow, establishing connectivity between the lagoon systems and the marine environment (Albaret 2017, Padilla-Serrato et al. 2017).

Different life development stages of fish have specific habitat and environmental requirements (Ramos et al. 2016). Spawning and nursery grounds are essential habitats where survival of early fish life stages is the most likely to occur. Important areas are estuaries, coastal lagoons, and upwelling zones (Zorica et al. 2020). Because of the environmental complexity, low predator incidence, and continuous nutrient supply, coastal lagoons greatly benefit the fish communities that inhabit them (Arceo-Carranza et al. 2010). Their seasonal variation serves as an ecological filter that defines favorable conditions for the life cycle stage in which the organism is found, thus influencing growth and survival (Peguero-Icaza et al. 2008).

Studies of community structure and life stages in coastal lagoons in temperate, tropical, and subtropical regions agree that ichthyofauna is mainly constituted by juveniles using these spaces for feeding and nursery (Ramos et al. 2016, Cabrera-Páez et al. 2018, Lanzoni et al. 2021), which are the main functions of the lagoons since they contribute to growth and survival and later recruited to the adult population inhabiting the adjacent areas (Cabrera-Páez et al. 2020). Adult fish use the coastal lagoons as feeding and breeding grounds, but generally, spawning occurs in areas adjacent to the lagoon (Nagelkerken 2009, Ramos et al. 2016). Only some species complete all the biological processes of their life cycle within the coastal lagoon (Whitfield 1999).

The ecological functions of coastal lagoons and their effects on fish communities vary over time due to their environmental variability (Yáñez-Arancibia et al. 1988, Pérez-Ruzafa et al. 2019, Whitfield et al. 2022). Some recent studies indicate that because of the characteristics of each coastal lagoon, ecological functioning should be analyzed particularly to identify fish species dependency and movement between the coastal lagoon and the marine environment (Aguilar et al. 2014, Pérez-Ruzafa et al. 2018, 2019). In addition, their study is essential for the proper evaluation and conservation strategies because these areas are ecosystems that have a key role in the ecological functions of fish communities and as sentinel systems under extreme environmental changes (Pérez-Ruzafa et al. 2019).

Studies of fish in coastal lagoons of the Gulf of California (GC) have focused on composition, abundance, and distribution (Rodríguez-Romero et al. 2011, Padilla-Serrato et al. 2017, Amezcua et al. 2019). In the Mexican Pacific, some research has been carried out on the composition and sizes of the specimens (González-Sansón et al. 2014, Cabrera-Páez et al. 2018, 2020). The Navachiste coastal lagoon in the GC was declared a Ramsar site in February 2008 (Sánchez-Bon et al. 2010). It was established as a site of international importance and has been subject to several studies (Montes et al. 2012, Félix-Salazar et al. 2020), including their ichthyofauna (Amezcua et al. 2019, Moreno-Pérez 2019), but none on the use of the coastal lagoons by fish that have been recorded in the area. Based on the above, the study on fish assemblages and sizes in the coastal lagoon of the GC was developed. For this case study, the coastal lagoon is assumed to function as an important growth and development area that provides a habitat for nursery, feeding, and protection for the different life stages of fish species. Therefore, this research aims to define the specific composition, diversity and dominance, seasonal juvenile-adult ratio, and movement of ichthyofauna between the coastal lagoon and the marine environment. Finally, the fish ecological usage of this subtropical coastal lagoon in the GC is determined.

MATERIALS AND METHODS

Study area

The Navachiste coastal lagoon in Sinaloa, Mexico (Gulf of California) is an ecosystem within Ramsar sites located at 25°30'-25°60'N and 108°45'-109°05'W, in the municipalities of Guasave and Ahome. (Fig. 1). This area is a semi-enclosed lagoon system (195 km^2 and 0.5-5 m in depth), where the San Ignacio Island barrier separates it from the GC (Martínez-López et al. 2007, Sánchez-Bon et al. 2010), and the adjacent coastal area has an irregular depth and numerous shallow zones (Félix-Salazar et al. 2020). The mangrove forest covers 11,324 ha of the coastal lagoon and almost the entirety of the several islands and islets (Sánchez-Bon et al. 2010, Carrasquilla-Henao et al. 2013). Its climate is warm and dry, with an average annual temperature of 23.5°C. It shows seasonal variations in water temperature in the cold periods (December-February) from 19 to 22°C and warm periods (July-September) from 31 to 32°C. Water salinity ranges from 33 to 40, and the lagoon has a 16-day water replenishment (Escobedo-Urías et al. 2007, Montes et al. 2012, Amezcua et al. 2019). The rainy season occurs between summer and autumn, with an annual average precipitation of 365 to 450 mm (Martínez-López et al. 2007).

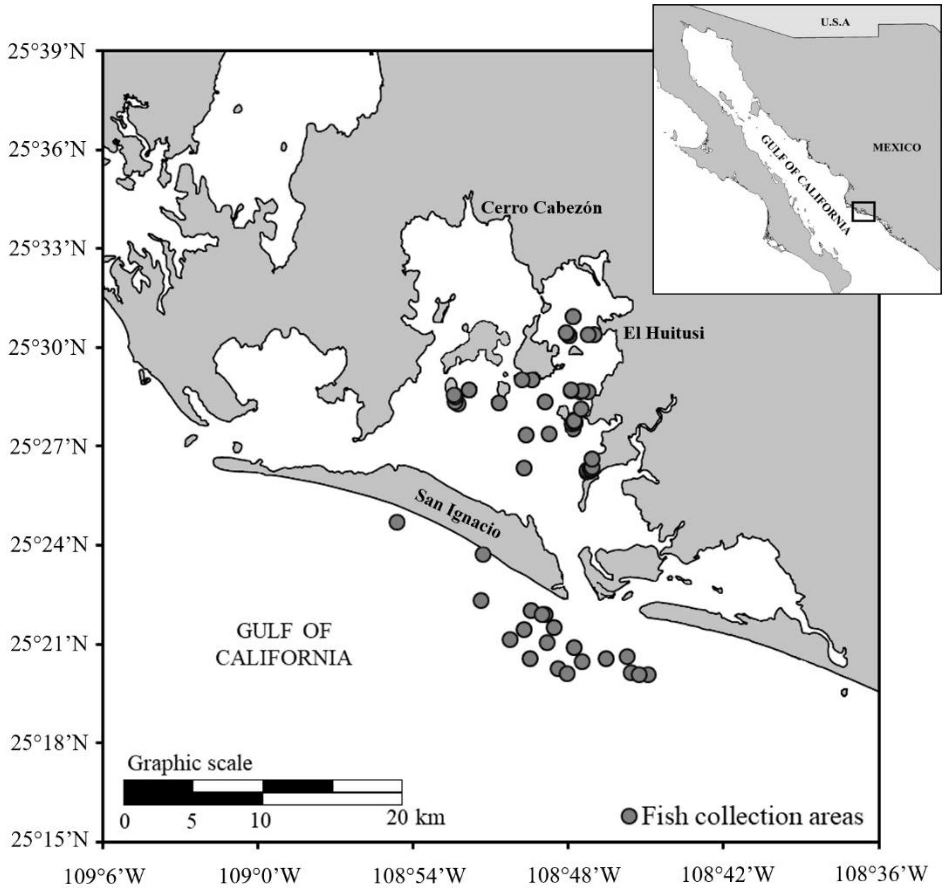

Figure 1. Study area and fish sampling locations in the Navachiste coastal lagoon system and the marine environment in the Gulf of California, México.

Table 1. Number of samplings by fishing gear (gillnets, casting net, trawling net) conducted in the Navachiste coastal lagoon (CL) and marine environment (ME) in the Gulf of California, Mexico, during the four seasons in the 2016-2017 period. WS: warm season, CS: cold season.

Fishing gear	WS (March 2016)		CS (December 2016)		CS (February 2017)		WS (September 2017)	
	CL	ME	CL	ME	CL	ME	CL	ME
Gillnets	0	2	2	1	1	2	6	3
Casting net	20	0	10	0	0	0	0	0
Trawling net	0	0	0	9	5	0	0	3

Biological sampling

Four fish samplings were performed in 2016 and 2017, which were classified into warm (WS) and cold (CS) seasons according to Amezcua & Amezcua-Linares (2014) and López-Martínez et al. (2023). WS included March 2016 and September 2017 sampling and CS December 2016 and February 2017 sampling. The organisms were collected on board - small vessels with 110 HP outboard motors from 64 stations during the samplings in the Navachiste coastal lagoon (Table 1); from the total stations sampled, 44 were located within the lagoon (internal zones) and 20 in the marine environment (external nearby zones) (Fig. 1) to compare and assess fish species spatial movement, length composition, and maturity. The fish collection was carried out with three fishing gears, using gillnets (600 m long, 3.6 m high, and mesh size of 7.62 cm), cast nets (3 m diameter and 1.2 cm mesh size), and trawl nets (20 m footrope and 3.8 cm mesh size and dragging the net to 3.7 km h^{-1}) to capture the largest possible number of species (pelagic and benthic-demersal) and better characterizing the community. Due to its sampling coverage in the study area, the unit of measurement for effort standardization was the gillnet (2160 m^2 and 30 min set) to allow comparisons between samplings. The standardized catch per unit effort (CPUE) was calculated from the abundance data of fish species *i* observed in the fishing gear *j* divided by the gillnet effort (2160 m^2 and 30 min) (Fig. 2) following the method of Sparre & Venema (1997) and Gibson-Reinemer et al. (2017). Standardized abundance data (CPUE) of fish species *i* were accommodated according to the season (warm and cold) and zone (coastal lagoon - marine environment) to describe the community used to evaluate ecological parameters.

The collected fish were placed in marked bags and transferred under refrigeration to the laboratory; the fish were identified to species level, using the keys: Jordan & Evermann (1896-1900), Meek & Hildebrand (1923-1928), Miller & Lea (1976), Eschmeyer et al. (1983), Fischer et al. (1995), Castro-Aguirre et al. (1999), Robertson & Allen (2015), Nelson et al. (2016) and Froese & Pauly (2021). Fish sex and maturity were based on the morphochromatic scale proposed by Nikolsky (1963), and morphometric characters and meristic counts were obtained for every specimen; the sex ratio was obtained for the total organisms.

Environmental variables

To evaluate the seasonal changes of the environment, sea surface temperature (SST), salinity (S), and chlorophyll (Chl-*a*) values were obtained. SST and S were recorded *in situ* (during the biological sampling) using YSI model 556 pro plus multiparameter equipment (Thomas Scientific, NJ, USA). The SST and S data were also used to analyze the variation between the lagoon and the marine environment; the statistical analysis was performed using the software Statistica v12 (StatSoft, Inc., MS, USA). For Chl-*a* concentration (mg m^{-3}) in the study area (Navachiste coastal lagoon) for 2016-2017, monthly satellite image composites of 1 km resolution HDF4 format were obtained. These images are the products of the merged simple averages of all valid data from sensors: SeaWiFS, MODIS Terra, MODIS Aqua, MERIS, VIIRS, and OLCI, all available at https://www.wimsoft.com/CAL/ (images accessed and obtained in January 2022). Image processing to obtain the Chl-*a* monthly data was carried out using Windows Image Manager Software (WIM version 9.06; 1991-2015, Mati Kahru, San Diego, CA, USA).

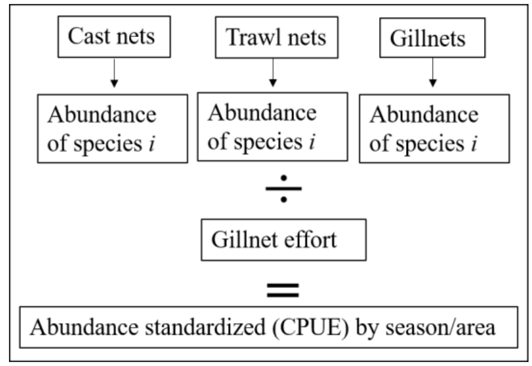

Figure 2. Diagram of the steps required to standardize the data in the Navachiste coastal lagoon and marine environment by season of the year.

Data analysis

The ecological parameters were calculated with standardized abundances (CPUE), used as community descriptors were Shannon diversity (H') and evenness (E), which were determined using PRIMER v6 (Clarke & Gorley 2015). Dominance was determined by using Sanders's (1960) biological value index (BVI) modified by Loya-Salinas & Escofet (1990) because this index has the advantage of combining the property of relative abundance with species consistency. By assigning a numerical value to each sample abundance, more consistent species during sampling are more important than those with high abundance in fewer samplings (Loya-Salinas & Escofet 1990).

The length at first maturity (L_{50}) (the length at which 50% of the fish are mature) allows for the separation of juveniles from adult organisms (Rábago-Quiroz et al. 2020). L_{50} of the species was used as reported by Moreno-Pérez (2019) and the online database FishBase (Froese & Pauly 2021), where juvenile individuals were those with sizes smaller than L_{50}, while adults were those with sizes equal to or larger than L_{50}. In this manner, the seasonal relative abundance of juvenile and adult organisms was identified. With the information previously described, correlations among diversity (H'), evenness (E), relative abundance of juveniles and adults, and environmental variables were tested by Pearson's correlation test.

The dominant species were determined by the BVI, and size distributions were evaluated using a box-and-whisker plot, given that they rarely meet a normal distribution (González-Sansón et al. 2014). Thus, asymmetry of the distributions is established based on the position of the median and location of 25-75% quartiles concerning the range of non-extreme values.

Additionally, some of these dominant species were used to obtain a box-and-whisker plot to identify the seasonal size ranges and percentage of non-breeding and breeding adults considering immature (stages I and II) and mature organisms (stages III-V). This information was used to characterize the fish community behavior, seasonal movement, and use of the subtropical coastal lagoon and the marine environment.

RESULTS

Environmental variables

The SST and S values from data *in situ* show the mean annual SST of the internal side of the Navachiste coastal lagoon was 22.6 ± 4.0°C, while the marine environment (near external zones) mean annual SST was 22.5 ± 3.9°C. Generally, the highest SST recorded for the study area was in WS, and the lowest in CS. The average S in the lagoon was 35.0 ± 0.8 and 34.9 ± 0.4 in the marine environment (Fig. 3a). The Kruskal-Wallis test showed that both variables had no significant differences (SST H (1, 28) = 0.0048, P = 0.94; S H (1, 19) = 0.169, P = 0.68) between the coastal lagoon and the marine environment. The annual average Chl-*a* was 4.1 ± 1.3 mg m^{-3}, with a maximum value in CS and minimum in WS (Fig. 3a). The environmental conditions showed evident inverse trends as SST increases, Chl-*a* decreases, and *vice versa*.

Fish species composition and community characteristics

The fish community identified was grouped into 95 species collected during the WS (March 2016 and September 2017) and CS (December 2016 and February 2017). Of the total, 43 species were caught by the three gears, the trawl net contributing to most of the abundance (32) followed by the gillnet (10), while 33 species were caught only by trawl net, 15 by gillnet and 4 by cast net. The coastal lagoon and the marine environment showed a difference in the abundance of fish species. The highest species abundance recorded in the internal coastal lagoon were *Haemulopsis nitidus* and *Eucinostomus dowii*, while *E. dowii* and *Diapterus brevirostris* in the marine environment. Regarding dominance (BVI), 20 fish species were the most important (Table 2).

Shannon diversity (H') showed the highest diversity during WS ($H'_{March\ 2016}$ = 3.3 ± 0.2 - $H'_{September\ 2017}$ = 3.9 ± 0.3) and the lowest in CS ($H'_{December\ 2016}$ = 3.6 ± 0.5 - $H'_{February\ 2017}$ = 2.8 ± 0.6). Evenness (E) showed species evenly distributed with very similar values in WS ($E_{March\ 2016}$ = 0.81 ± 0.09 - $E_{September\ 2017}$ = 0.74 ± 0.08) and CS ($E_{December\ 2016}$ = 0.74 ± 0.08 - $E_{February\ 2017}$ = 0.70 ± 0.08). During the season, a higher abundance of juveniles was observed in CS, while the relative abundance of adults increased in WS (Fig. 3b). H' and adult relative abundance correlated with SST and S, and juvenile relative abundance with Chl-*a*, SST-Chl-*a*, and S-Chl-*a* showed a negative correlation. In contrast, SST-S showed a positive one (Table 3).

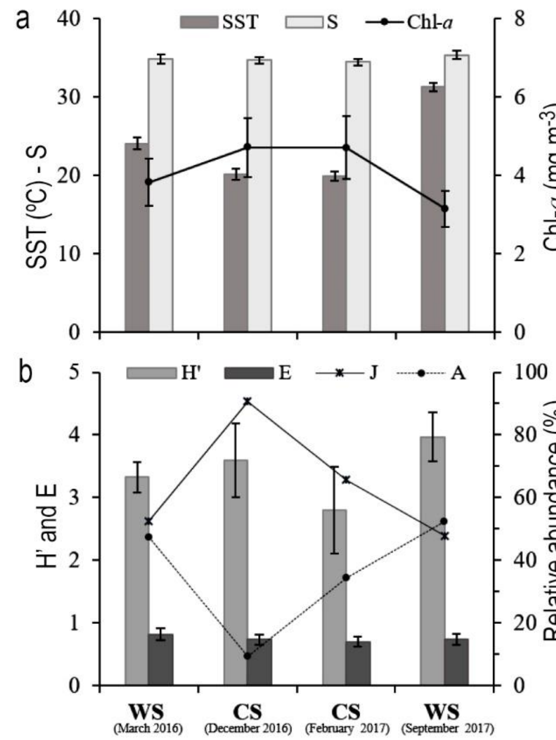

Figure 3. a) Seasonal sea surface temperature [SST mean ± standard error (SE)], salinity (S mean ± SE) and chlorophyll-*a* (Chl-*a* mean ± SE), and b) seasonal diversity (H' ± SE), evenness (E ± SE), relative abundances of juveniles (J) and adults (A) in the Navachiste subtropical coastal lagoon and marine environment system in the Gulf of California, Mexico, during the study period (2016-2017). WS: warm season, CS: cold season.

The size composition of dominant species (BVI) showed that juvenile organisms predominated (75%). However, adult sizes were also recorded in some species (Fig. 4). In the case of *Pseudupeneus grandisquamis*, only juvenile organisms were captured. For *Eucinostomus entomelas*, *Paralabrax maculatofasciatus*, and *Achirus mazatlanus*, 80% of the captured organisms were adults. In contrast, the rest of the species, both juveniles and adults were observed with greater relative abundance of juveniles for each species: *Diapterus brevirostris* (79%), *Urolophus halleri* (92%), *Haemulopsis nitidus* (70%), *Eucinostomus dowii* (85%),

Table 2. Ichthyofauna caught by cast nets (cn), gillnets (gn), trawl nets (tn), and in gray the fishing gear that contributed most of the abundance. Standardized abundance catch per unit effort (CPUE) of the Navachiste coastal lagoon (CL) and marine environment (ME) system in the Gulf of California, Mexico, during the study period. D: dominance. *Represents the species with the highest biological value index (BVI).

Species	cn	gn	tn	CL	ME	D
Sphyrna lewini (Griffith & Smith, 1834)			ME	-	1.57	
Pseudobatos glaucostigma (Jordan & Gilbert, 1883)			CL-ME	14.27	73.13	
Urolophus halleri Cooper, 1863	CL	ME	CL-ME	471.40	267.54	*
Urotrygon chilensis (Günther, 1872)			CL-ME	49.93	48.64	*
Albula gilberti Pfeiler & van der Heiden, 2011		CL-ME		0.24	0.60	
Albula pacifica (Beebe, 1942)		ME		-	2.86	
Albula esuncula (Garman, 1899)		CL		1.11	-	
Gymnothorax equatorialis (Hildebrand, 1946)			ME	-	2.94	
Ophichthus zophochir Jordan & Gilbert, 1882			ME	-	3.37	
Cynoponticus coniceps (Jordan & Gilbert, 1882)		ME		-	2.00	
Anchoa ischana (Jordan & Gilbert, 1882)			CL-ME	35.68	141.33	*
Anchoa lucida (Jordan & Gilbert, 1882)	CL	ME	CL	7.33	2.00	
Anchovia macrolepidota (Kner, 1863)			ME	-	3.14	
Cetengraulis mysticetus (Gunther, 1867)	CL		ME	0.80	2.94	
Lile stolifera (Jordan & Gilbert, 1882)			ME	-	841.06	
Opisthonema libertate (Günther, 1867)	CL	CL-ME	CL	91.73	6.55	*
Ariopsis guatemalensis (Günther, 1864)		CL	ME	14.29	3.37	
Ariopsis seemanni (Günther, 1864)		CL	CL	149.82	-	
Bagre panamensis (Gill, 1863)	CL	ME	CL-ME	7.33	57.36	*
Bagre pinnimaculatus (Steindachner, 1876)	CL	ME		0.20	2.00	
Occidentarius platypogon (Günther, 1864)		CL		3.33	-	
Synodus scituliceps Jordan & Gilbert, 1882			CL-ME	74.90	30.93	
Mugil cephalus Linnaeus, 1758	CL	CL		1.51	-	
Colpichthys regis (Jenkins & Evermann, 1889)	CL			0.20	-	
Nematistius pectoralis Gill, 1862	CL	CL-ME	ME	12.08	8.98	
Caranx caballus Günther, 1868		CL	ME	5.56	6.29	
Caranx caninus Günther, 1867		ME		-	17.26	
Caranx vinctus Jordan & Gilbert, 1882		ME		0.20	8.98	
Chloroscombrus orqueta Jordan & Gilbert, 1883		ME	ME	-	4.58	
Hemicaranx leucurus (Günther, 1864)		CL-ME		1.25	2.38	
Hemicaranx zelotes Gilbert, 1898		CL		1.11	-	
Oligoplites altus (Günther, 1868)		CL		1.59	-	
Oligoplites refulgens Gilbert & Starks, 1904	CL	ME	CL-ME	7.53	48.39	
Oligoplites saurus (Bloch & Schneider, 1801)	CL			1.02	-	
Selene brevoortii (Gill, 1863)			ME	-	4.62	
Selene peruviana (Guichenot, 1866)		ME	CL-ME	33.88	287.99	*
Trachinotus kennedyi Steindachner, 1876	CL	CL-ME	ME	2.53	5.73	
Trachinotus paitensis Cuvier, 1832		CL-ME		0.48	1.19	
Sphyraena ensis Jordan & Gilbert, 1882		ME	CL-ME	7.13	2.17	
Citharichthys gilberti Jenkins & Evermann, 1889			ME	-	1.68	
Citharichthys platophrys Gilbert, 1891			ME	-	1.68	
Cyclopsetta panamensis (Steindachner, 1876)			ME	-	2.94	
Cyclopsetta querna (Jordan & Bollman, 1890)			CL-ME	7.13	12.03	
Etropus crossotus Jordan & Gilbert, 1882	CL	ME	CL-ME	7.35	475.79	*
Paralichthys aestuarius Gilbert & Scofield, 1898	CL			1.02	-	
Syacium maculiferum (Garman, 1899)			ME	-	1.68	
Syacium ovale (Günther, 1864)		CL	ME	1.11	56.43	
Achirus mazatlanus (Steindachner, 1869)	CL		CL-ME	328.16	28.67	*
Achirus scutum (Günther, 1862)			ME	-	2.94	
Symphurus chabanaudi Mahadeva & Munroe, 1990			ME	-	23.56	
Scomberomorus sierra Jordan & Starks, 1895		CL-ME	ME	21.25	12.17	*

Continuation

Species	cn	gn	tn	CL	ME	D
Peprilus medius (Peters, 1869)		ME		-	1.60	
Centropomus robalito Jordan & Gilbert, 1882			ME	-	3.14	
Diapterus brevirostris (Sauvage, 1879)	CL	CL-ME	CL-ME	285.12	1068.81	*
Eucinostomus currani Zahuranec, 1980			CL-ME	21.40	24.10	
Eucinostomus dowii (Gill, 1863)			CL-ME	891.67	1095.57	*
Eucinostomus entomelas Zahuranec, 1980	CL	CL	CL-ME	31.68	51.16	*
Eucinostomus gracilis (Gill, 1862)	CL		CL-ME	18.45	188.77	*
Eugerres lineatus (Humboldt, 1821)		CL	ME	2.86	282.67	
Gerres simillimus Reagan, 1907			CL	42.80	-	
Pseudupeneus grandisquamis (Gill, 1863)		CL-ME	ME	12.14	33.40	*
Diplectrum macropoma (Günther, 1864)			ME	-	4.42	
Diplectrum pacificum Meek & Hildebrand, 1925		CL	CL-ME	22.51	30.92	
Paralabrax maculatofasciatus (Steindachner, 1868)	CL	CL	CL-ME	136.16	11.15	*
Haemulon maculicauda (Gill, 1862)			ME	-	1.47	
Haemulon scudderii Gill, 1862			ME	-	1.47	
Haemulon steindachneri (Jordan & Gilbert, 1882)		ME	CL	7.13	2.00	
Haemulopsis elongatus (Steindachner, 1879)	CL	CL-ME	CL-ME	45.22	32.26	*
Haemulopsis leuciscus (Günther, 1864)		CL-ME	CL-ME	18.77	4.33	
Haemulopsis nitidus (Steindachner, 1869)	CL	CL	CL-ME	1037.37	729.27	*
Orthopristis reddingi Jordan & Richardson, 1985		ME	ME	-	6.37	
Pomadasys macracanthus (Günther, 1864)		CL-ME	ME	12.14	33.40	
Pomadasys panamensis (Steindachner, 1876)		ME	ME	-	10.94	
Hoplopagrus guentherii Gill, 1862			ME	-	4.42	
Lutjanus argentiventris (Peters, 1869)			ME	-	2.94	
Lutjanus guttatus (Steindachner, 1869)			ME	-	5.89	
Polydactylus opercularis (Gill, 1863)		ME		-	0.60	
Scorpaena sonorae Jenkins & Evermann, 1889	CL		ME	1.20	1.68	
Prionotus birostratus Richardson, 1844			ME	-	1.68	
Prionotus ruscarius Gilbert & Starks, 1904			ME	-	2.94	
Chaetodipterus zonatus (Girard, 1858)	CL	CL-ME	ME	3.98	117.61	*
Bairdiella icistia (Jordan & Gilbert, 1882)			CL-ME	7.13	9.67	
Cynoscion nannus Castro-Aguirre & Arvizu-Martinez, 1976		CL	ME	2.22	5.50	
Cynoscion reticulatus (Günther, 1864)		ME		-	1.60	
Cynoscion stolzmanni (Steindachner, 1879)		ME	ME	-	4.33	
Larimus acclivis Jordan & Brisol, 1898		ME	ME	-	41.45	
Menticirrhus panamensis (Steindachner, 1875)		CL		5.71	-	
Menticirrhus nasus (Günther, 1868)			ME	-	15.35	
Micropogonias ectenes Jordan & Gilbert, 1882	CL	ME	ME	1.20	9.17	
Paralonchurus rathbuni (Jordan & Bollman, 1890)			ME	-	1.10	
Umbrina xanti Gill, 1862		ME	ME	-	2.89	
Balistes polylepis Steindachner, 1876	CL		CL-ME	80.88	67.96	*
Sphoeroides annulatus (Jenyns, 1842)	CL	ME	CL-ME	107.02	18.42	*
Sphoeroides lispus Walker in Walker & Bussing, 1996	CL			1.02	-	
Sphoeroides lobatus (Steindachner, 1870)			ME	-	1.10	

Balistes polylepis (53%), *E. gracilis* (88%), *Opisthonema libertate* (68%), *Sphoeroides annulatus* (96%), *H. elongatus* (73%), *Etropus crossovers* (51%), *Bagre panamensis* (78%), *Selene peruviana* (75%), *Chaetodipterus zonatus* (98%), *Scomberomorus sierra* (84%) and *Anchoa ischana* (85%) (Fig. 4). In general, the same behavior was observed with higher frequencies of females than males, ratio of 2.1:1 ± 0.96 (H:M), except for *U. halleri* with a higher presence of males, ratio of 1.2:1 (M:H).

The seasonal movement and developmental characteristics of some of the area's most dominant fish species were *D. brevirostris*, *U. halleri*, *H. nitidus*, *E. dowii*, *O. libertate*, and *E. crossotus* are described (Figs. 5-6). In WS (March 2016), species distribution was wide; in the coastal lagoon and the marine environ-

Table 3. Pearson's correlation values between ecological characteristics and environmental parameters. SST: sea surface temperature (°C); Chl-*a*: chlorophyll-*a* (mg m^{-3}); and S: salinity. Positive correlations are highlighted in bold.

Environmental parameter	Diversity (H')	Evenness (E)	Juvenile relative abundance	Adult relative abundance	SST	Chl-*a*
SST	**0.76**	0.20	-0.88	**0.88**		
Chl-*a*	-0.68	-0.46	**0.96**	-0.96	-0.95	
S	**0.49**	-0.47	-0.54	**0.54**	**0.77**	-0.56

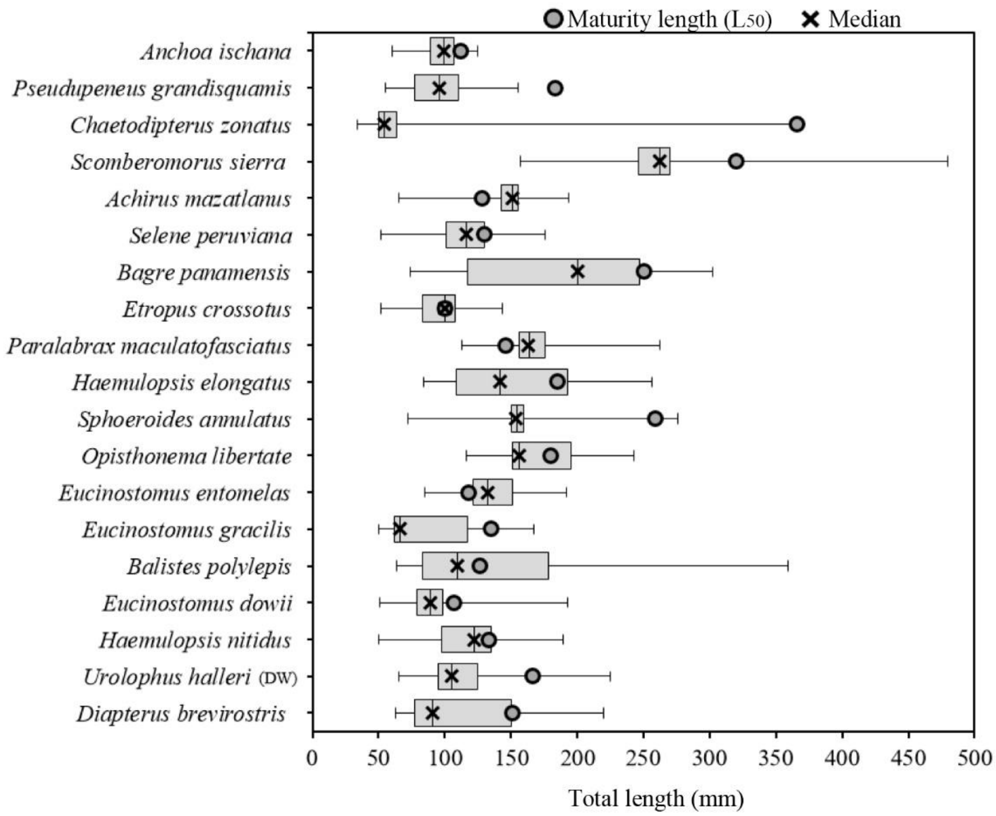

Figure 4. Size distribution of the dominant species by biological value index (BVI) in the study area; quartiles 25-75% (rectangle) and extreme interval values (solid line). DW: disc width.

ment, *U. halleri* (61%) and *O. libertate* (75%) juveniles predominated; for *D. brevirostris* (56%) and *H. nitidus* (75%), more adults were found. In this season, the species showed mature adults, but in the case of *U. halleri*, only immature adults were present.

During CS (December 2016), juveniles predominated for *D. brevirostris*, *H. nitidus*, *E. dowii*, *U. halleri*, and *E. crossotus* in the marine environment and the coastal lagoon. Mostly immature adults were observed. In CS (February 2017), more than 80% of the organisms were found within the coastal lagoon, of which *D. brevirostris*, *E. dowii*, and *O. libertate* were represented by 53% of juveniles and 47% of adults. On the other hand, *H. nitidus* were mainly adults (77%), and *U. halleri* were mostly juveniles (95%). Immature adults were mostly found for all the species.

During WS (September 2017), more than 80% of the organisms were found in the marine environment. Here, adults predominated for the species *D. brevirostris*, *H. nitidus*, *E. dowii*, *O. libertate*, and *E. crossotus*, except for *U. halleri*, where mostly juveniles were found. The species were mainly mature adults, except for *U. halleri* and *E. crossotus*, with the majority being immature adults.

The spatial-temporal fish species distribution in the Navachiste coastal lagoon showed that in WS (March

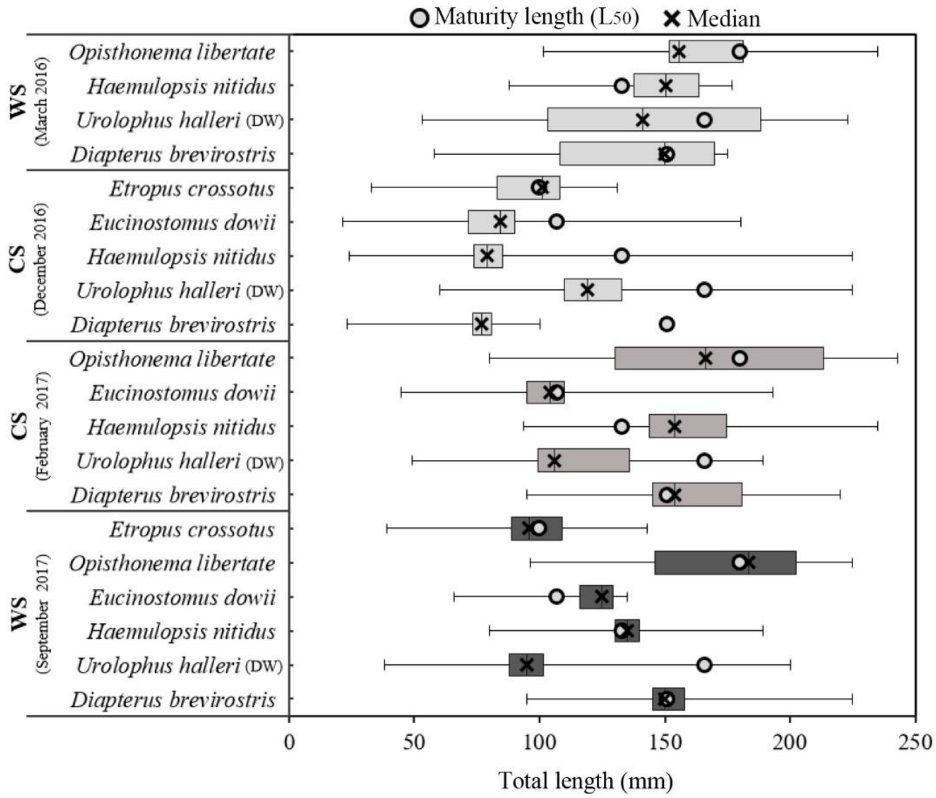

Figure 5. Size distribution for some of the most characteristic fish species by season in the subtropical Navachiste coastal lagoon and marine environment system in the Gulf of California, Mexico. Quartiles 25-75% (rectangle), the rectangles (light gray) represent that the community was almost equally distributed in the marine environment and coastal lagoon; (gray) >80% of the distribution is in the coastal lagoon and (dark gray) >80% of the distribution is in the marine environment, and extreme interval values (solid line). DW: disc width, WS: warm season, CS: cold season.

2016 and September 2017), predominant adults moved between the marine environment and the coastal lagoon. However, mature adults were mainly found in the marine environment. On the other hand, fewer juveniles were observed within the lagoon, which may have moved to the marine environment. In CS (December 2016 and February 2017), a decrease in adults and an increase in juveniles were observed moving between the marine environment and the coastal lagoon. Nonetheless, juveniles predominated within the coastal lagoon (Fig. 7).

DISCUSSION

Environmental variables

Globally, coastal lagoons are habitats with important environmental characteristics and different uses for the fish species that inhabit them, and they are decisive in their life cycles. The particular case of the Navachiste coastal lagoon showed seasonal environmental variability. SST and S showed maximum values during WS and minimum during CS, which agrees with Montes et al. (2012) and Amezcua et al. (2019). Temperature seasonality is well-defined because the lagoon is in a subtropical and semi-arid zone (Padilla-Serrato et al. 2017). SST strongly influences season and spatial changes in fish community structure (Albaret 2017, Lanzoni et al. 2021) as the primary factor controlling key physiological, biochemical, and life history processes (Bruno et al. 2013). Thus, variations in the abundance of juveniles and adults indicate species seasonality, commonly associated with biological processes such as protection, feeding, and growth (Padilla-Serrato et al. 2017).

The S values showed that pattern due to water exchange with the marine environment, low freshwater inputs during the rainy season, and high annual evaporation rates (Carrasquilla-Henao et al. 2013, Padilla-Serrato et al. 2017). Similar SST and S values between internal and external areas indicate water exchange through the mouths of the coastal lagoon and a strong interaction between both zones, allowing

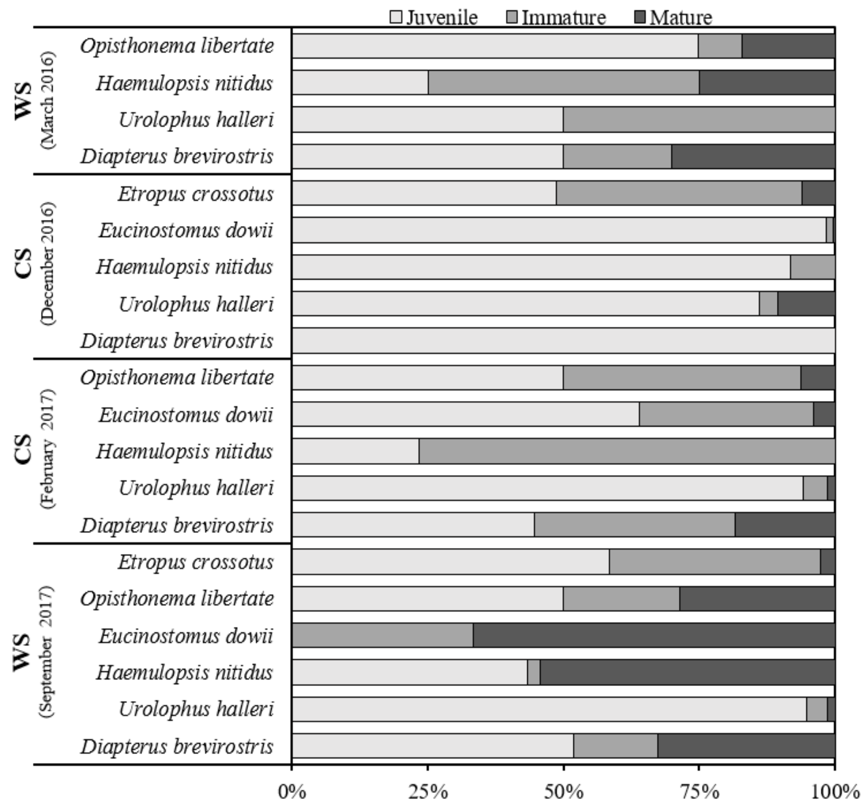

Figure 6. Seasonal relative abundance of juveniles, immature and mature adults of some of the most characteristic fish species in the Navachiste subtropical coastal lagoon and marine environment system in the Gulf of California, Mexico. WS: warm season, CS: cold season.

species movement and distribution (Díaz-Ruiz et al. 2018, Amezcua et al. 2019).

A variability was observed in Chl-*a* values, also reported by García-Morales et al. (2017), indicating increases in Chl-*a* concentration from November to April and decreases from May to October. During CS, the coastal upwelling of cold and nutrient-rich subsurface water occurs in the eastern coasts of the GC, which is determined by wind intensity, depth, and heterogeneity of the coastline, all generating an increase in Chl-*a* concentration along the coasts (Farach-Espinoza et al. 2021, López-Martínez et al. 2023). Chl-*a* levels in the lagoon are associated with farmland runoffs, seasonal rains, and wastewater effluents (Martínez-López et al. 2007, García-Morales et al. 2017). Environmental variables showed an inverse correlation between SST and Chl-*a* values when SST increases, Chl-*a* decreases and *vice versa* (García-Morales et al. 2017, López-Martínez et al. 2023).

The conditions foreseen for in the Gulf of California by 2100 year are temperature increases up to 2.5-4° (López-Martínez et al. 2017). An approximate of the effects could be obtained by evaluating the fish community and behavior during strong El Niño periods. The National Oceanic and Atmospheric Administration (NOAA) reported the strong event that occurred during 2015-2016 named "El Niño Godzilla," which caused notable environmental differences and strong seasonal variabilities in the mid-Gulf of California such as low Chl-*a* concentration, deeper thermocline, upwelling decrease, and high SST for longer periods (Coria-Monter et al. 2018, Farach-Espinoza et al. 2021). Conditions that occurred during the conduction of the present study provide background on the fish community structure and behavior during an El Niño event and serve as a point of comparison for future long-term studies.

Fish community characteristics

The fish community in the subtropical coastal lagoon was composed of 95 species. The combination of gillnets, cast nets, and trawl nets provides greater representativeness of the fish community in the coastal lagoon by catching a broad spectrum of species and size range. The different fishing gears are necessary to eva-

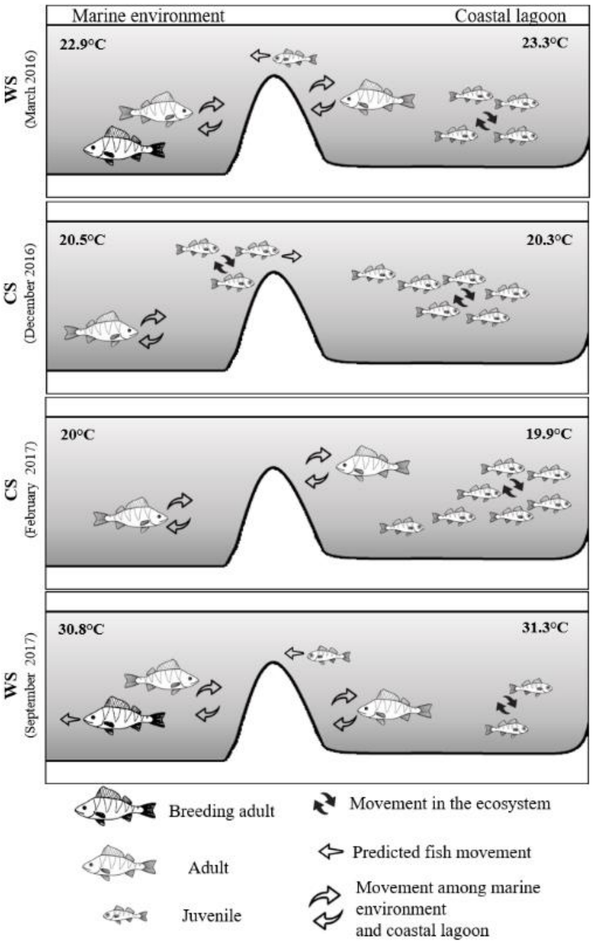

Figure 7. Conceptual diagram of the seasonal movement and life cycle of the Navachiste coastal lagoon fish community and marine environment system in the Gulf of California, Mexico. WS: warm season, CS: cold season.

luate the fish communities, the distinct ecological and biological processes of the community, life stages, and habitats (Amezcua et al. 2006, Amezcua & Amezcua-Linares 2014, Padilla-Serrato et al. 2017). The standardizing CPUE allows different gears to be compared to one another by equaling effort over sampling time, which is a method widely used by Amezcua et al. (2006), Gibson-Reinemer et al. (2017), and Lanzoni et al. (2021) to assess fish communities.

Coastal lagoon characteristics and environmental conditions influence fish species composition and abundance, thus directly influencing diversity and evenness (Amezcua et al. 2019). The highest diversity values occurred during the WS, reflecting that temperature controls patterns of diversity, as reported by Díaz-Ruiz et al. (2018), just as the changes in the presence and abundance are associated with seasonal changes (Rodríguez-Romero et al. 2011, Amezcua & Amezcua-Linares 2014).

The fish that characterize this coastal lagoon are resident species since they showed the highest BVI (Loya-Salinas & Escofet 1990). Dominant species are common in other coastal lagoons in the region because they have a wide distribution from temperate to tropical zones, high environmental tolerance, capacity to evade their predators, broad trophic spectrum, and environmental utilization (Rodríguez-Romero et al. 2011, Padilla-Serrato et al. 2017). Dominant species are important because they act as controllers of the entire fish community structure and function, so they are useful to illustrate the community's adaptive capacity and life history role (Yáñez-Arancibia et al. 1988).

The different 1:1 sex ratios found can have different connotations. In fish, sex is determined by genetics, environment - temperature being the most important - stress, or interaction between factors (Geffroy & Wedekind 2020). The sex ratio should be maintained 1:1, but commonly, this is not the case (Fryxell et al. 2015). The difference in sex ratio can vary between populations and the life cycle because of factors such as habitat preference, depth, feeding, reproductive and mortality aspects (Lucano-Ramírez et al. 2022). The highest proportion of females in the study coincides with that reported in other works (Ruiz-Ramírez et al. 2017, Rábago-Quiroz et al. 2020), which could be the result of displacement to refuge areas to avoid predators or in search of food in preparation for reproduction (Rábago-Quiroz et al. 2020), because coastal lagoons function as important food and energy sources, a greater presence of females is possible (Padilla-Serrato et al. 2017).

On the other hand, chemicals from anthropogenic impacts have been shown to influence the sex ratio (Dang & Kienzler 2019). García-Gasca et al. (2016) argue that the sex ratio female-biased could be due to exposure to estrogenic chemical compounds during the critical periods of sex determination or gonadal differentiation. The coastal lagoon of Navachiste is constantly impacted by aquaculture and agricultural activities, which could also influence the presence of females (Montes et al. 2012). Sex ratios have long been of interest in population ecology; despite the attention paid to the causes of natural variation, the consequences for communities and ecosystems remain untested. The lack of attention may be due to the assumption that the sexes of most species are ecologically equivalent in their effects on communities and ecosystems (Fryxell et al. 2015). Future research is needed on this topic.

The present research has provided information on how ichthyofauna structure is arranged in response to cyclic variations driven by seasons, highlighting that the lagoon delivers distinct ecological functions throughout the year. According to Nagelkerken (2009), more robust research is needed to understand the ecological function, which requires much broader and more specific data and analyses. Thus, the analysis of size composition - combined with size at first maturity (L_{50}) of each species - allowed the identification of juvenile and adult specimens, and by including sexual maturity, the reproductive use of the coastal lagoon was verified. These analyses are of great importance to determine the life stages of the species that use these important ecosystems. Furthermore, the analyses are consistent with the research conducted by González-Sansón et al. (2014), and Cabrera-Páez et al. (2020), who applied size and L_{50} information to demonstrate that the coastal lagoon is inhabited mainly by juveniles, so lagoons constitute potential nursery areas. In the Navachiste coastal lagoon, 75% of the fish species that inhabit the lagoon are juveniles; thus, the system is used as a nursery habitat, while the rest are adults that periodically use the lagoon as a refuge and feeding area. These results agree with those observed in Mar Chiquita coastal lagoon, Argentina (Bruno et al. 2013), Nador Lagoon, Morocco (Jaafour et al. 2015), Barra de Navidad Lagoon, Mexico (Cabrera-Páez et al. 2018), and Fattibello Lagoon, Italy (Lanzoni et al. 2021).

Juvenile fish predominance and adult presence indicate seasonal succession in different stages of the ichthyofauna life cycle. These seasonal patterns of functional use display the importance of connectivity between the coastal lagoon and the marine environment, ensuring individuals' movement and exchange. This connectivity is essential for understanding key ecological processes that guarantee the survival, success, and dynamics of fish populations and has become an increasingly important consideration in spatial conservation planning (Aguilar et al. 2014, Pérez-Ruzafa et al. 2018). Seasonal succession has also been documented in the Goiana Estuary, Brazil (Ramos et al. 2016), La Mancha Lagoon, Mexico (Díaz-Ruiz et al. 2018), Bahía Portete, Colombia (Gallego-Zerrato & Giraldo 2018), Mar Menor Lagoon, Spain (Pérez-Ruzafa et al. 2018) and Barra de Navidad Lagoon, Mexico (González-Sansón et al. 2018, Cabrera-Páez et al. 2020). Thus, the spatial-temporal distribution scheme of the species proposed in the present study can be generalized, at least for the coastal lagoons in subtropical and transitional zones.

The fact that most organisms collected in the samplings were juveniles is an aspect to consider, given that they were caught with commercial fishing gear and could appear in commercial catches. The consequences of catching juveniles in terms of conservation could be dramatic, affecting population recruitment (Salas-Singh et al. 2022). Figure 4 shows the L_{50} of the species and can serve as a first approximation to implement a minimum species catch size. Likewise, it should also be noted that most of the species in the present study do not appear as subjected to fishing National fishing charter in Mexico, which is a gap in the information necessary for sustainable management of the species using the coastal lagoons.

Coastal lagoons are simultaneously used by multiple species, revealing the importance of these ecosystems for biological populations (Lanzoni et al. 2021). Therefore, knowing the life history and specific movements of fish species is important to understand the location and ecological function of these habitats for the organisms (Aguilar et al. 2014). The life history of the fish community in this subtropical coastal lagoon stands out because not all species are found in seasons; the distribution and habitat use, as reproduction, feeding, and refuge areas follow patterns that depend on environmental conditions and specific physiological requirements of each species (Aguilar et al. 2014, Whitfield et al. 2022).

Fish in early stages feed mainly on zooplankton, which is crucial for their survival and growth. Thus, the high density of organisms in these early stages regularly coincides with high food availability in the ecosystem (Gallego-Zerrato & Giraldo 2018, Farach-Espinoza et al. 2021), promoting the growth and increasing successful fish recruitment in early stages (Gallego Zerrato & Giraldo 2018, Payan-Alejo et al. 2020). On the other hand, to maximize reproduction, it is synchronized with environmental signals, and for species survival to increase, a common tactic in tropical and subtropical species is multiple spawning (Spíndola-Linhares et al. 2014). Reproduction occurs in WS, coinciding with the low Chl-*a* concentration period in the study area, representing low food availability and fish species' energy allocation toward gonad maturation (Payan-Alejo et al. 2020).

Season patterns of the coastal lagoon's functional use depend on species ecology differences (Lanzoni et al. 2021). Juveniles of different species were observed throughout the year, predominantly in CS and with the mangrove cover, a primary nursery and recruitment habitat (Nagelkerken 2009, Sánchez-Bon et al. 2010).

This result indicates using the Navachiste coastal lagoon as a feeding and nursery (growth) habitat because it provides them protection and high food availability, favoring fish survival and recruitment when facing high vulnerability to predators in these stages (Cheminée et al. 2021).

Fish preferred specific nursery habitats, but the species used multiple ones. Thus, coastal lagoons play an important ecological role by providing different habitats for many fish species (Nagelkerken 2009, Jaafour et al. 2015). During the CS, juvenile fish were observed in shallow areas of the marine environment and within the coastal lagoon that has mangroves, several islands, and islets, which indicated that these organisms could use different habitat types in both ecosystem zones for nursery and feeding purposes during their life stage as observed by Nagelkerken (2009), González-Sansón et al. (2014) and Cheminée et al. (2021). This connectivity between the external and internal zones of the lagoon provides favorable conditions for the species to increase their success in survival and subsequent recruitment (Pérez-Ruzafa et al. 2018, Whitfield et al. 2022).

During WS, the adult specimens increase within the coastal lagoon for refuge and feeding (Díaz-Ruiz et al. 2004). The increase in mature adults indicates that reproduction occurs in the marine environment near the coastal zone, where optimal environmental conditions for growth areas, defense, and survival increase are found (Spíndola-Linhares et al. 2014, Ramos et al. 2016). This strategy ensures permanence of larvae in suitable areas for subsequent recruitment, seeking favorable conditions for both biological (food abundance and low predation) and physical (temperature and salinity) conditions, which explain the increase in number of juveniles that enter and distribute within the coastal lagoon during CS (Peguero-Icaza et al. 2008, Díaz-Ruiz et al. 2018).

Based on the results, the Navachiste coastal lagoon is an important nursery and feeding area representing a priority habitat for the fish community and species' survival. These ecological functions are especially important during unfavorable environmental conditions, such as the "Godzilla El Niño event". Nevertheless, this potential response should be addressed in subsequent long-term studies. Considering that an increase of SST from about 2.5 to 4°C is expected to occur in the GC by 2100 year (López-Martínez et al. 2017), and due to coastal lagoons ability to act as sentinel systems (Pérez-Ruzafa et al. 2019), the study of fish communities will become a study topic of maximum interest in the future of coastal lagoon ecology and management. Finally, the results of the present research demonstrate the ecological importance of the coastal lagoon for many fish species and make it relevant and applicable to other sub-tropical coastal lagoons in the world, all in the quest to direct efforts for the proper management and preservation of these ecosystems.

CONCLUSIONS

The present study has demonstrated that the subtropical coastal lagoon in the Gulf of California is an important area that provides feeding and nursery habitats of vital relevance for different fish species' life cycles. Likewise, the environmental variables influence the behavior and requirements of ichthyofauna, thus reinforcing the importance of evaluating the fish community structure during and after environmental anomalous events, such as El Niño Southern Oscillation. Thus, further studies are needed to evaluate the biological communities, their ecological use, and environmental variability and establish preservation plans for this ecosystem.

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