

Article

## Ecomorphological relations of sympatric juveniles of Clupeiformes from a Brazilian sandy beach

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**ABSTRACT.** Surf zones are important for early life stages of several fish species for presenting characteristics such as high phytoplanktonic production, diverse food availability and shelter against predators. The action of waves in this environment provides nutrient cycling and increase the turbidity making surf zones ideal nursery environments for diverse species of fish, including clupeiforms. Clupeiform species have a great ecological and economic value for being abundant fish in tropical sandy beaches surf zones with significant fisheries importance. Studies about their feeding ecology and environment use are relevant, and one of the methods improving this knowledge is the application of ecomorphological analyses, which helps understanding species ecological interactions and their adaptations. In this context, the present study aimed to identify the ecomorphological relations and infer about the feeding ecology of eight sympatric clupeiform species in a Brazilian tropical sandy beach. Ten ecomorphological variables were analyzed of individuals belonging to the species *Anchoa tricolor* (Spix & Agassiz, 1829), *Anchoa januaria* (Steindachner, 1879), *Anchovia clupeioides* (Swainson, 1839), *Anchoviella lepidentostole* (Fowler, 1911), *Lycengraulis grossidens* (Spix & Agassiz, 1829), *Chirocentrodon bleekermanus* (Poey, 1867), *Harengula clupeola* (Cuvier, 1829) and *Opisthonema oglinum* (Lesueur, 1818), whose values were employed in a principal component analysis (PCA) with the two first axis explaining 58.92% of the total variance. A high morphological overlap between the species of Engraulidae was observed with the exception of *A. clupeioides*, which differed from the others for presenting higher values of the compression index and caudal peduncle compression index. The Clupeidae species differed from the other families due to higher values of relative height and relative head length which also showed differences between the species themselves, having *H. clupeola* presented the highest values of these variables. The representative of Pristigasteridae showed an intermediate overlap between the species of the other families because of its highly compressed body but with low scores of relative height, caudal peduncle relative length and mouth aspect ratio. The morphological differentiation between the families and even between species from the same family indicates niche divergences, showing that besides their phylogenetical proximity there are differences in their ecological interactions which possibly contribute to their coexistence.

**KEYWORDS.** Morphological overlap; coexistence strategy; interspecific competition.

**RESUMO.** Relações ecomorfológicas de juvenis simpátricos de Clupeiformes de uma praia arenosa brasileira. Zonas de arrebentação são importantes para os estágios iniciais de várias espécies de peixes por apresentarem características como alta produção fitoplanctônica, disponibilidade alimentar diversificada e abrigo contra predadores. A ação das ondas nestes ambientes proporciona a ciclagem de nutrientes e eleva a turbidez, tornando as zonas de arrebentação ambientes de berçário ideais para diversas espécies de peixes, incluindo os clupeiformes. Espécies de Clupeiformes possuem alto valor ecológico e econômico, por serem peixes abundantes em zonas de arrebentação em praias arenosas tropicais com significativa importância pesqueira. Estudos sobre sua ecologia alimentar e utilização do ambiente são relevantes, e um dos métodos para aprimorar este conhecimento é a aplicação de análises ecomorfológicas, que auxiliam no entendimento das interações ecológicas das espécies e suas adaptações. Nesse contexto, o presente estudo teve como objetivo identificar as relações ecomorfológicas e inferir sobre a ecologia alimentar de oito espécies de clupeiformes simpátricas em uma praia arenosa tropical Brasileira. Foram analisadas dez variáveis ecomorfológicas de indivíduos pertencentes as espécies *Anchoa tricolor* (Spix & Agassiz, 1829), *Anchoa januaria* (Steindachner, 1879), *Anchovia clupeioides* (Swainson, 1839), *Anchoviella lepidentostole* (Fowler, 1911), *Lycengraulis grossidens* (Spix & Agassiz, 1829), *Chirocentrodon bleekermanus* (Poey, 1867), *Harengula clupeola* (Cuvier, 1829) e *Opisthonema oglinum* (Lesueur, 1818), cujos valores foram empregados em uma análise de componentes principais (PCA) com os dois primeiros eixos explicando 58,92% da variância total. Uma elevada sobreposição morfológica entre as espécies de Engraulidae foi observada, com exceção de *A. clupeioides*, que se diferenciou das demais por apresentar maiores valores do índice de compressão e índice de compressão do pedúnculo caudal. As espécies de Clupeidae diferiram das demais famílias devido aos elevados valores de altura relativa e comprimento relativo da cabeça, o que também mostrou diferenças entre as próprias espécies, tendo *H. clupeola* apresentado maiores valores destas variáveis. O representante de Pristigasteridae apresentou sobreposição intermediária entre as espécies das demais famílias, devido ao seu corpo altamente comprimido, mas com baixos escores de altura relativa, comprimento relativo do pedúnculo e aspecto da boca. A diferenciação morfológica entre as famílias, e até mesmo entre espécies de uma mesma família, indica divergências de nicho, mostrando que apesar de sua proximidade filogenética, existem diferenças em suas interações ecológicas, possivelmente contribuindo para a sua coexistência.

**PALAVRAS-CHAVE.** Sobreposição morfológica; estratégias de coexistência; competição interespecífica

Surf zones are highly energetic environments where much of the waves' energy is dissipated as they break on the shore (PEREGRINE, 1998). Despite presenting intense wave action over the communities that live there (MCLACHLAN, 1990), surf zones serve as nursery environments to several marine species as they present high phytoplankton productivity, elevated turbidity, nutrients cycling and shelter against predators (SALANT & SHANKS, 2018; IZUMIYAMA *et al.*, 2020). In this way, they serve as an adequate habitat to larval stages of fish species which develop into adult phase in this environment (GODEFROID *et al.*, 1999), and for others that complete their life cycle in surf zones (MONTEIRO-NETO *et al.*, 2003). Among these, representative of Clupeiforme with slender body, which provides good swimming ability in turbulent waters, such as sardines, anchovies and pilchards are included (WATSON & BALON, 1984; SILVA & ARAÚJO, 2000; NASCIMENTO *et al.*, 2019; REIS *et al.*, 2020).

Clupeiformes species present long and often numerous gill rakers and a predominantly planktonic feeding habit, in addition to having high importance for the industrial and artisanal fisheries around the world (NELSON *et al.*, 2016; JULIANI *et al.*, 2019; WANG *et al.*, 2021). Members of this order are found in many different habitats along their life cycle, with juveniles being more commonly found in estuarine environments and surf zones, while adults are found in deeper portions of coastal areas. Several species deserve conservation concern due to threats by pollution, habitat modification and overexploitation (ARAÚJO *et al.*, 2008; MAI *et al.*, 2014; BIRGE *et al.*, 2020).

Despite species belonging to the same order tend to present similar phenotypical characteristics, even those from a same family may have different osteological development or explore distinct habitats during their life cycle, what can lead to distinct adaptations to the environment among species (BLOOM & EGAN, 2018; DIZAJ *et al.*, 2020).

Fish feeding ecology brings up a range of information relating species body shape, prey selection and predation (NIKOLSKII, 1963), which are valuable for a responsible exploitation of fish stocks and development of conservation strategies for threatened species (BOYLE & HORN, 2006; SIMPFENDORFER *et al.*, 2011; BRAGA *et al.*, 2012; KARACHLER & STERGIU, 2013).

The coexistence of fish species with similar body shape and feeding preferences leads to niche partitioning (CORREA & WINEMILLER, 2014), which promotes different interactions with the environment, and exploitation of food resources in a different way in order to avoid competition. A good approach to understand such interactions is the use of ecomorphological analysis (WIKRAMANAYAKE, 1990; ADITE & WINEMILLER, 1997; OLIVIER *et al.*, 2019).

Ecomorphological studies in teleost fish have been developed as an important tool to understanding how morphology influences feeding patterns and environment use, assuming that there is correlation between species shape and life cycle (WINEMILLER, 1991; TEIXEIRA & BENNEMANN, 2007). In a short period of time body morphology is expected to influence fish diet, although in a larger period diet may

influence the morphology due to factors, such as phenotypic plasticity, according to the environmental conditions in which species thrive and their ecological interactions (MITTELBACH *et al.*, 1999; SVANBÄCK & EKLÖV, 2002).

Ecomorphology may be an important indicator of species diet and trophic position (BLASINA *et al.*, 2016), being able to identify adaptative convergence in phylogenetically distant species, and adaptative divergences in phylogenetically close ones (REILLY & WAINWRIGHT, 1994; CASSATI & CASTRO, 2006). It helps classifying the feeding habits associated with linear models, identifying possible changes in species feeding patterns and trophic levels according to the phase of the life cycle and infer about swimming ability (VORSATZ *et al.*, 2019; SOUZA & POMPEU, 2020; PODDER *et al.*, 2021a,b; SANTOS *et al.*, 2021).

In this context, the present study aimed to identify the morphological relations and infer about the feeding ecology of *Anchoa januaria* (Steindachner, 1879), *Anchoa tricolor* (Spix & Agassiz, 1829), *Anchoa clupeoides* (Swainson, 1839), *Anchoiella lepidostole* (Fowler, 1911), *Lycengraulis grossidens* (Spix & Agassiz, 1829), *Harengula clupeola* (Cuvier, 1829), *Opisthonema oglinum* (Lesueur, 1818) and *Chirocentrodon bleekermanus* (Poey, 1867), common syntopic Clupeiformes representatives in a sandy beach surf zone in northeastern Brazil.

## MATERIAL AND METHODS

The clupeiform individuals used are part of the Fish Collection of the Ichthyology Laboratory of *Universidade Federal Rural de Pernambuco*. They were collected in the Jaguaribe Beach, a sandy beach located in the north part of Itamaracá Island (Northern Coast of Pernambuco), located 50 km from the capital Recife, and separated from mainland by an estuarine channel called Santa Cruz Channel (ALMEIDA & VASCONCELOS-FILHO, 1997). The beach substrate is mainly compound by a sand substrate with dead or inactive coral formations and calcareous algae supported on a sandstone foundation (MEDEIROS & KJERFVE, 1993) with a well-documented fish fauna composition (SANTANA & SEVERI, 2009; SANTANA *et al.*, 2009).

The specimens were collected monthly between March 2005 and February 2006 in new and crescent moon phases, during the day and the night in low tide. The samples were obtained using a "picaré" beach seine net, 20 meters long, 2.5 meters high and 5 mm mesh internodes [see SANTANA & SEVERI (2009) for more details about the sampling]. The specimens were fixed in 4% formaldehyde, preserved in 70% ethanol and identified according to FIGUEIREDO & MENEZES (1978) and CARPENTER (2002).

Twenty individuals from each species, except *A. januaria* and *H. clupeola* (respectively 14 and seven individuals) were measured with the aid of a digital caliper (0.01 mm), to their standard length (SL), body height (BH), medium body height (MHB), body width (BW), head length (HL), head height (HH), relative eye height (ERH), pectoral fin length (PFL), pectoral fin width (PFW), caudal fin height

(CFH), caudal peduncle length (CPL), caudal peduncle height (CPH), caudal peduncle width (CPW), mouth width (MW) and mouth diameter (MD) (Fig. 1, adapted from ALBOUY *et al.*, 2011) (KEAST & WEBB, 1966; GATZ, 1979; WATSON & BALON, 1984; BEAUMORD & PETRERE JR, 1994).

Based on the measurements taken from each individuals, the following ecomorphological variables were calculated: Compression index ( $CI=BH/BW$ ) (WATSON & BALON, 1984): indicate the fish's position in the water column; high scores indicating laterally compressed fish; Relative height ( $HR=BH/SL$ ) (GATZ, 1979): directly related to the ability to make vertical turns; low scores indicating elongated fish; Relative peduncle length ( $RPL=CPL/SL$ ) (WATSON & BALON, 1984): elongated peduncles indicate fish with good swimming ability; Caudal peduncle compression index ( $CPCI=CPH/CPW$ ) (GATZ, 1979): high scores are typical in less active swimmers; Index of ventral flattening ( $IVF=MHB/BH$ ) (WATSON & BALON, 1984): low scores indicate fish inhabitants of waters with high hydrodynamics; Aspect of pectoral fin ratio ( $APFR=PFL/PFW$ ) (KEAST & WEBB, 1966): high scores indicate long and narrow fins; Relative eye position ( $REP=ERH/BH$ ) (GATZ, 1979): indicate the vertical habitat preference, benthic fish have eyes localized more dorsally and nektonic fish eyes localized laterally; Relative head length ( $RHL=HL/SL$ ) (WATSON & BALON, 1984): relatively longer heads indicate that the fish is able to handle larger prey items; Relative mouth width ( $RMW=MW/SL$ ) (GATZ, 1979): indicate the relative size of the prey items; and Mouth aspect ratio ( $MAR=MD/MW$ ) (BEAUMORD & PETRERE JR, 1994): the mouth aspect ratio is related to the shape of the feed items; elevated scores indicating narrow but wide-open mouths.

In order to check the development phase of the individuals used, their length of first maturity (L50) of all

species was based on literature (OSORIO & ACERO, 1996; SILVA-JUNIOR *et al.*, 2013; MAI & VIEIRA, 2013; PETERMANN & SCHWINGEL, 2016; COSTA *et al.*, 2018; FROESE & PAULY, 2022).

To evaluate eventual correlations between morphological similarities, the species and feeding were classified into the following trophic guilds: carnivore first order (FAVERO *et al.*, 2019): individuals that feed primarily of benthic invertebrates; carnivore second order (FAVERO *et al.*, 2019): fish with the diet based on invertebrates which may occasionally consume fish; planktivore (FAVERO *et al.*, 2019): species that feed predominantly on phytoplankton occasionally also feeding on zooplankton; zoobenthivore (ELLIOTT *et al.*, 2007): fish species that feed predominantly on invertebrates associated with the substrate, specially animals that live just above the sediment; and zooplanktivore (ELLIOTT *et al.*, 2007): fish species with diet predominantly composed by zooplankton, such as planktonic crustaceans and fish eggs and larvae. Species feeding guilds classification was based on literature (MAI & VIEIRA, 2013; ANDRADE-TUBINO *et al.*, 2019; FAVERO *et al.*, 2019; LIRA *et al.*, 2021).

With the aid of the software R (version 4.0.3) the normality of the ecomorphological variables was checked using a Shapiro-Wilk test followed by a Kruskal-Wallis test, to identify significant differences of each measured value between species, and a Dunn multiple comparison test (R CORE TEAM, 2009). The scores of the ten variables were examined through a principal component analysis (PCA) through the R built-in function "prcomp()" (R DEVELOPMENT CORE TEAM, 2009) to calculate the principal components, use the package "factoextra" (KASSAMBARA & MUNDT, 2020) to graphically visualize the affinity of the ecomorphological attributes with the axes of the PCA and the clusterization of the species based on the scores of their ecomorphological attributes.

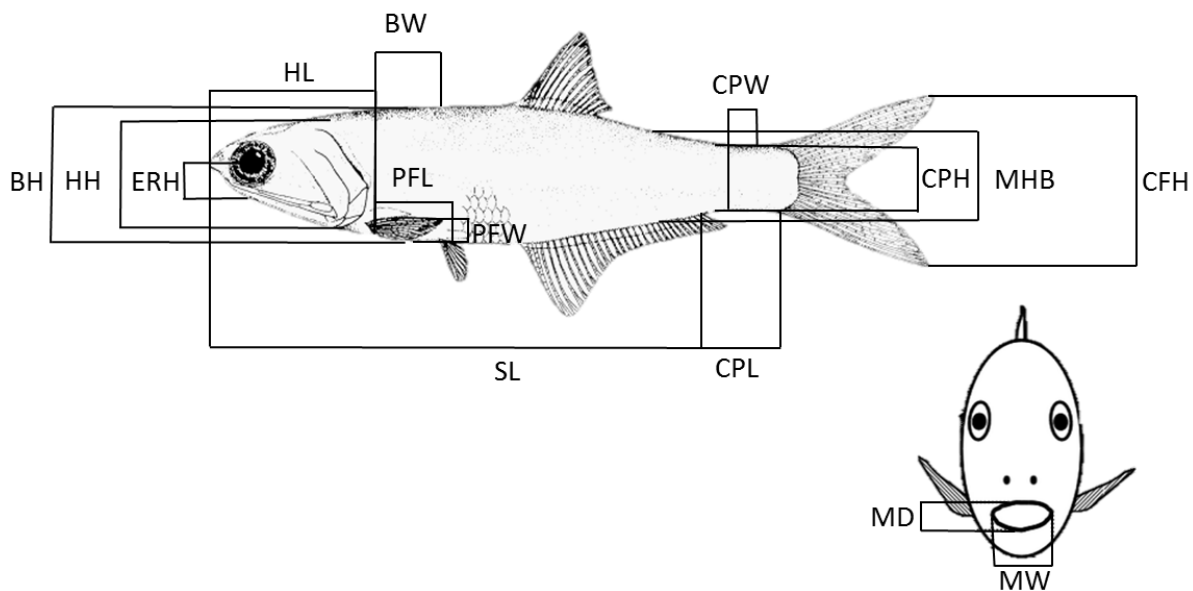


Fig. 1. Morphological measures taken to calculate the ecomorphological variables (adapted from ALBOUY *et al.*, 2011) (SL, standard length; BH, body height; MHB, medium body height; BW, body width; HL, head length; HH, head height; ERH, relative eye height; PFL, pectoral fin length; PFW, pectoral fin width; CFH, caudal fin height; CPL, caudal peduncle length; CPH, caudal peduncle height; CPW, caudal peduncle width; MW, mouth width; MD; mouth diameter).

## RESULTS

Individuals of all species were considered juveniles, since they presented standard length lower than their reported length at first maturity (L50), and were classified into distinct trophic guilds. *Anchoa januaria*, *A. clupeioides* and *H. clupeiola* were classified as planktivore fishes, *L. grossidens* and *O. oglinum* as zooplanktivore, *C. bleekermanus* as zoobenthivore, *A. lepidentostole* as carnivore first order and *A. tricolor* as carnivore second order (Tab. I).

Based on the ecomorphological data, higher values of CI were found in *A. clupeioides*, indicating its larger compression in relation to the other species, besides presenting the second smallest scores of HR, and together with *C. bleekermanus*, *O. oglinum* and *H. clupeiola* had the smallest values of RPL and CPCI (Tab. II). There were statistical significant differences of all ecomorphological variables between species.

The first two axis of the PCA explained together 58.92% of the total variance (Tab. III), the first axis representing 34.14% of the total and correlating more positively with HR, RHL and APFR, what differentiated *H. clupeiola* and *O. oglinum* from all other species (Fig. 2). The second axis represented 24.78% of the total, and

evidenced positive relations with CI, CPCI and IVF and a strong negative correlation with MAR, differentiating *A. clupeioides* from the other engraulids and positioning *C. bleekermanus* in an intermediate position between the species, besides presenting high scores of CI, CPCI and IVF, and also intermediate scores of MAR.

A considerable morphological overlap of some species was evidenced by the PCA (Fig. 2), and a strong correlation between the Engraulidae with the exception of *A. clupeioides*, because of its deeper body and higher caudal peduncle compression in relation to the other members of the family. The Clupeidae differentiated from the remainders, and the representative of Pristigasteridae occupied an intermediate position between the other families, due to its low scores of RHL and HR when compared with the clupeids, and low scores of MAR and elevated values of IVF, CI and CPCI when compared with the engraulids.

Despite the engraulids, with the exception of *A. clupeioides*, had presented high morphological overlap, they all belonged to distinct trophic guilds, clupeids presented morphological differences and belonged to different guilds, and the representative of Pristigasteridae was morphologically different from the other families and was the only zoobenthivore fish among the analyzed species.

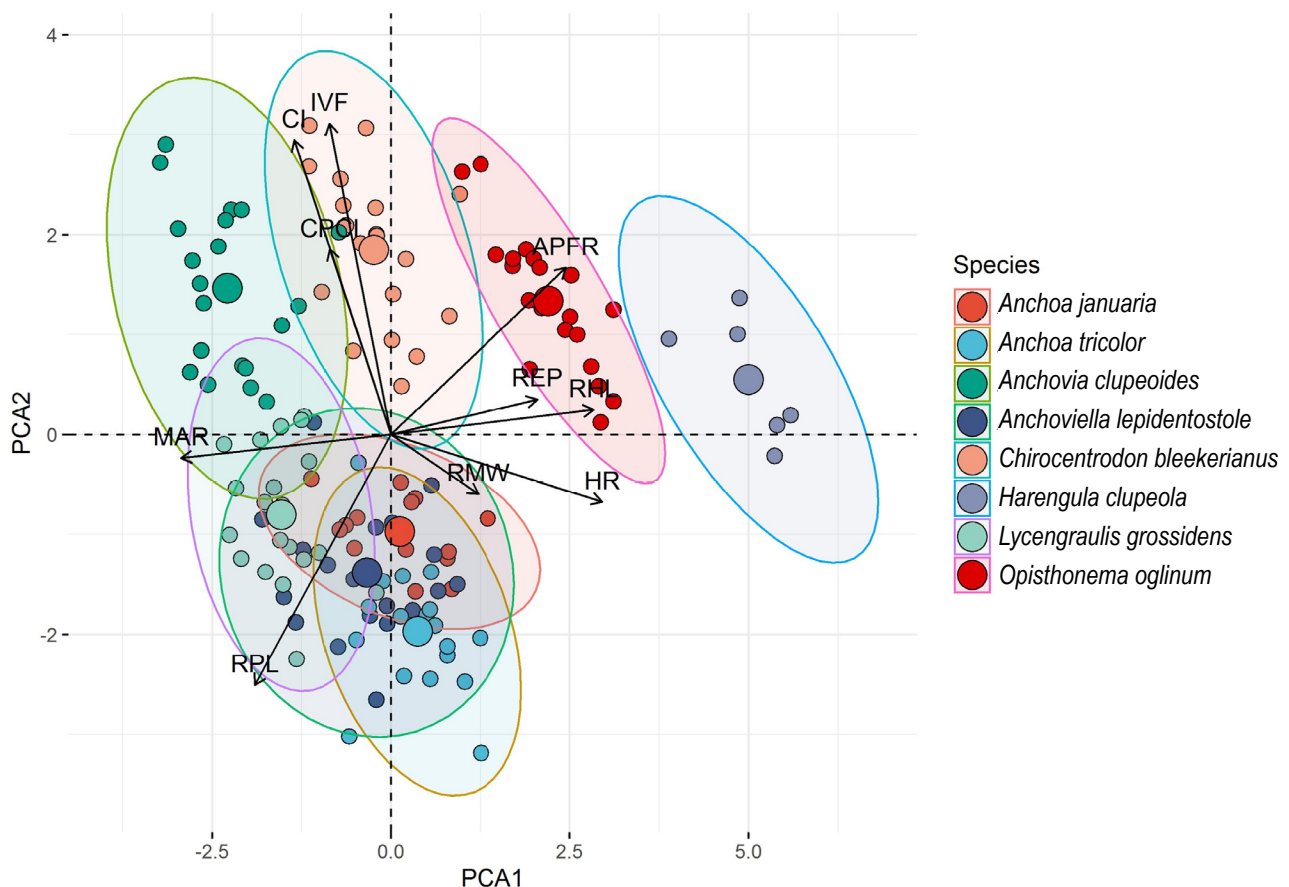


Fig. 2. Ordination diagram of the ecomorphological variables and clusters of the analyzed clupeiform species according to their relation with the first two axis of the PCA (CI, Compression index; HR, Relative height; RPL, Relative peduncle length; CPCI, Caudal peduncle compression index; IVF, Index of ventral flattening; APFR, Aspect of pectoral fin ratio; REP, Relative eye position; RHL, Relative head length; RMW, Relative mouth width; MAR, Mouth aspect ratio).



Tab. I. Range of the species standard length, their respective length of first maturity (L50) and trophic guild. \*References to L<sub>50</sub>: 1, FROESE & PAULY, 2022; 2, SILVA-JUNIOR *et al.*, 2013; 3, OSORIO & ACERO, 1996; 4, MAI & VIEIRA, 2013; 5, COSTA *et al.*, 2018; 6, PETERMANN & SCWINGEL, 2016. #References to trophic guild: 1, ANDRADE-TUBINO *et al.*, 2019; 2, FAVERO *et al.*, 2019; 3, MAI & VIEIRA, 2013; 4, LIRA *et al.*, 2021.

Species	Lmin-max (mm)	L50 (mm)*	Trophic guild#
<i>Anchoa januaria</i> (Steindachner, 1879)	35.22-52.07	65.0 <sup>1</sup>	Planktivore <sup>1</sup>
<i>Anchoa tricolor</i> (Spix & Agassiz, 1829)	47.35-73.69	76.0 <sup>2</sup>	Carnivore second order <sup>2</sup>
<i>Anchovia clupeioides</i> (Swainson, 1839)	48.45-111.49	151.0 <sup>3</sup>	Planktivore <sup>2</sup>
<i>Anchoviella lepidentostole</i> (Fowler, 1911)	31.96-53.59	94.0 <sup>1</sup>	Carnivore first order <sup>2</sup>
<i>Lycengraulis grossidens</i> (Spix & Agassiz, 1829)	48.73-66.61	112.0 <sup>4</sup>	Zooplanktivore <sup>3</sup>
<i>Chirocentron bleekermanus</i> (Poey, 1867)	43.94-74.55	76.0 <sup>2</sup>	Zoobenthivore <sup>4</sup>
<i>Harengula clupeola</i> (Cuvier, 1829)	34.24-58.66	85.0 <sup>5</sup>	Planktivore <sup>2</sup>
<i>Opisthonema oglinum</i> (Lesueur, 1818)	46.96-56.41	195.8 <sup>6</sup>	Zooplanktivore <sup>4</sup>

Tab. II. Median, minimum, maximum and p values of the ecomorphological attributes of the analyzed species (CI, Compression index; HR, Relative height; RPL, Relative peduncle length; CPCI, Caudal peduncle compression index; IVF, Index of ventral flattening; APFR, Aspect of pectoral fin ratio; REP, Relative eye position; RHL, Relative head length; RMW, Relative mouth width; MAR, Mouth aspect ratio).

Species		CI	HR	RPL	CPCI	IVF	APFR	REP	RHL	RMW	MAR
<i>Anchoa januaria</i> (Steindachner, 1879)	Median	22.960	0.0966	0.1397	32.023	19.550	18.900	0.6094	0.1933	0.0557	35.317
	Min	21.504	0.0790	0.1085	24.564	18.673	15.699	0.5318	0.1733	0.0516	29.474
	Max	24.849	0.1046	0.1639	38.780	21.558	30.180	0.7130	0.2282	0.0613	39.828
<i>Anchoa tricolor</i> (Spix & Agassiz, 1829)	Median	21.043	0.1022	0.1332	33.397	17.443	11.325	0.5149	0.2095	0.0700	36.111
	Min	19.239	0.0920	0.1070	27.805	14.567	0.9237	0.4283	0.1935	0.0629	33.441
	Max	23.633	0.1091	0.1718	43.839	19.275	13.701	0.5997	0.2302	0.0830	42.385
<i>Anchoa clupeioides</i> (Swainson, 1839)	Median	32.335	0.0878	0.1333	37.355	26.066	13.150	0.4061	0.1914	0.0626	42.888
	Min	29.806	0.0782	0.1100	26.618	21.236	10.280	0.3005	0.1693	0.0537	31.484
	Max	35.566	0.0993	0.1509	47.276	29.234	16.166	0.5312	0.2264	0.0722	49.925
<i>Anchoviella lepidentostole</i> (Fowler, 1911)	Median	21.991	0.1003	0.1517	31.694	18.054	26.801	0.3795	0.2007	0.0515	36.176
	Min	20.086	0.0869	0.1162	25.814	15.920	17.599	0.3186	0.1738	0.0446	26.468
	Max	25.936	0.1089	0.1755	39.603	21.823	38.297	0.4782	0.2210	0.0628	41.840
<i>Lycengraulis grossidens</i> (Spix & Agassiz, 1829)	Median	23.927	0.0891	0.1357	36.095	19.781	11.966	0.4135	0.1889	0.0552	36.394
	Min	22.033	0.0827	0.1199	27.547	17.785	10.642	0.3583	0.1758	0.0473	27.535
	Max	25.591	0.1045	0.1770	43.014	24.092	16.059	0.4802	0.2102	0.0644	46.102
<i>Chirocentron bleekermanus</i> (Poey, 1867)	Median	27.614	0.0866	0.0897	38.892	22.829	30.485	0.5401	0.1937	0.0544	35.311
	Min	23.454	0.0708	0.0737	32.394	18.442	23.356	0.4873	0.1637	0.0487	30.137
	Max	30.691	0.1064	0.0978	43.968	26.546	48.244	0.5733	0.2169	0.0623	41.129
<i>Harengula clupeola</i> (Cuvier, 1829)	Median	23.390	0.1391	0.0851	29.754	21.196	41.045	0.5672	0.2410	0.0848	19.667
	Min	22.006	0.1166	0.0791	27.109	19.286	33.682	0.4711	0.2335	0.0676	13.359
	Max	27.412	0.1692	0.0978	36.013	23.982	46.077	0.6153	0.2652	0.0964	24.178
<i>Opisthonema oglinum</i> (Lesueur, 1818)	Median	25.496	0.1143	0.0855	35.806	21.624	38.060	0.5174	0.2239	0.0531	30.174
	Min	22.500	0.0998	0.0625	31.818	18.474	33.270	0.4444	0.2103	0.0427	24.482
	Max	28.730	0.1273	0.0917	48.770	24.048	45.668	0.6085	0.2402	0.0597	37.923
	p	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Tab. III. Resulting values of the PCA first two axis scores for the ecomorphological attributes of the clupeiform species analyzed (CI, Compression index; HR, Relative height; RPL, Relative peduncle length; CPCI, Caudal peduncle compression index; IVF, Index of ventral flattening; APFR, Aspect of pectoral fin ratio; REP, Relative eye position; RHL, Relative head length; RMW, Relative mouth width; MAR, Mouth aspect ratio).

Ecomorphological attributes	PC1	PC2
CI	-0.2038325	0.52146680
HR	0.4459233	-0.11998855
RPL	-0.2865882	-0.44410825
CPCI	-0.1289963	0.32786086
IVF	-0.1293550	0.55045322
APFR	0.3694365	0.29529239
REP	0.3091174	0.06223093
RHL	0.4276741	0.04369443
RMW	0.1844571	-0.10588502
MAR	-0.4417382	-0.04195680
Variance proportion	34.14%	24.78%
Cumulative proportion	34.14%	58.92%

## DISCUSSION

The first two axis of the PCA showed a clear separation of *H. clupeola* and *O. oglinum* from the other clupeiforms, owing to their high scores of relative height and relative head length. These variables are directly related to the body stretching and to the ability to feed on bigger prey items (GATZ, 1979; WATSON & BALON, 1984). This not only morphologically differentiated these clupeids, for being species of carnivorous food habit, but also showed differences between them, since *H. clupeola* presents a more planktivore habit than *O. oglinum* which has a feeding preference for crustaceans (VEGA-CANDEJAS *et al.*, 1997; CHAVES & VENDEL, 2008; SOARES *et al.*, 2018; FAVERO *et al.*, 2019; BOMFIM *et al.*, 2020).

It was also observed the separation of engraulids, as a group with higher scores of mouth aspect ratio, whose big scores indicate fishes with wide-open but narrow mouths (BEAUMORD & PETRERE JR, 1994), thus contributing to the similarity between their species. In contrast, the second axis of the PCA grouped positively species with the highest scores of compression index, index of ventral flattening and caudal peduncle compression index, which are respectively related to body compression, occupation of environments with high hydrodynamics and to swimming intensity (GATZ, 1979; WATSON & BALON, 1984). This differentiated *A. clupeoides* from the remaining engraulids for being more compressed, corroborating with the data found by PESSANHA *et al.* (2015), who registered the compression index as responsible for the differentiation of *A. clupeoides* from all the other fish species analyzed from the surf zone estuary of the Mamanguape River (Paraíba, Brazil). The species with the highest scores of the relative peduncle length reinforced the ecomorphological resemblance between *A. januaria*, *A. tricolor*, *A. lepidentostole* and *L. grossidens*.

Although fish species belonging to the same taxonomic group tend to have similar body shape (CATELLA & PETRERE

JR, 1998), ecomorphological analyses can infer differences between them and their way of life, according to differences of their morphological variables (PIET, 1998; GARCIA *et al.*, 2020). In the studies of NUNES & HARTZ (2006) about two Characidae species inhabiting the Fortaleza Lake (State of Rio Grande do Sul, Brazil), the authors observed differences in their morphology and diet besides their morphological similarity. Such differences were also found in the present study, since although the species belong to the same order, morphological differences are perceived even in species from the same family, such as *A. clupeoides* and the other engraulids, and the separation between the clupeids.

Despite the ecomorphological similarity of engraulids, except for *A. clupeoides*, it can be said that species belonging to this family have distinct ecological niches in the Jaguaribe Beach. *Lycengraulis grossidens* and *A. lepidentostole* have a more generalist feeding habit depending on the food source available in the environment (BENEDITTO, 2020), thus indicating plasticity in their diet. In addition, exclusion mechanisms can be observed between species, such as species abundance seasonal variability, as reported by SANTANA & SEVERI (2009) in the Jaguaribe Beach surf zone, where *A. tricolor* is more abundant in the rainy season, *A. clupeoides* in the drought season, whereas *L. grossidens* is commonly found in both seasons.

Morphological differences may be an excellent proxy for variation in the diet of fish belonging to the same family or to species living in distinct environments without genetical exchange (DELARIVA & NEVES, 2020). Temporal variation of environment conditions can be an explanation to the coexistence of morphologically similar species, because disturbances in the environmental variables such as temperature, pluviosity, luminosity and food supply can significantly alter interspecific interactions in consonance with distinct species' response to these variations (MEFFE, 1984; GODINHO *et al.*, 2000; BEYST *et al.*, 2001; HELLAND *et al.*, 2011).

These variations may result in changes in species abundances which may imply different use of environmental food resources, altering the feeding habit of some species according to the food resources' availability and use based on prey behavior or size (MEFFE, 1984; WINEMILLER, 1990). Therefore, the choice for different prey items is one of the factors that may allow the coexistence of species (ROBERTSON, 1996; GROSSMAN *et al.*, 1998; SÁNCHEZ-HERNÁNDEZ *et al.*, 2011).

Such difference in the choice of prey among clupeiforms was observed by MEDEIROS *et al.* (2017) for *A. clupeioides*, *A. tricolor*, *H. clupeola* and *O. oglinum*. These authors observed distinct feeding preferences between species, *A. clupeioides* being a piscivorous one, *H. clupeola* showing a phytoplanktonic preference in its diet, and *A. tricolor* together with *O. oglinum* a zooplanktonic preference. These differences in feeding habit between the species corroborate with literature, as they are reported to belong to distinct trophic guilds (MAI & VIEIRA, 2013; ANDRADE-TUBINO *et al.*, 2019; FAVERO *et al.*, 2019; LIRA *et al.*, 2021) coupled with differences in ecomorphological attributes which possibly contribute to their coexistence.

Surf zone environments are used by several fish species in their early life stages due to their dynamism that provides nutrient cycling and stimulates the phytoplanktonic activity. This provides a considerable availability of food, not only for fishes alone but also for their potential prey items, such as microcrustaceans (BEYST *et al.*, 1999; YU *et al.*, 2003; SALANT & SHANKS, 2018; IZUMIYAMA *et al.*, 2020; GUERREIRO *et al.*, 2021), an important factor for the occurrence of Clupeiformes juveniles in such environment. Besides their phylogenetic proximity, their morphological differences and temporal variation in abundance throughout the year imply in distinct environmental interactions and resource use (CHESSON, 1985; MOUCHET *et al.*, 2013; SILVA *et al.*, 2017) responsible for the coexistence of these clupeiforms in coastal areas.

It is concluded that besides their phylogenetic proximity, the clupeiform species of the Jaguaribe Beach have distinct ecomorphological characteristics, indicating adaptative responses to the environment, such as the variation of their abundances along the year and occupation of distinct portions of the water column, as indicated by their ecomorphological attributes. Further studies of the feeding ecology of clupeiforms are necessary to better assess other aspects contributing to their coexistence in surf zones, and the role of these environments for the survival of their early life stages in these environments.

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