



## Seagrass and rhodolith beds are important seascapes for the development of fish eggs and larvae in tropical coastal areas

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### ABSTRACT

In this study, the ichthyoplankton in two distinct tropical seascapes, gravelly sand with rhodolith beds (SRB) and muddy sand with seagrasses, were compared. The number of eggs was higher in the seagrass beds; however, the number of fish larvae was slightly higher in the SRB. Seagrass beds present less turbulent hydrodynamics and favor the retention of eggs and spawning. A more structured habitat provides better shelter, especially for eggs. However, as ontogeny progresses, the fish can explore areas with less shelter. This behavior was observed in this study, where the less structured SRB habitat had a high density of larvae in the later developmental stage. The dominance of earlier larval stages demonstrates a preference for more protected and less turbulent seascapes for nursery and offspring rearing. The results highlight that mapping of these seascapes (e.g., seagrass and rhodolith beds) will help to establish conservation measures to protect ecological connectivity and important tropical species.

### 1. Introduction

Shallow coastal areas provide important habitats for many species (Sánchez-Caballero and Borges-Souza, 2018; Reis Filho et al., 2019). Essential fish habitats (EFHs) are environments that are necessary to maintain fish populations. Substrates within these habitats are used for multiple developmental stages, such as spawning, breeding, feeding, and growing to maturity (Benaka, 1999; Rosenberg et al., 2000).

One of the important types of coastal seascape, classified as EFHs, are seagrass, rhodolith, and seaweed beds (Amado-Filho et al., 2016; Eggerstsen et al., 2017). Seagrass beds (or seagrass meadows) and rhodolith beds have greater fish diversity and density than adjacent flattened areas (Heck et al., 1997; Horta et al., 2016), as they provide three-dimensional structures that are used as nursery, settlement, forage, and refuge areas (Berkström et al., 2012; Thiriet et al., 2014; Díaz et al., 2015). These structural complex areas are also used by important species that act as links in the marine food web and by fishery target species as spawning grounds (Bell et al., 1987; Huijbers et al.,

2008; von Nordheim et al., 2018).

Like terrestrial forests, seagrass meadows store large amounts of carbon, and there are initiatives to protect these blue carbon seascapes (Fourqurean et al., 2012; Macreadie et al., 2019). Moreover, rhodolith beds are important in global biogeochemical cycles, considering that they may form large biogenic carbonate deposits (Amado-Filho et al., 2016). However, because seagrass meadows and rhodolith beds are located in coastal areas, they have been under intense pressure from human activities, such as climate change, eutrophication, oil spills, habitat destruction, microplastics, and fishing (Kraufvelin et al., 2018; Huang et al., 2020; Magris and Giarrizo, 2020; Soares et al., 2020).

In coastal seascapes, larval fish can find food and protection throughout their development (Heck and Thoman, 1984; Barletta-Bergan et al., 2002; Bonecker et al., 2007). The preference for habitats with specific types of substrate (Petry et al., 2003; Maynou et al., 2006) indicates that fish larvae can actively choose favorable habitats for their development (Grioche et al., 1997). Therefore, it is fundamental to understand the role of coastal seascapes in the recruitment and

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distribution of tropical fish eggs and larvae so that management and conservation strategies can be implemented (Hedberg et al., 2018). Important processes in the fish life cycle, such as settlement, distribution, and recruitment, are closely related to characteristics of the seascapes they inhabit. For example, some organisms prefer seagrass beds that are less turbulent than unvegetated areas (Dorenbosch et al., 2004). When close to other connected shallow seascapes (e.g., coral reefs), seagrass and rhodolith beds can lead to increased density of some species and affect the assemblage structure (Gullström et al., 2008; Berkström et al., 2013; Carvalho et al., 2020). In this way, seagrass and rhodolith beds provide substrates and structural complexity that favor spawning and development (von Nordheim et al., 2018).

Despite the importance of identifying spawning and nursery areas, few studies about them have been conducted. In particular, a comparison of tropical ichthyoplankton in distinct seascapes, such as seagrass beds and unvegetated areas, has not yet been performed (Marcolin et al., 2010; Katsuragawa et al., 2011; Moussa et al., 2020). This kind of research will help to establish conservation measures to protect important fishes and may provide information about the ecological connectivity and overlap of species. The aim of this study was to examine how the diversity and density of eggs and fish larvae at different developmental stages vary in shallow coastal seascapes (muddy sand with seagrass beds versus gravelly sand with rhodolith beds).

## 2. Materials and methods

### 2.1. Study area

The study area is in the Equatorial Southwestern Atlantic (Ceará coast, NE Brazil) (Fig. 1) and is characterized by a marine ecosystem with warm waters ( $>26\text{ }^{\circ}\text{C}$ ) and stable sea surface temperatures ( $<5\text{ }^{\circ}\text{C}$

of intra- and inter-annual variation) (Teixeira and Machado, 2013; Soares et al., 2019). This area is localized in the continuous sub-equatorial atmospheric circulation of the trade winds, which are persistent and intense throughout the year and show a mean wind velocity of  $7.2\text{ m/s}$  (Maia et al., 2001; De Barros Corrêa et al., 2019). The climate is semi-arid, and the estuaries are shallow with low river flow (Schettini et al., 2017). The Aracatimirim, Aracatiaçú, and Acaraú estuaries and the estuarine-lagoonal system related to coastal barriers are close to the study area (Fig. 1). They are a freshwater-deprived system, due to irregular interannual rainfall distribution (e.g.,  $572.4\text{ mm}$  in 2005 and  $2497.7\text{ mm}$  in 2009) and multiple dams along the watershed (Pessoa, 2015). Moreover, precipitation is mainly influenced by the Inter-tropical Convergence Zone (ITCZ). The rainy season occurs between January and June, peaking from February to May, which was the period in which these samples were taken, and the dry season falls between July and December. Moreover, the sampling area is governed by a mesotidal regime and a westerly current (Maia et al., 2018).

The pelagic zone is characterized by a well-mixed surface layer with a nutrient deficit in the euphotic layer. This means that this nutrient-poor area is classified as oligotrophic with low nitrate concentrations, chlorophyll-a biomass, and primary production (Ekau and Knoppers, 1999; Souza et al., 2013; Queiroz et al., 2016). Moreover, the continental shelf in the study area is narrow ( $<80\text{ km}$ ) but supports high fish diversity (Freitas and Lotufo, 2015; Freitas et al., 2019).

The equatorial southwestern Atlantic shelf (Ceará coast) comprises a mixed sedimentological pattern, including a significant carbonate supply, relict siliciclastic grains, and a mixing of carbonates and siliciclastics. The modern siliciclastic supply is most common in nearshore bottoms, and discharge from shallow estuaries is low because of the semi-arid climate, droughts, and multiple dams (Ximenes Neto et al., 2018a, b; Morais et al., 2019). In this way, different types of seascape

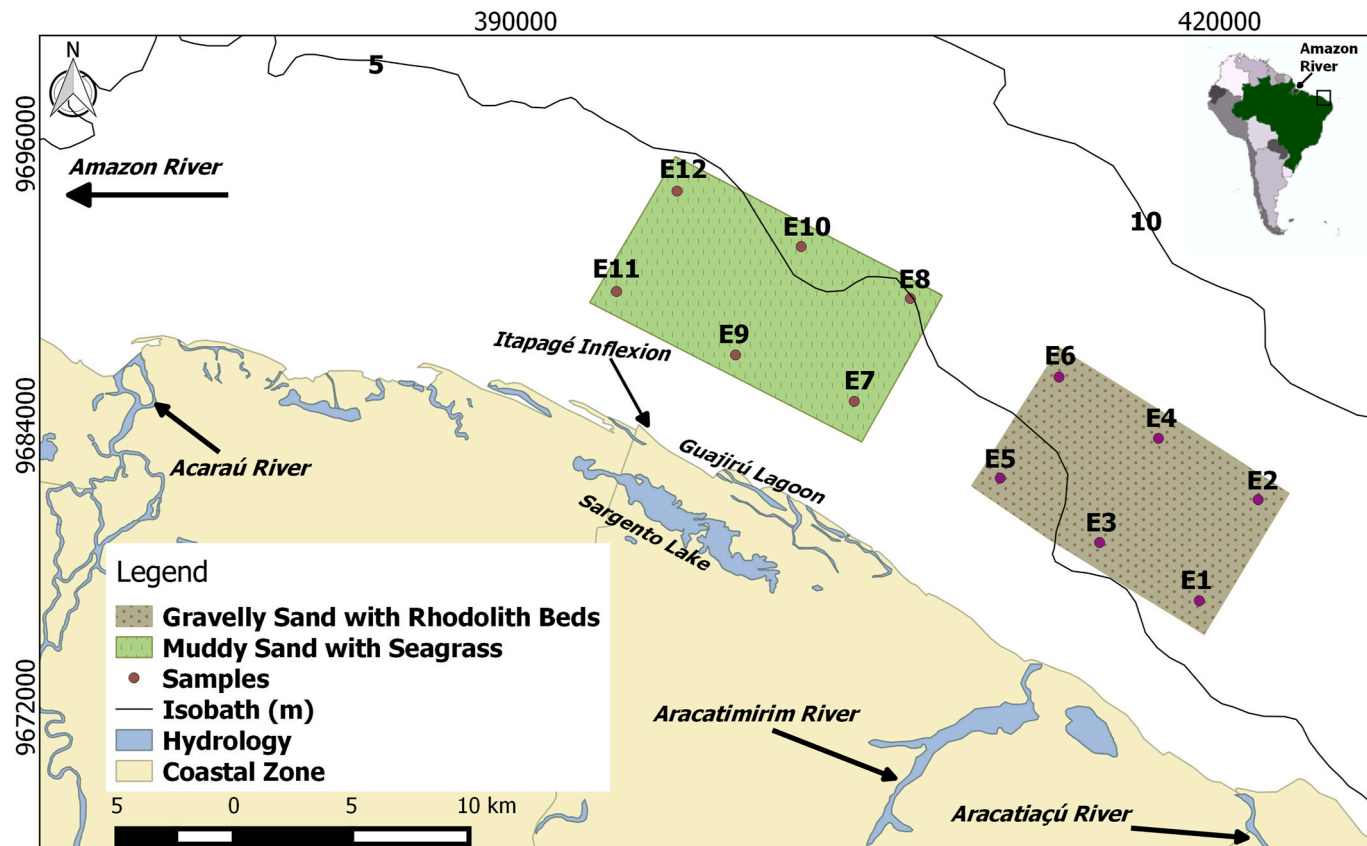


Fig. 1. Map of the area assessed (Equatorial Southwestern Atlantic, Ceará coast, NE Brazil): stations on the gravelly sand with rhodolith beds (E1 to E6) and muddy sand with seagrasses (E7 to E12) seascapes.

habitats are found in the inner shelf, such as rhodolith beds, seagrass beds (Fig. 1), *Halimeda* beds, and marginal coral reefs (Horta et al., 2016; Soares et al., 2017; Morais et al., 2019). Along the northeast coast of Brazil, there is a large area of seagrass meadow, composed of six different grass species (Barros et al., 2016; Copertino et al., 2016; Magalhães and Barros, 2017). Along the entire coast, patches of seagrass meadows are found in the intertidal zones and in shallow waters (<10 m depth). *Halodule wrightii* Ascherson, 1868 is the most common habitat-forming species (Barros et al., 2016; Copertino et al., 2016), and it benefits from the input of nutrients and the reduced wind speed during the rainy season (Barros and Rocha-Barreira, 2014). There is also an unvegetated seascape analyzed in this study that was formed by high modern carbonate sedimentation associated with calcareous red algae that consists of unconsolidated sediments (gravelly sand) and rhodolith beds. Rhodolith beds generally have epiphytes, such as seaweeds, and other organisms (Fig. 2) (Ximenes Neto et al., 2018a, b).

The shallow shelf studied is related to the Itapagé Inflection that favored the development of the Acaraú High, which provided a low sloping seafloor (Ximenes Neto et al., 2018b). This geomorphologic pattern favors the occurrence of two different coastal seascapes in a mixed carbonate-siliciclastic system of shallow waters (<10 m depth): an extensive bank of *Halodule wrightii* seagrass in muddy sand, located near the Guajirú Lagoon, and an unvegetated area composed of gravelly sand with rhodolith beds (Fig. 2), located close to the Aracatimirim River estuary. The samplings were designed for the collection of ichthyoplankton inhabiting both the coastal seascapes (Fig. 1).

## 2.2. Data samples

Ichthyoplankton sampling was carried out at 12 stations (distance of 5 km between stations in the same seascape) (Fig. 1) on the inner continental shelf, six of which were located on the rhodolith bed areas and six in the seagrass meadows. Two campaigns were carried out in the same season (rainy period): the first in April 2017 and the second in March 2018. The sampling was nocturnal, and a low-speed boat (no more than 3 knots) was used. Zooplankton samples were collected via 5 min sub-surface trawls with two conical nets (mouth diameter: 50 cm and mesh size: 300  $\mu$ m and 200  $\mu$ m), equipped with a General Oceanics

flowmeter (General Oceanics, Miami, FL, USA). The samples were fixed in 4% formalin solution buffered with sodium tetraborate. Vertical profiles of salinity and temperature were recorded with a YSI CastAway-CTD at each station (3.3 - 10.7 m depth, according to the station) to detect possible hydrologic differences in these shallow seascapes.

## 2.3. Data analysis

In the laboratory, fish eggs and larvae were sorted and counted. The identification of the larvae at the lowest possible taxonomic level was based on their morphometric and meristic characteristics and pigmentation patterns with the help of specialized literature (Richards, 2005; Bonecker et al., 2014). The identification of fish eggs was difficult, because the egg stage descriptions were much less detailed than the larval stage descriptions. Thus, we analyzed the total abundance of eggs. The development stages were classified into yolk sac, preflexion, flexion, and notochord postflexion, according to Ré (1999). All organisms were deposited in the collection of plankton, “Professor Mariana Ferreira de Menezes” of the Federal University of Ceará (UFC).

The density of fish eggs and larvae was expressed as the number of organisms per 100 m<sup>3</sup> of filtered water, and standardized according to the formula  $D = N/V$ , where N is the total number of each taxon in the sample, and V is the volume of filtered water recorded by the flowmeter. The non-parametric Kruskal-Wallis test ( $p < 0.05$ ) was used to compare the densities of larvae at each stage of development between the two seascapes (muddy sand with seagrass beds and gravelly sand with rhodolith beds, hereafter, called seagrass and rhodolith beds, respectively) and the two sampling years (2017 and 2018). The Venn Diagram was drawn to show the number of families exclusive to each habitat and the number that occurred in both seascapes.

## 3. Results

There was no variation in salinity (<0.50 g/kg between the maximum and minimum) and temperature (<0.8 °C) between the seascapes or the years (Table 1). In addition, the salinity and temperature distributions were well mixed in the shallow water column at all stations, with no stratification (Figures S1 and S2).

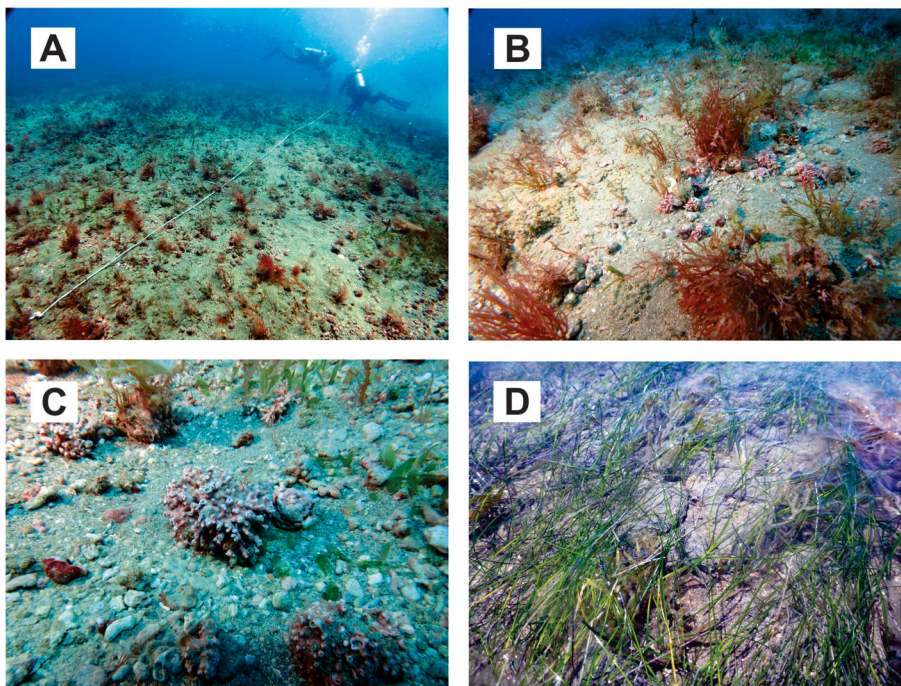


Fig. 2. Benthic seascapes on the equatorial southwestern Atlantic shelf (Ceará coast, northeastern Brazil). A) General view of the seascape comprised of gravelly sand with rhodolith beds; B) Subtidal seaweeds (*Rhodophyta*) populations growing on rhodoliths. In this view, we observed that rhodolith beds provide an important habitat for epibenthic communities, including macroalgae, invertebrates, and vertebrates; C) A detailed image of some rhodoliths in the study area (source: Morais et al. 2019); and D) Muddy sand with a seagrass (*Halodule wrightii*) bed.

**Table 1**

Average and standard deviation of salinity (g/kg) and sea temperature (°C) in the seascapes for both years (Equatorial Southwestern Atlantic, Ceará coast, NE Brazil).

|                  | 2017          |                | 2018          |                |
|------------------|---------------|----------------|---------------|----------------|
|                  | Seagrass beds | Rhodolith beds | Seagrass beds | Rhodolith beds |
| Salinity (g/kg)  | 36.13 ± 0.08  | 36.29 ± 0.11   | 36.87 ± 0.06  | 36.65 ± 0.19   |
| Temperature (°C) | 29.56 ± 0.09  | 29.32 ± 0.09   | 29.88 ± 0.09  | 29.80 ± 0.07   |

8.

A total of 8,094 eggs and 185 larvae were collected from the seagrass meadow seascape, and 2,014 eggs and 241 larvae were collected in the rhodolith beds using mesh nets (Table 2). Meanwhile, the highest density ( $P < 0.05$ , Kruskal-Wallis) of eggs was recorded in the seagrass meadow area in both years and nets (Figs. 3A and 4A). For the organisms collected with the 200 µm net, the eggs and yolk-sac larval stage showed a significant difference ( $p < 0.05$ ) between years and seascapes, since this stage was not registered in rhodolith beds in 2018 or in seagrass beds in 2017 (Fig. 3B). Moreover, there was a significant difference ( $p < 0.05$ ) between the eggs and yolk-sac stage (300 µm net), because they were absent in the seagrass beds in 2018 (Fig. 4A and B).

In the seagrass beds, the most abundant taxa collected with the 200 µm net in 2017 were the subfamily Syngnathinae and the family Atherinopsidae. In 2018, Atherinidae, Engraulidae (*Anchovia clupeioides* Swainson, 1839), and subfamily Syngnathinae (Table S1) were the most abundant. For organisms collected with the 300 µm net in 2017, the most abundant taxa were Syngnathinae, Atherinidae, and Hemiramphidae (*Hemiramphus* sp.). In 2018, the most abundant were Achiridae (*Achirus lineatus* Linnaeus, 1758), Engraulidae (*A. clupeioides*), and Atherinidae (Table S2).

In the rhodolith beds, among the organisms collected with the 200 µm net, the most abundant were representatives of the family Gobiidae, Engraulidae (species *A. clupeioides*) and Sciaenidae in 2017. In 2018, the most abundant organisms were members of the Engraulidae family (species *A. clupeioides*), Gobiidae, and Achiridae (species *A. lineatus*) (Table S3). For organisms collected with the 300 µm net in 2017, the most abundant organisms were Syngnathidae (subfamily Syngnathinae), Engraulidae (species *A. clupeioides*), and Gobiidae. In 2018, the most abundant taxa were Engraulidae (species *A. clupeioides*) and Gobiidae (Table S4).

The Venn diagram shows that the number of families that are common in each seascape was higher than the number of exclusive taxa (Fig. 5). In the rhodolith beds, exclusive taxa were higher in 2017 (Fig. 5), while in the seagrass beds, exclusive taxa were higher in 2018 (Fig. 5).

#### 4. Discussion

The importance of coastal seascapes such as rhodolith and seagrass beds for the life cycle of tropical fishes is highlighted in this study. The homogeneity of environmental data on sea temperature and salinity between the two seascapes indicates that they are not outstanding in explaining the differences in diversity and density of eggs and larvae. Therefore, structural physical differences between seascapes (seagrass

**Table 2**

Total number of eggs and fish larvae collected in each seascape using mesh nets (200 versus 300 µm) (Equatorial Southwestern Atlantic, Brazil).

| Seascape                          | Mesh nets | eggs (n) | larvae (n) |
|-----------------------------------|-----------|----------|------------|
| Gravelly sand with rhodolith beds | 200 µm    | 768      | 122        |
|                                   | 300 µm    | 1,246    | 119        |
| Muddy sand with seagrass beds     | 200 µm    | 3,478    | 106        |
|                                   | 300 µm    | 4,616    | 79         |

and rhodolith beds), ecological aspects of reproduction and connectivity of species, and other environmental factors (e.g., currents and tides) should be relevant to the patterns found. In this way, the study area of the muddy sand with seagrass beds is characterized by low depth and declivity (Fig. 1). The flat geomorphology of this marine area favors colonization by the plant *Halodule wrightii*, providing the formation of an important seascape for the fish community.

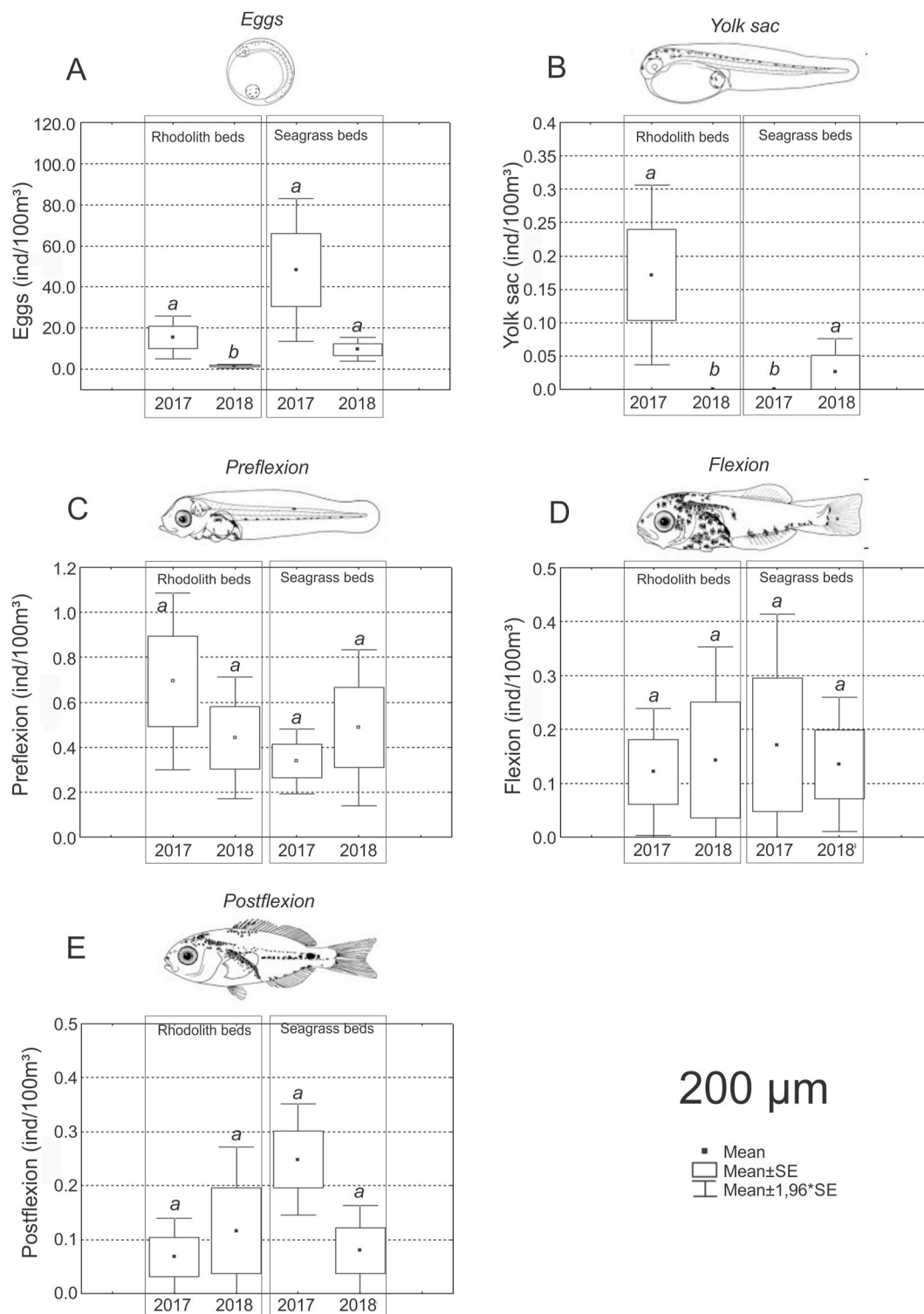
There were more eggs recorded in the seagrass beds than in the rhodolith beds, reaffirming the role of this seascape in the initial phases of fish life cycles as spawning and nursery areas. In this sense, the larvae of Engraulidae, Gobiidae, and Syngnathidae were among the most abundant and are common inhabitants at some stage of their life cycle in both seascapes. The most abundant taxa were common inhabitants of coastal shallow habitats, and were grouped as follows: *Chloroscombrus chrysurus* and *Achirus lineatus* in estuaries; organisms of genus *Lutjanus*, *Microdesmus*, and *Sparisoma* in coral reefs; *Hemiramphus* sp. and organisms previously registered as inhabitants of the coastal environments of Brazil's northern waters, like *A. clupeioides*, in seagrass beds (Mafalda et al., 2008; Mota et al., 2017). These organisms are common in larval fish assemblages in tropical southwestern coastal ecosystems, suggesting that coastal seascapes are not only important for planktonic larvae but also for organisms that present other reproductive and spawning strategies, such as demersal eggs and parental care.

Recent studies have highlighted the role of seagrass and rhodolith beds as nursery and feeding areas for several organisms (Berkström et al., 2013; Bertelli et al., 2014; Amado-Filho et al., 2016; Moussa et al., 2020). Seagrass beds are associated with less turbulent hydrodynamics than unvegetated habitats, which favors the retention of organisms, especially in these initial phases (Bell et al., 1987; Björk et al., 2008). Seagrass beds may also act as important areas of ecological and genetic connectivity between mangroves, rhodolith beds, and marginal coral reefs (Soares et al., 2017; Soares, 2020), influencing the survival of juvenile fish and increasing the abundance of reef species (Unsworth et al., 2008; Eggertsen et al., 2017; Mota et al., 2017). The number of families common to both seascapes suggests physical and ecological connectivity between the seagrass and rhodolith beds, which is an important finding for these seascapes, given their proximity to key areas, such as shallow and hypersaline estuaries with mangrove forests (Barroso et al., 2018) (Fig. 1).

In the present study, the high number of eggs and yolk-sac larvae demonstrate a preference (and/or retention) for protected and less turbulent seascapes as nursery and offspring rearing areas. The distribution of eggs is influenced by the biogeography of broadcast spawners, spawning habitat characteristics, and regime flow that can act by transporting or retaining these organisms (Pörtner and Peck, 2010). Tropical fish spawn continuously throughout the year, but some species have peaks associated with the rainy season (Johannes, 1978). In this study, sampling was carried out in the rainy season under a tropical semiarid climate, which may explain the high number of eggs recorded. Moreover, the current over the study area (equatorial western Atlantic continental shelf) flows predominantly westward, owing to the intense and persistent trade winds (Dias et al., 2013, 2018). In this sense, the inner shelf circulation is barotropic with wind-driven westward currents (Dias et al., 2018). However, during the rainy months of the sampling activities, the wind speed is the lowest throughout the year (<2.5 m/s) (Soares et al., 2019). This reduces the current speed in the inner shelf and, consequently, the transport of eggs and larvae, favoring retention and habitat preference.

Despite the lower density of larvae found in the postflexion stage, compared to the preflexion stage in the evaluated tropical region, studies indicate that these larvae in the later developmental stages also use the seagrass beds to seek refuge from predators (Bell et al., 1987; Guidetti and Bussoti, 2002). In this way, larvae can be passively transported to suitable habitats or actively guide and swim to such structurally complex vegetated habitats (Montgomery et al., 2006).

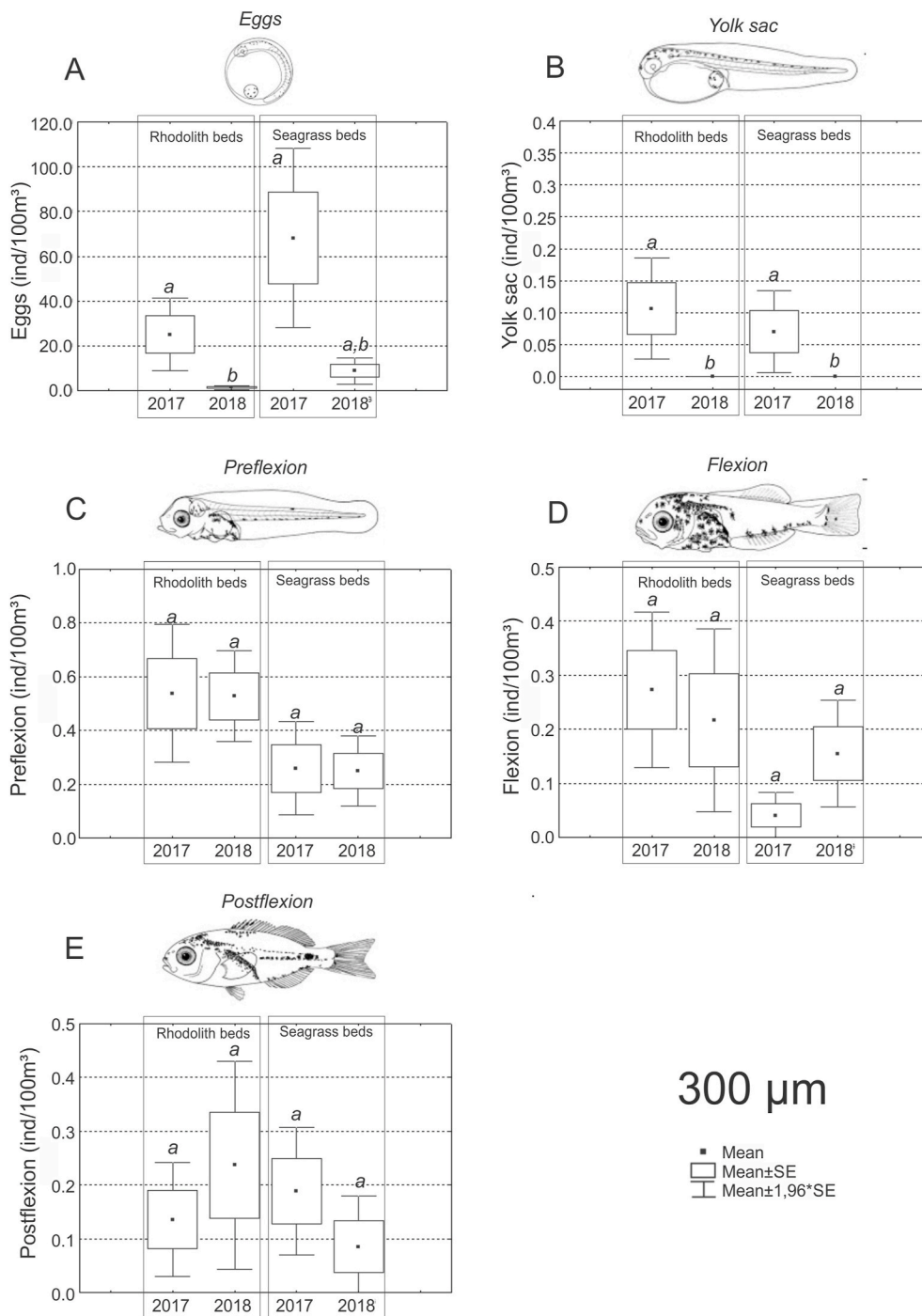
Habitat complexity and heterogeneity determine shelter and food



**Fig. 3.** Comparison between eggs and larval stages (A: eggs; B: yolk sac; C: preflexion; D: flexion; E: postflexion) collected with 200  $\mu$ m net per seascape per year of the area assessed (Equatorial Southwestern Atlantic, Brazil). Illustration of larval stages was adapted from Ré and Meneses (2008).

availability (García-Charton et al., 2004; Carvalho and Barros, 2017). Tolan et al. (1997) suggested that the greater the complexity of the coastal habitat, the greater the density of fishes. The authors also highlighted that seagrass beds not only serve as nursery areas for the early larval stages of fish, but the post-larvae and young juveniles of several species also appear to be strongly associated with specific seagrass and rhodolith habitats. In this way, microhabitat characteristics drive ontogenetic changes (Cuadros et al. 2017), and the greater the

structural complexity of the spawning grounds, the greater the survival rates of fish in the early stages of life. This has already been demonstrated for Atlantic herring (von Nordheim et al., 2018). Thus, habitat connectivity is defined by the combination of dispersion and factors that favor the survival of dispersed organisms (Cowen and Sponaugle, 2009). The more structured the habitat, the more shelter it provides, especially for larvae in the early stages of development, such as the present case in tropical shallow-water seascapes. However, as ontogeny progresses,



**Fig. 4.** Comparison between eggs and larval stages (A: eggs; B: yolk sac; C: preflexion; D: flexion; E: postflexion) collected with 300 µm net per seascape per year of the area assessed (Equatorial Southwestern Atlantic, Ceará coast, NE Brazil). Illustration of larval stages was adapted from Ré and Meneses (2008). A total of 15 families were identified in this study: Achiridae, Atherinidae, Atherinopsidae, Carangidae, Engraulidae, Gobiidae, Hemiramphidae, Lutjanidae, Microdesmidae, Paralichthyidae, Scaridae, Sciaenidae, Sparidae, Sygnathidae, and Tetraodontidae (Tables S1 to S4).

larvae in the later stages can explore tropical areas with less shelter (Sogard, 1997).

### 5. Conclusions

The dominance of organisms in the early stages of development (eggs and yolk sac larvae) demonstrates a preference for the more protected and less turbulent seascapes for nursery and offspring rearing. The study of larval development phases is essential to characterize the environment and its use by organisms at each stage of their life cycle. The data collected in this study reinforced the idea that the bottom seascape may influence ichthyoplankton assemblage.

Many seagrass and rhodolith beds worldwide are threatened

(Amado-Filho et al., 2016; Kraufvelin et al., 2018; Huang et al., 2020; Magris and Giarrizo, 2020; Soares et al., 2020) and are not yet adequately protected by fishery regulations, restoration efforts, marine protected areas (MPAs), or marine spatial planning (MSP) (Copertino et al., 2016; Horta et al., 2016; Macreadie et al., 2019). Moreover, our results highlight the importance of understanding the physical and biological connectivity and movement of fish life stages among tropical seascapes (Berkström et al., 2013; Endo et al., 2019). Thus, the establishment of MPAs and MSP can only be effective if connectivity among seascapes is recognized. This research reaffirms the need for management of different tropical coastal seascapes and the need for knowledge of local processes for the conservation of marine biodiversity.

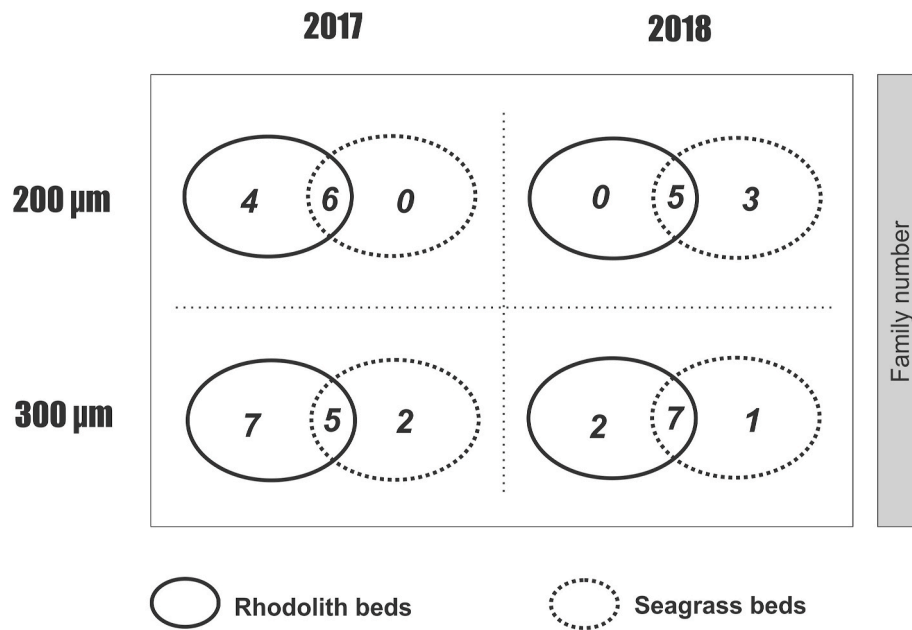


Fig. 5. Venn diagram based on the number of families for 200 µm and 300 µm plankton nets in 2017 and 2018, considering the coastal seascapes studied (Equatorial Southwestern Atlantic, Ceará coast, NE Brazil).

#### CRediT authorship contribution statement

**Ana Cecília Pinho Costa:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Writing - original draft, Writing - review & editing. **Tatiane Martins Garcia:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing - original draft, Writing - review & editing. **Bárbara Pereira Paiva:** Data curation, Formal analysis, Investigation, Methodology, Validation, Writing - review & editing. **Antônio Rodrigues Ximenes Neto:** Formal analysis, Investigation, Methodology, Validation, Writing - review & editing. **Marcelo de Oliveira Soares:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing - original draft, Writing - review & editing.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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humankind and all marine species.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2020.105064>.

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