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Cephalopods in the upwelling-influenced transition zone of Arraial do Cabo, Brazil, SW Atlantic: diversity, habitat use and sustainable management implications

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A R T I C L E I N F O

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A B S T R A C T

Despite the important role of cephalopods in demersal and pelagic trophic webs and their economic value as a fishing resource, they are still an understudied group in regional and local scales. Here, we evaluate the diversity of cephalopods in subtropical rocky reefs in Arraial do Cabo, a major upwelling region in southeastern Brazil, reporting information on distribution, habitat use, oceanographic conditions and biogeography. Using data obtained from underwater surveys, artisanal fisheries monitoring, citizen science and social media, a total of 15 species were identified, including three new records for the region and one new record for the Brazilian Province. Overall, the cephalopod fauna of Arraial do Cabo exhibited a mixture of warm- and cold-water species, as well as neritic and oceanic taxa. The co-occurrence of so many cephalopods in such a geographically limited area was mostly explained by the variety of bottom substrates and live covers. Thus, the combination of this feature with different sets of thermal and oceanographic conditions increases the habitat heterogeneity, probably accommodating octopus and squid species with diverse environmental preferences and tolerances.

1. Introduction

Cephalopods are fast-growing marine mollusks with short life cycles that sum approximately 820 species distributed globally across all oceans and inhabiting from coastal to deep-sea and even artificial habitats (Drazen et al., 2003; González et al., 2008; Lima et al., 2021; Freitas et al., 2022). They play a pivotal ecological role in food webs as both prey and predators (Gasalla et al., 2010; de la Chesnais et al., 2019; Dantas et al., 2022) and constitute a vital fishery resource for several coastal communities (Leite et al., 2008a; Rodhouse et al., 2014).

In Brazil, the Cephalopoda is still considered an underestimated group, with 93 valid species and at least 7 in the process of being described (Machado et al., 2023; Haimovici et al., 2025). This fauna is composed primarily of tropical and subtropical species (>70%), including 16% of species with a latitudinal distribution encompassing temperate regions, as well as 4% that reach subantarctic regions. In total, 14 species are classified as exclusively coastal, of which only a few are abundant enough to constitute relevant fishing resources (Haimovici et al., 2025).

Coastal and shelf industrial and artisanal modalities in south and southeast regions attain more than 90% of the production (Freire et al., 2015; Tosadori, 2022), mainly targeting the species *Octopus americanus* Froriep, 1806, *Doryteuthis pleii* (Blainville, 1823) and *Illex argentinus* (Castellanos, 1960), but at least five other species may comprise the

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bycatch fauna (Arkhipkin et al., 2015; Sauer et al., 2019; Haimovici et al., 2025). An important Brazilian coastal site for cephalopod fisheries can be spotted in the Arraial do Cabo region (Rio de Janeiro), where diverse artisanal octopus and squid fishing practices have persisted for over a century (Costa and Haimovici, 1990; ICMBio, 2020a).

Arraial do Cabo harbors a unique marine biodiversity composed of species with different thermal affinities (Batista et al., 2020), encompassing the southern and northern distribution limits of many groups occurring in the Western Atlantic, including the tropical and subtropical malacofaunas of Brazil (Petuch, 2013; de Paula et al., 2020). Besides this transitional aspect, the combination of prevailing NE winds and coastal morphology promotes the displacement of superficial waters, allowing the upwelling of colder, nutrient-rich South Atlantic Central Water (SACW) to the euphotic zone (Valentin, 2001). It directly enhances local primary productivity in spring and summer months and, consequently, the artisanal fisheries as well (Valentin, 2001; Coelho-Souza et al., 2012; Batista et al., 2020).

Previous studies on cephalopod local diversity also point to a transitional fauna composed of warm- and cold-water species (Haimovici et al., 1989). In the early 1990s, nine coastal species were recorded in the Arraial do Cabo region, and 16 oceanic or deep-sea shelf species were recorded for the state of Rio de Janeiro (Haimovici and Perez, 1991). Later in this decade, Costa and Fernandes (1993a,b) studied the seasonal and spatial variation of coastal cephalopods and the reproductive cycle of *Doryteuthis sanpaulensis* (Brakoniecki, 1984). Since then, numerous species have been described, redescribed, or newly recorded along the Brazilian coast and its oceanic islands, accompanied by major advances in ecological understanding and *in situ* identification based on external morphology and species-specific body patterns (Leite and Mather, 2008; Leite et al., 2008b, 2021; Lima et al., 2017a; Sales et al., 2019; Jesus et al., 2021; Alvarenga et al., 2024; González-Gómez et al., 2024; O'Brien et al., 2025). Furthermore, the first evaluation of cephalopod endangered species along the Brazilian coastline was recently published by the Ministry of the Environment (ICMBio, 2025). Although no species were considered vulnerable (VU) or endangered (EN), six species were classified as data deficient (DD), indicating that the limited knowledge of their life history and the potential human impacts on them are important red flags in this subject.

This study aimed at evaluating the diversity of cephalopods in the Arraial do Cabo region, reporting information on the species' distribution, habitat use, oceanographic conditions and biogeography. This is an unprecedented effort using five different data sources/methods at a local scale after a hiatus of more than 30 years (previous studies based solely on fisheries data). It is also a first step towards generating reliable information on species diversity to support future assessments of their conservation status and to assist in the cephalopod artisanal fishing management.

2. Material and methods

2.1. Study site

This study was performed within the Arraial do Cabo Marine Extractive Reserve (23°00′04.60″S/42°06′57.51″W), a sustainable use conservation unit (i.e. category of Brazilian marine protected area, MPA, that allows controlled human activities) that covers about 516 Km^2,

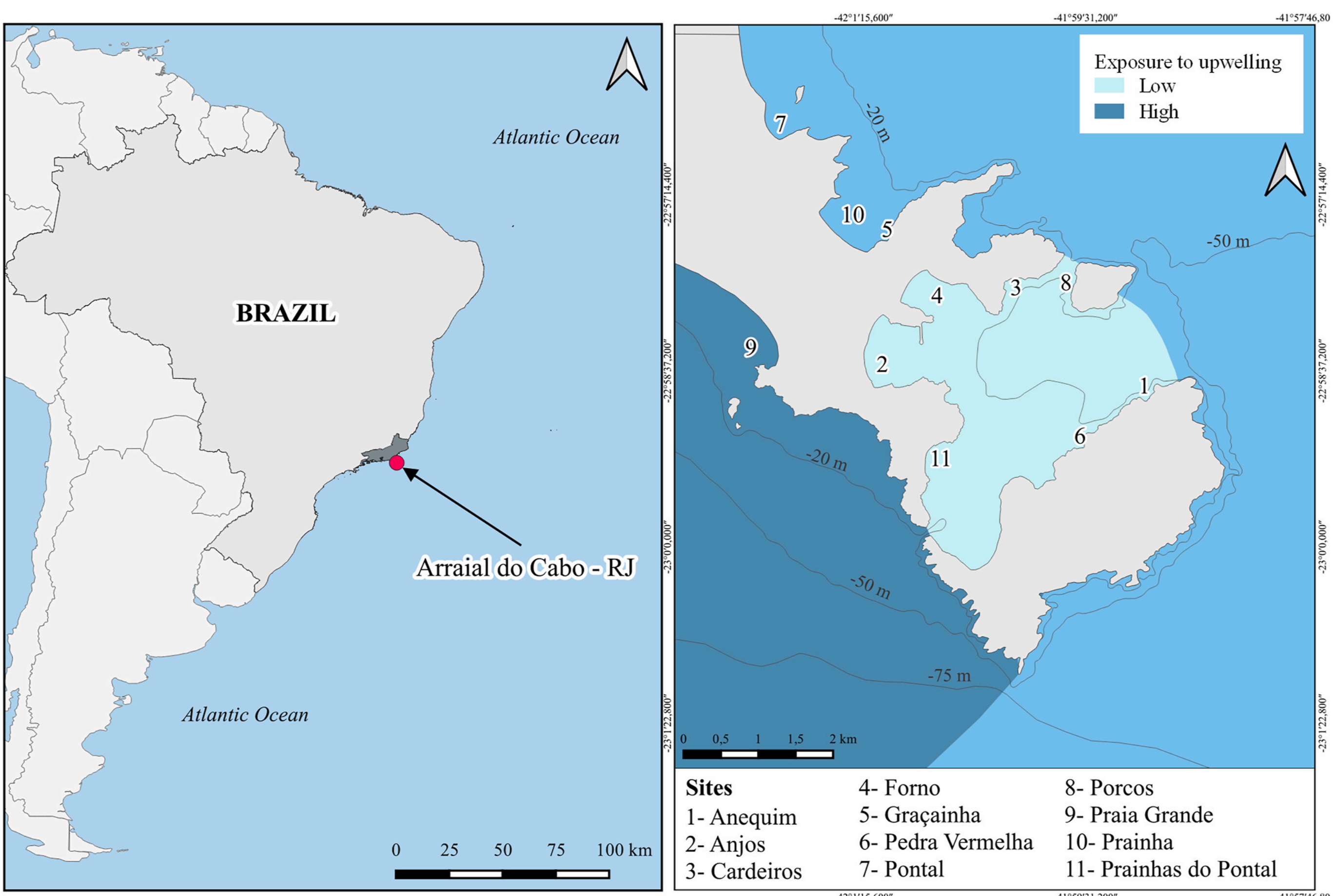

Fig. 1. Location of the study area in Arraial do Cabo, Rio de Janeiro, with indication of the coves and beaches where data collection was carried out via diving (i.e. active search, citizen science). Temperatures in the area of low exposure to upwelling are >22°C, whereas those in the area of high exposure to upwelling (i.e. fishing grounds) are <18°C.

where intense nautical tourism and various artisanal fisheries occur, including cephalopod fishing (Costa and Haimovici, 1990). This MPA was created in 1997 and has the only legislation in the national territory that regulates small-scale cephalopod fishing, establishing criteria and standards for squid and octopus captures (ICMBio, 2020a).

The Arraial do Cabo region (Fig. 1) is composed of an isthmus and four islands, mostly surrounded by rocky shores interspersed with sandy beaches of varying lengths and depths ranging from 2 to 45 m (Batista et al., 2020). The western and more exposed side of the isthmus, where most of the fishing occurs, is directly affected by the cold upwelling waters (<18°C), while the eastern side, more protected and with numerous coves and beaches (see diving sites listed in Fig. 1), preserves comparatively warmer waters (~22°C). The inner and more protected bay is composed of low slope rocky shores, formed by numerous different shaped rocks with maximum depths between 2 and 12 m, consequently presenting a high structural complexity. Shallower areas (≤4 m) have high abundances of sea urchins, with mosaics of "barren" patches, sessile invertebrates and epilithic algal matrix (EAM) mainly constituted by filamentous and articulated coralline algae. The deeper reefs (>4 m) have a major cover of macroalgae and EAM, with colonies of massive coral species (Cordeiro et al., 2014, 2020; Batista et al., 2020). The climate is tropical monsoon, with dry winters and generally very low precipitation (<850 mm/year); also, there is no significant freshwater supply within a 40 Km radius (Cordeiro et al., 2020).

2.2. Sampling

To assess the Arraial do Cabo cephalopod diversity (juvenile to adult individuals), data collected through different methodologies were used, including scientific diving, fisheries monitoring and analysis of photos and videos obtained by third parties (citizen scientists and social media). Considering the important role of diving-based approaches in studies focused on the ecology of cephalopods (Pak and Leite, 2025), an active search was done from July/2023 to May/2025 by SCUBA and free diving along the coves and beaches of the study area (Fig. 1). Divers would always swim parallel to the rocky shore and zigzag from the shallowest to the deepest part of it, where there is a transition to the unconsolidated bottom. Dives were conducted regularly (average: 6.0 ± 3.0 times/month, range: 1-12 dives), lasting 1 to 2 h, and at depths of up to 15 m; most searches were performed in the morning or afternoon, with only a few occurring at night ($n = 2$). Whenever cephalopods were encountered, the species name, number of individuals, predominant substrate and live cover, den type (only for octopuses), depth, temperature, and other pertinent observations (e.g. behavior, animal condition) were recorded. Temperature data was collected *in situ* with the aid of a diving computer and obtained through a fixed buoy positioned near Farol's beach, Cabo Frio Island (Aqualink, 2025 - https://aqualink.org/sites/1187). Photos and videos were made whenever possible with GoPro Hero 5 and Canon G1X cameras in waterproof housings.

During the same period, artisanal cephalopod fisheries were monitored monthly to identify and quantify the target species, as well as those that comprised the by-catch. Artisanal squid fishing took place at night with the aid of light lures, being practiced primarily in the "outer sea" (western side of the isthmus), off Praia Grande beach (Costa and Haimovici, 1990). This sector is dominated by fishermen at fixed points on the rocky shore (the "pesqueiros") and on small and medium-sized vessels (called "caícos" and "boca aberta", respectively), operated by one to three fishermen. Fishing gear is diverse and includes hand nets ("puçás"), squid-jigs ("zangarilhos", artificial bait combined with handlines) and gillnets. Another older method involves a different type of gillnet called "gancho" that is placed in the left corner of the beach using a long canoe. The "gancho" is pulled ashore every 2 h throughout the night. Monitoring of squid fishing could take place during captures (at the "pesqueiros") or after it, by accompanying the landings. Artisanal octopus fishing took place during the day on medium-sized vessels operated by three fishermen in the "outer sea", from Gruta Azul, on Cabo Frio Island, to Praia Grande, using five pot longlines arranged transversely to the coast (ICMBio, 2020b). These longlines, which remain on the bottom, serve as artificial refuges for the octopuses, which are captured manually when the gear is removed from the water. Monitoring of octopus fishing was done whether onboard or during landings at the local port. Octopus hookah fishing also occurs along the rocky shores of the study site during the day and with the aid of a hook called "bicheiro" but could not be monitored due to its uncertain frequency.

Third-party photos and videos were also analyzed, and the authors were consulted for details on the date, location, time, depth, temperature, and context of the observations. These records were obtained from the following sources: 1) database of the Reef Systems Ecology and Conservation Lab/Universidade Federal Fluminense (LECAR/UFF), which consists of a collection of photos and videos obtained *in situ* by the laboratory coordinator (C.E.L. Ferreira) from December/2000 to June/2023; 2) records on social media Instagram and YouTube found using the keywords "octopus", "squid" and "arraial do cabo" and referring to the period from April/2015 to April/2025; 3) contributions from citizen scientists to the Cephalopoda Project image bank, based at the Cephalopod and Underwater Studies Lab/Universidade Federal de Santa Catarina (LAMECE/UFSC). All third-party records were analyzed and screened to eliminate duplicate records, those from locations outside the study area, or those whose origins could not be verified.

2.3. Ethics statement

Due to this project involvement with the traditional knowledge of fishermen and local community, it was evaluated and approved by the Ethics Committee of the Universidade Federal de Santa Catarina (Statement No. 6.422.124). Sampling activities were authorized under the environmental license SISBIO 86899-1.

2.4. Data analysis

Octopus species were recognized based on morphological features, such as color patterns around the eyes, presence and extension of eye bars, presence and shape of ocelli, ventral color and reticular pattern of the arms' crown and other observed external features (e.g. behavior-related deimatic displays). Even though octopus can change body's color, form and texture, the range of variability obtained by each taxon is specific, allowing their identification *in situ*, in fishing landings or even in visual records, as shown by recent studies focused on West Atlantic coastal species (O'Brien et al., 2021; Alvarenga et al., 2024; Avendaño et al., 2025; Cedillo-Robles et al., 2026). Squid species were also recognized through morphological features, including color and body patterns, besides other components already described in ethograms and identification keys (Byrne et al., 2003; Mather et al., 2010; Postuma and Gasalla, 2015; Fernández-Álvarez et al., 2020; Migliavacca and Simone, 2020; Deville et al., 2024; Haimovici et al., 2025).

When observed in their natural environment, cephalopods were initially identified through a combination of clear morphological and habitat characteristics and, subsequently, identification was confirmed by analyzing images recorded at the time of observation. Specimens eventually sampled during fieldworks and those observed during fisheries monitoring underwent an individual thorough morphological and biometric analysis. Third-party images were also evaluated based on morphological, behavioral and habitat features and then compared to a wide reference material (see below). In any of these contexts, specimens that could not be effectively identified based on a representative set of characters were excluded from the study. The material that served as the basis for these analyses included literature such as 1) cephalopod identification guides reporting species morphology, habitat characteristics, distribution records and general ecology (Haimovici et al., 2009, 2025; Jereb and Roper, 2010; Jereb et al., 2016; Alvarenga et al., 2024);

2) species description articles (e.g. Haimovici, 1988; Leite et al., 2008b; Guerrero-Kommritz and Camelo-Guarin, 2016; Jesus et al., 2021; Leite et al., 2021); 3) images (photos and videos) of specimens already identified and catalogued in the Cephalopoda Project database.

A Canonical Correspondence Analysis (CCA) was employed to identify and quantify the relationship between the species presence-absence and the environmental data matrices. The variables included site, depth, temperature, and the main and secondary substrate types (i.e., first and second major substrate types), which included the categories rock, gravel, sand, mud, shell, coral and algae. ANOVA-like permutation tests were used to evaluate the global significance of the model tested through CCA, as well as the sequential and marginal significance of the environmental data. The analyses were performed in R software 4.5.1 (R Core Team, 2025) with the aid of the RStudio interface and the *'vegan'* package.

3. Results

A total of 2813 cephalopods belonging to 15 species and 6 families (i.e. Argonautidae, Eledonidae, Octopodidae, Loliginidae, Ommastrephidae and Thysanoteuthidae) were registered through the different methodologies employed in this study (Table 1, Supplementary Material Figs. S1 and S2). Of these, 11 species were previously reported from Rio de Janeiro and/or Arraial do Cabo, and three other species represent new records for the region: the octopuses *Octopus insularis* and *Amphioctopus burryi* and the pygmy octopus *Paroctopus cthulu*, endemic to southeastern and southern Brazil. Furthermore, one species was recorded/identified for the first time in Brazil: the Caribbean ocellated octopus *Octopus taganga*.

The dominant species in artisanal fisheries, *Doryteuthis pleii* (n = 761) and *Octopus americanus* (n = 701), were also the most frequently observed during underwater surveys (n = 33 and 60, respectively),

Table 1
List of cephalopods from Arraial do Cabo, Rio de Janeiro, with habitat characteristics, distribution, data source, total number of individuals observed, their condition, and threat level according to IUCN criteria. Abbreviations: habitat: SD-sand, MD-mud, GV-gravel, SH-shell, RC-rock, CR-coral, AG-algae, AF-artificial substrate/litter; distribution: ASPSP-San Peter and San Paul Archipelago, AFN-Fernando de Noronha Archipelago, ARC-Rocas Atoll, ATMV-Trindade and Martim Vaz Archipelago, STP-São Tomé and Príncipe, ASC-Ascension Island, STH-Saint Helena Island; data source: AS-active search, FS-fishing, LD-LECAR database, SM-social media, CS-citizen science; threat level: LC-least concern, DD-data deficient, NE-not evaluated. *According to T.S. Leite, personal communication (see Discussion section).

Taxon	Habitat	Distribution	Temperature range (°C)	Data source	Total number	Condition	IUCN status
Family Argonautidae							
Argonauta nodosus [Lightfoot], 1786	Epipelagic, oceanic	ASPSP, AFN, Rio de Janeiro to Argentina, South Pacific and Indian	23.4-25.2	AS, LD, SM	26	Senescent, spawning, paralarvae	LC
Family Eledonidae							
Eledone gaucha Haimovici, 1988	Benthic, shelf and slope, SD, MD	Rio de Janeiro to Argentina (North Patagonia)	21.4	FS	1	Dead, preyed upon	LC
Family Octopodidae							
Amphioctopus burryi (G. L. Voss, 1950)	Benthic, coastal, SD, GV, SH	North Carolina to Rio de Janeiro, East Atlantic (West Africa, Canary Islands)	22.5-22.7	CS	4	Alive	LC
Macrotritopus cf. *defilippi* (Vérany, 1851)	Benthic, coastal, SD, GV, MD	AFN, ARC, Florida to Santa Catarina	22.6-25.3	AS, LD, SM, CS	16	Alive	LC
Octopus americanus Froriep, 1806	Benthic, coastal, GV, SD, SH, RC	Virginia to North Argentina	20-24	AS, FS, LD, SM, CS	759	Alive, spawning, senescent	LC
Octopus taganga Guerrero-Kommritz & Camelo-Guarin, 2016	Benthic, coastal, RC, CR	Colombia, AFN*, Alagoas* to Rio de Janeiro	23.7-24	SM, CS	4	Alive	NE
Octopus insularis Leite & Haimovici, 2008	Benthic, coastal, RC, CR, AG	ASPSP, AFN, ARC, ATMV, Florida to Rio de Janeiro, East Atlantic (STP, ASC, STH)	21-27	AS, FS, LD, SM, CS	82	Alive	LC
Octopus tehuelchus A. d'Orbigny, 1835	Benthic, coastal, RC, MD, AF	South Bahia to Argentina (North Patagonia)	14-22.2	FS	12	Alive, spawning, dead	DD
Paroctopus cthulu Leite, F. D. Lima, S. M. Q. Lima & Haimovici, 2021	Benthic, coastal, AF	Espírito Santo to Santa Catarina	24.6-25.1	SM	2	Alive	DD
Family Loliginidae							
Doryteuthis pleii (Blainville, 1823)	Pelagic, coastal	Venezuela to North Argentina	21.7-25.3	AS, FS, LD, SM	861	Alive, spawning	DD
Doryteuthis sanpaulensis (Brakoniecki, 1984)	Pelagic, coastal	South Bahia to Argentina (North Patagonia)	20.3	FS	3	Alive	LC
Pickfordiateuthis pulchella G. L. Voss, 1953	Benthopelagic, coastal	South Florida to São Paulo	22.5-22.6	AS, LD	5	Alive	LC
Sepioteuthis aff. *sepioidea* (Blainville, 1823)	Pelagic, coastal	Florida to São Paulo	20-26.4	AS, LD, SM	1035	Alive, spawning	LC
Family Ommastrephidae							
Ommastrephes cylindraceus (A. d'Orbigny, 1835)	Epipelagic, nerito-oceanic	ASPSP, AFN, Rio Grande do Norte to South Argentina, South Indian	21.2-21.8	SM	2	Senescent	LC
Family Thysanoteuthidae							
Thysanoteuthis rhombus Troschel, 1857	Epipelagic, oceanic	ASPSP, AFN, Ceará to Rio Grande do Sul, North and South Atlantic, Mediterranean	20.9	FS	1	Senescent	LC

surpassed only by the squid *Sepioteuthis* aff. *sepioidea* (n = 498). This squid was likewise the most frequent species in historical records from the LECAR database (n = 329) and on social media (n = 208). The octopus *O. insularis* was the second most frequent species in social media records (n = 30) and was occasionally captured in pot longline fishery (n = 43) targeting *O. americanus* (Fig. 2). In general, species records varied according to the method employed, and some observations only occurred thanks to a single specific method (Fig. 2).

About 44% of the observed variation in the occurrence of cephalopod species was explained by the set of environmental variables analyzed (Fig. 3). The model was built with presence/absence data for the five most frequent cephalopods (i.e. *O. americanus*, *O. insularis*, *M.* cf. *defilippi*, *D. pleii*, and *S.* aff. *sepioidea*) based solely on records from underwater surveys and citizen science (79 observations). This restricted model was statistically significant (F = 2.015, p = 0.001) and the first two canonical axes (CCA1 and CCA2) captured 32.4% and 30.1% of the explained inertia, respectively. At first, main and secondary substrate types, site and depth seemed all important for cephalopod's occurrence (i.e. sequential significance test), but the evaluation of the marginal effects of each environmental variable pointed to the secondary substrate as the only factor presenting an independent and statistically significant contribution (Table 2).

Regarding habitat use, *O. americanus* and *M.* cf. *defilippi* were frequently associated with unconsolidated bottoms composed of gravel, sand and shells; *O. insularis* showed a preference for consolidated bottoms mostly covered by algae and coral. As for the squids *S.* aff. *sepioidea* and *D. pleii*, a preference was observed for habitats close to the rocky shores with coral cover and exposed rocks, respectively (Fig. 3).

4. Discussion

The present assessment of the local cephalopod diversity in an upwelling region of the Southwest Atlantic showed a mix of species with different thermal affinities from both neritic and oceanic realms. Furthermore, it allowed for the ecological characterization of several of these taxa in very heterogeneous habitats, which was an important first step in understanding their occurrence in the Arraial do Cabo Marine Extractive Reserve. A total of 15 octopus and squid species were recorded, 11 of which are from shallow coastal environments (up to 200 m depth), representing 69% of the coastal cephalopods reported in the whole Brazilian Province. Also, considering the total set of valid cephalopod taxa for this biogeographic province (94 spp., including shelf, slope and oceanic habitats), the Arraial do Cabo region potentially holds approximately 43% (~40 spp.) of this known diversity (Haimovici and Perez, 1991; Haimovici et al., 2025; ICMBio, 2025).

Analyses of cephalopod communities at regional and local scales around the world show that the coastal diversity observed in this study is proportionally high, reaching almost the same number of coastal species present along the entire coast of the Kermadec Islands in New Zealand (9 spp.), the Canary Islands in Spain (13 spp.), Chile (15 spp.), Mauritania (17 spp.), the East coast of China (17 spp.), the Pacific coast of Mexico (17 spp.) and half of those in the Caribbean region (23 spp.) (Ibañez et al., 2009; Judkins et al., 2010; Rocha et al., 2017; Braid and Bolstad, 2019; Escánez et al., 2021; Urbano and Arroyo-Lambaer, 2025; Liang et al., 2025). The co-occurrence of several cephalopod species with distinct habitat affinities observed in Arraial do Cabo is generally associated with transition zones, where local richness is often higher precisely because they accumulate components from two adjacent regions/subprovinces (Odum, 1971; Morrone, 2004; Ferro and Morrone, 2014).

In the Western Atlantic, biogeographic transition zones between the Carolinian and Caribbean provinces, as well as between the Brazilian and Patagonian provinces, exhibit high diversity and endemism for gastropods and bivalves (Petuch, 2013). Similar patterns have been documented between the Brazilian states of Bahia and Rio de Janeiro for prosobranch gastropods, sponges, tunicates, reef fish and macroalgae (Moreno et al., 2014; Barroso et al., 2016; Aued et al., 2018; Pinheiro et al., 2018; Cord et al., 2022; Jørgensen et al., 2022; Anderson et al., 2023). Driven by the warm Brazil Current and SACW upwelling, this zone represents a special center for molluscan evolution, marking the southern boundary for tropical malacofauna and serving as a barrier to subtropical and temperate species (Floeter and Soares-Gomes, 1999; Petuch, 2013), a transitional character that clearly encompasses the cephalopods of Arraial do Cabo as suggested by Palacio (1982) and Haimovici et al. (1989). Furthermore, its diverse spatial and trophic resources sustain ecologically similar or sympatric species through

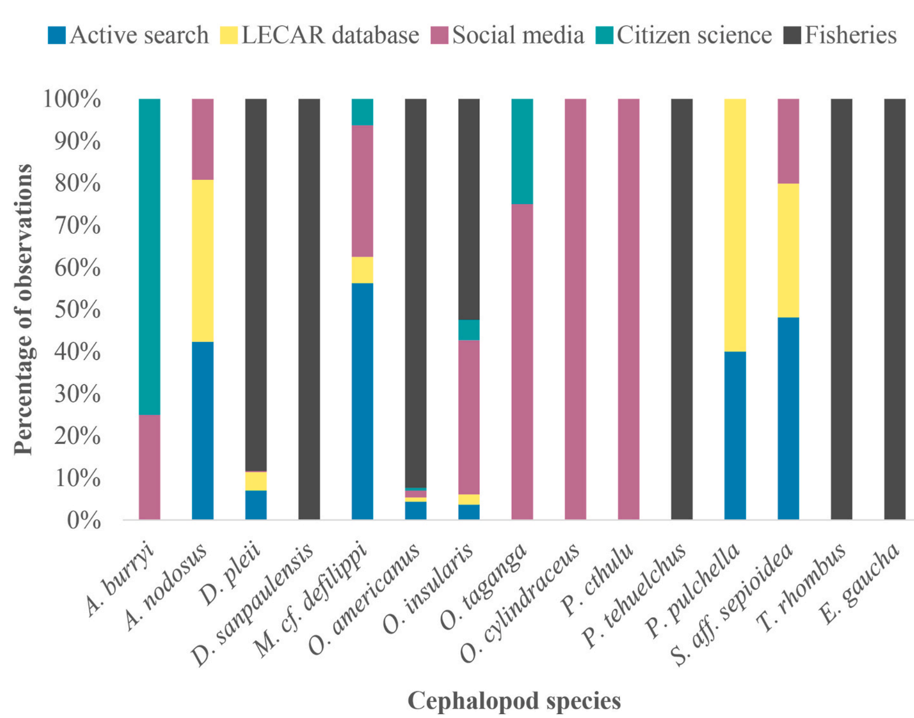

Fig. 2. Percentage of observations for each cephalopod species recorded through different types of datasets.

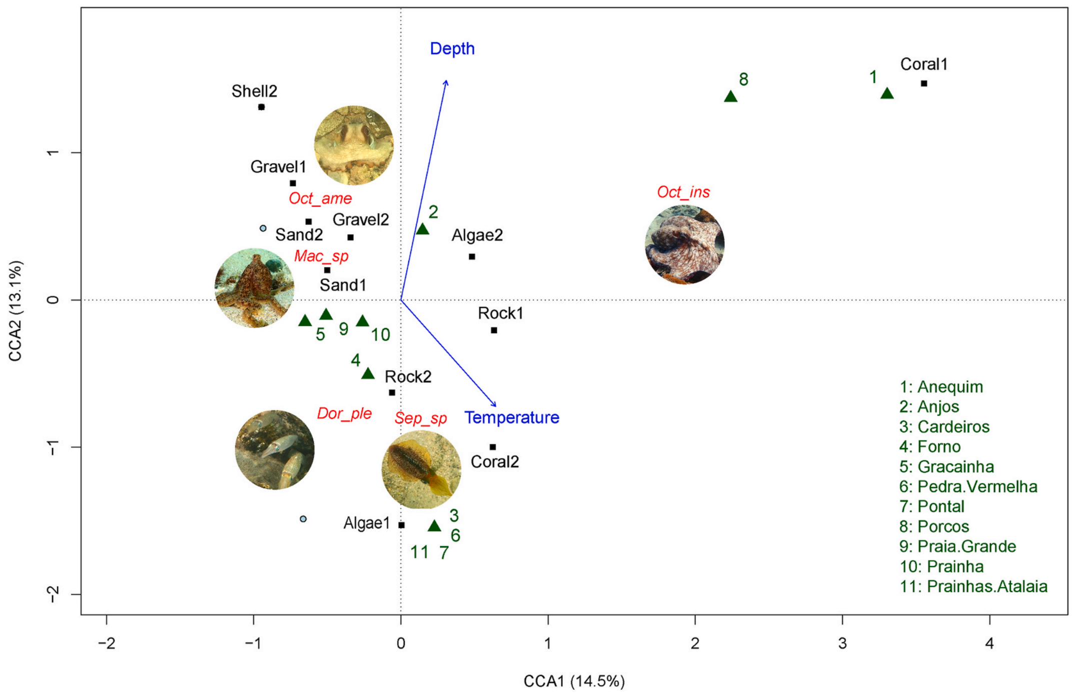

Fig. 3. Graphical representation of the preference of cephalopod species for the environmental characteristics and conditions of the study area (green – centroids [▲] and numerical labels of the collection/observation sites; black – centroids [■] and labels of the main [1] and secondary [2] substrate categories; blue – vectors and labels of the temperature and depth variables; red – cephalopod species *D. pleii*: Dor_ple, *M.* cf. *defilippi*: Mac_sp, *O. americanus*: Oct_ame, *O. insularis*: Oct_ins, *S.* aff. *sepioidea*: Sep_sp). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Results of permutation tests (ANOVA) for the sequential and marginal significance of environmental variables on the occurrence of cephalopod species.

Variables	df	Sequential Test			Marginal Test		
		Chi-square	F	p	Chi-square	F	p
Site	10	0.71593	1.7418	**0.018***	0.44920	1.0928	0.377
Depth	1	0.12508	3.0431	**0.019***	0.05749	1.3986	0.258
Temperature	1	0.7502	1.8251	0.129	0.03942	0.9590	0.418
Main substrate	4	0.42701	2.5971	**0.001*****	0.20857	1.2686	0.229
Secondary substrate	5	0.39625	1.9281	**0.011***	0.39625	1.9281	**0.010***
Residual	55	2.26070			2.26070		

resource partitioning, including differential habitat use, activity period, diet and morphological divergence (Chaves et al., 2021; Lear et al., 2021; Barrett and Brazier, 2024; Cardozo-Ferreira et al., 2026).

Spatial partitioning is well documented in Arraial do Cabo and species generally segregate based on temperature and wave exposure. Thus, some taxa concentrate in warmer sheltered waters to the east (inner bay of the isthmus), while others are related to the colder (upwelling-influenced) wave-exposed waters to the west (outer sea) (e.g., reef fish, turtles, benthic community, see Cordeiro et al., 2016; Mello-Fonseca et al., 2021). Although some cephalopod species were indeed exclusively reported in the east (i.e. *O. insularis*, *P. pulchella*) or the west (i.e. *E. gaucha*, *O. tehuelchus*, *O. cylindraceus*, *T. rhombus*) sides of the study area, niche partitioning directly related to temperature was not observed and a more in-depth evaluation is needed. Habitat type and species natural behavior, on the other hand, seemed more important.

For instance, *O. americanus* and *O. insularis* were observed in distinct habitats and activity periods, sometimes even sharing the same area. The former preferred dens in the transition between rocky shores and sand/gravel/shell beds and was only seen foraging at night, while the latter sheltered exclusively in dens on the rocky shore and foraged mainly during the day, matching what has been described in previous studies on their ecology and behavior (O'Brien et al., 2023; Côrtes et al., 2025, 2026). The octopus *M.* cf *defilippi* frequently co-occurred with *O. americanus* in unconsolidated bottoms, exclusively inhabiting burrows and deep galleries excavated directly in the substrate, whereas *O. americanus* occupied sandy plain areas always close to rocky shores and with a greater presence of small rocks, shells and living cover (e.g., algae) in the vicinity. This scenario was equally observed in Florida by Bennice et al. (2019), who thoroughly investigated the partitioning mechanisms between the two species. Although not statistically tested due to its low occurrence, the brown-striped octopus *A. burryi* also used specific microhabitats of the sandy bottoms of the Graçainha and Anjos coves, taking refuge in shells of other mollusks, mainly bivalves, dispersed in the substrate (see Guerra et al., 2013).

Coastal squid species likewise seemed to segregate in space and time. *Sepioteuthis* aff. *sepioidea* dominated the shallow warm waters of protected coves and beaches (e.g., Forno, Cardeiros, Prainha), forming numerous large schools near rocky shores during the day. In fact, Arraial do Cabo and Baía de Todos os Santos (state of Bahia, see Nunes et al., 2007) are the only sites on the Brazilian coast where substantial schools of this species were ever reported. Groups of *Doryteuthis pleii*, on the other hand, were observed almost exclusively at night in the colder waters near exposed shores (e.g., Praia Grande), where they are fished year-round. *D. pleii* individuals were exceptionally seen during the day in a sheltered sandy area of Graçainha's cove in apparent reproductive aggregations (Supplementary Material Fig. S3), as separate schools of males and females could be identified through body patterning (e.g. see 'accentuated testis and oviducal gland' chromatic components described by Postuma and Gasalla, 2015), something previously reported for this squid genus (Arkhipkin and Middleton, 2002). Records from the LECAR database indicate that this difference in habitat also occurs when choosing a substrate for spawning, with *S.* aff. *sepioidea* nesting on consolidated substrate (LaRoe, 1971) and *D. pleii* using sandy bottoms (Roper, 1965; Judkins and Vecchione, 2013) (Fig. 4).

Regarding the novel records of this study, the relatively frequent presence of *O. insularis* in the shallow reefs of Arraial do Cabo's inner bay and its mild occurrence in pot longline fishing points to its expansion to the subtropics as predicted by studies that modeled changes in its ecological niche (Lima et al., 2020, 2023). Nevertheless, it is difficult to determine when it began, what caused such change, or even whether the species managed to establish itself in the area; photos of *O. insularis* from the LECAR database date back to at least 2002 and fishermen recognize the species and call it the "African octopus". Moreover, as a by-catch of the pot longline fishing (alongside *O. tehuelchus* and *E. gaucha*), this record confirms the mixed production of the local artisanal octopus landings, stressing the importance of a species-specific monitoring to properly assess the stocks (Vecchione et al., 2000; Lima et al., 2017b, 2020; Barrett et al., 2023; Barrett and Brazier, 2024).

The ocellated octopus *O. taganga*, here in its first record in Brazil, was also present during the day on rocky shores. However, it only took shelter in crevices between rocks covered by colonies of the anthozoan *Palythoa caribaeorum*, where it was seen foraging as well. This species was described a few years ago in Colombia and there are still no studies addressing its ecology (Guerrero-Kommritz and Camelo-Guarin, 2016); hence, these observations are important for understanding its occurrence in Brazilian reef environments. After this record, lots identified as *Octopus hummelincki* Adam, 1936 (the only ocellated octopus known until then for the Brazilian coast, see Haimovici et al., 2025) were re-evaluated and other specimens of *O. taganga* from different Brazilian localities were found (sampled during activities of the Cephalopoda Project, T.S. Leite, personal communication), indicating the need for a revision of this species in Brazil.

The respective southward and northward expansions in the distributions of *A. burryi* and *P. cthulu* just highlight the effectiveness of integrating multiple data sources in the detection of cephalopod cryptic diversity by enhancing the temporal and spatial coverage of sampling (Bender et al., 2014; Coll et al., 2014; Robinson et al., 2020; Roberts et al., 2022). Further studies are already underway to clarify ecological, behavioral and population genetic aspects, but simpler diversity analyses like this are needed in other locations along the Brazilian coast, where there is still insufficient data on these and other cephalopod species (ICMBio, 2025).

Oceanic and nerito-oceanic cephalopods were observed through individual or massive strandings. In 2021, Tolla et al. (2024) recorded several spawning and senescent females of the octopus *A. nodosus* stranding in Praia Grande in a classic upwelling scenario (temperatures of 16-18°C). However, the most recent event (March/2025, this study) occurred at temperatures between 23 and 25°C, more closely resembling the stranding conditions reported by Demicheli et al. (2006) on the Uruguayan coast. Spawning females arrived at Praia Grande over three days, some even with their eggs already hatching, making it possible to visualize the live paralarvae. Ortiz et al. (2024) found *A. nodosus* paralarvae in southeast–south Brazilian outer shelf and slope mainly under the influence of Tropical Water (TW) and SACW, whereas Vidal et al. (2010) found high abundances of small male and female juveniles in the midshelf associated with high chlorophyl-*a* concentration and under the influence of SACW as well. Therefore, the stranding of mature females in Arraial do Cabo and the transport of paralarvae to offshore are probably related to the alternation of these two water masses along the southeastern coast, although it is difficult to define a distribution pattern for the family Argonautidae, as observed by Vasconcellos et al. (2024). The rare capture of senescent individuals of *O. cylindraceus* and *T. rhombus* by fishermen was also recorded, but their occurrence in the region for feeding and reproductive purposes and even in earlier stages was known already (Haimovici et al., 1989; Jereb and Roper, 2010; Cunha and Oliveira, 2014; Fernández-Álvarez et al., 2020; Ortiz et al., 2024; Vasconcellos et al., 2024).

Overall, the occurrence of the most frequent octopus and squid

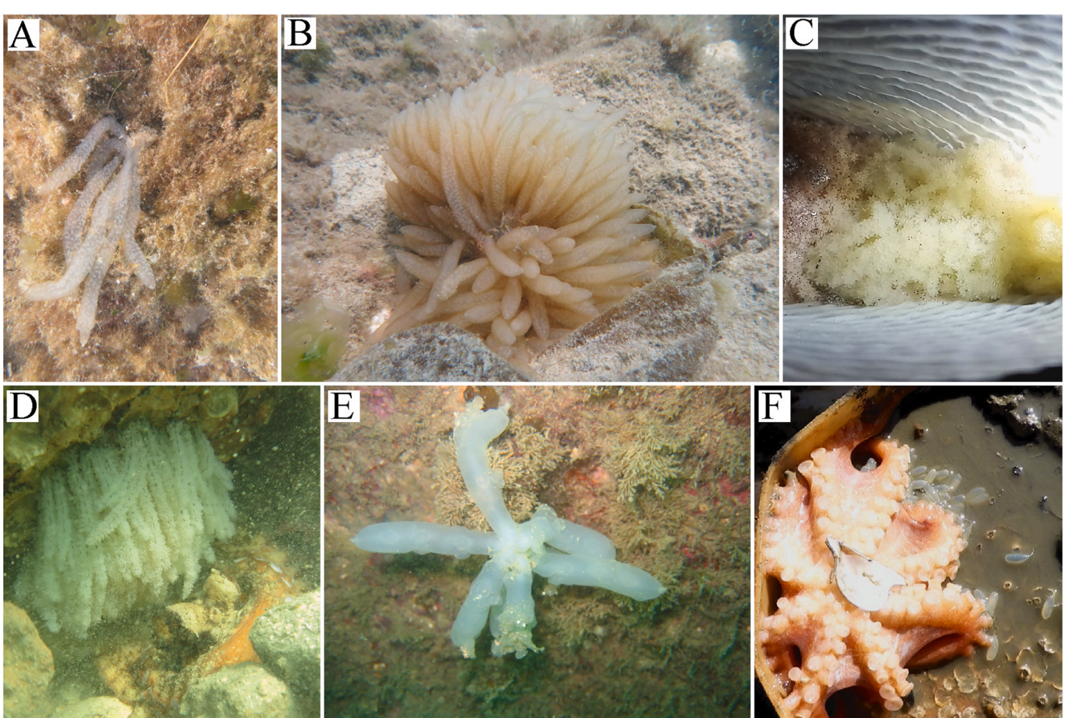

Fig. 4. Cephalopod spawning records in the study site: A) unidentified Loliginidae; B) *Doryteuthis pleii*; C) *Argonauta nodosus*; D) *Octopus americanus*; E) *Sepioteuthis* aff. *sepioidea*; F) *Octopus tehuelchus*. Photos: Cadu Ferreira (A, B, D and E) and Renato Dantas (C and F).

species was explained by the variety of bottom substrates and live covers (e.g. grain size, coral and algae cover) and their own pattern of habitat use. Arraial do Cabo presents a combination of different sets of thermal and oceanographic conditions that increase the habitat complexity and heterogeneity, sustaining a high diversity of different groups (e.g. Ferreira et al., 2001; Brasileiro et al., 2009; Sarmento et al., 2012; Cordeiro et al., 2016; Granthom-Costa et al., 2016). Such special features seem to benefit the coexistence of cephalopods as well and the spawning of at least five species (Fig. 4) indicates that some of them can even complete their life cycle in the region. Nevertheless, broader analyses are still needed as this current snapshot of the cephalopod assemblage is susceptible to changes, particularly those fishing-related.

5. Conclusions and knowledge gaps

The present evaluation of the cephalopods at Arraial do Cabo increased the total number of species recorded for Brazil (i.e. 94 spp., see Haimovici et al., 2025 for the most recent list) and expanded the distribution of some of them. Also, it allowed for a proper identification of octopus and squid species comprising local artisanal fishing resources (i. e. *O. americanus* and *D. pleii*). Bycatch species were identified as well and their occurrence in the landings should be monitored, as their biology in Brazilian waters is still poorly understood (e.g. *O. tehuelchus* and *E. gaucha*). The same can be said about the species not related to fisheries and only detected in the natural environment (e.g. *A. burryi*, *M.* cf. *defilippi*, *P. pulchella*). Therefore, this study may serve as baseline to assess future changes in the local assemblage, representing an important step in cephalopod conservation within this MPA.

Even though species occurrence in the area was elucidated, there is still more to understand about their habitat use and ecology. More studies specifically analyzing species niche partitioning are encouraged, since habitat heterogeneity and behavior seemed more relevant than temperature in the present investigation. The use of pictures and videos from social media clearly implies difficult source reliability but have potential to assist this type of study if proper citizen science guidelines and training are provided. For instance, the inclusion of temperature, depth, date, time and other relevant data in visual records would be a great advance from citizen scientists to accurately analyze species distribution. Despite being a local study, it may help understand cephalopod assemblage composition in other upwelling sites, as well as serve as an example of a proper start in fishery management in such diverse locations.

CRediT authorship contribution statement

Renato Junqueira de Souza Dantas: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft, Writing – review & editing. **Carlos Eduardo Leite Ferreira:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing. **Mariana Osório Côrtes:** Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Ana Beatriz Bauer:** Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Weslley Almeida da Silva:** Data curation, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Tatiana Silva Leite:** Conceptualization, Data curation, 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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2026.110150.

Data availability

Data will be made available on request.

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