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Improving the Knowledge on the Distribution and Ecology of the Protected Echinoid *Centrostephanus longispinus* (Philippi, 1845) in the Alboran Sea

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Abstract

Centrostephanus longispinus (Philippi, 1845) is a sea urchin widely distributed across the tropical and temperate Atlantic Ocean (including the Caribbean) and Mediterranean Sea. Although it is present along the Alboran Sea coastline (Western Mediterranean), it is generally considered rare and is listed under conservation and protection lists and conventions due to fragmented populations threatened by seabed degradation. This study provides the first density and size distribution data for this echinoid in the circalittoral and bathyal bottoms of the Alboran Sea, aiming to relate its presence to seabed features, environmental variables, and human pressures. A series of 131 (62 ROV and 69 TASIFE transects) underwater image transects were collected during CIRCAESAL expeditions (2021, 2023, 2024) using a ROV and a photogrammetric sledge from infralittoral to bathyal bottoms (17–856 m depth). Images were processed with OFOP software to quantify and classify individuals by size classes, depth, substrate, seafloor roughness, micro-habitat, and coverage of key benthic structuring species. A total of 524 individuals of *C. longispinus* were detected in 13 transects, with the highest densities recorded at 48–100 m depths in rough, rocky substrates with crevices and a moderate to low coverage of key benthic structuring species. Differences in habitat use were also observed across depth strata: individuals in shallower zones tend to remain hidden within crevices and structurally complex substrates, displaying a more cryptic behaviour, whereas those in deeper strata rely less on refuge and occupy less complex habitats. The largest aggregations occurred near the Guadiaro Canyon, outside the "*Estrecho Oriental*" Special Area of Conservation (SAC), suggesting this area may serve as a population reservoir deserving conservation. Despite these findings, ecological knowledge of *C. longispinus* remains limited, and future studies should improve the knowledge gaps, particularly in the eastern and southern Alboran Sea.

Keywords: abundance; echinoderm; habitat preference; hatpin urchin; Mediterranean Sea; population structure; species conservation

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1. Introduction

Centrostephanus (Peters, 1855) is a genus of diadematoid sea urchin widely spread in temperate and tropical waters of the Atlantic and Indo-Pacific Oceans as well as smaller basins located close by [1]. At present, there are eight nominal accepted species and one subspecies of *Centrostephanus*, with all of them characterised and distinguished from the rest of the diadematoid genera by the presence of globiferous pedicellariae [2–4]. Most of the poor knowledge on the ecology and biology of *Centrostephanus* has been obtained from just three species, including C. *rodgersii* (A. Agassiz, 1864) from southeastern Australia and northern New Zealand; *C. coronatus* (Verrill, 1867) from the eastern Pacific, and *C. longispinus* (Philippi, 1845) from the Atlantic Ocean and Mediterranean Sea [1,3,5]. *Centrostephanus longispinus* (Philippi, 1845) is the type species of the genus and is found from tropical to temperate areas of the Atlantic Ocean as well as in the Mediterranean and Caribbean Sea. Two subspecies are distinguished within this species: the nominal subspecies of the eastern Atlantic and Mediterranean and *Centrostephanus longispinus* ssp. *rubicingulus* Clark, 1921, of the western Atlantic and Caribbean Sea [1,6]. *Centrostephanus longispinus* could be considered as a relict species in the Mediterranean [6] and can co-occur with other diadematoid species such as the lessepsian species *Diadema setosum* (Leske, 1778) in the Mediterranean Sea [7–9] and the amphiatlantic species *D. antillarum* in some Macaronesian Islands [6,10]. *Centrostephanus* sea urchins are ecologically important organisms that can modify habitats, creating barrens and affecting kelps and other macroalgae as well as macrofaunal invertebrate species [3,11–13]. These diadematoids are highly sensitive to light, often foraging at night and hiding during the day in crevices [3,6,14,15]. They serve as a food source for large predators, including lobsters, large starfish and gastropods, groupers and trigger fishes, and the sea otter, among others [6,16,17]. Due to the ecological significance of many species belonging to the genus *Centrostephanus*, it is important to understand their habitat and micro-habitat preferences, as well as their relationship with other structuring species.

The hatpin urchin *C. longispinus* has been mainly studied in the infralittoral and upper circalittoral bottoms [18–20] and just in specific locations of the Mediterranean (Tunisia, where it was first cited [21]; National Parc of Port-Cros, in the northwest Mediterranean [22]; Provence, France [23]; and Ischia Island in the gulf of Naples [24]) but also in some areas of the Atlantic Ocean (*C. longispinus rubricingulus* in northeastern Brazil [5]; Banco de La Concepción at the north of the Canary Islands [25]). The distribution of *C. longispinus* spans largely across the western Atlantic but also the eastern Atlantic—in this case, from the southern Iberian Peninsula to Angola, including the Macaronesian Islands (Azores, Madeira, Canary Islands, and Cabo Verde) and some seamounts of the northeastern Atlantic (e.g., Banco de la Concepción)—and extends along the Mediterranean Sea, including the Adriatic, the Aegean, and the Marmara Sea [8,19,26–32]. In the Alboran Sea the species is catalogued as rare, despite being distributed along a large part of its coastline [28]. In the Macaronesian region, the species is uncommon and appears to have a dispersed distribution below 30 m depths [1,6]. However, this echinoid appears to be relatively frequent on the Saharan continental shelf [6,33]. The species is described as stenothermic, with a narrow temperature range between 12 and 18 °C and a depth range from 3 to 335 m [19,28]. The optimum ecological niche seems to correspond to rocky bottoms of the continental shelf below 50–60 m, with the highest abundances generally detected between 60 and 130 m depths [6]. Additionally, some populations have been found in sandy or muddy bottoms at 335 m [25,34]. Recently, the maximum depth limit has been updated from 379 [35] to 550 m with one specimen found in the northern Alboran Sea [36].

This echinoid has separate sexes, although hermaphroditic individuals have also been encountered [3]. There is hardly any data about its reproduction; however, it is thought that, like other species of diadematoids, it develops a planktonic larval phase that compensates for the low dispersion of the adults [22]. There is little knowledge of the recruitment, size class distribution, and longevity of the species. Possible factors that may interfere with recruitment include the role of bottom and surficial currents, the type of substrate, the presence of calcareous algae, and the presence of healthy populations with reproductive adults [6]. As observed in other diadematoids, it also has an important role as a grazer of macroalgae, seagrass, and small invertebrates (mainly bryozoans, tunicates, sponges, and cnidarians), shaping and altering the composition, structure, and distribution of some benthic habitats [3,37]. *Centrostephanus longispinus* may also have the potential ability to utilise dissolved organic carbon, and particulate organic matter has also been suggested [23,38,39]. Its capacity to feed on *Posidonia oceanica* (Linnaeus) Delile meadows has also been reported [39]. Possible predators of this species can be large starfish such as *Marthasterias glacialis* (Linnaeus, 1758) and gastropods such as *Charonia lampas* (Linnaeus, 1758), as well as fishes such as *Balistes capriscus* (Gmelin, 1789) [6].

The hatpin urchin is the only species of the *Centrostephanus* genus included in different conservation lists of endangered or threatened species (Table 1) due to its rarity and sparse and scattered populations, which are at risk of disappearing because of threats to the seabed, including contamination, general discharges, trawling disturbances, coastal developments that lead to habitat destruction [6,40,41], and the deterioration of environmental conditions such as ocean acidification [42].

Table 1. Conservation lists, directives, and conventions in which *Centrostephanus longispinus* is currently included. National and regional–local protection lists are marked with *.

Directives, Conventions, and Conservation Lists	Annex/Category
Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora—consolidated version 01/01/2007 (EU Habitats Directive)	Annex IV
Convention on the conservation of European wildlife and natural habitats (Bern Convention)	Annex II
Barcelona Convention Protocol concerning Specially Protected Areas and Biological Diversity in the Mediterranean (SPA/BD Protocol)	Annex II
Listado de Especies Silvestres en Régimen de Protección Especial y del Catálogo Español de Especies Amenazadas *	Vulnerable
Libro Rojo de los Invertebrados de Andalucía *	Vulnerable
Catálogo Andaluz de Especies Amenazadas *	Species of special interest

Quantitative and semi-quantitative data on *C. longispinus* are very scarce across its distribution range and mostly available only for the infralittoral and upper circalittoral populations [19–24,33,43], including some from bathyal zones [31]. The first abundance data for the distribution of *C. longispinus* along the Spanish coasts (including the northern Alboran Sea margin, Alboran Island, Balearic Islands, and Columbretes Islands) were provided by a previous study [28], although no density data could be reported. The environmental drivers of the distribution of *C. longispinus* on a seamount in the eastern Atlantic (Banco de la Concepción, Canary Islands) were first analysed in another study [25], but no density data were provided in that case either. Even Francour, who has studied this species in detail along the French coastline [18,19,22], published a biological approach without providing data on the density of its populations. The absence of density data in different bathymetric areas of the distribution of this echinoid complicates the evaluation of the environmental status of the species and its potential vulnerability to environmental changes or anthropogenic pressures.

Therefore, the main aims of the present study are to obtain the first density estimations of the hatpin urchin in the less studied populations occurring in the circalittoral and bathyal bottoms of the northern Alboran Sea in relation to seabed features, environmental variables, key benthic structuring species, and anthropogenic activity indicators. This study aims to enhance the knowledge of the environmental status of *C. longispinus* and, if necessary, propose appropriate conservation measures to improve its protection.

2. Materials and Methods

2.1. Study Area

The Alboran Sea is defined as a biogeographical entity within the Mediterranean Sea, bounded by the Strait of Gibraltar in the west and an imaginary line spanning from Cabo de Gata (Cape of Gata) (located in Almería, southern Spain) to Cap Fegalo (close to Oran, Algeria) [44] (Figure 1). The Alboran Sea exhibits one of the highest biodiversities in the Mediterranean basin, making it a biodiversity hotspot within the Mediterranean [45–49]. This is due to its position as a transitional zone between the Atlantic Ocean and the Mediterranean Sea, where species from warm waters (from North Africa's Atlantic) and cold and temperate waters (from the northeastern Atlantic) and Mediterranean species coexist, along with some endemic organisms restricted to the Strait of Gibraltar and specific locations of the Alboran Sea [50].

The margin of the Alboran Sea generally features a narrow shelf and deep areas dominated by significant topographic irregularities [51]. The shelf includes depositional, erosional, landslide, and anthropogenic features. On the other hand, the distal margins and adjacent sub-basins contain features of different origins, for example tectonic structures (folds and faults) [52]; seamounts, distributed along the continental slopes and sub-basins [53]; fluid outflows (mud diapirs, mud volcanoes, pockmarks, and patches of authigenic carbonates), primarily in the western sector [54,55]; depositional contourite features (drifts), erosional (moats, channels, and scarps) and mixed (terraces), from the continental shelf break to the basins [56,57]; mass movement features (turbidite systems, canyons, and slides), found both on the Iberian margin and the African continental slopes, as well as on the flanks of the Alboran Ridge; and biogenic structures, present on both the Iberian and African shelves [58].

The water mass circulation of the Alboran Sea is linked to the exchange through the Strait of Gibraltar, driven by excess evaporation over precipitation and river runoff in the Mediterranean. These currents are modulated by the Coriolis force [59]. The Atlantic water mass, with lower salinity than the Mediterranean one, enters as a narrow and fast-moving current, forming a permanent anticyclonic gyre in the western part of the Alboran Sea, extending from southern Spain to northern Morocco [60,61]. Additionally, another anticyclonic gyre is described in the eastern sub-basin, formed by the confluence of incoming Atlantic water and the westward current on the southern side of the gyre [60–62]. These anticyclonic gyres, along with the dynamics between the water masses and winds, create a series of upwellings that can be considered constant, bringing cold deep waters rich in nutrients, thus promoting high primary production in the northern part of the Alboran Sea basin [61,63]. On the other hand, the outflow of the Mediterranean water through the Strait of Gibraltar draws deep waters from the Mediterranean basin and contributes high-salinity water masses to the intermediate and deep circulation of the North Atlantic [64].

The Strait of Gibraltar and Alboran Sea are unfortunately some of the Mediterranean basins with the highest number of cumulative impacts, including climate change, pollution, fishing, maritime traffic, and highly invasive alien species, among others [65]. On the other hand, there are ca. 40 areas of ecological and conservation interest in the Strait of Gibraltar and Alboran Sea, which include Marine Protected Areas and Key Biodiversity Areas, with 23 located in the northern sector [66]. These protected areas are an opportunity to concentrate efforts and resources for protecting marine wildlife and benthic habitats, being a reservoir for species that can seed other areas through the export of adult biomass (spillover effect) and/or larvae (recruitment effect) [66–69]. These areas are of special importance because they contain a good representation of habitats listed in the Habitats Directive [70], such as coastal lagoons, *Posidonia* beds, reefs, sandbanks, etc., and also harbour important populations of species that are included in lists of protection, such as *Patella ferruginea*, Gmelin, 1791, *Madrepora oculata,* Linnaeus, 1758, *Charonia lampas* (Linnaeus, 1758), *Corallium rubrum* (Linnaeus, 1758), or the echinoid *Centrostephanus longispinus* [66], which is the focal species of the present study.

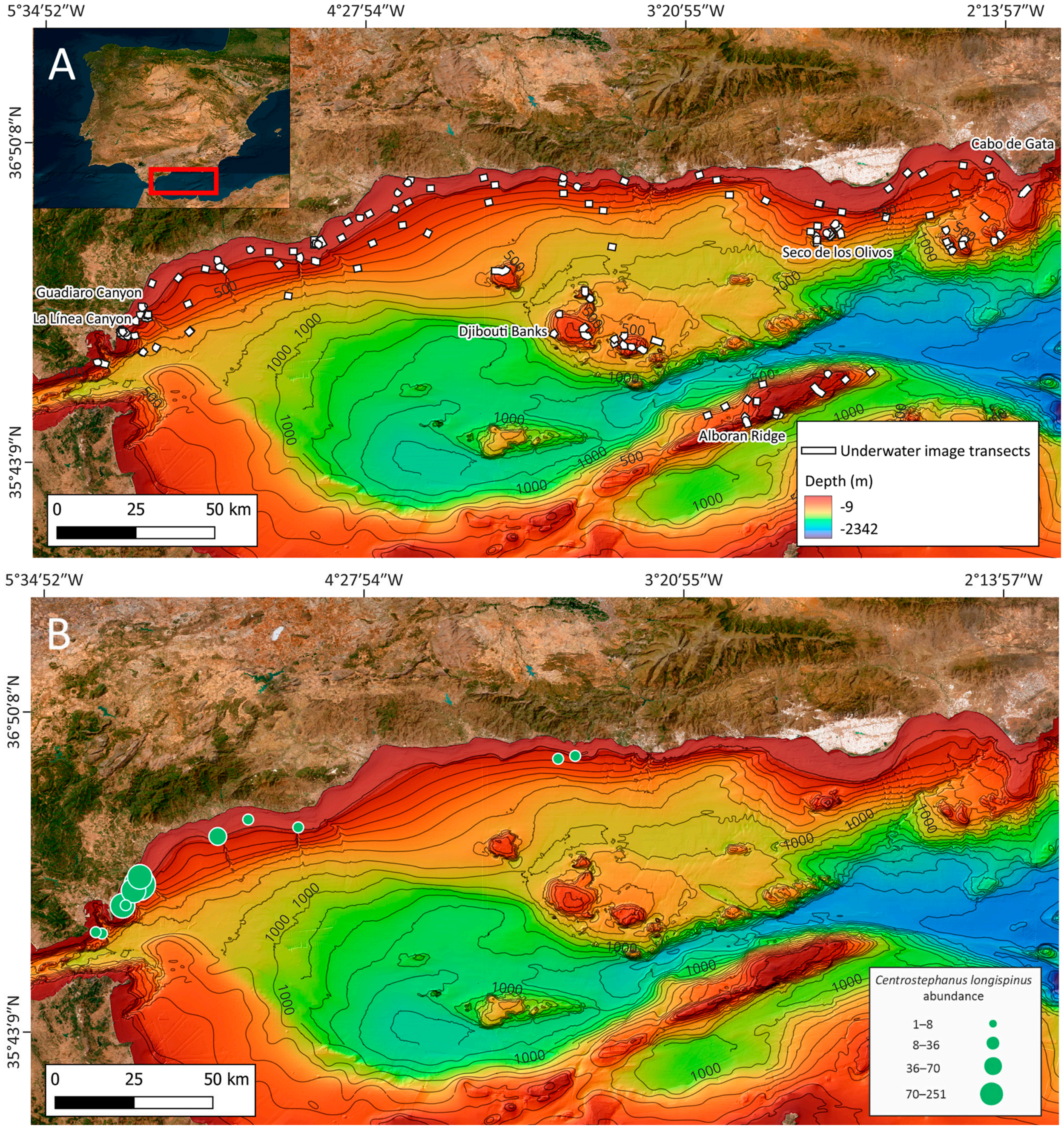

Figure 1. (**A**): Underwater image transects corresponding to the CIRCAESAL expeditions across the northern Strait of Gibraltar and Alboran Sea, as well as in some seamount-like features (Djibouti Banks, Seco de los Olivos) and the Alboran Ridge. (**B**): Abundance of *Centrostephanus longispinus* detected in each underwater image transect. Bathymetry colours vary according to depth, and negative values indicate depth below sea level; 100 m separated isobaths are marked with the 500 m and 1000 m depth isobaths indicated.

2.2. Underwater Image Acquisition

Quantitative data of *C. longispinus* in the Alboran Sea were obtained in daylight during three CIRCAESAL expeditions carried out by *Instituto Español de Oceanografía* (IEO-CSIC). Nevertheless, the collected data could be considered semi-quantitative and underestimated in some explored rocky bottoms with abundant crevices where *C. longispinus* usually hides and also because of the limitations of deep-sea underwater imagery equipment for monitoring crevice organisms [71]. The expeditions were carried out within the framework of the Marine Strategy Framework Directive (Directive 2008/56/CE), and the monitoring activities of circalittoral and bathyal benthic habitats were conducted under Descriptor 1 (Biodiversity) and Descriptor 6 (Seabed) frameworks. The CIRCAESAL expeditions have the objective of assessing the health status of the circalittoral and bathyal benthic habitats and their key species in the Strait of Gibraltar and northern Alboran Sea. The present study uses data from the expeditions conducted in July–August 2021, November 2023, and July 2024 (CIRCAESAL 0721, 1123, and 0524, respectively). During those expeditions, transects of underwater images were obtained by a Remotely Operated Vehicle (ROV LIROPUS 2000) and a photogrammetric sledge (TASIFE) in 14 sectors of the northern Strait of Gibraltar and the Alboran Sea. Many of these transects were located in Marine Protected Areas from the Natura 2000 Network or Marine Reserves (e.g., "*Estrecho Oriental*" SAC—Special Area of Conservation, the platform of the Alboran Ridge), while others were situated in areas with moderate to high levels of human activity and fishing pressure, such as the Málaga and the Algeciras Bays. The CIRCAESAL 0721 expedition consisted of 33 ROVs and 3 TASIFE transects, while the CIRCAESAL 1123 expedition carried out 55 TASIFE transects, and the CIRCAESAL 0524 expedition included 29 transects using the ROV, and an additional 11 transects were carried out using the TASIFE (*Instituto Español de Oceanografía, Centro Oceanográfico de Canarias*, Spain) (Table S1). High-resolution and georeferenced underwater images obtained with those two devices were analysed for identifying and quantifying *C. longispinus* individuals of different size classes as well as key benthic and demersal species, substrate types, and seafloor features, as well as human activity indicators. Underwater images were acquired using a HiPAP system for precise submarine navigation. Generally, the images were taken 0.5 to 2.5 m above the seafloor during dives lasting approximately 1 to 8 h for ROV dives and 20 min to 1.3 h for TASIFE dives, at depths ranging from 17 to 856 m. Laser points were employed (for scaling with 10 cm separation for ROV; 10 and 25.5 cm for TASIFE) to measure certain biological features (e.g., size of *C. longispinus*) and seafloor characteristics (e.g., substrate type) within each transect.

2.3. Underwater Image Processing

The 131 underwater imagery transects from all the corresponding dives were processed and georeferenced using the software VLC (VideoLAn Client) version 3. 0. 21 and the OFOP (Ocean Floor Observation Protocol) version 3.3.9. For each transect all the individuals of *C. longispinus* were counted and classified in different categories based on their size, type of substrate where they were located, seafloor roughness, micro-habitat (referring to where exactly each sea urchin was located), and coverage of key benthic structuring species. The size of each hatpin urchin was classified as small (1/3 of the maximum size), medium (2/3 of the maximum size), or large (2/3–3/3 of the maximum size), with a maximum size of 6 cm for the test diameter, as stipulated in [2]. It should be noted that these selected size classes are theoretical and do not correspond to reproductive aspects (i.e., gonad maturity, reproductive individuals, etc.). The type of substrate detected in the images was categorised into mud, sand, pebbles–boulders, or bedrock, while the seafloor roughness was categorised into low (generally flat surfaces without crevices) or high (heterogeneous surfaces with moderate to high availability of crevices). The coverage of key benthic structuring species was divided into three categories: low (less than 10 colonies or individuals/m^2), medium

(10–20 colonies or individuals/m^2), and high (more than 20 colonies or individuals/m^2). For the micro-habitat where each hatpin urchin individual was detected, 4 categories were used: (1) on the ledge or under rocks, (2) in rock crevices, (3) between rock and sedimentary substrates, and (4) on the rock outside crevices. Depth and also temperature and salinity where each hatpin urchin was detected were annotated and recorded from the CTD of the ROV. Additionally, data from human activities where each hatpin urchin was detected (e.g., lost longline gears, litter, etc.) and the presence of invasive species (mainly the brown algae *Rugulopteryx okamurae* (E.Y.Dawson) I.K.Hwang, W.J.Lee & H.S.Kim, 2009) were recorded as well.

The density of *C. longispinus* was estimated from the number of individuals detected in each photogram and the area of the photogram, which was calculated using the software ImageJ version 1.54. Density estimations were then standardised to 1 m^2. For the analysis, only data obtained in photograms with a similar area and taken 1 m from the seafloor were used in order to avoid the extreme density values from zoomed-in photograms or the low ones from zoomed-out photograms.

The variability in *C. longispinus* density values regarding size classes, substrates, depth strata, seafloor roughness, micro-habitats, and coverage of key benthic structuring species was assessed using a non-parametric test (Kruskal–Wallis). A pair-wise test using the non-parametric U Mann–Whitney test was also applied to ascertain patterns of differences among categories. In relation to the micro-habitat and the diel behavioural patterns of *C. longispinus*—most notably its preference to occupy crevices during daylight hours in the infralittoral and upper circalittoral zones, as well as its pronounced preference for rocky substrates in the lower circalittoral—separate datasets were utilised to enable a stratified analysis of different depth strata. The proportion of individuals of different size classes detected in different substrate types, micro-habitats, seafloor roughness, and coverages of key benthic structuring species in relation to different depth strata (infralittoral and upper circalittoral, with high–moderate irradiance; lower circalittoral with low irradiance; and bathyal with very low irradiance) was tested using a parametric Z-test for proportions. All statistical analyses were performed using the software IBM SPSS (Statistical Package for the Social Sciences) version 20.

3. Results

3.1. General Results and Comparissons of Proportions in Relation to Depth and Seafloor Features

In the present study, 131 transects of underwater images were conducted during daylight on deep infralittoral, circalittoral, and bathyal bottoms, from the Strait of Gibraltar to Cabo de Gata and also including seamounts and the Alboran Ridge (Figures 1 and 2). The bathymetric range explored ranged from 17 to 856 m, and the explored areas included various bottom types (from rocky to muddy bottoms, as well as mixed and detritic bottoms). A total of 524 individuals of *Centrostephanus longispinus* were detected in the analysed underwater images (Figure 2). Nevertheless, the hatpin urchin was only found in 13 transects, corresponding to ca. 10% of the studied underwater images, which may still indicate the rarity of the species in the studied area. Most individuals (98.66%) were detected in the circalittoral bottoms (and occasionally bathyal bottoms) of the western sector of the Alboran Sea (from the Strait of Gibraltar to the bay of Málaga), while the remaining ones were detected in the central sector (from the bay of Málaga to Motril, Granada) (Figures 1 and 2). Those individuals were found in water masses with temperatures between 13 and 16 °C and salinity values ranging from 37 to 38.2 ppm.

The majority of individuals corresponded to medium sizes (440 individuals, 83.97%), followed by small-size (56 ind., 10.69%) and large-size individuals (28 ind., 5.34%), and this was consistent across different depth strata (Figure 3). No significant differences were detected in the proportion of small and medium individuals across depth strata (two proportion Z-test: Z values between −0.68 and 0.01, $p > 0.05$ in all comparisons). However, a trend towards a higher proportion of large individuals in the infralittoral and upper circalittoral when compared to the lower circalittoral and bathyal was observed, although no significant differences were detected (Z values between 0.18 and 1.58, $p > 0.05$ in all comparisons).

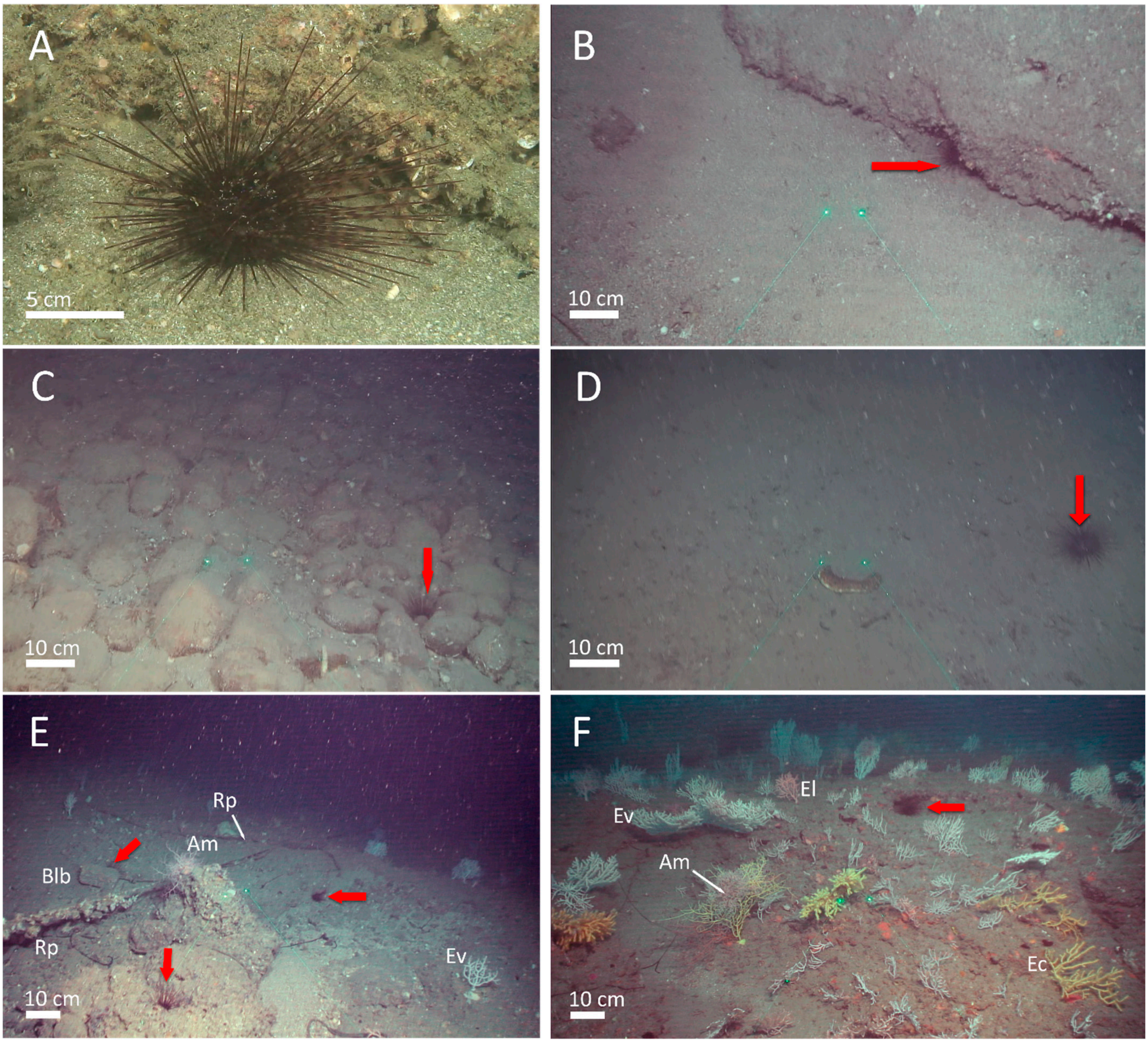

Figure 2. (**A**): Detail of a medium-size *Centrostephanus longispinus*; 130 m depth. (**B**): *C. longispinus* individual between rocks and sedimentary substrates; 116 m depth. (**C**): *C. longispinus* individual found on pebbles–boulders; 116 m depth. (**D**): *C. longispinus* individual detected on muddy bottoms; 245 m depth. (**E**): evidence of anthropogenic activity, mainly of cables and ropes used in longline fisheries in areas with *C. longispinus*; 109 m depth. (**F**): *C. longispinus* individual detected in an area with high coverage of key benthic structuring species; 67 m depth. Red arrows indicate individuals of *C. longispinus*; Blb: ballast block; Rp: Ropes and cables; Am: *Astrospartus mediterraneus*; Ev: *Eunicella verrucosa*; Ec: *Eunicella cavolini*; and El: *Eunicella labiata*.

Regarding bathymetric ranges, most individuals were detected in the shallowest strata of the present study between 48–75 m (198 individuals, 37.79%) and 75–100 m (167 ind., 31.87%). Fewer individuals were detected in those strata ranging from 100 to 125 m (73 ind., 13.93%), 125 to 150 m (46 ind., 8.78%), 150 to 175 m (20 ind., 3.82%), and 175 to 200 m (16 ind., 3.05%). Finally, four individuals (0.76%) were detected at depths greater than 200 m (corresponding to the bathyal zone) in La Línea and Guadiaro submarine canyons.

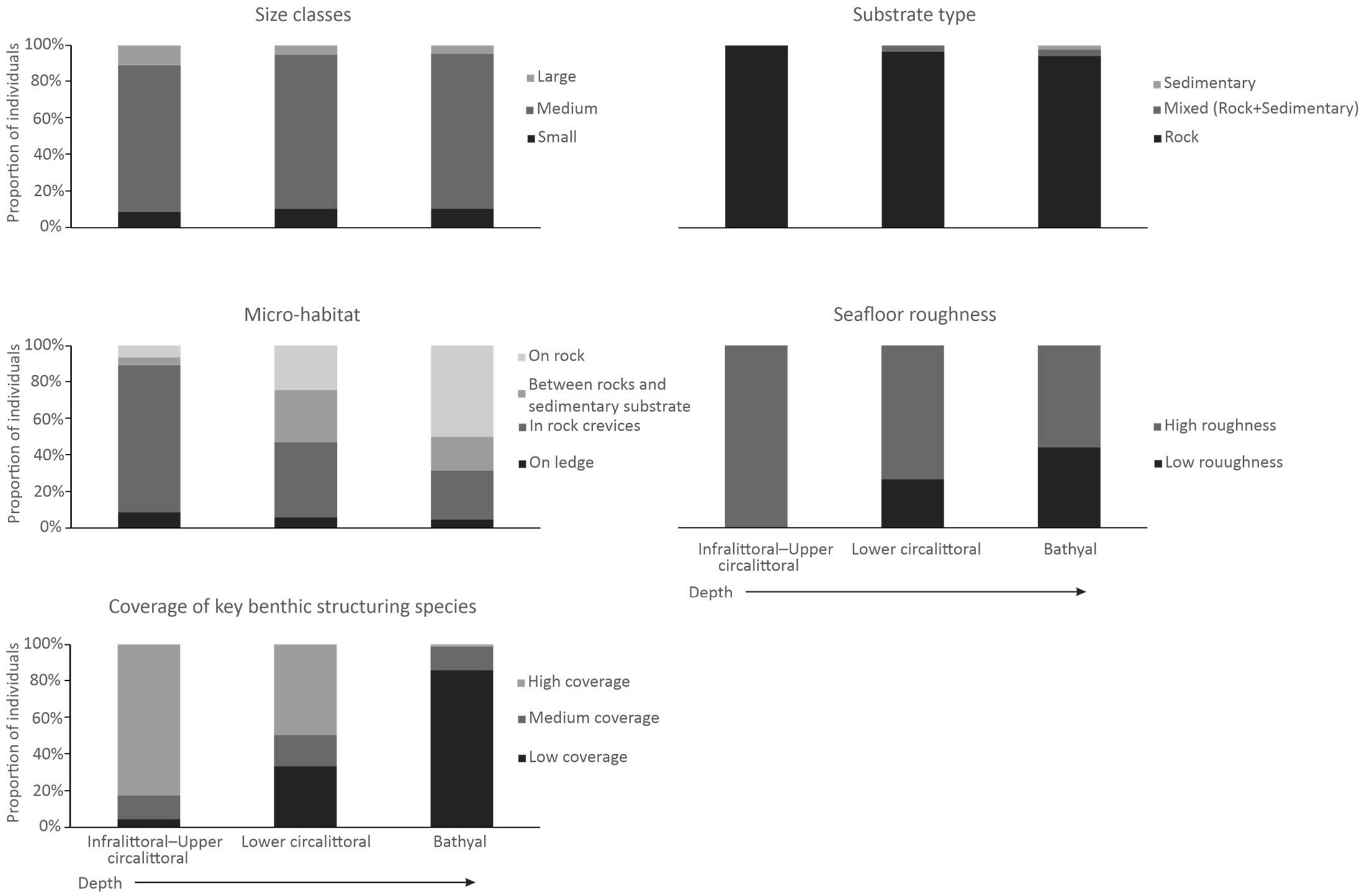

Figure 3. Proportion of individuals from different depth strata of the northern Strait of Gibraltar and Alboran Sea in relation to different size classes, main substrate types, micro-habitats, seafloor roughness, and coverages of key benthic structuring species.

Most individuals were detected in transects with a high availability of hard substrates (341 ind., 65.08%) or in those with mixed substrates (hard and sedimentary substrates) (183 ind., 34.92%). In the latter case, most individuals were mainly detected on the hard substrates or adjacent to those. Nevertheless, in one of the transects (DIVE14_ROV12, La Línea Canyon), a small- and a medium-size individual were detected on muddy bottoms. Locally, *C. longispinus* can be very rare, as no or very few individuals were detected in some areas with abundant hard bottoms located in those depth strata where most individuals were generally detected in other areas (e.g., the Alboran Ridge or the platform of the Seco de los Olivos Seamount, located in the northeast Alboran Sea).

The proportion of individuals associated with rock was consistently and significantly high in all depth strata considered (infralittoral and upper circalittoral, lower circalittoral, and bathyal), but no significant differences were detected in the proportion across depth strata (two proportion Z-test: Z values between 1.09 and 1.66, $p > 0.05$ in all comparisons) (Figure 3). Individuals on mixed substrates were only present on the deep strata, but no significant differences were detected (Z values between -1.28 and -0.07, $p > 0.05$ in all comparisons). However, individuals on sedimentary substrates were exclusively detected in the bathyal depth range, showing a significantly higher proportion when compared to the shallower strata ($Z < -3.01$, $p < 0.005$ in all comparisons).

Regarding the micro-habitat preference, the proportion of individuals on ledges was consistently low and did not differ significantly among the depth strata (Z values between 0.45 and 0.92, $p > 0.05$ in all comparisons) (Figure 3). Nevertheless, a significant decline of the proportion of individuals in rock crevices with depth was detected, with maxima in the infralittoral and upper circalittoral stratum ($Z > 2.46$, $p < 0.05$ in all comparisons). In contrast, the proportion of individuals between rocks and sedimentary substrates was significantly lower in the infralittoral and upper circalittoral when compared to both the lower circalittoral and bathyal strata ($Z < -2.27$, $p < 0.05$ in all comparisons), with no significant difference between the lower circalittoral and bathyal strata ($Z = 1.91$, $p = 0.05$). Finally, the proportion of individuals on rock significantly increased with depth, with maxima in the bathyal stratum ($Z < -2.74$, $p < 0.01$). In conclusion, individuals were significantly more abundant in crevices than in any other micro-habitat across all depth strata. This pattern was consistent in the infralittoral–upper circalittoral ($Z > 2.83$, $p < 0.005$ in all comparisons), lower circalittoral ($Z > 2.08$, $p < 0.05$), and bathyal strata ($Z > 2.69$, $p < 0.01$).

Regarding seafloor roughness, proportions of individuals in areas with low seafloor roughness were significantly higher in the lower circalittoral and bathyal strata than in the infralittoral and upper circalittoral ($Z < -3.21$; $p < 0.005$ in all comparisons) (Figure 3). Conversely, the proportion of individuals in areas with high seafloor roughness was significantly higher in the infralittoral and upper circalittoral than in both the lower circalittoral and bathyal strata ($Z > 3.21$, $p < 0.005$ in all comparisons).

Centrostephanus longispinus individuals were mainly detected in two habitat types, classified based on their resemblance to those of the "*Lista Patrón de Hábitats Marinos*" (LPHM) (Marine Spanish Habitats List) present in Spain [72], the Barcelona Convention (BC), and EUNIS classifications [73,74]. These were (1) infralittoral and circalittoral cobbles and gravels (LPHM 030401; BC: MC4.5 Mediterranean circalittoral mixed sediments; EUNIS: A5.4—sublittoral mixed sediments) and (2) non-concretionary circalittoral rock dominated by invertebrates with *Eunicella verrucosa* (Pallas, 1766) (LPHM 0302022304; BC: MC1.519 circalittoral rock with dominance of invertebrates with *Eunicella verrucosa*; EUNIS: A4.26—Mediterranean coralligenous communities moderately exposed to hydrodynamic action). Among the species detected with the hatpin urchin, the most dominant ones were generally gorgonians (*E. verrucosa, Eunicella cavolini* (Koch, 1887) and *Eunicella labiata* (Thomson, 1927)), the ophiuroid *Astrospartus mediterraneus* (Risso, 1826), and several unidentified encrusting and globular sponges (Figure 2).

Regarding the coverage of key benthic structuring species, a significantly higher proportion of *C. longispinus* individuals was found in areas with a high coverage of key benthic structuring species in the infralittoral and circalittoral bottoms, with a significant decline in the proportion in both the lower circalittoral and bathyal strata ($Z < -4.04$, $p < 0.001$) (Figure 3). In contrast, an increasing trend of the proportion of *C. longispinus* was detected in areas with a low coverage of key benthic structuring species when increasing the depth, with maxima in the bathyal strata ($Z > 4.25$, $p < 0.001$). The proportion of individuals in the medium coverage of key benthic structuring species was more evenly distributed across strata, with no significant differences detected (Z values between -0.71 and 0.99, $p > 0.05$). In conclusion, a significantly high proportion of individuals of *C. longispinus* was detected in areas with a high coverage of key benthic structuring species in the infralittoral and upper circalittoral stratum ($Z > 2.65$, $p < 0.01$) and in areas with a low coverage of key benthic structuring species in the bathyal stratum ($Z > 2.65$, $p < 0.01$).

Most of the hatpin urchins were detected in areas with low anthropogenic activity (386 ind., 73.66%). Nevertheless, some individuals occurred in areas with remains of longline gears (99 ind., 18.89% on bottoms with longline remains, cables/ropes/lines, and 6 ind., 1.15% on bottoms with longline ballast blocks) and with drifted thalli of the invasive algae *Rugulopteryx okamurae* (43 ind., 8.21%) (Figure 2). No damaged individuals or individuals entangled in longline cables were detected in the analysed underwater images. Nevertheless, one individual was detected in close contact with a ballast block used in longline fishing.

3.2. Density Estimations and Comparisons in Relation to Depth and Seafloor Features

The mean density of *C. longispinus* for the circalittoral and bathyal bottoms of the northern Alboran Sea and Strait of Gibraltar was 0.76 ± 0.032 ind/m^2 (individuals/m^2), ranging from 0.07 to 3.12 ind/m^2, when excluding the data where the species was absent. The mean density estimations, including areas with no *C. longispinus*, are significantly much lower, >0.001 ind/m^2. In contrast, considering only transects with *C. longispinus* on hard substrates between 48 and 100 m depths, the estimated density is still low but is a bit higher between 0.01 and 0.001 ind/m^2.

Density values were high for small-size individuals of *C. longispinus* (0.81 ± 0.089 ind/m^2), followed by medium-size (0.69 ± 0.031) and large-size ones (0.54 ± 0.073) (Figure 4). Nevertheless, no significant differences in the density were detected between size classes (Kruskal–Wallis non-parametric test; X^2 = 3.346; $p > 0.05$).

Density values were significantly higher in the depth strata between 75 and 100 m (0.94 ± 0.065 ind/m^2) and between 48 and 75 m (0.75 ± 0.047) in comparison with the deeper strata between 100 and 200 m (0.63 ± 0.084), 125 and 150 m (0.595 ± 0.114), 150 and 175 m (0.373 ± 0.078), and 175 and 200 m (0.66 ± 0.217) (Kruskal–Wallis non-parametric test; X^2 = 26.121; $p < 0.001$) (Figure 4). Similar significant trends were detected for medium and large individuals, generally with high densities in the 48–75 m and 75–100 m depth strata, with significant differences in the medium size class in the 75–100 m depth strata when compared with the other strata, except the 175–200 m depth strata (non-parametric U Mann–Whitney test, U > 186; $p < 0.001$) (Tables S2–S4). Small-size individuals displayed higher densities in the 100–125 m and 125–150 m depth strata.

In hard bottoms, mean density values of *C. longispinus* were significantly higher in areas where the main substrate type was pebbles–boulders (1.16 ± 0.107 ind/m^2) compared to areas with bedrock (0.71 ± 0.033) (Kruskal–Wallis non-parametric test; X^2 = 19.151; $p < 0.001$) (Figure 4). Regarding size classes, only medium-size individuals displayed significantly larger densities in bedrock (0.75 ± 0.790) when compared to pebbles–boulders (1.22 ± 0.119) (non-parametric U Mann–Whitney test, U = 1831.00; $p < 0.001$) (Figure 4). Densities of *C. longispinus* were significantly lower and generally null in sedimentary bottoms (Kruskal–Wallis non-parametric test; $p < 0.001$), as commented previously.

Regarding micro-habitats, density values for *C. longispinus* individuals were higher for the micro-habitat categorised as "on ledge" (0.80 ± 0.129 ind./m^2) and lower for "on rock" (outside crevices) (0.61 ± 0.484), with intermediate values for "between rock and sedimentary substrate" (0.77 ± 0.067) and "in rock crevices" (0.66 ± 0.044) (Figure 4). Nevertheless, no significant differences in the density were detected concerning the four micro-habitat categories (Kruskal–Wallis non-parametric test; X^2 = 3.647; $p = 0.302$) (Figure 4). As commented previously, the density estimations of individuals for "in crevices" and "on ledge" could be underestimated due to the cryptic behaviour of *C. longispinus* and the limitations of exploring those micro-habitats with the ROV or the photogrammetric sledge.

When comparing mean density values of *C. longispinus* among micro-habitats and across depth strata (infralittoral–upper circalittoral, 17–60 m depth, vs. lower circalittoral–Bathyal, >60 m depth), the highest densities in the shallow strata were observed "on ledge" (1.16 ± 0.211 ind./m^2), followed by "in rock crevices" (0.80 ± 0.071) and "on rock" (0.60 ± 0.133), whereas the lowest value was recorded "between rocks and sedimentary substrate" (0.13 ± 0.000). In the deep stratum, density values were highest "between rocks and sedimentary substrate" (0.79 ± 0.067), intermediate "on rock" (0.62 ± 0.053) and "in rock crevices" (0.64 ± 0.054), and lowest "on ledge" (0.76 ± 0.142) (Figure 5). Nevertheless, no significant differences were detected within either the shallow strata (Kruskal–Wallis non-parametric test; $\chi^2 = 5.787$; $p = 0.122$) or the deeper strata (Kruskal–Wallis non-parametric test; $\chi^2 = 5.067$; $p = 0.167$). In contrast, the analysis of each micro-habitat across depth strata revealed significant differences only for the "in crevices" category (non-parametric U Mann–Whitney test, U = 1077, $p < 0.005$), with higher densities recorded in the infralittoral–upper circalittoral strata than in the lower circalittoral–bathyal strata.

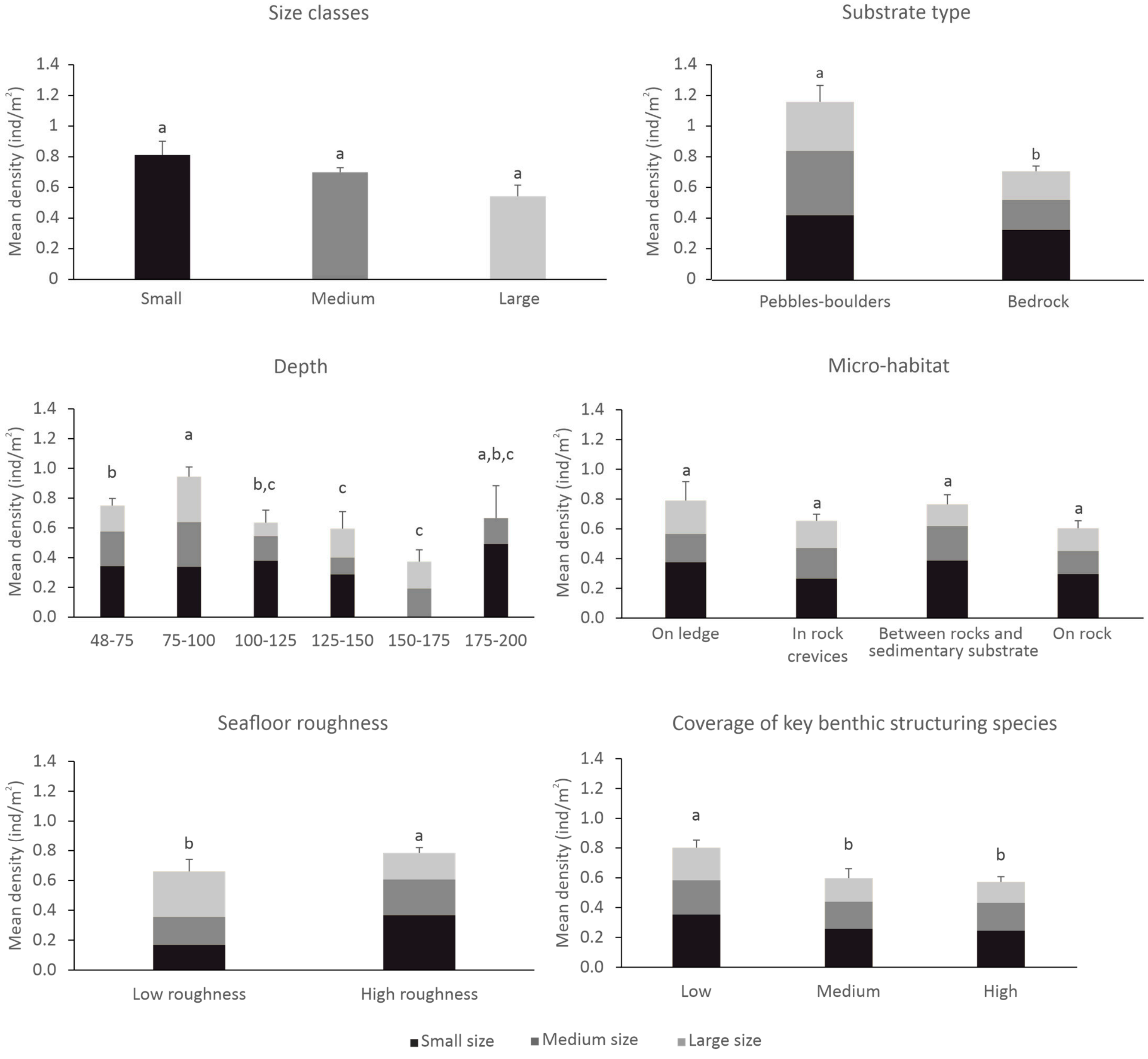

Figure 4. Density of *Centrostephanus longispinus* (individuals/m^2) in infralittoral, circalittoral, and bathyal bottoms of the northern Strait of Gibraltar and Alboran Sea in relation to different size classes, depth strata, main substrate types, micro-habitats, seafloor roughness and coverages of key benthic structuring species. Different letters indicate significant differences obtained in pair-wise comparisons using the non-parametric U Mann–Whitney test ($p < 0.05$). Mean ± standard error. Contribution of the different size classes of *C. longispinus* are also represented: small (1/3 of the maximum size), medium (2/3 of the maximum size), and large (2/3–3/3 of the maximum size), with the maximum size of the test diameter being 6 cm, as stipulated in [2].

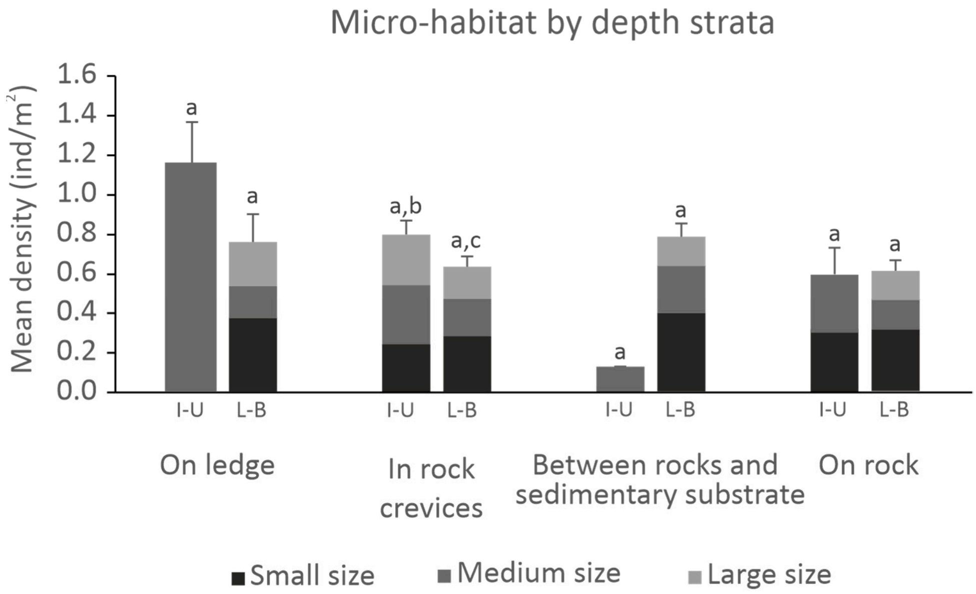

Figure 5. Density of *Centrostephanus longispinus* (individuals/m^2) in infralittoral, circalittoral, and bathyal bottoms of the northern Strait of Gibraltar and Alboran Sea in relation to different micro-habitats and depth strata (I-U: infralittoral–upper circalittoral vs. L-B: lower circalittoral–bathyal). Different letters indicate significant differences obtained in pair-wise comparisons between depth strata within each microhabitat using the non-parametric U Mann–Whitney test ($p < 0.05$). Mean + standard error. Contributions of the different size classes of *C. longispinus* are also represented: small (1/3 of the maximum size), medium (2/3 of the maximum size), and large (2/3–3/3 of the maximum size), with the maximum size of the test diameter being 6 cm, as stipulated in [2].

Concerning other seafloor features, mean density values of individuals were significantly higher in rocks with high seafloor roughness (0.78 ± 0.035 ind./m^2), when compared to rocks with low seafloor roughness (0.66 ± 0.080) (Kruskal–Wallis non-parametric test; $X^2 = 5.129$; $p < 0.05$) (Figure 4). Regarding size classes, although higher mean density values were observed for all classes (small: 0.86 ± 0.036; medium: 0.71 ± 0.030; and large: 0.52 ± 0.020), significant differences were only detected in the medium size class when comparing individuals in high-seafloor roughness with individuals in low-seafloor roughness (non-parametric U Mann–Whitney test, U > 1830; $p < 0.001$) (Figure 4).

Combining data obtained at different depths, the mean density values of *C. longispinus* were significantly higher in areas with a low density of key benthic structuring species (0.92 ± 0.062 ind./m^2), when compared to areas with a medium (0.687 ± 0.072) or high (0.65 ± 0.040) density of key benthic structuring species (Kruskal–Wallis non-parametric test; $X^2 = 11.041$; $p < 0.005$) (Figure 4).

In relation to human activities, mean density values of *C. longispinus* were higher in areas with a medium abundance of longlines (0.90 ± 0.300 ind./m^2), followed by areas without them (0.78 ± 0.030) and even with a low abundance of longlines (0.62 ± 0.060). Nevertheless, no significant differences in the density of *C. longispinus* were detected in relation to the abundance of longlines (Kruskal–Wallis non-parametric test; $X^2 = 3.647$; $p > 0.05$). Mean density values of *C. longispinus* were significantly higher in areas with no long-line ballast blocks (0.766 ± 0.030 ind./m^2) than those areas with the ballast blocks (0.28 ± 0.098) (Kruskal–Wallis non-parametric test; $X^2 = 4.254$; $p < 0.05$).

Regarding invasive alien species, mean density values of *C. longispinus* were significantly higher in areas with a small presence of drifted thalli of the invasive algae *Rugulopteryx okamurae* (1.31 ± 0.119 ind./m^2) than those areas with a medium presence (1.21 ± 0.494) and also those without the invasive algae species (0.71 ± 0.03) (Kruskal–Wallis non-parametric test; $X^2 = 24.567$; $p < 0.001$). A similar trend was also detected in pair-wise comparisons using the non-parametric U Mann–Whitney test ($U = 1275.00$; $p < 0.001$ in all comparisons).

4. Discussion

The present study has dealt with the distribution, density, and population structure of *Centrostephanus longispinus* from low infralittoral to bathyal bottoms of the northern Strait of Gibraltar and Alboran Sea using underwater imagery techniques. To date, research on the distribution of this species has been limited throughout the Mediterranean Sea, and, therefore, information is also scarce in the study area, with optimal populations reported at *El placer de las bóvedas*, a promontory located on the west coast of Málaga, southern Spain [6,25,28]. Stable populations, with high numbers of individuals, have also been reported in southern France (near Marseille), the Gulf of Naples, and the rocky escarpments of southeastern Menorca [6,19,22,24,29,43]. On the other hand, several studies of the hatpin urchin have focused on its pigment cells [75–78] rather than on providing population density values or insights on the ecological role of this echinoid. The lack of knowledge about its distribution area may be due to the absence of data rather than the actual absence of the species, especially when considering unstudied populations located in the circalittoral and bathyal bottoms. Moreover, the fragmented distribution can also be related to its daily behaviour and its concentration in crevices during daylight hours in the infralittoral and upper circalittoral zones and the limitations involved with exploring these micro-habitats using scuba diving or the traditional deep-sea underwater imagery equipment [6,71]. Additionally, the apparent rarity of *C. longispinus* may be due to several factors—either because it can also be a component of the circalittoral or deep rocky environments that have generally been prospected minimally or because it is a relict species, and its populations are in regression due to natural causes [28,79]. In the present study, *C. longispinus* was not detected in some pristine areas with very high abundances of branching corals and gorgonians, such as the Alboran Ridge, Seco de los Olivos (Chella Bank), and the surroundings of the Alboran Island [46], where it remains an uncommon species [80]. It is possible that the high complexity of the habitat complicated the detection of *C. longispinus* individuals in the present study using underwater images, so further exploration would be desirable in those areas.

Previous records on *C. longispinus* mostly documented the infralittoral zone, with just a few anecdotal records for deeper areas [6,43,81]. According to a previous study [28], areas below the 50–60 m depth could host the largest densities of this echinoid species due to the presence of strong currents. This supports the fact that one of the highest density values detected in the present study is found in the depth strata between 75 and 100 m, with significant differences compared to the other depth strata. However, the highest density values of the present study correspond to the strata between 48 and 75, which is more consistent with the records previously reported in the literature [20,22,28]. Regarding size classes, a similar trend was detected in the medium-size individuals with significantly higher density values in the 75–100 m depth strata, while the small-size individuals showed higher density values in deeper strata, between 100 and 150 m. This could serve as evidence supporting the idea that reproductive populations are found between 60 and 130 m depths [6]. Moreover, at the deepest strata, no large individuals were detected and at the 150–175 m depth strata, no small individuals were detected. When comparing individual proportions among the depth strata, no significant differences were detected, with the medium-size individuals representing the greatest percentage in all strata when compared to both small and large individuals. This study is one of the few to assess the population structure in relation to size classes of *C. longispinus* using a Remotely Operated Vehicle (ROV). The use of an ROV allows us to access deeper areas where the species has been less studied, extending our knowledge of its ecological niche, as has been proven with *C. rodgersii* [82] and to report the presence of reproductive populations at such depths.

Four individuals were found very deep, between 200 and 250 m, and were located inside La Línea Canyon and the head of the Guadiaro Canyon. Notably, these individuals were also the only ones found on muddy bottoms. This could be the result of transport processes in the submarine canyons, highlighting the important role that canyons play for sediment, organisms, and litter transport from the continental shelf to the bathyal zone [83–86]. In previous studies other individuals detected in the bathyal zone (208 m depth) were obtained by dredging at the Josephine bank off the coast of the Iberian Peninsula, in the Atlantic Ocean [22], and using a beam trawl at a ca 400 m depth in the northern slope of the Gulf of Cádiz—where some MOW erosive channels occur that may serve as pathways for transporting water masses, particles, and organisms (González-García, pers. comm)—and 500 m in front of Motril, at the Granada Coast [36]. These particular cases can be attributed to water mass dynamics and transport processes driven by bottom currents. Compared to other species of the genus, *C. longispinus* seems to have a deeper bathymetric range, like *C. tenuispinus* [87], with the rest of the species more closely linked to infralittoral areas (*C. coronatus* between 3 and 10 m, *C. rodgersii* between 5 and 30 m) [3,88]. The wide depth range of *C. longispinus* may somehow be linked to its wide distributional range (spanning from temperate to tropical areas) and flexibility to live in different environmental conditions. In the present study, the temperature of the water masses where the individuals were detected ranged from 13 to 16 °C, matching the temperature range reported in the literature and highlighting the stenothermal nature of the species [2,6,22]. The wide depth range and distribution of the species may also explain the limited knowledge that is still available for this echinoid, since a large part of its populations occur in the circalittoral zone.

Despite the fact that *C. longispinus* is widespread throughout the Mediterranean [6,28], the densities recorded in the present study, and more specifically at the eastern Strait of Gibraltar, have been observed to be the highest to date. This finding is in accordance with the species distribution model developed by [8]. The Strait of Gibraltar is a transition zone between the Atlantic Ocean and the Mediterranean Sea and is exposed to complex and strong hydrodynamic conditions [89–91]. The interaction of water masses together with wind dynamics produces upwelling processes, which contribute to a process of fertilisation of the coastal zone, increasing the production and food supply for larger trophic components and key benthic structuring species of the ecosystem [92]. These peculiar environmental conditions, with the supply of nutrients, could contribute to the development of populations of suspension feeders and of organisms that may benefit from food particle fluxes [93]. Moreover, planktotrophic larvae could benefit from the flux of these particles, resulting in a significant recruitment for some species [94]. It should be noted that the influence of Atlantic water currents could increase the larval abundance, and the western Atlantic gyre may act as a hydrodynamic trap, keeping the larvae close to the coast [95]. The high density values detected around the northern Strait of Gibraltar and western Alboran Sea, with a high presence of small-size individuals, may support this hypothesis, suggesting that this sector could potentially constitute an important reproductive hot spot for *C. longispinus* in the Mediterranean Sea, even though the species is widespread throughout the basin. Further and similar studies obtaining density estimations of *C. longispinus* across the Mediterranean and eastern Atlantic may be helpful for detecting other important hotspots for this species.

One of the largest and most dense populations of *C. longispinus* was detected at the head of the Guadiaro Canyon. This submarine canyon is located near the Special Area of Conservation (SAC) "*Fondos marinos del estuario del río Guadiaro*", in the western part of the Guadiaro River, between the provinces of Málaga and Cádiz (northwestern Alboran

Sea) [66]. Another important population was detected in the "*Estrecho Oriental*" SAC, situated close to the Guadiaro Canyon, in the northeastern part of the Strait of Gibraltar, bordering the Gibraltar Rock and La Línea de la Concepción (Cádiz) [66]. Although Guadiaro Canyon is close to those SACs, the head of the canyon itself is currently not under any form of protection. Given that this area hosts one of the largest *C. longispinus* populations recorded in the northern Alboran Sea to date, its inclusion within the "*Estrecho Oriental*" SAC should be considered. In addition, the second largest population of the species occurred in the SAC "*Estrecho Oriental*", emphasising the importance of these Marine Protected Areas for the conservation of this and other species, where some potential threats such as different fishing activities (trawling, longline, etc.) are regulated.

According to the literature and the present study, the hatpin urchin has been generally found on rock and coralligenous habitats, but there are also some records in *Posidonia oceanica* meadows [6,9,19,24,81]. The present study detected a higher proportion of individuals and higher density values of individuals on hard substrates with a higher complexity (high seafloor roughness). An interesting trend was detected in the deep strata, where a higher proportion of individuals could occur in mixed and sedimentary substrates with a low seafloor roughness and coverage of key benthic structuring species. Experimental evidence from previous research [14,96] demonstrated that when boulder refuges are created, *C. rodgersii* individuals preferentially occupy these refuges over forest like habitats. Similarly, other studies indicate that the diadematids have a greater reliance on shelter in comparison to other echinoid species [80,97,98]. This evidence supports the trend detected in the shallowest strata (infralittoral and upper circalittoral), in which *C. longispinus* individuals of all size classes have significantly higher density values in areas with greater habitat complexity, specifically in pebble–boulder and high seafloor roughness areas, and larger individuals could rely less on high seafloor complexity (when compared to medium and small individuals) as they have higher density values for low seafloor roughness. Such habitat complexity provides better shelter opportunities, a factor on which this and other similar echinoid species heavily relies. Little is known about the ecology of *C. longispinus* at large depths [8,28,29,41], but considering its diel behaviour detected in the infralittoral, with a preference for hiding in crevices during daylight [1,3,22], it is possible that at greater depths this echinoid may be less sensitive to light changes and is more flexible, expanding its ecological niche to other bottom types.

In relation to the micro-habitat, the higher density values corresponded to the "on ledges" category, followed by "between rocks and sedimentary substrate", "in rock crevices", and, finally, "on rocks outside crevices". This finding aligns with the ecological niche of this species, suggesting a preference for crevices or habitats with some level of complexity that serve as refuges [6,18]. This trend has also been detected in other *Centrostephanus* species that generally occur in infralittoral rocky reefs [3,71,87,96,99,100]. When comparing the micro-habitat preference of *C. longispinus* across depth strata, individuals were more frequently associated with ledges and crevices in the infralittoral and upper circalittoral zones, but they were detected less in these micro-habitats with increasing depths. In the deepest strata they were more often found in exposed micro-habitats such as between rocks and sedimentary substrate or on rocks. This depth-related shift suggests that individuals in the infralittoral and upper circalittoral zones, being more dependent on light, exhibit more cryptic behaviour, as is known for the *Centrostephanus* genus [3,88,96,101,102], whereas they tend to be less concealed and occupy more open habitats in the deeper strata. This is reinforced by the fact that the bathyal strata, in particular, showed the greatest proportion of individuals on rock, with significant differences compared to the shallower depth strata. Moreover, most *C. longispinus* individuals of the infralittoral and upper circalittoral zones occurred in areas with a high coverage of key structuring benthic species, reinforcing the hypothesis of a higher need for shelter in the shallow strata when compared to the deep strata, where most *C. longispinus* individuals were detected in areas with a low coverage of key benthic structuring species. In part, the detected trend could be attributed to the limitations of the ROV when acquiring underwater images for studying certain cryptic species as opposed to the increased surveying capability that scuba diving allows in terms of being able to search through crevices, caves, and hollows [71,103]. In addition, the species grazes at night [6,14], whereas the ROV transects were conducted during the day, which may have resulted in more individuals remaining hidden in their refuges due to the species' circadian rhythms and thus going undetected, which is supported by the higher density values and proportion of individuals observed in ledges and crevices in the infralittoral–upper circalittoral stratum, contrasting with the predominance of individuals on rock in the bathyal stratum. Given the high density of *C. longispinus* individuals detected in the present study and the limitations of the ROV and the cryptic behaviour of the species, it must be considered that the density values for some micro-habitats could be underestimated, especially for those occurring on ledges and in crevices. Consequently, the fact that higher proportions of individuals were nonetheless detected in crevices reinforces the hypothesis of a strong ecological reliance on habitat complexity and suggests that circalittoral populations may play an even greater ecological role for this species. Although the data collected for this species in some micro-habitats are to be considered semi-quantitative, particularly in the infralittoral and upper circalittoral rocky bottoms with abundant crevices, the micro-habitat preference trends could even be larger when adding all those individuals occurring in crevices and on ledges that could not be detected in the present study. Moreover, a further study contrasting the density data of *C. longispinus* obtained during daylight and night time hours in both shallow and deep strata could greatly improve the population size estimations and our knowledge on ecological aspects of this species in different parts of its biogeographical distribution.

In general, significantly higher density values were found in areas with a low coverage of key benthic structuring species when compared to those with medium and high coverages. Nevertheless, an opposite trend was detected in different depth strata, with a significantly high proportion of individuals occurring in areas with a high coverage of key benthic structuring species in the infralittoral and upper circalittoral regions, whereas a significantly high proportion of individuals was detected in areas with a low coverage of key benthic structuring species in the deep strata. This supports the hypothesis mentioned before, where the individuals would be more sheltered by the key benthic structuring species, as the coralligenous habitat represents an important component in the *Centrostephanus* ecology [3,6,96,104]. However, the increasing prevalence of individuals in low-coverage habitats with depth suggests that this dependency decreases in deeper strata, where individuals tend to occupy more exposed environments. A similar pattern was detected by [105], where the lowest density of echinoids occurred in an area with the highest coverage of branching corals. In that study, the authors noted that this should not be interpreted as an indication of low echinoderm density but rather as a regulatory component due to the role of corals in providing settlement surfaces and refuge for other species. It should be noted that *C. longispinus* is highly sedentary, with records showing individuals moving only around 2 m over a span of 5 years [22]. As a grazer, this species mainly feeds on encrusting algae and invertebrates [3], and its grazing pressure could also explain why a lower coverage of key benthic structuring species is observed in deep areas where the hatpin urchin is very abundant and may move more because they seem to be less dependent on crevices and shelter. Indeed, the creation of barrens by species of the genus *Centrostephanus* is well documented [3,14,87,99,106]. This possible competition for space and grazing activity, combined with its sedentary nature and the difficulty of movement caused by its long spines in structurally complex habitats (as observed in other sea urchins [107]), should be investigated in areas with different coverages of key benthic structuring species and different depths.

Regarding areas with signs of anthropogenic activity, higher densities and abundance values of hatpin urchins were detected together with low signs of anthropogenic activity. In the specific case of longline fisheries, higher sea urchin densities were observed in areas with medium longline abundances; however, these differences were not statistically significant. Nevertheless, significantly higher densities of *C. longispinus* were detected in the absence of ballast blocks and in areas with a low coverage of the drifted thalli of the invasive algae *Rugulopteryx okamurae*. Despite the effect of trawling activity on echinoids being known [41], the longline fisheries do not have a major impact on echinoids [108], which may indicate the absence of significant differences detected in the presence of this fishing gear. On the other hand, although the presence of ballast blocks (with holes) might appear to increase the structural complexity in the seabed, they are generally avoided by the sea urchins (only one individual was detected on a ballast block). This suggests that the blocks may not increase the availability of hard substrates or crevices that could offer shelter for the hatpin urchins. In any case, this human activity related to longline fisheries should be studied in detail for this and other benthic species since the deployment of blocks has increased greatly in recent decades in some areas of the northern Strait of Gibraltar and Alboran Sea and is producing an acute change in the seafloor composition and structure. Additionally, according to observations by professionals working in the area, the use of baited fishing pots for octopus attracts several species of echinoids, including the hatpin urchin. The impact of this type of fishery should also be further studied, and awareness should be raised among fishermen so that by-catch can be released back into the sea.

In relation to the potential effect of the invasive algae *R. okamurae*, it is well known that the sea urchin prefers areas without this invasive species. Little is known about the effects of the invasive algae *R. okamurae* on the circalittoral and bathyal benthic organisms [65,109], but a high coverage of the drifted thalli could lead to a decline in the biodiversity of the area [110], decreasing the food availability for *C. longispinus* or even hindering the settlement of their larvae. Further research should be carried out to learn more about the effects of longline fisheries and *R. okamurae* coverage, not only for *C. longispinus* but for other invertebrates in general.

5. Conclusions

This study is the first to assess density data and population structure of the Diadematidae *Centrostephanus longispinus* in the Strait of Gibraltar and Alboran Sea, an important biodiversity hotspot within the Mediterranean Sea. The use of underwater imagery has made possible the prospection of deeper rocky areas inaccessible through traditional sampling (e.g., beam trawl or scuba diving), enabling the study of a broader bathymetric range in which the hatpin urchin appears to have its ecological niche.

In the present study, an important population of *C. longispinus* was located in the northeast of the Strait of Gibraltar, with maximum density values of 0.76 ± 0.032 ind./m^2. The oceanographic conditions of this zone—dominated by the western Atlantic gyre, promoting upwelling events and larvae retention near the coast [78]—could be supporting these abundant populations. In addition, the high presence of small individuals suggests that this sector could potentially serve as a significant reproductive population of the hatpin urchin for this part of the Mediterranean Sea. Moreover, this population is located at the head of the Guadiaro Canyon, just outside two different SACs, and should therefore be considered for inclusion within any of those SACs to ensure the protection of this and other detected species.

On the other hand, this study reinforces two hypotheses: that of [20], according to which areas located below depths of 50–60 m harbour the highest densities of this species of echinoid, and that of [8], which suggests that reproductive populations are found between 60 and 130 m depths. It should also be noted that at shallower depths, in the infralittoral and upper circalittoral zones, the species behaves cryptically during daylight hours (when sampling was conducted), often concentrating in crevices and in more structurally complex habitats that provide refuge, as also observed in this and other studies, which may lead to an underestimation of its abundance in those habitats using underwater imagery methods. In deeper strata, however, the species tends to occupy a greater diversity of habitats, increasingly using more exposed ones and relying less on coralligenous habitats, with structuring species indicating a lesser need for shelter. Densities in crevices may therefore be higher than those recorded here, potentially resulting in significant differences in micro-habitat use that could not be fully demonstrated in this study. In fact, previous research has consistently reported greater numbers of individuals in crevices compared to exposed rock [14,87,88,100]. Therefore, it may be interesting to collect data during the night time to obtain a more accurate estimation of the species distribution and ecology but also for the assessment of this species under different directives (Habitat Directive, Marine Strategy Framework Directive) and conventions (Barcelona Convention). The preferred habitat of *C. longispinus* is circalittoral rock dominated by invertebrates with *Eunicella verrucosa*, suggesting that the species' conservation is closely tied to the integrity of coralligenous habitats.

The presence of fishing gear debris (e.g., ballast blocks) as well as a high coverage of the drifted thalli of the invasive algae *Rugulopteryx okamurae* on the seabed appears to have a negative impact on *C. longispinus* densities. However, further and more detailed studies are needed to assess the actual impacts of these pressures on this and other key benthic species in this part of the Mediterranean Sea.

Regarding areas where no individuals were found or where the species was recorded at low densities in the present study, these are mainly located in the eastern Alboran Sea —including sites where previous studies had reported its presence (e.g., *El Placer de las Bóvedas*) and the central Alboran Sea (e.g., Alboran platform). Further surveys should target these areas to determine if the species is still present but was undetected in this study using underwater images or whether it is undergoing a regression.

Despite the findings presented, the ecological knowledge of *C. longispinus* remains incomplete, particularly in the northeastern and southern Alboran Sea. Species distribution models and targeted expeditions in areas predicted to have a high abundance of this echinoid should be prioritised to address existing knowledge gaps on this species.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/d17110758/s1: Tables S1–S4. Table S1: Transects of underwater images from the different expeditions, and the abundances of *Centrostephanus longispinus* individuals in total and separated in size categories. Lat: latitude; Long: longitude; N: abundance of individuals; S: abundance of small individuals; M: abundance of medium individuals; L: abundance of large individuals; Table S2. *p*-values from Mann–Whitney U tests comparing depth strata for Centrostephanus longispinus, for individuals in the small-size category. Bolded values indicate statistically significant differences ($p < 0.05$). X values indicate the absence of individuals on that depth strata.; Table S3. *p*-values from Mann–Whitney U tests comparing depth strata for Centrostephanus longispinus, for individuals in the medium-size category. Bolded values indicate statistically significant differences ($p < 0.05$). X values indicate the absence of individuals on that depth strata.; Table S4. *p*-values from Mann–Whitney U tests comparing depth strata for Centrostephanus longispinus, for individuals in the large-size category. Bolded values indicate statistically significant differences ($p < 0.05$). X values indicate the absence of individuals on that depth strata.

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