Article

Factors Influencing Habitat Selection of Three Cryptobenthic Clingfish Species in the Shallow North Adriatic Sea

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Abstract: Cryptobenthic fishes were often overlooked in the past due to their cryptic lifestyle, so knowledge of their ecology is still incomplete. One of the most poorly studied taxa of fishes in the Mediterranean Sea is clingfish. In this paper we examine the habitat preferences of three clingfish species (*Lepadogaster lepadogaster*, *L. candolii*, and *Apletodon incognitus*) occurring in the Gulf of Trieste (Northern Adriatic). The results show that all three species have a cryptic lifestyle and are well-segregated based on their depth distribution and macro- and microhabitat preferences. *L. lepadogaster* inhabits shallow waters of the lower mediolittoral and upper infralittoral, where it occurs on rocky bottoms under stones. *L. candolii* similarly occurs in the rocky infralittoral under stones, but below the lower distribution limit of *L. lepadogaster*, and in seagrass meadows, where it occupies empty seashells. Such hiding places in seagrass meadows are also occupied by *A. incognitus*, which mostly occurs below the lower distribution limit of *L. candolii*. Despite the overlap of depth and macrohabitat, the probability of individuals of two species encountering each other or competing in the same habitat is low when the depth range is combined with the microhabitat preferences of these species.

Keywords: cryptobenthic fish; clingfish; habitat selection; depth distribution; *Lepadogaster lepadogaster*; *Lepadogaster candolii*; *Apletodon incognitus*

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1. Introduction

Knowledge of species habitat preferences is essential, since it provides basic information about the suitability of the environment for a particular species [1]. Habitat preferences are important species traits that have many ecological consequences, ranging from the fitness of individuals [2,3] to the abundance and distribution of species in the environment [4]. As habitats can be diverse, with numerous variables shaping them, it can be quite challenging to determine the critical factors that affect habitat preferences [5]. The individual chooses the habitat that positively affects its fitness by providing a sufficient amount of adequate food [6] or allowing the possibility of increased survival due to reduced predation and mortality risk [7]. Such habitat choice is known especially in cryptobenthic fish species, based on Miller's definition [8] as those whose "small body size permits exploitation of restricted habitats, where food and shelter are obtained in, or in relation to, conditions of substrate complexity and/or restricted living space, with a physical barrier likely to be interposed between the small fish and sympatric predators". Consequently, by exhibiting such a cryptic lifestyle, fish are hardly observed by divers and are usually not detected in conventional ichthyofaunal surveys [9]. Smith-Vaniz et al. [10] concluded that around 64% of fish fauna can be overlooked by visual censuses due to their hiding habits. Therefore,

knowledge about the occurrence and ecology of cryptobenthic fishes remains fragmented at a global scale. Recent studies have shown that cryptobenthic fish species are not rare, as previously assumed [11], but rather common [12–14]. Ackerman and Bellwood [15] proved that cryptobenthic fishes from tropical reefs, due to their high abundance, can potentially influence the ecosystem. Recently, many authors have reported the importance (e.g., energy transfer) of cryptobenthic fish species in tropical seas (e.g., [15–17]), while there is still a lack of knowledge on cryptobenthic fish species from the Mediterranean and their ecology [13,18].

One of the less-studied taxa of fishes in the Mediterranean Sea is clingfish (family Gobiesocidae) [12,13]. Clingfish, all species of which are cryptobenthic, are poorly known due to their small size, cryptic way of life, good camouflage, and the fact that only a few ichthyologists have worked on this family [19]. Furthermore, since they are cryptobenthic, it is not possible to collect specimens with common methods (e.g., nets or baited traps) [19]; collection requires scuba equipment and the use of anesthetic. The aim of this study is to provide information on the habitat preferences of three clingfish species (*Lepadogaster lepadogaster* (Bonnaterre 1788), *L. candolii* (Risso 1810), and *Apletodon incognitus* (Hofrichter and Patzner 1997)) in the Gulf of Trieste. *L. lepadogaster* and *L. candolii*, despite being poorly studied, are the most common species of European clingfishes (family Gobiesocidae) and are widespread throughout Mediterranean Sea and, also, in the Eastern Atlantic coast from England to Northwest Africa, the Canary Islands, and the Madeira Islands [9,20–28]. *A. incognitus* is a recently described species [29,30] with poorly known biology and ecology. The species presence has been confirmed for the northern part of the Mediterranean Sea, including the Adriatic Sea, and in the Eastern Atlantic at the Azores Islands [29,31,32].

2. Materials and Methods

2.1. Study Area

The study was conducted in the Slovenian part of the Gulf of Trieste, the northernmost part of both the Adriatic and Mediterranean Seas. The Gulf of Trieste is a shallow gulf (20–25 m) isolated from the rest of the Northern Adriatic and restricted by a transect from Grado to Savudrija Peninsula. It occupies an area of about 500 km² [33]. The seabed of the Slovenian Sea is a predominantly soft sedimentary bottom of fluvial origin, while the coastal bottom is mostly rocky, consisting mainly of Eocene Flysch layers. The coastal bottom consists of boulder fields and banks of pebbles, where the sizes of the boulders, rocks, stones, and substrate particles decrease with the distance from the shore. The rocky bottom extends to a depth of about 10 m, where it changes to a sedimentary bottom. Inside bays, soft sedimentary bottoms of fluvial origin prevail [33]. On the shallow coastal sedimentary bottom, seagrass meadows appear between 1- and 11-m depths [34].

2.2. Data Collection

2.2.1. Field Work

Sampling of clingfish specimens was performed from October 2016 to March 2019. In addition, 166 specimens of *A. incognitus* and 9 specimens of *L. candolii* from the collection of the Marine Biology Station Piran, National Institute of Biology (Piran, Slovenia) collected from 2005 to 2008 were included in the research. Samplings were performed at different localities in the coastal waters of the Slovenian part of the Gulf of Trieste. Altogether, 206 samplings (approximately 1 h each) were performed within 72 locations (Figure 1) that were randomly selected. Clingfishes were found within 107 sampling sites.

Figure 1. Sampling locations (black dots) along the Slovenian coastline where clingfishes were searched.

Specimens were collected by snorkeling and scuba diving in mediolittoral (41 sampling locations) and infralittoral belts (31 sampling locations). Additionally, some specimens were collected in tide pools during low tide. The main types of habitats studied were as follows: (a) Sandstone boulder fields, consisting of arrangements of sandstone boulders and mostly rectangular-shaped stones in one layer of bedrock extending from the mediolittoral to approximately 10 m. (b) Banks of pebbles, occurring mostly in protected bays. Sandstone pebbles were flatter, while limestone pebbles were rounded. Pebbles were arranged in layers, with larger pebbles (3–10 cm) on the surface and smaller pebbles (1–3 cm) in the deeper layers. Banks of pebbles were present mostly in mediolittoral and upper infralittoral. (c) Seagrass meadows of *Cymodocea nodosa* and *Posidonia oceanica*, where clingfish were sought in rhizomes (matte) and seashells in particular. (d) Sandy–muddy bottoms.

2.2.2. Fish Collection

Fish were randomly sought in different hiding places, such as under stones, boulders, and shells, or inside natural cavities such as caves, cavities, holes, clefts, etc. To facilitate the collection, the narcotic quinaldine (Sigma-Aldrich, St. Louis, MO, USA) diluted to 1:15 solution with alcohol [12,35] was used. The narcotic was sprayed into the hiding places using a laboratory wash bottle. The anesthetized fish were then caught with a hand net. Specimens of *L. lepadogaster* were also collected without anesthetic by lifting stones and catching them with the hand net. Specimens that were attached to the lower surface of the stones dropped themselves right into the net. Specimens of *A. incognitus* sighted in oyster shells were captured by placing a plastic bag over the oyster shell and chasing them into the bag. In the case of clingfish species, we also checked the hiding places to see if there were nests inside them. We also sampled banks of pebbles in the mediolittoral and upper infralittoral with a bucket and checked for fish with a sieve [36]. After sampling, stones and rocks that were checked for the presence of cryptobenthic fishes were placed in their former position, so that we did not cause damage to the natural habitat. Clingfishes were caught and stored in 100-mL plastic chambers with small holes in the cover that provided fresh water with oxygen.

2.2.3. Habitat Survey

Basic ecological data on the sampling location were obtained at each site. We collected the date and location; and environmental variables: macrohabitat (e.g., rocky area, sediment bottom, and seagrass meadow) and microhabitat (e.g., under stones and in seashells); and depth of finding.

Since 2 species were hiding under stones, they were analyzed in more detail to determine the differences in their habitat preferences. To this end, we measured the length, width, and height of stones and collected data on the presence of algal and sponge overgrowth on the stones and particular substrate under the stones. When mediolittoral sampling was done, the depth was calculated based on the depth of the sampling point and the zero point from the tide amplitude calendar [37–39].

2.2.4. Laboratory Work

After sampling, fish were transferred as soon as possible (less than 1 h after sampling was completed) to Marine Biology Station Piran (MBS) of the National Institute of Biology, where they were photographed with an Olympus TG-4 (Olympus, Tokyo, Japan) and cautiously measured to the nearest 0.01 mm with a caliper. The sex of the clingfish specimens was determined based on the length and size of the urogenital papillae, which are larger and more elongated in males than in females [18,24], while, in *A. incognitus*, the sex was also determined based on the size of caniniform teeth, which are larger in males [18]. Fish were identified at the species level by using the identification keys of Jardas [40] and Marčeta [41] and by scientific articles with species diagnoses, descriptions, and keys for identification [9,19,29,42]. After laboratory examination, the clingfish specimens were released at the sites where they were collected.

2.2.5. Data Analysis

During the survey, altogether, 641 clingfish specimens were recorded in the field, and 419 of them were measured (194 specimens of *L. lepadogaster*, 177 specimens of *L. candolii*, and 108 specimens of *A. incognitus*). In the next step, the sex ratio was calculated for each species. Potential differences in the sex structure within species were tested with chi-square (χ^2) statistics ($\alpha = 0.05$) in R statistical software (R Foundation for Statistical Computing, Vienna, Austria) [43]. Water depth recordings for the observed sample ($N = 419$) enabled a depth distribution comparison between species. Here, ANOVA and the corresponding Tukey's post hoc test were applied. Since the studied fish species prefer different pebble morphology, the stone dimensions (length, width, and height) where the fish were caught were measured. These data were then used to calculate the stone volume and shape (flatness). The latter was determined by applying the ratio of the surface area to the volume ($SA:V = S/V$, where S is surface (cm^2) and V is volume (cm^3)). The higher the ratio, the flatter the stone. In the next step, a linear regression analysis in the R statistical environment [43] was used to compare the influence of combinations of the habitat factors on the studied fish species: depth distribution and fish size, undersurface area of the stone and fish size, and flatness ($SA:V$) of the stone and depth distribution.

3. Results

3.1. Size Distribution and Sex Ratio of Three Species

The sizes of the *L. lepadogaster* specimens ranged from 28.06 to 78.02 mm (57.60 ± 8.54 mm). The sex ratio of 182 specimens of *L. lepadogaster* whose sex was determined (others were immature) showed no statistical differences ($\chi^2 = 2.66$; $df = 1$; $p > \alpha$; $\alpha = 0.05$), although the ratio was 1:1.3 in favor of males. The average male size was measured as 59.8 mm, and the maximum size was 78.02 mm in total length, while the average female size was 55.7 mm and they reached 72.12 mm in total length.

The size of the *L. candolii* specimens ranged from 13.97 to 86.94 mm (41.48 ± 16.00 mm) in total length. The sex ratio calculated from 56 specimens whose sex was determined (others were immature) did not statistically differ from 1:1 ($\chi^2 = 12.07$; $df = 1$; $p < \alpha$;

$\alpha = 0.05$) and was 1:2.7 in favor of females. Males measured an average of 64.2 mm and reached a maximum of 86.94 mm in total length, while females measured an average of 52.4 mm and reached a maximum 66.08 mm in total length.

The size of *A. incognitus* specimens ranged from 12.24 mm to a maximum of 50.69 mm (31.16 ± 9.40 mm) in total length. The sex ratio calculated from 66 specimens whose sex was determined was statistically different from 1:1 ($\chi^2 = 8.72$; $df = 1$; $p < \alpha$; $\alpha = 0.05$) and was 1:2.1 in favor of males. Males measured an average of 36 mm and reached a maximum of 50.69 mm in total length, while females measured an average of 22 mm and reached a maximum of 29.35 mm in total length.

3.2. Habitat Preferences of *Lepadogaster lepadogaster*

All 242 specimens of *L. lepadogaster* were found in the exposed or partially exposed rocky coastal area and were absent in sheltered areas. Specimens occurred between 0.4- and 2.2-m depths, with 75% of specimens found between 0.7 and 1.2 m. The results showed a positive correlation ($p < \alpha$; $\alpha = 0.05$) between the fish size and sea depth of fish occurrence. Most of them were found in boulder fields and banks of larger stones, where they were hiding under stones (98.3%), while a few specimens were found hiding in banks of pebbles. The specimens were mostly attached to the smooth and bare undersides of stones. In only a few cases, they were present under stones on the substrate. The average sizes of stones under which specimens were found were $26.0 (\pm 11.0) \times 14.3 (\pm 5.7) \times 7.6 (\pm 4.0)$ cm (length $\times$ width $\times$ height), with an average bottom surface of 409.8 ± 349 cm², while the average volume of the stones was 4027.7 ± 8269.4 cm³. The bottom surface area positively influenced the clingfish size, as large specimens preferred stones with larger surface areas (t -test, $p < \alpha$; $\alpha = 0.05$). Furthermore, our data showed a significant negative linear relation ($p < \alpha$; $\alpha = 0.05$) between stone flatness (SA:V) and depth of occurrence, showing that occupied stones were flatter with the decreasing depth. Stones were mostly overgrown with turf vegetation (58.4%) or were bare (36.6%). Under stones where clingfishes were found, the most common substrate was pebbles (63.8%), which were sometimes mixed with sand (20.4%) or rarely occurred together with a sandstone terrace. The pebbles under stones were of different sizes and rectangular in shape and mostly in one layer. Only rarely was the substrate made of a sandstone terrace (7.2%). In seven cases, more than one specimen was found under the same stone.

3.3. Habitat Preferences of *Lepadogaster candolii*

During the survey, 177 specimens of *L. candolii* were observed in the field. Specimens were found from 0.7- to 5.3-m depths, mostly (75%) in the depth range from 1.8 to 3.3 m. Four specimens were also found in tide pools. The results showed a significant negative linear relation ($p < \alpha$; $\alpha = 0.05$) between fish size and depth occurrence, as large specimens occurred in shallower waters and small specimens occurred somewhat deeper. Specimens were mostly found in the rocky coastal area (82.5%) in boulder fields and under solitary rocks on sand patches, while 17.5% of them were found in a seagrass meadow of *C. nodosa* and *P. oceanica*. Specimens were mostly attached to the underside of objects (such as stones and seashells) or were sometimes present in the substrates under objects. Specimens were mostly found under stones (90.4%) and rarely under sandstone terraces, seashells (e.g., *Pinna nobilis* and *Ostrea edulis*), or artificial objects (e.g., plastic and metal plates) on the sea bottom. In four cases, juvenile specimens were found outside the shelter on shells of living *P. nobilis*. The average sizes of stones under which specimens were found were $26.9 (\pm 12.7) \times 17.1 (\pm 7.5) \times 6.7 (\pm 4.0)$ cm (length $\times$ width $\times$ height), and they had an average bottom surface of 530.9 ± 533.1 cm², while the average volume of the stones was 4487.6 ± 9655.5 cm³. The obtained data showed that fish sizes increase along the bottom surface area gradient, as larger specimens preferred stones with larger surface areas. Our data showed a positive correlation between depth and stone flatness (SA:V), indicating that stones were flatter with the increasing depth. Furthermore, our data showed a significant linear relation ($p < \alpha$; $\alpha = 0.05$) between stone flatness (SA:V) and depth of occurrence. The

surface on the underside of stones occupied by *L. candolii* was relatively rough, due to small holes made by different biota, and was also covered with tubes of serpulid polychaetes. Different kinds of small sponges were usually also present on the undersides of the stone surfaces, but their presence was not included in the analyses. All stones were overgrown with algae, 25.3% of them with algal turf and 62.4% with macroalgae (e.g., *Padina pavonica*, *Dictyota* sp., and *Cystoseira* sp.). Less often (12.4%), the stones were also overgrown also with sponges (e.g., *Aplysina aerophoba*). The most common substrate under the stones was pebbles, which were most often mixed with sand (54.2%).

3.4. Habitat Preferences of *Apletodon incognitus*

Altogether, 222 specimens were observed during the survey. Specimens were found from 1.6- to 6.6-m depths, mainly (75%) in the depth range from 3.45 to 4.5 m. The results showed a significant linear relation ($p < \alpha$; $\alpha = 0.05$) between the size and depth occurrence of *A. incognitus*, as large specimens occurred somewhat deeper. Most specimens (98.2%) were found in a seagrass meadow of *C. nodosa* and only few in a seagrass meadow of *P. oceanica*. Less than 2% of specimens were found on the sediment bottom but only in the immediate vicinity of the seagrass meadow. Specimens were found in various hiding places (Figure 2). Specimens occupied mostly dead oyster shells (66.0%), especially oysters attached to *P. nobilis* (82.8% of all specimens found in oyster shells), and less often in clusters of oyster shells on the sea bottom (9.4% of all specimens found in oyster shells). Many specimens were also found on living adult *P. nobilis* (22.2%) that were overgrown with an epibiota cover (e.g., oysters, bryozoans, serpulid polychaetes, and algae). Only 4.6% of specimens were found on isolated stones that were present in the seagrass meadow. Smaller juvenile and subadult specimens of *A. incognitus* (<35 mm, with a narrow head in the cheek area) were often found outside the shelter on shells of living *P. nobilis* (73.1% of all specimens found outside *P. nobilis*), while bigger adult specimens (>35 mm, with a wide head in the cheek area) were mostly found hiding inside empty oyster shells. Specimens of *P. nobilis* on which specimens of *A. incognitus* were found were mostly adult and did not have spines (a characteristic feature of juvenile noble pen shells), which would disable the clinging ability. Shells of *P. nobilis* were normally overgrown with epibiota, which provided cover for the fish. Disturbed fish sometimes moved to seagrass leaves, but they were never found hiding among the leaves.

3.5. Comparison of Three Clingfish Species

3.5.1. Size Distribution and Sex Ratio

Although *L. candolii* reached the largest maximum size of all three species, the specimens were on average smaller than those of *L. lepadogaster*, while *A. incognitus* was the smallest. In *L. lepadogaster* and *A. incognitus*, males prevailed in the population, while, in *L. candolii*, females were more abundant. In all three species, males were, on average, larger than females and reached a larger maximum body size.

3.5.2. Depth Distribution

All three species were clearly separated based on depth segregation (ANOVA and Tukey's post hoc test; $p < \alpha$; $\alpha = 0.05$) (Figure 3). *L. lepadogaster* occurred in the shallowest water from the lower mediolittoral to upper infralittoral. The depth distribution of *L. lepadogaster* in the upper infralittoral (down to a 2-m depth) overlapped with the upper limit of occurrence of *L. candolii*. However, specimens of *L. candolii* mostly occurred deeper in the infralittoral and were most abundant below the limit of the distribution of *L. lepadogaster*. Although there was a slight overlap in the depth range with *L. lepadogaster*, it is necessary to take into account the preference to habitat exposure. In the sheltered bay of St. Jernej (Ankaran), *L. lepadogaster* was absent, and this was the only location where *L. candolii* occurred in tide pools, so there was no habitat overlap between the species. However, in exposed or partially exposed locations where both species were present, *L. candolii* was mostly found below the lower limit of distribution of *L. lepadogaster*. In only a few cases,

L. lepadogaster and *L. candolii* were found together at the border of their occurrence in the upper infralittoral. *L. candolii* also had an overlap in its lower limit of depth distribution with *A. incognitus*, which occurred in deeper waters than the other two species. However, *L. candolii* occurred mostly above the depth distribution of *A. incognitus*, while there was almost no overlap in the depth distribution between *L. lepadogaster* and *A. incognitus*.

In all three species, intraspecific depth segregation based on the sizes of the specimens was observed. Inside the limit of depth distribution, large specimens of *L. lepadogaster* and *A. incognitus* were present in deeper water, while juveniles were more abundant in shallow water (Figure 4). Conversely, large specimens of *L. candolii* were more abundant in shallow water, while juveniles were more abundant deeper inside their depth distribution. Our data confirmed a significant linear relation ($p < \alpha$; $\alpha = 0.05$) between fish size and depth occurrence. However, the largest specimens of *L. lepadogaster* and *L. candolii* were the most abundant in waters between 1.5 and 2 m, while smaller specimens of *L. lepadogaster* were more abundant in shallower water, and juveniles of *L. candolii* were more abundant in deeper water inside their depth distribution. Based on these results, there is a low chance of overlap between large specimens of both species and almost no chance of overlap in the depth distribution between small specimens of these species.

Figure 2. Specimens of hiding *Apletodon incognitus*: (A) on the shell of *Pinna nobilis*, (B) nesting male occupying a slightly open dead oyster shell, (C) non-nesting specimen occupying a wide-open dead oyster shell, and (D) disturbed specimen that moved from shelter to seagrass leaf (Photos: D. Trkov.).

Figure 3. Depth distribution of three clingfish species. There is statistically significant difference (marked: a, b and c) between species based on depth of occurrence (Tukey's post-hoc test). Blue rectangle: *Lepadogaster lepadogaster*, orange rectangle: *Lepadogaster candolii* and gray rectangle: *Apletodon incognitus*.

Figure 4. Depth distribution of three clingfish species based on their sizes. Inner concentration ellipses cover 50% of all data for a given species, and outer concentration ellipses cover 75% of data for a particular species.

3.5.3. Habitat Selection

The three species showed different macrohabitat preferences. *L. lepadogaster* and *A. incognitus* were very specific in their habitat choices. *L. lepadogaster* was found only in rocky environments, while *A. incognitus* was strictly associated with seagrass meadows (Figure 5), and *L. candolii* was found in both.

Figure 5. Macrohabitat preferences of three clingfish species. Blue bars: *Lepadogaster lepadogaster*, orange bars: *Lepadogaster candolii*, and gray bars: *Apletodon incognitus*.

The macrohabitat preferences of *L. lepadogaster* and *L. candolii* overlapped, with both occurring mostly in the rocky bottom under stones (Figure 6). These were mostly made of sandstones (the characteristic rock type in the area) that were mostly rectangular in shape. Further, the two species showed various differences in microhabitat choices in addition to their depth range. *L. candolii* occupied stones with larger average undersurface areas (1.3 times larger) than *L. lepadogaster*, and the stones were flatter, which prevents them from sinking into the sediment; deeper in the infralittoral where *L. candolii* occurred, a sedimentary bottom (e.g., sand) was present, so only flat stones had not sunk into the sediment. This is further supported by observations that stones occupied by *L. candolii* were flatter with the increasing depth (Figure 7). A statistically significant difference in the substrate under the occupied stones between *L. lepadogaster* and *L. candolii* was found ($\chi^2 = 130.59$; $df = 1$; $p < \alpha$; $\alpha = 0.05$). Pebbles as substrates under stones were typical for *L. lepadogaster*, while pebbles with sand were typical for *L. candolii* (Figure 8). A statistically significant difference in overgrown stones between *L. lepadogaster* and *L. candolii* was also found ($\chi^2 = 228.53$; $df = 1$; $p < \alpha$; $\alpha = 0.05$). Bare stones and stones with turf vegetation were typical for *L. lepadogaster*, while stones with macroalgae were typical for *L. candolii* (Figure 9).

Figure 6. Shelters occupied by three species of clingfish. Blue bars: *Lepadogaster lepadogaster*, orange bars: *Lepadogaster candolii*, and gray bars: *Apletodon incognitus*.

Figure 7. Ratio between the depth and surface area-to-volume ratio (SA:V) of stones for *Lepadogaster lepadogaster* and *Lepadogaster candolii*. Inner concentration ellipses cover 50% of all data for a given species, and outer concentration ellipses cover 75% of the data for a particular species. Both axes are log-transformed.

Figure 8. Substrate coverage under stones occupied by *Lepadogaster lepadogaster* (blue bars) and *Lepadogaster candolii* (orange bars).

Figure 9. Overgrowth on stones occupied by *Lepadogaster lepadogaster* (blue bars) and *Lepadogaster candolii* (orange bars).

For both species, it was observed that the undersurface area was positively correlated with the fish size, as larger specimens occupied stones with larger undersurface areas (Figure 10). Furthermore, our data showed a significant linear relation ($p < \alpha$; $\alpha = 0.05$) between the undersurface area and fish size for both species. The undersurface areas of the stones were rougher for *L. candolii* than *L. lepadogaster* due to small holes made by different excavators, and their cover was overgrown with tubes of serpulid polychaetes.

Figure 10. Ratio between the undersurface area of inhabited stones and sizes of *Lepadogaster lepadogaster* and *Lepadogaster candolii*. Inner concentration ellipses cover 50% of all data for a given species, and outer concentration ellipses cover 75% of the data for a particular species. Both axes are log-transformed.

Although specimens of *L. candolii* also occurred in seagrass meadows at the same depth as *A. incognitus* and both specimens occupied seashells, there were evident differences in choice of hiding place between these two species. Adult specimens of *L. candolii* occupied shells of dead *P. nobilis* lying on the sea bottom. Such pen shells were also occupied by big males of *Parablennius tentacularis* and *Gobius niger* but almost never by *A. incognitus*. The latter mostly hide inside empty oyster shells, which are too small for adult *L. candolii*. Furthermore, juvenile specimens of *L. candolii* mostly occupied the undersurface of oyster shells on the sea bottom and were almost never observed inside the shells. However, *A. incognitus* prefer oyster shells attached to living *P. nobilis*, which further reduces the possibility of competition with *L. candolii* and with other invertebrates and potential predators (e.g., crabs). Despite the overlap of depths and macrohabitats, the chance of an encounter or competition between individuals of two species in the same habitat is quite low when combining their depth range and microhabitat preferences.

Of all three species, *A. incognitus* most often occurred outside the shelter. In contrast, specimens of *L. lepadogaster* were never observed outside the shelter. Contrary to expectations, the present quantitative data on individual occurrences showed that *A. incognitus* and *L. candolii* are not strictly cryptobenthic species, while *L. lepadogaster* is.

4. Discussion

4.1. Size Distribution and Sex Ratio

All three studied species are well-adapted to the environments in which they are found. All of them are small-sized coastal fish (smaller than 10 cm) or very small (*A. incognitus* is less than 6 cm long), which enables the efficient exploitation of cryptic habitats and better food availability [8]. The size of the fish species is correlated with their preferred microhabitat choice. Specimens of *A. incognitus* were found to effectively explore oyster shells, which are the smallest shelters compared to the other two species. The other two

species are bigger and hide mostly under stones, where space is not so restricted. All three species are dorsoventrally flattened, which is another adaptation from exploiting their preferred cryptic habitats, where space is a limiting factor [44,45]. The larger body size of males of all three species could be correlated with territoriality and nest guarding, as bigger males can protect their nests more easily. This dominance rank that is positively correlated with the size of the fish was also observed in blennies, in which male territoriality and nest guarding is also known [46–48].

The sex ratio of *L. lepadogaster* was not significantly different from 1:1, which is in accordance with other studies [24,26]. The higher number of collected males than females of *A. incognitus* is not necessarily the result of a real population sex ratio but, rather, is related to their habitat choice; males are bigger and hide mostly in seashells, while females are smaller and can hide among seagrass leaves [13,18] and other cryptic habitats where it is much harder to observe them. However, it is hard to provide a hypothesis for the higher number of female *L. candolii*.

4.2. Habitat Selection Patterns in Three Clingfish Species

4.2.1. Species Occurrence and Abundance

All three clingfish species were found in shallow coastal waters, where they were distinctly in conjunction with the substrate, which is typical for many clingfish species in general (sensu [24]). Of the three species, *L. lepadogaster* specimens were most often found, which is in accordance with many studies [21–27] reporting that this species is locally common and is considered as one of the most common clingfish species in the Mediterranean Sea.

4.2.2. Depth Segregation

Many coastal fish are syntopic. Separation into different ecological niches enables them to coexist in the ecosystem [49]. The separation of ecological niches is also evident in the three studied clingfish species. The three clingfish species differ in terms of depth segregation, with just a little overlap between them. The occurrence of *L. lepadogaster* in the lower mediotlittoral and upper infralittoral is in agreement with observations by Hofrichter and Patzner [13], who reported that the species was the most abundant at a depth of 0.8 m. However, Gibson [50] and Hofrichter [24] reported that some specimens could be found much deeper in the infralittoral (down to a 12-m depth). Hofrichter [24] noted that, for *L. lepadogaster*, there is no seasonal shift to deeper waters due to low winter temperatures, but he observed that the fish moved to deeper water in bad weather conditions (e.g., storms and extreme surf). The occurrence of *L. candolii* below the lower limit of distribution of *L. lepadogaster* was also observed by Brandstätter and Körbek [51]. Hofrichter and Patzner [13] reported that the species is most abundant at a depth of around 2 m, where it reaches a maximum density of 10 ind./m². *A. incognitus* occurred in deeper bottoms than the other two species, which is related to the availability of seagrass meadows present in the Slovenian Sea from 1 to 11 m in depth [34].

The three species were segregated by changes in sea depth preferences according to the size of individuals. Furthermore, depth segregation of different sizes of fish within the same species is known in many fish species and is the result of intense intraspecific predation or competition [52,53]. Intraspecific depth segregation could be due to the avoidance of competition for food and shelter between specimens of different sizes, as well as the avoidance of cannibalism, since large specimens can prey on smaller specimens. The predation of large specimens of *L. candolii* on smaller ones was observed when they were kept together in a 10-L bucket (personal observation). Cannibalism is also known in other clingfishes [54,55]. Another very likely reason is that larger specimens of *L. lepadogaster* occurred somewhat deeper than smaller ones, which could be related to the presence of crabs (especially *Pisidia* sp.), which are an important source of food for large specimens [56] and occur mainly in the upper infralittoral [57,58]. This is also supported by the occurrence of the largest specimens of *L. candolii*, which were abundant especially in the upper

infralittoral belt, where crabs represent important prey for them (unpublished data). The occurrence of large specimens of *L. lepadogaster* in the upper infralittoral could also be linked to strong territorial behavior by males [59], which hide under the same stone for several months [24]. Since specimens were never found outside of the water at low tide, specimens from the lower mediolittoral need to move somewhat deeper or remain in tide pools. Furthermore, the movement of males into slightly deeper water during the mating season was previously reported by Hofrichter [24]. In addition, the distribution of small specimens of *L. lepadogaster* in the upper part of the lower mediolittoral and of *L. candolii* in the lower infralittoral is probably also due to the avoidance of competition and to the interspecific predation of large specimens, which were most abundant in both species at the mediolittoral–infralittoral boundary. Predation by *L. lepadogaster* on smaller *Gouania willdenowi* (Risso 1810) was observed by Hofrichter [24].

L. lepadogaster and *L. candolii* showed similar macrohabitat preferences but with somewhat different exposures to wave action. *L. lepadogaster* specimens were mostly found in boulder fields and banks of large stones, where this species achieved a density of a maximum of 8 ind./m² [12], while Hofrichter and Patzner [13] reported a maximum 23 ind./m² in such habitats. Adaptation to strongly exposed habitats and the avoidance of calm waters, which were observed for *L. lepadogaster*, are also known in other clingfishes, although adequate shelter and food are provided [54,60]. The occurrence of *L. candolii* in mediolittoral in such areas shows that this species probably has different preferences for habitat exposure or just takes advantage of the free habitat niches. The preference for less turbulent water by *L. candolii* was previously reported by Gonçalves et al. [61]. Boulder fields were recognized as the most suitable habitat for those two species, as well as other Mediterranean clingfishes [13], by Hofrichter [18,24] and Patzner [12]. Patzner [12] noted that, in boulder fields, *L. candolii* can reach a maximum density of up to 12 ind./m². *L. candolii* also occurred in seagrass meadows, as observed by other researchers [12,13,18], where it is syntopical with *A. incognitus*. Although *A. incognitus* mostly occurred deeper than *L. candolii*, both species were found at the same time in some locations but were collected from different hiding places.

4.2.3. Habitat Selection

All three clingfish species exhibit a cryptic lifestyle, which provides them with protection against predators [13]. *L. lepadogaster* and *L. candolii* show similar microhabitat preferences, as both species prefer stones of a similar size and a similar substrate under the stone. Due to a high water turbulence and factors associated with low tide, many stones occupied by *L. lepadogaster* were devoid of vegetation. Meanwhile, *L. candolii* appeared slightly deeper or in sheltered areas where conditions were more favorable for macroalgae growth, and consequently, algae were more abundant on those stones. The habit of *L. lepadogaster* to occupy flat stones covered with algae was previously reported by King [26], while the occurrence of *L. candolii* in the biocenosis of photophilic algae has been reported in other studies [13,18,62], which also reported the selection of bare stones by *L. lepadogaster*.

L. lepadogaster and *L. candolii* occupied stones that were big enough that wave action could not move or turn them around but not so big that they would be heavy enough to sink into the sediment. Our results on preferred stone sizes (undersurface areas) by *L. lepadogaster* are in accordance with a study by Henriques et al. [9] showing that *L. lepadogaster* occupied stones with a similar bottom surface area (477 cm²). *L. candolii* showed a preference for larger undersurface areas than *L. lepadogaster*. As *L. lepadogaster* specimens were, on average, bigger than *L. candolii*, the size of the fish species is probably not related to the surface area of the stones. At the same time, it should be noted that the sizes of the stones decreased with the distance from the coast. One reason why *L. candolii* prefer stones with larger undersurface areas could be that they inhabit deeper and less turbulent waters, which means less food for potential prey (detritivore crustaceans). This may be reflected in lower prey abundances, and consequently, *L. candolii* needs a bigger shelter to obtain

enough food. Another reason could be related to the substrates under stones (e.g., sand, which is more common in deeper areas), which provides less shelter for potential prey groups (especially decapods [63]) and could also be compensated by the choice of stones with larger undersurface areas. Furthermore, *L. candolii* also prey outside the shelter, as observed by Gonçalves et al. [61], which could be due to an insufficient amount of suitable prey under the stones. Conversely, specimens of *L. lepadogaster* were not observed outside the shelter, which is in accordance with observations of many researchers (e.g., [18,24,61]). Gonçalves et al. [61] noted that *L. lepadogaster* does not make many movements, probably due to the turbulent environment in which it lives. An association between little movement and a turbulent environment was also observed in blennies [64]. Velasco et al. [65] noted that, in the rocky intertidal habitat, the availability of prey is relatively high, which is reflected in a higher dietary overlap of intertidal fish. Furthermore, a high density of suitable prey could be an important factor, as it allows feeding without major movement. These observations indicate that *L. lepadogaster* exhibit the most exclusive cryptic behavior compared to *L. candolii*, which was previously confirmed in other studies, while *A. incognitus* is even less strict in cryptobenthic occurrence than *L. candolii* [18,24,61]. The present research shows that the degree of cryptic behavior of cryptobenthic fishes should be concluded from quantitative data, e.g., from observations of the microhabitat positions of a large number of individuals, and not presumed in advance or from qualitative data and individual observations.

The sizes of *L. lepadogaster* and *L. candolii* were found to be positively correlated with the undersurface area of the stones, as larger specimens preferred larger surface areas. The reason for the intraspecific occupation of stones with a larger undersurface area by large specimens could be that they offer more space, as well as a larger area in which to search for prey.

L. lepadogaster and *L. candolii* showed a preference for similar substrates under occupied stones. For both species, pebbles were the most common substrate. Pebbles probably provide enough space under stones for clingfish specimens to live under them. Furthermore, pebbles are a favorite habitat for decapods *Pisidia* sp. and *A. nitescens* [63], as well as isopods and amphipods, which are important food items for clingfishes [26,50,56,65,66]. However, under stones occupied by *L. candolii*, pebbles were usually mixed with sand. This is probably related to the depth, since *L. candolii* occur in deeper waters distant from the coast, where finer sediments are more prevalent. In the case where only fine substrate (e.g., sand) was present under the stones, there was usually not enough space between the stone and the substrate (stones were usually sunken) for the clingfish, while big stones as substrates cause the hiding place underneath to be too exposed and offer no protection against predators.

Specimens of *L. candolii* also occupied seashells (mostly *P. nobilis* and *O. edulis*) and artificial structures. *L. candolii* exploited these microhabitats mostly in seagrass meadows, where shells are almost the only hard remains that can be used for shelter, so their availability is a limiting factor. Artificial structures such as metal and plastic plates can be used as alternative shelters. The exploitation of artificial structures as hiding places by *L. candolii* and *Diplecogaster bimaculata*, a related species, was also reported by Brandl et al. [19]. Most of the stones on the sedimentary bottom near the coast are also the result of human activities (stones thrown by people). However, most of these are unsuitable for clingfish occupation, as they sunk into the seabed due to their weight. Under such stones, specimens of *Gobius niger* (Linnaeus 1758) were mostly observed, which can dig shelters under stones. *G. niger* and big males of *Parablennius tentacularis* (Brünnich 1768) were the most common fish species observed under shells of dead *P. nobilis*. As each shell is usually occupied by only one fish, we can assume there is ongoing interspecific competition for such shelters. Strong intra- and interspecific competitions for shelter, which limit resources in the environment, were already demonstrated in blennies [46,47,67,68].

The presence of specimens of *L. candolii* outside the shells of *P. nobilis* confirms that they move around outside the shelter, which was already suspected by Kovačić [62] and

reported by other researchers [13,18,61]. However, the specimens were never observed freely swimming between shelters in the field, as some authors reported [12,13], except when they were disturbed from the shelter. In that case, specimens sometimes swam more than 1 m to the next shelter, not necessarily the nearest one, as was observed in *L. lepadogaster*.

Some researchers [13,18,30] reported that juvenile and subadult specimens of *A. incognitus* were commonly found on leaves of *P. oceanica* and under different species of sea urchins, where they reached a maximum abundance of up to 40 ind./m². However, in this study, specimens of *A. incognitus* and *L. candolii* were never found under sea urchins, even though these hiding places were checked many times. In fact, this is the first study to show the preference of adult specimens of *A. incognitus* for empty oyster shells attached to *P. nobilis*. A flattened body and small body size enable them to effectively occupy dead oyster shells. However, the oyster shells are also inhabited by other fish species, such as small specimens of *P. tentacularis*, *Symphodus cinereus*, and *Zebrus zebrus* (personal observation). This may indicate that there is competition for shelter between certain coastal fish. However, it seems that *A. incognitus* prefers empty oyster shells, which are less open than those occupied by *P. tentacularis*, especially during the nesting period. The occupation of such shells is possible due to their smaller body height, which is, besides Blenniidae and Gobiidae, the most pronounced in Gobiessocidae [44,45]. This gives *A. incognitus* a competitive advantage in exploiting such hiding places. Furthermore, adult males of *A. incognitus* have wide heads in the cheek area [18], which makes them seem bigger from a frontal view. Having a disproportionally wide mouth for their body size, they display their caniniform teeth, which probably serve for defense, as they are not used for feeding. Many other small territorial fish species also have big caniniform teeth that are not used for feeding but, rather, for deterring predators and displaying during antagonistic interactions [69]. Teeth displays (yawning) were observed in the interactions of specimens of all three species kept in the aquariums (unpublished data), and such behavior was also observed in *L. lepadogaster* by Hofrichter [24].

5. Conclusions

Marine fish are involved in many critical ecosystem processes and provide a variety of ecosystem goods and services [70]. Research on cryptobenthic fish species is thus essential in order to understand the functioning of the marine ecosystem. Due to their cryptic way of life, their importance was usually overlooked in the past. However, new discoveries about cryptobenthic fish species show that they represent an essential part of coastal biodiversity and can importantly affect ecosystem functions [15]. Knowledge about the ecology of small cryptobenthic gobies and gobiessocids from the Mediterranean Sea is still insufficient [12], and studies like the present research are still rare.

Habitat loss and fragmentation are major threats to biodiversity [71] and, also, the biggest threat to cryptobenthic fish communities [72]. Cryptobenthic fish species with specific habitat preferences are usually the most vulnerable to changes of microhabitats, even if some species show plasticity in habitat use [73]. Cryptobenthic fishes in general have a small dispersal range (due to the small body size [55,72,74]), so they can be affected by the fragmentation of a suitable habitat, making it difficult for them to recolonize [72]. Habitat degradation is also very problematic in the Slovenian part of the Adriatic Sea, especially in the coastal part, as less than 20% of it is still in a natural state. As the most degraded parts are coastal zones of the supralittoral, mediolittoral, and infralittoral [75], this has a big impact on *L. lepadogaster*, which exclusively occupies this coastal zone. Due to the specific habitat requirements of *L. lepadogaster* and isolated locally abundant populations, a serious disturbance of habitats and specimens in their collection might seriously affect their populations [26].

In recent years, seagrass meadows have been disappearing not only along the Slovenian coast [34] but, also, in other parts of the Mediterranean Sea and the Atlantic Ocean [76,77]. Furthermore, in the Mediterranean Sea, there is high mortality of *P. nobilis* [78], whose

population is declining, and the species is now considered to be critically endangered [79]. *P. nobilis* is an important bioconstructor, since its big shell offers shelter or a solid basis for the settlement of many other organisms [78,80,81]. Among them, empty oyster shells offer important shelters and nests for *A. incognitus*. The decline of *P. nobilis* and seagrass meadows can have a significant impact on populations of *A. incognitus* and other fish species that are strongly associated with them. Among the three species, it seems that *L. candolii* is the least negatively affected by human activities. This is due to its distribution in the infralittoral belt, which is less affected by humans, its euryecious habitat and microhabitat preferences, and even its potential to use artificial objects on the sea bottom as shelter.

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