Defining the role of Sabellaria alveolata reefs as nursery areas for juvenile fish: first evidence from drone-based imagery and underwater visual census data

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Abstract :

The biogenic reefs built by the honeycomb worm Sabellaria alveolata constitute priority habitats along Atlanto-Mediterranean coastal areas. Despite their wide extent and important ecological role, the nursery value of S. alveolata reefs remains unclear, and more information is needed to define how such structured habitats affect juvenile fish assemblages. In this study, habitat use by juveniles of 7 fish species was investigated by underwater visual census (UVC) at 3 study sites representing a gradient of complexity of Sabellaria reef habitats, spanning from a large and uniform reef to patchy and isolated small reef formations. Sabellaria reef metrics derived by drone-based cartography and GIS analysis were used to quantitatively monitor the seasonal structural changes occurring due to the natural dynamics of the reefs. We also tested the potential effect of Sabellaria habitats on the growth and relative condition factor (Kn) of white seabream Diplodus sargus juveniles. Five of the 7 surveyed species, especially sparid fishes, showed a clear preferential association with Sabellaria formations. Generalized additive modelling revealed a significant effect of the compactness ratio on estimated fish densities at high and low index values. The juvenile fish sampled on Sabellaria reefs exhibited higher values of Kn than those sampled

on rocky habitats, supporting the hypothesis that structural complexity positively affected their condition. We provide evidence on habitat use by juveniles, suggesting that the presence of the Sabellaria reef may act as a nursery and affect local fish density in Mediterranean coastal waters.

Keywords : Fish habitats, Habitat complexity, Biogenic reef, UAVs, Mediterranean Sea

47 **1. INTRODUCTION**

48 Marine coastal habitats provide several ecosystem services to nearshore human populations, 49 including shoreline protection, commercial fisheries, recreational activities, and nutrient cycling. The ecosystem goods and services provided by coastal habitats, such as seagrass beds, estuarines 50 51 mudflats, and saltmarshes are appreciably higher per unit area than those provided by terrestrial 52 habitats (Costanza et al. 1997, Lefcheck et al. 2019). Coastal marine ecosystems encompass highly productive areas such as estuaries and bays that provide food resources and refuge for adult and 53 juvenile fish and invertebrate species, contributing significantly to local and global biodiversity. As 54 a result, they are widely recognized as nursery grounds for the growth and development of juvenile 55 56 fish and shellfish (Paterson & Whitfield 2000, Beck et al. 2003). Over the last decades, a great effort 57 was made to define a standard framework to rigorously measure the importance of juvenile habitats 58 as nurseries and to support their protection (Beck et al. 2003, Dahlgren et al. 2006, Nagelkerken et 59 al. 2015). The Nursery Role Hypothesis (NRH) formalized by Beck et al., (2001) states: 'a habitat is a

60 nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other 61 habitats in which juveniles occur'. This definition constitutes a standard framework for rigorously 62 measuring, comparing, and categorizing nursery habitats through the ecological processes capable 63 of supporting greater contributions to adult recruitment, depending on any combination of four 64 65 factors: (i) density, (ii) growth, (iii) survival of juveniles and (iv) movement to adult habitats. 66 Therefore, the concept of a nursery must extend beyond simply the numbers of juveniles present 67 but also may entail higher specific growth rates due to the abundance of food resources, higher survival owing to protection from predators, and effective juvenile-adult linkage, resulting in more 68 juveniles reaching the adult population (Heck Jr et al. 2003). Although some aspects of the NRH have 69 70 been contested (Sheaves et al. 2006, Baker & Sheaves 2007) and some modifications, therefore, 71 suggested (Dahlgren et al. 2006, Nagelkerken et al. 2015), the core framework provided by NRH for measuring juvenile habitat quality remains widely agreed upon. However, despite wide acceptance 72 73 of NHR by marine biologists, fisheries managers and other stakeholders, and its recurrent use as 74 justification for the protection and conservation of these specific widely distributed nursery habitats 75 such as seagrass beds, estuaries, saltmarshes, mangroves forests, oyster beds, and shallow rocky 76 reefs (Nagelkerken et al. 2002, Dahlgren et al. 2006, Nagelkerken 2009, Litvin et al. 2018), few 77 attentions have been dedicated to other less common coastal habitats that can yet play an 78 important role in ecosystem functioning at the local scale. Among these, the role played by temperate biogenic reefs made by the polychaetes of the genus Sabellaria (Annelida, Sabellariidae) 79 80 for the juvenile fish remains unevidenced and poorly documented. The honeycomb worm Sabellaria 81 alveolata (Linnaeus, 1767) is a common filter-feeding gregarious species that builds wave-resistant 82 reefs of various types (i.e. mushrooms, pillows, barriers, and platforms; Curd et al. 2019) by 83 assembling mobile sand grains into solid tubes (Le Cam et al. 2011, Lisco et al. 2017). These worms

84 collect with specific tentacular filaments calibrated sediments and bioclast particles between 63 µm and 2 mm (belonging to the 'sand' class on the Wentworth scale), resuspended by wave action, that 85 are then cemented with proteinaceous adhesives to create a rigid but elastic tube (Le Cam et al. 86 2011, Deias et al. 2023). Due to their ability to transform soft-sedimentary habitats into engineered 87 88 hard bioconstructions and to modulate resource availability to other species via structural 89 modifications of the environment, Sabellaria worms are defined as 'ecosystem engineers' (Jones et 90 al. 2018, 2021). Sabellaria reefs are widespread along European Atlantic coasts, occurring on 91 intertidal and subtidal shores of west Scotland to the south of Morocco (Dubois et al. 2002, Firth et al. 2015, Curd et al. 2019). In the Mediterranean Sea, important sabellariid reef formations can be 92 found along the peninsular Italian coast (Gravina et al. 2018, Ingrosso et al. 2018, Bonifazi et al. 93 94 2019) and Sicily (Borghese et al. 2022, Sanfilippo et al. 2022), where they occur 95 from the lower shore to the sublittoral fringe. S. alveolata can be regarded as the most important building organism along intertidal sandy coastal habitats, where it plays key ecological functions 96 97 such as creating biodiversity hotspots (Dubois et al. 2006, Jones et al. 2020, Muller et al. 2021), 98 increasing microphytobenthic primary production and promoting benthic-pelagic coupling (Jones et 99 al. 2021) or filtrating phytoplankton biomass resulting in high clearance rates (Dubois et al. 2003). 100 As a result, these reefs are listed under Annex I of the EC Habitats Directive (European Council Directive 92/43 on the Conservation of Natural Habitats and of Wild Fauna and Flora) as a marine 101 102 habitat to be protected by the designation of 'Special Areas of Conservation'. Despite their relevant ecological role, sabellarid reefs are listed as "Data Deficient" in the European Red List of Habitats by 103 104 the IUCN (Franzitta et al. 2022). While macrofauna biodiversity assemblages associated with 105 Sabellaria reefs are well investigated (Bonifazi et al. 2019, Muller et al. 2021), very little is known 106 regarding motile-associated megafauna using this habitat, especially fish assemblages. In this 107 context, defining the role of S. alveolata reefs in providing the specific ecosystem service of 108 supporting juvenile life stages and thus sustaining adult fish populations is a fundamental requirement for characterizing and better managing coastal areas. It is well known that habitat 109 complexity provided by three-dimensional structures constructed by marine polychaete worms in 110 the families Sabellariidae (Sabellaria alveolata, S. spinulosa) and Terebellidae (Lanice conchilega) 111 112 can serve as nursery grounds for larvae of several invertebrate species (Dias & Paula 2001, Dubois 113 et al. 2006, Bremec et al. 2013, Seitz et al. 2014, Bonifazi et al. 2019, Aviz et al. 2021). However, 114 regarding fish species, only a few studies reported L. conchilega (Rabaut et al. 2010) and S. spinulosa (Pearce et al. 2011b a, Gibb et al. 2014) reefs as nursery grounds for certain fish species of 115 commercial interest (i.e. flatfish) because the high abundance of juveniles hosted. Since the role of 116 117 S. alveolata reefs as nursery grounds remains unclear, the main objective of this study is to assess if S. alveolata biogenic habitats play a key role in the Mediterranean fish population by investigating 118 119 juvenile fish species' juvenile density, growth, and survival.

120 Over the past 50 years, a variety of in situ non-destructive underwater visual census (UVC) techniques have been used to quantitatively estimate relative abundances, densities, sizes, 121 122 biomass, habitat types, and community structure of both adult and juvenile fish species in tropical (Brock 1954, Sale & Douglas 1981, Bohnsack & Bannerot 1986, St. John et al. 1990) and temperate 123 areas (Harmelin-Vivien et al. 1985, 1995, Francour 1997, Vigliola & Harmelin-Vivien 2001, Cocheret 124 125 De La Morinière et al. 2002, Ribeiro et al. 2005). Aside from the nature of the UVC method (e.g. 126 point counts, strip transects, line transects, rapid visual counts) and the equipment used (e.g. SCUBA diving, baited remote underwater stereo-video stations, rotating video apparatus), UVC has proven 127 helpful in expanding our knowledge in fish assemblages. However, no single approach is best suited 128 129 for all circumstances, with each variant designed to examine a specific aspect of fish assemblages 130 (Ribeiro et al. 2005). Moreover, the spatial distribution of juvenile fish assemblages is related to 131 fine-scale variations in habitat structure (Harmelin-Vivien et al. 1995, Copp & Kovác 1996, Russo et 132 al. 2007, Ventura et al. 2015), making the presence of adequate habitats critical during the settlement of juvenile stages. As a result of this site-specificity determined by the availability of 133 microhabitats, juvenile fishes typically show regular and predictable patterns of dispersal from the 134 onset of settlement until recruitment to the adult population (Garcia-Rubies & Macpherson 1995). 135 136 Therefore, it is crucial to integrate habitat surveys in UVC sampling to understand better organisms' 137 distribution patterns in relation to available habitats. Using a combination of observational 138 techniques, spatial monitoring surveys can provide a more comprehensive perspective on fish 139 ecosystems, aimed at describing specific aspects linked to species and habitats association (Murphy & Jenkins 2010). Underwater imagery derived from single photographs and video sequences 140 acquired by underwater cameras mounted on remotely operated vehicles (ROVs) and 141 142 autonomous underwater vehicles (AUVs), as well as acoustic data (side scan sonar, multibeam echo 143 sounders), represent the most employed remote observational techniques used to support UVC (Kenny et al. 2003, Chabot et al. 2017, Egerton et al. 2018, Wetz et al. 2020, Cheal et al. 2021). 144 Emerging technologies and recent advances in aerial imagery, such as multispectral satellite imagery 145 (Collin et al. 2017) and airborne light detection and ranging -LiDAR- (Collin et al. 2018b) have the 146 147 potential to increase our ability to accurately map remote or inaccessible areas, improving habitat 148 discrimination within complex reef seascapes at large spatial scales. Also, at a finer scale and more specifically regarding Sabellaria reefs, low-cost but promising unmanned aerial vehicles (UAVs) 149 150 applications has been efficiently used to generate ultra-high spatial resolution orthophoto mosaic s of honeycomb worm reefs, using a photogrammetric approach (Collin et al. 2018a, 2019, Ventura 151 152 et al. 2018a, Jackson-Bué et al. 2021). Although these cartographic outputs can guide fish censuses 153 more effectively in identified habitats of interest and finely depict reef topography to reduce time 154 and costs considerably in underwater surveys, no attempts have been made to connect such 155 mapping efforts to direct UVC data. Considering that data on the recruitment of demersal coastal

156 fishes along the Italian coasts are still scarce and generally related only to the arrival of 0-group fishes in bays or lagoons (Vigliola et al. 1998), without no quantitative information available for 157 specific microhabitat requirements such as those constituted by Sabellaria formations, we 158 examined patterns of habitat utilization by seven juvenile species. Therefore, we investigated for 159 160 the first time the role of *S. alveolata* reefs in providing an effective nursery habitat for juvenile fish 161 among coastal waters by integrating GIS information derived from drone-based cartography with 162 traditional UVC abundance estimates. We also explored the importance of S. alveolata reef structure on the recruitment dynamics by associating the observed fish densities with reef shape 163 complexity measured during winter (bioconstructions in the retrograding phase) and summer 164 months (bioconstructions in the prograding phase). Finally, to provide a complete picture of the 165 NRH, we also investigated growth and body condition for the white seabream Diplodus sargus, 166 167 besides juveniles 'abundance patterns. The interest in this species was driven by its socioeconomic importance being exploited in local/artisanal and recreational fisheries throughout the year (Biagi 168 169 et al. 2002, Tiralongo et al. 2021).

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171 **2. MATERIAL AND METHODS**

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173 **2.1 Study site**

This study was carried out along 1.3 km of sandy coastline in the Central Mediterranean Sea (Tyrrhenian Sea, west coast of Central Italy) south of Anzio harbour, near the Natural Reserve of Tor Caldara. Along this coast, water turbidity is high during most of the year because of fine sandy sediments mixed with terrigenous particles derived from river runoff and high hydrodynamic force (high exposure to winds and wave energy from the southern sectors), making the area suitable for the settlement of *S. alveolata* which is well adapted to turbid systems and capable of maintaining
its filtering activity even under high seston loads (Dubois et al. 2003).

Three sampling sites (S1, S2 and S3, Fig. 1) were identified according to a gradient of structural 181 complexity of S. alveolata bioconstructions. Large ball-shaped structures (up to 2 m diameter), some 182 183 of them fused to form barriers and small platforms from the water surface up to 3 m depth, 184 characterized the reef at the S1 site (41°29'34.345 "N; 12°35'9.088 "E). Due to its persistence and 185 high ecological interest, this area has already been studied from geological (Moretti et al. 2019) and biological perspectives (La Porta et al. 2009, Ventura et al. 2018a). A smaller S. alveolata reef, mainly 186 composed of mushroom-shaped formations (up to 1 m diameter) over a pebbly bottom from 0.5 to 187 3.5 m depth, characterized the S2 site (41°29'18.224 "N; 12°35'18.977 "E). The site S3 (41°29'13 "N; 188 12°35'19.172 "E) was characterized by reef type composed of isolated veneers and small pillow-189 190 shaped hummocks over a calcareous (upper Plicocene bioclastic calcarenites) substrate. Sites S1 and S2 mainly exhibited prograding formations (i.e. evidence of recent building activity and expanding 191 biogenic formations). In contrast, site S3 exhibited retrograding phases (i.e. evidence of degraded 192 reef portions and empty tubes), with biogenic formations showing signs of biofilm and epibiont 193 194 cover, also represented in the surrounding bedrock covered by a dense carpet of photophilous 195 algae. In this study, we cannot identify a standard control site with only rocky substrata since it is not present along the coast, especially considering reasonable distances from the other two sites 196 197 (S1 and S2) where Sabellaria forms complex and stable reefs. In fact, the promontory at the S3 Site, 198 which presents only small and isolated portions of *Sabellaria* growing on rocks, is the only stretch 199 of coast with hard calcareous seabed. While areas displaying only rocky outcrops, such as Capo 200 Circeo and Capolinaro, are present at around 60 km southward and 80 km northward, respectively, 201 at such distances, other local factors related to oceanography and larval supply might have 202 influenced juvenile densities, masking the effects of habitat type.

204 **2.2 UAV-based imagery and GIS analysis**

In late September 2019, an aerial survey with a low-cost UAV (Quanum Nova CX-20 equipped with 205 206 a GoPro Hero 8 action camera) was used to produce a coarse map of the coast from an 207 altitude of 120 m to identify the three study sites (Fig. S1 in supplementary material). Subsequently, 208 to effectively support the UVC survey, from October 2020 to November 2021, six high-209 resolution/low-altitude mapping missions were carried out both in fall-winter (September-210 February), following the main retrograding reef phase during autumnal storms and in springsummer (March-August), following the main prograding reef phase after larval recruitment focused 211 212 during the spring (Ventura et al. 2021). Mapping missions were carried out always with calm sea conditions and low wind < 1 knot (0-1 on the Beaufort scale) to ensure optimal detection of targeted 213 214 habitats and low local turbidity. Aerial mapping was conducted from an altitude of 30 m using a modified DJI Mavic 2 Pro UAV equipped with an additional L1/L2 GNSS receiver with Post Processing 215 Kinematics (PPK) capabilities to provide an improved cartography in terms of spatial resolution and 216 positional accuracies of the three sites. This consumer-grade off-the-shelf UAV was a lightweight 217 218 (0.9 kg) and easy-to-carry (322 L × 242 W × 84 H mm) quadcopter equipped with a fully stabilized 3-219 axis gimbal Hasselblad L1D-20c camera RGB camera with a 1-inch CMOS sensor. Each Li-Po Battery (3850 mAh) offered up to 30 minutes of flight time with good weather conditions and low wind. 220 221 Considering that the Mavic 2 Pro Hasselblad L1D- 20c camera produced 20 Megapixel format (5472 222 x 3648) photos, the sensor width was 13.2 mm, the actual focal length was 10.3 mm, and the UAV 223 flew at a constant height of 30 m above the mean sea level (AMSL); we applied the following formula 224 to estimate the ground sample distance (GSD, the distance between two consecutive pixel centres 225 measured on the ground):

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$$GSD_{cm/pix} = \left(\frac{Sensor \ width \ _{mm} \times Flight \ height \ _{m}}{Focal \ lenght \ _{mm} \times Image \ width \ _{pix}}\right) \times 100 \quad (1)$$

to get a GSD of 0.7 cm per pixel, allowing an excellent identification of above and below-water *S. alveolata* formations. The PPK routine was performed in Toposetter 2.0 Pro software, which allowed
an accurate georeferencing (less than 10 cm-level accuracy in horizontal/vertical positioning) of the
acquired imagery along the UAV track using as input the UBX files recorded by the L1/ L2 GNSS
receiver mounted on the UAV and Rinex 3.03 files derived by a near Continuously Operating
Reference Station (Ventura et al. 2023a).

233 The UAV-based imagery was processed using Agisoft Metashape v 1.6.1, a low-cost Structure from Motion (SfM) photogrammetric software, to generate orthorectified photomosaics of the study 234 235 area. SfM outputs included Digital Surface Models (DSMs) of the mapped locations. Still, we did not 236 include height information since the surface/elevation numerical model of the submerged part of the reef was affected by considerable inaccuracies due to water movements and light scattering. 237 238 Orthophoto mosaics generated in Metashape were exported as raster images (GeoTIFF format, in 239 the reference system WGS84/UTM zone 33 N, EPSG:32633) into a geographical information system 240 using ArcMap 10.6 software (Esri 2011) for subsequent Object-Based Image Classification (OBIA). 241 Before classification, we reduced the pixel complexity by segmenting the orthophoto mosaics into more compact image objects through the mean-shift (MS) segmentation function available in the 242 Spatial Analyst extension (Ventura et al. 2022, 2023b a). The spectral details, spatial details, and 243 244 minimum segment size parameters were set to 20, 18 and 800, respectively. After segmentation, 245 we manually selected 30 image objects for each cover class (Sabellaria reef, sandy bottoms, and rocky substrata) as training samples to train the Support vector machine (SVM) algorithm. The SVM 246 model uses each band's mean and standard deviation to classify the image objects in the whole 247 248 dataset. The classification results were verified using confusion matrices to compare OBIA results 249 against 50 assessment points (20 ground-truthed and 30 random points visually sampled on the 250 orthophoto mosaic). Validation points were first compared with the resulting classification, and the

analyses included an overall map and per-class accuracies. We did not include the kappa coefficient 251 252 because the chance agreement is irrelevant in an accuracy assessment (Foody 2020). After cover class identification through OBIA, the Patch Shape extension available in the opensource plugin 253 WhiteBox Tools v.1.4.0 (Lindsay 2014) was used to add indicators of shape complexity to the 254 255 identified S. alveolata polygons, using three complementary metrics: (1) the 'Compactness Ratio 256 (CR)' which expresses the Area/Perimeter ratio, a measure of shape complexity, for vector polygon 257 where an increase in fragmentation leads to an increase in perimeter more rapidly than a change in 258 area and therefore a decrease in CR; (2) the 'Shape Complexity Index (SCI)' which relates a polygon's shape to that of an encompassing convex hull, defined as SCI = 1 - A / Ah. Where A is the polygon's 259 260 area, and Ah is the area of the convex hull containing the polygon. As the shape of the polygon becomes more complex, the SCI approaches 1, and (3) the 'Hole Proportion (HP)' which calculates 261 262 the proportion of the total area of a polygon's holes relative to the area of the polygon's hull. It can be a valuable measure of shape complexity or a patch's discontinuity (Lindsay 2014). Mean values 263 264 of CR, SCI and HP were derived using all the polygons attributed to *S. alveolata* reef for each study site and survey period. The percentage cover for each seabed class was calculated by dividing the 265 266 area covered by the respective polygon by the total mapped area of the site. The aerial mapping 267 mission was conducted using precise GPS information, ensuring that the total mapped area 268 remained constant throughout summerly to winterly surveys.

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271 **2.3 Underwater Visual Census Sampling**

Data on juvenile fish abundance and microhabitat use were collected twice per month from October
2020 to November 2021 by UVC. Censuses were carried out between 11:00 am and 3:00 pm and in
the depth range of 0.3 - 2.5 m. To standardize the sampling effort, the UVC was carried out along

275 predefined pathways, previously defined on UAV cartography, with different lengths according to the extent and complexity of each site, to cover an area of 600 m² (200 m in length x 3 m in width) 276 in sites S1 and S3 and an area of 570 m² (190 m L x 3 m W) in site S2. One snorkeler swam slowly 277 following the reef border while simultaneously recording all individuals within a fixed distance of 278 279 1.5 m per side. This distance was chosen because of the limited maximum horizontal underwater 280 visibility and the small sizes of juveniles. To follow the correct path during each UVC survey, the 281 snorkeler was equipped with a real-time track system through a water-resistant tablet running the 282 GPS LoggerPro App, directly mounted on the marker buoy. The number of individuals of seven target species (Diplodus sargus, D. puntazzo, D. vulgaris, Salpa salpa, Dicentrarchus labrax, Umbrina 283 cirrosa and Atherina hepsetus), time of the day, tide level, and preferred habitat type according to 284 two main categories (S. alveolata reef and hard substrata encompassing rocks with photophilic 285 286 algae, pebbles, and gravel) were recorded. When juveniles were observed for more than 5 min on a specific substrate type, we considered it a preferred substratum, as young juveniles typically show 287 a strong site-specificity, the microhabitat they were found in was assumed to be the one they 288 preferentially used (Garcia-Rubies & Macpherson 1995, Macpherson 1998). 289

290 Size classes for sparid fishes were chosen to define three principal periods of juvenile ontogenetic 291 development (Macpherson 1998, Vigliola et al. 1998): settlement phase (smallest juveniles, from 10 to 20 mm total length, TL), intermediate phase (medium-size juveniles, from 20 to 45 mm TL) and 292 293 pre-dispersal phase outside the surveyed nursery areas (large-size juveniles, from 45 to 66 mm TL). 294 For other species, fish sizes were recorded in 30 mm size intervals. Plastic tablets with fish 295 silhouettes and a ruler attached to the end of a meter stick were used to reduce magnification errors 296 in estimating fish length (Bohnsack & Bannerot 1986, Harmelin-Vivien et al. 1995). When large 297 shoals were observed, the count was carried out later in the lab, using FULL-HD (1920 X 1080p)

frames captured from video footage acquired by a Sony Alpha 6000 camera within a Sea Frogpolycarbonate housing.

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301 **2.3 Estimation of condition factor and growth of** *Diplodus sargus*

To determine the role of S. alveolata reef on D. sargus juveniles' condition, 153 fish (ranging in size 302 303 from 16 to 66 mm TL) were collected monthly from May to August 2021 in the three sites, using 304 specific hand-nets with a 5 mm mesh size. We adapted the sampling effort proportionally to the extent of the total cover of the habitats (i.e. S. alveolata reef dominant in sites S1 and S2 and other 305 hard substrates encompasses rocks, pebbles and gravel mainly represented in Site S3) to ensure 306 comparable fish samples between sites. Therefore, we collected D. sargus juveniles on S. alveolata 307 in S1 and S2 sites, whilst juveniles associated with rocky areas were sampled only from site S3. 308 309 Monthly size distributions of D. sargus juveniles were estimated for each sampling site and preferential habitat to estimate growth variation over time. Considering the different extents of 310 311 each site's two main habitat types and the selective sampling method, the site could be used as a proxy for associating juveniles with the two main habitat types (Sabellaria and rocky substrata). 312 313 Moreover, juveniles of *D. sargus* were never found free-swimming on sandy areas but always 314 sampled in small shoals, stationary in proximity to the two substrata considered. Covariance analysis 315 (ANCOVA) and linear regressions were used to test for slope differences between juvenile growth 316 rate and habitat type.

The relative condition factor K_n was used to study the variation in juvenile conditions while avoiding the effect of length (Ferraton et al. 2007). For each specimen, the total length TL, in cm) and the eviscerated wet body weight (We, in g) were used to compute the formula as follows:

$$K_n = \frac{We}{We'} \quad (2)$$

where *We* is the measured individual eviscerated weight and *We'* is the estimated eviscerated weight from the $\log_{10}We - \log_{10}TL$ relationship (We'=10^{-intercept} x TL^{slope}).

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324 2.4 Data Analysis

Juvenile fish densities (D, expressed in the number of juveniles per 100 m²) were estimated using UVC data as follows:

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$$D_i = \frac{n_i}{W*L}$$
 (3)

where n_i is the number of individuals detected, W is the path width (in metres), and L is the path length (in metres). Generalized additive models (GAMs) were used to investigate the influence of reef metrics on juvenile fish densities among the three study sites. GAMs are non-parametric extensions of generalized linear models (GLM) that allow for non-linear relationships between predictor and response variables common to ecological data (Guisan & Zimmermann 2000, Zuur et al. 2007). The following equation gives general GAM construction:

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$$E[Y|\mathbf{X}] = g^{-1}(\mathbf{X}_{a}\boldsymbol{\beta} + \sum_{k} s(X_{k})) \quad (4)$$

335 where E[Y|X] is the expected value of the response variable (log-transformed fish densities) given all independent information, g is a link function, X_a is a set of predictors linearly related to the 336 dependent variable. At the same time, X_k represents one of the K predictors not linearly related to 337 the dependent variable, and S_k is a smooth function of the predictor variable, X_k. A GAM with 338 339 Gaussian distribution (with identity link function) was fit with a cubic regression spline as a smooth 340 function using the 'mgcv' library in R version 4.2.1 (Wood 2001). Smooth functions were used to model the relationship between the response variable and the reef metrics estimated from UAV-341 based cartography. In the current study, cubic splines were restricted to a maximum of 5 knots for 342 343 the full set of independent variables (i.e. site, species, size class, season, tide level, Sabellaria reef 344 cover, substratum type, CR, SCI, and HP) to prevent overfitting (Dance & Rooker 2016). Independent

345 variables influencing juvenile densities were selected for the final model using a backwards stepwise procedure based on minimizing the Akaike information criterion (AIC), which measures goodness of 346 fit while accounting for model complexity (number of variables). The approximate significance of 347 the smoothed predictor (p-values) was used to guide the backward selection procedure, where the 348 349 variable with the highest p-value (above 0.05) was removed first. When removing a predictor 350 returned model with a smaller AIC (with Δ AIC > 2 between models), the same variable was excluded 351 from the analysis. Stepwise selection continued until removing any remaining predictors increased 352 in the model AIC (Anderson et al. 1998). Non-significant (p > 0.05) terms retained in the final model 353 were removed if model AIC was comparable (<2) after removal. In addition, as a secondary criterion to AIC, the overall model fit was assessed with percent deviance explained: DE = [(null deviance -354 residual deviance) / null deviance] × 100. The relative influence of each independent variable was 355 356 assessed by removing each variable individually from the final model and comparing the percent change in DE (ΔDE) and change in AIC (ΔAIC). The 'gam.check' tool of the 'mgcv' package (Wood & 357 358 Wood 2015), which plots the deviance residuals against approximate theoretical quartiles of the residual deviance distribution according to the fitted model, was used to check the model's 359 360 residuals. Models with overdispersed and anomalous distribution of residuals were discarded. 361 Significant differences for either fish habitat/site association and K_n were tested with the nonparametric Wilcoxon signed rank test using the 'wilcox.test' function in the 'rstatix' package. The 362 363 Bonferroni correction was applied to the resulting p-values to account for the influence of multiple tests. Results of the tests, expressed with significance codes, were reported directly on plots using 364 'ggpubr' and 'ggsignif' R packages (Kassambara 2020, Ahlmann-Eltze & Patil 2021). 365

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367 **3 RESULTS**

368 **3.1** Sabellaria reef metrics and their relationship with juvenile densities

369 The UAV-based orthophoto mosaics generated after SfM processing showed a spatial resolution of 0.66 cm/pix (Fig. 2 a-d and Fig. S2 supplementary material). The high level of detail supported the 370 UVC sampling by providing the snorkeler with accurate cartographic support that was helpful for 371 survey management and data acquisition. The OBIA classification approach effectively identified the 372 most important features of the coastal zones, including Sabellaria reefs, resulting in an overall mean 373 374 (± SD) accuracy of 86.9 % (± 0.3). Major land-cover misclassification errors involved spectral 375 confusion among the class 'rocks with algae' with a total of 8.16% and 16.3% of samples interpreted 376 as S. alveolata reef and sandy bottoms, respectively (Overall, producer and user accuracies are reported in Table S1 of the supplementary material). S. alveolata reef cover in S1 (Wilcoxon signed-377 ranks test; W = 3986, p-value = 0.0001) and S2 (Wilcoxon signed-ranks test; W = 2257, p-value = 378 379 0.01) sites significantly differed from S3 site considering both the winter and summer months. The S1 site exhibited the most considerable reef extent (2056 m²) in summer, covering more than 33% 380 of the whole area, whilst only limited S. alveolata reef bioconstructions were reported in the S3 site, 381 with an average cover of 5.2% throughout the year (Table 1). Generally, we observed a reduction in 382 S. alveolata reef cover (up to 10% in the S1 site) with an increase in the areas covered by sandy 383 384 bottoms from summer to winter due to natural erosion of the bioconstructions and sand deposition 385 during severe storms occurring more frequently from late summer.

S. alveolata reef metrics Compactness Ratio (CR)', 'Shape Complexity Index (SCI)' and 'Hole Proportion (HP)', derived after polygon delineation based on OBIA classification, exhibited large habitat variability among sites and seasons (Fig. 3). Generally, the three metrics reported significative differences from summer to winter months, denoting their ability in detecting natural dynamics of *S. alveolata* reefs. The S1 site showed the highest CR among the studied reefs both in summer and winter, being well-structured with a compact shape denoting reef stability. High CR values in the S1 site corresponded to a reef composed of large and continuous colonies (high surface 393 for low perimeter) that can offer a more stable structure capable of withstanding the intensity of wave action and little prone to retrograding phase in winter. As expected, smaller CR values 394 indicated smaller and more fragmented reef structures at sites S2 and S3. Consequently, SCI 395 increased significantly in S1 (Wilcoxon signed-ranks test; W = 266, p-value < 0.001) 396 and S2 397 (Wilcoxon signed-ranks test; W = 589, p-value < 0.001) sites from summer to winter, highlighting 398 reef fragmentation. Conversely, site S3 showed larger values of SCI in winter because of isolated 399 reef formations constituted by small and low veneers between rocks, offering limited surfaces exposed to waves and therefore less prone to damage (Curtis 1975). In the S1 and S3 sites, HP 400 did not significantly increase in winter, whilst hole formation significantly (Wilcoxon signed-ranks 401 test; W = 560, p-value < 0.001) occurred in *S. alveolata* reefs in the S2 site. 402

The final selected GAM model (DE = 64.9% and pseudo-R² = 0.62) fitted on 256 observations included four retained variables, with species, site, size class, and CR resulting as the most influential (Table 2). This model includes information on all relevant sources of variability when referring to the juveniles' density. The GAM formula we chose according to the AIC selection procedure and diagnostic plots were reported in the supplementary material as Equation S1 and Figure S3, respectively.

For all the considered species, densities showed a significant negative effect from site S1 to S3, which is especially marked for sparid species (higher for *Diplodus* spp. and minimum for *Salpa salpa*), *D. labrax* and *U. cirrosa*. Among *Diplodus* species, the white seabream *D. sargus* seemed the most influenced in terms of site selection, similar to *D. labrax*. The response plot of the non-linear term showed a sinusoidal trend indicating that juvenile fish densities were lowest at moderate values (0.3-0.5) of *Sabellaria* reef CR, whilst larger densities were reported both at lower (< 0.3) and higher (> 0.5) CR values (Fig. 4).

417 **3.2** Temporal and spatial variability of juvenile fish

A total of 3395 juveniles belonging to the seven target species were censused among the three sites 418 over the whole study period. The most abundant species were two sparid fishes (Diplodus vulgaris 419 and D. sargus), accounting for 32.3 % and 27 % of the total juvenile assemblage, followed by 420 Atherinidae (Atherina hepsetus, 21.2%) and Salpa salpa (10.5%). Diplodus puntazzo, Umbrina cirrosa 421 422 and Dicentrarchus labrax were reported occasionally, representing a small fraction of the assemblage (5.8%, 2% and 1.3%, respectively). Within-month variation of juveniles' density was 423 424 high, especially for sparid fishes (Fig. S4 Supp. material). Diplodus sargus and D. vulgaris were found mainly from late spring to mid-summer, whilst S. salpa and D. puntazzo were observed in winter. 425 The other species (A. hepsetus, D. labrax and U. cirrosa) were censused mainly in late summer or 426 427 early autumn.

During summer months, juvenile density significantly differed from S1 to S2 sites (Wilcoxon signed-428 ranks test; W = 3399, p-value < 0.001) and from S1 and S3 sites (Wilcoxon signed-ranks test; W = 429 3554, p-value = 0.003), with the highest average (\pm SD) density of 14.3 \pm 16.8 (n = 82) Ind. 100 m⁻² 430 recorded in the S1 site (Fig. 5). The sea breams *D. sargus* (Wilcoxon signed-ranks test; W = 1645, p-431 432 value < 0.001) *D. puntazzo* (Wilcoxon signed-ranks test; W = 129, p-value = 0.01) and the sea bass 433 D. labrax (Wilcoxon signed-ranks test; W = 27, p-value = 0.04) showed significant decreasing density values passing from S1 to S3 sites (Fig. 6). The shi drum (*U. cirrosa*) juveniles were reported only in 434 435 the S1 site. The other sparid fishes (D. vulgaris, S. salpa) and the Mediterranean sand smelt (A. hepsetus) were censused with comparable mean densities in all sites. 436

437

438 **3.3 Juveniles' habitat use**

439 The three juvenile species of the genus *Diplodus* (*D. sargus, D.vulgaris, D. puntazzo*)showed a 440 significant association with *S. alveolata* biogenic formations when compared to the other rocky 441 habitats, mainly constituted by hard substrates covered by photophilic algae (Fig. 7). U. cirrosa 442 juveniles were only reported in proximity to *S. alveolata* formations. Conversely, the mean densities of A. hepsetus, D. labrax, and S. salpa juveniles did not differ among the two habitat types, with the 443 latter mostly forming large shoals over rocky substrates. Small and medium-sized juveniles (2-5 cm 444 TL) were observed prevalently (> 70%) near *Sabellaria* formations (Fig. 8). This habitat association 445 446 was particularly evident for sparid species (especially for D. sargus) and D. labrax being almost all 447 the juveniles observed on Sabellaria reef, also several months after settlement. By contrast, largesized juveniles of S. salpa (7-8 cm TL) and A. hepsetus (2-3 cm TL) showed a preference for rocky 448 substrates covered by photophilic algae. 449

450

451 **3.4 Relative condition factor (K**_n) and growth of *Diplodus sargus* juveniles

Monthly size distributions of the sampled *D. sargus* juveniles from May to August differ significantly between months and substrate type (Fig. 9 a) in June (Wilcoxon signed-ranks test; W = 286, p-value < 0.001) and July (Wilcoxon signed-ranks test; W = 55, p-value = 0.004). *D. sargus* juveniles associated with *Sabellaria* reef in S1 and S2 sites exhibited higher increases in monthly size (regressions' slopes were significantly different among habitat types in both slopes and intercepts (ANCOVA, regression slope: F = 4.33, df = 1, p = 0.03) than juveniles settling on other hard substrates in the S3 site (Fig. 9b).

The K_n significantly differed (Wilcoxon signed-ranks test; W = 1396, p-value < 0.001) in juvenile *D.* sargus living near Sabellaria reef compared to specimens collected on hard rocky substrates. These differences were particularly strong among small-sized (25.3 ± 3.1 mm TL; Wilcoxon signed-ranks test; W = 70, p-value < 0.001) and medium-sized (35.1 ± 4.8 mm TL; Wilcoxon signed-ranks test; W = 63, p-value = 0.01) juveniles, whilst for larger juveniles (55.1 ± 4.7 mm TL), the effect of habitat on fish condition was not significant (Fig. 10). 465 **3 DISCUSSION**

The function of shallow coastal habitats as essential nursery grounds for marine fishes has become 466 an accepted ecological concept (Amara et al. 2007, Searcy et al. 2007). However, not all coastal 467 areas are equally important as nursery grounds. Quality nursery habitats contribute 468 469 disproportionately to the adult population by supporting increased densities, faster growth, better 470 survival, and successful movement of recruits to adult habitats (Beck et al. 2001). Juvenile fish 471 densities, growth, survival, and connectivity are essential indicators of juvenile habitat quality that 472 must be understood in an ecosystem-based approach to implementing comprehensive fisheries management strategies (Beck et al. 2003, Schloesser & Fabrizio 2019). Therefore, the dynamics 473 affecting essential fish habitats must be recorded accurately and extensively in marine monitoring 474 475 surveys, especially in complex coastal environments where microscale variability may affect the 476 estimates (Edgar et al. 2004). To date, this assessment is generally missing for temperate biogenic reefs made by the tube-building worm S. alveolata, which, analogously to other biogenic worm 477 reefs, are considered hotspots of biodiversity capable of providing refuge to an array of organisms, 478 479 including hard and sandy bottom invertebrates (Bremec et al. 2013, Gravina et al. 2018, Ingrosso et 480 al. 2018, Giangrande et al. 2020).

481 Our results indicated that juveniles of five commercially important species (Diplodus sargus, D. puntazzo and D. vulgaris, D. labrax and U. cirrosa) made a preferential use of S. alveolata reef 482 483 habitats with more cohesive reef structures with little or no fragmentation as those occurring in the S1 site. Fish densities were non-linearly linked to the compactness ratio (CR) metric, a common 484 485 estimate of the reef fragmentation: higher densities of juveniles were associated with high and low 486 levels of reef CR, with lowest densities at moderate CR values. As expected, a massive, 487 unfragmented, and compact reef (i.e. high CR values) has the greatest effect on the density and 488 diversity of juvenile fish. It offers shallow, sheltered areas with reduced hydrodynamic forces and

489 lower predation rates (Ruiz et al. 1993). Paradoxically, a similar refuge effect can also be observed when reef habitat fragmentation is maximal (i.e. low CR values) due to an increase of faults and 490 anfractuosities due to biogenic structures degradation (Dubois et al. 2002, Stone et al. 2019). This 491 492 effect has been demonstrated in macrofaunal diversity, where numerous small sessile epibionts 493 colonized degraded and fragmented reef structures (Dubois et al. 2006, Bonifazi et al. 2019). 494 Similarly, as shown in degraded coral reefs, prey vulnerability increases, leading to an initial rise in 495 resource availability and productivity for a significant part of the reef fish community, particularly herbivores and invertivores (Brandl et al. 2016, Olán-González et al. 2023), confirming that habitat 496 degradation allows the exploitation of novel resources by fishes that feed on macroinvertebrates 497 498 such as juvenile sparid fishes (Ventura et al. 2017, 2018b).

Moreover, when the loss of one microhabitat type occurs due to reef degradation during winter 499 500 storms, there is a simultaneous replacement by another microhabitat type, and, typically, massive 501 S. alveolata structures are replaced mainly by sandy rubble on degraded reefs, and some juvenile 502 fishes that prefer rubble microhabitats benefit from reef degradation. On the other hand, the lowest densities of juveniles reported at moderate CR values may be due to the transitional morphology of 503 504 the reef between prograding and retrograding stages (Curd et al. 2019, Firth et al. 2021). This study 505 shows that the refuge effects of S. alveolata habitats are just as important whether the reef is massive and little fragmented or made up of small, highly fragmented structures, providing valuable 506 nursery grounds hosting high juvenile densities throughout the year. This result should have 507 508 consequences in terms of management and restoration (Franzitta et al. 2022) of this reef habitat so as not to target exclusively extensive reefs (in size or surface area). Still, it should also make it 509 510 possible to justify important ecological functions in nursery areas for the smallest and most 511 fragmented biogenic reefs.

512 It should be noted that the predicted effect size is minimal (approximately 5 fish per 100 m²), especially considering the considerable measurement uncertainty characterizing UVC sampling. 513 Moreover, the limited deviance explained by the CR term also suggested that the relationship was 514 not particularly strong. While accepting that structure does not significantly affect juvenile fish 515 densities at the scales and extents examined here, our results confirmed that the reef, in all its 516 517 forms, acts as a preferential habitat for juveniles. Consequently, we can argue that *S. alveolata* reefs 518 play an essential role as a nursery area for juvenile fish even though its degree of compactness and 519 fragmentation. Similar results are reported for plant traits such as shoot density and aboveground biomass, which are only weakly correlated with the diversity of the associated fauna and may not 520 provide good proxies for diversity for another engineered habitat constituted by eelgrass (Zostera 521 marina) meadows (Muller et al. 2023). In fact, no significant differences were found between 522 523 communities from the centre to the edges of the meadows, indicating that both habitats provide similar benefits to biodiversity and highlighting that the shape of the community was directly 524 mediated by the presence of the meadow more than its health status (Muller et al. 2023). 525

Estimates of the ecological values of nursery areas, which are particularly important in monitoring 526 527 the effects of fishing and protection strategies on the structure of coastal fish assemblages, are 528 available for a variety of coastal benthic systems, including those supported by engineering species such as seagrasses (Jackson et al. 2001, Dorenbosch et al. 2004), mangroves (Mumby et al. 2004), 529 530 oyster reefs (Beck et al. 2003) and other reef-building polychaetes such as Lanice conchilega (Rabaut 531 et al. 2009, 2010), Ficopomatus enigmaticus (Méndez Casariego et al. 2004) and S. spinulosa (Reise 532 2012, Tillin & Gibb 2018). By contrast, virtually no data are available to quantify the importance of 533 S. alveolata formations for coastal juvenile fish assemblages, especially in the Mediterranean Sea. 534 Therefore, considering that the most common and widely accepted criterion for defining the nursery 535 function of habitats is their ability to provide food and refuge (Paterson & Whitfield 2000), the

536 efforts directed at evaluating habitat quality in the context of the nursery-role concept should not be limited to abundances, but should also take into account growth, survival and linkage (Beck et al. 537 2001, 2003, Dahlgren et al. 2006, Lefcheck et al. 2019). In this respect, we also evaluated the 538 potential effects on growth rate and fish condition exerted by S. alveolata reefs compared to 539 adjacent hard substrata. Fish condition is critical because it dramatically influences growth, 540 541 reproduction and survival. Fish condition has seldom been used to assess habitat quality in marine 542 ecosystems, where most of the research dealt with differences in abundance and biomass between habitats (Lloret et al. 2002, Cantafaro et al. 2017). Although we quantified growth and K_n for a single 543 sparid species (i.e. *D. sargus*), our results provided an important baseline for other species that 544 utilized the S. alveolata reef as a nursery area. S. alveolata reef hosts a high diversity of associated 545 546 fauna, including sessile (bivalves), burrower (tanaidaceans) and infaunal (isopods, amphipods and 547 polychetes) invertebrates, which could themselves support other benthic infaunal assemblages and, in turn, provide food for fish, as confirmed by previous studies on feeding habits of sparid fishes 548 (Sala & Ballesteros 1997, Costa & Cataudella 2007, Ventura et al. 2017, Bonifazi et al. 2018). The 549 highest K_n and growth rate were reported for small and medium-sized classes of juveniles, as larger 550 551 juveniles already expand their feeding ground outside the reef structures: the high density in small 552 invertebrates offers a head start in development for fish juveniles exploiting reef habitat as a feeding ground. The species S. alveolata is also a potential food source that may direct influence the 553 554 condition of fish: worms can be sucked out from their tube by juveniles with enough suction power, 555 such as sparids (Christensen 1978) or during reef destruction (i.e. during storms and periods of high wave energy). Considering, however, that juveniles of predators (*D. labrax*) were found in the same 556 557 sites, the refuge effect from consumer pressure provided by shallow bottoms may be 558 overestimated, suggesting that the refuge paradigm may be too simplistic for diverse and complex 559 nursery grounds (Baker & Sheaves 2007). Thus, the factors that more likely influence the distribution

of juvenile fishes in shallow water are probably related to the availability of food resources (Le Pape
& Bonhommeau 2015).

In Mediterranean environments, especially inside complex communities such as seagrass meadows 562 and biogenic reefs, UVC results can be affected by some typical sources of error linked to 563 environmental conditions, such as water clarity that may affect the detectability of fishes (La Manna 564 565 et al. 2021), the surveyed area dimensions (Jones et al. 2015), the census methodology (Pais & 566 Cabral 2018), the trait of target fishes with different behaviour (Kulbicki 1998, Pais & Cabral 2017), 567 intra-observer variability due to divers' experience, and habitat spatio-temporal variability and complexity (Friedlander & Parrish 1998, De Girolamo & Mazzoldi 2001, Green et al. 2013, Kislik et 568 al. 2020). This latter aspect deserves particular attention in planning accurate UVC monitoring to 569 570 estimate the specific association between juvenile fish and microhabitats, likely occurring at small 571 spatial scales (Harmelin-Vivien et al. 1995, Ventura et al. 2015, 2018b). In this context, recent mapping technologies based on ultra-high resolution imagery acquired by small UAVs coupled with 572 OBIA classification can be a valuable tool in identifying and characterizing coastal areas (Goncalves 573 & Henriques 2015, Papakonstantinou et al. 2016, Ventura et al. 2016, 2018a, 2023b, Jeong et al. 574 575 2018, Adade et al. 2021), providing accurate GIS data of heterogeneous stretches of coasts where 576 the environmental variability of the seabed is a critical aspect capable of influencing the distribution of juvenile and adult fish assemblages. We demonstrated that the use of UAV-based cartography 577 578 could be a valuable tool to integrate UVC surveys considering both the spatial planning of sampling campaigns and data acquisition of geomorphological features related to specific habitats such as 579 580 sabellariid reefs that are characterized by high spatial 2D/3D heterogeneity, even at small spatial 581 scales (Bertocci et al. 2017, Jackson-Bué et al. 2021, Ventura et al. 2021). The potential of UAVs for 582 environmental assessment is increasingly being demonstrated, especially in monitoring 583 programmes of shallow marine habitats, which are more and more frequently carried out using

584 aerial UAV photography in conjunction with field surveys to map seagrass beds directly (Ventura et al. 2018a), submerged aquatic vegetation (SAV) such as macroalgal beds (Rossiter et al. 2020, 585 Ventura et al. 2023b), coral reef (Casella et al. 2017, Collin et al. 2018b, Nguyen et al. 2021), rocky 586 reef (Tait et al. 2021) and other biogenic reefs (Collin et al. 2019, Donnarumma et al. 2021, Brunier 587 et al. 2022). Mapping and monitoring these habitats may provide valuable information on fish-588 589 habitat associations, eventually helping to identify optimal monitoring designs and to establish the 590 most effective schemes of temporal and spatial acquisition of data to achieve the specific objectives 591 of the study, including, for example, the estimation of seasonal variability at target sites (Murphy & Jenkins 2010). Although topographic features (e.g. Topographic Position Index, surface roughness, 592 slope) derived from elevation data (DEMs) were not explicitly considered here, they could provide 593 594 additional variables such as complementary fragmentation metrics or reef morphotypes descriptors 595 (Brunier et al. 2022) usable for the estimation of reef health status (Desroy et al. 2011, Bajjouk et al. 2020). However, our approach demonstrated that RGB orthophoto mosaic and polygon 596 delineation in GIS could provide simple and relevant indicators of the shape and complexity of 597 Sabellaria reefs related to their potential role as nursery grounds for juvenile fish. 598

599

600 4 Conclusions

Using UAV-based cartography reveals the potential for high-resolution remote sensing imagery to be implemented into traditional UVC-based monitoring efforts by quantifying biogenic reefs' finescale attributes (Murfitt et al. 2017). The present study adds new perspectives to on-ground surveys, giving insight into the distribution and abundance of juvenile species associated with complex coastal habitats formed by reef-building polychaetes. The ability of UAVs to capture fine-scale (cm) georeferenced imagery of the whole reef, depicting morphological changes occurring between accretion and erosion processes due to environmental dynamics, is crucial for improving spatial 608 monitoring and assessing the spatial variability of reef habitat types. Although UAVs may not be able to fully replace *in situ* monitoring techniques on sabellariid reefs, they can provide complementary 609 data suited to obtain a more comprehensive understanding of biogenic reef ecology and, in 610 particular, their nursery role. Because the nursery role concept aims to identify high-quality areas, 611 612 we encourage precise monitoring even on relatively small habitats, such as Sabellaria reefs 613 presented here. Despite their limited size, they can represent essential nursery habitats that can 614 support more adult recruits per unit of space compared to other habitats used by juveniles of the same species. This is a crucial aspect for prioritizing spatially explicit management (e.g. 615 establishment of marine protected areas) when costs or other logistic constraints limit the amount 616 of space that can be protected (Dahlgren et al. 2006). Finally, although this study is relatively limited 617 in spatial coverage and temporal resolution and further studies are required to fully understand 618 619 connectivity and ecological habitat linkages (Nagelkerken et al. 2015), our findings can serve as a starting point for examining the effects of S. alveolata bioconstructions on juvenile fish assemblages, 620 confirming that habitat structure should be included as a biodiversity component during evaluations 621 of its nursery role, especially under the predicted increase of the impact of human activities and 622 623 climate change on biogenic formations in the next few years (Dubois et al. 2006, Curd et al. 2023).

624

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626

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TABLES

- **Table 1:** Site overall extent (m²) and reef habitat cover (%) in the three sites (S1, S2, S3) as derived
- 976 from UAV-based aerial imagery OBIA classification.

Site (m ²)	Season	Habitat m ² (% cover)					
		Sabellaria reef	Sandy bottoms	Rocks with algae			
S1 (6100)	Summer	2056.4 (33.4)	4067.2 (66.1)	27.9 (0.5)			
	Winter	1406.2 (23)	4709 (77)	0 (0)			
S2 (2700)	Summer	354 (12.9)	2229.4 (81.4)	155.5 (5.7)			
	Winter	267.6 (9.8)	2448.5 (89.5)	18.6 (0.7)			
S3 (4100)	Summer	227.3 (7.2)	813.5 (25.9)	3103.1 (66.9)			
	Winter	203.8 (3.3)	982.4 (29.7)	2954.5 (67)			

Table 2: Output of the GAM model on log-transformed juvenile densities (expressed in number of juveniles per 100 m²), reporting the model's linear and non-linear terms. Significant p-values are

981	highlighted in bold.	

Linear terms								
Explanatory variable	Estimate	Std. Error	t value	P-value				
Intercept	4.4059	0.2326	18.944	<0.001				
Site: S2	-0.507	0.2446	-2.073	0.039				
Site: S3	-0.7244	0.2388	-3.033	0.003				
Species: D. labrax	-2.6066	0.2904	-8.975	<0.001				
Species: D. puntazzo	-2.211	0.225	-9.828	<0.001				
Species: D. sargus	-2.4086	0.1857	-12.97	<0.001				
Species: D. vulgaris	-1.0024	0.2196	-4.565	<0.001				
Species: S. salpa	-0.5664	0.2616	-2.165	0.031				
Species: U. cirrosa	-1.8902	0.3736	-5.059	<0.001				
Size class: Medium	-0.3964	0.1143	-3.469	<0.001				
Size class: Large	-0.6955	0.1516	-4.587	<0.001				
Non-linear (smooth) terms								
Explanatory variable	edf	Ref. df	F	p-value				
CR (<i>Sabellaria</i> reef complexity Ratio)	3.38	3.78	2.605	0.0218				

985 FIGURES

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Figure 1: Map of the Latium coast south of Rome (Central Tyrrhenian Sea) where the three study sites (S1, S2, S3) were located. The main urban complex and the limit of the Tor Caldara Natural Reserve are reported by grey and green polygons, respectively. The dotted lines represent bathymetric depth contours.

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Figure 2: High spatial resolution mapping of Sabellaria reef using Unmanned Aerial Vehicles (UAV)-995 based orthophotmosaic and imagery classification. Orthophoto mosaic of the S1 site in summer (a) 996 997 with the resulting classification derived by object-based image analysis (OBIA) leading to feature 998 extraction and identification of the three main seabed cover classes (rocks with algae, S. alveolata reef and sandy bottoms) (b). Orthophoto mosaic of the S1 site in winter (c) with the resulting 999 classification based on OBIA(d). Note the modification of reef boundaries and cover. The mean 1000 snorkeler's underwater visual census (UVC) path with a covered area of 600 m² (200 m Length x 3 1001 1002 m Width) derived by multiple global positioning systems (GPS) tracks interpolation is reported in 1003 grey. The mapping and OBIA results of the S2 and S3 sites were reported in Fig. S1 as supplementary 1004 material.



1007Figure 3: Mean values (± SE) of Sabellaria alveolata polygons-related reef metrics estimated after1008OBIA classification of UAV-based imagery. CR = Compactness ratio, SCI = Shape complexity, HP =1009Hole proportion. The Wilcoxon signed rank tests were used for pairwise comparisons. The alpha1010value was set at 0.05, and the Bonferroni adjustment was applied for multiple comparison.1011Significance codes: ****p <0.0001; ***p < 0.001; *p < 0.05; ns = non-significant. See Fig. 1 and Fig.</td>1012S1 in the supplementary materials for mapping results and visualization of *S. alveolata* reef polygons1013over seasons.



Figure 4: Response plots showing the influence of the retained non-linear term (*S. alveolata* reef
Compactness Ratio, CR) on juvenile fish densities among the three sites according to the final
generalized additive model (GAM). Model fit was assessed with Akaike's information criterion (AIC)
and % deviance explained (DE). Solid lines represent smoothed values, and dotted lines represent
95% confidence intervals. N = 256 observations (site x species x size classes).



Figure 5: Seasonal variation in juvenile fish densities (expressed as N. of individuals per 100 m²)
recorded in the three sites from October 2020 to November 2021. The Wilcoxon signed rank tests
were used for pairwise comparisons. The alpha value was set at 0.05, and the Bonferroni
adjustment was applied for multiple comparison Significance codes: ****p <0.0001 = 0; **p <
0.01; ns = non-significant.



Figure 6: Mean (± SE) juvenile densities (expressed as N. of individuals per 100 m²) of the seven fish
 species recorded in the three sites from October 2020 to November 2021. The Wilcoxon signed rank
 tests were used for pairwise comparisons. The alpha value was set at 0.05, and the Bonferroni
 adjustment was applied for multiple comparisons. Significance codes: ****P <0.0001; *P < 0.05; ns
 = non-significant.



applied for multiple comparisons. Significance codes: ****p <0.0001; *p < 0.05; ns = non-significant.



Figure 8: Relative abundance (expressed as %) of the seven juveniles species recorded in the three
study sites (S1-S3), according to habitat type (i.e. *Sabellria alveolata* formations and other rocky
substrates) and their size class (small, medium, and large).

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Figure 9: Monthly mean size (total length TL mm ± SE) variation of *Diplodus sargus* juveniles (N = 173) according to preferential substrate type from the arrival of juveniles (May) until dispersal outside the surveyed sites (August). (a) Line plot showing the mean size variation over time (month), the Wilcoxon signed rank tests were used for pairwise comparisons. The alpha value was set at 0.05,

and the Bonferroni adjustment was applied for multiple comparisons (Significance codes: ***p < 0.001; ns = non-significant). (b) Boxplot of the TL with superimposed regression lines between the two substrate types reporting significant differences in slopes (rate of change in TL) tested with ANCOVA. Values per habitat type were obtained by combining all size measurements of sampled specimens from Site S1 and S2 for *Sabellaria alveolata* reef and Site S3 for hard substrates (i.e. rocks, pebbles, and gravel), respectively, over the entire 2-year study period.

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Figure 10: Mean (\pm SE) relative condition factor (K_n) of *Diplodus sargus* juveniles grouped by size class and habitat type. The Wilcoxon signed rank tests were used for pairwise comparisons. The alpha value was set at 0.05, and the Bonferroni adjustment was applied for multiple comparisons. Significance codes: ****p <0.0001; *P < 0.05; ns = non-significant. Values in parentheses indicate sample size.