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5 **Gigantic breeding colonies of a marine fish in the Mediterranean**

6

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21

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24

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29 SUMMARY: We report the discovery of a massive fish breeding ecosystem in the
30 Mediterranean Sea. On the coast of Corsica Island, the breeding colonies of picarels
31 (*Spicara smaris*) cover more than 134.6 ha between 37 and 50 m deep. More than 18 million
32 nests, each guarded by a male, were estimated, attracting numerous predators, including
33 critically endangered species like angel shark (*Squatina squatina*), and promoting amazing
34 behaviors.

35 CORRESPONDENCE

36 While breeding colonies are well known in seabirds, they remain exceptional for marine
37 fishes. Fifteen massive breeding colonies of picarels (*Spicara smaris*), a small
38 hermaphrodite zooplanktivorous fish, made of nests each guarded by a male, were observed
39 by chance during video transects in spring 2021 along the East coast of Corsica (French
40 Mediterranean). In total, these colonies covered more than 134.6 ha within a surveyed area
41 of 712.1 ha, a single colony covering from 2.2 to 28 ha between 37 and 50 m deep. The
42 seabed, including the lower limit of *Posidonia oceanica* meadows, soft bottoms, and the
43 predominant rhodolith beds, have been completely rebuilt in circular jointed nests measuring
44 55 cm in diameter on average. With a density of 2.6 nests per m², the estimated number of
45 nests exceeds 18 million, each guarded by a male. Females swim in groups above the nests
46 and sometimes lay eggs. A rich macrofauna including threatened species (IUCN red list) can
47 be observed around the nests, eating eggs or adults. This finding highlights the exceptional
48 ecological role of this small fish as an ecosystem engineer crating oasis of marine life. This
49 warrants further studies and better protection of the area, at least during this short breeding
50 season.

51 Picarels, *Spicara smaris* Linnaeus 1758 (Actinopterygii: Sparidae), are benthopelagic
52 marine fish found all around the Mediterranean Sea, Black Sea, and the surrounding Atlantic
53 coasts including the Canary Islands¹. *S. smaris* is a protogynous hermaphroditic species, it
54 starts life as a female before becoming a male, with one seasonal breeding peak per year
55 from spring to autumn depending on the locality². During this period, males (20 cm long)
56 display a more intense blue coloration, gather in large groups and dig small circular
57 depressions over which they parade³. In these nests, the females (up to 15 cm long) lay
58 sticky eggs that are immediately fertilized by the male. Each male then actively protects and
59 ventilates the eggs⁴ in his nest. This aggregative breeding strategy has been known for
60 several decades³ but has only been described in four sites along the French Mediterranean
61 continental coast^{5,6}. Yet, the number and extent of these aggregations, the factors
62 influencing site choice, the distances travelled by breeding adults to reach them, and the
63 ecological role of these aggregations remain unknown.

64 In May 2021, fifteen picarel breeding colonies were discovered during a large-scale survey
65 focusing on the critically endangered angel shark (*Squatina squatina*)⁷. These colonies were
66 spaced from 150 m to 2500 m. The nests were close to each other (Figure 1) and clearly
67 differentiated from the surrounding seabed by the absence of any macroalgae or other
68 organisms inside the nests themselves, and by uniform sediments with a roughness lower
69 inside the nest (1.02) than at the edge (1.18) (t-test, $p < 0.001$). Each active nest contained
70 thousands of 0.5-mm eggs guarded by a male showing his large raised dorsal fin (Figure 1).
71 Four weeks after our observation (early June 2021), the nests were no longer visible,
72 confirming the ephemeral nature of these engineered ecosystems.

73 Depositing the eggs on the gravel may maintain aeration and cleanliness while nest edges
74 (1.39 to 7.67 cm high; average 3.84 cm) may prevent the eggs from being swept away or
75 facilitate surveillance by the males. Males may also aerate the eggs by moving their caudal
76 fin (fan) in the same way they maintain the integrity of the nests. Paternal care is a scarce
77 phenomenon in marine fishes (16% of families) compared to their freshwater counterparts
78 due to the lower environmental fluctuations in the ocean⁸. Divers observed male guardians

79 repelling benthic predators (hermit crabs, rays) with mouth and caudal fin strikes. Certain
80 troublesome elements (Codium algae, sand urchins) can even be passed from male to male
81 until they were thrown away from the breeding area. Divers also observed sudden looting
82 behavior. With no obvious trigger, all the males in the vicinity suddenly pounced on a nest
83 and devoured the eggs in a matter of seconds before returning to guard their own nest.
84 Video analyses (see also Table S1) revealed that a male spends an average of 91 % of his
85 time defending the nest (, 6 % maintaining the nest and regularly "pecking" the sediment
86 around and in the nest, and 1 % interacting with females. The remaining 2 % of the time
87 period could not be analyzed because the lens was obstructed.

88 Besides picarels, the divers and underwater remote cameras observed species rarely
89 spotted together in such abundance and diversity like cephalopods (*Octopus vulgaris*, *Loligo*
90 *spp*, *Sepia officinalis*) but also predator fishes (*Zeus faber*, *Lophius piscatorius*, *Trachinus*
91 *draco*, *Scyliorhinus canicular*) including IUCN Red List¹⁴ chondrichthyans like *Raja clavata*
92 (Least concern), *Dasyatis sp.*, *Torpedo marmorata* (Vulnerable), *Torpedo torpedo*
93 (Vulnerable) (see also the video in Table S1). They hunted picarels or fed on their eggs. To
94 complement visual observations, we also performed video and environmental DNA surveys.
95 We detected the presence of *Squatina squatina* DNA while the towed camera recorded a
96 *Myliobatis aquila*, a *Dasyatis sp* and octopus nests. Static cameras set among active *Spicara*
97 *smaris* breeding colonies recorded seven other fish species like *Atherina hepsetus*, *Coris*
98 *julis*, *Lichia amia*, *Mullus sp*, *Serranus cabrilla*, *Symphodus cinereus* and *Symphodus*
99 *mediterraneus*.

100 Picarels are known to play a crucial role in the flow of energy between the bottom and top
101 trophic levels of benthic and pelagic food webs in the Aegean Sea⁹. Without having in-depth
102 knowledge of areas covered and seascape ecosystems engineered, local fishers are aware
103 of this phenomenon, which they call "arènes de reproduction" (breeding arenas) and target
104 them for *Z. faber*, but many rays and sharks are also part of by-catch even if they are
105 released alive when possible. The aggregation of angel sharks in these areas might be
106 linked to the concentration of prey and their own life cycle with breeding adults and
107 newborns observed in the same location at the same period.

108 Since 2022, *Spicara spp* has been on the list of additional regulated species recommended
109 by the FAO¹⁰. The temporal survey of the sites reported here could help to improve our
110 knowledge of this fish (population estimates, survival, intra-specific interactions) but also
111 provide important data for improving the conservation of threatened species that still live in
112 this area and guide the future need to achieve 30% of coverage by marine protected areas
113 in the heavily impacted Mediterranean Sea.

114

115 See supplemental Information for complementary results, methods and short videos.

116

117

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146 AUTHOR CONTRIBUTIONS

147 Towed Camera, sonar, eDNA: FH, AB, JD, NF; Photogrammetry: FH for acquisition, GM for
148 modelling and analyses; Temperature sensor (set and analysis): FH, GM, Environmental
149 data analysis: TB; Images: AB and LB; Video analysis: AB; Writing and editing: all the
150 authors; Group leader, coordination: JD, DM and FH

151

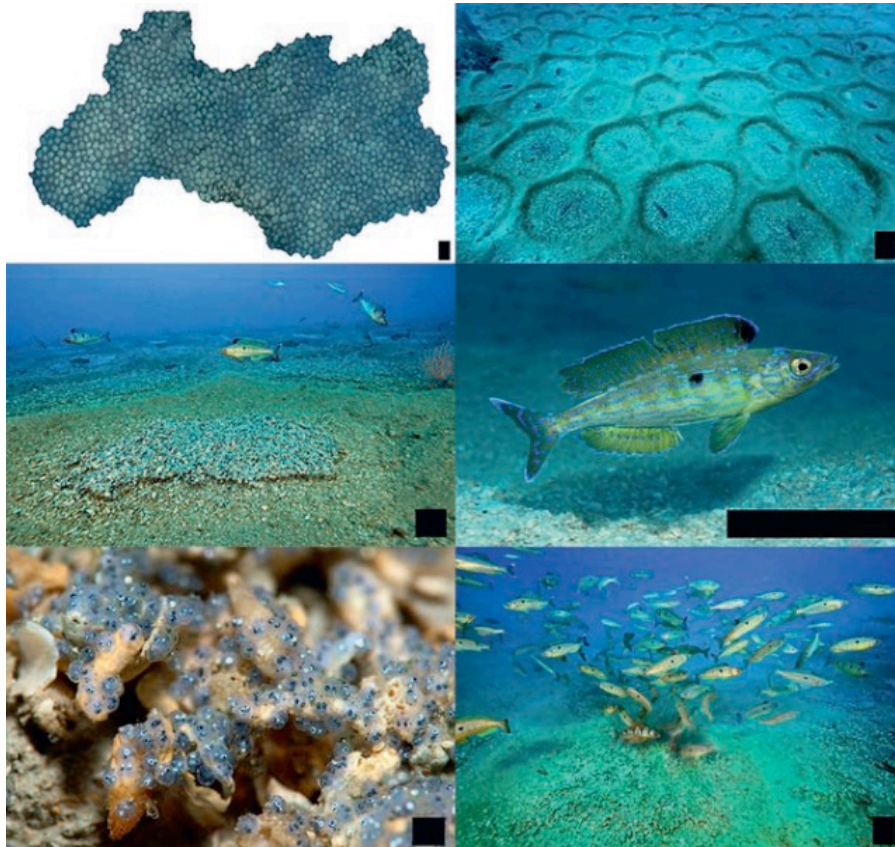
152 DECLARATION OF INTERESTS

153 Florian Holon and Laurent Ballesta are two of the three co-founders of Andromède
154 océanologie.

155

156

157 FIGURE LEGENDS



158

159 **Figure 1. Picarel breeding colony**

160 *Spicara smaris* breeding colonies cover hectares and are constituted of hundreds circular
161 hexagonal depressions (A, see also Figure S1), each one guarded by one male (B, C)
162 showing an accentuated blue color (D). Thousands embryonated eggs are clearly visible in
163 the nests (E). Observation of intra-specific aggressive behavior with a male individual under
164 attack (in the centre) showing marked contrasting colors (F). A corresponds to a captured 3D
165 model of a breeding colony portion (497 m²), constructed using photogrammetry; B-E are
166 photos by the photograph Laurent Ballesta.

167

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