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Gigantic breeding colonies of a marine fish in the Mediterranean

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

CORRESPONDENCE

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

Picarels, *Spicara smaris* Linnaeus 1758 (Actinopterygii: Sparidae), are bentho-pelagic marine fish found all around the Mediterranean Sea, Black Sea, and the surrounding Atlantic coasts including the Canary Islands[1]. *S. smaris* is a protogynous hermaphroditic species, it starts life as a female before becoming a male, with one seasonal breeding peak per year from spring to autumn depending on the locality[2]. During this period, males (20 cm long) display a more intense blue coloration, gather in large groups and dig small circular depressions over which they parade[3]. In these nests, the females (up to 15 cm long) lay sticky eggs that are immediately fertilized by the male. Each male then actively protects and ventilates the eggs[4] in his nest. This aggregative breeding strategy has been known for several decades[3] but has only been described in four sites along the French Mediterranean continental coast[5,6]. Yet, the number and extent of these aggregations, the factors influencing site choice, the distances travelled by breeding adults to reach them, and the ecological role of these aggregations remain unknown.

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

Depositing the eggs on the gravel may maintain aeration and cleanliness while nest edges (1.39 to 7.67 cm high; average 3.84 cm) may prevent the eggs from being swept away or facilitate surveillance by the males. Males may also aerate the eggs by moving their caudal fin (fan) in the same way they maintain the integrity of the nests. Paternal care is a scarce phenomenon in marine fishes (16% of families) compared to their freshwater counterparts due to the lower environmental fluctuations in the ocean[8]. Divers observed male guardians

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

Besides picarels, the divers and underwater remote cameras observed species rarely spotted together in such abundance and diversity like cephalopods (*Octopus vulgaris, Loligo spp, Sepia officinalis*) but also predator fishes (*Zeus faber*, *Lophius piscatorius, Trachinus draco, Scyliorhinus canicular)* including IUCN Red List[14] chondrichthyans like *Raja clavata* (Least concern), *Dasyatis sp*., *Torpedo marmorata* (Vulnerable), *Torpedo torpedo* (Vulnerable) (see also the video in Table S1). They hunted picarels or fed on their eggs. To complement visual observations, we also performed video and environmental DNA surveys. We detected the presence of *Squatina squatina* DNA while the towed camera recorded a *Myliobatis aquila*, a *Dasyatis sp* and octopus nests. Static cameras set among active *Spicara smaris* breeding colonies recorded seven other fish species like *Atherina hepsetus, Coris julis, Lichia amia, Mullus sp, Serranus cabrilla, Symphodus cinereus* and *Symphodus mediterraneus*.

Picarels are known to play a crucial role in the flow of energy between the bottom and top trophic levels of benthic and pelagic food webs in the Aegean Sea[9]. Without having in-depth knowledge of areas covered and seascape ecosystems engineered, local fishers are aware of this phenomenon, which they call “arènes de reproduction” (breeding arenas) and target them for *Z. faber*, but many rays and sharks are also part of by-catch even if they are released alive when possible. The aggregation of angel sharks in these areas might be linked to the concentration of prey and their own life cycle with breeding adults and newborns observed in the same location at the same period.

Since 2022, *Spicara spp* has been on the list of additional regulated species recommended by the FAO[10]. The temporal survey of the sites reported here could help to improve our knowledge of this fish (population estimates, survival, intra-specific interactions) but also provide important data for improving the conservation of threatened species that still live in this area and guide the future need to achieve 30% of coverage by marine protected areas in the heavily impacted Mediterranean Sea.

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

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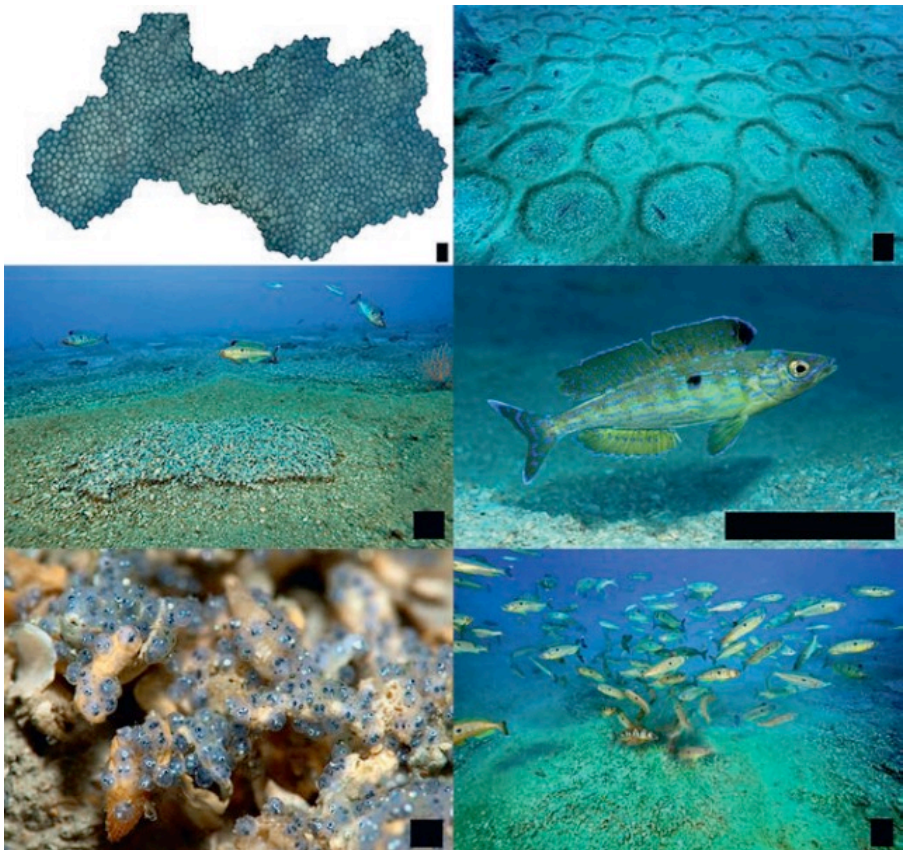
AUTHOR CONTRIBUTIONS

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

DECLARATION OF INTERESTS

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

157 FIGURE LEGENDS



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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.
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198