

SHORT COMMUNICATION

Bivalve living in bivalve shells: The hidden occurrence of the date mussel *Lithophaga lithophaga*

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Abstract: The date mussel *Lithophaga lithophaga* is a protected, long-lived endolithic bivalve typically associated with calcareous rocky substrata. In this study, we report its occurrence within the shells of two bivalve species, opportunistically collected in Mali Ston Bay, Adriatic Sea. Twelve *Ostrea edulis* and five *Spondylus gaederopus* specimens were analysed by carefully examining their shells and extracting the boring bivalves. The shell length, abundance and position of *L. lithophaga* within each host valve were recorded, together with visible alterations of the host shell. In *O. edulis*, *L. lithophaga* ranged from 2.2 to 36.4 mm in shell length, with up to ten individuals recorded in a single host. Larger specimens were restricted to the thicker region of the left valve near the hinge, whereas smaller individuals also occurred in other parts of the shell and in the right valve. Only small individuals were observed in *S. gaederopus*. These findings indicate that the thick shells of bivalves can serve as substrata for *L. lithophaga*. The concealed presence of this strictly protected species within shells of commercially interesting bivalves also raises practical conservation and regulatory questions, because its presence may remain undetected until the host shell is opened or processed.

Keywords: date mussel; endolith; bivalve aquaculture; Mediterranean; Adriatic; *Ostrea edulis*; *Spondylus gaederopus*

Sažetak: ŠKOLJKAŠ KOJI ŽIVI U LJUŠTURAMA ŠKOLJKAŠA: SKRIVENA POJAVA PRSTACA LITHOPHAGA LITHOPHAGA. Prstac *Lithophaga lithophaga* zaštićeni je dugovječni endolitski školjkaš koji je uobičajeno vezan uz vapnenačke stjenovite podloge. U ovom radu izvještavamo o njegovoj pojavi unutar ljuštura dviju vrsta školjkaša, prikupljenih u Malostonskom zaljevu u Jadranskom moru. Analizirano je dvanaest primjeraka vrste *Ostrea edulis* i pet primjeraka vrste *Spondylus gaederopus*, pri čemu su njihove ljuštire pažljivo pregledane, a ukopani školjkaši izvađeni. Zabilježeni su duljina ljuštire, brojnost i položaj *L. lithophaga* unutar svake ljuštire domaćina, kao i vidljive promjene na ljušturi domaćina. Duljine ljuštura *L. lithophaga* ukopanih u vrsti *O. edulis* iznosile su od 2,2 do 36,4 mm, a u jednom domaćinu zabilježeno je deset jedinki. Veći primjerci bili su ograničeni na deblji dio lijeve ljuštire u blizini brave, dok su se manje jedinke pojavljivale i u drugim dijelovima ljuštire te u desnoj ljušturi. U vrsti *S. gaederopus* zabilježene su samo male jedinke. Ovi nalazi pokazuju da deblje ljuštire školjkaša mogu služiti kao podloga za vrstu *L. lithophaga*. Skrivena prisutnost ove strogo zaštićene vrste unutar ljuštura komercijalno zanimljivih školjkaša također otvara praktična pitanja zaštite i primjene propisa jer njezina prisutnost može ostati neotkrivena sve dok se ljuštura domaćina ne otvori ili obradi.

Ključne riječi: prstac; endolit; akvakultura školjkaša; Sredozemno more; Jadransko more; *Ostrea edulis*; *Spondylus gaederopus*

INTRODUCTION

Bivalves are a diverse class of aquatic molluscs, and there are ~ 9200 known species inhabiting various marine habitats (Huber, 2010). They exhibit a wide range of modes of life, including endolithic, which involves boring holes in hard substrata by chemical and/or mechanical means (Collins *et al.*, 2023). The date mussel *Lithophaga lithophaga* (Linnaeus, 1758) is one of the endolithic bivalves inhabiting subtidal calcareous rocks into which it bores chemically using secretions produced by the pallial glands (Jaccarini *et al.*, 1968). It attains a size of 95 mm, with occasional specimens reaching a shell length of 110 mm (Poppe and Goto, 1993).

The distribution of *L. lithophaga* includes the Mediterranean Sea and the Atlantic coasts, from Spain to Angola (Poppe and Goto, 1993). It is a long-lived,

slow-growing bivalve, with age estimates indicating a lifespan exceeding 54 years (Galinou-Mitsoudi and Sinis, 1995; Peharda *et al.*, 2015). Shell growth progressively declines with increasing age, while the excavated borehole is, on average, approximately 1.5 times longer than the shell (Galinou-Mitsoudi and Sinis, 1995). First reproduction occurs at an age of 2+ years and at a shell length greater than 0.9 cm (Galinou-Mitsoudi and Sinis, 1994).

Exploitation of *L. lithophaga* affects not only the target species, but also the calcareous rocky substratum and the associated benthic assemblages, because extraction requires the physical demolition of the rock in which the bivalves live (e.g., Hrs-Brenko *et al.*, 1991; Fanelli *et al.*, 1994; Colletti *et al.*, 2020). Therefore, date mussel fishing has been described as one of the most destructive human pressures on shallow Mediterranean rocky reefs

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and is forbidden in all Mediterranean countries (see supplement in Colletti *et al.*, 2020) and included in several international and European conservation instruments (Bern Convention, 1979; Council of European Communities, 1992; UNEP/MAP-SPA/RAC, 2018).

Bivalve shells can function as biogenic hard substrata for diverse associated organisms (Mackensen *et al.*, 2012). In the Mediterranean Sea, *Rocellaria dubia* (Pennant, 1777) is the best-documented native bivalve borer inhabiting the shells of oysters *Ostrea edulis* Linnaeus, 1758 and *Magallana gigas* (Thunberg, 1793), but also several other bivalve species, including *Glycymeris nummaria* (Linnaeus, 1758), *Modiolus barbatus* (Linnaeus, 1758), *Pinna nobilis* Linnaeus, 1758, *Spondylus gaederopus* Linnaeus, 1758, and *Venus verrucosa* Linnaeus, 1758 (Trigui El-Menif *et al.*, 2005; Šiletić, 2006; Morton *et al.*, 2011; Ćurin *et al.*, 2014; Mikac *et al.*, 2021). To the best of our knowledge, boring by *L. lithophaga* has not previously been documented in live-collected bivalve shells from the Adriatic Sea. However, the fossil record from South Dobrogea, Romania, provides evidence of *L. lithophaga* boring into the thick valves of the extinct oyster †*Cubitostrea fimbriata crassa* (Munteanu and Munteanu, 2001), while the species has also been reported to be encapsulated within the shell of the non-indigenous Indo-Pacific bivalve *Spondylus spinosus* Schreibers, 1793 in the Gulf of Iskenderun, eastern Mediterranean (Delongueville and Scaillet, 2006).

Outside the Mediterranean Sea, several rock-boring mussels of the family Mytilidae have been investigated as endolithic borers of oyster shells. In the south-western Atlantic, *Leiosolenus patagonicus* (A. d'Orbigny, 1846) has been studied in living *Ostrea puelchana* A. d'Orbigny, 1842, while borings have also been examined in the fossil oysters *Cubitostrea alvarezii* (A. d'Orbigny, 1839) and *Crassostrea patagonica* (A. d'Orbigny, 1839), with research addressing the abundance and distribution of borings within the valves, age and growth, effects on oyster condition, and substrate-related variation in mussel shell morphology (Mauna *et al.*, 2005; Bagur *et al.*, 2013; Diez *et al.*, 2014). In the north-western Gulf of Mexico, *Leiosolenus bisulcatus* (A. d'Orbigny, 1853) was recorded boring into living *Crassostrea virginica* (Gmelin, 1791) and *Ostrea equestris* Say, 1834, while *Leiosolenus aristatus* (Dillwyn, 1817) was also found in *O. equestris*. On the Mexican Pacific coast, *L. aristatus* was documented as an endobiont of the rock oyster *Striostrea prismatica* (J.E. Gray, 1825) (Sanchez-Telumbre *et al.*, 2021). *Leiosolenus plumula* (Hanley, 1843) was recorded as a boring endobiont of *Spondylus crassiquama* Lamarck, 1819 off the northern coast of Ecuador (Mackensen *et al.*, 2012). In all studies cited above, the species currently assigned to *Leiosolenus* P.P. Carpenter, 1857 were reported under the genus *Lithophaga*; however, subsequent phylogenetic analyses supported the recognition of *Leiosolenus* as a distinct genus (Owada, 2007; Liu *et al.*, 2018).

Two relatively large, thick-shelled bivalve species

occurring in the Mediterranean Sea, *O. edulis* and *S. gaederopus*, may provide suitable substrata for colonisation by *L. lithophaga*. The European flat oyster, *O. edulis*, is a native bivalve of high ecological and economic importance in European marine ecosystems and occurs in both natural populations and aquaculture (Antepli *et al.*, 2026; Ezgeta-Balić *et al.*, 2026). It naturally attaches to the substrate with its left valve. The European thorny oyster *S. gaederopus* is a relatively large-sized edible bivalve. Adults occur mainly on shallow sublittoral hard substrata at relatively low density, where they are cemented to rocks or dead coral with their right valve (Lamprell *et al.*, 2001; Galinou-Mitsoudi *et al.*, 2019).

The aim of this study is to report and characterise the occurrence of *L. lithophaga* within the shells of the European flat oyster *O. edulis* and the European thorny oyster *S. gaederopus*, with particular emphasis on the abundance and size of the boring individuals, their distribution within the host valves, and the shell alterations associated with their presence.

MATERIAL AND METHODS

Specimens of the European flat oyster (*Ostrea edulis*; N=12) and the European thorny oyster (*Spondylus gaederopus*; N=5) with *Lithophaga lithophaga* in their shells were opportunistically collected from the wild. They were harvested by commercial fisherman in the Mali Ston Bay (~3 m depth, Adriatic Sea; ~42° 55' 25" N, 17° 31' 44" E) during the spring and summer of 2026 (see Table 1). Upon collection, specimens were kept frozen until transportation to the laboratory at the Institute of Oceanography and Fisheries in Split, Croatia. In the laboratory, oyster shells were slowly defrosted, measured using vernier callipers, and photographed. Their shells were carefully fragmented to enable the extraction of *L. lithophaga* shells and the evaluation of their abundance and size. The shell length of each extracted *L. lithophaga* was measured using a vernier calliper and millimetre paper. Because oyster shells were not stored in individual plastic bags upon collection, two *L. lithophaga* specimens were accidentally removed from their hosts during transport and processing, and we could not link them to their host shell (OE_9 and OE_11). In such cases, a note was made, and the *L. lithophaga* shell was not measured. Age of *O. edulis* was estimated based on information provided by local fishermen and aquaculture producers. Due to the extreme hardness and density of cross-lamella shell structure of *S. gaederopus* (Kennedy *et al.*, 1969), only some shells of *S. gaederopus* were fragmented, while others were examined under a microscope and *L. lithophaga* specimens present in them were counted. The age of *S. gaederopus* specimens was estimated from growth rings visible on their external shell surface. To validate these age estimates, we cut the specimen SG_5 through the hinge region, using a Struers Labotom-3 saw, and counted the growth rings. Photographs were taken using an Olympus OM-D E-M5

Table 1. Data on collected specimens, including date of collection, host specimen size (OE = *Ostrea edulis*, SG = *Spondylus gaederopus*, L – shell length, H – shell height, W – shell width, N – number of *Lithophaga lithophaga* in host shell). All measurements are presented in millimetres.

ID	Date	L	H	W	N in right valve	L in right valve	N in left valve	L in left valve
OE_1	1 st Jul 2026	106	109	32	1	10.1	1	23.8
OE_2	1 st Jul 2026	69	91	51	1	7.0	1	36.4
OE_3	5 th Jul 2026	82	110	52	0		1	31.0
OE_4	5 th Jul 2026	73	95	37	0		8	2.5, 8.0, 9.4, 10.5, 11.8, 13.2, 18.0, 24.8
OE_5	5 th Jul 2026	56	105	23	0		1	22.4
OE_6	5 th Jul 2026	72	91	34	0		1	11.9
OE_7	5 th Jul 2026	73	109	47	3	8.0, 9.7, 12.7	4	14.0, 16.7, 30.0, 30.6
OE_8	5 th Jul 2026	97	109	33	0		1	18.6
OE_9	5 th Jul 2026	85	74	32	4	4.5, 5.0, 10.1, 11.4	1	*
OE_10	5 th Jul 2026	85	91	39	6	2.2, 2.9, 3.5, 3.9, 5.1, 5.5	4	4.9, 16.1, 20.1, 25.3
OE_11	5 th Jul 2026	77	67	31	0		1	*
OE_12	5 th Jul 2026	66	70	21	0		1	19.6
SG_1	15 th Mar 2026	86	112	51	0		22	<10**
SG_2	29 th Apr 2026	91	108	54	0		1	8.0
SG_3	Spring 2026	84	92	61	0		5	<10**
SG_4	5 th Jul 2026	91	104	52	2	<10**	11	<10**
SG_5	5 th Jul 2026	91	93	63	1	<10**	2	<10**

* Holes of *L. lithophaga* from which the shell was lost during the transportation of samples, so shell length measurements were not possible.

** Due to the hardness of *S. gaederopus* shells, it was not possible to fragment them to extract all small *L. lithophaga* specimens without damaging them, so their number was estimated by counting holes with *L. lithophaga* present under microscope magnification. Their shell size was conservatively estimated as <10 mm based on one extracted specimen.

Mark III digital camera equipped with an M. Zuiko Digital ED 30 mm f/3.5 Macro lens and a Zeiss Stemi 508 microscope equipped with an AxioCam 212 color camera.

RESULTS AND DISCUSSION

Lithophaga lithophaga were found living in the shells of all live-collected *Ostrea edulis* and *Spondylus gaederopus* specimens from Mali Ston Bay. A total of 12 *O. edulis* shells were analysed, with shell lengths ranging from 56 to 106 mm (Table 1). We found evidence of

Lithophaga lithophaga in all 12 left (concave) valves, but only in the right (flat) valves of five analysed oysters. In the left valves of two *O. edulis* specimens (OE_9 and OE_11), clearly recognisable *L. lithophaga* holes were present, but associated specimens were not measured, as they were accidentally removed from their holes during transport. Lengths of extracted *L. lithophaga* ranged from 2.2 to 36.4 mm, and specimens larger than 13 mm were found only in the left valve near the hinge area, where the *O. edulis* shell is the thickest and oldest chronologically, as that part of the shell is deposited during early ontogeny (Fig. 1). No specimens of *L. lithophaga*

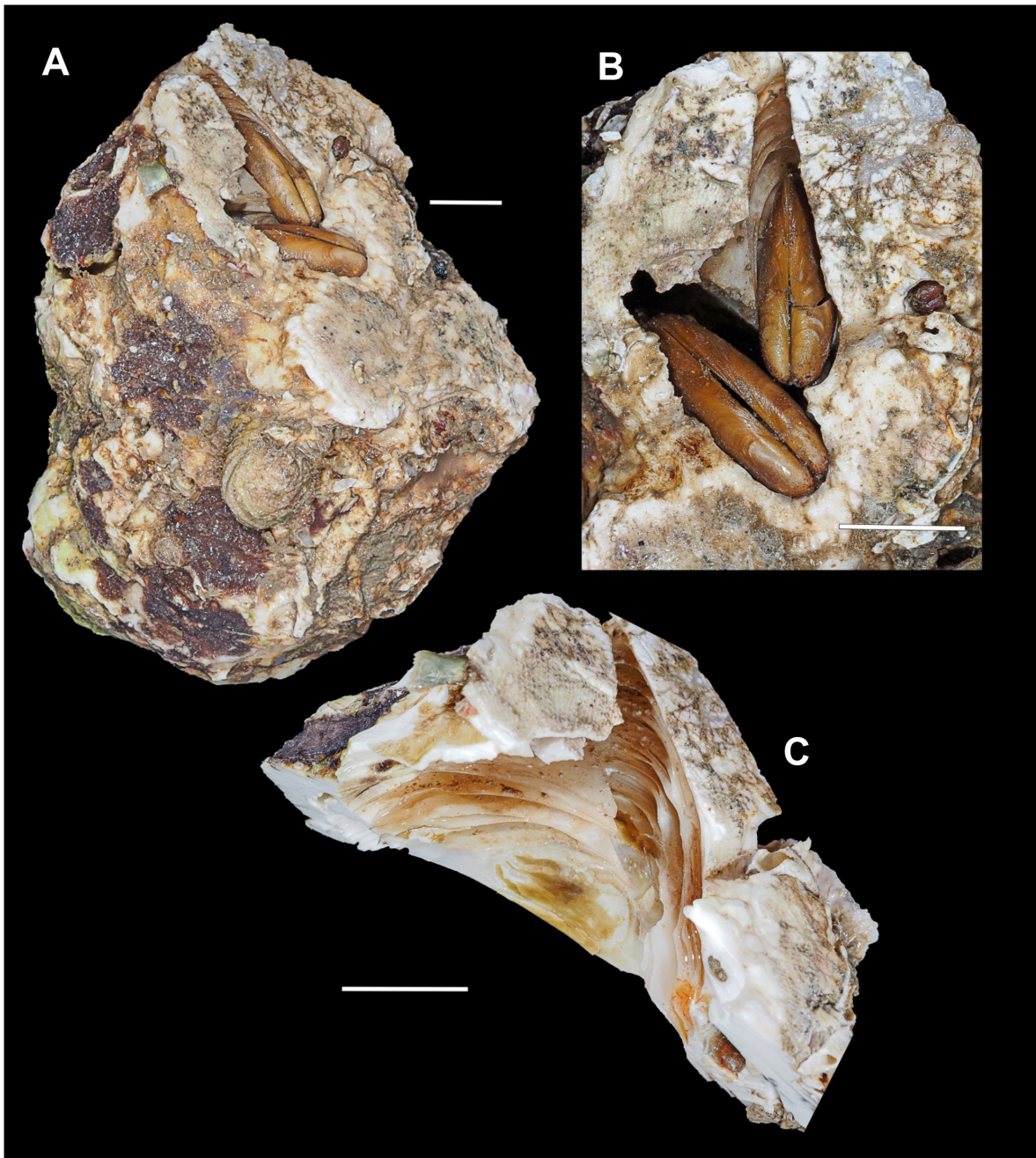


Fig. 1. *Lithophaga lithophaga* in *Ostrea edulis* (OE_4) shell **(A)**; close-up of two *L. lithophaga* specimens with shell lengths of 24.8 and 18.0 mm **(B)**; appearance of holes in *O. edulis* shell made after removal of *L. lithophaga* showing the shell layers **(C)**. Scale bars: 1 cm.

were found near *O. edulis* shell margin. Left and right oyster valves are structurally different, and the left one, due to its thickness and shell structure, seems to provide more favourable physical conditions for *L. lithophaga* growth. A future study should map the position within the host shell and size of *L. lithophaga* specimens to better understand preferred bioerosion areas. Such analysis should include both wild and aquaculture *O. edulis* populations.

Consistent with the present findings, Mauna *et al.* (2005) and Diez *et al.* (2014) found a similar pattern for

the related boring mytilid *Leiosolenus patagonicus* in *O. puelchana*, while Mauna *et al.* (2005) reported the same pattern in the fossil oyster *Cubitostrea alvarezi*, with borings more abundant in the left valve and concentrated mainly in the thicker shell regions around the umbo and hinge area. In contrast, no difference in boring abundance between the left and right valves was observed in fossil oyster *Crassostrea patagonica*, which the authors related to its different life habit, with the shells oriented almost vertically. Munteanu and Munteanu (2001) likewise reported *L. lithophaga* borings in thick

fossil oyster valves, particularly around the umbo. The maximum number of *L. lithophaga* shells extracted from one single analysed *O. edulis* was 10 (OE_10), and they ranged from 2.2 to 25.3 mm, most likely representing different recruitment years. As the estimated age of these *O. edulis*, based on their size and information obtained from the aquaculture producers and local fishermen, is two to three years, the maximum age of the extracted *L. lithophaga* with a shell length of 36.4 mm (present in OE_2) is less than three years.

The analysed *S. gaederopus* specimens contained only smaller-sized *L. lithophaga* specimens and they were visible on the external shell surface of the host shell (Fig. 2). The largest number (22) of *L. lithophaga* specimens was found in a left valve of the shell SG_1 (Table 1), and their estimated shell lengths were <10 mm. In one of the analysed shells (SG_4), one *L. lithophaga* specimen was observed boring between the shell of its main host and its epibiont *Chama gryphoides*, with visible boring areas in shells of both species. Based on growth rings observed on the external shell surface of the analysed *S. gaederopus* specimens, and growth rings in the shell cross-section of specimen SG_5, age of all analysed *S. gaederopus* specimens was estimated at ~5 years.

While *O. edulis* shells consist of prismatic calcite foliated with chalk lenses and are therefore soft and brittle, *S. gaederopus* shells contain internal layers of crossed lamellar microstructures (e.g., Kennedy *et al.*, 1969), and are much harder and more challenging for boring. The type and hardness of substrate influence the growth rates of endolithic bivalves (e.g., Devescovi and Iveša, 2008; Bagur *et al.*, 2013). Thereby, the shell structure and hardness of *S. gaederopus* most likely limit the growth rates of *L. lithophaga* and influence their position. In the examined host specimens, *L. lithophaga* made larger holes in *O. edulis* shells than into *S. gaederopus* (see Fig. 2 vs Fig. 3). This was achieved by drilling at a smaller angle, almost parallel to the host growth, as it is visible in Fig. 2. In cases of both host species, some *L. lithophaga* penetrated through the entire host shell thickness. It is possible that larger-sized *L. lithophaga* can live in *S. gaederopus*, but as this species is relatively rare, targeted sampling should be conducted to evaluate the relationship between these two bivalve species.

Žuljević *et al.* (2018) observed a massive *L. lithophaga* spawning event in the coastal area of Hvar Island, Adriatic Sea, in late August and early September. The observations are consistent with earlier studies, including Galinou-Mitsoudi and Sinis (1994), according to whom gamete release in Greek waters occurs almost simultaneously after a decline in the highest water temperatures. The observed range of *L. lithophaga* shell lengths indicates that they probably represent several different recruitment years, including possibly fall 2025 (~10 mm), fall 2024 (~20 mm) and fall 2023 or earlier (>30 mm). Furthermore, the smallest *L. lithophaga*

(~2 mm) might indicate recruitment during different parts of the year, which is in accordance with findings of Galinou-Mitsoudi and Sinis (1994), who observed a lower percentage of mature individuals during winter months.

The presence of *L. lithophaga* causes changes in the shell deposition process, as the host shell needs to deposit additional shell material in order to protect itself. While holes caused by endolithic organisms are visible on the host external shell surface, disruptions in shell deposition are often more evident on the internal shell surface (Figs. 2D, 3A). Other endolithic organisms can also disrupt the shell growth of the host, including the bivalve *Rocellaria dubia* (Morton *et al.*, 2011). In our study, *R. dubia* was observed in both *O. edulis* and *S. gaederopus*. Previous studies have clearly documented boring by *R. dubia* in shells of several bivalve species, including oysters (Morton *et al.*, 2011; Mikac *et al.*, 2021). Besides its impact on the shell, Mikac *et al.* (2021) pointed out that infestation by *R. dubia* can affect the soft tissues of the host, causing a decrease in the fitness of aquaculture *M. gigas*. As the estimated longevity of *L. lithophaga* ~54 years (Galinou-Mitsoudi and Sinis, 1994; Peharda *et al.*, 2015) exceeds that of *O. edulis* 14 years (Richardson *et al.*, 1993) and *S. gaederopus* 18 years (Galinou-Mitsoudi *et al.*, 2019), growth of *L. lithophaga* individuals boring in these bivalve hosts could ultimately have both sublethal and lethal effects on the host organism.

The occurrence of *L. lithophaga* within commercially harvested oysters raises a previously unrecognised conservation and regulatory issue. *Lithophaga lithophaga* is listed as a strictly protected species, and its deliberate capture or killing is prohibited (Bern Convention, 1979; Council Directive 92/43/EEC, 1992; UNEP/MAP-SPA/RAC, 2018). In fishing activities, accidentally caught specimens must not be harmed and must be promptly released into the sea. However, these provisions are difficult to apply when *L. lithophaga* is completely enclosed within an oyster shell. In the specimens examined here, its presence became apparent only later on, once ashore, after careful inspection of the shell. This may create regulatory uncertainty for fishers, aquaculture producers, inspectors and conservation authorities, particularly because oysters are commercially important species that are routinely harvested and processed.

The principal conservation rationale for protecting *L. lithophaga* is the severe and potentially long-lasting destruction of shallow Mediterranean rocky habitats caused by its targeted extraction (e.g., Fanelli *et al.*, 1994; Guidetti and Boero, 2004; Colletti *et al.*, 2020). The species is additionally vulnerable because of its slow growth and considerable longevity, which limit the recovery rate of exploited populations (Peharda *et al.*, 2015; Colletti *et al.*, 2020). In contrast, the incidental removal of individuals inhabiting commercially harvested bivalve species does not require the destruction of natural rocky substrata. Moreover, as noted by Bagur *et*

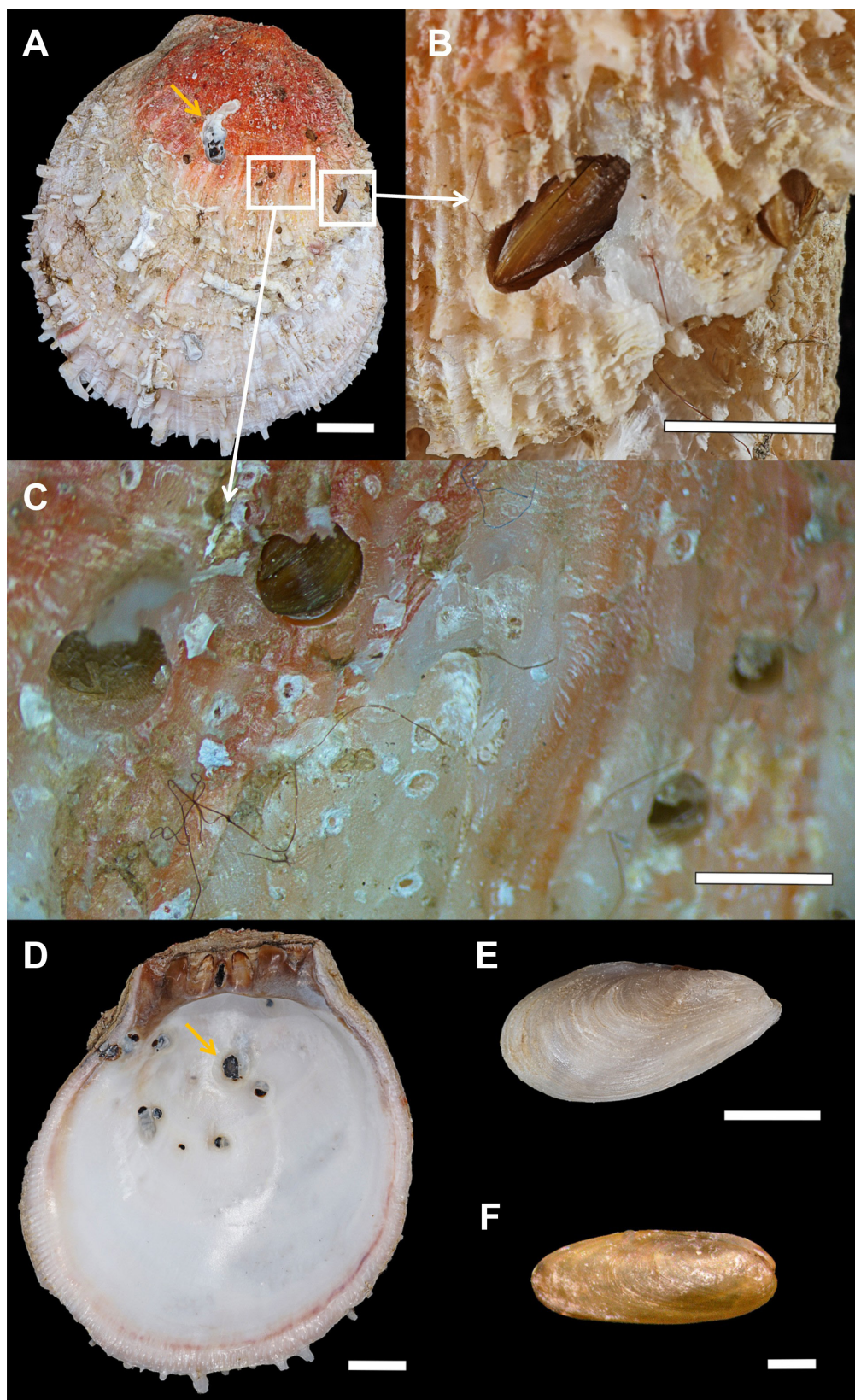


Fig. 2. *Lithophaga lithophaga* in *Spondylus gaederopus* shell (SG_1). External shell surface with *L. lithophaga* holes and the position inhabited by *Rocellaria dubia* indicated by the orange arrow (**A**); areas with *L. lithophaga* marked with white rectangles are shown in close-ups in parts (**B**) and (**C**). Internal shell surface of *S. gaederopus* illustrating disturbance areas (**D**); *R. dubia* specimen extracted from *S. gaederopus* (**E**); *L. lithophaga* specimen extracted from *S. gaederopus* (**F**). Scale bars: A, 1 cm; B, 5 mm; C, 2 mm; D, 1 cm; E, 5 mm; F, 1 mm.

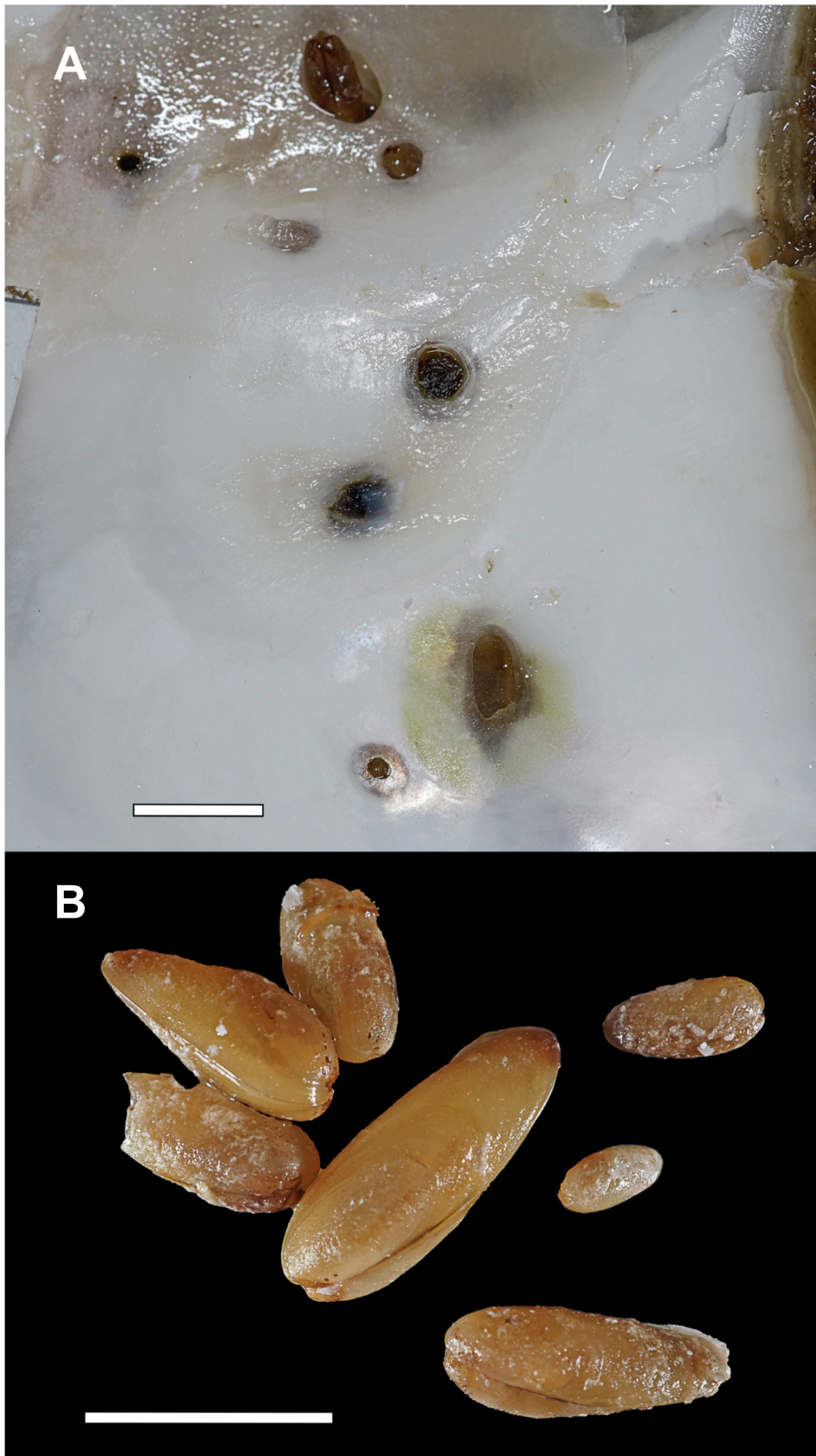


Fig. 3. *Lithophaga lithophaga* in *Ostrea edulis* (OE_10) shell. Inner shell side of *O. edulis* with damage caused by *L. lithophaga* protruding all the way through the shell and showing some evidence of shell repair (**A**); some of the *L. lithophaga* specimens extracted from OE_10 (**B**). Scale bars: 5 mm.

al. (2013), the limited thickness and lifespan of the host shell may constrain the size and longevity attainable by the endolith.

Further research should analyse a larger number of specimens in order to quantify the occurrence of *L. lithophaga* in *O. edulis* shells in their natural habitats as well as in aquaculture. It should be conducted in other parts of the Adriatic and Mediterranean Seas and should include other potential host bivalves that have sufficiently thick shells for survival of *L. lithophaga*.

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DECLARATION OF COMPETING INTEREST

Given her role as Editor-in-Chief of Acta Adriatica, Melita Peharda had no involvement in the peer review of this article and had no access to information regarding its peer review. Full responsibility for the editorial process for this article was delegated to another journal editor.

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