scientific reports

OPEN

Growth and skeletal structure of the parasitic zoantharian *Savalia savaglia* (Bertoloni, 1819)

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The gold coral *Savalia savaglia* parasitizes gorgonians in coralligenous habitats, causing tissue necrosis in its hosts and overgrowing their skeletons with its coenenchyme. While previous studies have mainly focused on its distribution, biology, ecology, and conservation, limited information is available about its skeletal architecture and growth patterns. Photographic observations of the same specimens over time revealed that *S. savaglia* grows rapidly during early colonization, slowing once the host is completely overgrown. In the Tavolara Channel (NE Tyrrhenian Sea), large, old dead specimens—radiocarbon-dated to approximately 800 years—resulted from the coalescence of several colonies, highlighting their evolution over a long timescale. Colonies merge when trunks or apical branches come into contact, forming polygonal meshes. Scanning Electron Microscopy (SEM) analysis revealed a laminar skeletal structure covered with small blunt spines, resembling those observed in antipatharians. These spines cement adjacent layers, increasing the skeleton's resistance to currents and affecting its susceptibility to mechanical damage. These findings support early descriptions by H. Lacaze-Duthiers in the 18th century. Chemical analysis revealed the presence of 7% chitin in the skeleton, along with a high protein content.

Keywords Parazoanthidae, Age estimation, Growth rate, Chitin, Anastomoses

The gold coral *Savalia savaglia* (Bertoloni, 1819) (Anthozoa, Hexacorallia, Zoantharia, Parazoanthidae) is distributed in the Mediterranean Sea and also reported along the Northeastern Atlantic coasts and in Macaronesian region[1,2].

According to Bell[3] the first reference to "*Savaglia*" is attributed to Ferrante Imperato, who cited this species in his *Dell'hystoria naturale*, published in Naples in 1599. The name was also mentioned in the *Opere Postume* of Giuseppe Ginanni and by Vitaliano Donati (in Nardo[4)]. Finally, the species was formally described in 1819 as *Gorgonia savaglia* by the botanist Antonio Bertoloni, based on a specimen present in the collection of Francesco Ginanni, coming from Ragusa (now Dubrovnik) on the eastern coast of the Adriatic Sea[5]. This species was considered to belong to Antipatharia by Milne-Edwards and Haime and called *Leiopathes lamarcki*[6]. Lacaze-Duthiers[7] made the first record of its presence in the western Mediterranean Sea based on specimens collected along the Algerian coast, where Italian red coral fishermen referred to the species as "*Palma Negra*" (black palm tree). In this paper Lacaze-Duthiers considered the species as belonging to a different antipatharian genus named *Gerardia* in honor of his mother recently died. Nardo[4] moved this species within the genus *Savalia* and suggested a separation from the antipatharians due to the number of tentacles. Finally, Carlgren[8] on the basis of the macrocnemic arrangement of the septa, clearly stated the taxonomic position of the species inside Zoantharia.

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Savalia savaglia is one of the few zoantharians capable of secreting a skeleton composed of a hard, multi-layered, proteinaceous material[9,10] allowing for an erect, arborescent corallum. It typically begins growing with an encrusting habitus on the gorgonians' ramifications. Once the host is completely covered, the zoantharian thickens the skeleton over the host's basal plate, stem and major branches and begins producing proper apical branches[3,11].

Lacaze-Duthiers[7] was the first scientist to highlight this unusual parasitic behaviour: "*Définitivement je m'arrêtai à cette opinion, que la* Gerardia *était d'abord à son origine un parasite, mais que plus tard elle sécrétait un axe et déposait un polypier sur les charpentes qui lui avaient servi de premier soutien*". Zibrowius[11] first quantified the phenomenon, estimating through underwater experiments that *S. savaglia* overgrew the branches of the gorgonian *Paramuricea clavata* (Risso, 1827) at a rate of 0.7 cm per month (8 cm in 11 months). Moreover, it is known that the zoantharian can overgrow other gorgonian species, such as *Eunicella* spp. and *Leptogorgia* spp. and it can also be found associated with antipatharians[12]. Finally, colonies have been observed producing an erect, non-parasitic skeleton in areas where gorgonians are rare of absent[9,13].

Due to the increase of recreative diving, this large species, although generally rare, became more and more popular. In 1958, at Punta Manara (Ligurian Sea, Italy), the first north Mediterranean specimens was recorded during a diving survey by the pioneer of scientific diving Gianni Roghi[5,14]. In the following years, the diving activity and, more recently, Remote Operative Vehicle (ROV) prospections demonstrated the wide distribution of this species in the western and eastern Mediterranean basins[15,16]. Today, the occurrence of the species has been assessed in the whole Mediterranean Sea and on the Atlantic coast of Portugal, Spain, the Canary Archipelagos and Madeira[1,17–22]. Most recently the species was recorded along the French Basque coast of the Bay of Biscay, with colonies presumably established on *Paramuricea grayi* (Johnson, 1861) at 35–40 m depth[23]. Also, from the ecological point of view, this species has been the subject of several studies, focusing primarily on its role as an ecosystem engineer[12,] its reproductive biology[24] and its conservation[1,13,25–27]. Additionally, the chemistry of its proteinaceous skeleton was studied, revealing an unusually high concentration of histidine[28,29]. Notably, *S. savaglia* is the only known organism to produce ajugasterone-C, an ecdysteroid previously found only in terrestrial plants[30,31]. Radiocarbon analyses conducted on Pacific gold corals estimated the longevity and slow growth rate of the colonies, showing a radial growth rate of 4 to 35 µm per year. Some colonies have lifespans of thousands of years, with the longest-lived *Savalia* specimens of this genus being as old as 2,700 years[32,33]. No such analyses have ever been carried out on the Mediterranean *S. savaglia*.

Being particularly prone to be damaged or collected by fishing activities[34–36] it is included in Annex II of Specially Protected Areas of Mediterranean Importance (SPAMI-Barcelona Convention) for the protection of threatened species, the Appendix II of the Berne Convention on the Conservation of European Wildlife and Natural Habitats, and currently considered as Near-Threatened by the International Union for Conservation of Nature (IUCN) Red List since 2015 [37]. Despite the increasing interest in this species, the only information available on its growth patterns comes from Lacaze-Duthiers' study, which is over 160 years old. Furthermore, the description of its skeletal architecture is still incomplete, and since Zibrowius' findings in 1985, no additional data have been gathered regarding its parasitic dynamics.

This study aims to provide new insights into the colony morphology, skeletal ultrastructure and composition, growth patterns, and colony radiocarbon age of *S. savaglia*.

Materials and methods

Overgrowth and growth patterns

The temporal dynamics of *Savalia savaglia* overgrowth and subsequent growth were investigated using an extensive underwater photographic archive comprising gorgonian colonies partially or completely covered by the zoantharian coming from different localities of the Mediterranean Sea (Table 1).

The dynamics of *S. savaglia* growth were estimated over time by calculating the positive variation in the fan surface in photos of the same specimen with available metric references and suitable perspectives taken at different time intervals. Considering that the fan shape of the gorgonian host *Paramuricea clavata* is roughly

Locality		Depth (m)	Monitoring period	*N* specimens	Gorgonian condition	Estimated features	Photo credits
Portofino MPA	Ligurian Sea	45	2016; 2022	1	Partially covered	Fan surface	Alessandro Grasso
Costacuti Shoal	C Tyrrhenian Sea	45	2018–2023	1	Partially covered	Fan surface	Alessandro Diotallevi
Mortoriotto, Portorotondo	C Tyrrhenian Sea	35	1966; 2005; 2023	1	Completely covered	Fan surface, branch length	Eleonora de Sabata
Tavolara MPA	C Tyrrhenian Sea	35	2002–2024	1	Partially covered	Fan surface, branch length	Egidio Trainito
Tavolara MPA	C Tyrrhenian Sea	35	2017; 2023	2	Completely covered	Basal plate surface	Egidio Trainito
Capo Carbonara	C Tyrrhenian Sea	35	2017; 2023	1	Completely covered	Basal plate surface	Egidio Trainito
Ustica	S Tyrrhenian Sea	30	2018–2024	11	Completely covered	Fan surface	Maria Cristina Gambi, Riccado Cingillo, Elisa Manganelli, Lucio Bellomo
Scilla	Messina Strait	40	1999–2003	1	Partially covered	Fan surface	Francesco Turano

Table 1. *Savaglia Savalia* colonies examined in the photographic material used for the growth and overgrowth estimation.

planar[38] the fan surface was calculated on the projected area of the branches following the contour of the colony as precisely as possible. When possible, particularly in small specimens, the growth rate of the zoantharian was calculated by estimating the total branch development.

Image analysis was performed using the graphic software ImageJ (1.53t Version)[39].

Finally, the morphological structure of two old, dead, large colonies (C1 and C2) collected by SCUBA diving on 06/10/2023 at 45 m in the Tavolara-Punta Coda Cavallo Marine Protected Area (TPCCMPA) in Northeastern Sardinia (Tyrrhenian Sea) was described. In particular, cross-sections made by diamond saw of the base and apical branches were analysed and photographed under stereomicroscope to describe their internal skeletal structure. The two specimens were deposited in the collection of the Zoological section of the University of Genoa Museum (IZUG-16137; IZUG-16138).

Skeleton ultrastructure

For Scanning Electron Microscope (SEM) observations, portions of the C2 skeleton were washed with distilled water, dehydrated in a series of ethanol solutions of increasing concentration, and dried in a critical point dryer. Finally, they were coated with gold-palladium in a Balzer Union evaporator and examined with a Philips Tescan Vega 3 LM EM 515 SEM. Cross-sections of the skeleton (20 µm thick) were also analysed.

Age estimation

Ten samples, corresponding to basal portions and apical branches of the colony C2, were radiocarbon-dated to reconstruct the temporal development of the colony. The age was obtained by Accelerator Mass Spectrometry (AMS) at the Center of Applied Physics, Dating and Diagnostic (CEDAD) of the University of Salento[40,41].

The selected samples were crushed to powder in a mortar, demineralised by 1% HCl at room temperature and gelatinised in acidified water (HCl, pH = 3) at 85 °C. Gelatine was then filtered on 0.45 µm pore silver filters[42] and then combusted to carbon dioxide in sealed quartz tubes, together with CuO and silver wool and finally reduced to graphite at 600 °C by using hydrogen as a reducing agent and iron powder as a catalyst[43]. The extracted graphite (1 mg ca.) was then pressed in the target holders of the accelerator mass spectrometer for the measurement of $^{14}C/^{12}C$ and $^{13}C/^{12}C$ isotopic ratios. Conventional radiocarbon ages were calculated from the measured isotopic ratios according to[44]. Conventional radiocarbon ages were calibrated to calendar years using the MARINE20 calibration curve valid for marine data[45] and the OxCal Vers. 4.0 Software[46]. A local reservoir correction $\Delta R = -162 \pm 15$ years was used as the average value for the Tyrrhenian Sea obtained from the database[47].

Chitin extraction process

After preliminary treatment and proximate analysis of the C1 and C2 skeleton (Supplementary Material S1), the chitin dosage was performed by applying the protocol reported by Bo et al.[48] with some modifications.

Step 1: The micronised raw material was washed thrice with distilled water at room temperature to remove water-soluble substances, including seawater salts. The total soluble solids (TSS) of the washing solutions were measured by a digital refractometer at 20 °C (Hanna Instruments, Italy) and expressed as Brix degree (°Brix).

Step 2: The protein fraction was extracted with alkali-based extraction at room temperature with a 2.5% w/V NaOH solution, with a solid/solvent ratio equal to 1/10 w/V. This extraction phase removes the alkali-soluble protein fraction, eventual lipids, and pigments. The procedure was repeated until the liquid fraction presented a lighter colour, and its UV-visible spectrum showed no more peaks around 280 nm.

Step 3: The dried alkali-treated material was washed for 2 h with HCl 0.5 M to neutralise the pH, ensure the removal of any acid-soluble proteins, and perform a demineralisation[49]. Then, the purified material was dried in the oven at 37 °C, and the corresponding ATR-FTIR spectrum was recorded and compared to the spectrum of commercial chitin purchased by Sigma-Aldrich S.r.l (CAS number: 1398-61-4).

Finally, the yield of the extracted chitin was calculated by comparing the weight of the final solid residue to the raw material weight (g/100 g).

Attenuated total reflectance fourier transform infrared spectroscopy analysis

The ATR-FTIR spectra of the raw material and the final extract (chitin) obtained after the HCl treatment were recorded using an FT-IR spectrophotometer (Perkin Elmer, Inc., Waltham, MA, US) from 4000 to 600 cm^{-1}, with a resolution of 4 cm^{-1}, collecting 16 scans per sample. The spectrum of commercial chitin (used as a reference standard) has been recorded to compare the extracted product tentatively.

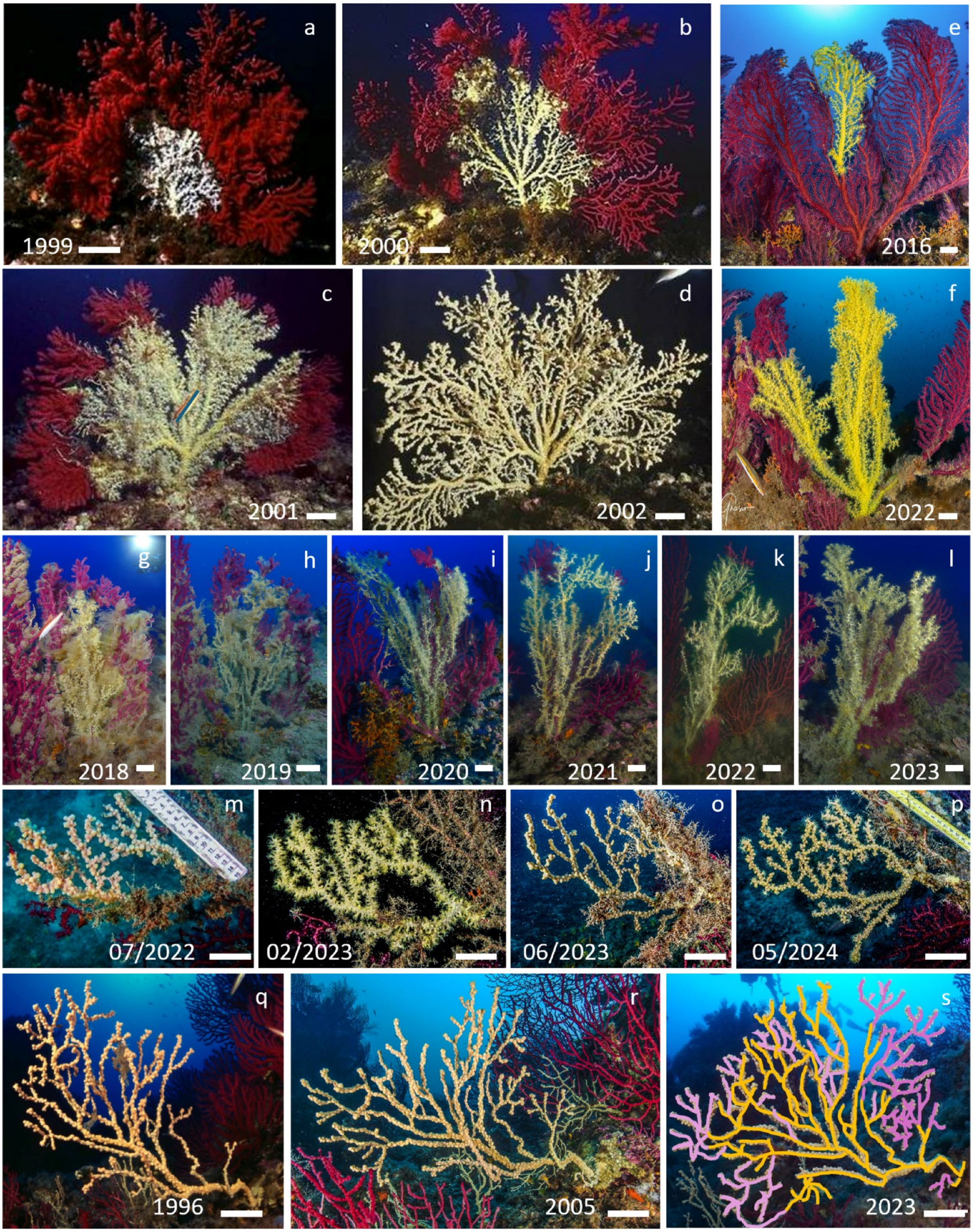
Results

Overgrowth and growth patterns

The overgrowth of gorgonians by *Savalia savaglia* was estimated by comparing images of the same colony taken after different periods (Table 1).

In 1999, a diver grafted a small branch of *S. savaglia* at the base of a colony of *Paramuricea clavata* with a fan surface of 2651 cm^2 at Scilla (Messina Strait) at a depth of 40 m. The development of the graft was annually monitored photographically over four years (Fig. 1a–d). Initially, the gorgonian was affected by the zoantharian on a central portion of the fan, including the basal trunk, covering about 11% of its surface (291 cm^2) (Fig. 1a). Over time, the overgrowth increased exponentially, completely covering the gorgonian in four years, with an annual average increase of 590 cm^2 of fan surface (Figs. 1b–d and 2a).

Another example comes from a colony photographed along the Portofino Promontory (Ligurian Sea) at a depth of 45 m in 2016 and again in 2022. In this case, the colony of *P. clavata* was naturally affected by the epibiosis. The gorgonian consisted of four main branches originating from a short joint base. In 2016, the epibiosis involved the apical portion of a central branch, covering 13% of the total fan surface (372 cm^2) (Fig. 1e).



Six years later, the affected branch was fully colonised from the base to the apex, and a second branch was nearly covered, reaching 61.7% of the *P. clavata* fan surface (1198 cm²) (Figs. 1f and 2b), with an annual increase of about 140 cm².

A long-term series of images (2018–2023) was taken on a colony of *P. clavata* affected by epibiosis (Fig. 1g–l) at Costacuti Shoal, at a depth of 45 m (central Tyrrhenian Sea). At the beginning of the monitoring, the overgrown surface measured 500 cm² (28% of the gorgonian fan surface) and reached 1630 cm² (69%) (Fig. 2c) after five years, with an average annual increase of about 220 cm².

◀**Fig. 1**. Examples of the overgrowth and successive growth of several specimens of *Paramuricea clavata* by *Savalia savaglia* after different periods. (**a–d**) A grafted portion of the zoanthid completely covered the gorgonian of Scilla after four years (1999–2002) (photo credits: Francesco Turano); (**e**, **f**) a specimen recorded at the Portofino Promontory quickly colonised a large portion of the sea fan in six years (2016–2022) (photo credits: Alessandro Grasso); (**g–l**) annual record of *S. savaglia* overgrowth at the Costacuti Shoal from 2018 to 2023 (photo credits: Alessandro Diotallevi); (**m–p**) a new-settled colony on a damaged *P. clavata* monitored four time between 2022 and 2024 at Tavolara – Punta Coda Cavallo MPA; (**q–s**) a colony monitored thrice between 1996 and 2023 at Mortoriotto site, showing the growth after the complete covering of the gorgonian skeleton (**s**, new apical portions are indicated in pink, while gorgonian branches covered by the zoanthid are indicated in yellow) (photo credits: Eleonora de Sabata). Scale bars: 5 cm.

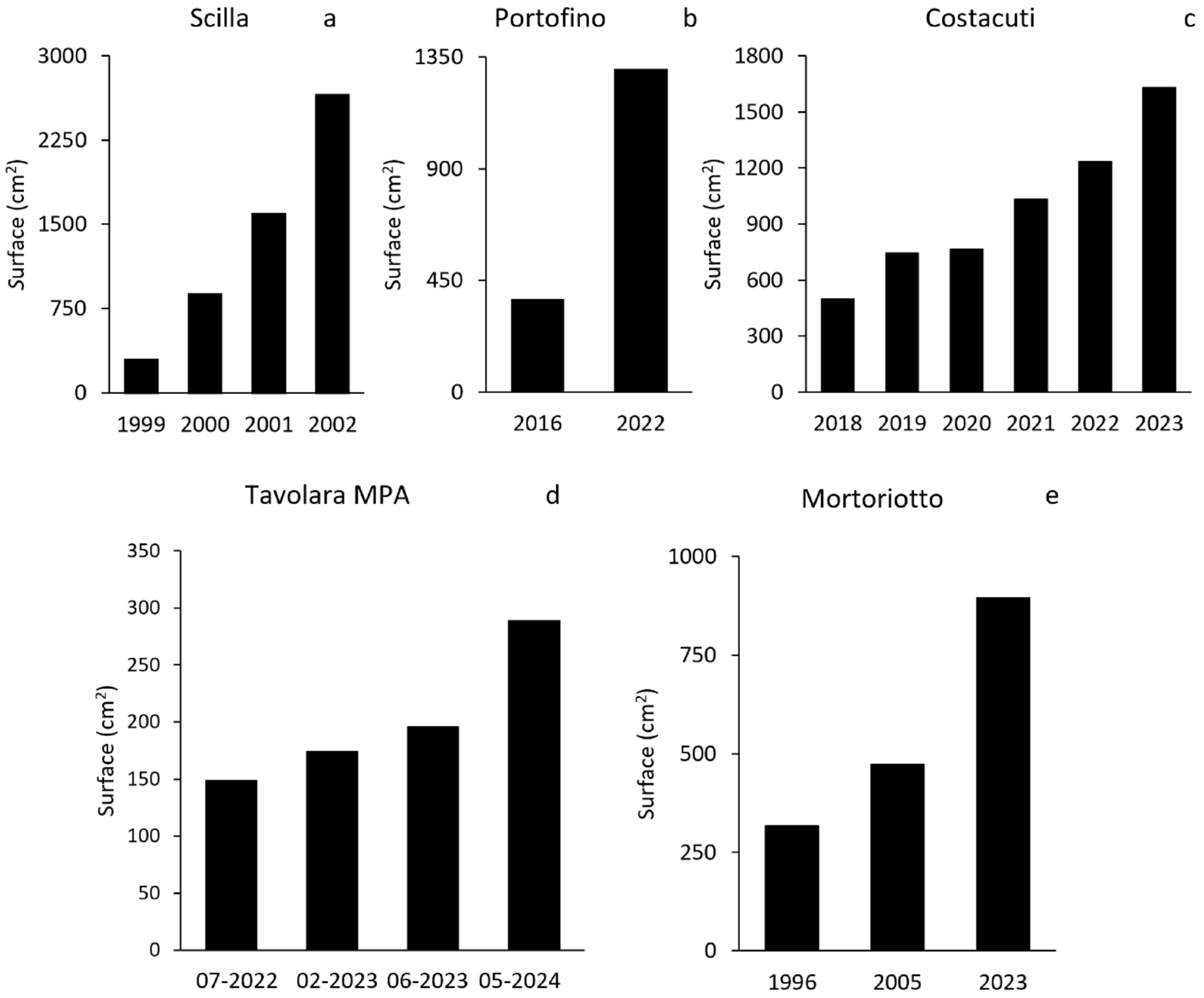


Fig. 2. The annual increase of *Savalia savaglia* surface (cm^2) for (**a**) Scilla, (**b**) Portofino MPA, (**c**) Costacuti, (**d**) Tavolara MPA and (**e**) Mortoriotto specimens.

At the Tavolara Punta Coda Cavallo MPA, a small colony settled on a damaged *P. clavata* was recorded in July 2022 and the growth was followed for 22 months (Figs. 1m–p and 2d); the annual increase resulted in 85 cm^{2}y^{-1} in fan surface. Moreover, the resulting estimated total branch length development was 29 cm per year. When *S. savaglia* finishes covering its host, it continues to grow by producing new branches reinforced only by its proper skeleton. One colony photographed at the Mortoriotto site (Portorotondo, Sardinia) at a depth of 35 m completely covered a *P. clavata* in 1996 (Fig. 1q). The size of the colony increased about 156 cm² of fan surface after nine years (Fig. 1r) and by 423 cm² after further 18 years (Fig. 1s) resulting in a regular annual growth rate of about 21 cm² (Fig. 2e). In this case, the colony doubled its branches after 18 years (from 202 cm in 2005 to 411 cm in 2023), resulting in a linear growth rate of about 11 cm y^{-1}.

At Ustica, eleven colonies at a depth of 30 m fully covered *P. clavata* were monitored over six years (2018–2024). The comparison showed an average surface increase of 63 ± 28 cm^2 per year.

In some cases, the increase in the surface area of the basal plate could be estimated. Two colonies from TPCCMPA and one from Capo Carbonara MPA showed an average annual growth of 5.6 ± 1.3 cm^2 over six years (2017–2023).

Skeleton deposition, coalescence and ultrastructure

The growth of *Savalia savaglia* at a broad time scale was reconstructed by studying the large specimens found dead within the Tavolara MPA (Fig. 3). Specimen C1 was 101 cm tall and 75 cm wide (Fig. 3a, Supplementary Material S2) while specimen C2 was smaller, standing 51 cm high and 21 cm wide at the base. Both colonies exhibited a planar development (Fig. 3b; Supplementary Material S2).

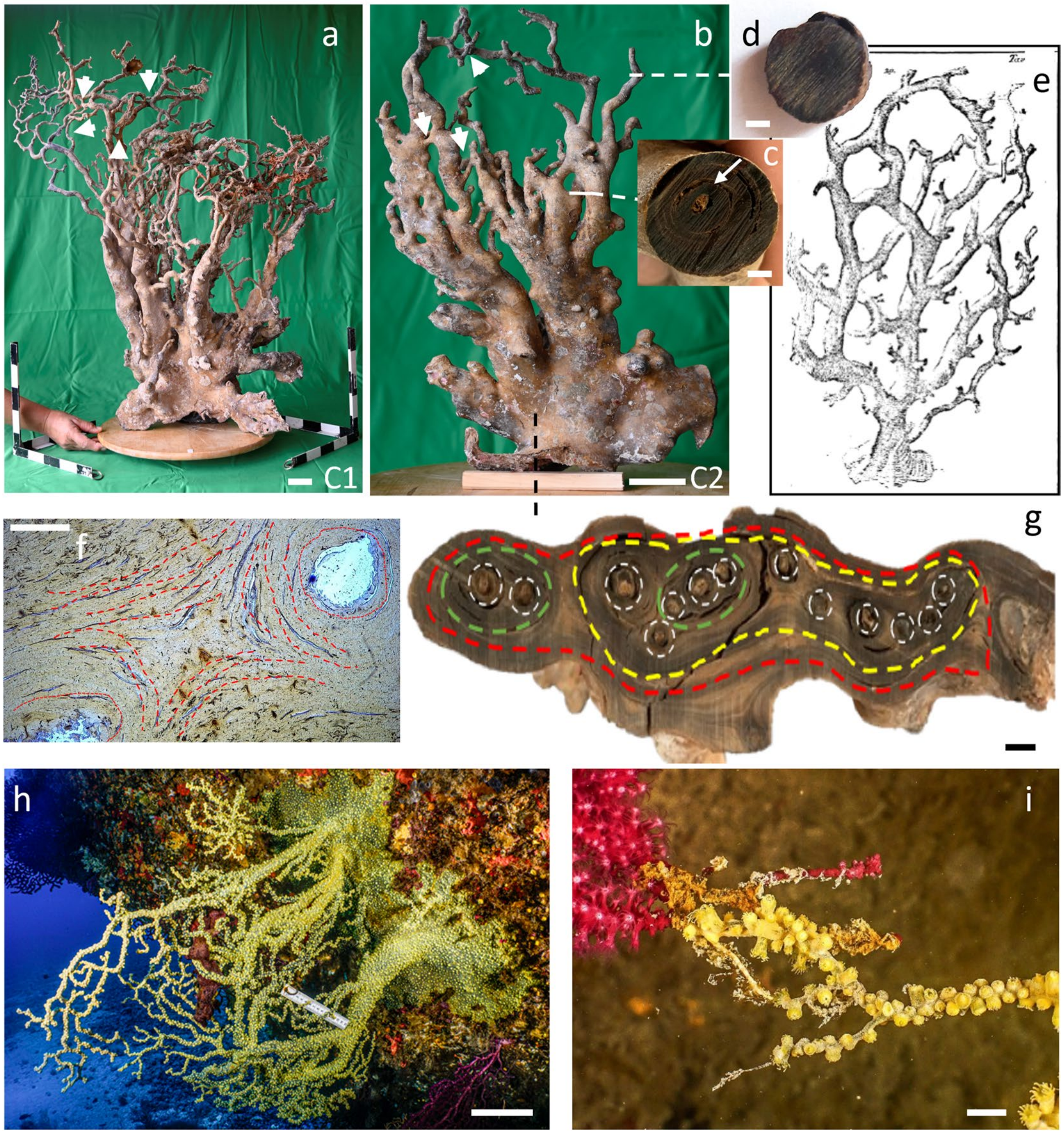


Fig. 3. (**a,b**) The two large dead specimens C1 and C2 of *Savalia savaglia* collected at Tavolara – Punta Coda Cavallo Marine Protected Area, characterized by several anastomosed branches (white arrows); (**c**) cross-section of a large branch where the presence of the gorgonian host is visible in the core (white arrows) and (**d**) apical portion where the gorgonian skeleton is absent. (**e**) Anastomoses of *S. savaglia* branches documented in Ginanni's Opera[56]. (**f**) Cross-section of two anastomosed branches showing merged skeletons (red dotted lines). (**g**) Cross-section of C2 base, highlighting the presence of 13 gorgonian basal plates and stems (white dotted circles) enveloped by *S. savaglia* at different moments (green, yellow and red dotted lines, progressively). (**h**) Basal plates from merging close colonies produce large specimens; (**i**) the colonization of the zoanthid starting from the apical portion of a damaged *Paramuricea clavata* and reaching another close gorgonian. Scale bars: **a**-**b**: 5 cm; **c**: 3 cm; **d**:1 cm; **f**: 500 µm; **g**: 1 cm; **h**: 15 cm; **i**: 1 cm.

When the zoantharian's coenosarc covers the gorgonian, it deposits its organic skeleton on that of the host. When the covering is complete, the zoantharian continues its growth by producing branches, not taking advantage of the strength of the host skeleton. This pattern is easily observable in cross-sections, where the original gorgonian skeleton is visible in the center, encased by a thick layer of the zoantharian's skeleton, which is characterised by notable density (Fig. 3c). When the tips of the branches continue to grow, being supported exclusively by *S. savaglia* skeleton, the cross-sections appear completely homogeneous without any residual skeletal elements from the host (Fig. 3d). These new branches tend to anastomosise with each other's, forming large polygonal meshes (Fig. 3a, b, e). In cross-section, it is evident that when two branches come into contact, their skeletons merge and are coated by a continuous layer of new skeleton enveloping them (Fig. 3f).

A peculiar feature of *S. savaglia* during growth is the coalescence of close colonies. A cross-section at the base of the colony C2 revealed the presence of the skeletons of 13 different colonies, presumably of *Paramuricea clavata* (Fig. 3g). By observing living colonies at Capo Carbonara MPA at 45 m, it can be hypothesised that this process begins with the fusion of the basal plates of different specimens. As the trunks grow in diameter and make contact, they merge thanks to an encrusting layer of new skeleton enveloping them (Fig. 3h). The fusion may also result from the infesting of close colonies (Fig. 3i).

SEM analysis of the skeletal features of *S. savaglia* highlighted its structure, consisting of several concentric layers, each 10–20 µm thick (Fig. 4a). Each layer is covered by numerous conical processes, similar to blunt spines, with a basal diameter of about 50 µm and a height of approximately 80 µm (Fig. 4b). These processes, with a density of 15 ± 2 mm^{-2}, are hollow and appear as depressions on the underside of the layer (Fig. 4c). The processes of one layer interlock with those of the successive one.

Mechanical injuries

The skeletal structure in the oldest colonies of *Savalia savaglia* is tough and rigid but, at the same time, relatively fragile. These characteristics make the colonies extremely prone to mechanical damage, such as that caused by fishing gear. In the Tavolara MPA, mechanical damage affects 38% of the colonies, with large broken branches (Fig. 5a–h). Completely uprooted colonies have also often been observed, still entangled in the fishing lines (Fig. 5i–k). Large branches, broken by mechanical impacts, cannot recover, as demonstrated by ten-year monitoring (Fig. 5a–c; d–f). Some Ustica colonies, living in shallow waters (30 m), showed portions of naked skeleton due to an unknown cause. If the damaged surface involved is small, this damage is recovered in one year (Fig. 5l, m), while wide areas need more time (Fig. 5n, o).

Colony age and growth rate estimation

The radiocarbon age was estimated in different portions of the basal and apical sections of specimen C2 (Fig. 6; Table 2). Starting from the base, the first colony of *Paramuricea clavata* became epibionted approximately 800 years before present (YBP) (1), followed by two other gorgonian colonies, with estimated ages of 550 and 590 years (2). Then, around 315 YBP, these three colonies fused (3) as suggested by the age estimate of a common sheet of skeleton enveloping them (Fig. 6a). This data allowed us to estimate a very low tangential growth rate, ranging from 0.035 to 0.04 mm $year^{-1}$.

A large branch located 19 cm from the base was determined to be 560 years old, while the distal apexes had ages ranging between 330 and 340 YBP (Fig. 6b).

Chitin determination

The preliminary purification step performed on the raw material to eliminate water-soluble compounds showed low values of TSS content, decreasing from 0.3 ± 0.1°Brix in the first washing water to 0°Brix in the last one. Considering that the decrease of the Brix degree is related to the reduction of the extracted water-soluble substances, especially salt, soluble pigments and proteins[50]the third washing water was considered to contain a percentage of proteins and other substances too low to be detected, and the material was considered ready for the following extraction step.

The following alkali-based extraction was performed 12 times until reaching a light colour liquid fraction without a visible peak at 280 nm in the UV-visible spectra to ensure the removal of both the pigments and the alkaline-soluble protein fraction, respectively[50]. Then, the acid treatment (HCl 0.5 M) of the previously alkali-treated material was performed to neutralise the pH, to remove the remaining acid-soluble proteins, and as a demineralisation step[49]. The final yield of the extraction procedure was about 7.1%, which can be attributed to the extracted chitin.

FTIR spectroscopy has been employed as a convenient and non-destructive method for rapidly evaluating and confirming chitin extraction[51]. The ATR-FTIR profile (Fig. 7) of the coral residue seems quite similar to that of one of the commercial chitin used as a reference standard. Slight differences could be attributed to the different origins of the material; in fact, the commercial chitin is extracted from shrimp exoskeletons.

Concerning the evaluated ATR-FTIR profile, the wideband that ranges from 3700 to 3000 cm^{-1} corresponds to the stretching of O-H and N-H bonds. In particular, the peak at 3100–3110 cm^{-1} is associated with NH symmetric stretching and occurs at 3100 cm^{-1} in the chitin extracted from the zoantharian and 3094 cm^{-1} in the commercial chitin. The band around 2890 cm^{-1} represent the stretching vibration –CH2 in the CH2OH groups and is evident at 1880 cm^{-1} in the extracted one and at 2871 cm^{-1} for the commercial one[52]. Amide I band is evident in the range 1600–1680 cm^{-1}, assigned to the C = O group for extracted and commercial chitin. Amide I can be divided into two peaks, as characteristic of α-chitin, evident in the case of the commercial chitin. At approximately 1550–1560 cm^{-1} and 1650–1655 cm^{-1} in the chitin spectrum, corresponding to stretching vibration N–H and C = O (in the NHCOCH3 group), respectively, Amide I can be observed at 1555 cm^{-1} in the extracted and at 1551 cm^{-1} in the commercial[53]. Also, the peaks at about 1310–1320 cm^{-1} (amide III,

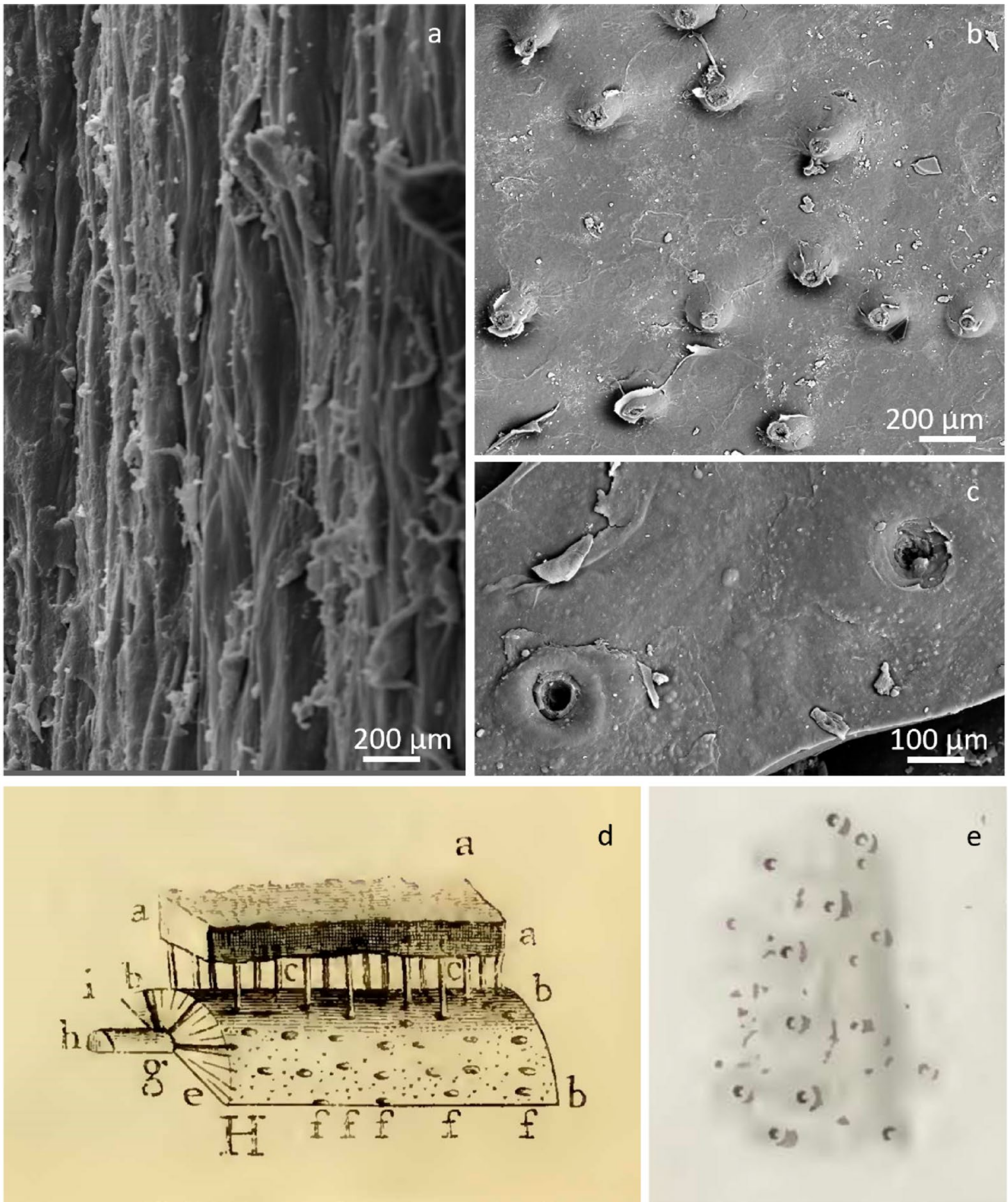


Fig. 4. (**a**) The concentric, tree-like ring arrangement of *Savalia savaglia* skeletal layers. (**b**) The conical processes, similar to spines, appear as depressions on the underside of the layer (**c**). Original drawings of Donati[61] (**d**) and Lacaze-Duthiers[7] (**e**) showing the skeletal structure and tissue organisation of *S. savaglia*. Scale bars: **a**, **b**: 200 µm; **c**: 100 µm.

corresponding to CN stretching) can be observed in the spectra at 1310 cm^{-1} and 1306 cm^{-1} in the extracted and commercial chitin, respectively.

Discussion

This study highlights novel or previously underexplored aspects of *Savalia savaglia*'s growth dynamics. Firstly, although notable variability exists, the zoantharian's colonization of its host appears to be a relatively rapid process. Complete overgrowth clearly requires the parasite's growth rate to exceed that of its host. In a few years, a large gorgonian could be covered entirely (140–220 cm^2 y^{-1}). The extremely high growth rate of the specimen from Scilla (about 600 cm^2 y^{-1}) could be due to the peculiar environmental conditions of the site, characterised by high water movement and consequent high trophic supply[54,55]. Although the present data refer to the covered fan surface of the host, they seem congruent with the data experimentally obtained by Zibrovious[11] recording a linear covering of 9–11 cm y^{-1}.

When the host is completely covered, *S. savaglia* continues its growth, producing branches. Our data indicates a surface increase of 21 cm^2 y^{-1} and a linear growth of the branches of 11 cm y^{-1}. The slower progression of this process, compared to the rapid overgrowth phase, is consistent with the requirement that the internal skeleton of new branch segments must be secreted by the zoantharian itself.

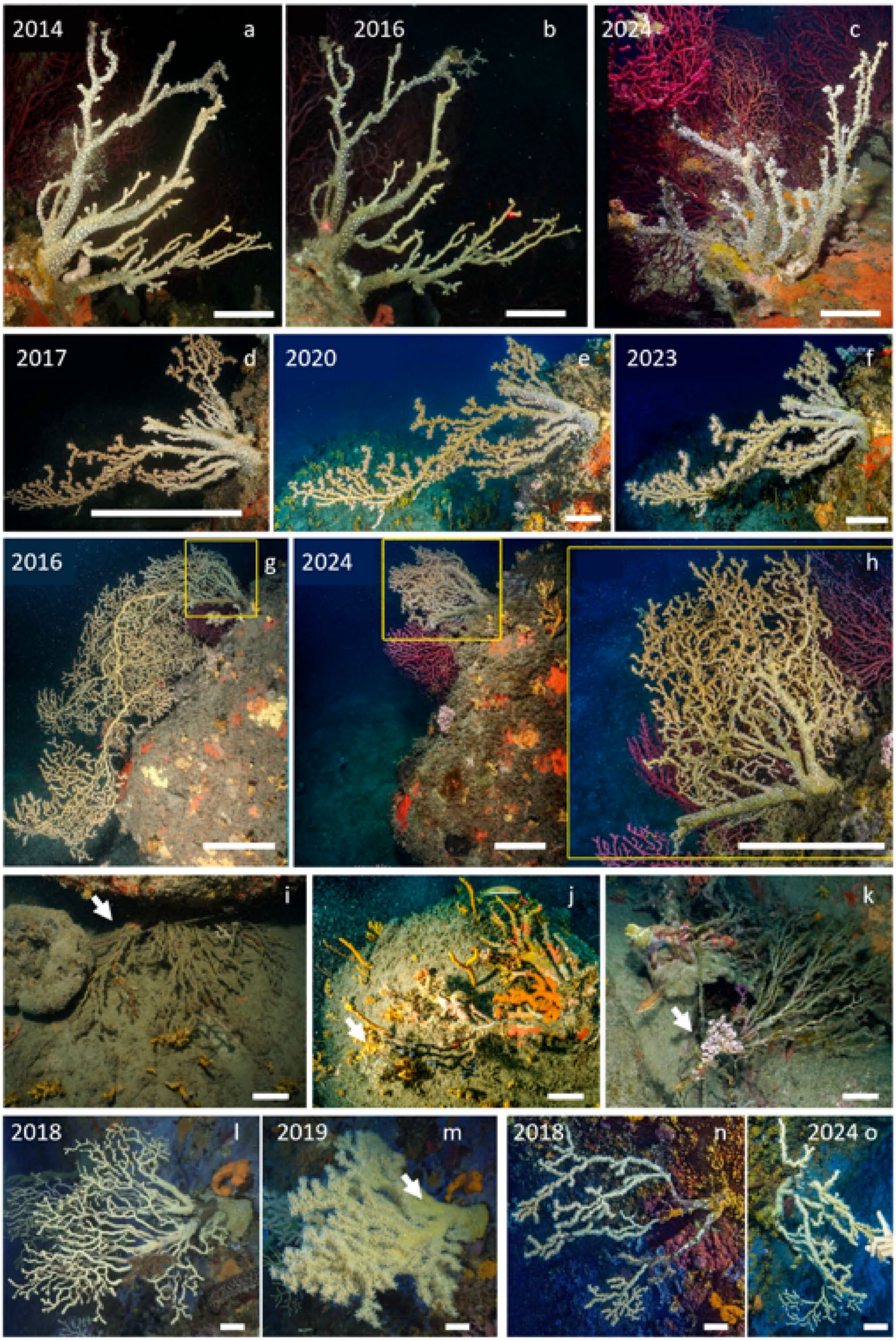


Fig. 5. (**a–h**) Examples of large, injured colonies of *Savalia savaglia* at Tavolara – Punta Coda Cavallo Marine Protected Area, showing the tendency of the zoanthid to not recover from injuries caused by mechanical damage even after more than ten years (yellow squares (**g**, **h**) indicated a close-up of the damaged large specimens). (**i–k**) Extirpated dead colonies entangled by fishing lines (white arrows). (**l–o**) Recovery from tissue loss caused by thermal stress in two colonies from Ustica (North Sicily) (photo credits: Maria Cristina Gambi, Elisa Manganelli and Riccardo Cingillo). A small portion of the damaged surface recovered in one year (white arrows) (**l**,**m**); a colony severely hit completely recovered from the damage after 6 years (white arrows) (**n**,**o**).

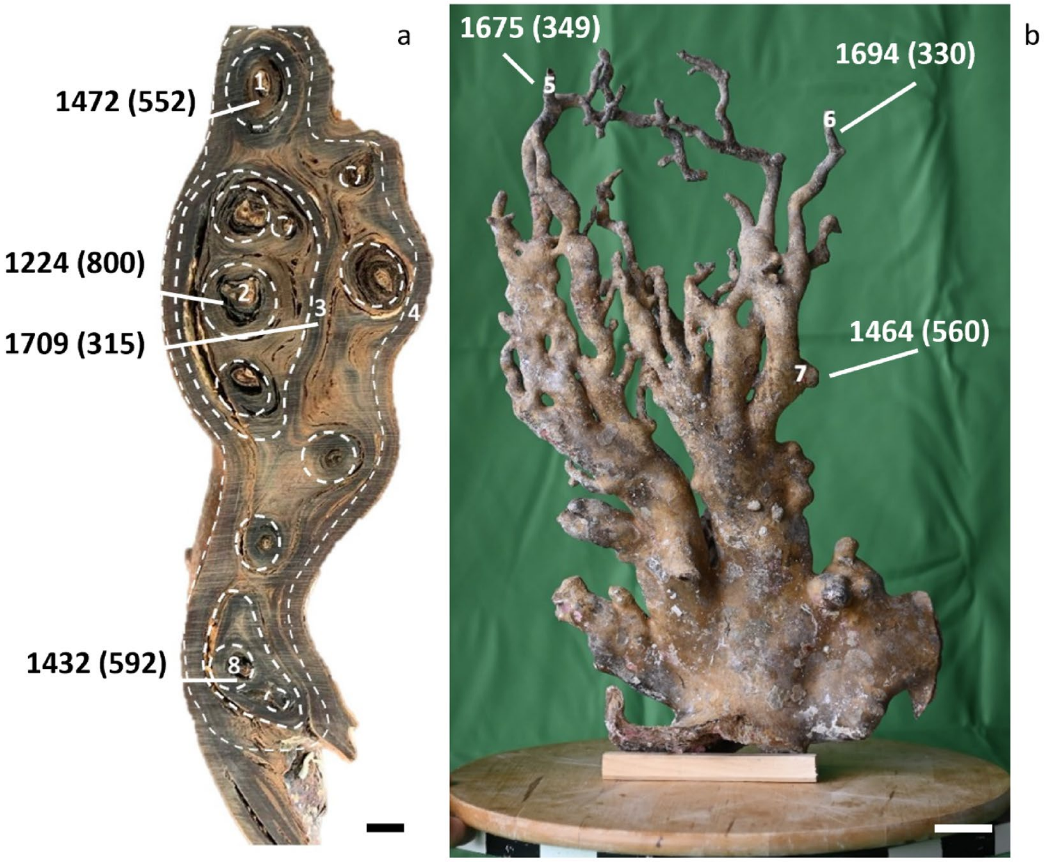


Fig. 6. Radiocarbon age estimation of different portions of the basal and apical sections of specimen C2, showing the progression in time of the *Savalia savaglia* development. Scale bars: **a**: 1 cm; **b**: 5 cm.

Sample ID	Radiocarbon age (BP*)	Calibrated age
S1	705 ± 40	1472AD – 1784AD
S2	1035 ± 40	1224AD – 1464AD
S3	474 ± 35	1709AD – 1952AD
S4	758 ± 40	1437AD – 1705AD
S5	526 ± 40	1675AD – 1952AD
S6	497 ± 40	1694AD – 1952AD
S7	713 ± 40	1464AD – 1772AD
S8	772 ± 40	1432AD – 1692AD

Table 2. Radiocarbon age estimation of the basal and apical portion of the C2 specimen collected at the Tavolara – Punta coda Cavallo MPA. Uncertainties correspond to two standard deviation confidence level (95.4% probability). (*) BP = Conventional Radiocarbon years Before the Present.

In old specimens, the new branches are easily recognisable for their tendency to produce anastomoses, resulting in intricate meshes. A high level of branch fusion, rare or absent in the colonies of *Paramuricea clavata*, is, on the contrary, typical of *S. savaglia*, which is also observed in non-parasitical specimens[13]. The aptitude of the branches to produce anastomoses was perfectly described by Lacaze-Duthiere[7] Moreover, the anastomoses were already evident in the sketch present in the *Opere postume* by Giuseppe Ginanni[56] (Fig. 3e). The formation of the anastomoses in the specimens studied here is elucidated in the cross-sections, where the skeletons of two apical branches become fused by a further layer of skeleton that envelops both in a unique superstructure.

The aptitude to merge skeletal portions in *S. savaglia* is particularly relevant also because different colonies, originally infesting different gorgonians, can fuse to produce stately specimens. The cross-sections at the base of a large colony highlighted a group of several colonies that fused through a continuous layer of a common

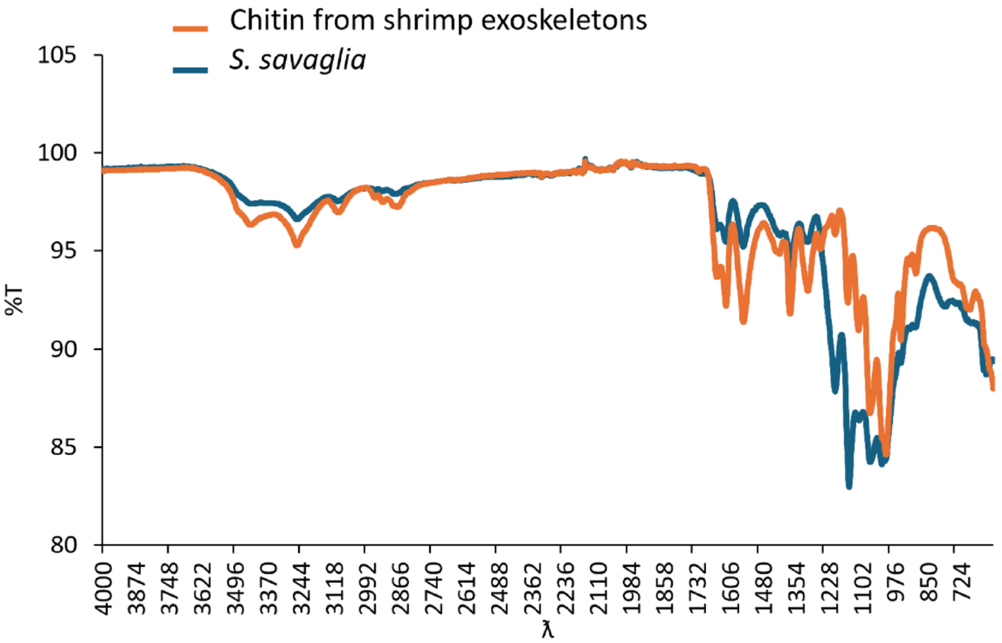


Fig. 7. ATR-FTIR profile of *Savalia savaglia* residue (blue line) and commercial chitin (extracted from shrimps) used as reference standard (orange line).

skeleton as their stem grew larger and came into contact. In this way, the coalescence of different colonies plays a key role in shaping, together with the environment, the final morphology of the specimens.

Two hypotheses, not mutually exclusive, can be made regarding the dynamic of this process. The first hypothesis is based on the expanding ability of the basal plate of the zoantharian, which, when touching another gorgonian, starts to colonise it (infestation bottom-up). *S. savaglia*, indeed, is probably the branched Mediterranean anthozoan that produces the largest basal plates[9]. Our results indicate that it develops with a 4–10 cm^2 y^{-1} growth rate. A second hypothesis involves separate episodes of larval colonisation of different close-by hosts (including adults and juvenile gorgonians) and the subsequent coalescence of the zoantharian colonies. The formation of chimeric colonies has been extensively studied, mainly in tropical scleractinians, where it has been shown that such colonies grow faster than solitary ones, indicating chimerism as an important strategy to maximise the survival of the vulnerable stages of coral life history[57–59]. The genetic compatibility of the zoantharian colonies that come into contact remains an open issue. It is plausible that they derive from larvae of a single reproductive event, but further studies will be necessary to clarify this issue. Poliseno et al.[22] studying several *S. savaglia* populations, recorded that asexual reproduction seems to be the dominant reproductive strategy in this species.

Regarding the age determination, the radiocarbon dating of the large *S. savaglia* colony from the Tavolara MPA (C1 and C2) indicated a secular age. This datum agrees with previous findings for deep Pacific specimens of gold corals[29,32,59,60], representing the first reference for the Mediterranean Sea, as well as the first for the species. On the base of these determinations, authors indicated a radial growth of the skeleton for five samples of Hawaiian gold corals ranging from 15 to 45 µm yr^{-1}. This datum perfectly agrees with that obtained for the Tavolara's colony with a radial growth rate of 30 µm y^{-1}. The carbon ages determined in different points of the basal transversal section reconstructed the story of the colony formations that joined together various gorgonian colonies in a period of about three centuries through a series of different anastomotic episodes. The age estimated for the apical branches is more difficult to interpret. As demonstrated, the gorgonian overgrowth is a rapid process, and the difference in age between the base and the apical branch probably reflects the time necessary to reach the thickness of the branch.

The study of the ultrastructure of the skeleton allowed us to recognise a laminar structure of organic material. The thickness of the laminas (about 20 µm) is very similar to the obtained annual radial growth. In this way, it is possible to hypothesise the deposition of one lamina per year. The laminas are characterised by numerous small blunt spines that are functionally analogous but different in shape from those of black corals (Hexacorallia, Antipatharia). These conical processes were first highlighted in the *Opere postume* of Vitaliano Donati[61]. This Author drew a portion of the skeleton with blunt spines with fibers connecting the coenenchyme to the skeleton (Fig. 4d). The presence of the spines was already observed by Lacaze-Duthiers[7] (Fig. 4e).

The blunt spines are stacked one on the other, layer by layer, increasing the surface area for cementing one skeletal layer to the next. They can also function as continuous rivets, preventing the delamination of the skeleton. This type of structure is responsible for the typical mechanical characteristics of the species' skeleton, particularly its resistance to currents. However, it also gives rigidity and subjects large specimens to a high risk of mechanical damage, as described for black corals[1,19,21].

The present study verifies the occurrence of chitin in this species for the first time after the first presumed affinity with *Cirrhipathes* Blainville, 1834 (Antipatharia) in biochemical composition of the axis [62]. Our data indicated the presence of about 7% of chitin in the *S. savaglia* skeleton, while higher values were recorded for black corals (5–20%)[62–66]. The presence of chitin is congruent with the finding in this species of high amount of ecdysterone, a hormone typically involved in arthropod moulting and chitin synthesis[26]. The systematics position of *S. savaglia* was problematic for a long time because of its resemblance to antipatharians. The presence of chitin and spines increased this affinity. Nevertheless, the anatomy of the polyps and the cnidome indicate that this species belongs to Zoantharia[62–68].

This finding provides additional evidence for the widespread distribution of chitin within Cnidaria, where it occurs not only in skeletal elements but also in the soft tissues of several species[65]. Cnidarians with a chitinous skeleton are hexacorals (black[48,65–68] and gold corals) and hydrozoans[69,70]. Intriguingly, all these groups can produce spines. In hydrozoans, the spines are typical of the family Hydractiniidae[71–74], Rosalindidae[75] and Solanderiidae[76].

As the final morphology of large colonies may be severely shaped by mechanical damage due to limited flexibility linked to colony age, the MPAs managing authorities should implement effective protection measures[77] to regulate fishing activities to preserve the rare, localised small populations of this habitat engineer, who promotes the development of high biodiversity and ecosystem services[12]. Lacaze Duthiers[7] says that, for red coral fishermen, the collection of intact *S. savaglia* colonies was a sure mark of pristine hardground. In contrast, broken colonies indicated that a bank was already commercially exploited. The sensitivity of *Savalia savaglia* colonies to mechanical damage is indirectly evidenced by the intact specimens observed within the Ustica, Tavolara and Capo Carbonara Marine Protected Areas, where colonies typically develop beneath overhanging rocks, thus avoiding entanglement with fishing gear. Due to its distinctive morphological and ecological traits, *S. savaglia* has long attracted the attention of marine biologists. Nevertheless, several structural and compositional aspects of this iconic zoantharian remained poorly understood. Among the existing scientific literature, the seminal work of Henry Lacaze-Duthiers stands out as the most comprehensive monograph ever dedicated to the species. Many of his pioneering observations remain highly relevant and continue to serve as a valuable source of inspiration for contemporary marine biologists.

Data availability

The analyzed specimens are deposited in the zoological collection of the museum of the Department for the study of Earth, Environment and Life of the Genoa University. No datasets were generated or analysed during the current study. The photographic materials collected and/or analysed during the current study are available from the corresponding author on reasonable request. All data generated or analysed during this study are included in this published article (and its Supplementary Information files)" as data availability.

Received: 14 November 2024; Accepted: 25 August 2025

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Acknowledgements

The authors would like to thank Alessandro Diotallevi, Maria Cristina Gambi, Alessandro Grasso, Eleonora de Sabata, Francesco Turano, Riccardo Cingillo, Elisa Manganelli e Lucio Bellomo for making photographic and video materials available. We also thank Paolo Guidetti for carrying out the unusual role of courier transporter with diligence and contempt for danger. A particular thank goes to the management of Tavolara and Capo Carbonara MPAs for permission to use the GIS environment and the possibility of independently developing the underwater surveys, Pier Augusto Panzalis, Nicoletta Cadoni. Lara Carozzo e Maria Leonor García-Gutierrez, Franca Dessì and the "Slow Dive" team for the support during diving activities and data collection.

Author contributions

G. B., M. C. and E. T. designed the study. E. T. collected the specimens and provided part of the photographic material of Figs. 1, 3 and 5. M. C. performed the image analyses, R. B., V. O., and F. T. carried out the chemical analysis and L. C., M. D'E. G. Q. the radiocarbon age estimation. G. B. and M. B. led the interpretation of the results. G. B. and M. C. wrote the first draft, with frequent discussions with E. T. and M. B.; M. C. prepared Figs. 1, 2, 3, 4, 5 and 6 and F. T. prepared Fig. 7. All authors contributed substantially to revisions and gave final approval for publication.

Funding

This research was supported by the National Biodiversity Future Center – NBFC project, code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP D31B21008270007.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-025-17541-w.

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