

Distribution, population structure and life cycle of the Mediterranean endemic *Laminaria rodriguezii* (Laminariales, Phaeophyceae)

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Contributing Editor: Sotiris ORFANIDIS

Received: 09 June 2025; Accepted: 26 August 2025; Published online: 21 October 2025

Abstract

Laminaria rodriguezii is a rare deep-water kelp species, endemic to the Mediterranean Sea, known in only 19 locations, 5 along the Eastern Provence and 14 in Corsica (French coasts). Populations are found at depths ranging from 48 to 100 m; the oldest record dates back to 1954. This study aims to better understand its distribution, biology, and ecology by analyzing recent data from *in situ* observations and sampling. In July 2019, a population at Magaud Bank (France) was studied at 75 m depth. A total of 154 individuals were collected in quadrats, showing an average density of 15.7 ± 2.2 individuals per m² (mean $\pm$ SE). The population consists mostly of small blades, with 80% measuring < 40 cm in total length. The blades generally have a single lobe, corresponding to the year 2019, but sometimes 2 to 3 superimposed lobes, corresponding to the growth of the years 2018 and 2019 respectively. Lobe density ranged from 6 to 84 lobes per m², and the dry mass (DM) varied from 24 to 1160 g DM m⁻². A small percentage (17%) of individuals bore small, mostly released sori on the 2018 lobes, and some blades showed signs of herbivory (7%) and breakage (44%). In culture, we verified the typical heteromorphous haplodiplontic life cycle of *Laminaria* species, with microscopic dimorphic male and female gametophytes. In addition, we showed that vegetative sporophyte reproduction is possible from hapters and stolons. Except for 7 locations (in Corsica) that were not examined, all the French historical populations are still present, and we propose a Least Concern IUCN status for the species. Considering their resistance to the few disturbances likely to threaten the species (mainly fishing using tremail nets), proposals for conservation measures along the French coast are discussed.

Keywords: Mediterranean kelp; distribution; life cycle; IUCN statut.

Introduction

Marine algal forests are the dominant ecosystems of shallow rocky coasts in temperate and cold-water marine habitats (Steneck *et al.*, 2002). The kelp forests are among the most productive marine habitats in the ocean, structuring the seabed and providing numerous ecosystem services (Smale *et al.*, 2013). In the Mediterranean Sea marine algal forests are mostly composed of fucoids species and kelp forests are rare. Only two *Laminaria* species are present: the Atlantic *Laminaria ochroleuca* Bachelot Pylae and the endemic *L. rodriguezii* Bornet (Guiry & Guiry, 2025). The latter species is characterized by stolons with branched holdfasts with multiple hapters, and by blades developing from the stolons. A blade has a short stipe, is undivided and can reach up to 150 cm

in length and 30 cm in width, with undulate margins. In the following year, the initial blade (year n-1) is pushed upward by the growth of a new blade, resulting in a structure with two superimposed blades (years n and n-1) (Boisset *et al.*, 2016); in some cases, a third blade can occur (years n, n-1 and n-2). Hereafter, we will call each of these superimposed blades 'lobes'; a blade can thus be composed of 1, 2 or 3 lobes. As in other species of *Laminaria*, blades, stolons and holdfasts represent the sporophyte, which is macroscopic, while the gametophyte, until now not observed in *L. rodriguezii*, would be microscopic and reduced to a few cells. This species dwells at depths ranging from 50 to 120 m on deep-water coralligenous beds as well as seamount flanks, slopes, and rocky ledges of offshore islands with highly transparent waters and strong currents (Pérès & Picard, 1964; Fredj, 1972;

Ballesteros, 2006; Bo *et al.*, 2011). Large, detached leaves are often found in deeper areas (Fourt & Goujard, 2012), down to 260 m depth in the Adriatic Sea, (Ercegović, 1960), suggesting the export of organic material to adjacent ecosystems. Reproduction occurs both clonally and sexually (Reynès *et al.*, 2021). Within the order Laminariales, the only other species capable of clonal growth via stolons is the Northeast Pacific kelp *Laminaria sinclairii* (Harvey ex J.D. Hooker & Harvey) Farlow, Anderson & Eaton (Demes & Graham 2011). *Laminaria rodriguezii* has been documented throughout the whole of the Mediterranean Sea: in Spain, (Catalonia, the Balearic Islands, the Valencia region), Italy (Ustica, Pianosa, Stromboli, Sardinia, Sicily), Algeria, Tunisia, Morocco, Turkey, and Croatia (Bornet, 1888; Giaccone, 1969; Ben Maiz *et al.*, 1987; Perret-Boudouresque & Seridi, 1989; Boudouresque *et al.*, 1990; Ribera *et al.*, 1992; Cossu & Gazale, 1999; Benhissoune *et al.*, 2002; Taşkin *et al.*, 2008). In France, *L. rodriguezii* has been documented along the coasts of Corsica and the Eastern Provence (Huvé, 1955; Boudouresque & Perret-Boudouresque, 1987; Reynès *et al.*, 2021; Boudouresque *et al.*, 2022). This taxon has not yet been assessed for the IUCN Red List and is currently categorized as ‘Not Evaluated’ (NE) (IUCN, 2025). It is listed in Annex I of the Bern Convention as strictly protected (Council of Europe, 1979) and in Annex II of the Barcelona Convention, as an endangered or threatened species (UNEP/MAP-SPA/RAC, 2018); yet it is not protected in France.

Due to the considerable depths at which *L. rodriguezii* thrives, the population structure of this Mediterranean deep-water kelp remains poorly known. Sampling techniques reported in the literature, including dredging (Huvé, 1955; Gautier & Picard, 1957; Joher *et al.*, 2012; Farriols *et al.*, 2025), research submersibles (Fredj, 1972) and ROV imagery (Joher *et al.*, 2015; Küpper *et al.*, 2019; Farriols *et al.*, 2025), are insufficient for precise sampling or preserving intact specimens during collection.

Recent advances in scuba diving technologies, along with the increasing accessibility of rebreathers and trimix diving for scientific research, now enable the implementation of diver-based sampling protocols in the mesophotic zone. In July 2019, the Gombessa V expedition (<https://gombessa-expeditions.com/>) successfully collected samples from the *L. rodriguezii* population at the Magaud Bank. This study aims to describe the distribution of *L. rodriguezii* along the Mediterranean French coast and analyze its population structure using precise sampling methods that prevent the loss or destruction of collected specimens. Since the complete life cycle of the species remains unknown, we utilized these samples to cultivate and document its full life cycle.

Materials and Methods

Distribution

We gathered all records of *L. rodriguezii* along the French Mediterranean coast through time, including gray

literature, herbarium vouchers where specimens were present, i.e., the National Natural History Museum at Paris (PC) and the MIO herbarium at Marseille (HCOM). All information has been included in a GIS database to provide accurate distribution of the species.

Sampling

The *L. rodriguezii* population sampled in this study was located on the Magaud Bank, at a depth of 75 meters, east of Île du Levant, France (Fig. 1). Sampling was conducted by the Andromède Océanologie diving team during the Gombessa V expedition in July 2019. The team of four divers used autonomous saturation diving, a new technic specially developed for the expedition, mixing saturation diving and closed-circuit diving. This method allows the divers to stay at the bottom for several hours (2 h for this study) since all the decompression stops are done in one go at the end of the three-week expedition.

We define an individual of *L. rodriguezii* as a set of stolons, with the blades and holdfasts they bear, in physical connection. These individuals may result from the fragmentation of a pre-existing individual; they are therefore genetically identical (clones) and are called ramets. They may also be genetically different and are then called genets. Since we do not know whether they are ramets or genets, we will hereafter use the term “individuals”.

Within 10 quadrats of 1 m² randomly placed on the substrate, all *L. rodriguezii* individuals were collected in bags, ensuring the preservation of all holdfasts, stolons, and delicate blade structures. The samples were sent to the surface immediately after collection using a lifting parachute. Environmental parameters (CTD profile from surface to bottom) were registered through a SBE 19plus V2 SeaCAT[®] Seabird profiler (Deter *et al.*, 2020). At the rocky bottom (-81 m), we recorded the following variables: temperature = 13.8°C, pH = 7.91, salinity = 38.20 g.kg⁻¹, conductivity = 4.52 S/m, dissolved oxygen = 5.00 mL/L (saturation = 87.55 %), turbidity = 0.29 NTU, and fluorescence = 0.41 mg.m⁻³ and light = 1.98 µmol m⁻² s⁻¹.

Population structure

In the laboratory, a biometric analysis was performed to assess the following parameters: the density of individuals per quadrat (ind. m⁻²), the length and width (cm) of each blade type (L_n , L_{n-1} , and L_{n-2}), the stipe length (cm), the wet mass (WM) of *L. rodriguezii* individuals (g), and the wet mass of *L. rodriguezii* per quadrat (g.m⁻²) (see Fig. 2 for details on the anatomy of *L. rodriguezii* and see Table 2 for the compilation of the mean ± SE, the median, the minimum and the maximum values of each of the measured parameters). Additional observations included the presence of sori (i.e., spore-producing zones), the condition of individuals (e.g., intact or broken leaves), and evidence of grazing marks.

The relationship between wet mass and blade size was evaluated assessed using Spearman’s rank correlation on

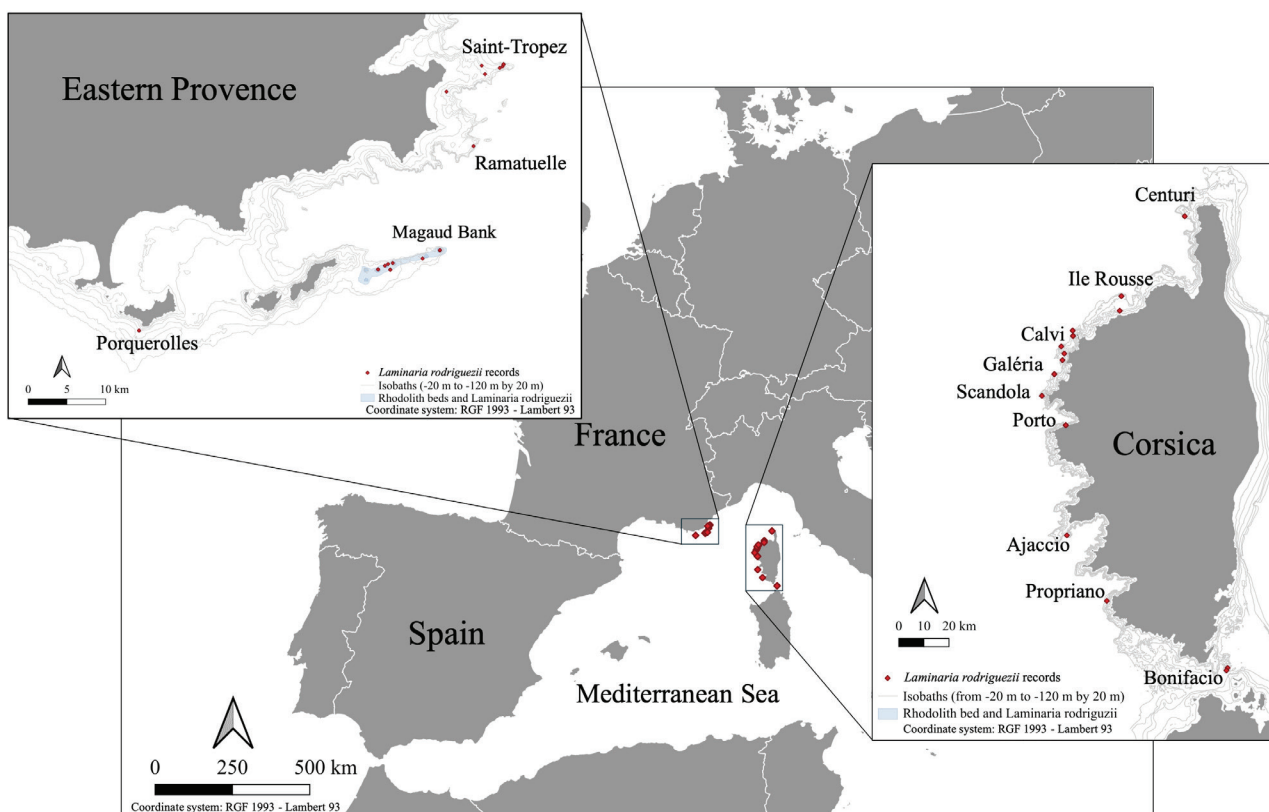


Fig. 1: Locations of *Laminaria rodriguezii* populations along the French Mediterranean coast.

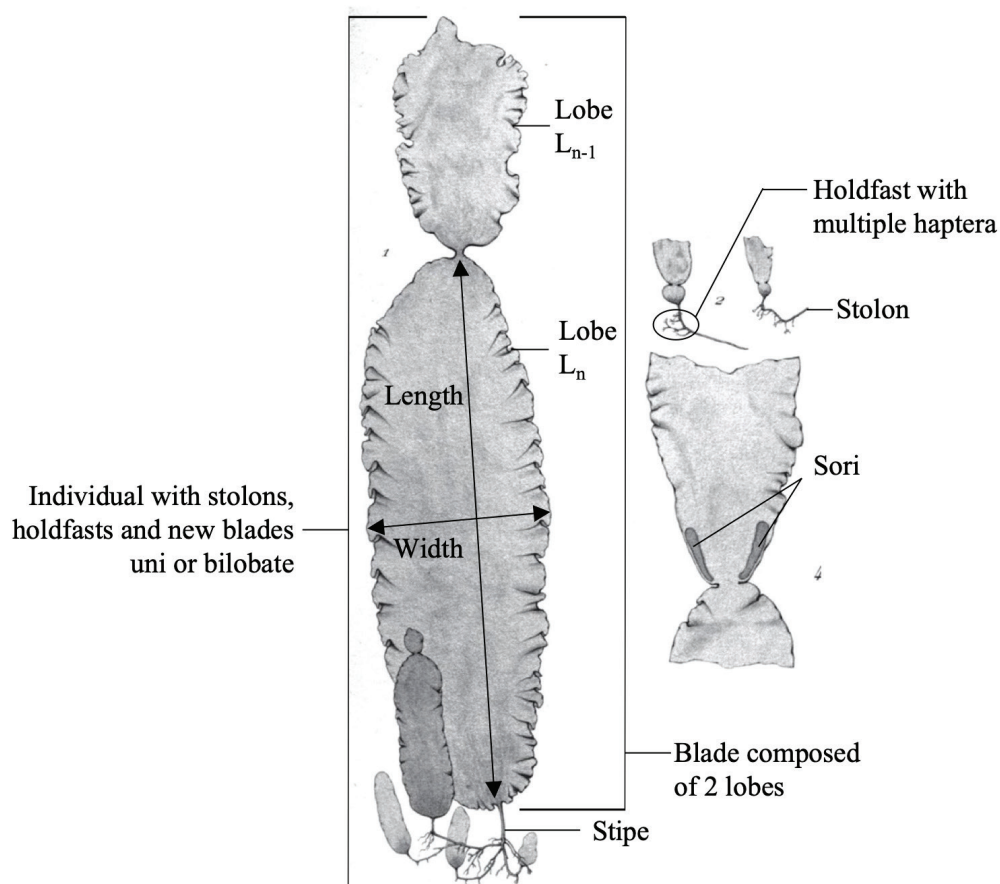


Fig. 2: Measured parameters for the different individuals of *Laminaria rodriguezii* from the Magaud Bank population. L_n lobes correspond to those from the current year, while L_{n-1} lobes are from the previous year. A blade can thus be composed of several lobes. The illustrations are adapted from Bornet (1888).

log₁₀-transformed data, which were log-transformed to approximate linearity.

Isolation of clonal gametophytes and life cycle observations

In general, sori were few, present along the blade margins as small oval areas, and spores had already been mostly released in July, visible by the very weak brown to whitish colour and patchy appearance of the sori (Fig. 7). For spore release and gametophyte isolation in principle we followed the method described in Bartsch (2018).

Sori from 11 individuals were cut out from blades in the laboratory at Marseille, cleaned with fresh paper towels and transferred into Falcon tubes (50 mL, Sarstedt AG & Co, Nürnbrecht, Germany) filled with two glass slides and one drop of sterile seawater to produce a wet chamber. These tubes were kept at 15°C overnight before they were filled with sterile artificial seawater (Instant Ocean SeaSalt) at 38 g kg⁻¹. Sori were removed after 24 h to reduce the risk of contamination and tubes were transferred to the Alfred Wegener Institute within 2 days with constant cooling at 15 °C. In the home laboratory, the glass slides were transferred into petri dishes and cultivated in iron-free ½ PES (Provasoli, 1968; modifications: HEPES-buffer instead of TRIS, double concentration of Na₂glycerophosphate, iodine enrichment after Tatewaki, 1966) in sterile North Sea seawater (approx. 31.5 g kg⁻¹). For a short period GeO₂ was added to suppress potential diatom growth (Shea & Chopin 2007). Dishes were kept at 15°C, long days (16:8 h light: dark LD) and in very low white LED light (2 µmol photons m⁻² s⁻¹) [Mitras Lightbar 2 Daylight, controlled by a Profilux 3 computer; GHL Advanced Technology; measured with a LI-COR LI-185B Photometer (LI-COR-Biosciences, Lincoln, NE, USA)] for several weeks before isolation of clonal gametophytes. When gametophytes were multicellular and big enough to discriminate sexes, male and female clonal gametophytes were isolated from 8 different sporophytes in total (resulting in AWI stock culture numbers: 3582 – 3597). After isolation cultures were kept in red LED light and otherwise the same conditions for vegetative growth.

Gametophytes from one parental sporophyte became fertile under the above conditions and produced juvenile sporophytes. Sporophytes were then cultivated in 5 L beakers with a higher irradiance of 15 µmol photon m⁻² s⁻¹ and weekly change of ½ PES. These sporophytes were cultivated up to a length of several centimeters in aerated glass beakers for further experiments (Pageault, 2020).

In order to verify whether haptera and stolons are able to form new blades, we cut haptera from some sporophytes and further cultivated them in petri dishes under the same conditions as above.

Results

Distribution

A total of 20 populations of *L. rodriguezii* have been recorded since 1954 for France: 6 along the coast of Eastern Provence and 14 off the island of Corsica (Table 1, Fig. 1). The depth of occurrence ranges from 48 to 100 m, with populations dwelling on rhodolith beds or coralligenous assemblages.

Population structure

The studied site is a seascape of hills interspersed with valleys of white shell sand. The kelp field at Magaud Bank dwells between 71 and 81 m depth mainly on rocks. Several drift individuals of *L. rodriguezii* have been observed at greater depths. This bank hosts a highly diverse array of communities, such as rhodoliths, nutrient-rich biogenic detritus, and coralligenous habitat dominated by large gorgonians *Paramuricea clavata* (Risso, 1826) and *Paramuricea macrospina* (von Koch, 1882), yellow coral colonies of *Dendrophyllia cornigera* (Lamarck, 1816) and some sponges (Fig. 3). Divers observed many melon sea urchins *Echinus melo* Lamarck, 1816, several sunfish *Mola mola* (Linnaeus, 1758) and red scorpionfish *Scorpaena scrofa* Linnaeus, 1758. Several abandoned fishing lines were observed on the seabed.

A total of 154 individuals were collected within 10 quadrats interspersed over an area of approximately 500 m², with densities ranging from 5 to 25 ind. m⁻² and an average density of 15.7 ± 2.2 ind. m⁻² (mean ± SE, median = 15.5 ind. m⁻², Table 2). Among these individuals, 117 were single blade individuals while 37 others had stolons supporting 1 to 12 blades resulting in 100 additional blades from those 37 individuals.

Altogether, 253 blades were recorded (117 isolated blades plus 100 additional blades on stolons); the density of blades ranged between 6 and 52 blades m⁻² with an average of 25.4 ± 4.8 blades m⁻² (mean ± SE, median = 21.5 blades m⁻², Table 2). All blades bore the lobe from 2019 (L_n); of these, 117 still carried the lobe from 2018 (L_{n-1}), and lobes retained lobes from 2017 (L_{n-2}) and were thus three years old. The lobe density (lobe m⁻²) of the *L. rodriguezii* population at Magaud ranged from 6 to 84 lobe m⁻², with an average of 37.7 ± 8.6 lobe m⁻² (mean ± SE, median = 27.5 lobe m⁻², Table 2).

The length of L_n lobes ranged from 2.0 cm to 120.0 cm, with an average length of 18.8 ± 1.2 cm (mean ± SE, median = 11 cm, Table 2). Their widths varied between 1.5 cm and 33.0 cm with an average of 9.0 ± 0.4 cm (mean ± SE, median = 6 cm, Table 2). The L_{n-1} lobes measured between 0.5 cm and 144.0 cm in length, with an average of 20.6 ± 2.3 cm (mean ± SE, median = 10 cm, Table 2), and their widths ranged from 1.0 cm to 29.0 cm, with an average of 8.3 ± 0.6 cm (mean ± SE, median = 5 cm, Table 2). Finally, the L_{n-2} lobes were shorter, measuring between 2.5 cm and 18.0 cm in length (average 8.7 ± 2.7 cm, median = 6.5 cm, Table 2) and between 3.0 cm

Table 1. Records of *Laminaria rodriguezii* along the French Mediterranean coast. MPA = Marine Protected Area. HCOM: Herbarium held at Aix-Marseille University - MIO; MNHN-PC: Herbarium held at the National Natural History Museum at Paris.

Region	Municipality	Site	Protection status	Longitude	Latitude	Depth (m)	Date of record	Reference
Eastern Provence	Hyères-les-Palmiers	Porquerolles Island	Core area of the Port-Cros National Park (PCNP), Natura 2000	6.19167°E	42.97797°N	55-62	2013, 2023	Unpublished record
				6.57417°E	43.03714°N	80	1954	HCOM: H1158, H1159
	Maugaud Bank		Adjacent Marine Area (AMA) of the PCNP, Natura 2000	6.57432°E	43.03705°N	80	1954	MNHN-PC: PC0467438, PC0467439
				6.58530°E	43.04106°N	75-95	1956	HCOM: H1165
				6.59356°E	43.03620°N	80	1957	Gautier & Picard, 1957
				6.59355°E	43.03603°N	80	1980	Falconetti, 1980
				6.59790°E	43.04370°N	80	2008	Pedel & Fabri, 2011
				6.59790°E	43.04370°N	79	2014	Unpublished record from Andromède team
				6.64560°E	43.04740°N	80	2014	Unpublished record from Andromède team
				6.67350°E	6.67350°N	80	2014	Unpublished record from Andromède team
				6.59800°E	43.04380°N	76	2018	Unpublished record from Andromède team
				6.59047°E	43.04286°N	71	2018	Reynès <i>et al.</i> , 2021
				6.67375°E	43.05625°N	75	2019	Andromède Océanologie, 2020
				6.73535°E	43.17501°N	80	2004, 2018	Reynès <i>et al.</i> , 2021
	Ramatuelle	Cap Camarat	Adjacent Marine Area (AMA) of the PCNP, Natura 2000	6.69582°E	43.24000°N	50-78	1990	Harmelin <i>et al.</i> , 1991
	Saint-Tropez	Cap Pinet						

Continued

Table 1 continued

Region	Municipality	Site	Protection status	Longitude	Latitude	Depth (m)	Date of record	Reference
Corsica	Centuri	Saint-Julien	Natura 2000	6.75396°E	43.26827°N	78	2011	Safège Cettis, 2011
		Les roches des Maines	Natura 2000	6.75849°E	43.25839°N	50	2004	Unpublished record
		Le Grand-Arbois	Natura 2000	6.78239°E	43.26457°N	70	2000	Unpublished record
				6.78857°E	43.26843°N	65-70	2000	Unpublished record
				6.78876°E	43.26865°N	65-70	2000	Unpublished record
				6.78858°E	43.2684°N	65-70	2000	Unpublished record
				6.78859°E	43.26845°N	65-70	2000	Unpublished record
				6.78875°E	43.26864°N	65-70	2000	Unpublished record
				6.78876°E	43.26865°N	65-70	2000	Unpublished record
				6.78718°E	43.26638°N	80	2025	Unpublished record
	Centuri	Centuri Bank	Natura 2000	9.28400°E	42.97245°N	100	1955, 2014	HCOM: H6459, Molinier, 1956, Unpublished record from Andromède team
	Ile Rousse	Ile Rousse Bank	Local MPA	8.94500°E	42.7037°N	85-100	1957	HCOM: H6461, H6462
	Calvi	Punta Rossa	Natura 2000	8.93177°E	42.65186°N	48	2024	Unpublished record from Andromède team
				8.93149°E	42.65174°N	50	2024	Unpublished record from Andromède team
				8.69592°E	42.57400°N	52-70	1962	MNHN-PC: PC0467428, PC0467429, PC0467430, PC0467432, PC0467433, PC0467434, PC0467435, PC0467436

Continued

Table 1 continued

Region	Municipality	Site	Protection status	Longitude	Latitude	Depth (m)	Date of record	Reference
		Capu di à Mursetta	Natura 2000	8.63612°E	42.49000°N	70-90	1962	Fredj, 1972
		Punta Arajagia	Natura 2000	8.64726°E	42.51300°N	70-90	1962	Fredj, 1972
		Capo Cavallo	Natura 2000	8.63500°E	42.53932°N	70-90	1962	Fredj, 1972
		Punta Revellata	Natura 2000	8.69600°E	42.59329°N	70-90	1962	Fredj, 1972
Galéria		I Scuglietti	Natura 2000	8.59204°E	42.44171°N	80	1976, 1979, 1980	HCOM: H1158, H1159, H6452, H6453, H6454, H6455, H6456, H6458, H6460
		Gàrgalu	Natural Reserve of Scandola	8.52456°E	42.36713°N	74	2011	Andromède Océanologie, 2011
Porto		Punta Piana	Natura 2000	8.63000°E	42.25588°N	90	1962	MNHN-PC: PC0467418, PC0467419, PC0467421, PC0467422, PC0467423, PC0467424, PC0467426, PC0467427
Ajaccio		Les Sanguinaires	Natura 2000	8.59744°E	41.86082°N	80	2004	Ganteaume <i>et al.</i> , 2004
Propriano		Punta Di Manna Mulina	Natura 2000	8.76594°E	41.61587°N	75-85	1962	MNHN-PC: PC0467420
Bonifacio		Bonifacio Bank	Natural Reserve of Bouches de Bonifacio	9.31000°E	41.33430°N	70	2012	Reynès <i>et al.</i> , 2021

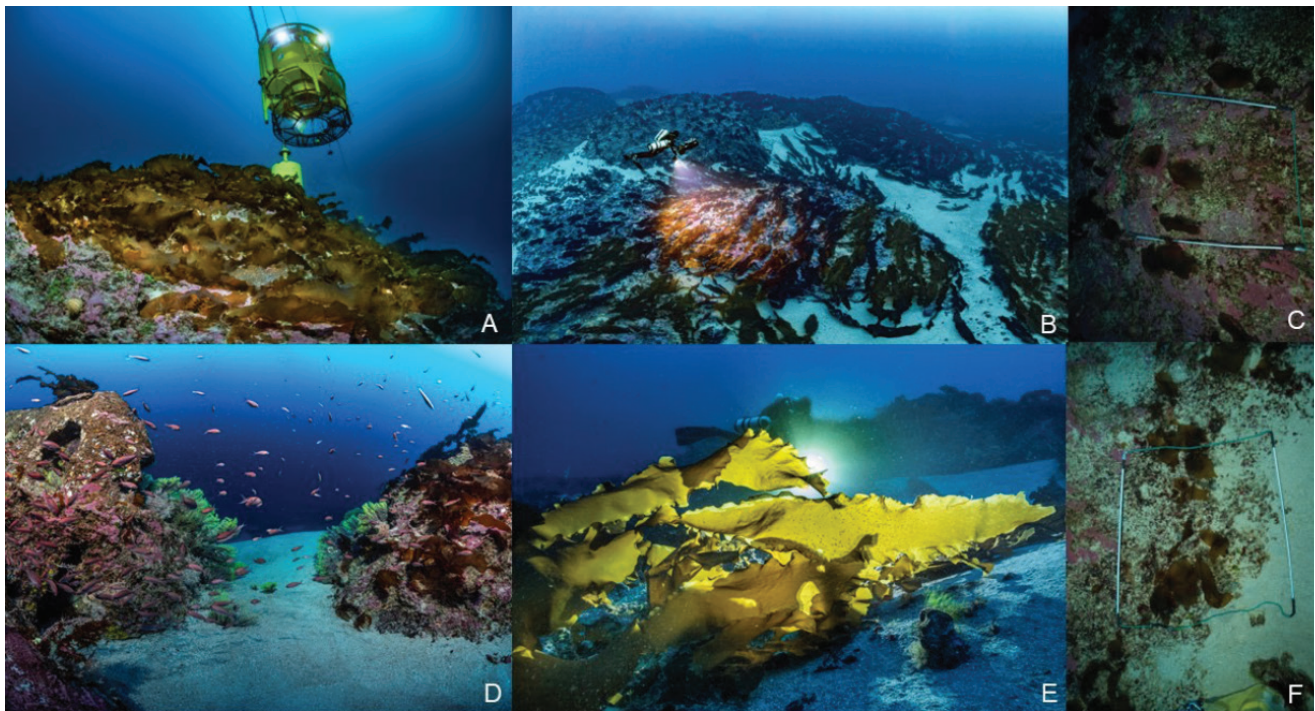


Fig. 3: Impressions of the sampling area at Magaud Bank characterized by strong currents: A) *Laminaria rodriguezii* bed at Magaud Bank, the lift was used by the divers for the collection by autonomous saturation dive, B) the Magaud Bank seascape with small rocky and coralligenous hills interspersed with valleys of white shell sand, C) a 1-m² quadrat on coralligenous substrate, D) *L. rodriguezii* and gorgonians on a massif (hill), E) *L. rodriguezii* blades in the current, F) a 1-m² quadrat on sandy and rhodolith substrate. Photo Credits: Laurent Ballesta.

Table 2. Biometric parameters of population of *Laminaria rodriguezii* sampled at the Magaud Bank in July 2019. Blades can be composed of a single, or two or three superimposed lobes. L_n: lobes from the year (2019); L_{n-1}: lobes from the previous year (2018); L_{n-2}: lobes from 2017.

		units	Mean ± SE	Median	Min	Max	n
Density of individuals		ind. m ⁻²	15.7 ± 2.2	15.5	5	25	10
Density of blades		blade m ⁻²	25.4 ± 4.8	21.5	6	52	10
Lobe density		lobe m ⁻²	37.7 ± 8.6	27.5	6	84	10
Length of lobes							
	L _n	cm	18.8 ± 1.2	11	2	120	253
	L _{n-1}	cm	20.6 ± 2.2	10	0.5	144	117
	L _{n-2}	cm	8.7 ± 2.7	6.5	2.5	18	6
Width of lobes							
	L _n	cm	9.0 ± 0.4	6	1.5	33	253
	L _{n-1}	cm	8.3 ± 0.6	5.5	1	29	117
	L _{n-2}	cm	6.0 ± 0.9	6	3	9	6
Stipe length		cm	2.8 ± 0.1	2	0.3	15	243
Total length [stipe (if present) + all lobes] of blades		cm	31.3 ± 2.3	18.5	2.5	271	253
Single-lobed blades		cm	17.2 ± 1.2	13	2.5	79	136
Two-lobed blades		cm	47.8 ± 4.6	26	7	271	111
Three lobed blades		cm	41.2 ± 11.9	27.5	18.5	88	6
Number of haptera per blade			10.6 ± 0.7	9	1	60	164
Longest haptera per blade		cm	6.3 ± 0.4	5	0.1	25	164
Total length of stolon per quadrat		cm	10.8 ± 5.6	0.5	0	55.5	10
Wet mass of <i>Laminaria rodriguezii</i> per quadrat		g WM m ⁻²	452.4 ± 141.9	302.5	23.9	1160.3	10

and 9.0 cm in width (average 6.0 ± 0.9 cm, median = 6 cm, Table 2).

Most lobes were shorter than 20 cm, regardless of type: 71.7% of L_n lobes, 68.1% of L_{n-1} lobes, and 100% of L_{n-2} lobes (Fig. 4).

Taking into account the stipe length, which ranges from 0.3 cm to 15.0 cm with an average of 2.8 ± 0.1 cm (mean $\pm$ SE, median = 2 cm, Table 2), the total length (i.e., stipe + all lobes) of *L. rodriguezii* blades varies from 2.5 cm to 271.0 cm, with an average of 31.3 ± 2.3 cm (mean $\pm$ SE, median = 18.5 cm, Table 2). The population on the Magaud Bank is dominated by small blades, with 79.9% measuring less than 40 cm in total length. The longest blades are two-lobed blades (Fig. 5), with the single-lobed blades ranging from 2.5 to 79 cm with an average of 17.2 ± 1.2 cm (mean $\pm$ SE, median = 13 cm, Table 2), the two-lobed blades ranging from 7 to 271 cm with an average of 47.8 ± 4.6 cm (mean $\pm$ SE, median = 26 cm, Table 2) and finally the three-lobed blades ranging from 18.5 to 88 cm with an average of 41.2 ± 11.9 cm (mean $\pm$ SE, median = 27.5 cm, Table 2).

The structure of the holdfasts (i.e., the structures that anchor *L. rodriguezii* to the substrate) varies among blades, ranging from 1 to 60 haptera per holdfast, with an average of 10.6 ± 0.7 haptera (mean $\pm$ SE, median = 9, Table 2). The longest hapteron per holdfast measures between 0.1 cm and 25.0 cm, with an average length of 6.3 ± 0.4 cm (mean $\pm$ SE, median = 5 cm, Table 2).

Few stolons were observed, with their total length within the quadrats ranging from 0 to 55.5 cm, averaging 10.8 ± 5.6 cm (mean $\pm$ SE, median = 0.5 cm, Table 2).

The wet mass (WM) of the individuals is proportional to their size ($\log_{10}$ transformed to linearize the relation, Spearman correlation $\rho = 0.94$, $p < 0.0001$; Fig. 6), with the lightest individual weighing 0.2 g WM and the heaviest 364.8 g WM, resulting in an average weight of 22.8 ± 3.23 g WM (mean $\pm$ SE, median = 5 g WM). The biomass of *L. rodriguezii* within the quadrats ranged from 23.9 to 1160.3 g WM m^{-2} , with an average biomass of 452.4 ± 141.9 g WM m^{-2} (mean $\pm$ SE, median = 302.5 g WM m^{-2} Table 2).

Out of the 154 individuals analysed, only 26 bore blades with sori, representing 16.9%. Among these 26 individuals, sori were carried 21 times by lobes from 2018 (L_{n-1}) and 5 times by lobes from 2019 (L_n).

Of the 376 lobes sampled during this campaign, 26 showed signs of herbivory, representing 6.9%. However, 164 leaves (43.6%) exhibited signs of erosion or breakage.

Life cycle

We observed the life cycle of *L. rodriguezii* for the first time in the laboratory (Fig. 7). This species follows the same heteromorphous haplodiplobiontic life cycle known for *Laminaria* species; macroscopic sporophytes (with blades, holdfasts and stolons) discharge spores from sori which germinate into male and female gametophytes. These gametophytes are microscopic and produce male and female gametes. Gametogenesis happens under a very low irradiance of 2 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

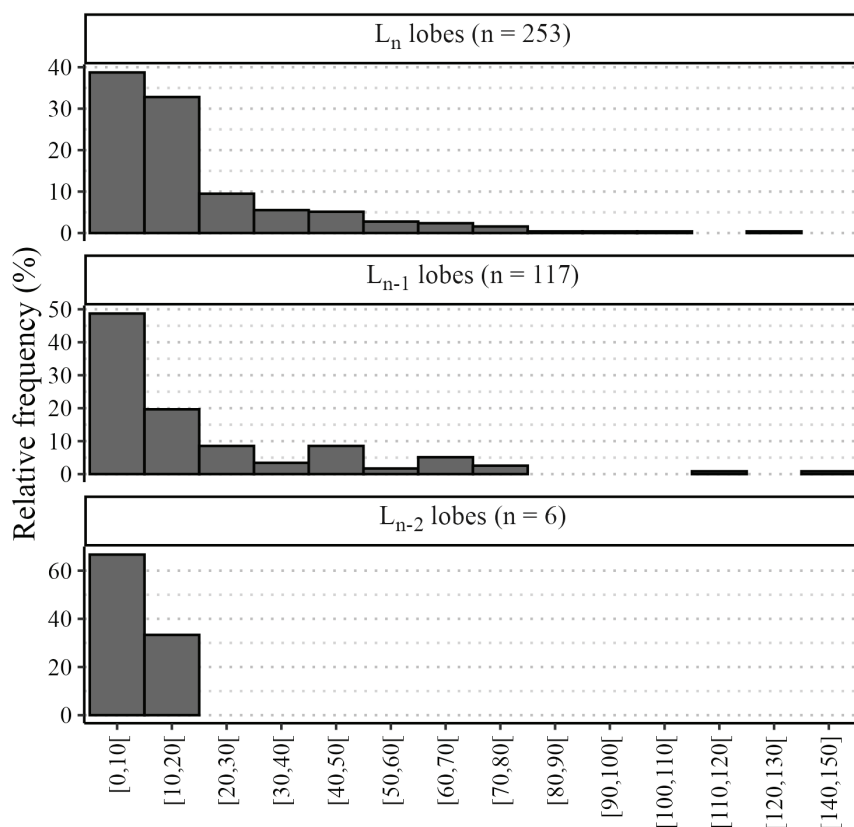


Fig. 4: Relative frequency of each length class (in cm) of each lobe type. L_n lobes correspond to those from 2019, L_{n-1} lobes to those from 2018 and L_{n-2} lobes to those from 2018.

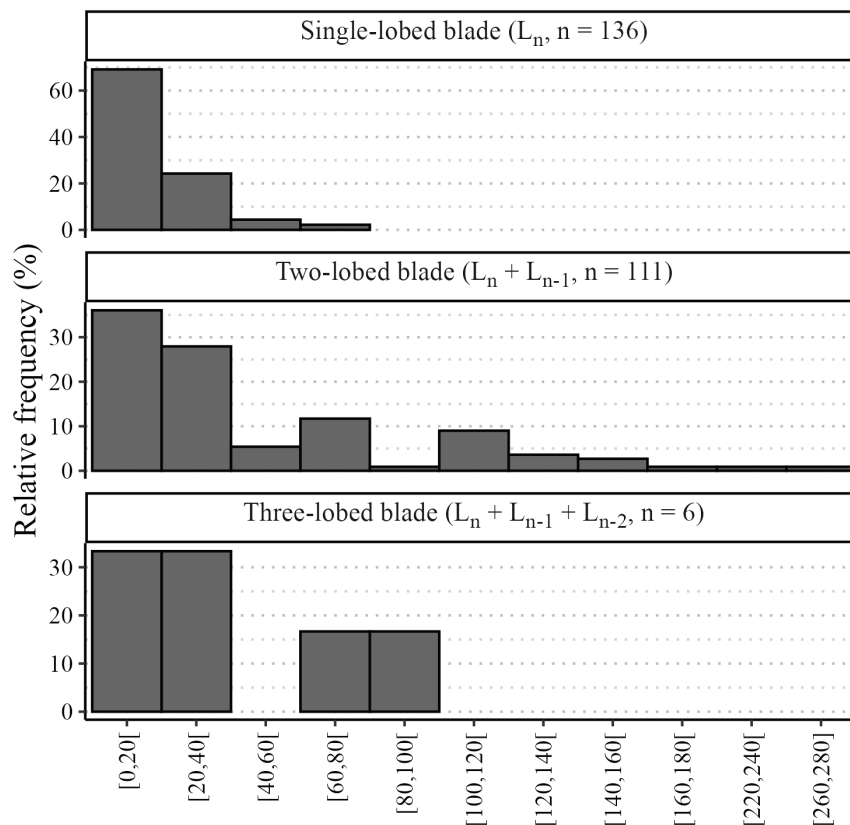


Fig. 5: Relative frequency of each total length class [stipe plus all lobes (L_n , L_{n-1} , L_{n-2})] in cm of each configuration of blades (i.e., single, two or three-lobed blade).

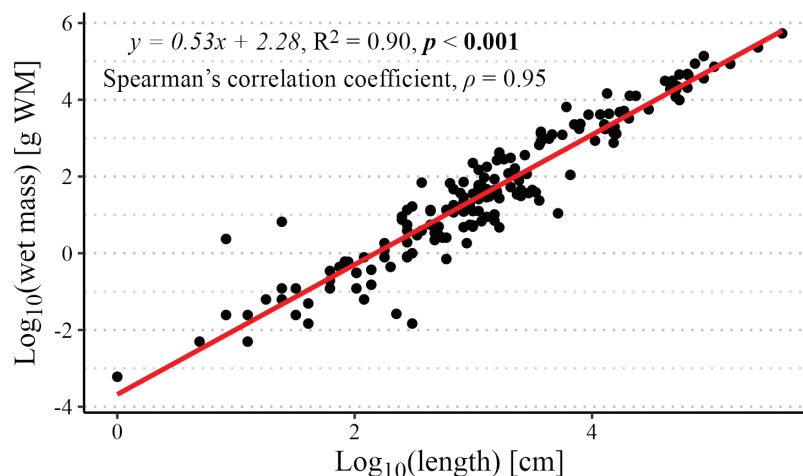


Fig. 6: Linear regression between the length and the wet mass, WM, ($\log_{10}$ transformed) of *Laminaria rodriguezii* blades ($n = 164$).

Fertilization produces zygotes which germinate into new sporophytes (stolons, holdfasts and blades).

In addition to this mode of propagation *via* spores and gametes, the ability to form clonal sporophytes without sexuality from holdfasts and stolons has been observed in the laboratory as well. After cutting of holdfasts and stolons, first callus-like signs of regeneration were observed 16 weeks later and within a few days new blades grew out. This mode of propagation seems to be very effective as even a sporophyte culture which nearly disintegrated due to being overlooked, grew out into many new sporophytes after regular medium change was continued.

Discussion

Laminaria rodriguezii is present in 19 locations along the coast of Eastern Provence and Corsica and all are located in Marine Protected Areas (MPAs), including “paper parks” without any regulations such as Natura 2000 sites. The Magaud Bank is the most frequently observed location, with regular observations since 1954, from the early Cousteau explorations to ROV surveys and deep-diving expeditions. The densities recorded at our site (between 6 and 52 blades. m^{-2}) are much lower than those recorded at the Columbretes Islands (Balearic Islands, Spain) (55 to 210 blades. $0.25 m^{-2}$) (Linares *et al.*, 2015). At the Magaud Bank, which is much deeper than

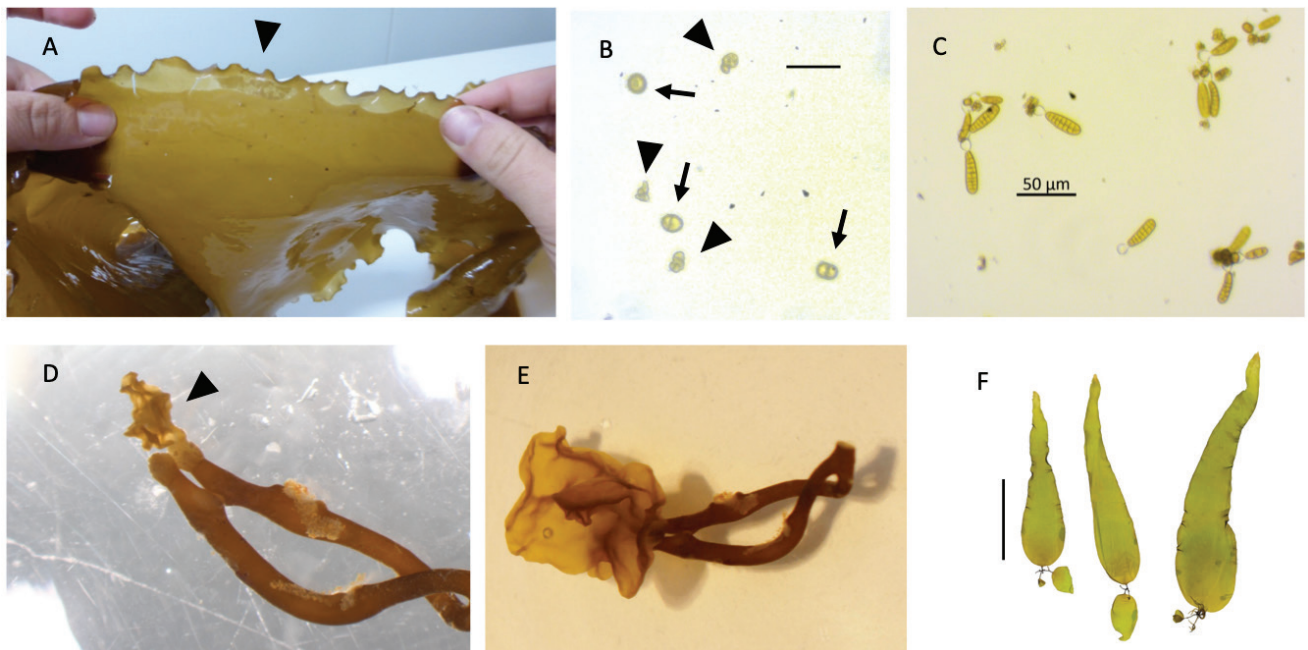


Fig. 7: Life cycle stages of *Laminaria rodriguezii*. A. Blade with marginal sori, mostly released (whitish zone) except for patchy area (arrowhead). B. Early gametophyte stages after germination of the spores (males: arrowhead, females: arrows). C. Young microscopic sporophytes which developed at 15°C and an irradiance of 2 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. D. Stolon with regenerating clonal sporophyte at tip (arrowhead) first having a callus like appearance. E. Same stolon a few days later. F. Sporophytes (herbarium material) on 29.6.2020 approx. one year after spore release (8.7.2019) cultivated in 50% PES, 15 °C, irradiance of 15 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and long daylength (16:8 LD). Scale bars: B: 50 μm , F: 5 cm. Photos: A: Klaus Valentin, B-E: Andreas Wagner.

the Columbretes location (75 m versus 40 m), the blades never overlap highlighting the fundamental role of light in the distribution of this species. At such a depth, always located beneath the thermocline, the temperature remains low all year-round constant over time, around 13 °C.

The assemblages of this bank were mapped between 1969 and 1977, revealing *L. rodriguezii* populations mixed with large rhodolith beds (Falconetti, 1980). The total population area has been estimated at 1,146 ha (based on Falconetti's data). Recurrent observations at different points of the bank suggest that the large area covered by *L. rodriguezii* has remained unchanged since then despite lost fishing gear which were frequently observed at all locations. These deep marine forests are well known to local fishermen, who refer to them as “le tabac” (tobacco, in French) due to their appearance. They serve as habitats for large shoals of fish (Fig. 8).

Unlike fucoids, which do not have a heteroromorphic life cycle with a free-living sexual stage, are highly vulnerable and show low resilience to disturbances (Blanfuné *et al.*, 2025), *L. rodriguezii* exhibits clonal reproduction *via* stolons and in addition *via* their digenetic haplodiplontic life cycle with free-living minute sexual gametophytes. As kelp gametophytes are extremely tolerant against low light and may even survive long phases of darkness (Tom Dieck, 1993), as they can propagate over > 35 years without losing their ability to reproduce (Martins *et al.*, 2019 - used gametophytes isolated in 1985) and as they generally also exhibit a higher temperature tolerance than the sporophyte phase (e.g., Tom Dieck, 1992; Tom Dieck & de Oliveira, 1993), they are an important reservoir and seed-bank for kelp beds (e.g., Car-

ney *et al.*, 2013, Schoenrock *et al.*, 2021), which probably also refers to *L. rodriguezii*. But, as we observed only very small sori compared to blade sizes, we assume that sexual reproduction and population resilience *via* gametophytes is less pronounced than clonal reproduction *via* stolons. Nevertheless, this double reproductive strategy may in part explain its resilience to their deep-water habitat. Sporophytes may easily generate from broken stolons and although gametophytes may become fertile at very low irradiances (this study) and sporophytes may even grow at low light (Pageault, 2020), we assume that clonal reproduction is more important for the species, a fact that is supported by molecular studies (Reynès *et al.*, 2021). Clonal propagation may also hint at a certain ability to withstand physical disturbances, particularly fishing activities, as even small stolons may regenerate sporophytes. However, intense trawling, as recorded in the Adriatic, may have led to the complete extinction of local populations (Žuljević *et al.*, 2016) and thus should be prevented throughout the deep-water habitats of France.

Accordingly, the conservation status of *L. rodriguezii* can be assessed in accordance with the IUCN Red List criteria (IUCN, 2012). Based on a comparison of historical and current records, as well as an assessment of anthropogenic pressures at each locality, we propose an IUCN-like status of *Least Concern* for *L. rodriguezii* in both French Mediterranean regions (Eastern Provence and Corsica). By contrast, Žuljević *et al.* (2016) classified the species as *Critically Endangered* in the Adriatic. As observed for other species constituting marine forests, the assessment should be conducted on a regional basis (Blanfuné *et al.*, 2016, 2025).



Fig. 8: Abundant fish populations above the *Laminaria rodriguezii* beds of Magaud Bank. A sunfish *Mola mola* (Linnaeus, 1758) can be seen in the upper part of the photo. In the foreground, a school of *Anthias anthias* (Linnaeus, 1758).

Although the species is listed in Annex I of the Bern Convention and Annex II of the Barcelona Convention (as a protected species), yet it is not protected in France. The effectiveness of listing a species for national protection is questionable, as *L. rodriguezii* faces limited threats at the depth where it thrives. Unlike shallow marine waters in the Mediterranean, where herbivory and habitat destruction are primary stressors, these factors do not significantly impact *L. rodriguezii* populations. Herbivores are scarce at these depths, with no herbivorous fish or sea urchins (*Echinus melo* is detritivorous), and the micro-herbivore community consists mainly of crustaceans, which do not appear to regulate biomass significantly. All sites are exposed to strong currents and are continuously enriched with nutrients, suggesting a bottom-up process regulating these marine forests.

Although *L. rodriguezii* populations are highly structured and lack connectivity between them, clonality may explain their persistence (Reynès *et al.*, 2021). The species' biology plays a role in its resilience; its stolons are highly fragile and easily break when touched, resulting in a strong dominance of clonal individuals. This characteristic may contribute to its resistance to fishing gear. Even if trawling is still not banned within some marine protected areas, trawling on rocky banks in Eastern Provence and Corsica is not feasible.

It would be preferable to consider populations rather than species in protection measures. A comprehensive mapping of existing populations and regular monitoring are necessary to best conserve this remarkable and endemic Mediterranean species.

Acknowledgements

Samples were collected during the GOMBESSA 5 cruise led by Andromède Océanologie and supported

by Manufacture de Haute Horlogerie Suisse Blancpain and Blancpain Ocean Commitment, the Prince Albert II de Monaco Foundation, the Société des explorations de Monaco and Agence de l'eau Rhône-Méditerranée-Corse (French Water Agency). The authors also want to thank Agathe Blandin, Gwenaëlle Delaruelle, ARTE, INPP (Institut National de Plongée Professionnelle), Les Gens Bien Production, Région Sud, Fondation IRIS, Fondation Véolia, Agence Française pour la Biodiversité, CNC, Métropole Nice Côte d'Azur, Parc National des Calanques, Océanopolis Brest, Ushuaïa TV, AP diving, Aqualung, Nikon, Syera, HE2B ISEK, Molecular, Seacam, Bigblue, Keldan, Neotek, enlaps, RG Blue, Azoth Systems, Subspace pictures, Topstar, without whom this expedition would not have been possible.

References

- Andromède Océanologie, 2011. *Étude et cartographie des biocénoses marines de la Réserve naturelle de Scandola, Corse*. Andromède Océanologie, Montpellier, 136 pp.
- Andromède Océanologie, 2020. *Etat des eaux et des écosystèmes de la zone crépusculaire en Méditerranée française – Surveillance DCE et DCSMM. Contrat Andromède Océanologie & Agence de l'eau Rhône Méditerranée & Corse*. Andromède Océanologie, Marseille. 202 pp.
- Ballesteros, E., 2006. Mediterranean coralligenous assemblages: a synthesis of present knowledge. p. 123-195. In: *Oceanography and marine biology: an annual review volume 44*. Gibson, R. N., Atkinson, R. J. A., Gordon, J. D. M. (Eds.). CRC Press, Boca Raton.
- Bartsch, I., 2018. Derivation of Clonal Stock Cultures and Hybridization of Kelps. p. 61-78. In: *Protocols for Macroalgae Research*. Charrier, B., Wichard, T., Reddy, C. R. K. (Eds.). CRC Press, Boca Raton.
- Benhissoune, S., Boudouresque, C.-F., Perret-Boudouresque,

- M., Verlaque, M., 2002. A check-list of marine seaweeds of the Mediterranean and Atlantic coasts of Morocco. II. Phaeophyceae. *Botanica marina*, 45, 217-230.
- Ben Maiz, N., Boudouresque, C.-F., Ouachi, F., 1987. Inventaire des algues et phanérogames marines benthiques de la Tunisie. *Giornale botanico italiano*, 121 (5-6) 259-304.
- Blanfuné, A., Boudouresque, C.-F., Verlaque, M., Thibaut, T., 2016. The fate of *Cystoseira crinita*, a forest-forming Fucale (Phaeophyceae, Stramenopiles), in France (North Western Mediterranean Sea). *Estuarine, Coastal and Shelf Science*, 181, 196-208.
- Blanfuné, A., Boudouresque, C.-F., Verlaque, M., Thibaut, T., 2025. Severe decline of *Gongolaria barbata* (Fucales) along most of the French Mediterranean coast. *Scientific Reports*, 15, 5701.
- Bo, M., Bertolino, M., Borghini, M., Castellano, M., Covazzi Harriague, A. *et al.*, 2011. Characteristics of the Mesophotic Megabenthic Assemblages of the Vercelli Seamount (North Tyrrhenian Sea). *PLoS ONE* 6, e16357.
- Boisset, F., Ferrer-Gallego, P. P., Furnari, G., Cormaci, M., Dennetière, B., 2016. Typification of the Mediterranean Endemic Deep-Water Macroalga *Laminaria rodriguezii* Bornet (Laminariaceae, Phaeophyceae). *Cryptogamie, Algologie* 37, 121-132.
- Bornet, M.Ed., 1888. Note Sur Une Nouvelle Espèce De Laminaria (*Laminaria rodriguezii*) De La Méditerranée. *Bulletin de la Société Botanique de France*, 35, 361-366.
- Boudouresque, C.-F., Perret-Boudouresque, M.M., 1987. *A checklist of the benthic marine algae of Corsica*. GIS Posidonie, Marseille, 121 pp.
- Boudouresque C.-F., Perret-Boudouresque M., Blanfuné A., 2022. Diversity of marine and brackish macrophytes in the Port-Cros National Park (Provence, France, Mediterranean Sea): taxa and research effort over space and time. *Diversity*, 14 (329), 1-41.
- Boudouresque, C.-F., Ballesteros, E., Ben Maiz, N., Boisset, F., Bouladier, E. *et al.*, 1990. *Livre rouge «Gérard Vuignier» des végétaux, peuplements et paysages marins menacés de Méditerranée*. Programme des Nations Unies pour l'Environnement (UNEP), IUCN Publishers, Athens, 250 pp.
- Carney, L.T., Bohonak, A. J., Edwards, M. S., Alberto, F., 2013. Genetic and experimental evidence for a mixed-age, mixed-origin bank of kelp microscopic stages in southern California. *Ecology*, 94, 1955-19654.
- Cossu, A., Gazale, V., 1999. Nuove segnalazioni per la flora marina bentonica della Sardegna. *Biologia Marina Mediterranea*, 6 (1), 368-371.
- Council of Europe, 1979. Convention on the Conservation of European Wildlife and Natural Habitats, Bern, 19.IX.1979. *European Treaty Series*, 104: 1-10 + Annexes.
- Demes, K. W., Graham, M. H., 2011. Abiotic regulation of investment in sexual versus vegetative reproduction in the clonal kelp *Laminaria sinclairii* (laminariales, Phaeophyceae). *Journal of phycology*, 47(3), 463-470.
- Deter, J., Juhel, J.-B. Boulanger, E., Guellati, N., Mauron, S. *et al.*, 2020. *Gombessa 5 cruise: CTD profiles in western Mediterranean, July 2019. SEANOE*.
- Ercegović, H., 1960. Limite inférieure des algues supérieures en Adriatique. *Rapports et Procès-verbaux des Réunions de la CIESMM* 15, 156-160.
- Falconetti, C., 1980. Bionomie benthique des fonds situés à la limite du plateau continental du banc du Magaud (îles d'Hyères) et de la région de Calvi (Corse). Ph.D. Thesis, University of Nice, France, 287 pp.
- Farriols, M.T., Joher, S., Ordines, F., Guijarro, B., Peteiro, C. *et al.*, 2025. Recovery and expansion of rhodoliths beds and *Laminaria rodriguezii* forests after bottom trawl ban. *Biodiversity and Conservation*, 34 (3), 895-915.
- Fourt, M., Goujard, A., 2012. *Rapport final de la campagne MEDSEASCAN (Têtes des canyons méditerranéens continentaux) Novembre 2008 - Avril 2010. Partenariat Agence des aires marines protégées*. GIS Posidonie, Marseille, 218pp.
- Fredj, G., 1972. Compte rendu de plongée en SP 300 sur les fonds à *Laminaria rodriguezii* Bornet de la Pointe de Revellata (Corse). *Bulletin de l'Institut océanographique de Monaco*, 71, 1-42.
- Ganteaume, A., Bonhomme, P., Ruitton, S., Verlaque, M., Boudouresque, C.-F., 2004. *Etat des lieux et potentialités du milieu marin autour des îles Sanguinaires (Corse du Sud)*. *Contract GIS Posidonie et Association des Amis du Parc de Corse*. GIS Posidonie, 60 pp.
- Gautier, Y., Picard, J., 1957. Bionomie du banc de Magaud (Est des Iles d'Hyères). *Recueil des travaux de la station marine d'Endoume*, 12 (21), 28-40.
- Giaccone, G., 1969. Note sistematiche ed osservazioni fitosociologiche sulle Laminariales del Mediterraneo occidentale. *Plant Biosystem* 103, 457-474.
- Guiry, M.D., Guiry, G.M., 2025. AlgaeBase. World-wide electronic publication, University of Galway. <https://www.algaebase.org>; (Accessed 5 March 2025).
- Harmelin, J.G., Zibrowius, H., Arnoux, A., Romana, L., 1991. *Evaluation de l'état des peuplements benthiques du haut-fond St Julien (Région de St Tropez)*. *Campagnes Cyana de mars et Juin 1990*. Ifremer, Paris, 41pp.
- Huvé, H., 1955. Présence de *Laminaria rodriguezii* Bornet sur les côtes françaises de la Méditerranée. *Recueil des travaux de la station marine d'Endoume*, 15, 73-91.
- IUCN, 2012. IUCN Red List Categories and Criteria: Version 3.1. (IUCN, Gland, Switzerland and Cambridge).
- IUCN, 2025. The IUCN Red List of Threatened Species. Version 2025-1. <https://www.iucnredlist.org> (Accessed 21 March 2025)
- Joher, S., Ballesteros, E., Rodrigues-Prieto, C., 2015. Contribution to the study of deep coastal detritic bottoms: the algal communities of the continental shelf off the Balearic Islands, Western Mediterranean. *Mediterranean Marine Science*, 16 (3), 573-590.
- Joher, S., Ballesteros, E., Cebrian, E., Sánchez, N., Rodríguez-Prieto, C., 2012. Deep-water macroalgal-dominated coastal detritic assemblages on the continental shelf off Mallorca and Menorca (Balearic Islands, Western Mediterranean). *Botanica Marina* 55, 485-497.
- Küpper, F. C., Tsiamis, K., Johansson, N. R., Peters, A. F., Salomidi, M. *et al.*, 2019. New records of the rare deep-water alga *Sebdenia monnardiana* (Rhodophyta) and the alien *Dictyota cyanoloma* (Phaeophyceae) and the unresolved case of deep-water kelp in the Ionian and Aegean Seas (Greece). *Botanica Marina*, 62, 577-586.
- Linares, C., Vidal, M., Canals, M., Kersting, D. K., Amblas,

- D., Aspillaga, E., *et al.*, 2015. Persistent natural acidification drives major distribution shifts in marine benthic ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150587.
- Martins, N., Pearson, G. A., Gouveia, L., Tavares, A. I., Serão, E. A., *et al.*, 2019. Hybrid vigour for thermal tolerance in hybrids between the allopatric kelps *Laminaria digitata* and *L. pallida* (Laminariales, Phaeophyceae) with contrasting thermal affinities. *European Journal of Phycology*, 54, 548-561.
- Molinier, R., 1956. Les fonds à laminaires du Grand Banc de Centuri (Cap Corse). *Comptes Rendus de l'Académie des Sciences*, 342, 939-941.
- Pageault, L., 2020. *Growth and photosynthesis of the endemic Mediterranean deep-water kelp Laminaria rodriguezii along temperature and irradiance gradient*. MSc Thesis. University of Aix-Marseille, France, 47 pp.
- Pedel, L., Fabri, M.C., 2011. *Description et cartographie des biocénoses benthiques rencontrées au cours de la campagne MEDSEACAN (Aamp/Comex). Convention MED-DTL – Ifremer pour l'Evaluation Initiale de DCSMM*. Ifremer, Paris, 109 pp.
- Pérès, J.-M., Picard, J., 1964. Nouveau manuel de bionomie benthique de la mer Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, 31 (47), 3-137.
- Perret-Boudouresque, M.M., Seridi, H., 1989. *Inventaire des algues marines benthiques d'Algérie*. Gis Posidonie, Marseille, 117 pp.
- Provasoli, L., 1968. Media and prospects for the cultivation of marine algae. p. 63-75. In: *Cultures and Collections of Algae*. Watanabe, A., Hattori, A., (Eds.). *Proceedings of the US Japan Conference, Hakone 1966*. Japanese Society of Plant Physiology, Tokyo.
- Reynès, L., Thibaut, T., Mauger, S., Blanfuné, A., Holon, F., *et al.*, 2021. Genomic signatures of clonality in the deep-water kelp *Laminaria rodriguezii*. *Molecular Ecology*, 30, 1806-1822.
- Ribera, M.A., Gomez Garreta, A., Gallardo, T., Cormaci, M., Furnari, G. *et al.*, 1992. Check-list of Mediterranean Seaweeds. I. Fucophyceae (Warming, 1884). *Botanica Marina*, 35, 109-130.
- Safege Cetiis, 2011. *Étude préalable à la mise en place de l'observatoire marin du littoral des Maures le long des côtes de Ramatuelle. Rapport d'étude*. Contrat Safege Cetiis - SIVOM du Littoral des Maures. 170 pp.
- Schoenrock, K.M., McHugh, T.A., Krueger-Hadfield, S., 2021. Revisiting the 'Bank of microscopic forms' in macroalgal dominated ecosystems. *Journal of Phycology*, 57, 14-29.
- Shea, R., Chopin, T. 2007. Effects of germanium dioxide, an inhibitor of diatom growth, on the microscopic laboratory cultivation stage of the kelp, *Laminaria saccharina*. *Journal of Applied Phycology*, 19, 27-32.
- Smale, D.A., Burrows, M.T., Moore, P., O'Connor, N., Hawkins, S.J., 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast Atlantic perspective. *Ecology and Evolution*, 3, 4016-4038.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M. *et al.*, 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation*, 29, 436-459.
- Taşkin, E., Öztürk, M., Kurt, O., Öztürk, M. 2008. *The checklist of the marine flora of Turkey*. Manisa, Turkey, 87 pp.
- Tatewaki, M., 1966. Formation of a crustaceous sporophyte with unilocular sporangia in *Scytosiphon lomentaria*. *Phycologia*, 6, 62-66.
- tom Dieck, I., 1992. North Pacific and North Atlantic digitate *Laminaria* species (Phaeophyta): hybridization experiments and temperature responses. *Phycologia*, 31 (2), 147-163.
- tom Dieck, I., 1993. Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): Ecological and biogeographical implications. *Marine Ecology Progress Series*, 100, 253-264.
- tom Dieck, I., de Oliveira, E.C., 1993. The section Digitatae of the genus *Laminaria* (Phaeophyta) in the northern and southern Atlantic: crossing experiments and temperature responses. *Marine Biology*, 115, 151-160.
- UNEP/MAP-SPA/RAC, 2018. SAP/RAC: SPA-BD Protocol - Annex II: List of endangered or threatened species. SPA/RAC publ., Tunis, Tunisia.
- Žuljević, A., Peters, A.F., Nikolić, V., Antolić, B., Despalatović, M. *et al.*, 2016. The Mediterranean deep-water kelp *Laminaria rodriguezii* is an endangered species in the Adriatic Sea. *Marine Biology*, 163 (69), 1-12.