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

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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 m^2 (mean ± 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 m^2, 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 haptera 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 haptera, 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 m^2 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

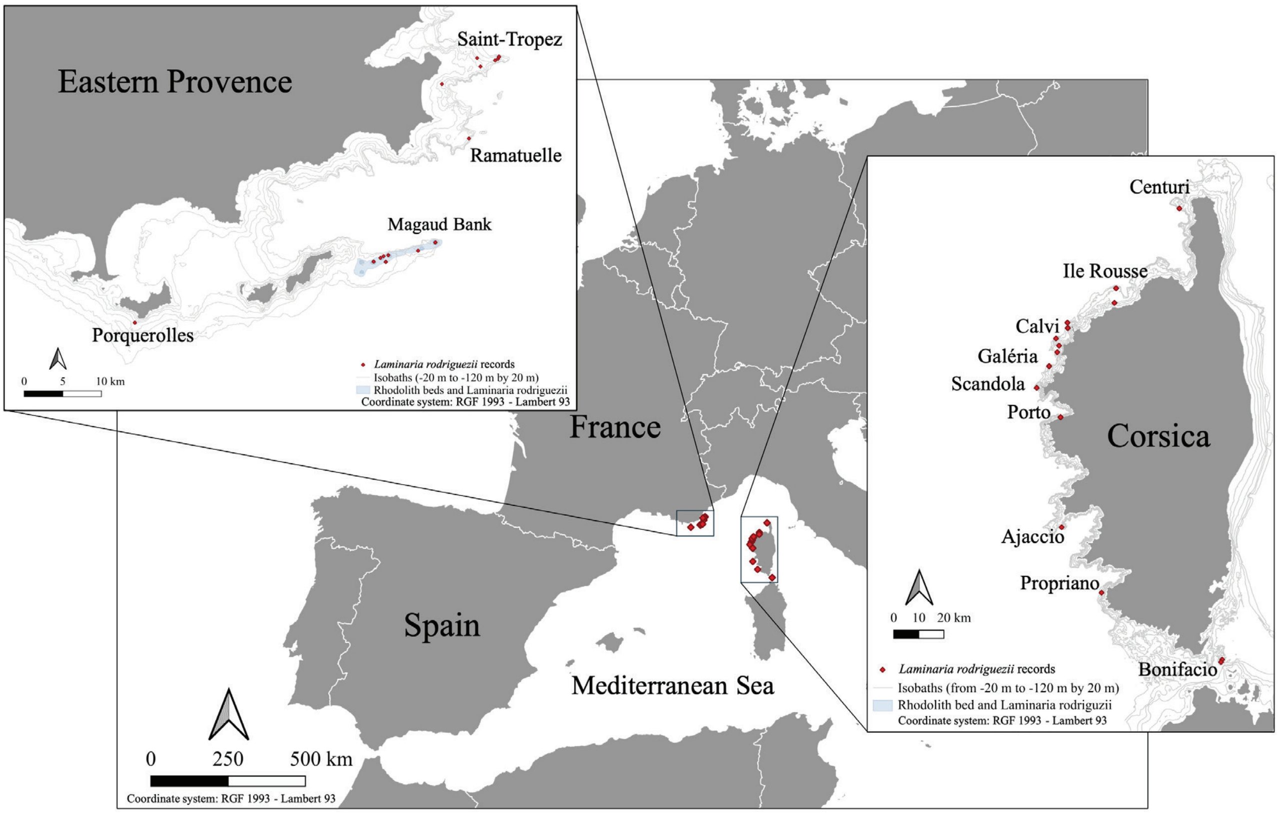

Fig. 1: Locations of *Laminaria rodriguezii* populations along the French Mediterranean coast.

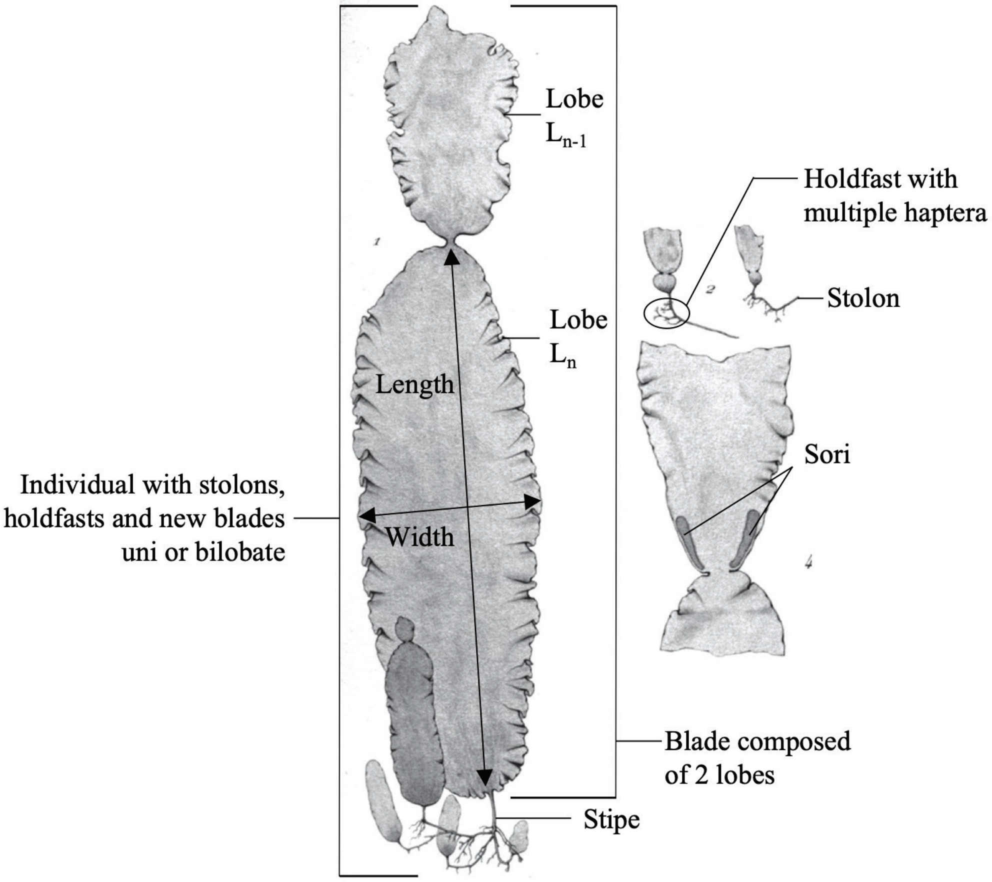

Fig. 2: Measured parameters for the different individuals of *Laminaria rodriguezii* from the Magaud Bank population. L_n lobes correspond to those from the current year, while L_{n-1} lobes are from the previous year. A blade can thus be composed of several lobes. The illustrations are adapted from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

log_{10}-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 Na_2glycerophosphate, iodine enrichment after Tatewaki, 1966) in sterile North Sea seawater (approx. 31.5 g kg^{-1}). For a short period GeO_2 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 m^2, 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
		Magaud Bank	Adjacent Marine Area (AMA) of the PCNP, Natura 2000	6.57417°E	43.03714°N	80	1954	HCOM: H1158, H1159
				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 *et al.*, 2021
				6.67375°E	43.05625°N	75	2019	Andromède Océanologie, 2020
	Ramatuelle	Cap Camarat	Adjacent Marine Area (AMA) of the PCNP, Natura 2000	6.73535°E	43.17501°N	80	2004, 2018	Reynès *et al.*, 2021
	Saint-Tropez	Cap Pinet	Natura 2000	6.69582°E	43.24000°N	50-78	1990	Harmelin *et al.*, 1991

Continued

Table 1 continued

Region	Municipality	Site	Protection status	Longitude	Latitude	Depth (m)	Date of record	Reference
		Saint-Julien	Natura 2000	6.75396°E	43.26827°N	78	2011	Safege Cetiis, 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
Corsica	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
				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
	Calvi	Punta Rossa	Natura 2000	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 *et al.*, 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 *et al.*, 2021

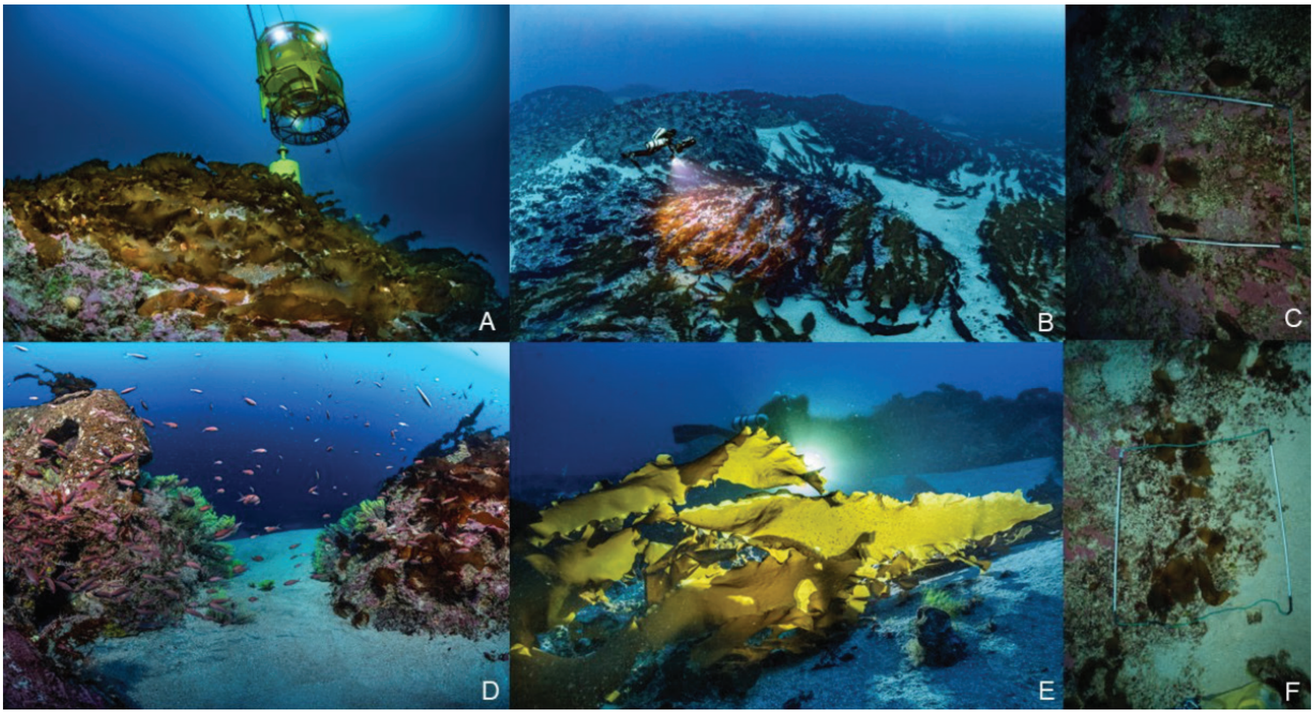

Fig. 3: Impressions of the sampling area at Magaud Bank characterized by strong currents: A) *Laminaria rodriguezii* bed at Magaud Bank, the lift was used by the divers for the collection by autonomous saturation dive, B) the Magaud Bank seascape with small rocky and coralligenous hills interspersed with valleys of white shell sand, C) a 1-m^2 quadrat on coralligenous substrate, D) *L. rodriguezii* and gorgonians on a massif (hill), E) *L. rodriguezii* blades in the current, F) a 1-m^2 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 *Laminaria rodriguezii* 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 ± 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± 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± 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± 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± 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± 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± 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± 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 ± 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 ±SE, median = 302.5 9 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 µmol photons m^{-2} s^{-1}.

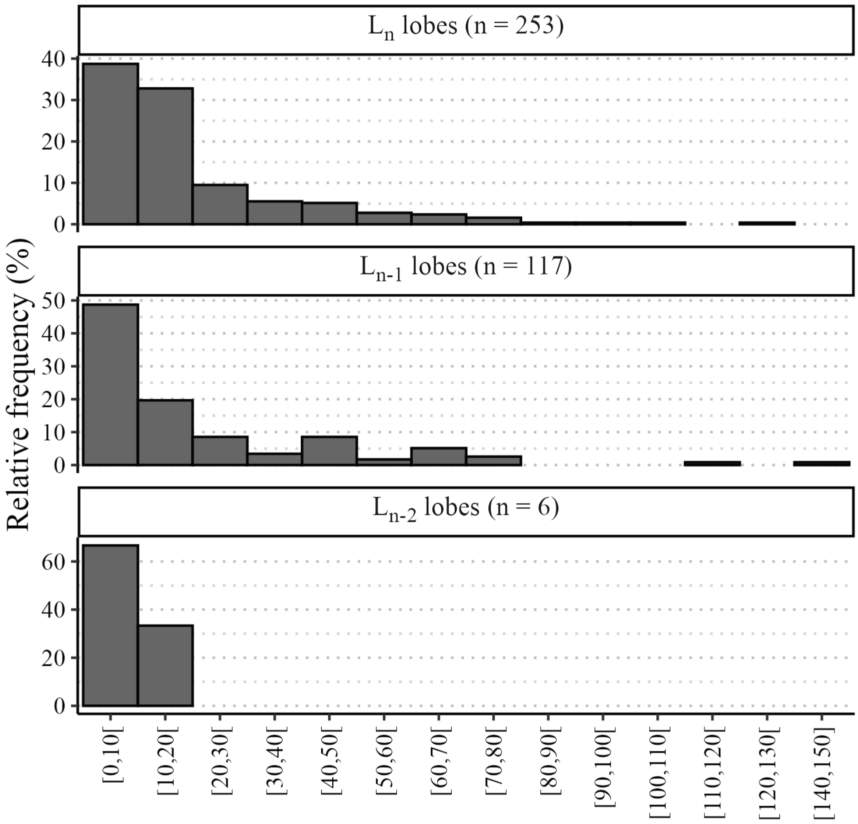

Fig. 4: Relative frequency of each length class (in cm) of each lobe type. L_n lobes correspond to those from 2019, L_{n-1} lobes to those from 2018 and L_{n-2} lobes to those from 2018.

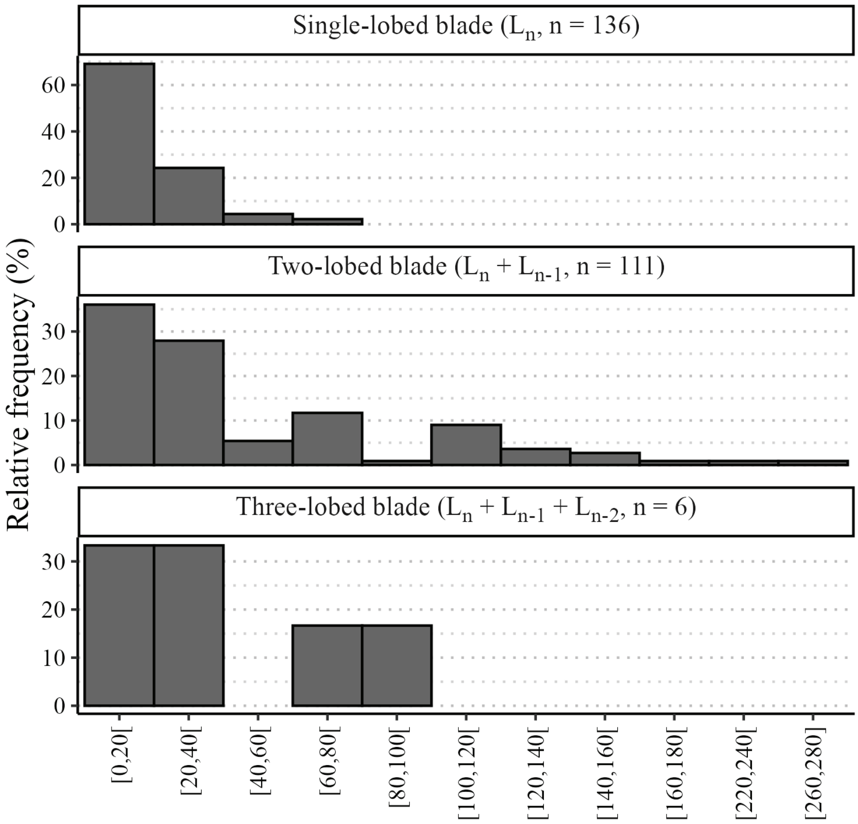

Fig. 5: Relative frequency of each total length class [stipe plus all lobes (L_n, L_{n-1}, L_{n-2})] in cm of each configuration of blades (i.e., single, two or three-lobed blade).

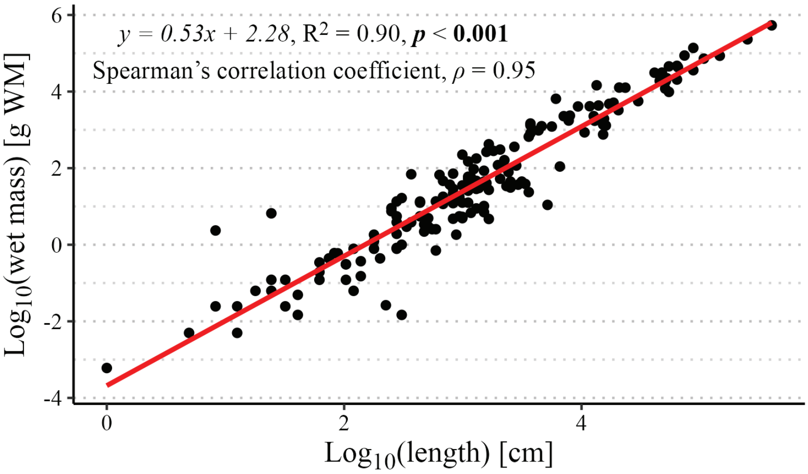

Fig. 6: Linear regression between the length and the wet mass, WM, ($\log_{10}$ transformed) of *Laminaria rodriguezii* blades (n = 164).

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

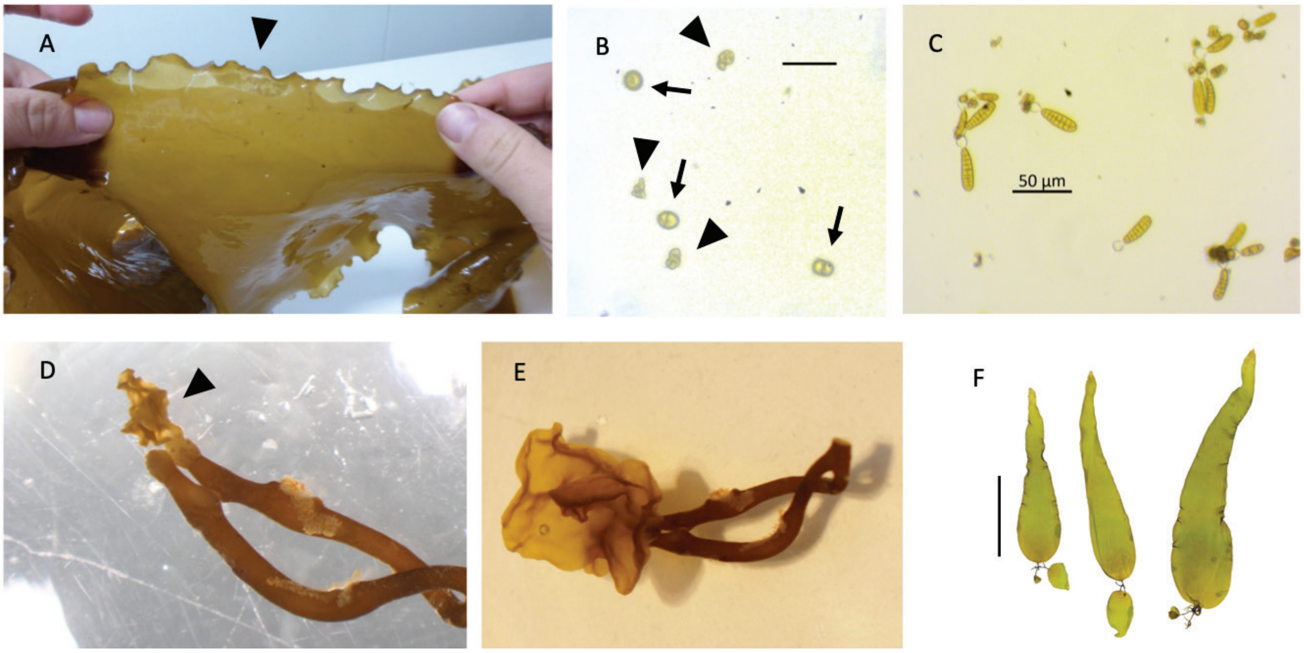

Fig. 7: Life cycle stages of *Laminaria rodriguezii*. A. Blade with marginal sori, mostly released (whitish zone) except for patchy area (arrowhead). B. Early gametophyte stages after germination of the spores (males: arrowhead, females: arrows). C. Young microscopic sporophytes which developed at 15°C and an irradiance of 2 µmol photons m^{-2} 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 µmol photons m^{-2} 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 heteroromophic 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., Carney *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.

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