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Ecology and distribution patterns of *Chara connivens* (Charophyta, Characeae) on the Canary Islands – the first record from Fuerteventura

by

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Abstract

The paper presents the first record of a Chara connivens (Characeae) stand from Fuerteventura (Canary Islands, Spain). The species was previously recorded only on Tenerife and Lanzarote, mostly in marine and artificial habitats. Physicochemical parameters of water and morphological features of the thalli and plant community were analyzed. General habitat requirements of C. connivens populations located in Europe, North Africa, and South-West Asia were reviewed. The newly described stand was located in a natural rock crevice that was part of a riverbed in El Barranco de las Peñitas (Penitas Canyon). This habitat was unshaded and filled with brackish water. C. connivens co-occurred with Cladophora glomerata and Ruppia maritima. Our report on the presence of C. connivens in the Spanish territory of the Atlantic Ocean is the first in almost 40 years. The distribution of C. connivens and its plant associations on the Canary Archipelago are poorly explored, which is why this topic requires further research.

Key words: Canary Islands, *Chara connivens*, charophytes, Fuerteventura, macroalgae, Spain

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Introduction

Charophytes, often called stoneworts, are a group of autotrophic and macroscopic algae represented by more than 400 species assigned to the Characeae family within the Charophyta phylum (Schneider et al. 2015; Guiry & Guiry 2019). Its first members evolved nearly 420 million years ago (Graham & Wilcox 2000). Charophytes are a highly developed and diverse group of macroalgae (Kotta et al. 2004; Schneider et al. 2015). They are widely distributed in freshwater as well as brackish and marine habitats, from tropical to polar regions (Wood 1965). The occurrence of Characeae taxa is mostly limited to clear, freshwater lakes with low fertility (Dambska 1964; Krause 1969; 1981; 1997; Martin et al. 2003; Brzeska et al. 2015). Many stonewort species are characteristic of hard, oligo-mesotrophic water ecosystems (Krause 1981; 1997). Some species of the genus Chara are capable of developing in eutrophic or even hypertrophic habitats (Urbaniak & Gabka 2014).

Chara connivens P. Salzmann ex A. Braun, known as a convergent stonewort, belongs to the group of brackish charophytes. To date, C. connivens has been reported mainly from Western Europe, the Mediterranean Sea basin region and the Baltic Sea (Krause 1981; 1997; Torn & Martin 2003; Torn et al. 2004; Urbaniak & Gabka 2014; Brzeska et al. 2015). Several stands of C. connivens were also located in the inland saline waters of Central and Southern Europe (Dąmbska 1964; Krause 1997; Torn & Martin 2003). Furthermore, this alga was also found in North Africa and Central Asia (Corillion 1957; Krause 1997; Cirujano et al. 2008). Communities with C. connivens are mostly pioneer in ephemeral shallow waterbodies (Felzines & Lambert 2012). In Europe, C. connivens stands were recorded in Albania (Zeneli & Kashta 2016), Bulgaria (Temniskova et al. 2008), Estonia (Torn & Martin 2003; Kotta et al. 2004; Torn et al. 2015), Finland (Appelgren et al. 2004), France (Hy 1913; Corillion 1957), Georgia (Barinova & Kukhaleishvili 2014), Germany (Wood 1965; Luther 1979; Ludwig & Schnittler 1996), Great Britain (Stewart & Church 1992; Bryant & Stewart 2002; John et al. 2011), Greece (Langangen 2010; 2012), Ireland (Stewart & Church 1992), Latvia (Skuja 1928; Kostkevičienė & Sinkevičiene 2008), the Netherlands (Simons et al. 1994; Bruinsma 2000; Bruinsma et al. 2018), Poland (Urbaniak & Blaženčić 2012; Urbaniak & Gąbka 2014; Brzeska et al. 2015; Krajewski et al. 2015), Portugal (Corillion 1957; Cambra Sánchez et al. 1998), Romania (Caraus 2002; 2012; 2017), Russia (Kaliningrad Oblast) (Romanov et al. 2018a,b), Spain (Reyes Prósper 1910; Aboal 1985; Cambra Sánchez et al. 1998; Cirujano et al. 2008; del Pozo et al. 2011), and Sweden (Luther 1979; Blindow 1988; Wallström & Persson 1999; Tolstoy & Österlund 2003; Torn & Martin 2003; Torn et al. 2004; Langangen 2007). In Africa, populations of C. connivens were found in Algeria (Wood 1965; Muller et al. 2017), Egypt (Corillion 1957), Morocco (Wood 1965; Muller et al. 2017), and Tunisia (Corillion 1957; Wood 1965; Muller et al. 2017). Unfortunately, the presence of C. connivens in South-West Asia has been poorly investigated and the species was recorded only in India (Gupta 2012), Iran (Ahmadi et al. 2012) and Israel (Romanov & Barinova 2012; Barinova & Romanov 2015). All of the above-mentioned data come from published research papers. However, some data on the identified stands of this alga have not yet been published. Herbaria can also provide information on the distribution of C. connivens (see collections deposited at the Academy of Natural Sciences, Adam Mickiewicz University in Poznań, Butler University, Drexel University, Field Museum of Natural History, Harvard University, Miami University, New York Botanical Garden, University of California and University of Michigan). Interestingly, these unpublished herbarium notes inform about C. connivens populations in Australia (9 stands) as well as in Europe (France - 2 stands, Germany - 1, Kaliningrad Oblast - 1, the Netherlands - 1, Poland - 2, Spain – 1, Sweden – 1, and the United Kingdom – 2).

In some European countries, C. connivens is protected by law. In Poland, for example, C. connivens is a strictly protected species. The "Red list of plants and fungi in Poland" classifies this alga as extinct or most likely extinct (EX) species (Siemińska et al. 2006). In Great Britain, C. connivens is an endangered (EN) species (Stewart & Church 1992). In Ireland, the convergent stonewort is classified as a regionally extinct (RE) species. The conservation status of this species is inconsistent due to discoveries of new stands or confirmed recolonization of the historical ones. Initially, in 1993, the German government classified C. connivens as a regionally extinct species (Schmidt 1994), but following the identification of new stands, its status was changed to critically endangered (CE) in 2012 (Korsch et al. 2013). Finally, the latest update of the "Red list of stoneworts (Charophyceae) from Mecklenburg-Western Pomerania, Germany" presents C. connivens as an endangered (EN) species (Teppke et al. 2015). This alga is also a red-listed species in Sweden and, based on recent research, it should be likewise promptly classified as highly threatened in Finland (Appelgren et al. 2004). On the other hand, the Helsinki Commission (HELCOM) database from 2013 classified C. connivens as a "not native" species to the Baltic Sea area. Moreover, in some of the Baltic Sea countries (Denmark, Germany and Lithuania - verified in 2017), C. connivens is considered as an invasive species requiring special attention (DAISIE 2006; Drake 2009;



NOBANIS 2015; Pagad et al. 2018). Unfortunately, the origin of the convergent stonewort in the Baltic Sea area is unclear and the Baltic Marine Biologists (BMB) working group "Non-indigenous estuarine and marine organisms" characterized it as cryptogenic (Torn & Martin 2003; Kautsky & Snoeijs 2004). According to some theories, this species arrived in the Baltic Sea as a consequence of shipping from the Mediterranean region and was introduced together with the ballast, e.g. wet sand (Luther 1979; Torn & Martin 2003; Tolstoy & Österlund 2003). This idea is supported by the fact that many of the identified Baltic Sea stands of C. connivens are convergent with the ballast sites of harbors. However, Appelgren et al. (2004) challenged this hypothesis based on coastal stands of C. connivens on the Åland Archipelago (Finland) outside the important shipping routes in the 19th or 20th century. Considering that the population of C. connivens in the Baltic Sea is guite stable at the regional scale, i.e. neither severely dispersed nor continually declining, the species is currently classified as the least concern (LC) species (HELCOM 2013).

The objectives of the current study were (1) to characterize the unknown and unique stand of *C. connivens* from Fuerteventura and (2) to determine the relationships between environmental gradients and distribution of this algae. This work presents revised data on the occurrence and ecology of the convergent stonewort.

Materials and methods

Research location

The study involved the *Chara* population from its stand located in the canyon El Barranco de las Peñitas on Fuerteventura (Spain), one of the largest (1657 km²) and oldest (20 million years) islands of the Canary Archipelago (Schmitz et al. 2018). This area is of volcanic origin and is currently highly eroded as well as the most arid region of Macaronesia. Temperatures are very stable (17–20°C) throughout the year, although air masses from neighboring Africa can suddenly increase the temperature (Schmitz et al. 2018). Precipitation is irregular and low, i.e. less than 200 mm per year, but winds and insolation (2800 hours per year) are very intense.

The research site was located in the western part of the island, between the cities of Mazquez and Vega de Rio Palmas ($28^{\circ}23'17.6''$ N; $14^{\circ}06'13.2''$ W), at an elevation of 172 m a.s.l. (Fig. 1). The canyon is part of the rural park of Betancuria. The sampling site was located in a longitudinal, narrow rock crevice (25.31×3.56 m),

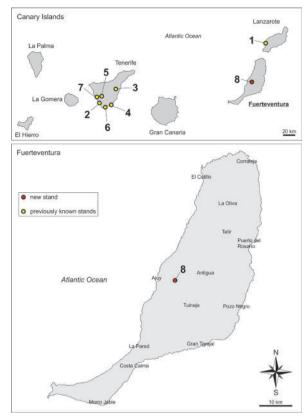


Figure 1

Distribution map of *Chara connivens* populations on the Canary Islands (Spain). Red circle: new stand; yellow circles: previously known stands. Stands: 1 – El Golfo, 2 – Las Cuevitas, 3 – Añocheza, 4 – Adeje, 5 – El Barranco del Infierno, 6 – Costa del Silencio, 7 – Armeñime, and 8 – El Barranco de las Peñitas. The number assigned to a given stand is consistent with the numbering used in Table 1.

partly filled with water (Fig. 2A), which constitutes a unique natural habitat on the island. A slight flow of water was observed. The bottom was rocky and sandy-organic.

Species identification

The identification of species was based on the examination of morphological features as presented by Cirujano et al. (2008), Bryant & Stewart (2011), and Urbaniak & Gąbka (2015). Moreover, the identification keys created by Dąmbska (1964), Moore (1986), Krause (1997), Pełechaty & Pukacz (2008) and John et al. (2011) were used. All specimens of *Chara* were classified to one species only – *Chara connivens* P. Salzmann ex A. Braun. The current nomenclature of algae, mosses and vascular plants was used according to AlgaeBase (Guiry & Guiry 2019) and the World Checklist of Selected Plant Families (WCSP 2019).



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Table 1

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Stands of *Chara connivens* on Canary Islands (Spain). The number assigned to a given stand is consistent with the numbering used in Figure 1

Island	Stand	Habitat	Date	Collector(s)	Herbarium, voucher number	References
Lanzarote	1. El Golfo	marine	07.1975	M.C. Gill Rodriguez	TFC Phyc., 2193	Rodriguez et al. 1981
Tenerife	2. Las Cuevitas	marine	12.1976	E. Beltrán	TFC Phyc., 2195	Rodriguez et al. 1981
	Ibid.	marine	12.1978	W. Wildpret E. Beltrán C. Rodriguez	TFC Phyc., 2196	Rodriguez et al. 1981
	3. Añocheza	artificial pool	04.1980	W. Wildpret E. Beltrán C. Rodriguez	TFC Phyc., 2197	Rodriguez et al. 1981
	4. Adeje	marine	09.1982	J.C. van Raam	JVR & L., 8201	Raam & Gonzalez-Henriquez 1995
	5. El Barranco del Infierno	river	09.1982	J.C. van Raam	JVR & L., 8202	Raam & Gonzalez-Henriquez 1995
	6. Costa del Silencio	artificial pool	09.1982	J.C. van Raam	JVR & L., 8203	Raam & Gonzalez-Henriquez 1995
	7. Armeñime	artificial pool	09.1982	J.C. van Raam	JVR & L., 8204	Raam & Gonzalez-Henriquez 1995
Fuerteventura	8. El Barranco de las Peñitas	intermittent river	04.2019	A.S. Rybak A.M. Woyda-Ploszczyca	POZA, CH0009	(this paper)

Field samples

Thalli and water sampling was conducted on 12 April 2019. Thalli specimens were collected directly from the central part of the *Chara* meadow. In total, two subsamples of thalli (2×5 g of fresh weight) were collected from this stand.

The samples of water (1 I) were collected from the central part of the stonewort meadow. Long-sleeve veterinary gloves were used in the process to prevent contamination. Samples of water were filtered through a coarse plastic sieve to separate vascular plants and filamentous macroalgae. Subsequently, the water samples were placed into two 0.5 I sterile plastic containers, preserved with 0.5 ml of chloroform and cooled in a mobile refrigerator. In the laboratory, before the chemical analysis, the samples were filtered through a microbiological filter with a pore size of 0.45 microns (Sartorius, Goettingen, Germany).

Physicochemical analysis

In the field, water temperature, pH, electrolytic conductivity, total dissolved solids (TDS), oxidation-reduction potential (ORP), salinity and oxygenation were measured using the Professional Plus Multi-Parameter Instrument (YSI, Yellow Springs, OH, USA). In addition, water depth was measured using a plastic staff gauge. Chemical analyses, i.e.

ammonium nitrogen (N-NH₃), nitrate nitrogen (N-NO₃), total phosphate (P-PO₄), sulfate (SO₄) and total iron (Fe-total) concentrations, as well as water color, were performed in the laboratory using a HACH DR 2800 spectrophotometer (Fairborn, OH, USA) and applying standard hydrochemical methods (APHA 2002). Sodium chloride (NaCl) concentration was determined using the HACH Chloride Digital Titrator Kit (Fairborn, OH, USA). Water turbidity was measured using a EUTECH TN-100 turbidimeter (Thermo Scientific, Singapore). The applied equipment and standard analytical methods are presented in detail in Rybak & Gąbka (2018).

Microscopic observation

The morphology of the thalli was assessed directly after the collection of samples. A mobile MINI Magnum microscope (MINI, China) with a magnification of 5 to 20 and a magnifying glass were used in the field to quickly analyze the thalli.

Laboratory observations were performed using a Zeiss Stemi DV4 stereomicroscope (Zeiss, Germany) with a magnification of 8 to 32. Thalli were also analyzed under a light microscope (Zeiss Axioskop 2 MOT). Microphotographs of fresh samples (Fig. 3) were taken with the ProgRes Speed XT core 3 camera (Jenoptic, Germany).





Figure 2

Habitat of *Chara connivens* on Fuerteventura. A – view of El Barranco de las Peñitas canyon (in western direction), with a partially water-filled rock crevice (red arrow); B – *C. connivens* meadows (red arrows); C – dense meadow of convergent stonewort; and D – fresh thalli of *C. connivens* from the stand. Photographs by A.M. Woyda-Ploszczyca





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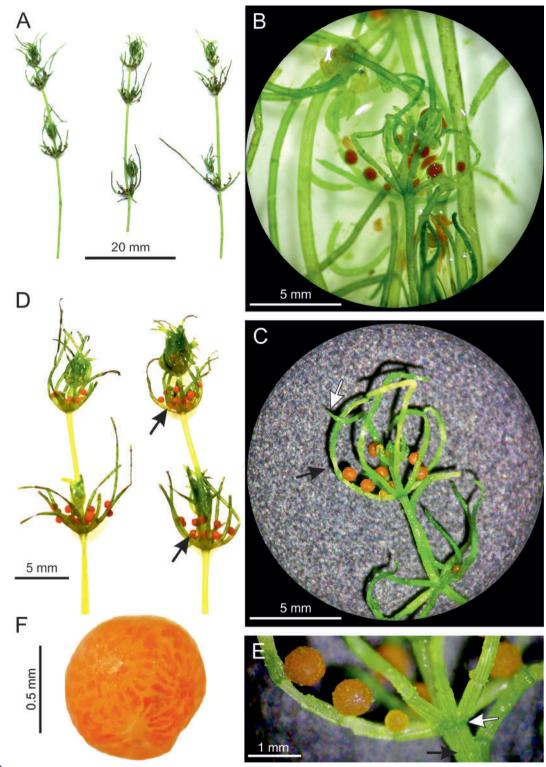


Figure 3

Male specimen of *Chara connivens* from the El Barranco de las Peñitas canyon (Fuerteventura Island). A – slender thalli; B – the upper part of the thallus (in the middle); C – an incurved branchlet (black arrow) and an ecorticate terminal segment of the branchlet (white arrow); D – slender thalli with visible male gametangia (antheridia); E – a node with a double whorl of rudimentary stipulodes (white arrow) and the main axis (stem) with triplostichous isostichous cortex (black arrow); and F – a single, typically orange-reddish male gametangium (antheridium). Photographs by A.S. Rybak



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Herbarium

Several individuals of *Chara* were selected for an herbarium. A herbarium sheet was prepared in accordance with the guidelines of Drobnik (2007), Kalmbach (2011) and Rybak (2015, 2018). Thalli samples were attached to the labelled sheet using Archer's method. The herbarium sheet was digitized based on the Gilroy (2001) protocol (Fig. 4). A voucher specimen (in Merrill's box) was deposited in the Natural History Collections at the Faculty of Biology [Poznań Algae Herbarium (acronym: POZA), voucher number: CH0009] at Adam Mickiewicz University in Poznań.

Results and discussion

Identification features

A detailed description of C. connivens presented by Dambska (1964), Wood (1965), Torn & Martin (2003), Moore (1986), Krause (1997), Cirujano et al. (2008), Pełechaty & Pukacz (2008), Bryant & Stewart (2011), Urbaniak & Gąbka (2014), Becker et al. (2016) was used. The plants are mostly small, up to 15 cm long, rarely longer (25-50 cm); slender thalli are delicate green and lustrous. An erect plant axis is usually 0.3-1.4 mm in diameter and not or slightly encrusted. C. connivens has 6-9 branchlets in a whorl. Fertile (male) plants often have branches that are strongly curved inwards (connivent) and sterile plants are similar. Internodes are shorter or as long as branches (in the upper part). Each branchlet has 6-10 segments, of which 6-8 are corticated; the last 1-3 segments can be without a cortex. The stem cortex is triplostichous and partly isostichous. Spine cells are lacking or rudimentary (papillous) if present. Stipulodes are also papillous, almost globular and occur in two rows. The plant is dioecious with gametangia at the lowest branchlet nodes. Bract cells (7–8) are very short, rudimentary, do not exceed the diameter of the branch. Bracteoles commonly papilliform or shorter than oogonium. Oogonia are 605–775 µm long and 330–410 µm wide. Oospores are long and ellipsoid-cylindrical in shape, usually dark brown or black, with a size of 485–595 imes205–325 µm. Antheridia (male gametangia) are solitary, clear orange-reddish, and up to 1100 µm in diameter.

Based on the description presented above, many morphological characteristics of *Chara* samples from Fuerteventura correspond to the *C. connivens* species, although only slightly encrusted male specimens were found (Figs 3 and 4). The fresh thalli were delicate, light green, up to 75 cm long, with axes from 0.4 to 1.1 mm in diameter. Antheridia were gaudy orange-reddish. Branches were strongly curved inward and ended with ecorticate terminal segments (Fig. 3).

C. connivens habitats

The C. connivens community on the Canary Islands grows mainly in hard freshwater, brackish water, small natural ponds and artificial irrigation tanks (del Arco Aguilar & Rodríguez Delgado 2018). To date, the Canary stands of C. connivens have been reported only from Lanzarote, a marine habitat (El Golfo) and Tenerife, marine (Las Cuevitas, and Adeje), riverine (El Barranco del Infierno) and artificial systems (Añocheza, Costa del Silencio) (Gil-Rodriguez et al. 1982; Raam & Gonzalez-Henriquez 1995) (Fig. 1, Table 1). The new stand of C. connivens on Fuerteventura Island was identified in a ravine-bed crevice of the canyon El Barranco de las Peñitas, 5.22 km from the ocean shoreline (Figs 1, 2). The sediment in this stand was rocky-organic. This type of sediment is not a necessary condition as in Germany C. connivens was

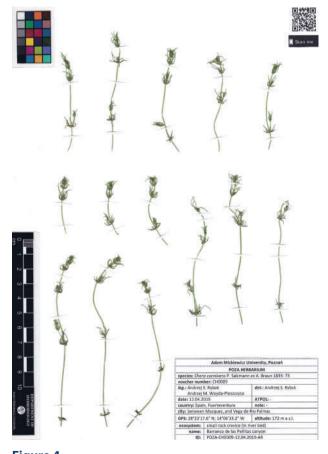


Figure 4

Herbarium specimen of *Chara connivens* from Fuerteventura Island (deposited in POZA herbarium). **Prepared and scanned by A.S. Rybak**



found on sandy and organic substrates (Becker 2008; 2010), in Spain and Greece – on loamy soil (Espinar et al. 2002; Langangen 2010), and in the Baltic Sea region (data from Estonia and Sweden) – on sand, muddy sand, muddy clay or mixtures of sand with pebbles (Torn & Martin 2003).

Plant communities with C. connivens

The C. connivens population of El Barranco de las Peñitas presented in this work occurred together with other species, i.e. macroalgae and vascular plants. The C. connivens meadow was accompanied by Cladophora glomerata and Rhizoclonium sp. mats (Fig. 5). Previously, Barinova & Romanov (2015) also observed C. connivens coexisting with filamentous algae, but in freshwater artificial pools (Northern Israel, Ein Afeg region). In this stand, C. connivens thalli were covered with unbranched filaments of the green alga Oedogonium sp. Vascular plants were represented by Ruppia maritima, which was a co-dominant species in the plant community (Fig. 5). So far, C. connivens associations on the Canary Islands have only been reported from Tenerife (Gil-Rodriguez et al. 1982; Raam & Gonzalez-Henriguez 1995) and Lanzarote (Gil-Rodriguez et al. 1982), where the convergent stonewort co-occurred with R. maritima, Potamogeton pusillus, and Myriophyllum spicatum (del Arco Aguilar & Rodríguez Delgado 2018). Specifically, the Canary Island populations of C. connivens in brackish habitats (marine lagoons) observed by Raam & Gonzalez-Henriquez (1995) were accompanied only by Ruppia maritima, but in rivulet stands, this alga coexisted with the moss species Fontinalis antipyretica and the vascular plant Nasturtium officinale. Moreover, the aforementioned authors observed that C. connivens meadows in freshwater artificial ecosystems (dammed reservoirs and agricultural water basins) could grow in the company of *P. pusillus*, but the meadows consisted mainly of the convergent stonewort completely covering the water surface of habitats. Therefore, the plant communities with C. connivens from the Canaries are rather poor in terms of species composition.

In the Mediterranean Sea region, *C. connivens* forms its own association, which dominates a habitat and is called *Ass.: Charetum conniventis* Velayos, Carrasco & Cirujano 1989 (Corillion 1957). According to many phytosociologists, *C. connivens* is a characteristic species of the halophilic alliance *All.: Charion canescentis* Fukarek ex Krausch 1964 (Krause 1969; 1981; Schaminée et al. 1995; van Raam 1998). *C. connivens* is also an accompanying species for other communities, i.e. *Ass.: Charetum hispidae* and



Figure 5

Chara connivens meadow (red arrows) accompanied by the "clouds" of *Cladophora glomerata* (yellow arrows) and shoots of *Ruppia maritima* (white arrow) covered with *Rhizoclonium* sp. filaments. **Photograph by A.S. Rybak**



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Charetum asperae (Schaminée et al. 1995; van Raam 1998). In other phytosociological works, the association *Charetum conniventis* is classified into a different alliance, namely *All.: Charion fragilis* Krausch 1964, which includes all groups of *Chara* communities from oligo-mesotrophic and calcium carbonate rich water (Becker et al. 2016; del Arco Aguilar & Rodríguez 2018).

In aquatic ecosystems of continental Europe, C. connivens occurs in various aquatic plant associations on habitats with different levels of salinity. In German inland lakes, C. connives occurred together with C. virgata, C. globularis and Nitella flexilis (Becker et al. 2016). The following vascular plant species can coexist with C. connivens, i.e. Elodea nuttallii, M. spicatum, Eleocharis acicularis, Elatine hexandra, and Potamogeton berchtoldii (Becker 2008; 2010; Becker et al. 2016). In marine brackish habitats (Fehmarn Island, Germany), C. connivens coexisted with other Chara species, i.e. C. aspera, C. canescens, C. vulgaris and C. globularis, while vascular plants were represented by Stuckenia pectinata, P. pusillus, Zannichellia palustris ssp. pedicellata and Ranunculus peltatus subsp. baudotii. This plant community also included the green alga Ulva intestinalis (Heinzel et al. 2010; Becker et al. 2016). On the other hand, in the coastal lake Cämmerer (Usedom Island, Germany), C. connivens grew together with C. aspera, C. canescens, C. tomentosa, C. papillosa, Najas marina ssp. intermedia, S. pectinate and M. spicatum (Becker et al. 2016). In the shallow peat lakes of the Netherlands, C. connivens grew together with C. aspera, C. globularis, C. hispida, C. aculeolata, C. contraria, Nitellopsis obtusa, Najas marina and the moss F. antipyretica (Simons et al. 1994; Becker et al. 2016). In the Baltic Sea, C. connivens species were usually recorded together with the algae C. aspera, C. globularis, C. tomentosa, C. contraria, N. obtusa and Tolypella nidifica as well as the vascular plants M. spicatum, S. pectinata, P. pusillus, and Z. palustris ssp. pedicellata, including nymphoides species and lemnids (Torn & Martin 2003; Brzeska et al. 2015; Becker et al. 2016). In addition, in the marine habitats of Finland and Estonia, C. connivens co-occurred with C. baltica and C. horrida (Appelgren et al. 2004; Torn et al. 2004; Becker et al. 2016). In the ephemeral lakes of Sardinia Island (Mediterranean Sea), C. connivens grew with C. aspera, Nitella opaca, Baldellia ranunculoides and R. peltatus ssp. baudotii (Becker et al. 2016). Furthermore, in salt marshes of southern Spain, C. connivens coexisted with C. canescens and Nitella hyalina (Espinar et al. 2002). Moreover, in freshwater lakes in Greece, C. connivens was observed only with C. globularis (Langangen 2010), but in France - with C. braunii and Nitella translucens (Corillion 1957; Becker et al. 2016).

Ecology of C. connivens

Unfortunately, the only literature concerning C. connivens on the Canary Islands (from the 1980s and 1990s) fails to mention physicochemical characteristics of water. The C. connivens population from Fuerteventura examined in this study grew in water with a neutral reaction and under good aerobic conditions (average oxygenation level - 83.4%, average concentration of oxygen – 7.4 mg l^{-1}). A phytoplankton bloom did not occur. The water was colorless and its color was at the average level of 20 Pt-Co units. The turbidity level ranged from 0.6 to 1.06 NTU (Nephelometric Turbidity Unit). The water in the habitat was also characterized by a high concentration of mineral compounds, which was reflected in a high level of electrolytic conductivity (10.11 mS cm⁻¹) and TDS (6.63 g l⁻¹). The high concentration of sodium chloride (3206.5 mg l-1) was the most important feature of the C. connivens stand. Furthermore, the water also contained many sulfates (196 mg l^{-1}), as well as nutrients, i.e., orthophosphates (2.73 mg l⁻¹) and nitrate nitrogen (from 0.8 to 1.10 mg l^{-1}). On the other hand, the total iron ion content was low (0.07 mg l^{-1} ; Table 2).

The available data describing the ecology of C. connivens are partly consistent with our results. Populations of this stonewort in north-western ponds of continental Spain grew in waters with turbidity ranging from 5 to 46 NTU, but the optimum turbidity value was 17 NTU (del Pozo et al. 2011). Moreover, the cover of C. connivens was significantly positively correlated with the level of orthophosphate. Such an observation was in line with findings that C. connivens prefers hypereutrophic waters (Lambert-Servien et al. 2006; Becker et al. 2016). However, mesotrophic to slightly eutrophic waters were also occupied by this alga (Felzines & Lambert 2012). Thus, C. connivens may tolerate relatively high concentrations of phosphates and ammonium (Simons et al. 1994). Nonetheless, it has been experimentally demonstrated that the growth of convergent stonewort thalli is significantly limited above 10 mg l⁻¹ of ammonium.

Populations of *C. connivens* are often found on limestone or in water with a certain amount of limestone, thus neutral to alkaline habitats (van Raam 1998). Some evidence indicates that optimum pH for *C. connivens* is between 7.0 and 9.0, and the optimum calcium level ranges from 45.6 to 180 mg l⁻¹ (Corillion 1957; Nat et al. 1994; Langangen 2010; Becker et al. 2016). Based on research performed in the Netherlands and Greece, this species tolerates a wide range of conductivity, i.e. from 0.35 to 3.07 mS cm⁻¹ (Nat et al. 1994; Langangen 2010). Similarly, *C. connivens* can grow



Parameter	Units	Minimum	Mean	Maximum
Depth of water	m	0.8	1.6	1.6
Temperature	°C	19.3	19.3	19.3
рН	-	6.4	6.6	6.8
Electrolytic conductivity	mS cm ^{−1}	9.8	10.1	10.3
TDS	g l ⁻¹	6.6	6.6	6.6
ORP	mV	64.0	64.4	65.2
Water color	Pt-Co mg l⁻¹	14.0	20.1	25.0
Turbidity	NTU	0.6	0.7	1.0
Oxygenation	%	80.0	83.4	86.4
Oxygen		7.0	7.4	7.8
N-NO ₃		0.8	0.8	1.1
N-NH ₃		0.1	0.1	0.2
Fe-total	mg l⁻¹	0.06	0.07	0.07
PO ₄		2.7	2.7	2.7
SO₄		168.0	196.0	216.0
NaCl		2821.5	3206.5	3382.5
Salinity	PSU	4.9	5.0	5.0

in ecosystems with varying chloride concentrations, ranging from 0 to 1070 mg l⁻¹ (Simons & Nat 1996). According to van Raam (1998), *C. connivens* can settle in mesohaline habitats from 5.0 to 18.0 PSU (Practical Salinity Units). It was experimentally demonstrated that the optimal growth of this alga needs 124 mg l⁻¹ of chloride and is significantly inhibited at approximately 2774 mg l⁻¹ (Simons et al. 1994). In the Baltic Sea, populations of *C. connivens* occurred in habitats with salinity ranging from 0.8 to 9 PSU, which is in line with other parameters describing the degree of water mineralization for this stonewort (Blindow 2000; Torn & Martin 2003; Appelgren et al. 2015; Becker et al. 2016).

C. connivens is a heliophilic species (Corillion 1957), therefore exposure to sunlight is a very important determinant of *C. connivens* growth (Simons et al. 1994; Rip et al. 2006). The unshaded stand in Fuerteventura supports this finding. Therefore, *C. connivens* grows mostly in shallow waters (1–1.5 m), but not deeper than 4 m (Torn & Martin 2003; Blindow 2008; Schories et al. 2009).

Conclusions

Undoubtedly, the distribution patterns and ecology of *C. connivens* from the Canary Islands require further detailed studies. It is difficult to monitor and protect inland macroalgae habitats on Fuerteventura, because its natural freshwater and brackish water ecosystems are rare, ephemeral and constantly exposed to anthropogenic pressure (eutrophication, tourist activity – see Figure 2A, and interference in the



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environment), as well as affected by extreme natural events (weather changes leading to the drying up of water bodies and rivers). We hope that our study will contribute to a better understanding of *C. connivens* ecology in the Atlantic Ocean region.

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