received: 2020-02-16 10.19233/ASHN.2020.10

# SEASONAL GROWTH PATTERNS OF *CYMODOCEA NODOSA* AND DIVERSITY OF ITS EPIBIOTA IN THE NORTHERN ADRIATIC SEA

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## *ABSTRACT*

*Growth patterns of the lesser Neptune grass,* Cymodocea nodosa*, and the distribution of epifauna and epiflora along its leaves were studied from May to October 2014 at two different depths (1.5 and 5 m) in the northern Adriatic Sea (Pula, Croatia). Generally, seagrass biomass, shoot density and number of leaves per shoot were higher in the shallow water, whereas leaf length was pretty similar between depths. The abundance of epibiota followed a leaf-age gradient. At both depths, autotrophic aufwuchs (mainly Rhodophyta) dominated throughout the study period. The epifauna recorded comprised representatives of Bryozoa, Annelida (Polychaeta), Mollusca and Cnidaria (Anthozoa, Hydrozoa). Above all, we document a major decline of the investigated* C. nodosa *patch from 2014 to the present, which highlights the importance for conservation and management efforts regarding seagrass meadows in the northern Adriatic Sea.*

**Key words**: aufwuchs, *Cymodocea nodosa,* seagrass meadow, sessile invertebrates

## MODELLI DI CRESCITA STAGIONALE DI *CYMODOCEA NODOSA* E DIVERSITÀ DEI SUOI EPIBIONTI NELL'ADRIATICO SETTENTRIONALE

## *SINTESI*

*I modelli di crescita di* Cymodocea nodosa *e la distribuzione di epifauna ed epiflora lungo le sue foglie sono stati studiati da maggio a ottobre 2014, a due diverse profondità (1,5 e 5 m) nell'Adriatico settentrionale (Pola, Croazia). In generale, la biomassa della pianta, la densità dei fasci e il numero di foglie per fascio sono risultati più alti a 1,5 m, mentre la lunghezza delle foglie era abbastanza simile tra le profondità. L'abbondanza di epibionti ha seguito un gradiente di età delle foglie. Ad entrambe le profondità, "aufwuchs" autotrofi (principalmente Rhodophyta) hanno dominato per tutto il periodo di studio. L'epifauna determinata ha compreso rappresentanti di Bryozoa, Annelida (Polychaeta), Mollusca e Cnidaria (Anthozoa, Hydrozoa). Gli autori hanno inoltre documentato un grave declino del prato di* C. nodosa *nella zona indagata dal 2014 ad oggi, il che evidenzia l'importanza degli sforzi di conservazione e gestione delle praterie di fanerogame nell'Adriatico settentrionale.*

**Parole chiave**: aufwuchs, *Cymodocea nodosa*, praterie di fanerogame, invertebrati sessili

#### INTRODUCTION

Seagrass meadows occur across the globe and cover 0.1 - 0.2 % of the oceans (Duarte *et al*., 2008). Concordant with a general decay of environmental quality in marine near-shore habitats, massive regressions of seagrass meadows have been observed in the last few decades (Zavodnik & Jaklin, 1990; Waycott *et al*., 2009). This poses a massive threat to coastal ecosystems, as seagrass meadows are important primary producers (Duffy, 2006) and play a crucial role as ecosystem engineers (Wright & Jones, 2006). By colonizing mobile substrata like sandy bottoms or silt at varying depths, they form a three-dimensional structure in an otherwise rather homogeneous environment and supply food, shelter and nursery areas for a variety of animals (Beck *et al.*, 2001; Duffy *et al*.*,* 2003; Cuadros *et al.*, 2017). Furthermore, seagrasses act as a substrate for a whole community of epiphytes and epizoans (Trautman & Borowitzka, 1999; Piazzi *et al.*, 2016), many of which are strictly associated with the plants and successfully adapted to live and grow on their leaves and rhizomes (Casola *et al.*, 1987; Trautman & Borowitzka, 1999). Despite the general high productivity of seagrass meadows, this aufwuchs plays a crucial role in the seagrass ecosystem functioning by serving as food for a variety of grazing organisms like snails, contributing to the overall productivity and thus representing an important part of the biological diversity in seagrass beds (Silberstein *et al*., 1986; Moncreiff *et al*., 1992; Cambridge *et al*., 2007; Gacia *et al*., 2009; Lepoint *et al.*, 2014; Piazzi *et al.*, 2016).

*Cymodocea nodosa* (Ucria) Ascherson, 1870 is one of five seagrass species native to the Adriatic Sea and inhabits mainly sheltered to semi-exposed sites, where it forms either mono-specific or mixed meadows with *Zostera noltei* Hornemann, 1832 (Mazzella *et al*., 1993; Mazzella *et al*., 1998). *Cymodocea nodosa* grows at varying salinity conditions down to a depth of 40 m (Procaccini *et al*., 2003; Boudouresque *et al*., 2009) and is usually found in places not favoured by the largest growing Mediterranean species, *Posidonia oceanica*  (Linnaeus) Delile, 1813 (Toccaceli 1990; Sánchez-Jerez *et al.*, 1999). Considered as a pioneer species, *C. nodosa* is often the first seagrass species to colonize newly established habitat (e.g. Van der Velde & Hartog 1992), but it is also present in degraded *P. oceanica* meadows facilitating the colonisation by other taxa such as the green algae *Caulerpa* spp. (Ceccherelli & Sechi, 2002; Montefalcone *et al*., 2007). Generally, shoot density and size in seagrasses are mainly determined by meadow depth, health and seasonality, but other factors such as branching frequency, seedlings' success, local sediment type and hydrodynamic conditions are also shaping their growth patterns (Pérez *et al*., 1994; Marbá *et al*., 2002; Leoni *et al*., 2008; Díaz-Almela *et al*., 2008; Martínez-Crego *et al*., 2008).

Hence, wave action and water currents strongly impact the establishment of *C. nodosa*, whereas in shallow waters (less than 5 m), *C. nodosa* forms patchy meadows that become more continuous in larger depths between 5 and 35 m (Reyes *et al.*, 1995). Maximum levels of biomass and cover are found at intermediate depths (Dring & Dring, 1991; Krause-Jensen *et al*., 2000).

Despite the important role of *C. nodosa* and its associated community for the functioning of coastal ecosystems (Orlando-Bonaca *et al*., 2015; 2016), studies about its epifauna and -flora are generally scarce and highly biased towards algal aufwuchs. Previous studies mainly focused on the morphology, diversity, temporal distribution, reproductive phenology, biomass, primary production and distribution of crustose red algae of the family Corallinaceae and other epiphytes on *C. nodosa* leaves (Reyes & Afonso-Carrillo, 1995; Reyes & Sanson, 1996, 1997; Reyes *et al*., 1998; Reyes & Sansón, 2001). In contrast, next to nothing is known about sessile invertebrates associated with *C. nodosa* (Guidetti *et al*., 2001). This lack



**Fig. 1: Sampling. (A) Investigated site Valsaline Bay (Pula, Croatia, 44°50'59.6"N, 13°50'10.0"E). Satellite pictures show a drastic decline in meadow size (dark areas) from 2013 to 2019. (B) Custom-built sampling device with a standardized frame (0.5 m x 0.5 m) attached to the mosquito net. (C) Standardized sampling pattern (black dots) for each replicate (= total of 13 investigated shoots).** 

**Sl. 1: Vzorčenje. (A) Raziskovana lokaliteta – zaliv Valsaline (Pulj, Hrvaška, 44°50'59.6"N, 13°50'10.0"E). Satelitski posnetki kažejo drastični upad v velikosti morskega travnika (temni predeli) od 2013 do 2019. (B) Vzorčevalni pripomoček s standardnim okvirjem (0,5 m x 0,5 m) in mrežico proti komarjem. (C) Standardiziran vzorčevalni pristop (črne točke) za vsako paralelko (=vsota 13 raziskanih šopov).**

of data on *C. nodosa* epibiota is quite surprising considering the wealth of studies investigating aufwuchs on *P. oceanica* (e.g. Mazzella *et al*., 1989; Mazzella *et al*. 1992; Marbá *et al*., 2002; Balata *et al*., 2007; Lepoint *et al*., 2014; Piazzi *et al*., 2016), which form the basis of our knowledge on seagrass aufwuchs and the factors and processes underlying its diversity and occurrence patterns.

The present study aims at characterizing the seasonal growth patterns of a *C. nodosa* meadow in the northern Adriatic Sea, by comparing two different water depths and relating the growth patterns to different environmental parameters. We further investigated seasonal changes of the diversity and frequency of the whole epibiotic (i.e. autotrophic and heterotrophic) community along the leaves and deliver an overview about the aufwuchs present on *C. nodosa* in the northern Adriatic Sea. Above all, we monitored a major loss of the investigated meadow between the study period (2014) and 2019. The documentation of this decline is of utmost importance for conservation and management efforts regarding *C. nodosa* in the northern Adriatic Sea.

### **MATERIAL AND METHODS**

The investigated *C. nodosa* meadow is located in the northern Adriatic Sea (Valsaline /Pula/Croatia - 44°50'59.6"N 13°50'10.0"E), situated in the southwest of the Istrian peninsula (Fig. 1A). The bay is exposed northwest and some sheltered areas exhibit mixed patches of *C. nodosa* and *Z. noltei*. The present study is focused solely on *C. nodosa* and areas of mixed patches of both species were avoided. Sampling was conducted monthly from May to October 2014 at 1.5 m and 5 m depth by snorkeling and scuba diving. Environmental parameters (surface water temperature, rainfall and wind) were recorded daily during the sampling period and summarized monthly (Tab. 1).

Each monthly sample consisted of four replicates per depth of a standardized area of 0.25 m² where seagrass was collected using a custom-built sampling device (Fig. 1B). For each replicate a smaller frame (14 cm x 14 cm) was used to visually count shoot density and leaves per shoot, which was later extrapolated to a size of  $1 \text{ m}^2$ . All other leaves were cut off for calculating the leaf area index (LAI – see below) following Bréda (2008) and kept in seawater with air ventilation for subsequent investigations of epiphytes and epizoans.

$$
\frac{T DW[g]*RL\,surface\,[mm^2]}{RL\,DW[g]} = T\,surface\,[mm^2] \tag{1}
$$
\n
$$
\frac{T\,surface\,[m^2]}{1\,m^2} = LAI \tag{2}
$$

 $(2)$ 

where:

 $1 \text{ m}^2$ 

 $T$  DW = total dry weight [g], surface  $T =$  total surface  $[mm^2]$ ,  $[m^2]$ RL surface = reference leaf surface [mm²], RL DW = reference leaf dry weight [g],

In a next step, leaves in a shoot were classified into three categories (*oldest*, *youngest* and *other leaves*). Determination of leaf ages was based on the classification by Reyes & Sansón (2001), with the youngest leaves originating in between the oldest leaves, which typically occupy the outer position in a shoot. Mean leaf lengths were determined for each leaf-age category.

To investigate the epibiota on the leaves, 13 shoots per replicate were harvested in a standardized way (Fig. 1C) (i.e. 52 shoots per month and depth). If possible, aufwuchs was determined to species level. Otherwise higher taxonomical units were used to rank the specimens (Tab. 2). Furthermore, frequency of occurrences as well as total number (i.e. mean and standard deviation) of epibiota on leaves per replicate for taxonomical unit and depth were calculated. For

**Tab. 1: Mean and standard deviation (SD) of environmental parameters (water surface temperature, wind speed and direction as well as rainfall) from daily measures during the study period (May-October). Tab. 1: Povprečje in standardna deviacija (SD) okoljskih parametrov (površinska temperature vode, hitrost in smer vetra ter padavine) na podlagi dnevnih meritev v vzorčevalnem obdobju (maj – oktober).** 

month	water surface $T$ in $^{\circ}C$		wind direction (abundance)								wind speed in km/h			rainfall in l/m <sup>2</sup>	
	Mean	<b>SD</b>	N	NΟ	O	SО	S	<b>SW</b>	W	<b>NW</b>	Mean	SD	max	Mean	SD
5	18.07	1.47	9	19	23	18	4	7	10	4	. .36	3.48	75	6.25	3.86
6	21.93	0.98	$\overline{2}$	33	19	10	6	6	13	10	11.57	5.12	55	23.00	15.39
7	24.26	0.86	$\overline{2}$	35	22	13	$\overline{2}$	9	11	11	9.64	2.63	55	15.43	9.32
8	24.90	0.30	7	32	19	20	$\overline{2}$	5	9	6	9.21	3.06	50	17.75	5.62
9	21.70	0.65	6	47	21	4	$\overline{0}$	$\overline{4}$	9	6	1.36	4.02	75	27.17	23.79
10	2.45	0.51	4	37	19	21	3	6	$\overline{2}$	4	1.50	5.06	75	9.67	4.51

**Tab. 2: Diversity and taxonomic identification of the found epiphytic and epizoic community their abbreviations used in the text and the figures. Insecure taxonomic identifications are marked with "cf." qualifiers. Tab. 2: Pestrost in taksonomska opredelitev epifitske in epizojske združbe ter njihove okrajšave, uporabljene v slikovnem gradivu in besedilu. Negotove taksonomske določitve so označene s "cf".**



visualizations we decided to show only frequency of occurrences, because they allow a better interspecific comparison between taxa. All graphical visualizations were performed in R v3.3.2 (R Core Team, 2013).

After the investigation period we determined a drastic decline of the seagrass meadow size in Valsaline bay. In order to track this change, we used historical images in GoogleEarthPro. Unfortunately, no high-resolution images were available from 2014. Hence, for visualization purposes (Fig. 1A), we decided to take an aerial image from 2013 and compared it with the situation in 2019. Above all, for a better comparability of the patch size, which can fluctuate seasonally, we show images taken in the same month (October).

## **RESULTS**

## **Environmental parameters**

The annual water surface temperature of the sampling site showed typical seasonal variations in





**Fig. 2:** Cymodocea nodosa **meadow structure of the investigated site (Valsaline, Pula) for the period May - October 2014. (A) Leaf area index (LAI – leaf area/m<sup>2</sup> ), (B) shoot density (shoots/m<sup>2</sup> ), (C) mean number of leaves per shoot for each sampling replicate (I-IV) and (D) comparison of leaf length for different depths, 1.5 m and 5 m. Sl. 2: Struktura morskega travnika kolenčaste cimodoceje na raziskani lokaliteti (Valsaline, Pulj) v obdobju med majem in oktobrom 2014. (A) Indeks listne površine (LAI – listna površina/m<sup>2</sup> ), (B) gostota šopov (št. šopov/m<sup>2</sup> ), (C) povprečno število listov v šopu za vsako paralelko (I-IV) in (D) primerjava dolžine listov na različnih globinah 1,5 m in 5 m.** 

the northern Mediterranean Sea, with a maximum in August (24.9  $\pm$  0.3 °C) and a minimum in May (18.07  $\pm$  1.47 °C) (Tab. 1). The prevailing wind direction was north-east ("Bora"). Average wind speeds did not exceed 11.57 km/h. Maximum wind speed was detected in Mai, September and October with 75 km/h. Highest values of rainfall (27.17 l/m<sup>2</sup>) were recorded in September.

#### **Meadow structure**

Throughout the study period, seagrass growth parameters were generally higher in 1.5 m compared to 5 m depth (Fig. 2). For both shallow and deep water, the LAI was highest during the summer months, with a maximum LAI observed in July (Fig. 2A). Interestingly, after a drop in August, the LAI in the shallow water reached a second peak in September.

Mean annual shoot density (Fig. 2B) reached values of 1292  $\pm$  433 per m<sup>2</sup> at 1.5 m depth and  $1000 \pm 385$  per m<sup>2</sup> at 5 m depth. Seasonal variation in the number of *C. nodosa* shoots was recorded, with lowest values in May at 1.5 m (803  $\pm$ 143 per m<sup>2</sup>) and October at 5 m (561  $\pm$ 72 per m²). Highest values were recorded in August at 1.5 m (1913  $\pm$  335 per m<sup>2</sup>) and September at 5 m (1441  $\pm$  274 per m²) (Fig. 2B).

The mean number of leaves per shoot (Fig. 2C) ranged from  $3.09 \pm 0.41$  at 1.5 m to  $2.91 \pm 0.45$  at 5 m. A seasonal pattern became evident, with highest values in July at 1.5 m  $(3.92 \pm 0.76)$  and in June and July at 5 m (June,  $3.46 \pm 0.52$ ; July,  $3.46$ ± 0.66). Lowest values were recorded in October for both depths (1.5 m, 2.38  $\pm$ 0.51; 5 m,  $2.08 \pm 0.28$ ) (Fig. 2C).

The mean leaf length over the entire study period (Fig. 2D) was 131.49 ± 19.15 mm for shallow water and 116.58 ± 18.1 mm for deeper water. The mean leaf lengths (Fig. 2D) of the oldest leaf in a shoot reached maximum values in July  $(152.61 \pm 32.39 \text{ mm})$  and June  $(133.98)$ ± 28.23 mm) and minimum values in September (108.56  $\pm$  31.2 mm) and May  $(86.77 \pm 20.36 \text{ mm})$ , in 1.5 and 5 m depth, respectively. The maximum values for the youngest leaf in a shoot were recorded in July for both shallow  $(97.68 \pm 33.35)$ mm) and deeper water  $(88.03 \pm 32.57)$ mm). Minimum values were observed in October for both depths  $(1.5 \text{ m}, 71.78 \pm$ 23.97 mm; 5 m,  $63.37 \pm 22.65$  mm).

## **Diversity and frequency of epiphytes**

A total of 18 taxa were identified, six of which could be determined to species level (Tab. 2). Autotrophic aufwuchs dominated throughout the study period at both depths and was most abundant on the oldest leaves (Fig. 3; Appendix 1, 2 & 3). In contrast, heterotrophic cover did not show



**Fig. 3: Frequency of occurrence (mean and standard deviation) of epiphytes and epizoans on leaves per replicate over the investigated period (May – October) for both depths. Abbreviations: cer:** Ceramium**; cly:** Clytia linearis**; cor:** Corallinaceae**; osc:** Oscillatoria**; ovi:**  Oviposition**; pol:** Polychaeta**; rh:** Rhodophyta**; tre:** Tretomphaloides concinna**; ATH: a**thecate hydroids**; bac:** Bacillariophyceae**; biv:**  Bivalvia**; bry:** Bryozoa**; buno:** Bunodeopsis strumosa**; fora:** Foraminifera**; kir:** Kirchenpaueria pinnata**; pach:** Pachycordyle pusilla**; qui: quiver (tube) of Polychaetes; schiz:** Schizobrachiella sanguinea**. For taxonomic position see Tab. 2.**

**Sl. 3: Frekvenca pojavljanja (povprečje in standardna deviacija) epifitov in epizojev na listih na paralelko v raziskanem obdobju (maj – oktober) na obeh globinah. Okrajšave: cer:** Ceramium**; cly:**  Clytia linearis**; cor:** Corallinaceae**; osc:** Oscillatoria**; ovi:** ovipozicija**; pol:** Polychaeta**; rh:** *Rhodophyta***; tre:** Tretomphaloides concinna**; ATH:** atekatni trdoživnjaki**; bac:** Bacillariophyceae**; biv:** Bivalvia**; bry:** Bryozoa**; buno:** Bunodeopsis strumosa**; fora:** Foraminifera**; kir:**  Kirchenpaueria pinnata**; pach:** Pachycordyle pusilla**; qui: cevke mnogoščetincev; schiz:** Schizobrachiella sanguinea**. Glej Tab. 2. za taksonomski položaj.**

a clear leaf-age gradient (Appendix 2 & 3). In 1.5 m depth, epibiota abundance reached a maximum in July and decreased later in the season (Fig. 3). Similar patterns were observed in 5 m depth, with a maximum in June and July, followed by a decrease later in the study period. *Ceramium* spp., Corallinaceae, various other Rhodophyta, *Tretomphaloides concinna* (Brady, 1884) and Polychaeta were the most frequently observed epibiota at both depth and in all months. Gastropod clutches and *Clytia linearis* (Thorneley, 1900) were present, but at low frequency, in all months at both depth. Oscillatoria, tubes of polychaetes and hydrozoans were present in several months at both depths. Foraminifera, *Schizobrachiella sanguinea* (Norman, 1868), other Bryozoa, Bivalvia, *Bunodeopsis strumosa* Andrès, 1881 were found only occasionally. Most of the hydrozoans, with the exception of *Clytia linearis*, appeared only in the second half (from July onwards) and Bacillariophyceae as well as Bivalvia were only present in the first half (until July) of the season. Taxa that were only present in the deep transect (5 m) included *Bunodeopsis strumosa, Schizobrachiella sanguinea* and various Foraminifera (Fig. 3; Appendix 1).

## **DISCUSSION**

#### **Meadow structure**

The structure and overall growth patterns of the studied *C. nodosa* meadow at Valsaline Bay, Croatia, are similar to those of other previously studied *C. nodosa* meadows in the Mediterranean Sea and around the Canary Islands (Bičanić & Baković, 2000; Cancemi *et al.*, 2002; Peduzzi & Vuković, 1990; Reyes *et al.*, 1995). Biomass (LAI) and shoot density were generally higher in 1.5 m as compared to 5 m water depth (Fig. 2A). Previous studies on *C. nodosa* from the Mediterranean Sea and the Canary Islands found maximum growth rates in late spring/ summer (Terrados & Ros, 1992; Peduzzi & Vukovic, 1990; Reyes *et al.*, 1995), the time with most favourable conditions for seagrass growth in the Mediterranean Sea (Marbá *et al.*, 1996; Guidetti *et al.*, 2001). Likewise, we found that, at both depths, biomass, shoot density and number of leaves per shoot reached their maxima in the summer months (Fig. 2B & 2C).

Patterns and processes determining meadow structure and seasonal growth patterns of seagrasses are highly complex (Duarte *et al.*, 2007; Garrido *et al.*, 2013), such that disentangling the explicit factors shaping meadow structure and growth patterns is not trivial. *Cymodocea nodosa* is particularly susceptible to seasonal fluctuations (e.g. seawater temperature) and, similar to other seagrasses, the

growth pattern is linked to abiotic conditions, particularly to heavy wave action as well as changes in temperature and light intensity (Marbá *et al.*, 1996; Reyes & Afonso-Carrillo, 1995). Mechanic turbulences such as waves could be responsible for discrepancies of growth patterns in different depths. Reduced water movement and an increase of sediment stabilization in deeper water layers enhance seagrass growth and the formation of continuous meadows (Vidondo *et al.*, 1998). In contrast, in shallow water, intense periods of wave action can lead to the fracture of old leaves or detachment of long-living aufwuchs organisms (Reyes & Sansón, 2001). However, we do not find a big difference in overall leaf length when comparing both depths. The investigated site, Valsaline Bay, is opened towards northwest and therefore exposed to western winds (e.g., "Zapadnjak" or "Lebić"). During the study period wind speeds of more than 45 km/h were repeatedly recorded (Tab. 1) from these directions. The prevalent wind direction throughout the study period, however, was north-east ("Bora"). The Bora can reach top speeds of up to 250 km/h (Grisogono *et al.*, 2009) and potentially impacts near-shore seagrass growth patterns. Even though the bay is in general protected from winds of this direction, deeper sites, due to their relative locations in the bay (i.e. larger offshore distance), may be more affected than shallow parts (i.e. closer to shore).

With increasing depth, light availability for photosynthesis decreases (Dring & Dring, 1991; Krause-Jensen *et al.*, 2000), which could explain generally lower LAI and shoot density values (Fig. 2A & 2B) in the deeper water. Furthermore, seagrass meadow structure is known to be influenced by the processes involved in recovering from natural and anthropogenic mechanic stressors (Duarte *et al.*, 2007). Decreasing LAI in August in shallow water could thus be the result of heavy rainfalls in July that discharged large amounts of terrestrial mud into the study area (Tab. 1; S. Bračun, personal observation).

### **Frequency and diversity of epibiota on** *Cymodocea nodosa* **leaves**

The characteristics of seagrass growth and the life strategies of epiphytes and epizoans are the major factors determining growth dynamics of the aufwuchs (Reyes & Sansón, 1997). A constant creation of leaf surface and the detachment of old parts result in a steadily changing environment that requires adaptations to short life spans and a linear growth/erosion of the substrate (Heijs, 1985; Reyes & Sansón, 2001). In addition, aufwuchs organisms are impacted by numerous abiotic and biotic factors, such as light availability and competition for space

(Heijs, 1985; Reyes & Sansón, 1997), resulting in typical ontogenetic and demographic turnovers. The oldest leaves usually occupy the outermost position of a shoot, and the youngest ones originate from the base between the older leaves of a shoot (Reyes & Sansón, 2001). Initial epibiotic colonizers are found already on the youngest leaves and if they persist and grow, they crucially contribute to an increased biomass of more mature leave stages (Reyes *et al.*, 1998; Reyes & Sansón, 2001).

In our study, autotrophic aufwuchs dominated throughout the study period at both depths (Fig. 3; Appendix 1) and increased with leaf age (Appendix 2 & 3). Reyes & Sansón (2001) showed that the contribution of epiphytes on the oldest leaves, concerning the total biomass of epibiota per shoot, was markedly higher than the contribution of epiphytes from all other leaves. Generally, older leaves are larger (Fig. 2D; Reyes & Sansón, 2001), which offers more leaf surface, but could, especially in nutrient rich areas, affect epiphytic growth due to self-shading effects (Pérez *et al.*, 1994).

Among autotrophic taxa we found various Rhodophyta, Ceramiales (*Ceramium*) and Corallinaceae, all of them quite abundant throughout the year. This is supported by previous studies that recorded Rhodophyta as the most common phylum on seagrass leaves, which account for more than 90% of all algal divisions (Reyes & Sansón, 2001). Among the algal aufwuchs, sciaphilic Corallinaceae were clearly most prominent at both depths (Fig. 3). Crustose coralline algae can bear mechanical disturbances, like strong water movement, are able to grow under low light conditions and are considered as primary colonisers of seagrass leaves (Borowitzka *et al.*, 1990). Whereas in the deep transect (5 m) Corallinaceae could profit from generally lower light conditions, in shallow waters (1.5 m) stronger mechanic disturbances and the shading through leaves resulting from a denser meadow (Fig. 2B) could be explanatory factors for increased Corallinaceae growth.

Overall, epiphyte abundance in shallow water showed an increase until July, followed by a decrease later in the season, and in 5 m depth an increase between June and July, with a subsequent decrease between July and August. Reyes & Sansón (2001) investigated epiphyte biomass on *C. nodosa* leaves throughout the year in the Canary Islands and found an irregular annual variation of the epiphytic community with two maxima (winter, late spring-early summer) and one minimum (spring) that could be linked to the leaf lifetime in different seasons (Reyes *et al.*, 1995). In concordance with these findings, the low frequency of epiphytes in May, detected in our study, might be explained by the short leaf lifetime (45-75 d) (Reyes & Sansón, 1997), which limits the chance of aufwuchs establishment. In contrast,

the peak of epiphytes during summer months can be linked to high daily accumulation of epiphytes due to favourable light conditions in this period, and furthermore, could explain the delay of epiphytic growth in deeper water, where these conditions are achieved later in the season. Nonetheless, further studies, especially spanning over winter months, will be necessary to fully understand annual growth dynamics of epiphytes.

Heterotrophic cover appeared seasonally or occasionally, but rarely permanent on *C. nodosa*  and did not show a clear leaf-age gradient (Fig. 3; Appendix 2 & 3). Spatial competition could be a reason for the alternating frequency patterns of heterotrophic organisms, with autotrophes potentially suppressing the establishment of sessile epiphytic invertebrates by rapid growth at locations and in months with good light conditions (Borowitzka *et al.*, 1990). Thus, if autotrophic cover decreases, the frequency of heterotrophs can increase. Polychaeta were present throughout the season on leaves of different age, but were most abundant on the youngest leaves, independent of depth (Appendix 2 & 3). Colonisation of young leaves could be a strategy to cope with the enormous space competition in later leaf stages and requires a directed and active settling mechanism. Indeed, sedentary polychaeta larvae have chemotactic organs that might allow them to distinguish between leaf-ages (Pawlik, 1992; Helm *et al.*, 2018). In addition to polychaetes, other organisms such as *Tretomphaloides concinna* (Foraminifera), gastropod clutches and – an exception among Hydrozoans – *Clytia linearis* were present throughout the year. Occasionally found taxa were several Bivalvia, Bacillariophycea, *Bunodeopsis strumosa* and *Schizobrachiella sanguinea*. These occasional occurrences could either be explained by seasonality of organisms (which might be true for athecate hydrozoans, *Kirchenpaueria pinnata* (Linnaeus, 1758) and *Pachycordyle pussila* (Motz-Kossowska, 1905)), or that specimens accidentally settled down on seagrass even though not favorable to them. The sea anemone *Bunodeopsis strumosa* has been reported from different *Zostera* species before (Ates, 1992) and could – as a hemi-sessile animal – easily switch the host plant from adjacent mixed seagrass patches that grow at the investigated study site (Valsaline bay).

Compared to *P. oceanica*, which is considered well-studied regarding its aufwuchs (reviewed by Piazzi *et al.* 2016), the algal communities in *C. nodosa* dominate over sessile invertebrates and appear to be less species-rich (Mazella *et al.*, 1998). Several reasons might explain the discrepancy of auto- versus heterotrophic aufwuchs between *C. nodosa* and *P. oceanica*. Firstly, the size and width of *P. oceanica* leaves largely exceed those of *C. nodosa*, which

allows the establishment of large growing sessile organisms on the leaves. Secondly, *P. oceanica* forms a prominent rhizome layer (also called "matte") that provides settling space and perfect conditions for a variety of sessile invertebrates, many of which can also be found on rocky substrates (e.g. Mabrouk *et al.*, 2014). Hence, these multilayered rhizome structures are unique for *P. oceanica* among all other Mediterranean seagrass species and provide stable perennial conditions that are mostly necessary for invertebrates with longer developmental cycles (Boudouresque, 1974; Piazzi *et al.*, 2016). Several tunicates, poriferan and bryozoan species are associated with the rhizomes of *P. oceanica*, which clearly highlights the pivotal ecological role of this layer for the establishment of heterotrophic aufwuchs (Piazzi *et al.*, 2016). Hence, the absence of a rhizome layer in *C. nodosa* could explain why sponges and tunicates are missing in our samples. However, the whole epibiotic community found in this study is also present in *P. oceanica* (Piazzi *et al.*, 2016). Above all, an overlap in the aufwuchs community between *P. oceanica* and *C. nodosa* makes sense in the light of long-term dynamics and phase-shifts that strongly link these two seagrass species (Montefalcone *et al.*, 2007).

### **Conservation remarks and outlook**

From 2013 to 2019 the investigated seagrass meadow underwent a drastic change, which resulted in the disappearance of the whole patch (Fig. 1A). Several other places along the Istrian coast suffer from a decline of *C. nodosa* meadows (personal observation; L. Lipej, personal communication). Nonetheless, data on distribution and abundance of *C. nodosa* is largely lacking for the northern Adriatic Sea (Orlando-Bonaca *et al.*, 2016), which makes comparative studies and hence the implementation of proper conservation efforts difficult. Natural disturbances (i.e. extreme climatic events, heavy storms, or biological interaction and invasions) are often responsible for seagrass loss, which also affects the biomass and production of its aufwuchs (Reyes & Sansón, 2001; Tuya *et al.*, 2013). On the other hand, human induced disturbances like eutrophication and dredging lead to reduced

water clarity and overall quality with impacts on *C. nodosa* growth patterns, or cause direct physical damage (Short & Wyllie-Echeverria, 1996; Reed & Hovel, 2006; Orlando Bonaca *et al.*, 2019). Above all, rapid changes on a global scale affect coastal ecosystems too fast to allow adaptation of seagrass species to the changing environment (Montefalcone *et al.*, 2007; Chefaoui *et al.*, 2018). A loss of seagrass coincides with a deprivation of all the ecological services they provide and as a consequence, water quality, primary production and biodiversity will decline (Tuya *et al.*, 2014).

However, recolonization of seagrass seems still possible if disturbances are limited and growth conditions are suitable. Simulations show that small species of seagrass recover within a few years after a disturbance, while large species may require centuries (Duarte, 1995). Above all, more studies about the dynamics of different seagrass species and their epiphytic community, including *C. nodosa* are essential and of utmost importance for understanding close-shore ecosystem dynamics and changes. Although the knowledge about algal colonization of *C. nodosa* leaves is considered high (e.g. Reyes & Sansón, 1996), there is a lack of data on the diversity of epizoans. Reyes & Sansón (1996) rightly mentioned, that understanding the function of *C. nodosa* comes along with the complete inclusion of the whole aufwuchs community. Hence, further investigations including the creation of a catalogue about the species composition, with proper species determination of all common epifaunal taxa would be necessary, especially in the light of biological diversity and conservation strategies.

#### ACKNOWLEDGEMENTS

For field support and the implementation of the present study we thank the staff of the Morska Škola Pula (Croatia). Furthermore, we thank several colleagues for their input concerning the taxonomic determinations: Neela Enke, Martin Langer, Frans Jorissen, Caterina Morigi*,* Björn Berning, Robert A. Patzner, Bastian Brenzinger*,* Kristian Fauchald and Cinzia Gravili. Finally, we thank the Haus des Meeres (Vienna) for supporting S.B. with the Rupert-Riedl prize.

**Appendix 1: Frequency of occurrences (upper values) and total number (lower values, grey) of epiphytes on leaves given in mean (bold) and standard deviation (italics) per replicate for both depths. Taxonomic abbreviations correspond to organisms determined in Table 2.**

**Priloga 1: Frekvenca pojavljanja (zgornje vrednosti) in celotno število (spodnje vrednosti) epifitov in epizojev na listih, izražena s povprečno vrednostjo (krepko) in standardno deviacijo (kurziv) za različne starostne razrede listov na paralelkah v obeh globinah. Taksonomske okrajšave ustrezajo organizmom v Tabeli 2.** 



Appendix 2: Frequency of occurrences (upper values, white) and total number (lower values, grey) of epiphytes on leaves given in mean (bold) and<br>standard deviation (italics) for different leaf-ages per replicate for 1.5 m Appendix 2: Frequency of occurrences (upper values, white) and total number (lower values, grey) of epiphytes on leaves given in mean (bold) and standard deviation (italics) for different leaf-ages per replicate for 1.5 m depth. Taxonomic abbreviations correspond to organisms determined in Table 2. Priloga 2: Frekvenca pojavljanja (zgornje vrednosti na belem polju) in celotno število (spodnje vrednosti na sivem polju) epifitov in epizojev na listih,<br>izraženi s povprečno vrednostjo (krepko) in standardno deviacijo (ku okrajšave ustrezajo organizmom v Tabeli 2.



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Appendix 3: Frequency of occurrences (upper values) and total number (lower values) of epiphytes on leaves given in mean (bold) and standard deviation<br>(italics) for different leaf-ages per replicate for 5 m depth. Taxonomi Appendix 3: Frequency of occurrences (upper values) and total number (lower values) of epiphytes on leaves given in mean (bold) and standard deviation Priloga 3: Frekvenca pojavljanja (zgornje vrednosti) in celotno število (spodnje vrednosti) epititov in epizojev na listih, izraženi s povprečno vrednostjo<br>(krepko) in standardno deviacijo (kurziv) za različne starostne ra italics) for different leaf-ages per replicate for 5 m depth. Taxonomic abbreviations correspond to organisms determined in Table 2. Tabeli 2.



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## SEZONSKA RAST KOLENČASTE CIMODOCEJE (*CYMODOCEA NODOSA*) IN PESTROST NJENIH EPIBIONTOV V SEVERNEM JADRANU

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#### *POVZETEK*

*Avtorji so raziskovali rastne značilnosti kolenčaste cimodoceje* (Cymodocea nodosa) *in prostorsko poraščenost epifavne in epiflore na njenih listih od maja do oktobra 2014 na dveh globinah (1,5 in 5 m) v severnem Jadranu (Pulj, Hrvaška). Navadno so biomasa, gostota šopov in število listov v šopu višji v plitvini, medtem ko je dolžina lista bolj ali manj podobna na različnih globinah. Število epibiontov je sledilo gradientu starosti listov. Na obeh globinah so tekom raziskave kot obrast na listih prevladovale rdeče alge. Epifavno so sestavljali predstavniki taksonomskih skupin kot so Bryozoa, Annelida (Polychaeta), Mollusca in Cnidaria (Anthozoa, Hydrozoa). Avtorji opozarjajo na velik upad morskega travnika kolenčaste cimodoceje v obdobju od 2014 naprej, ki narekuje potrebo po varovanju in upravljanju morskih travnikov v severnem Jadranskem morju.* 

**Ključne besede**: aufwuchs, *Cymodocea nodosa,* morski travnik, sesilni nevretenčarji

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