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Tesi di Ricerca

Study of primary production of seagrasses in Venice Lagoon

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Coordinatore del Dottorato

prof. Enrico Bertuzzo

Supervisore

prof. Adriano Sfriso

Dottorando
Yari Tomio Matricola
83860

ABSTRACT

Seagrasses are a group of aquatic angiosperm monocots which adapted to live in marine, lagoonal and coastal environments in totally submerged conditions. Seagrass meadows provide high-value ecosystem services and represent one of the most important primary producers in marine-coastal and lagoonal ecosystems with an average net production of 27.2±5.8 mmol O_2 m^{-2} day^{-1}. Moreover, seagrass meadows are also considered a significant sink for atmospheric CO_2 with a great capacity to sequester and store carbon within their sediment, contributing to the sequestration of about 20% of the global carbon in marine sediments despite occupying only 0.1% of marine surface. The total ecosystem services provided by the presence of seagrass meadows are estimated in \$34,000 ha^{-1} $year^{-1}$. Nevertheless, since they are located in coastal-marine and transitional environments which are some of the most impacted areas by anthropogenic activities, seagrass meadows have declined due to human pressures at a rate of approx. 110 km^2 $year^{-1}$ between 1980 and 2006. The PhD thesis is part of this context and aims to carry out an update of primary production values after almost 20 years since the last ones available in bibliography (2003). The thesis also fits within the Corila Venezia2021 scientific research program which intends to monitor the testing phase of the tidal regulation project known as MOSE (MOdulo Sperimentale Elettromeccanico or Experimental Electromechanical Module). The thesis aimed at obtaining as complete a picture as possible of the primary production of seagrasses and their communities and their contribution to CO_2 capture and carbon sequestration in Venice Lagoon. The Net Primary Production (NPP) of four species (*Zostera marina*, *Zostera noltei*, *Cymodocea nodosa* and *Ruppia cirrhosa*) was calculated by the "leaf-marking" technique and/or the positive changes in monthly leaf and rhizome biomasses. In particular, NPPs of *Z. marina*, *Z. noltei* and *C. nodosa* were calculated by two annual sampling campaigns on a monthly basis in 2019 and 2020/2021 to update NPP combined with the mapping carried out in 2018 and 2021 and to assess possible impacts to seagrass communities from the MOSE project. NPP of *R. cirrhosa* was determined by one annual sampling campaign on a monthly basis in 2021/2022 in order to update its contribution to the global seagrass NPP after 25 years since the last study conducted in Venice Lagoon (1997). Biomasses collected in the 2019 sampling campaign have been analysed to calculate nutrient and carbon concentrations in order to obtain an estimation of carbon sequestration and total phosphorous and nitrogen contents. Moreover, a total of 5 sampling campaigns was carried out in 2019/2020 (August, October, February and June) and 2022 (July) in order to estimate the inter-seasonal and daily

primary production of two seagrass communities (*Z. marina* and *Z. noltei*) under the same environmental conditions in one station by variation on oxygen concentrations in benthic chambers using short incubation time (1.5-2 hours). Daily net community productions were calculated by repeated measurements in order to cover the whole photoperiod and at least two measurements of respiration at the end of photoperiod. All these measurements provide an important link between photosynthesis, primary production and carbon stored at the sediment level: a very important factor when taking into account the effects of climate change, its possible repercussions on aquatic and coastal ecosystems, the importance of meadows, the ecosystem services associated with them and their conservation.

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1 INTRODUCTION

Seagrasses are a group of aquatic angiosperm monocots, which adapted to live in marine, lagoonal and coastal environments in totally submerged conditions (Larkum et al., 2006; Orth et al., 2006). The seagrasses are not a taxonomic group. In fact, since the various seagrass families are not closely related (den Hartog and Kuo, 2006), the seagrasses form an ecological group. According to the classification of Angiosperm Phylogeny Group (APG), the different taxa belong to a limited number of families, all classified within the Kingdom Plantae, clade Angiospermae, Monocotyledones and order Alismatales R. Br. ex Bercht & J.Presl (Chase et al., 2016). All seagrass families are characterized by four common properties (Arber, 1920): (i) the plants are adapted to live in a saline medium, (ii) fully submerged, (iii) with a secure anchoring system and (iv) a hydrophilous pollination mechanism. However, this set of properties is satisfied also by several other taxa of aquatic plants (e.g. the "eurysaline" group (den Hartog, 1970; den Hartog, 1981): Ruppiaceae, Zannichelliaceae and Potamogetonaceae), although these species usually do not compete successfully with the seagrasses. This allows the introduction of another property (den Hartog, 1970): (v) the capacity to successfully compete with other organisms in the marine environment. According to den Hartog (1970)'s classification, species that live only in marine environments are referred to as "seagrasses", distinguishing them from "eelgrasses" that live in brackish or fresh waters.

1.1 TAXONOMY AND MORPHOLOGY

The first study of the morphological characteristics of seagrasses dates back to the late 18th century with the introduction of the generic name "Phucagrostis" (which means literally "seaweed grass") by Filippo Cavolini in 1792. However, until the early 20th century, marine angiosperms were less studied than most algae and misconceptions about their relationships were widespread. Nevertheless, all authors placed all seagrasses within the monocotyledonous subclass Alismatidae and divided them into separate families. A major step forward in the reconstruction of phylogenetic hypotheses was the introduction of cladistic methodology in late '80s of 20th century. The first study was conducted by Dahlgren and Rasmussen (1983) in which seagrasses were divided into three clades (Cymodoceaceae/Zannichelliaceae, Posidoniaceae/Zosteraceae and Hydrocharitaceae). The next big step was the incorporation of molecular data in cladistic analyses with Les et al.

(1993). However, the most complete study including molecular phylogenetic analysis was conducted by Les et al. (1997) and divided the seagrasses among five families: Hydrocharitaceae, Cymodoceaceae, Zosteraceaea, Posidoniaceae and Ruppiaceae (**Fig. 1**).

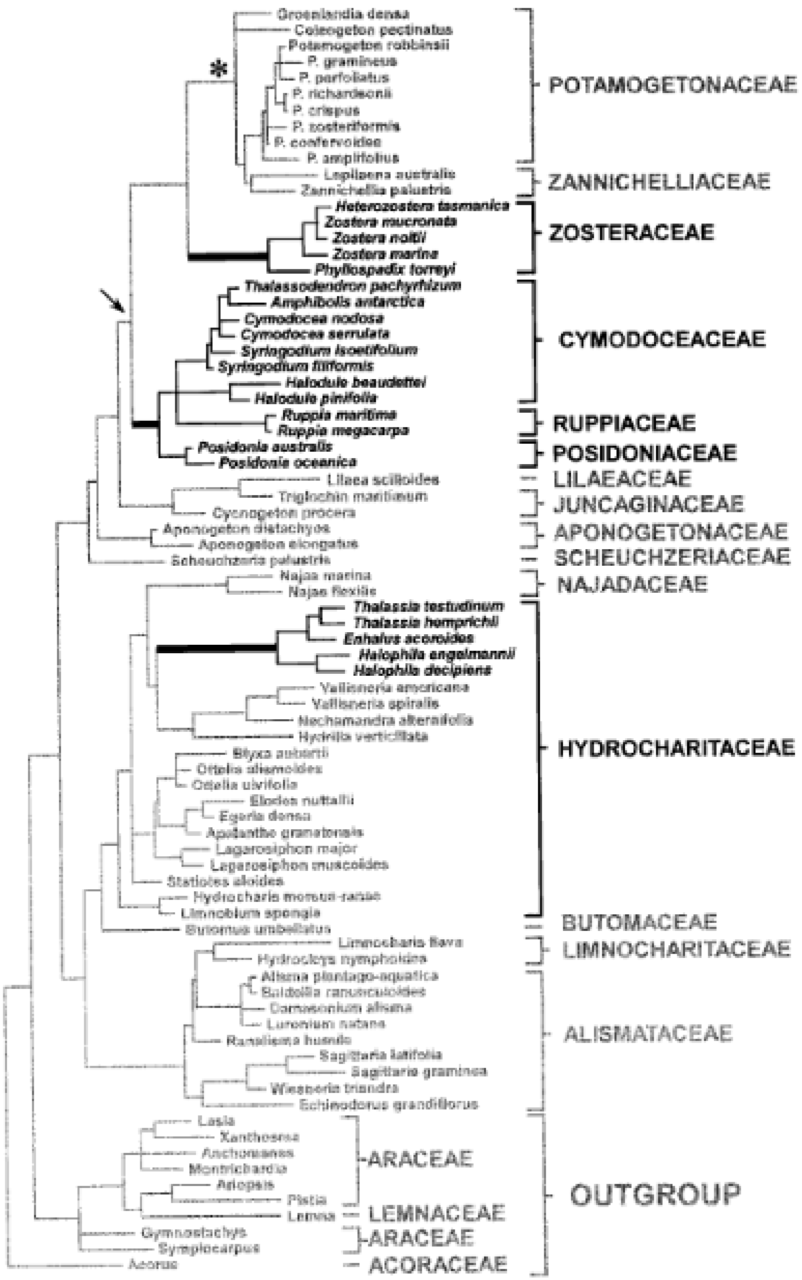


Figure 1: *rbcL* cladogram of species from the 15 families in the monocotyledon subclass Alismatidae. Five seagrass families are highlighted in bold type according to Les et al. (1997).

Seagrasses can be classified according to the shape and/or the presence/absence of erect stems into three main morphological categories (Kuo and den Hartog, 2006): (i) plants with strap-shaped leaves at the top of an erect stem (all genera of Cymodoceae Vines and *Thalassia* Banks ex König, 1805 of Hydrocharitaceae Jussieu), (ii) plants with strap-shaped leaves but without erect stems (species *Enhalus acroides* Royle, 1839 of Hydrocharitaceae, all genera of Posidoniaceae Vines and Zosteraceae Dumort.), and (iii) plants without strap-shaped leaves but with petiolate leaves at rhizome node or more leaflets on distal notes of erect stem (genus *Halophila* Du Petit-Thouars, 1806 of Hydrocharitaceae). As in all plants, the vegetative body of seagrasses presents the typical differentiation into three organs: roots, stems (which extended horizontally below the sediment surface and called rhizomes) and leaves. These organs are connected to each other by conducting vessels, not strongly lignified, that allow the transport of water, nutrients and gases (phloem and xylem). The presence of these three organs as well as flowers, fruits and seeds allows them to be unambiguously differentiated from thallophytes (**Fig. 2**).

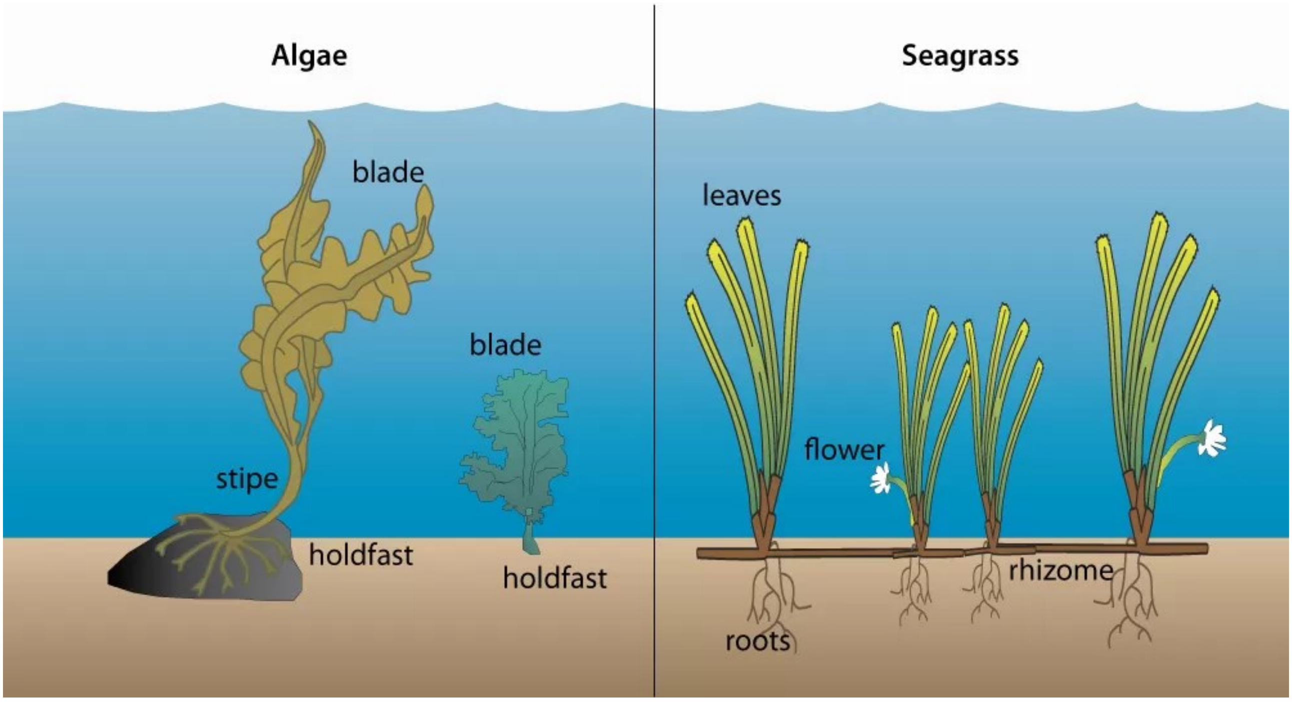


Figure 2: Difference in the vegetative body between algae and seagrasses (courtesy of ian.umces.edu, University of Maryland Center of Environmental Science)

The inconspicuous roots develop from the lower or basal portion of the rhizomes and present different root regions: root cap and root hairs. The roots have the function of anchoring the plant to the substrate and absorbing nutrients from the sediment. The stems are often buried or anchored to the substrate and are called rhizomes. The rhizomes are generally herbaceous (except for the genera *Thalassodendron* Hartog and *Amphibolis* C.Agardh and for species *Posidonia oceanica* (L.) Delile, 1813, in which they are lignified) and dimorphic, with both horizontal (plagiotropic rhizomes) and vertical (orthotropic rhizomes) growing directions (**Fig. 3**).

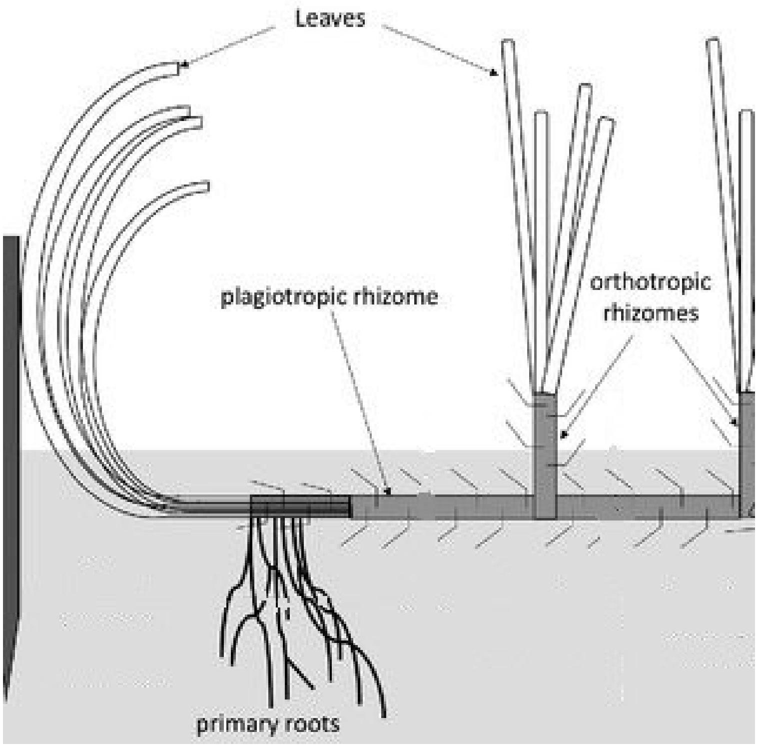


Figure 3: Schematic representation of seagrass organization (courtesy of Gobert et al. (2016))

Plagiotropic rhizomes allow the plant to anchor itself to the substrate and a horizontal advancement of the meadow, while the orthotropic ones allow vertical growth. Rhizomes have a high potential for growth and expansion. The clonal organisation allows to colonise the environment by forming interconnected meadows and functional units that can range from a couple of leaves to hundreds of thousands or millions (Rodriguez-Prieto et al., 2015). The seagrass leaves grow from a basal meristem at rhizome level with a leaf sheath. The sheath has the task of protecting the younger leaves and the meristematic tissue (**Fig. 4**).

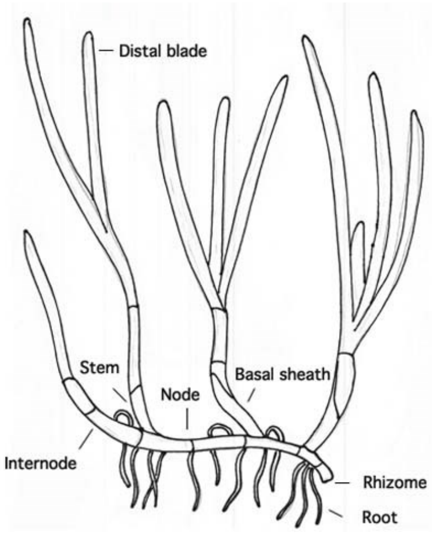


Figure 4: Scheme illustrating the morphological characteristics of seagrass leaves (courtesy of depts.washington.edu)

The most visible part of seagrasses are undoubtedly the leaves, which are generally ribbon-like and grouped in bundles of varying number depending on the species (**Fig. 4**). They do not have stomata or impermeable cuticles, but large gas-filled cavities, called aeriferous parenchyma (aerenchyma). The aerenchyma extend to the stem and roots and facilitate the transport of gas between the different parts of the plant, the oxygenation of the rhizosphere and the floating of the leaves (**Fig. 5**).

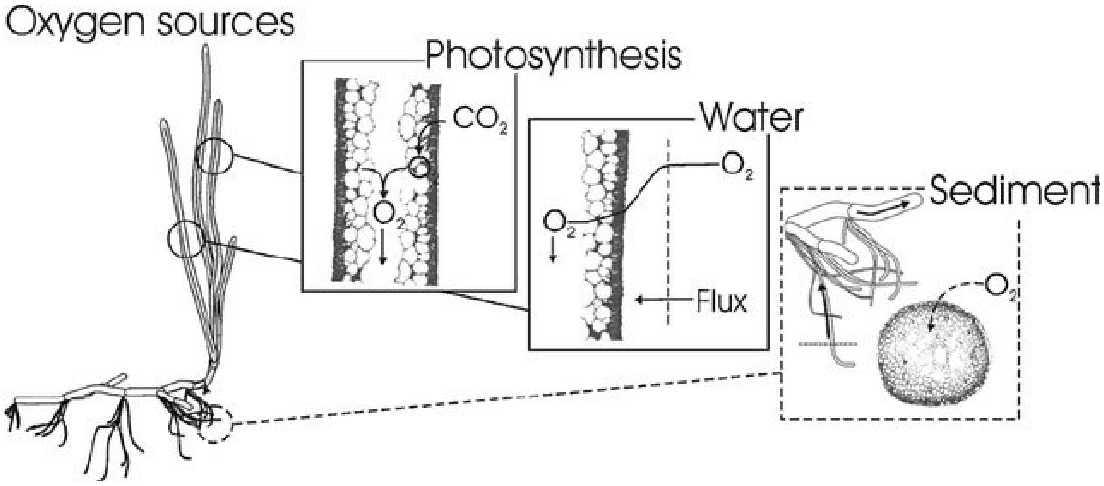


Figure 5: Schematic representation of the internal structures of leaves and roots and CO_2 and oxygen fluxes in seagrasses (courtesy of Borum et al. (2006))

These characteristics distinguish them from the leaves of terrestrial plants. The main pigments contained within the leaves are chlorophyll-*a* and *b*, which is why they always take on a green colour (light or darker) despite the presence of a few carotenoids (zeaxanthin, neoxanthin, lutein, violaxanthin, β-carotene and xanthophylls) (Casazza and Mazzella, 2002). The leaves contain veins that allow taxonomic distinction between species and are also characterised by the presence of a thin cuticle capable of absorbing nutrients and carbon from water. The flower (**Fig. 6** and **7**) has very little or no calyx and corolla (perianth), as the pollination process is passive and the dispersal of the trinucleate pollen grains is favoured by currents.

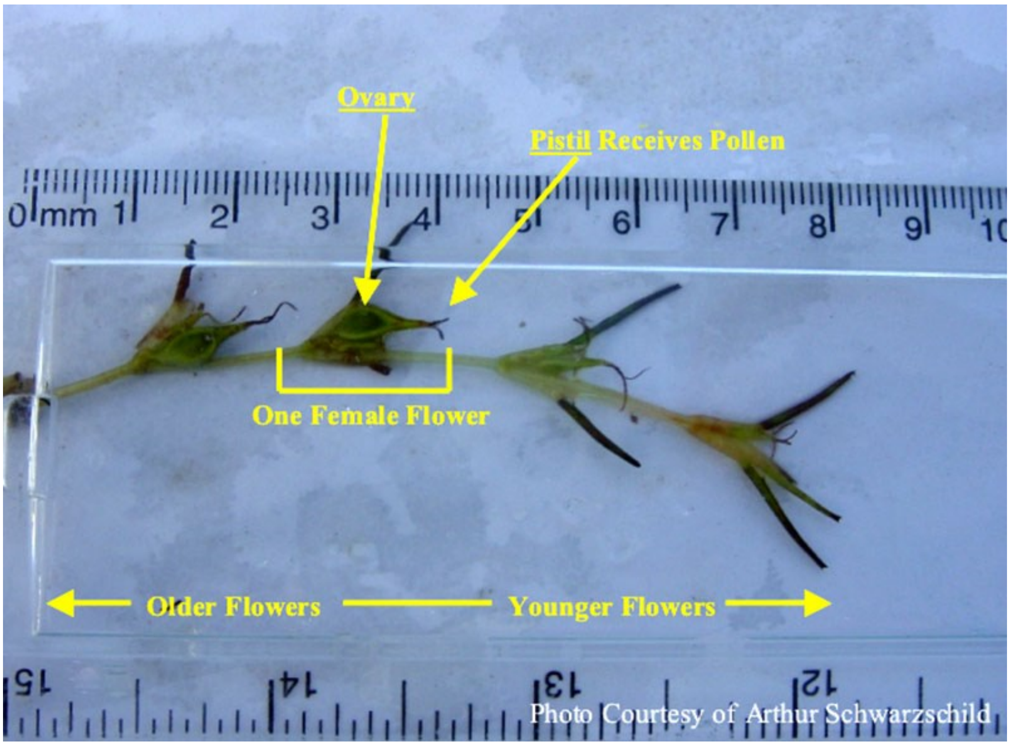


Figure 6: Example of female seeds of *Syringodium filiforme* Kurtz. (courtesy of teachoceanscience.org)

Furthermore, the flower comprises a gynoecium with one or more free and distinct carpels and an almost absent endosperm. The stamens and pistils can be found in separate flowers (unisexual) or on the same flower (hermaphrodite). These two organisations can both be found simultaneously in monoecious plant (genera *Posidonia* Köenig 1805, *Ruppia* L. and *Zostera* L.), or separately in dioecious plants (genera *Halophila* and *Cymodocea* K.D. Koenig). Once the pollen nuclei, released by the stamens, fertilise the ovules, fruits are formed. Fruits bear seeds of variable appearance in the various genera (**Fig. 7**). The seed thus consists of embryo, endosperm (nutritive tissue typical of Angiosperms) and seminal integuments. Modifications of parts of the flowers or inflorescences lead to the formation of the fruit (**Fig. 7**), whose purpose is to cover, protect and facilitate the dispersal of the seeds (**Fig. 7**).

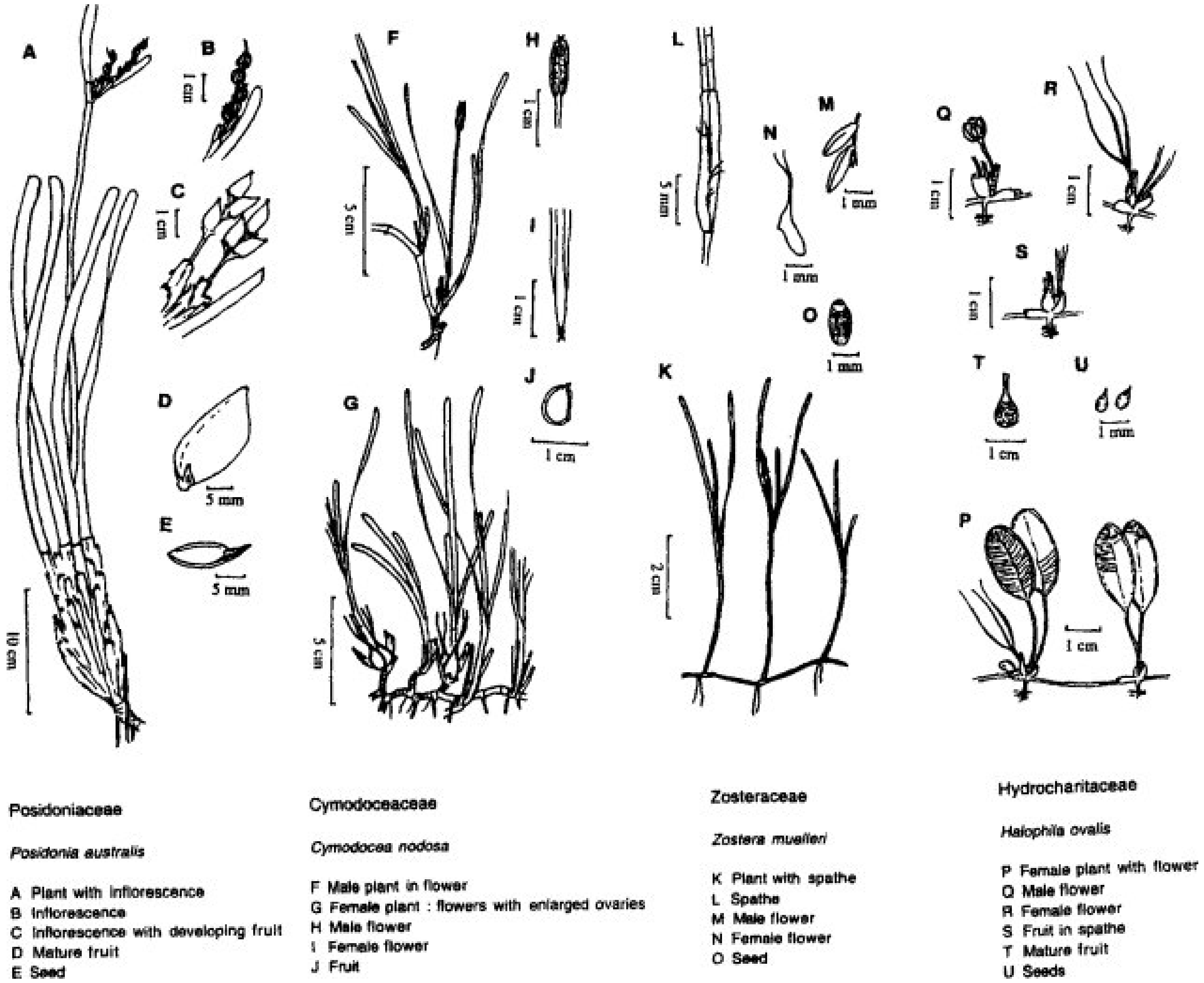


Figure 7: Flowers and fruits of 4 seagrass families: Cymodoceaceae, Posidoniaceae, Zosteraceae and Hydrocharitaceae (courtesy of Diana et al. (2001))

1.2 REPRODUCTION

As previously mentioned, seagrasses are marine angiosperms with capacity to reproduce both asexually, also called clonal growth (i.e., horizontal and local rhizome extension), or sexually (with production of flowers, fruits and seeds) (**Fig. 8**). The seeds can then be transported by tidal currents and waves, by the movement of sediment and/or by animals such as birds, Sirenia Illiger, 1811, turtles (McMahon et al., 2014; Tol et al, 2017), fish and invertebrates (**Fig. 8**).

The asexual reproduction allows plants to expand their meadows following colonisation of new habitats and/or the recovery after undergoing disturbance (Duarte and Sand-Jensen, 1990; Sherman et al., 2016). In fact, asexual reproduction maintains and propagates “good” genotypes, provides versions of the same genotypes in the event of mortality, removing the costs of reproduction (Ackerman, 2006). Whereas sexual reproduction is more favourable for

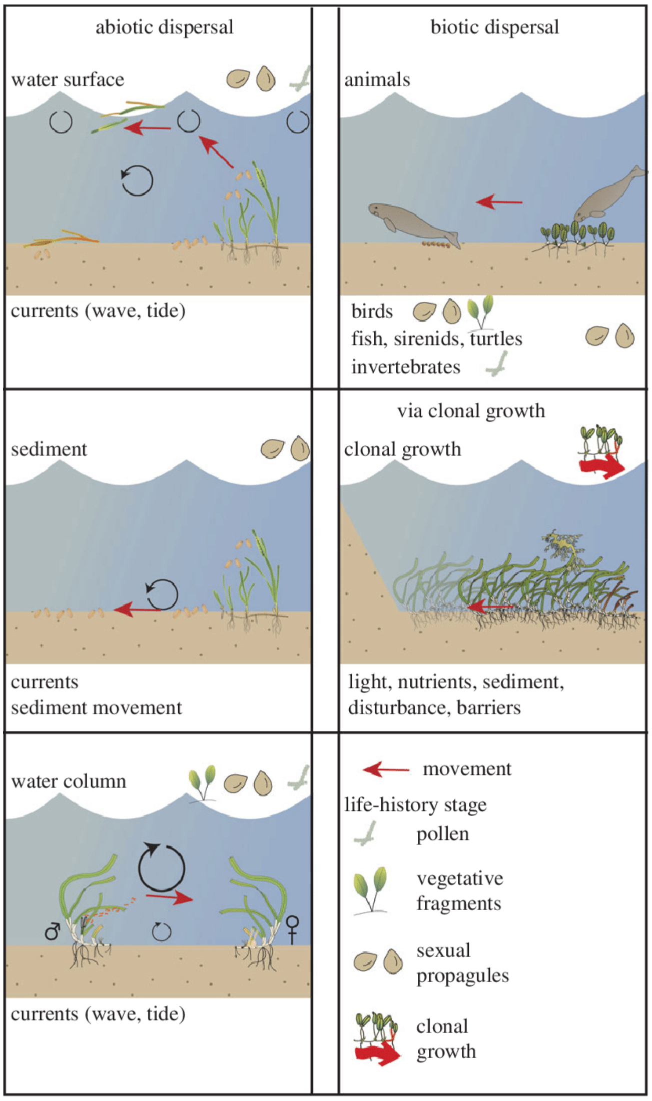


Figure 8: Asexual and sexual reproduction and seed dispersal methods of seagrasses (courtesy of McMahon et al. (2014))

the dispersal and colonisation of new areas and for maintaining the populations (Rasheed, 2004; McMahon et al., 2014). Indeed, sexual reproduction maintains the genetic variation, masking the deleterious genes and generating Sisyphean genotypes that can colonize new habitats or niches (Ackerman, 2006). As in all angiosperms, the reproductive cycle involves an alternation of generations between a diploid generation (sporophyte) and a haploid one (gametophyte) (Pasqua et al., 2019). All seagrasses present a heteromorphic two-phase cycle with dominant sporophyte, as the gametophytes are extremely reduced and have no free life (Rodriguez-Prieto et al., 2015). The diploid egg (2n), present inside the pistil, produces a haploid egg cell called the female gametophyte (n) by meiosis. Inside the anthers, grains of haploid pollen (n) are generated by meiosis. Each pollen grain divides by mitosis and generates a haploid (n) male gametophyte. When male gametophyte comes into contact with the upper end of the pistil, the pollen tube transports the male gamete to the egg cell (pollination), whose fusion produce a diploid zygote (2n) (Pasqua et al., 2019) (**Fig. 9**). All seagrasses, except *E. acoroides*, have hydrophilic pollination with pollen release in the form of gelatinous filaments in water or dispersal of the pollen by means of currents (hydrophilic pollination) until fertilisation of the female flower (McConchie and Knox, 1989). *E. acoroides* is the only species with subaerial pollination, with pollen dispersal during high tides, transport to the surface and fertilisation of the female flower at low tide (Pettitt, 1984).

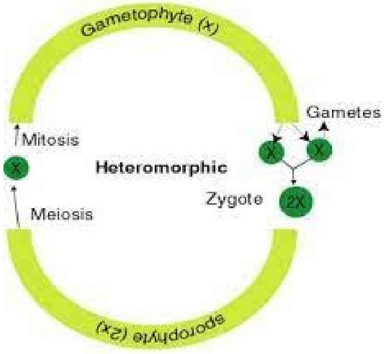
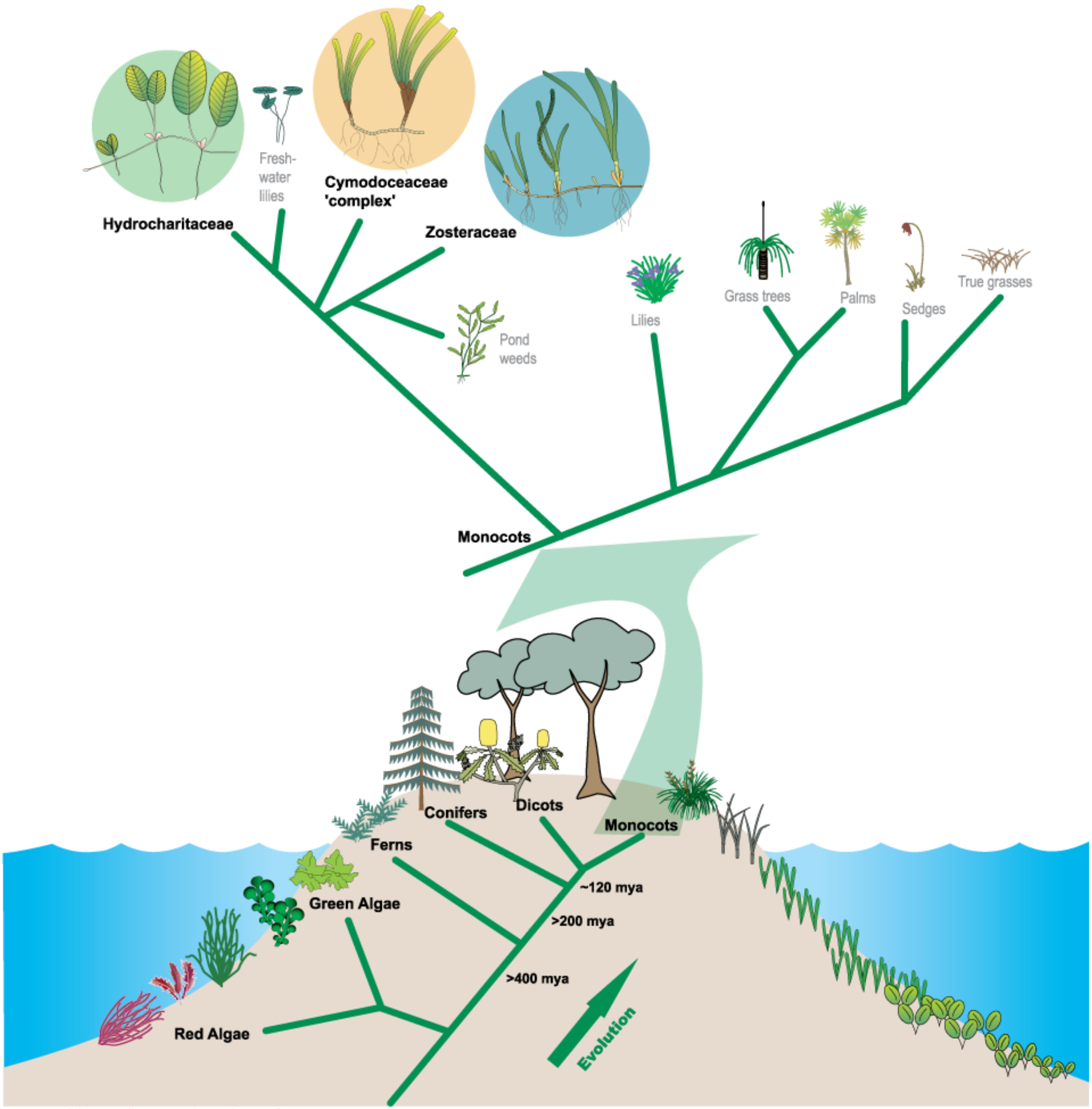


Figure 9: Schematic representation of heteromorphic two-phase cycle (courtesy of niobioinformatics.in)

1.3 ORIGIN AND EVOLUTION

The low number of species (around 60) had initially suggested a recent evolution of seagrasses (Orth et al., 2006). However, fossil remains and other indirect evidence (e.g. fossils of associated fauna) allowed to estimate that the colonisation by Angiosperms of the marine environment began around 100 million years ago, during the Cretaceous period (den Hartog, 1970; Brasier, 1975). Therefore, seagrasses evolved from primitive xerophile and halotolerant coastal terrestrial plants and from freshwater hydrophytes (Larkum and den Hartog, 1989). However, most of the seagrass genera evolved in late Eocene, around 40 million years ago (Larkum and den Hartog, 1989). The primitive plants were characterized by sympodial rhizomes, cymose inflorescence and the capacity to live in partially submerged conditions in salt waters (den Hartog, 1970). Therefore, seagrasses represent the only group of plants that have taken the reverse route back to the sea and adapted to live in condition of total immersion, bringing with them the terrestrial evolutionary characteristics of their ancestors. This evolutionary process (**Fig. 10**) was demonstrated by comparing the similar structures of the lignified stems of the genera *Amphibolis* and *Thalassodendron*, both viviparous as some mangrove taxa, and the herbaceous stems of hydrophytes (Larkum and den Hartog, 1989). Adaptation to the aquatic environment has led to the development of a basal meristem, allowing the plant to grow despite leaf damage, an extensive lacunar system for gas exchange for the maintenance of adequate oxygen levels in the underground structures (rhizomes and roots), subulate and sheathed leaves to resist waves and tidal motion and a pollination system adapted to the aquatic environment (Amber, 1920). Other adaptations led to the loss of the repertoire of stomatal, terpenoid synthesis, ethylene signalling pathway, ultraviolet protection and far red photocycles of the phytochrome superfamily in order to adapt instead to salinity and total submersion (Olsen et al., 2016).



Conceptual diagram illustrating the evolution of seagrass species.
Diagram courtesy of James Cook University, Australia.

Figure 10: Conceptual diagram illustrating the evolution of seagrass species (courtesy of James Cook University, Australia).

Although extinctions have been documented in fossils, speciation has been conservative, since the number of species has never deviated too far from today's numbers (Hemminga and Duarte, 2000). In fact, the low sexual reproduction rates and poor dispersal associated with pollination restrict the fluxes and diversity in meadows compared to terrestrial Angiosperms (Papenbrock, 2012). The majority of seagrass meadows are monospecific with the exception of the meadows in the Indo-Pacific region and the Red Sea (Duarte, 2000) and the mixed meadows of *Zostera noltei* Hornemann, 1832, *Zostera marina* L., and *Cymodocea nodosa* (Ucria) Ascherson in the Venice Lagoon (Rismondo et al., 2003). Moreover, species richness and diversity decrease from the equator to higher latitudes (**Fig. 11**) (Duarte, 2000) and as salinity increases (Terrados et al., 1999).

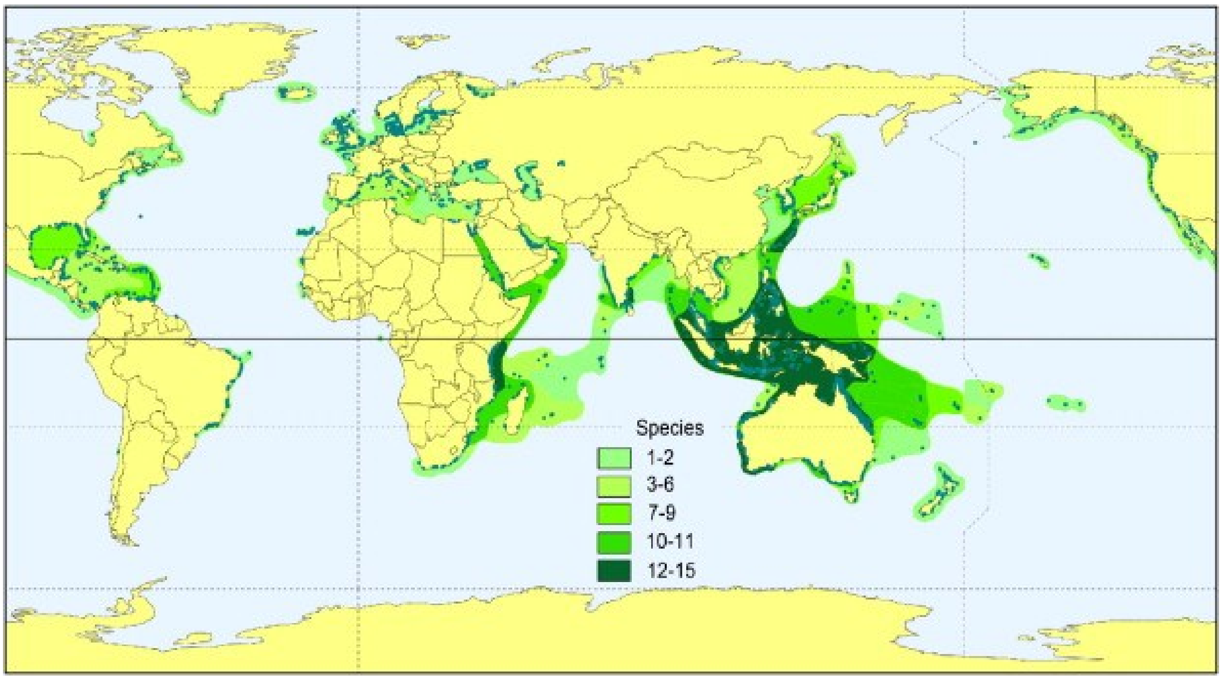
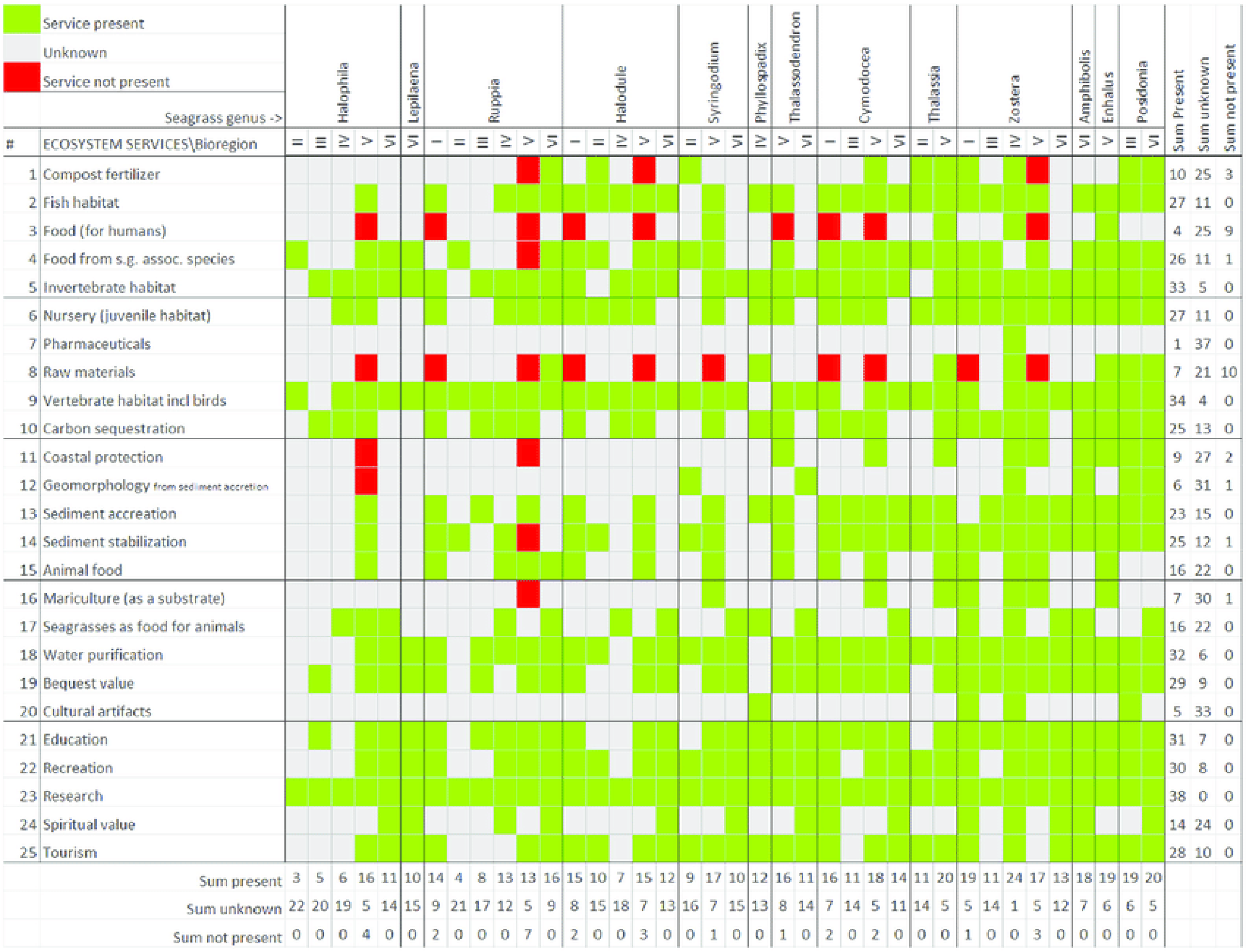


Figure 11: Global seagrass diversity and distribution depending on the number of species (courtesy of Short et al. (2007)).

1.4 BIOGEOGRAPHY AND ECOSYSTEM SERVICES

The number of Angiosperms adapted to the marine environment (about 12 genera with 60 species worldwide) is negligible in comparison to terrestrial Angiosperms (around 260,000 species) (Bremer et al, 2003). However, despite the low number of species, the seagrasses are widespread along the coasts of almost all continents, with the exception of Antarctica, up to a maximum depth of 50 m (infralittoral) depending on the transparency of the water (Hemminga and Duarte, 2000). Although there is no comprehensive measurement of the entire surface occupied by seagrasses, the currently documented area is approx. 177,000 km^2 (Green and Short, 2003). This appears to be an underestimation, as there are no data on the extension of the meadows in many countries (e.g. Indonesia and the Bahamas) (**Fig. 11**). However, estimates in the literature vary from a minimum of 300,000 km^2 to a maximum of 600,000 km^2 (Duarte et al, 2005a; Nellemann et al., 2009; Mcleod et al., 2011).

Seagrass meadows provide high-value ecosystem services (Duarte and Chiscano, 1999), providing habitat, shelter, nursery and source of food for different organisms of benthic and fish fauna (Rismondo et al., 1995; Hemminga and Duarte, 2000) (**Fig. 12**).



🟩 Service present
⬜ Unknown
🟥 Service not present

#	Seagrass genus ->	Halophila					Lepilaena	Ruppia						Halodule					Syringodium			Phyllospadix	Thalassodendron		Cymodocea				Thalassia		Zostera					Amphibolis	Enhalus	Posidonia		Sum Present	Sum unknown	Sum not present
#	ECOSYSTEM SERVICES\Bioregion	II	III	IV	V	VI	VI	I	II	III	IV	V	VI	I	II	IV	V	VI	II	V	VI	IV	V	VI	I	III	V	VI	II	V	I	III	IV	V	VI	VI	V	III	VI			
1	Compost fertilizer	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟥	🟩	⬜	🟩	⬜	🟥	⬜	🟩	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	🟩	🟩	🟩	⬜	🟩	🟥	⬜	⬜	⬜	🟩	🟩	10	25	3
2	Fish habitat	⬜	⬜	⬜	🟩	⬜	⬜	🟩	⬜	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	27	11	0
3	Food (for humans)	⬜	⬜	⬜	🟥	⬜	⬜	🟥	⬜	⬜	⬜	🟥	⬜	🟥	⬜	⬜	🟥	⬜	⬜	🟩	⬜	⬜	🟥	⬜	🟥	⬜	🟥	⬜	⬜	🟩	⬜	⬜	🟩	🟥	⬜	⬜	🟩	⬜	⬜	4	25	9
4	Food from s.g. assoc. species	🟩	⬜	⬜	🟩	🟩	🟩	⬜	🟩	⬜	⬜	🟥	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	⬜	⬜	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	⬜	🟩	🟩	🟩	🟩	26	11	1
5	Invertebrate habitat	⬜	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	33	5	0
6	Nursery (juvenile habitat)	⬜	⬜	🟩	🟩	⬜	⬜	🟩	⬜	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	⬜	🟩	⬜	🟩	🟩	⬜	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	27	11	0
7	Pharmaceuticals	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	⬜	⬜	1	37	0
8	Raw materials	⬜	⬜	⬜	🟥	⬜	⬜	🟥	⬜	⬜	⬜	🟥	🟩	🟥	⬜	⬜	🟥	⬜	⬜	🟥	⬜	🟩	⬜	⬜	🟥	⬜	🟥	⬜	⬜	🟩	🟥	⬜	🟩	🟥	⬜	⬜	🟩	🟩	🟩	7	21	10
9	Vertebrate habitat incl birds	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	34	4	0
10	Carbon sequestration	⬜	🟩	🟩	🟩	⬜	⬜	🟩	⬜	🟩	🟩	🟩	⬜	🟩	⬜	🟩	🟩	⬜	⬜	🟩	⬜	🟩	🟩	⬜	🟩	🟩	🟩	⬜	⬜	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	25	13	0
11	Coastal protection	⬜	⬜	⬜	🟥	⬜	⬜	⬜	⬜	⬜	⬜	🟥	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	🟩	⬜	⬜	🟩	⬜	⬜	🟩	🟩	⬜	🟩	🟩	🟩	🟩	9	27	2
12	Geomorphology from sediment accretion	⬜	⬜	⬜	🟥	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	🟩	⬜	🟩	🟩	6	31	1
13	Sediment accreation	⬜	⬜	⬜	🟩	⬜	⬜	🟩	⬜	🟩	⬜	🟩	⬜	🟩	⬜	⬜	🟩	⬜	⬜	🟩	⬜	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	23	15	0
14	Sediment stabilization	⬜	⬜	⬜	🟩	⬜	⬜	🟩	🟩	⬜	🟩	🟥	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩	⬜	⬜	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	25	12	1
15	Animal food	⬜	⬜	⬜	🟩	⬜	⬜	🟩	⬜	⬜	🟩	🟩	🟩	🟩	⬜	⬜	🟩	⬜	⬜	🟩	⬜	⬜	🟩	⬜	🟩	⬜	🟩	⬜	⬜	🟩	🟩	⬜	🟩	🟩	⬜	⬜	🟩	⬜	⬜	16	22	0
16	Mariculture (as a substrate)	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟥	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	🟩	🟩	⬜	🟩	🟩	⬜	⬜	🟩	⬜	⬜	7	30	1
17	Seagrasses as food for animals	⬜	⬜	🟩	🟩	🟩	⬜	⬜	⬜	⬜	🟩	⬜	🟩	⬜	⬜	🟩	⬜	🟩	⬜	⬜	🟩	🟩	⬜	🟩	⬜	⬜	⬜	🟩	⬜	⬜	🟩	⬜	🟩	⬜	🟩	🟩	⬜	⬜	🟩	16	22	0
18	Water purification	⬜	⬜	⬜	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	32	6	0
19	Bequest value	⬜	🟩	⬜	🟩	🟩	🟩	🟩	⬜	🟩	⬜	🟩	🟩	🟩	⬜	⬜	🟩	🟩	⬜	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	29	9	0
20	Cultural artifacts	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟩	⬜	🟩	⬜	⬜	⬜	⬜	🟩	⬜	5	33	0
21	Education	⬜	🟩	⬜	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	⬜	⬜	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	31	7	0
22	Recreation	⬜	⬜	⬜	🟩	🟩	🟩	🟩	⬜	⬜	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	30	8	0
23	Research	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	38	0	0
24	Spiritual value	⬜	⬜	⬜	⬜	🟩	🟩	⬜	⬜	⬜	🟩	⬜	🟩	⬜	⬜	⬜	⬜	🟩	⬜	⬜	🟩	⬜	⬜	🟩	🟩	⬜	⬜	🟩	⬜	⬜	🟩	⬜	🟩	⬜	🟩	🟩	⬜	⬜	🟩	14	24	0
25	Tourism	⬜	⬜	⬜	🟩	🟩	🟩	🟩	⬜	⬜	⬜	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	⬜	🟩	🟩	🟩	🟩	🟩	⬜	🟩	⬜	🟩	🟩	🟩	🟩	🟩	28	10	0
	Sum present	3	5	6	16	11	10	14	4	8	13	13	16	15	10	7	15	12	9	17	10	12	16	11	16	11	18	14	11	20	19	11	24	17	13	18	19	19	20			
	Sum unknown	22	20	19	5	14	15	9	21	17	12	5	9	8	15	18	7	13	16	7	15	13	8	14	7	14	5	11	14	5	5	14	1	5	12	7	6	6	5			
	Sum not present	0	0	0	4	0	0	2	0	0	0	7	0	2	0	0	3	0	0	1	0	0	1	0	2	0	2	0	0	0	1	0	0	3	0	0	0	0	0			

Figure 12: Ecosystem services provided by seagrass species. Red represents service not present; grey unknow and green service present (courtesy of Nordlund et al. (2016))

Seagrasses represent one of the most important primary producers in marine-coastal and lagoonal ecosystems (Smith, 1981; Charpy-Roubaud and Sournia, 1990). Duarte et al. (2010) estimated the gross primary production of seagrass in 224.9±11.1 mmol O_2 m^{-2} day^{-1}, a value that exceeds respiration, thus producing more biomass than their needs (autotrophic ecosystem). Therefore, seagrasses provide an average net production of 27.2±5.8 mmol O_2 m^{-2} day^{-1} (Duarte et al., 2010). Seagrass meadows are also considered a significant sink for atmospheric CO_2 with a great capacity to sequester and store carbon within their sediment (Duarte et al., 2005b). In fact, seagrasses contribute to the sequestration of about 20% of the global carbon in marine sediments despite occupying only 0.1% of marine surface (Duarte et al., 2005b; Kennedy et al., 2010). Duarte et al. (2010) estimated carbon production by seagrass meadows in 1 kg C dry weight m^{-2} $year^{-1}$ and their carbon storage capacity at a rate of 58 g C m^{-2} $year^{-1}$ (Duarte et al., 2013), almost five times the capability of carbon storage from North America wetlands (Duarte et al., 2010). Yet, a fraction of their production (almost 80%) is composed by roots and rhizomes which are laid in sediments and is not consumed by herbivores due to their low carbon and nutrient contents (Duarte, 1990) and low oxygen concentrations in the sediment (often anoxic) (Duarte et al., 2005b). As a result, rhizomes are preserved over long-time scales (Duarte et al., 2010), resulting in slow decomposition rates (Enriquez et al., 1993). Moreover, the dissipation of waves and tides by leaves prevents sediment resuspension, stabilising the associated carbon (Duarte et al., 2013). Thereby, considering an estimated extension between 300,000 and 600,000 km^2, Duarte et al. (2013) estimated that, thanks to their metabolism, seagrasses are able to store between 20 to 101*10^6 tonnes C year^{-1}, for a total carbon reserve that ranged between 4.2 and 8.4 × 10^9 tonnes C depending on the cover area considered (Fourqurean et al., 2012).

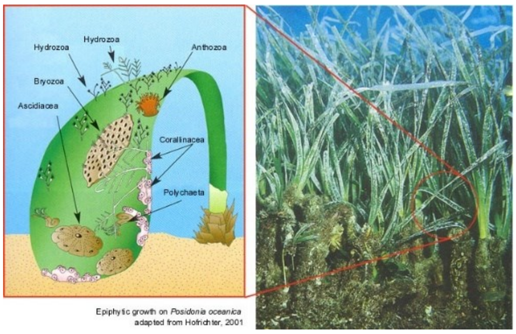


Figure 13: Example of epiphytes growth on seagrass leaf (courtesy of biophysics.sbg.ac.at)

Seagrasses also play an important structural role in coastal ecosystems. The dense foliage provides substrate for many epiphytes (**Fig. 13**) (also with growth and accumulation of carbonate structures by calcareous algae) and other aquatic organisms. In addition, the leaves capture suspended sediment and allow it to settle, thus increasing the clarity of the water column (Short and Short, 1984) (**Fig. 14**). Moreover, the dense root-rhizome system changes the substrate conditions allowing compaction and stabilisation, limiting the phenomena of erosion, resuspension and loss of fine sediments with consequent limitation of turbidity (**Fig. 14**).

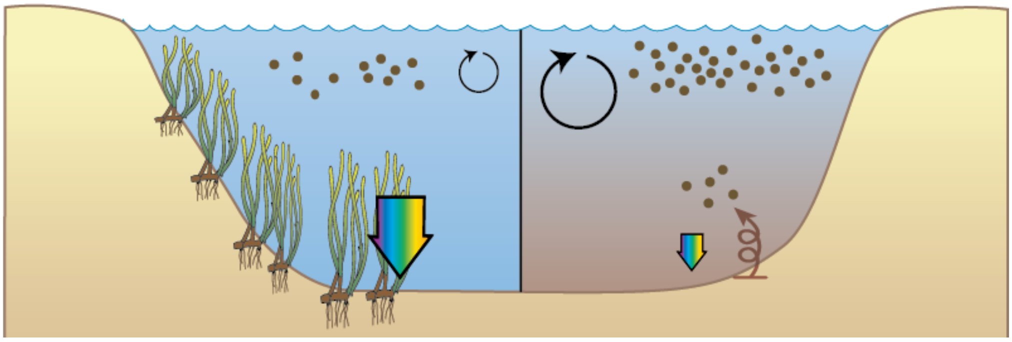


Figure 14: Conceptual diagram of sediment trapping by seagrass leaves and how seagrass can improve water clarity (courtesy of teachoceanscience.org)

The substrate in well-structured meadows is thus rendered homogenous and the rhizomes themselves are transformed into new substrate favouring the colonisation of epiphytes

(Hemminga and Duarte, 2000). The presence of seagrasses also reduces hydrodynamics and the amount of light radiation at the bottom allowing the growth of species with low lighting requirements and thus increasing biodiversity (Rodriguez-Prieto et al., 2015). Seagrasses also form the basis of the food chain, although few species feed directly on them (e.g. *Trichechus* L., *Chelonia mydas* L., Mugilidae Jarocki, 1822, *Aluterus scriptus* Osbeck, 1765, *Platybelone argalus* Lesueur, 1812, *Acanthurus bahianus* Castelnau, 1855, Brachyura Latreille, 1802, Nephropidae Dana, 1852, Scaridae Rafinesque, 1810 and Anatidae Vigors, 1825) (**Fig. 15**). Finally, seagrasses remove nutrients and oxygenate sediments, improving ecological quality (Terrados and Borum, 2004). Costanza et al. (1997) and Short et al. (2011) estimated the total ecosystem services provided by the presence of seagrass meadows in \$34,000 ha^{-1} year^{-1}.

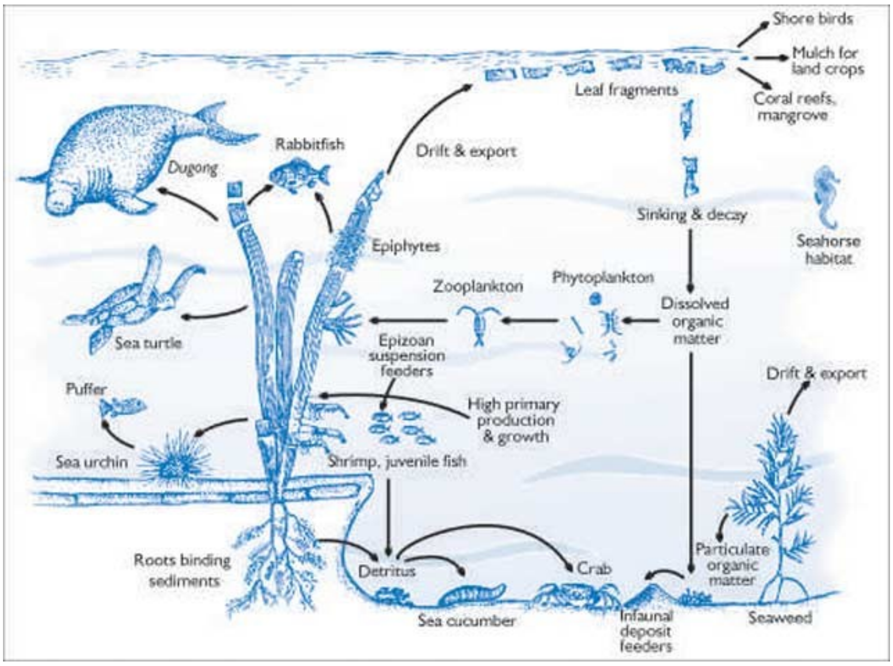


Figure 15: Schematic representation of seagrass food web (courtesy of oneocean.org)

1.5 PHYTOECOLOGY

The growth of aquatic plants is affected by different abiotic factors such as temperature, light, hydrodynamics, sedimentation rates, nutrient concentrations, depth, granulometric and physical characteristics of the sediments and biotic factors (such as grazing by aquatic vertebrates and birds) (Greve and Binzer, 2004). Seagrass productivity is determined by the balance of respiration and photosynthesis which are mainly influenced by four environmental factors: light (Silva et al., 2009), hydrodynamics (Maxwell et al., 2017), temperature

(Alcoverro, 1995; Collier and Waycott, 2014) and nutrient concentrations (Ourry et al., 1997; Pupillo et al., 2003).

The light radiation varies in both quantity and quality (wavelength) depending on the depth. The relationship between the seagrass colonisation depth (Z_c in m) and the light attenuation coefficients in water (K, in m^{-1}) is expressed by the equation (Duarte, 1991):

$$\log Z_c = 0.26 - 1.07 \times \log K$$

Therefore, colonisation decreases rapidly as turbidity increases (Hemminga and Duarte, 2000) and, in case of high turbidity water and/or phenomena that prevent the light from reaching the seabed, the presence of seagrasses is greatly limited if not prevented (Ralph et al., 2007). Hydrodynamics is another very relevant factor: on the one hand it ensures a continuous renewal of the water by providing nutrients necessary for plant growth, on the other hand it determines the plants' ability to remain attached to the substrate. Furthermore, the continuous resuspension and turbidity of water through wave action can also lead to damage to the leaf apparatus (Maxwell et al., 2017). Temperature is considered a major factor controlling seasonal growth (Lee et al., 2005), influencing the speed of metabolic reactions. Therefore, different species have adapted to live in certain temperature ranges. In fact, while photosynthetic capacity and shoot biomass of *Z. noltei* drops over 37°C (Massa et al., 2009), optimum water temperature for *Z. marina* lies between 10 and 20°C with photosynthetic rate dropping and increasing mortality at higher temperature (Nejrup and Pedersen, 2008). However, both temperature and solar irradiance show similar seasonal trends and often correlate, making it difficult to discriminate each contribution (Kaldy, 2006). Lastly, nutrient availabilities play a fundamental role in regulating productivity where light is plentiful (Lee et al., 2007). In fact, while low nutrient concentrations could limit seagrass growth, excessive concentrations could lead to macroalgal blooms, light attenuation and local anoxia/hypoxia (Hauxwell et al., 2001; Burkholder et al., 2007). These factors are particularly important in shallow-water environments and lagoons which are characterized by high daily and seasonal variations in temperature and irradiance due to tidal cycles, sediment resuspensions and characteristics, hydrodynamic and seasonal patterns (Franzoi et al., 2010; Canal-Vergés et al., 2016; Flindt et al., 2016; Amos et al., 2017).

All seagrasses need a source of inorganic carbon as raw material for the synthesis of organic compounds (carbohydrates) through photosynthesis (Hemminga and Duarte, 2000). This source is provided by the presence of CO_2 in water from the atmospheric reserve or from the respiratory activity of heterotrophic marine organisms (Hemminga and Duarte, 2000). The inorganic carbon is largely absorbed by diffusion through leaves directly from water as carbon dioxide carbon (CO_2) and bicarbonate ion (HCO_3^-) (Hemminga and Duarte, 2000). Carbon availability can become limiting especially in areas where hydrodynamics is very limited (Rodriguez-Prieto et al., 2015). However, such limitation does not occur except at a seasonal level (Rodriguez-Prieto et al., 2015). The two elements generally limiting the growth are nitrogen and phosphorus which are absorbed in dissolved form (nitrate, ammonium, and phosphorus) from water or interstitial water in the sediment (Hemminga and Duarte, 2000). Leaves are able to directly absorb ammonium, nitrate and phosphates, while roots and rhizomes absorb only ammonium and phosphates (Hemminga and Duarte, 2000). However, given the higher concentrations in the interstitial waters, the sediment turns out to be the largest source of nitrogen and phosphorus for seagrasses (Hemminga and Duarte, 2000). In particular, ammonium can enter the interior of the cells by diffusion through cation channels, while nitrate and phosphate via specific transporters (nitrate permease in symport with protons and phosphate transporters) (Ourry et al, 1997; Pupillo et al., 2003). These elements, together with other normally non-limiting elements such as magnesium, copper, manganese, zinc, iron and others, are essential for the synthesis of amino acids, nucleic acid and vital compounds such as chlorophylls (Larcher, 1995). The average percentage values of carbon, nitrogen and phosphorus in seagrass leaves (33.5%, 1.9%, respectively and 0.24% (Duarte, 1992)) were converted into a median atomic ratio median atomic C:N:P ratio of 435:20:1 (Hemminga and Duarte, 2000). Comparing these values with the Redfield ratio for the production of organic matter by phytoplankton (106:16:1 (Redfield et al., 1963)), it can be deduced that seagrasses require about a quarter of the nitrogen and phosphorus needed for phytoplankton (Hemminga and Duarte, 2000). However, under nitrogen-limiting conditions, the C:N ratio can increase from 20 to 40, whereas, under phosphorus-limiting conditions, the C:P ratio can even exceed 1000 (Hemminga and Duarte, 2000). When nutrient concentrations are low, seagrasses are the dominant species compared to macroalgae (Fourqurean et al, 1995) due to the competitive advantage given by the roots and rhizomes in the uptake of nutrients from the sediment (Hemminga, 1998; Vonk et al., 2008). The situation is reversed in the presence of high nutrient concentrations due to the greater efficiency of macroalgae in absorption through the thallus than through the leaves of the seagrasses, particularly the thionitrophilic and opportunist species (Burkholder et al., 2007; Vonk et al., 2008) (**Fig. 16**).

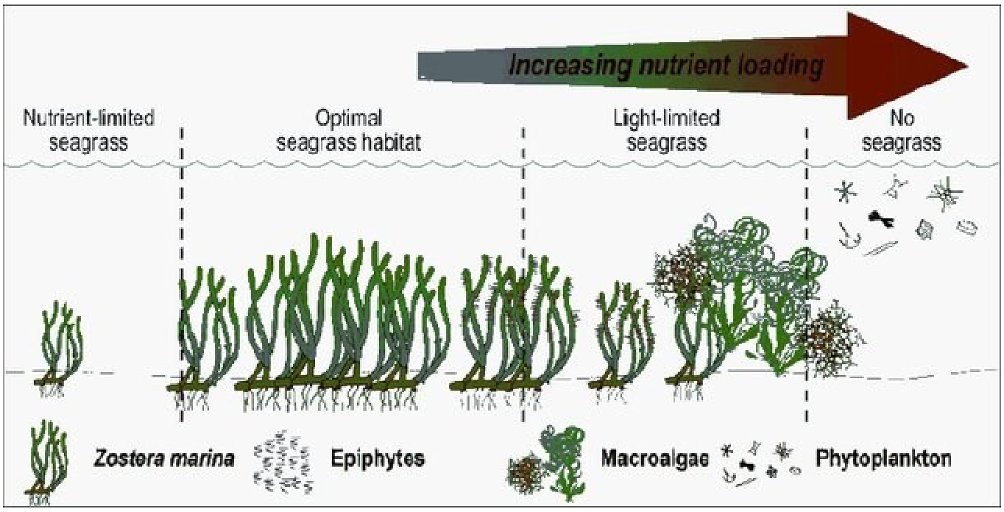


Figure 16: Conceptual diagram of seagrass habitat changes with increasing nutrient loading (courtesy of Kennish (2009))

1.6 PRIMARY PRODUCTION

Net community production and oxygen/CO_2 fluxes for a given meadow are generally estimated using different techniques, each affected by several biases (Silva et al., 2009). These techniques are based on metabolic approaches (Staehr et al., 2010; Campbell and Fourqurean, 2011; Long et al., 2015), PAM (Pulse -Amplitude Modulation) fluorometry (Beer and Björk, 2000; Duarte et al., 2017; George et al., 2020; Purvaja et al., 2020), oxygen/CO_2 variations and the most recent Eddy Covariance technique (Markwitz and Siebicke, 2019; Koopmans et al., 2020). Metabolism approaches estimate oxygen fluxes as the products of diel-changes measurements that, however, could be bias by several factors such as upstream contribution, changes in circulation, stratification and gas exchange calculation at the air-water interface (Staehr et al., 2010; Campbell and Fourqurean, 2011; Long et al., 2015). PAM fluorometry gives indications of photosynthetic traits of individual plants, photochemical efficiency and stress conditions but it is often impossible to compare such measurements with growth rates and community productions (Beer et al., 1998; Beer and Björk, 2000; Silva et al., 2008; Silva et al., 2009; Durako, 2012; Hoellein et al., 2013; Duarte et al., 2017; George et al., 2020; Purvaja et al., 2020). On the other hand, Eddy Covariance (EC) technique measures the ecosystem–atmosphere exchange of trace gases (Markwitz and Siebicke, 2019), estimating oxygen fluxes as the fluctuations of vertical velocity and oxygen concentration in turbulent flow (Koopmans et al., 2020), but it is traditional limited by high costs and complexity of EC set-ups (Markwitz and Siebicke, 2019). Instead, the use of benthic chambers in order to evaluate CO_2/oxygen variations is more practical and direct for estimating photosynthesis rates at community level over a known area (Baldocchi, 2014; Long, et al., 2015; Berger et al., 2020). However, chambers could be invasive cutting below-ground tissues, changing hydrodynamic movement and exchange and altering light availability and pH levels due to no gas exchange (Campbell and Fourqurean, 2011; Koopmans et al., 2020). CO_2 techniques analyse the evolution of CO_2 by directly measurements of fluxes by InfraRed Gas Analyzer (IRGA). However, these techniques are designed for measurements in the air and it is difficult to implement in water since their sensibility to changes in pH (Ouisse et al., 2014). Instead, oxygen techniques, measured traditionally by Winkler method (Olivé et al., 2016), represent the most common method to estimate seagrass productivity at community level (Silva et al., 2009).

Isolating the primary production of seagrasses alone is an important task in order to understand the contribution of individual species considering also that communities could vary considerably at local level. Local metrics could impact the abundance, diversity and community composition of seagrass-associated fish and invertebrates (Barry et al., 2021). In fact, the physical structures of vegetation (density/biomass), leaf surface area and root/rhizome biomass and thickness could correlate or not with abundance, species richness and diversity of seagrass-associated fauna (Hovel et al., 2002; Franco et al., 2006; Hosack et al., 2006; Unsworth et al., 2007; Almeida et al., 2008; Moore and Hovel, 2010; Parsons et al., 2013; Ávila et al., 2015). Moreover, the responses of certain taxa within the communities could vary not only spatially but also temporally (Hovel et al., 2002; Jelbart et al., 2007; Moore and Hovel, 2010; McCloskey and Unsworth, 2015). Finally, other factors can influence seagrass-associated flora and faunal communities, such as nutrient concentrations (Gil et al., 2006; Peterson et al., 2007; Armitage and Fourqurean, 2009; Daudi et al., 2012; Burghart et al., 2013; Tuya et al., 2013), exposure to waves and tides (Jelbart et al., 2007; Moore and Hovel, 2010; Parsons et al., 2013; Ávila et al., 2015), large-scale physical disturbances (Herkül et al., 2011; Patrick et al., 2020) and predator pressure (Mattila et al., 2008; Amundrud et al., 2015; Huang et al., 2015). All these factors make it difficult to extrapolate inferences from point sampling data. Consequently, growth measurements at seagrass species level are more useful in order to expand point values to a larger area (such as lagoon). Method for measuring seagrass growth is commonly directly by marking leaves, rhizomes and shoots at a fixed reference height, relocating the marks at a later time (usually

15 days) and measuring the distances (Short and Duarte, 2001). Coupling these results with monthly biomasses, it allows the calculation of annual net primary production of both rhizome and leaf apparatus and production/biomass ratios (P/B) (Sfriso et al., 1998; Short and Duarte, 2001).

1.7 ANTHROPOGENIC IMPACTS, LAWS FOR CONSERVATION AND ENVIRONMENTAL RESTORATION

Coastal-marine and transitional environments are some of the most impacted areas by anthropogenic activities, with two-thirds of the world's population living within 100 km of a coast (oceanconference.un.org). Human pressures, such as over-exploitation, physical modifications (e.g., loss of water transparency by sediment resuspension), aquaculture, mechanical fishing activities, nutrient and sediment pollution, introduction of non-native species and eutrophication phenomena (Short et al., 1995; Hauxwell et al., 2001; Burkholder et al., 2007), lead to meadow decline at a rate of approx. 110 km^2 $year^{-1}$ between 1980 and 2006 (Waycott et al., 2009; Marbà et al., 2014; Oprandi et al., 2014; Holon et al., 2015; Telesca et al., 2015). Moreover, physical stress from wave and current action, lack of sediment, bioturbators and other local feedback mechanisms (e.g. resuspension by drifting ephemeral macroalgae, seedling uprooting and lugworm burial of seeds) could reduce the capability of seagrasses to recolonize and survive (Valdemarsen et al., 2010; Kuusemäe et al., 2016). This resulted in the insertion of one-fifth of seagrass species as “Endangered, Vulnerable and Near Threatened” according to IUCN (International Union for Conservation of Nature) criteria (Short et al., 2011) (**Fig. 17**).

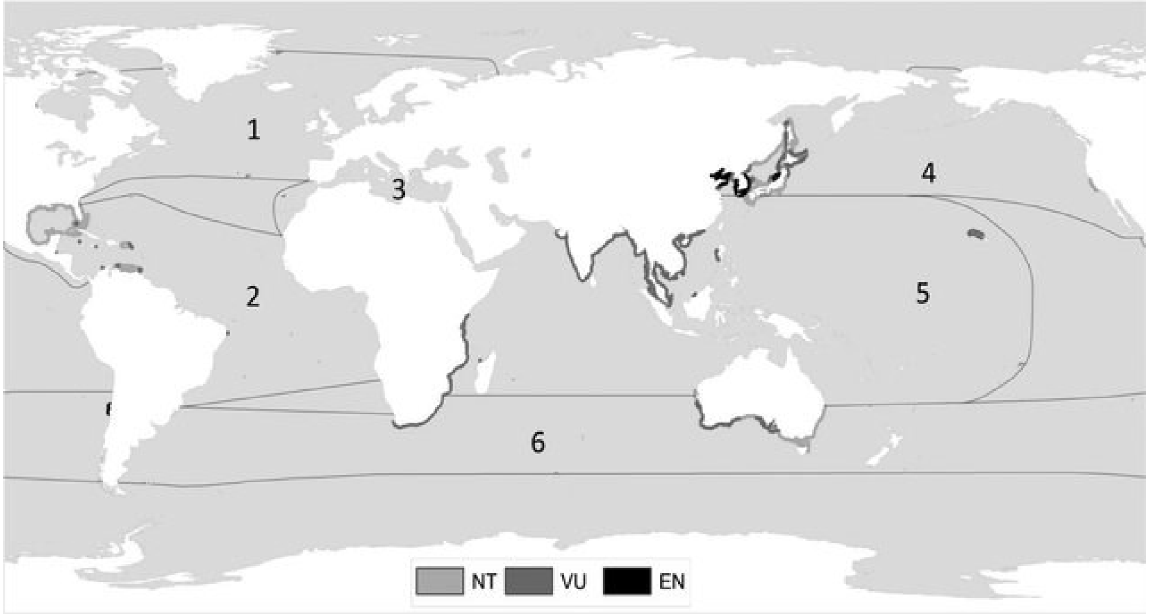


Figure 17: Distribution of Near Threatened (NT), Vulnerable (VU) and Endangered (EN) seagrasses across the globe. Numbers 1-6 indicate bioregions (courtesy of Novak and Short (2020))

In particular, European seagrass area was reduced by 1/3 due to disease, deteriorated water quality and coastal development between 1869 and 2016 (de los Santos et al., 2019). However, since then, loss rates slowed down for most of the species reversing the net rate of change in seagrass area due to management intervention and natural recovery and colonization (de los Santos et al., 2019). Nevertheless, the increasing human pressure on coastal systems and short- and small-scale stress events threat the resilience of seagrass ecosystems and their carbon reserves in global assessments (Soissons et al., 2018). In particular, the increase of nutrient concentrations along coastal areas has led to phytoplanktonic and opportunistic and thionitrophilic macroalgae blooms (Hauxwell et al., 2001; Burkholder et al., 2007), lowering the content of carbon within the leaves and rhizomes of seagrasses (Han et al., 2016) and leading to a decrease in their biomass or even their disappearance. For these reasons, seagrass meadows are considered 'sensitive' and therefore excellent bio-indicators of environmental quality for aquatic environments. The European Directive 2000/60/EC (Water Framework Directive, WFD), implemented by Italy with the Legislative Decree 152/2006, establishes a framework for the protection and management of community water resources, including marine-coastal and lagoonal systems. Ecological status can be assessed on the basis of monitoring and study of different Quality Elements (QEs) supported by hydromorphological and physico-chemical characteristics of the environment. The ecological status is thus defined by the structure and functioning of aquatic ecosystems through 5 classes: "high", "good", "moderate", "poor" and "bad". The Directive includes five QEs for both marine and coastal waters: macroalgae, seagrasses, phytoplankton, zoobenthos and ichthyofauna. In transitional water systems macroalgae and seagrasses are considered a single QE, called macrophytes. Several authors have proposed some indices using macrophytes as environmental indicators: Macrophyte Quality Index (MaQI) (Sfriso et al., 2007a, 2009, 2014); Ecological Evaluation Index (EEI) (Orfanidis et al., 2001, 2003, 2011), *Posidonia oceanica* Multivariate Index (POMI) (Bennett et al., 2011) and CARLIT (Ballesteros et al., 2007). Subsequently, the European Directive 2008/56/EC (Marine Strategy Framework Directive), implemented in Italy by Legislative Decree no. 190 of 13 October 2010, includes seagrasses among the 9 indicators (together with phytoplankton, zooplankton, jellyfish, bony fish, cartilaginous fish, piscivorous fish, marine reptiles and marine mammals) for the Environmental Status (ES) assessment with the aim to achieve “Good Environmental Status (GES)” by 2020 in all European water bodies. Since in 2020 the quality status of Europe’ seas portray a mixed picture with some species showing signs of recovery and other steep deterioration (COM, 2020), a new EU Biodiversity Strategy for 2030 was adopted in May 2020. The new strategy aims to strengthen the protection of marine ecosystems and to restore them to achieve “Good Environmental Status” through the expansion of protected areas and the establishment of strictly protected areas for habitats and fish stocks recovery. In addition, the *Posidonia oceanica* meadows, widely distributed throughout the Mediterranean Sea, are considered a priority habitat of European Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural and semi-natural habitats and wild flora and fauna.

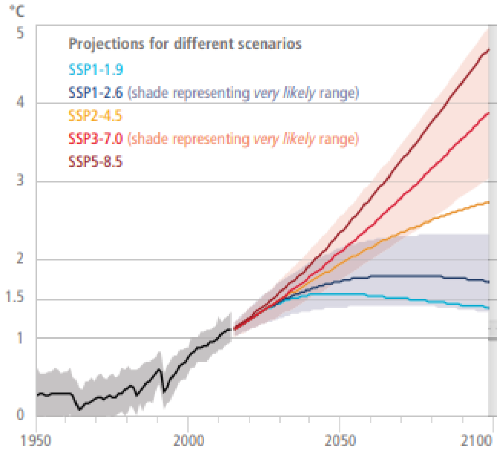


Figure 18: Projections of global surface temperature change. Increase relative to the period 1850-1900 (courtesy of IPCC (2022))

This series of conventions, directives and laws were introduced with the aim of slowing or halting the degradation of seagrasses, already under pressure as they are located close to the coasts and therefore in heavily anthropized environments (Ralph et al., 2006). In addition to local level forcing, Global Change could worsen the health status of seagrass meadows (Waycott et al., 2009; Chefaoui et al., 2018). In fact, the global ocean surface temperature has increased of approximately 0.11°C per decade over the period 1971-2010 in the first 75 m depth, with an average sea level rise of about 0.19 m between 1901 and 2010 (**Fig. 18**) from the beginning of the industrial age (IPCC, 2022). The continued emission of greenhouse gases (especially CO_2 and CH_4) in the coming years will lead to a further increase in ocean surface temperature (an estimated increase in the first 100 m at the end of the XXI between 1.5 up to 4.5°C compared to the period 1850-1900) and to sea level rise (between about 0.5 and 0.9 m in the period 2081-2100 compared to the period 1986-2005) (**Fig. 19**) (IPCC, 2022).

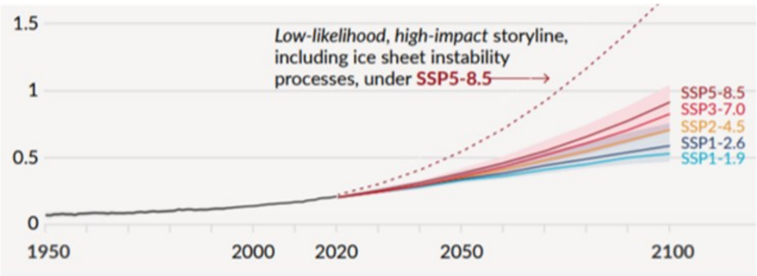


Figure 19: Projections of sea level rise (courtesy of IPCC (2022))

Such temperature variations will lead to alterations in the growth rates, photosynthesis, calcification and many biogeochemical processes of seagrasses, while the warming of the oceans will affect species, communities and ecosystems in ways not yet fully known. Indeed, an increment of temperature would lead to a “range contraction” of temperate species, interspecific competition with tropical species (Koch et al., 2013) and to carbon losses (Chefaoui et al., 2018). These effects vary depending on the depths of the seabed: the shallowest meadows will acclimatise through respiratory homeostasis and the activation of photo-protective mechanisms, while the deepest ones will suffer damage to the photosynthetic apparatus and the carbon balance (Marin-Guirao et al., 2016). Furthermore, a higher temperature will lead to an increase in the number of leaves with a brownish colour (indicative of dieback) and in the levels of pheophytins, thus decreasing photosynthetic capacity (Repolho et al., 2017). Sea level rise will increase the depth and thus decrease the availability of light on the bottom, reducing the productivity of seagrasses (Pachauri et al., 2014). Finally, the acidification of the sea, due to the increased concentration of carbon dioxide, will decrease the number of photosynthetic pigments (Apostolaki et al., 2014; Repolho et al., 2017).

In order to meet the conservation and restoration of seagrasses and mitigation and adaptation to climate change, a series of projects have been developed in areas where they were present and subsequently disappeared as a result of various anthropogenic pressures. The Life SeResto (SEagrasses RESTOration, LIFE12 NAT/IT/000331), Life Lagoon Refresh (LIFE16 NAT/IT/000663) and Life Transfer (LIFE19 NAT/IT/000264) projects fit into fully into this scenario. The aim is the restoration, preservation and acceleration of the priority aquatic habitat 1150* (Lagune Coastal Lagoons) in the Upper Lagoon of Venice SCI (IT3250031) and in 8 Natura 2000 sites in 3 Member States of EU (European Union: Italy, Greece and Spain), through the dispersal and the transportation of seagrass sods and rhizomes taken from areas where environmental conditions are high (according to WFD 2000/60/EC), in order to help the natural expansion of the meadows. In particular, Life SeResto project which finished in 2018 leads to the colonization of about 15 km^2 in the northern part of Venice Lagoon (Sfriso et al., 2021a).

1.8 VENICE LAGOON

The Venice Lagoon (**Fig. 20**) is located in the northern Adriatic Sea and lies from north to south between the Sile and Brenta rivers.

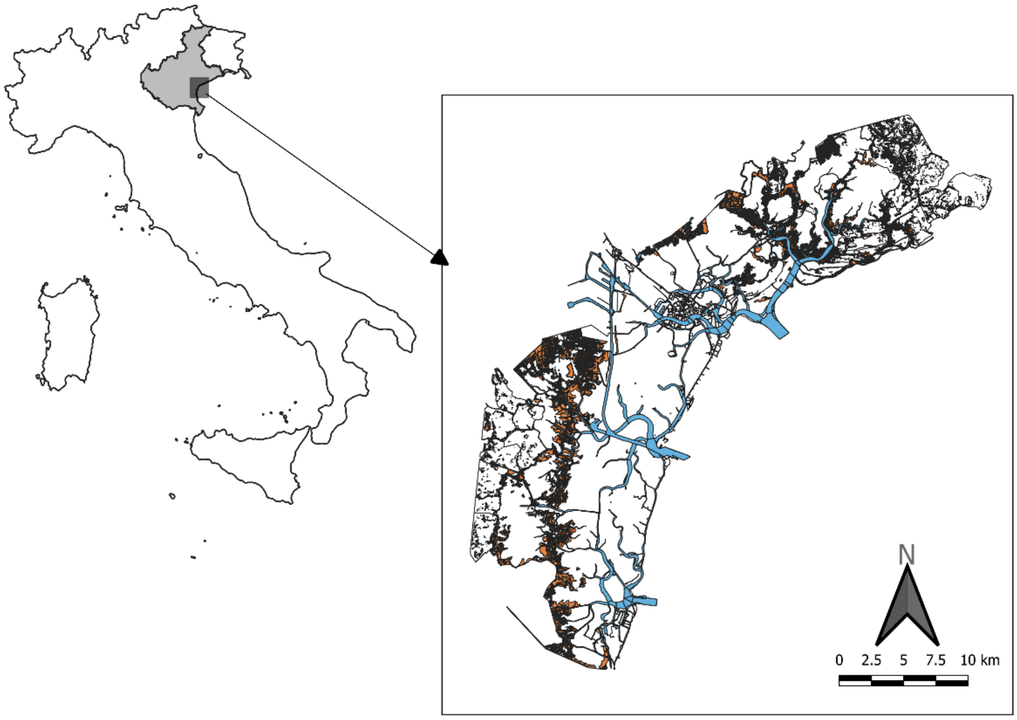


Figure 20: Venice Lagoon

Venice Lagoon, with an area of approximately 549 km^2 (10% made up of salt marshes and 5% of islands), is the largest transitional water system in the Mediterranean Sea. It is connected to the sea by a system of barrier islands formed from north to south by Cavallino, Lido, Pellestrina and Sottomarina. The barrier islands are separated from each other respectively by three inlets (Lido-San Nicolò, Malamocco and Chioggia). The latter divide the lagoon from the geographical point of view into three areas: northern, central and southern lagoons. In particular, the northern lagoon is a Site of Community Interest in the Natura 2000 network (SCI IT3250031 - Northern Venice Lagoon). Over the years, Venice Lagoon has undergone great variations in environmental parameters and in the chemical-physical characteristics of water and sediments. The main causes of these alterations are to be found in the excessive amount of nutrients in the water that has originated since the 1920s with the creation of the industrial pole of Porto Marghera and the spillage of eutrophic substances of organic and inorganic origin (Pavoni et al., 1992). Nutrient concentrations increased over the years until reaching a peak around the 1960s and 1970s (Pavoni et al., 1992), radically changing the hydrodynamics and trophic conditions. Ammonia concentrations reached values between 1000 and 3800 µM in water of the industrial area and within its canals, while phosphorous and nitrogen ones have increased by 2.4 and 30 times respectively (Giordani and Perin, 1974; Perin, 1975; Zucchetta, 1983; Cossu and De Fraja Frangipane, 1985; Sfriso et al., 1990). The seagrasses, in particular the species *Z. marina*, *Z. noltei* and *C. nodosa*, dominated the lagoon before 1960s, ensuring transparency and oligo-mesotrophic conditions. However, hydrodynamic changes and high nutrient concentrations led to a great development of macroalgae (mostly Ulvaceae J.V. Lamouroux ex Dumortier, 1822 and Gracilariaceae Willkomm, 1854 species), replacing seagrasses as the predominant species in the central and northern lagoon until between 1979 and 1990 (Sfriso et al., 1987, 1990; Sfriso and Facca, 2007b). Nevertheless, seagrasses still represented the dominant species in the southern lagoon. At the same time, the biodiversity decreased, reaching the minimum number of species present (Sfriso, 1987; Sfriso, 2010). The high biomass combined with the absence of wind, high temperatures and stagnant water led to the degradation of a large amount of organic matter and consequent anoxic events and death of macrofauna and ichthyofauna (Sfriso et al., 1988). After 1990 the cover and production of *Ulva* L. decreased, reaching values in 1998 similar to 2003 (Sfriso et al., 2003). The reduction in macroalgae biomasses was the result of the decrease of available light due to the increased sediment resuspended by clam fishing and their mechanised harvesting (Sfriso et al., 1994; Sfriso and Marcomini, 1996), the reduction of nutrient concentrations and, finally, the grazing by herbivorous invertebrates (Sfriso and Facca, 2007b). Between the years 1990 and 2002, the internal structure of populations of seagrasses changed with a drastic decrease of *Z. noltei*. In fact, comparing the data of distribution of seagrasses in these two years, there were different patterns in the three basins:

- In the southern lagoon, the species *Z. marina*, *Z. noltei* and *C. nodosa* increased appreciably in coverage, in particular *C. nodosa* had an increase of 12.0 km^2 in 12 years (Rismondo et al., 2003);

- In the central lagoon, there were discrete increases of total seagrass coverage due to improved ecosystem conditions. In particular, *Z. marina* increased its coverage of 7.47 km^2;
- In contrast, the northern lagoon recorded the greatest losses, amounting to 6.84 km^2, with the almost total disappearance of *Z. noltei*. In fact, antithetically to the other basins, after the regression of the 1980s and 1990s there was no recovery in the early 2000s (Sfriso and Facca, 2007b). The main cause of the different behaviour of the north is the limited water exchange, due to the peculiar morphological and hydrodynamic conditions of the area.

Globally, the seagrasses became the main primary producers in the lagoon in 2007 with the decreases of macroalgae and phytoplankton (Sfriso and Facca, 2007b). The further decrease of anthropogenic impacts (eutrophication and clam harvesting) and the project Life SeResto favoured the recolonization of aquatic angiosperms with an overall increase in surface of 70% between 2003 and 2018, going from 55.9 km^2 to 94.8 km^2 (Sfriso et al., 2021b). In fact, *C. nodosa*, *Z. marina* and *Z. noltei* expanded by 37.5%, 44.6% and 191% respectively (Sfriso et al., 2021b).

1.9 PURPOSE OF THE THESIS

The PhD thesis is part of this context and aims to carry out an update of primary production values after almost 20 years since the last ones available in bibliography (2003). The thesis also fits within the Corila Venezia 2021 scientific research program which intends to monitor the testing phase of the tidal regulation project known as MOSE (MOdulo Sperimentale Eletttromeccanico or Experimental Electromechanical Module). MOSE is a system of mobile gates installed at the three inlets (Lido, Malamocco and Chioggia) that are able to isolate the Venice Lagoon from the Adriatic Sea during exceptional high tide events. Thereby, the Venice Lagoon is now a regulated lagoon with numerous potential impacts on lagoon hydrodynamic circulation, on the physical-chemical characteristics of water, on tidal regimes and on lagoon communities and ecosystems.

The thesis is therefore structured in four parts, each one aimed at obtaining as complete a picture as possible of the primary production of seagrasses and their communities and their contribution to CO_2 capture and carbon sequestration in Venice Lagoon.

- Two annual sampling campaigns on a monthly basis were carried out in 2019 and 2020/2021 in order to update Net Primary Production (NPP) and to assess possible impacts to seagrass communities from the MOSE project. The net primary productions of the three most widespread seagrass species in the Venice Lagoon (*C. nodosa*, *Z. marina*, and *Z. noltei*) were therefore studied and the biomasses and monthly growth rates of each species were determined at 4 stations. This allowed the NPP determination of each species which, combined with the mapping carried out in 2018 and 2021, allowed to estimate the contributions to the net primary production in the lagoon by the different species of seagrasses;
- Biomasses collected in the 2019 sampling campaign have been analysed to calculate nutrient and carbon concentrations in order to obtain an estimation of carbon stock and total phosphorous and nitrogen contents;
- One annual sampling campaign on a monthly basis was carried out in 2021/2022 in order to estimate the contribution of *R. cirrhosa* to the global seagrass NPP in Venice Lagoon and to update its contribution after 25 years since the last study conducted in Venice lagoon (Cagnoni, 1997);
- A total of 5 sampling campaigns was carried out in 2019/2020 and 2022 in order to estimate the inter-seasonal and daily primary production of two seagrass communities (*Z. marina* and *Z. noltei*) under the same environmental conditions in one station. These studies gave an important contribution to carbon sequestration and sink potential in Venice Lagoon by *in situ* measurements with the oxygen variation method. Benthic chambers and short-time incubation periods were used in order to make these measurements under *in situ* hydrodynamic, illumination and weather conditions. Two meadows were selected in a station characterised by the same water depth in two different but choked areas of the same lagoon canal to capture the differences between species. These studies were conducted simultaneously for both species in 2019 (August and October) and 2020 (February and May) for the determination of inter-seasonal primary production and in July 2022 for daily one.

Moreover, water and sediment samples were collected at each station and sampling campaign in order to characterise the stations in terms of the main chemical parameters. Phosphate, nitrate, nitrite, ammonium, chlorophyll-*a* and total suspended sediment concentrations and salinity were determined in water column. Dry density, fines (grain-size fraction < 63 µm), organic carbon contents were determined in the top-5 cm of sediments. Moreover, water temperature, pH and redox potential were determined in water column and sediment by means of portable instruments.

All these measurements provide an important link between photosynthesis, primary production and carbon stored at the sediment level: a very important factor when taking into account the effects of climate change, its possible repercussions on aquatic and coastal ecosystems, the importance of meadows, the ecosystem services associated with them and their conservation.

2 MATERIALS AND METHODS

2.1 DESCRIPTION OF STUDY SPECIES

2.1.1 *ZOSTERA MARINA* LINNAEUS, 1753

Eelgrass *Z. marina* (**Fig. 21**) belongs to the Zosteraceae family and is the most widely distributed seagrass species, from temperate water up to northern Arctic regions from +2 m to -12 m mean sea level (MSL) (den Hartog, 1970; Short et al., 1993; Borum and Greve, 2004; Jarvis et al., 2012; Olesen et al., 2015). The rhizomes, whose colour varies from green on the surface to yellowish, present spaced nodes and internodes (**Fig. 21**).

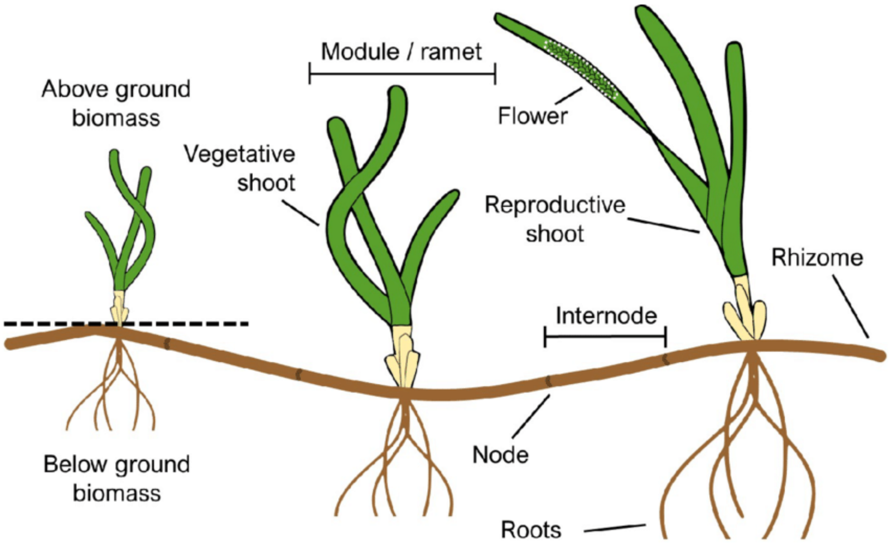


Figure 21: Key morphological structures of *Z. marina* (courtesy of Howarth et al. (2021))

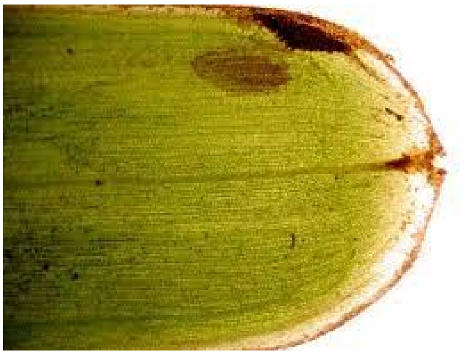


Figure 22: Image of leaf of *Z. marina* and the cavity in the middle (courtesy of lifeseresto.eu)

The rhizomes penetrate inside the sediments to a depth of 5-10 cm, thus making them easily uprooted. Shoots of variable number from 2 to 7 leaves 6-7 mm wide, up to 100-120 cm long and slightly curved are emitted from the nodes. Distinctive features of the species are the rounded leaf apices and the central depression formed by the central rib (**Fig. 22**). This central rib together with the other two more evident, approximately equidistant from each other, constitutes the areas where the phloem and xylem tubes pass. The leaves present reddish-brown tannic cells as defence against grazing by herbivorous invertebrates and internally have aeriform voids that allow erect posture to be maintained. Flowering occurs in the spring period and the flowers are arranged in spikes and are small-sized and green. Along the leaf axis, male and female flowers are arranged alternately, so that after each female flower there are two male flowers for a total of 15 female and 30 male flowers (**Fig. 23**). The fruits are dry and smooth, between 3 and 5 mm in size and ovoid-ellipsoid in shape. *Z. marina* colonises environments characterised by brackish water and shallow lagoon bottoms. This makes *Z. marina* the most widespread species in terms of coverage in the lagoon of Venice with 37.6 km^2 in 2018 (Sfriso et al., 2021b) which increased to 49 km^2 in 2021 (Sfriso, 2022).

Figure 23: Flowering and non-flowering shoots of *Z. marina* and seeds (courtesy of Erftemeijer and van Katwijk (2010))

2.1.2 *ZOSTERA NOLTEI* HORNEMANN, 1832

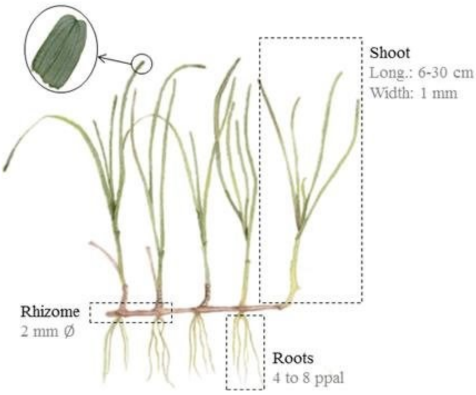


Figure 24: Schematic representation of *Z. noltei* species (courtesy of Valle (2014))

Z. noltei belongs to the family of Zosteraceae and is distributed from the southern coasts of Norway to the Mediterranean Sea (Borum and Greve, 2004) in confined environments, in mudflats and at the margins of salt marshes. It prefers environments characterised by fine-grained, loosely compact substrates (predominantly silty). The plants of *Z. noltei* are similar to *Z. marina* but smaller in size (**Fig. 24**). The rhizomes are pale or pinkish (**Fig. 24**), do not go deeper than 5 cm in the sediment and are therefore easy to uproot. The nodes and internodes are variously spaced and do not have leaf scars. The leaves are ribbon-shaped, grouped between 2 and 5, 0.7-1.5 mm wide and 10-20-(40) cm long (Sfriso, 2010). The bifid leaf apices present a central depression giving rise to a large bundle (**Fig. 24**). The three major veins constitute the areas where the phloem and xylem tubes pass through. *Z. noltei* has a greater number of reddish-brown tannic cells than *Z. marina*. Flowering of the plant occurs in May and August and the flowers, varying in number from 3 to 12, are united in a linear spadix. The male flowers are almost double the number of the female ones. Male flowers are reduced to unilocular anthers, while the female ones to a sessile, bifid ovary without a stigma. The fruits instead are flattened ellipsoidal and measure approx. 2 mm (Sfriso, 2010). *Z. noltei* can be found in monospecific populations or in association with *R. cirrhosa* or *Z. marina*. It prefers the lower mesolittoral but could also be found in the infralittoral in the absence of competition with other species. In Venice lagoon it occurs often sympatric with *Z. marina* in saltmarsh areas (upper meso-littoral/upper infra-littoral) characterized by fine sediment for a total cover area of about 11.8 (Sfriso et al., 2021b) in 2018 and 25.7 in 2021 (Sfriso, 2022).

2.1.3 *CYMODOCEEA NODOSA* (UCRIA) ASCHERSON

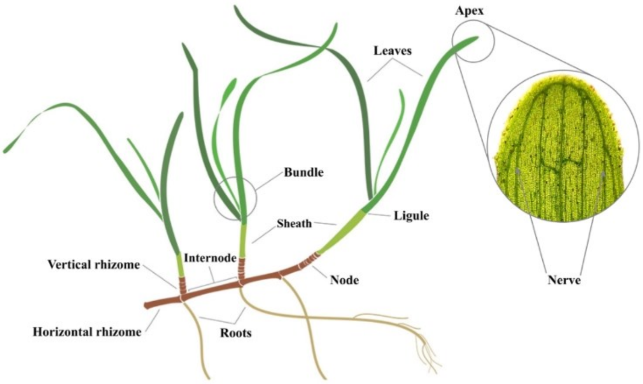


Figure 25: Schematic representation of *C. nodosa* (courtesy of Gutiérrez (2019))

C. nodosa (**Fig. 25**) belongs to the Cymodoceae family and is widely distributed along the coasts of the Mediterranean Sea (Borum and Greve, 2004), reaching a height up to 150 cm and colonising from shallow subtidal areas to very deep waters up to 60 m (Borum and Greve, 2004). It can be found in environments characterised by high salinity and mostly coarse sediment (sandy sediment) (Sfriso, 2010). Being a plant of sub-tropical origin, in the Venice Lagoon it reaches its maximum in terms of density and coverage in June and July. On the contrary, in the winter period it loses its leaves, remaining only with the rhizome below the sediment. The rhizomes are long horizontally and short vertically and take on the characteristic reddish-pink colour. At the nodes there are large solitary adventitious roots and very closely spaced annular scars. *C. nodosa* is the most suitable species for consolidating sediments as it forms a dense and intricate network capable of reach a depth of up to 30 cm (Sfriso, 2010). Sprouts are emitted between May and November at the rhizome nodes in variable numbers of 2-4 leaves about 3 mm wide and equipped with a 3-7 cm long sheath (Sfriso, 2010). Inward-facing hooked denticles which contain reddish-brown cells rich in tannins are present on the sides of the leaf, while the apex is rounded and without central depression. The leaves present a characteristic structure consisting of 7 vascular bundles of equal thickness where the phloem and xylem tubes pass through (**Fig. 25**). In the Venice lagoon, the reproduction of this species occurs almost exclusively asexually, so flowering is very rare. In Venice Lagoon, *C. nodosa* covered about 32.4 km^2 in 2018 (Sfriso et al., 2021b) and 32.1 km^2 in 2021 (Sfriso, 2022).

2.1.4 *RUPPIA CIRRHOSA* (PETAGNA) GRANDE, 1918

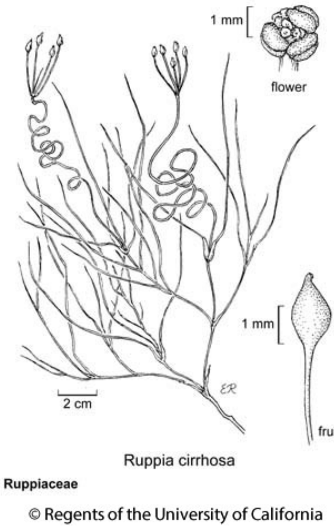


Figure 26: Schematic representation of *R. cirrhosa* (courtesy of ucjeps.berkeley.edu)

R. cirrhosa is a plant belonging to the Ruppiaceae family and is distributed in most countries bordering the Mediterranean Sea, reaching up to 45 cm in height (Mannino et al., 2015). It is an annual/perennial species colonising confined environments characterised by a wide range of salinity (15-60 psu), light and temperature (mainly between 5 and 30°C) conditions (Mannino et al., 2015) and by muddy sediments in which the rhizomes form hypogeal compartments that are easy to eradicate (**Fig. 26**). The rhizomes, whose diameter varies between 0.8 and 1.2 mm, are provided with many nodes and internodes yellowish in colour (Sfriso, 2010). The herbaceous stems carry packages of 3-5 leaves with a length between 15 and 17 cm long and between 0.8 and 1.0 mm wide that gradually taper to 0.5-0.6 mm at the apex (Sfriso, 2010). Brownish-red tannic cells are present along the apical part, stems, peduncles, flower stalks and basal sheaths. The leaves are regular, have a single central rib central rib and are serrated with numerous apical denticles with 2-3 prominent cells (**Fig. 26**). *R. cirrhosa* reproduces asexually with the formation of horizontal rhizomes with monopodial branching (Mannino et al., 2015). After some time, growth turns to vertical and, as soon as flowering begins, branching becomes sympodial with flower and fruit more abundant in small water bodies due to the limited turbulence (Mannino et al., 2015). *R. cirrhosa* has the lowest cover area in Venice Lagoon (6.03 km^2 in 2018 (Sfriso et al., 2021b) and 10.3 km^2 in 2021 (Sfriso, 2022), although in 2003 was not present in the lagoon open to the tidal expansion (Sfriso et al., 2021b).

2.2 SEAGRASS GROWTH AND NET PRIMARY PRODUCTION

Four stations (**Fig. 27**) were selected due to the presence of dense and stable monospecific meadows, each characterises by the presence of different species:

- *Z. marina* present at Ca' Roman (CR) station;
- *Z. noltei* present at Petta di Bò (PB) station;
- and *C. nodosa* present at San Nicolò (SN) and Santa Maria del Mare (SMM) stations.

Tab. 1 reports the coordinates of each station (according to coordinate system Monte Mario/Italy Zone 2 – Datum: Roma 40 – Projection: Gauss-Boaga – EPSG:3004):

Table 1: Coordinates of the 4 stations (EPSG:3004)

Stazioni	Latitude	Longitude
Ca' Roman (CR)	45° 15' 155" N	12° 17' 340" E
Petta di Bò (PB)	45° 16.165' N	12° 15.032' E
San Nicolò (SN)	45° 26' 3.50" N	12° 23' 17.30" E
Santa Maria del Mare (SMM)	45° 19.485' N	12° 18.446' E

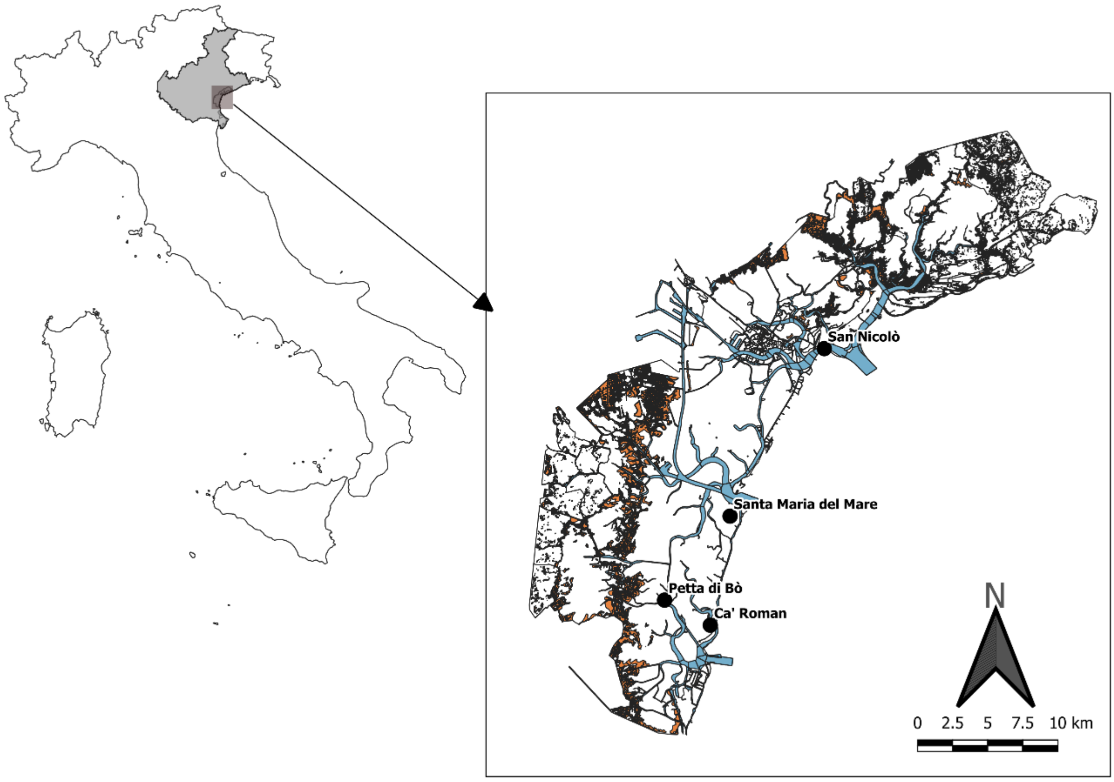


Figure 27: Locations of the 4 stations where the growth rates of the three seagrass species were studied

Two annual sampling campaigns were carried out on a monthly basis between January and December 2019 and between November 2020 and October 2021. Monthly sampling campaigns were carried out at each station for the determination of fresh weight of leaves, rhizomes, roots and dead parts by sampling at least 6 sub-samples of known area (20x25 cm, 0.05 m^2) (Sfriso and Ghetti, 1998; Short and Duarte, 2001). Biomasses were then sieved through a 3 mm mesh sieve in order to remove sediment, placed in polyethylene bags and transported to the laboratory. Here, samples were washed in tap water and carefully scraped to remove salts, epiphytes and sediment. Leaves, rhizomes, roots and dead parts (composed by dead leaves and rhizomes mixed together) were separated and weighted for each sod (precision: 0.01 g) after quickly drying with blotting paper. The number of shoots, leaves and shoot length was determined (precision: 0.1 cm). All the samples were frozen and lyophilised to calculate the dry weight (Sfriso and Ghetti, 1998). Leaf growth rates were assessed by marking the apical leaf sheath (“leaf-marking technique”) of at least 20 leaf bundles (Sfriso and Ghetti, 1998; Short and Duarte, 2001) with a hole, measuring the growth of each leaf every 15 days. The annual production (g ftw m^{-2} y^{-1}) for the leaves were estimated by means of the formula (Sfriso and Ghetti, 1998):

$$Leaf\ production = Leaf\ number \times Leaf\ weight \times \frac{365}{Mean\ leaf\ age}$$

Rhizome growth was instead assessed as the positive changes in monthly biomass in one year.

2.3 SEAGRASS NUTRIENT AND CARBON CONCENTRATIONS

Lyophilised samples were grounded and homogenised for total carbon, phosphorous and nitrogen contents. Carbon and nitrogen were obtained by means of Elemental Analyzer (vario MICRO Tube, Elementar Analysensysteme GmbH) in triplicate (coefficient of variation (CV) $\leq$5%). Phosphorous was determined colorimetrically after Teflon bomb digestion by a HNO_3 – $HClO_4$ mixture according to Kornfeldt (1982) and Sfriso and Marcomini (2003). The colorimetric quantification was performed following the procedures reported by Strickland and Parsons (1972) (coefficient of variation (CV) $\leq$5%).

2.4 *RUPPIA CIRRHOSA* GROWTH AND NET PRIMARY PRODUCTION

The study (**Fig. 28**) was conducted in a station at locality Lio Piccolo (Venice) in the northern part of Venice Lagoon. The station was selected due to the presence of dense and stable monospecific meadow of *R. cirrhosa* (EPSG:3004, coordinates: 45° 29.198’ N 12°28.977’ E).

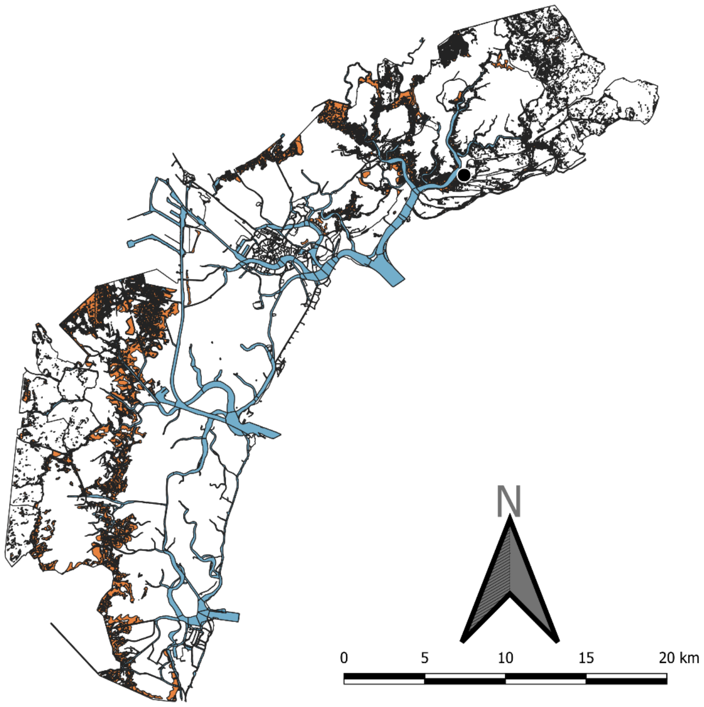


Figure 28: Location of the station in locality Lio Piccolo (Venice) where the growth rate of *R. cirrhosa* was studied

All measurements were carried out following the same methods explained in the section 2.2 on materials and methods, with the exception that leaf growth was assessed as the positive changes in monthly biomass due to the small size of the plant.

2.5 NET COMMUNITY PRODUCTION OF *ZOSTERA MARINA* AND *ZOSTERA NOLTEI*

The study on inter-seasonal net community production was conducted in a station at Cavallino-Treporti locality, in the northern part of the Venice Lagoon (EPSG:3004, coordinates: 45°28.12031' N, 12°26.767865' E), in four different seasonal sampling campaigns: August (summer) and October (autumn) 2019 and February (winter) and June (spring) 2020 (**Fig. 29**). The study on daily net community production was instead conducted in one sampling campaign in July 2022.

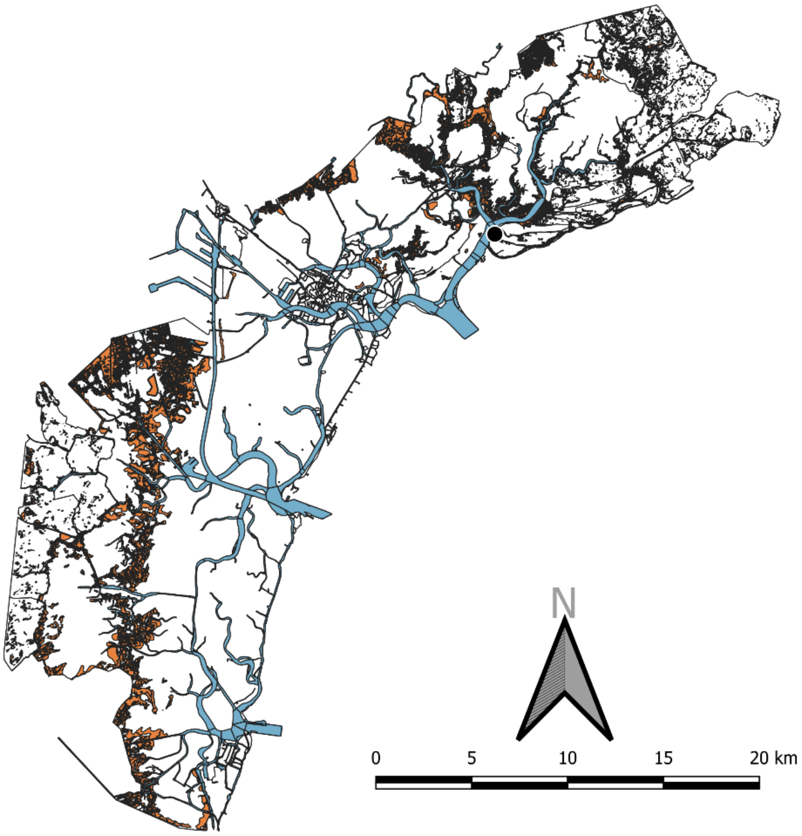


Figure 29: Study site for inter-seasonal and daily net community production

The station was selected due to its peculiar characteristics of water transparency, sandy sediment, shallow water (about 1 meter depth) and the presence of natural and dense meadows of both *Z. noltei* and *Z. marina*. Net Community Production (NCP) was derived from differences in oxygen concentrations of a community section (0.0314 m^2) enclosed within benthic incubation chambers, evaluated using Winkler method. The benthic chambers design was modified from the one described in Barrón et al. (2006). Each chamber consisted in a cylindrical metallic structure with holes on both sides (20 cm inner diameter, 25 cm height), inserted into the sediment usually for 10 cm to stabilize the chamber (**Fig. 30**). A gas-tight polyethylene plastic bag (60 cm long), with one sampling port to withdraw water samples by a syringe, was fitted into the metallic structure. The plastic bags allowed propagation of external turbulence, simulating natural conditions of the station like water flow and waves (Barrón and Duarte, 2009). A set of 9 incubation chambers were displayed: 3 in *Z. marina*, 3 in *Z.*

Figure 30: Example of benthic chamber structure

noltei meadows and 3 in bare sediment (called “Blank”). During first sampling campaign, we conducted a preliminary study on the effect of benthic chamber insertion on sediment resuspension. We then deployed one benthic chamber in seagrass meadows and monitored every 15 min the concentration of Total Suspended Sediment (TSS) over 2.5-hour incubation period filtering each time 250 ml through a 0.45 µm glass fiber filter (Whatman GF-F) in double replicates. We concluded that waiting 30 min before starting sampling procedures was better to let the TSS return to the initial value of the station (**Table 2**).

Table 2: Total Suspended Sediment variations to evaluate waiting time for fist water sampling inside benthic chamber

Time	TSS (mg l^{-1})
15 minutes	46.7
30 minutes	26.7
45 minutes	26.5
1 hour	26.3
1.25 hour	26.6
1.5 hour	26.8
1.75 hour	26.5
2 hours	27.3
2.25 hours	27
2.5 hours	26.6

Incubations were conducted along the day at twelve o’clock (solar noon, local time GMT+1) of sunny days to avoid problems with water transparency and photosynthesis activities. Water samples were then collected after 30 minutes and after 2.5 hours (for a total incubation period of 2 hours) with 100 mL plastic syringes through the sampling port installed in each bag. Once collected, syringes were emptied in dark glass bottles with beak caps, whose volumes were previously calculated in laboratory, avoiding bubbling and bobble formation. The volume of each benthic chamber was estimated by injecting 5.0 mL of KH_2PO_4 0.50 M at the end of the experiment, allowing 5 minutes for mixing and determining concentration of the dilution. The water samples were kept frozen until spectrophotometric determination of phosphorous concentration, following Strickland and Parsons (1972) and Italian Environmental Ministry (ICRAM-ANPA, 2001) procedures.

Net Community Production (NCP) rates were calculated by the difference between final and initial oxygen concentrations, normalized by the incubation time, the volume of water and the projected community area, according to the formula:

$$NCP = \frac{([Ox]final - [Ox]initial) \times V}{A \times T}$$

where [Ox] is the oxygen concentration (mmol), V is the volume (L) incubated in the chamber, A is the area enclosed in the chamber (0.0314 m^2), and T is the incubation time (2 hours). NCP values are expressed as mean±sd of three replicates (three benthic chambers). At the end of the experiment all seagrass biomass enclosed in each chamber was removed from sediment, stored in plastic bags, kept on the fridge until separation and weighted in laboratory to calculate biomasses of rhizome and leaves per area unit. Samples were then freeze-dried, weighted (dry weight (dtw) to fresh weight (ftw) ratios), grounded and homogenised for carbon concentration in rhizomes and leaves.

For the determination of daily net community production, a set of 12 incubation chambers were displayed: 6 in *Z. marina*, 6 in *Z. noltei* meadows, six of which (3 for each meadow) fitted with black plastic bags to simulate respiration and the remaining six (3 for each meadow) with transparent bags like the study on inter-seasonal primary production. Water samples were then collected after 30 minutes and after 2.5 hours (for a total incubation period of 2 hours), repeating the procedure in order to cover the whole photoperiod for transparent benthic chambers and to obtain two measurements of respiration for black benthic chambers at the end of photoperiod. The same procedures for calculation and analysis were followed as mentioned above. All community primary production data are coupled with measurements of Photosynthetically Active Radiation (PAR) at seabed depth by means of portable photometer (LI-COR, LI-250A, accuracy ±0.6%) equipped with a quantum sensor (LI-COR, LI-193 Spherical underwater quantum sensor, sensitivity: 4 µA per 1,000 µmol s^{-1} m^{-2}).

2.6 CHARACTERIZATION OF THE STATIONS

Water samples for the determination of chlorophyll-*a* (Chl-*a*), salinity, Total Suspended Sediments (TSS) and nutrient concentrations (reactive phosphorous (RP) and Dissolved Inorganic Nitrogen (DIN) = sum of nitrate, nitrite and ammonium) were also taken each sampling campaign to characterize all the stations, following Strickland and Parsons (1972) and Italian Environmental Ministry (ICRAM-ANPA, 2001) procedures. Three replicates of top-5 cm sediment were sampled in each sampling campaign to calculate dry densities and granulometries (fine fraction: <63µm) (Sfriso et al., 2005). Organic carbon concentrations of top-5cm were obtained by means of Elemental Analyzer (vario MICRO Tube, Elementar

Analysensysteme GmbH) in triplicate (coefficient of variation (CV) ≤5%), following freeze-drying of the samples. Organic carbon was calculated as the difference between the values obtained pre- and post-combustion at 440°C (Loss On Ignition technique) (Schumacher, 2002). Water temperature, pH and redox potential of water column and top-5 cm sediments were determined by means of portable pH/redox instrument (pHenomenal pH1100 H, VWR, water temperature accuracy: ±0.2°C; pH accuracy: ±0.005; mV accuracy: ±0.3 mV).

Results in the text, tables and figures are expressed as mean±sd and all statistical analyses were performed using R software version 4.1.2.

3 RESULTS

3.1 BIOMASSES AND PRIMARY PRODUCTION OF AQUATIC ANGIOSPERMS

3.1.1 PHYSICAL-CHEMICAL PARAMETERS OF THE STATIONS

Mean values of physico-chemical parameters of the water column and the 5-cm top sediment layer are reported in **Tab. 3-4-5-7-7** for each station sampled in 2019 and 2020/21.

Table 3: Mean±sd values of physical-chemical parameters at Ca' Roman (*Z. marina*)

Ca' Roman	**2019**	**2020/21**
Chl-*a* (µg/l)	1.23±0.02	1.46±0.06
Salinity (psu)	27.4±0.3	28.7±0.3
TSS (mg/l)	46.3±3.7	44.7±0.3
pH water	8.20±0.05	8.36±0.01
Water Eh (mV)	271±3	276±3
Water temperature (°C)	16.7±0.2	16.5±0.1
Reactive Phosphorous (µM)	0.29±0.55	0.15±0.04
DIN (µM)	6.92±14.1	5.60±3.42
Sediment pH	7.42±0.03	7.33±0.04
Sediment Eh (mV)	-81±9	-99±3
Sediment Dry Density (g cm^{-3})	0.92±0.06	0.96±0.04
Sediment Organic Carbon (OC) (%)	1.55±0.05	1.40±0.06
Sediment fine fraction (<63µm) (%)	50.4±1.6	45.3±2.4

Table 4: Mean±sd values of physical-chemical parameters at Petta di Bò *(Z. noltei)*

Petta di Bò	**2019**	**2020/21**
Chl-*a* (µg/l)	1.44±0.01	1.29±0.40
Salinity (psu)	29.3±0.3	29.9±0.1
TSS (mg/l)	73.6±5.4	34.5±0.5
pH water	8.19±0.40	8.29±0.01
Water Eh (mV)	292±3	295±3
Water temperature (°C)	17.7±0.2	15.6±0.1
Reactive Phosphorous (µM)	0.95±1.27	0.21±0.13
DIN (µM)	4.82±2.69	8.42±1.94
Sediment pH	7.41±0.04	7.51±0.02
Sediment Eh (mV)	33±2	-5±1
Sediment Dry Density (g cm^{-3})	0.99±0.03	1.15±0.05
Sediment Organic Carbon (OC) (%)	0.87±0.03	0.80±0.02
Sediment fine fraction (<63µm) (%)	16.8±1.2	14.6±1.4

Table 5: Mean±sd values of physical-chemical parameters at Santa Maria del Mare (*C. nodosa*)

Santa Maria del Mare	**2019**	**2020/21**
Chl-*a* (µg/l)	1.30±0.02	1.32±0.05
Salinity (psu)	26.3±0.3	29.4±0.3
TSS (mg/l)	47.7±2.3	48.3±0.7
pH water	8.29±0.20	8.50±0.01
Water Eh (mV)	289±2	271±4
Water temperature (°C)	17.2±0.2	17.8±0.1
Reactive Phosphorous (µM)	0.35±0.46	0.35±0.12
DIN (µM)	3.34±2.04	5.53±1.54
Sediment pH	7.41±0.04	7.36±0.04
Sediment Eh (mV)	-76±4	-73±2
Sediment Dry Density (g cm^{-3})	1.13±0.07	1.13±0.04
Sediment Organic Carbon (OC) (%)	1.26±0.04	1.06±0.04
Sediment fine fraction (<63µm) (%)	48.1±1.9	41.7±2.3

Table 6: Mean±sd values of physical-chemical parameters at San Nicolò (*C. nodosa*)

San Nicolò	**2019**	**2020/21**
Chl-*a* (µg/l)	1.98±0.02	1.93±0.70
Salinity (psu)	32.6±0.4	32.4±0.2

TSS (mg/l)	70.6±4.4	49.9±0.5
pH water	8.20±0.40	8.28±0.01
Water Eh (mV)	276±2	306±3
Water temperature (°C)	17.1±0.2	18.2±0.1
Reactive Phosphorous (μM)	0.42±0.54	0.15±0.11
DIN (μM)	6.26±5.08	7.51±3.22
Sediment pH	7.62±0.06	7.51±0.02
Sediment Eh (mV)	188±10	124±2
Sediment Dry Density (g cm^{-3})	1.34±0.06	1.35±0.05
Sediment Organic Carbon (OC) (%)	0.56±0.04	0.56±0.03
Sediment fine fraction (<63μm) (%)	2.55±1.05	5.00±0.55

Table 7: Mean±sd values of physical-chemical parameters at Lio Piccolo (*R. cirrhosa*)

Lio Piccolo	**2021/22**
Chl-*a* (μg/l)	2.69±1.63
Salinity (psu)	35.6±12.7
TSS (mg/l)	37.8±41.8
pH water	8.42±0.45
Water Eh (mV)	227.3±115.2
Water temperature (°C)	17.5±8.2
Reactive Phosphorous (μM)	0.21±0.15
DIN (μM)	10.9±24.2
Sediment pH	7.63±0.36
Sediment Eh (mV)	-204±48
Sediment Dry Density (g cm^{-3})	0.78±0.15
Sediment fine fraction (<63μm) (%)	81.8±4.5

Chl-*a* values were extremely low at all stations both in 2019 and 2020/21 with values more than 50% higher at Lio Piccolo. Salinity was higher at San Nicolò and Lio Piccolo. The former is close to the mouth of Lido, therefore is more affected by the influx of salty water from the Adriatic Sea. The latter is located in a choked area characterised by shallow waters which are subjected to strong evaporation, especially in the summer season. Mean values of RP at Petta di Bò in 2019 were almost three times higher than those of the stations close to the lagoon inlets and higher than the imperative value of Ronchi Costa decree of 28 March 1998

(0.80 µM). This difference was probably due to adverse weather events that affected the lagoon in the autumn 2019 (Sfriso et al., 2021c). However, when considering the values measured between late spring and early summer the values are within the means of those measured in the lagoon mappings carried out in 2011, 2014 and 2018 (Sfriso, 2012a,b; Sfriso, 2015; Sfriso, 2018). The Ehs and the dry densities of the sediments follow the patterns of grain-size with lower values at stations characterised by finer particles, such as Lio Piccolo and vice versa in sandy areas such as San Nicolò.

3.1.2 *Z. marina* at Ca' Roman

The mean biomass of *Z. marina* monitored in 2021-21 (3500 g fwt m^{-2}) was much higher than the one measured in 2019 (2399 g fwt m^{-2}) (**Fig. 31-32**). Higher values were also found for the biomass peaks. In 2020/21 the highest value reached 5,939 g fwt m^{-2}, while in 2019 it was 4,830 g fwt m^{-2}. Furthermore, in 2020-21 two peaks were recorded, one in April and one in August. On an annual basis in 2019, the biomass of shoots (975 g fwt m^{-2}) was slightly higher than that of rhizomes (950 g fwt m^{-2}), while in 2020/21 the biomass of rhizomes was markedly higher (1,807 g fwt m^{-2}) compared to 1,452 g fwt m^{-2} of shoots. Moreover, the biomass of death parts consisting mainly of rhizomes was also very high (474 and 240 g fwt m^{-2} in 2019 and 2020/21, respectively).

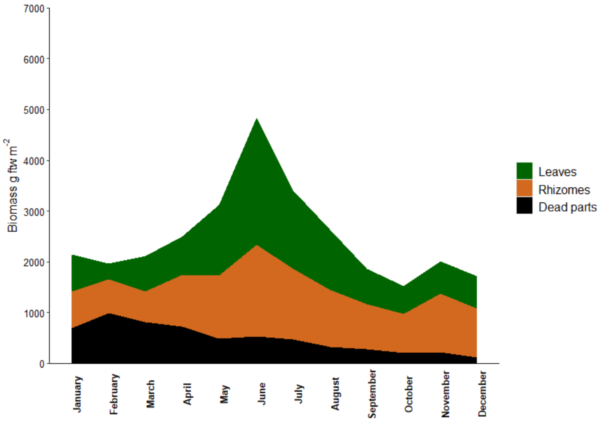


Figure 31: Biomass variation (g fwt m^{-2}) for *Z. marina* in 2019

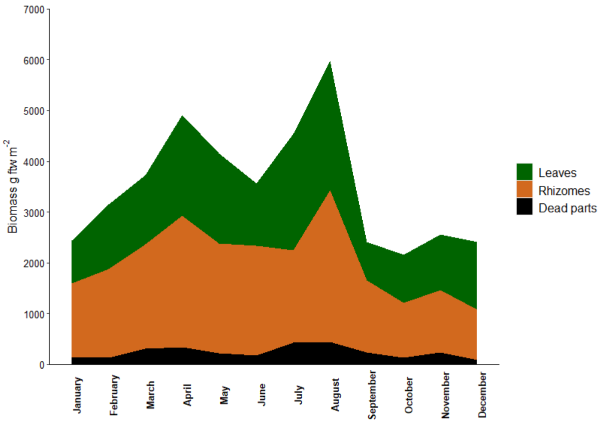


Figure 32: Biomass variation (g fwt m^{-2}) for *Z. marina* in 20210/21

Similarly, the mean number of shoots in 2020/21 was 974 shoots m^{-2} with a peak of 1,667 shoots m^{-2} in August, while in 2019 the mean value settled at 696 shoots m^{-2} with a peak of 1,327 shoots m^{-2} in June (**Fig. 33-34**).

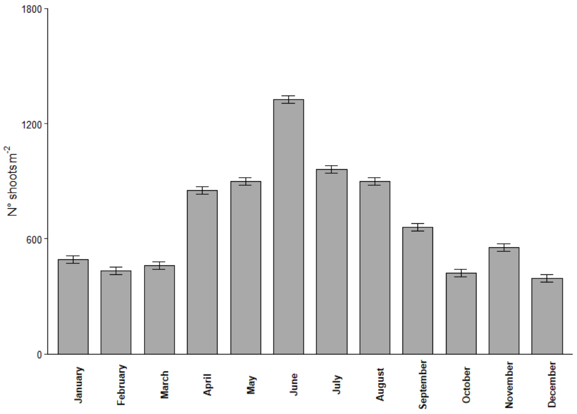


Figure 33: Number of shoots per m^2 for *Z. marina* in 2019

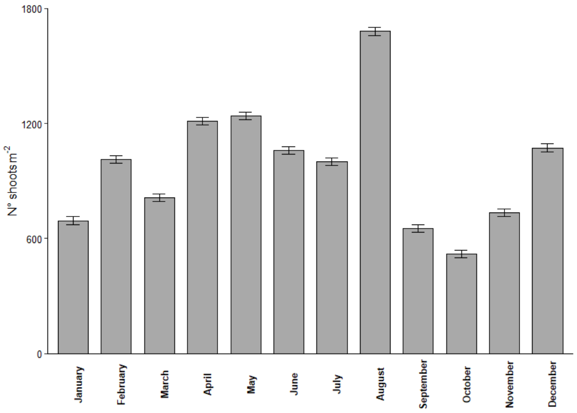


Figure 34: Number of shoots per m^2 for *Z. marina* in 2020/21

The mean length of *Z. marina* shoots in 2019 and 2020/21 were very similar with mean values of 37.7 and 39.2 cm respectively, and maximum values of 53.1 and 51.7 cm (**Fig. 35-36**).

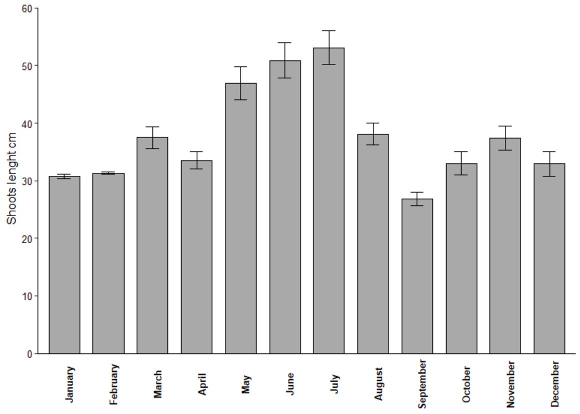


Figure 35: Shoot lengths of *Z. marina* in 2019

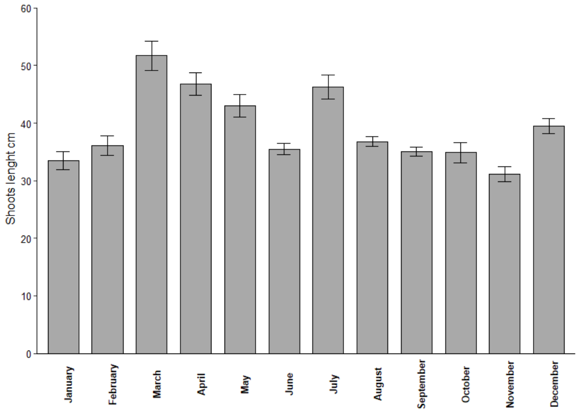


Figure 36: Shoot lengths of *Z. marina* in 2020/21

Moreover, the mean number of leaves per shoot in 2020/21 (4.16) was higher than that monitored in 2019 (3.35) as were the maximum peaks (5.17 and 4.60 leaves per shoot, respectively) that were recorded in June in both years (**Fig. 37-38**).

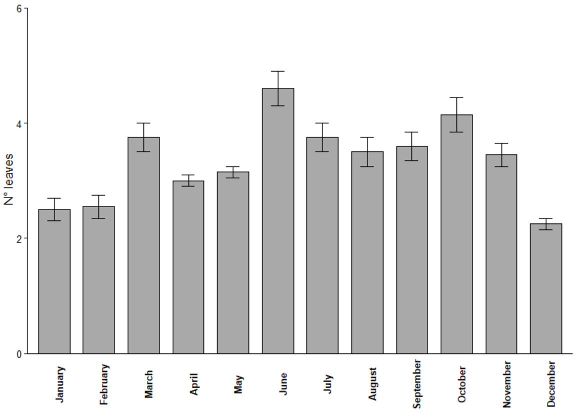


Figure 37: Number of leaves per shoot of *Z. marina* in 2019

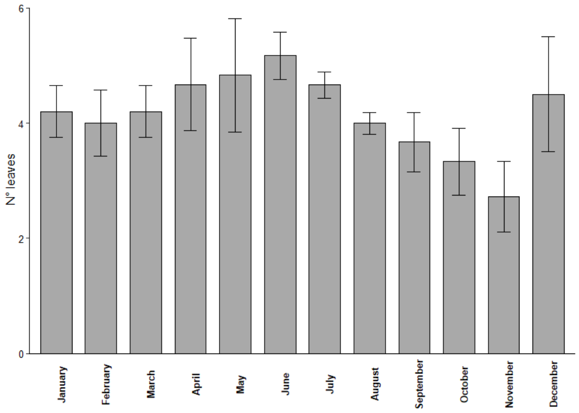


Figure 38: Number of leaves per shoot of *Z. marina* in 2020/21

The growth values of *Z. marina* reflect those of the biomasses and the variations in morphological parameters, showing higher values in 2020-21 than in 2019. This species, which grows all year round, showed the lowest values in December-January and August-September, although they were different in the two years (**Fig. 39-40**). The minimum average values were lower in 2019, with a shoot growth of 1.33 cm d^{-1} in January 2019 and 0.92 cm d^{-1} in August 2019. The maximum shoot growth was reached in May with 6.88 cm d^{-1} in 2019 and 9.27 cm d^{-1} in 2020-21. In autumn, *Z. marina* showed a second peak in accretion with a maximum value recorded in early October (3.60 cm d^{-1} in 2019 and 4.34 cm d^{-1} in 2020/21). On an annual basis, the mean growth of shoots was 2.73 cm d^{-1} in 2019 and 3.27 cm d^{-1} in 2020/21.

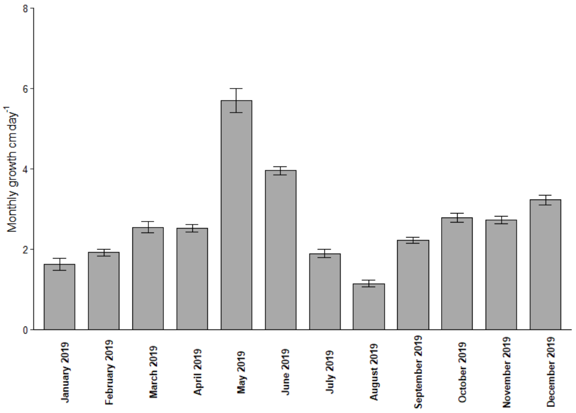


Figure 39: Monthly shoot growth (cm d^{-1}) of *Z. marina* in 2019

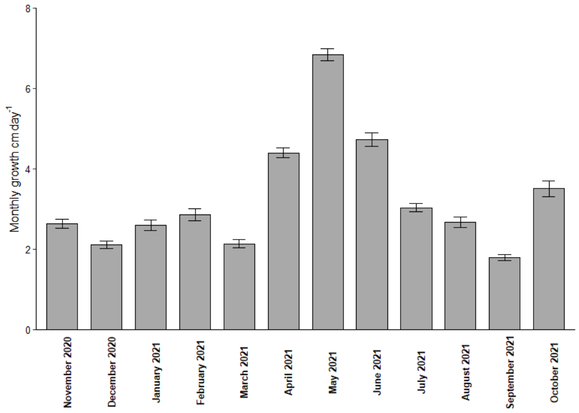


Figure 40: Monthly shoot growth (cm d^{-1}) of *Z. marina* in 2020/21

3.1.3 *Z. noltei* at Petta di Bò

Z. noltei had a similar pattern to *Z. marina* with significant differences in the two years. In 2019 the mean annual biomass was 1,991 g fwt m^{-2}, while in 2020-21 it increased to 2,610 g fwt m^{-2} (**Fig. 41-42**). The highest contribution to the total biomass was due to rhizomes with 1,392 and 1,803 g fwt m^{-2} in 2019 and 020/21, respectively. Shoots accounted for only about a third in comparison to the belowground biomass with 460 and 690 g fwt m^{-2}, respectively, while dead parts were only a negligible fraction of the total biomass varying from 139 to 117 g fwt m^{-2}.

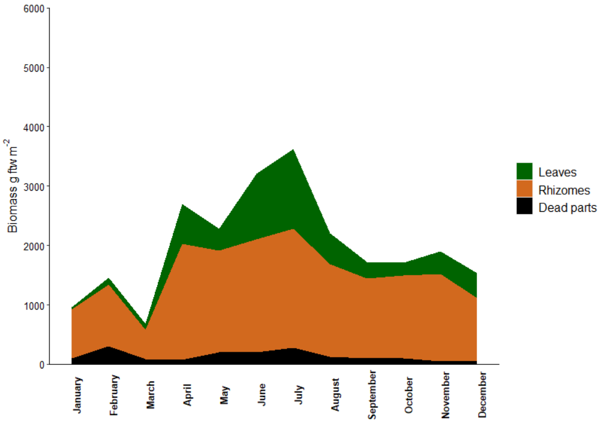


Figure 41: Biomass variation (g fwt m^{-2}) for *Z. noltei* in 2019

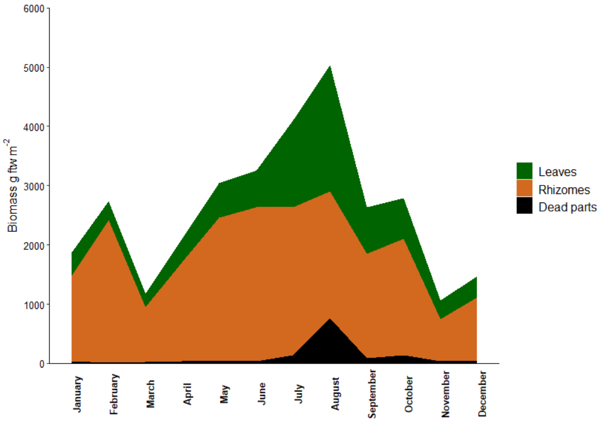


Figure 42: Biomass variation (g fwt m^{-2}) for *Z. noltei* in 2020/21

This species compensates for the smaller size with an increase in shoot number per unit area. The average annual values varied from 5,502 to 4,179 shoots m^{-2} in 2019 and 2020/21, respectively. In June 2019 and 2020/21, the maximum number of shoots varied from 13,021 to 8,990 shoots m^{-2} (**Fig. 43-44**).

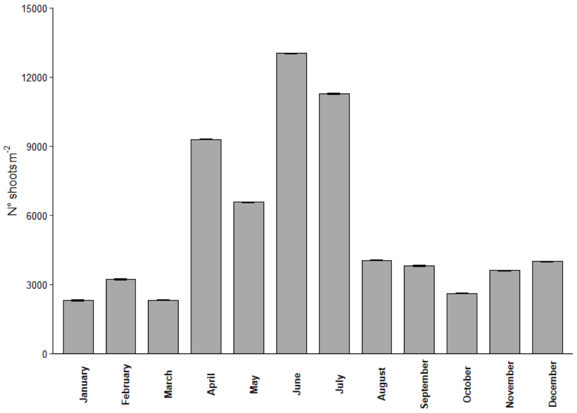


Figure 43: Number of shoots per m^2 for *Z. noltei* in 2019

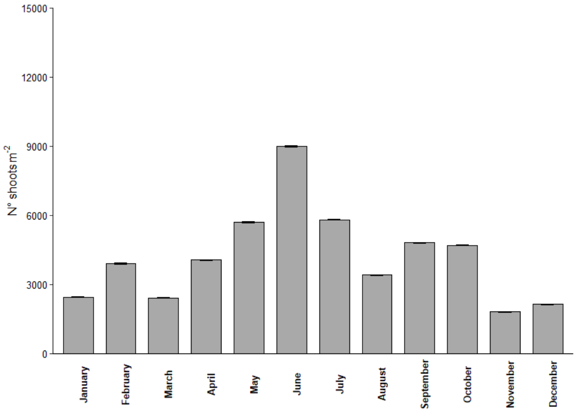


Figure 44: Number of shoots per m^2 for *Z. noltei* in 2020/21

The average length of the leaves was very similar in the two years, varying between 19.1 and 21.2 cm in 2019 and 2020/21, respectively, with maximum values in August (29.3 and 37.0 cm in 2019 and 2020/21) (**Fig. 45-46**). A second peak was observed in November 2019 (28.9 cm) and October 2021 (26.9 cm).

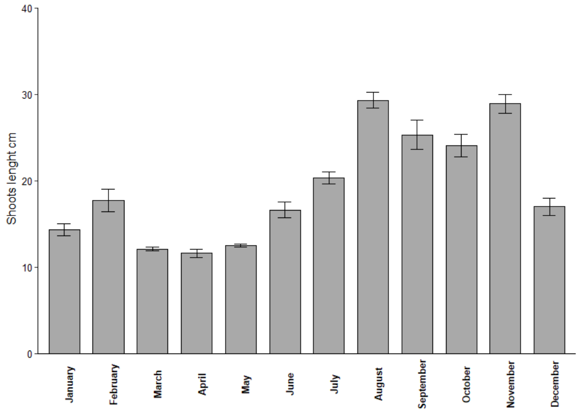


Figure 45: Shoot lengths of *Z. noltei* in 2019

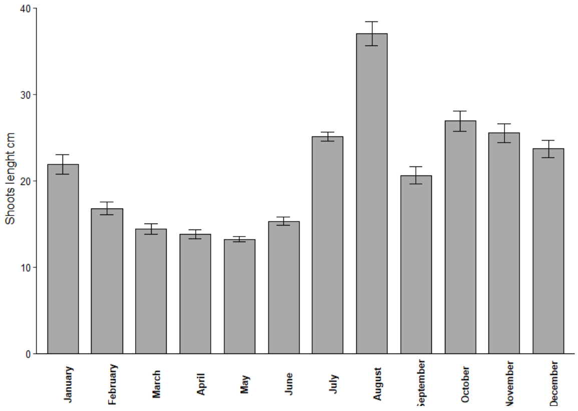


Figure 46: Shoot lengths of *Z. noltei* in 2020/21

The average number of leaves per shoot varied between 2.88 in 2019 and 3.00 in 2020/21 with a maximum of 3.35 in March 2019 and 3.86 in June 2021 (**Fig. 47-48**)

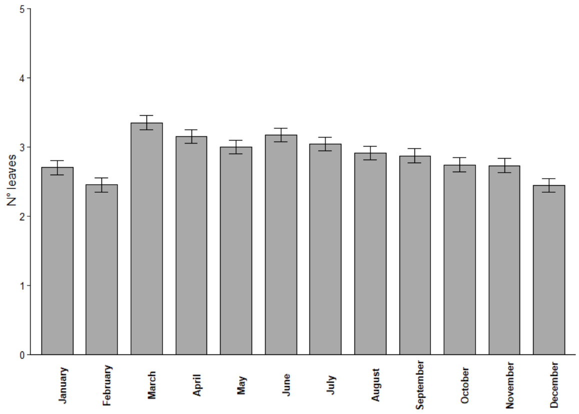


Figure 47: Number of leaves per shoot of *Z. noltei* in 2019

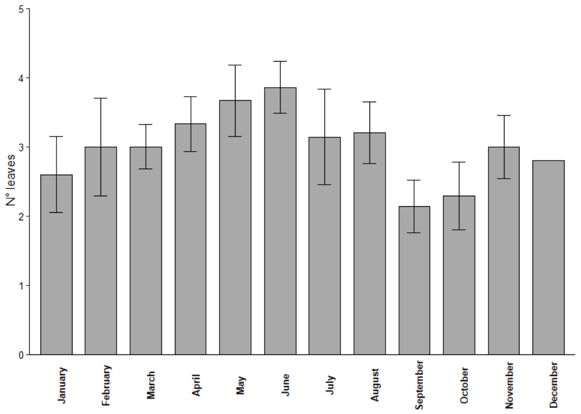


Figure 48: Number of leaves per shoot of *Z. noltei* in 2020/21

In contrast to *Z. marina*, this species showed its greatest growth in mid-summer, with maximum values varying between 1.70 and 1.81 cm d^{-1} in July and August (**Fig. 49-50**) and with a reduced but continued growth throughout the cold season. The average annual production of the individual shoots was practically the same with 0.82 and 0.81 cm d^{-1} in 2019 and 2020/21, respectively.

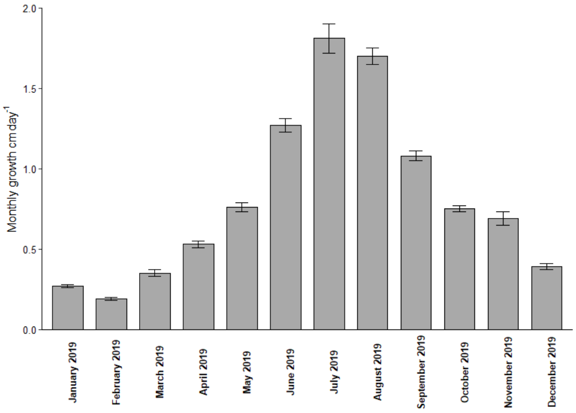


Figure 49: Monthly shoot growth (cm d^{-1}) of *Z. noltei* in 2019

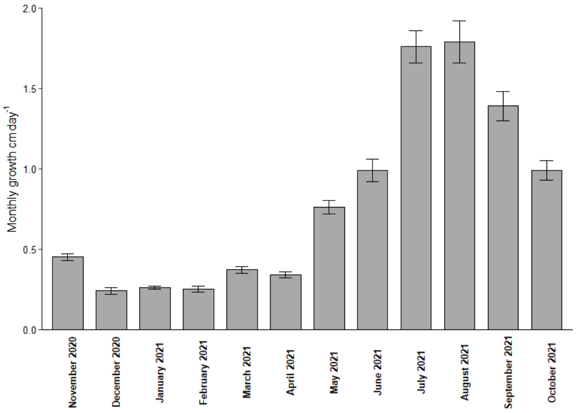


Figure 50: Monthly shoot growth (cm d^{-1}) of *Z. noltei* in 2020/21

3.1.4 *C. nodosa* at Santa Maria del Mare

The biomass of *C. nodosa* monitored at SMM in 2019 and 2020/21 is shown in **Fig. 51-52**. The mean annual value was higher in 2020/21 (3,459 g fwt m^{-2}) than in 2019 (3,095 g(fwt) m^{-2}) although the peak was more relevant in 2019 (7,067 g fwt m^{-2}) than in 2020/21 (5,497 g fwt m^{-2}). Furthermore, in 2020/21 the maximum biomass occurred in July instead of August as in 2019. On an annual basis, rhizomes constituted the majority of the biomass in both years and were absolutely dominant in the cold season when only the basal part with 1-2 dormant leaves remains. The weights of dead parts of shoots and rhizomes were very low: 143 g fwt m^{-2} in 2019 and 190 g fwt m^{-2} in 2020/21.

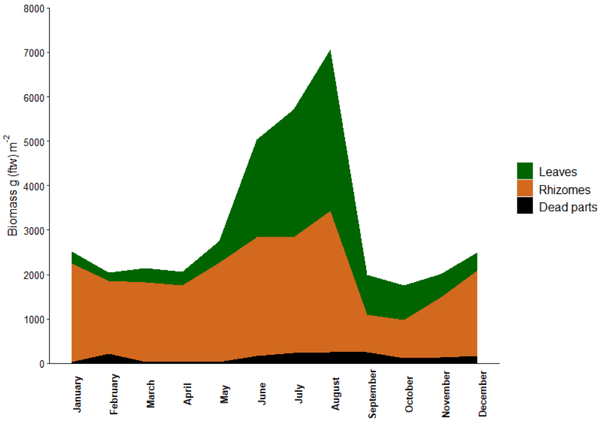


Figure 51: Biomass variation (g fwt m^{-2}) for *C. nodosa* in 2019 at Santa Maria del Mare

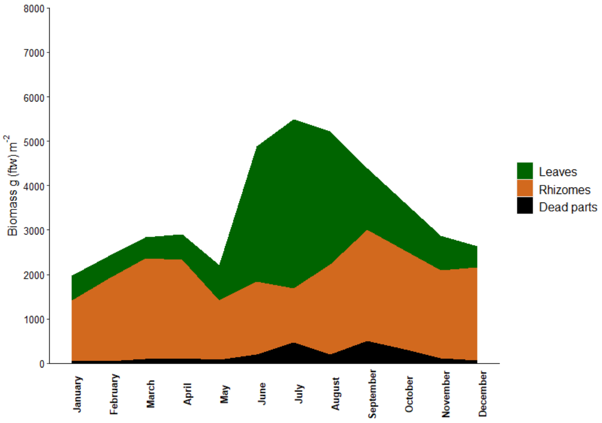


Figure 52: Biomass variation (g fwt m^{-2}) for *C. nodosa* in 2020/21 at Santa Maria del Mare

The mean number of shoots was higher in 2020/21 (1,373 shoots m^{-2}) than in 2019 (1,273 shoots m^{-2}). Similarly, the maximum mean number was recorded in July 2020/21 (3,804 shoots m^{-2}) while the peak mean value in 2019 was found in June (2,747 shoots m^{-2}) with a second peak in August (2,400 shoots m^{-2}) (**Fig. 53-54**).

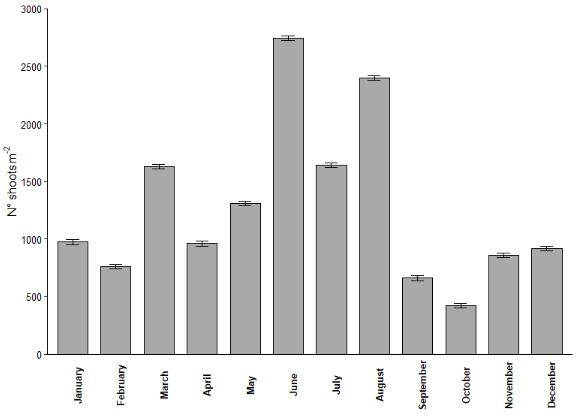


Figure 53: Number of shoots per m^2 for *C. nodosa* in 2019 at Santa Maria del Mare

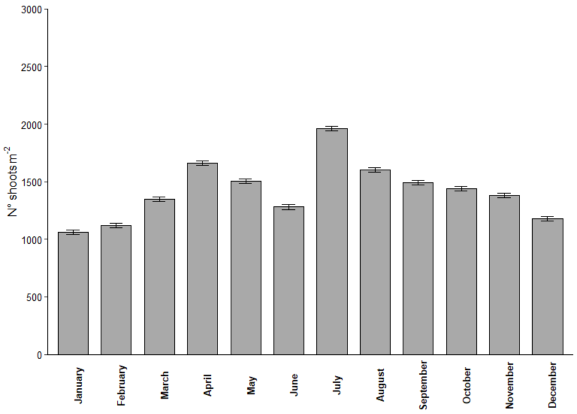


Figure 54: Number of shoots per m^2 for *C. nodosa* in 2020/21 at Santa Maria del Mare

The mean length of the leaves was slightly longer in 2019 (42.1 cm) with the maximum mean value of 86.6 cm in August (**Fig. 55-56**). In contrast, the mean length in 2020/21 was 41.3 cm while the peak value was found in July (77.7 cm).

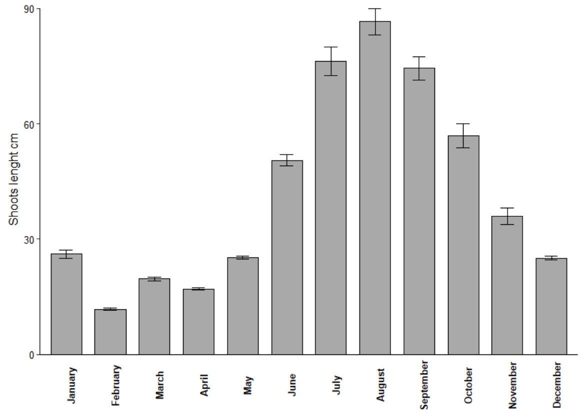


Figure 55: Shoot lengths of *C. nodosa* in 2019 at Santa Maria del Mare

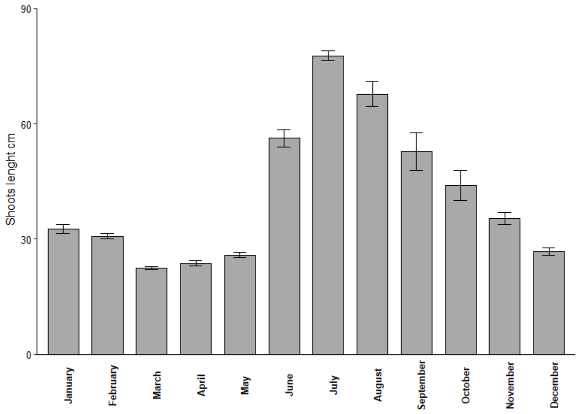


Figure 56: Shoot lengths of *C. nodosa* in 2020/21 at Santa Maria del Mare

The mean number of leaves per shoot in 2020/21 was 2.62 with a maximum average value of 3.70 leaves per shoot in July (**Fig. 57-58**). In 2019 the mean value was lower (2.45 leaves per shoot), but the maximum mean value was higher with 4.00 leaves per shoot in July. In winter shoots remained dormant with only two small leaves per shoot.

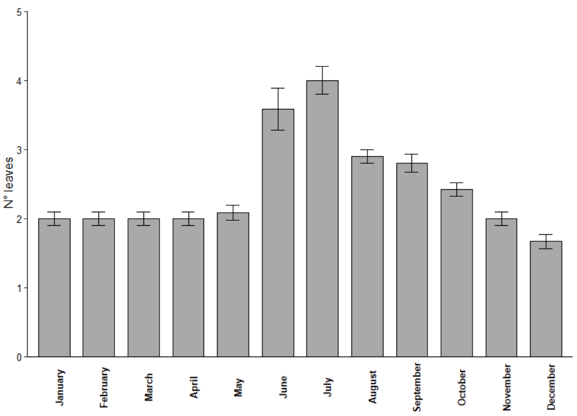


Figure 57: Number of leaves per shoot of *C. nodosa* in 2019 at Santa Maria del Mare

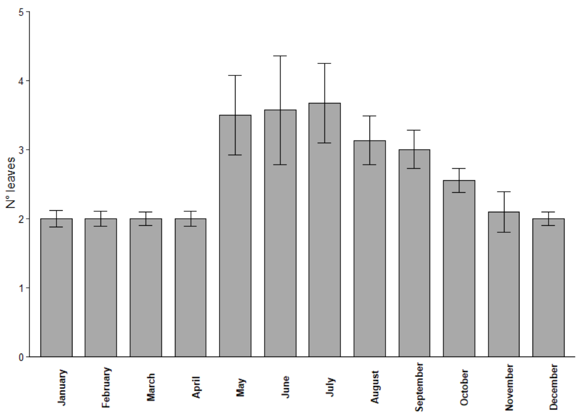


Figure 58: Number of leaves per shoot of *C. nodosa* in 2020/21 at Santa Maria del Mare

In 2020/21, the mean growth of shoots (1.63 cm d^{-1}) was higher than in 2019 (1.26 cm d^{-1}) (**Fig. 59-60**). Similarly, the average peak recorded in August 2021 (7.59 cm d^{-1}) was higher than in 2019 (5.39 cm d^{-1}). These values, calculated on a monthly basis, showed the highest mean growth in August 2021 (4.78 cm d^{-1}) and July 2019 (3.47 cm d^{-1}).

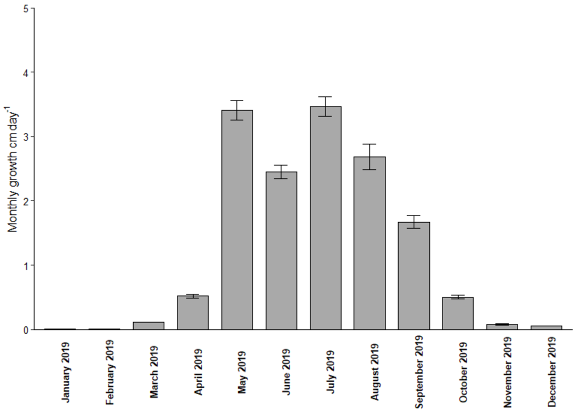


Figure 59: Monthly shoot growth (cm d^{-1}) of *C. nodosa* in 2019 at Santa Maria del Mare

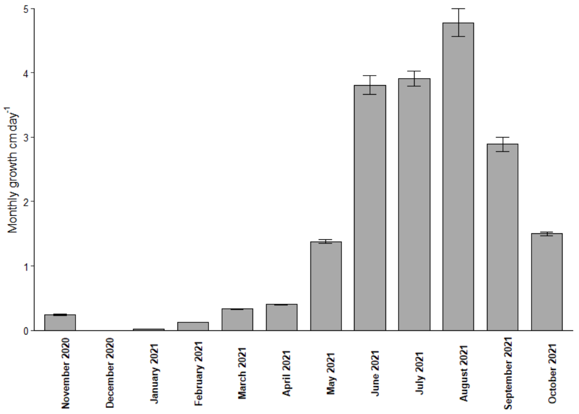


Figure 60: Monthly shoot growth (cm d^{-1}) of *C. nodosa* in 2020/21 at Santa Maria del Mare

3.1.5 *C. nodosa* at San Nicolò

The mean biomass recorded in 2020/21 (4,471 g fwt m^{-2}) was extremely higher than in 2019 (2,816 g fwt m^{-2}) (**Fig. 61-62)**. In fact, in July 2021 the mean biomass was 10,373 g fwt m^{-2}, while in 2019 it was more than halved (4,474 g fwt m^{-2}). On an annual basis, rhizomes constituted the majority of the biomass in 2019, while in 2020-21 the mean shoot biomass was similar to that of the belowground part. The weight of the dead parts of shoots and rhizomes was very low but in 2019 (123 g fwt m^{-2}) it was almost half than in 2020/21 (307 g fwt m^{-2}).

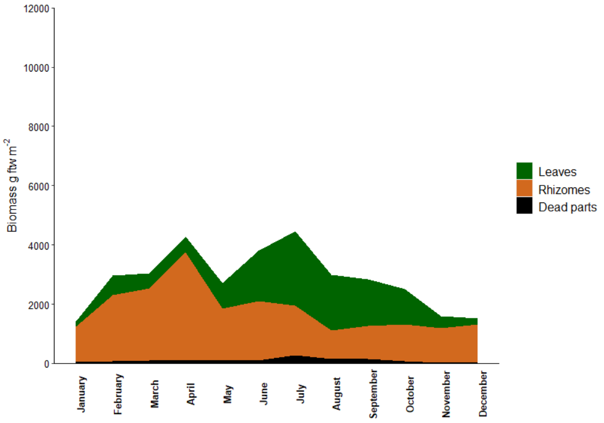


Figure 61: Biomass variation (g fwt m^{-2}) for *C. nodosa* in 2019 at San Nicolò

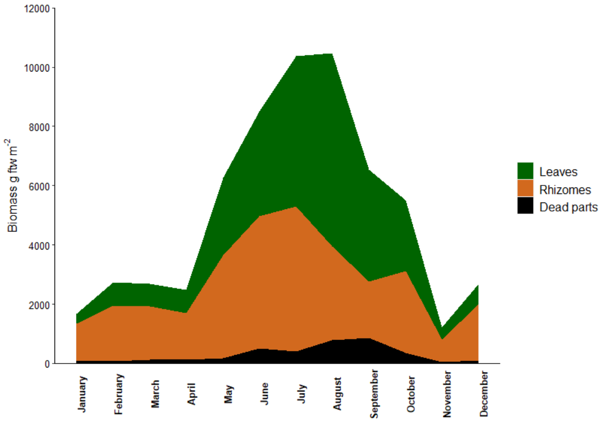


Figure 62: Biomass variation (g fwt m^{-2}) for *C. nodosa* in 2020/21 at San Nicolò

The mean number of shoots was higher in 2020/21 (1,809 shoots m^{-2}) than in 2019 (1,373 shoots m^{-2}). Similarly, the maximum number was recorded in July 2021 (2,880 shoots m^{-2}) and in June 2019 (2,333 shoots m^{-2}) (**Fig. 63-64**).

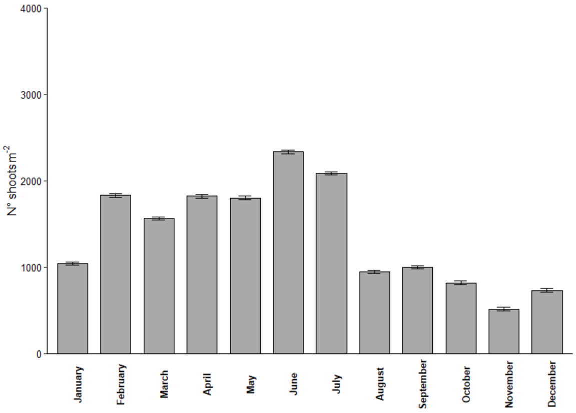


Figure 63: Number of shoots per m^2 for *C. nodosa* in 2019 at San Nicolò

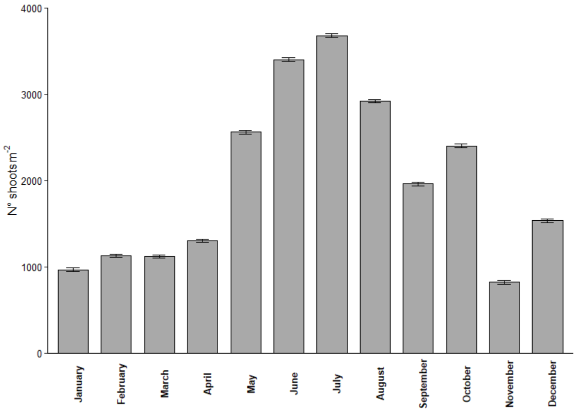


Figure 64: Number of shoots per m^2 for *C. nodosa* in 2020/21 at San Nicolò

The mean length of shoots was the highest in 2020/21 (41.3 cm) but the peak value was recorded in August (72.2 cm) (**Fig. 65-66**). In contrast, the mean length in 2019 was 36.4 cm, while the peak value was reached in July (89.4 cm).

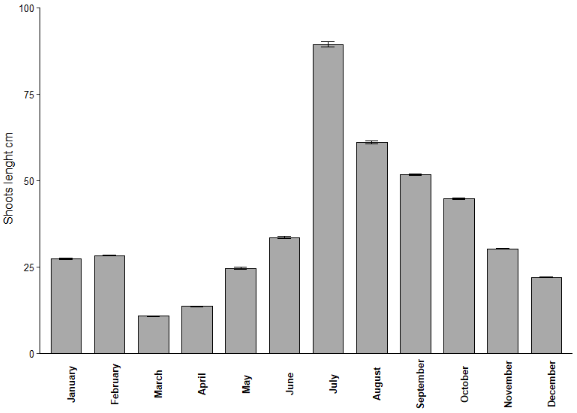


Figure 65: Shoot lengths of C. nodosa in 2019 at San Nicolò

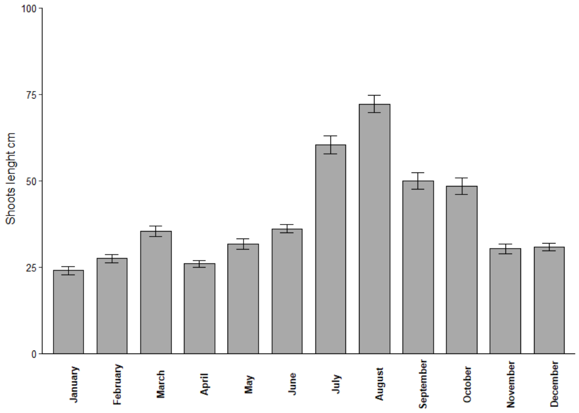


Figure 66: Shoot lengths of C. nodosa in 2020/21 at San Nicolò

The mean number of leaves per shoot was slightly higher in 2020/21 (2.62) compared to 2019 (2.46) (**Fig. 67-68**).

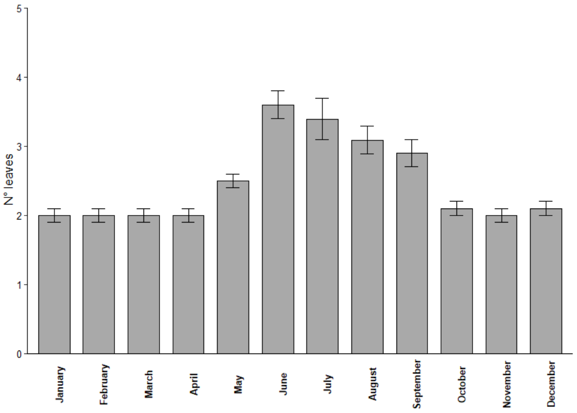


Figure 67: Number of leaves per shoot of *C. nodosa* in 2019 at San Nicolò

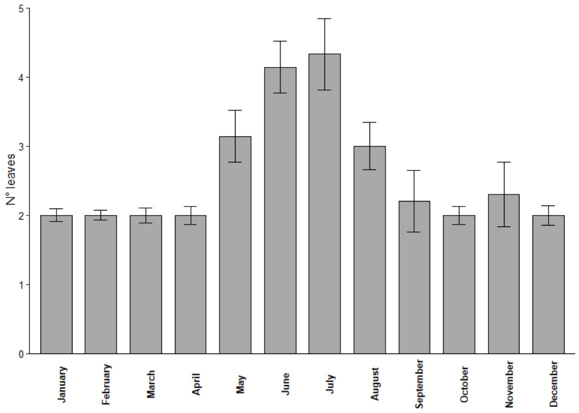


Figure 68: Number of leaves per shoot of *C. nodosa* in 2020/21 at San Nicolò

In 2020/21, the mean shoot growth (1.57 cm d^{-1}) was higher than in 2019 (1.39 cm d^{-1}) (**Fig. 69-70**). In contrast, the growth peaks occurred in July of both years and were very similar: 5.47 cm d^{-1} and 5.46 cm d^{-1} in 2019 and 2020/21, respectively.

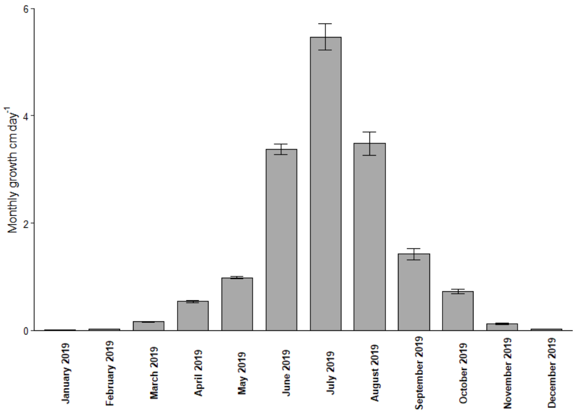


Figure 69: Monthly shoot growth (cm d^{-1}) of *C. nodosa* in 2019 at San Nicolò

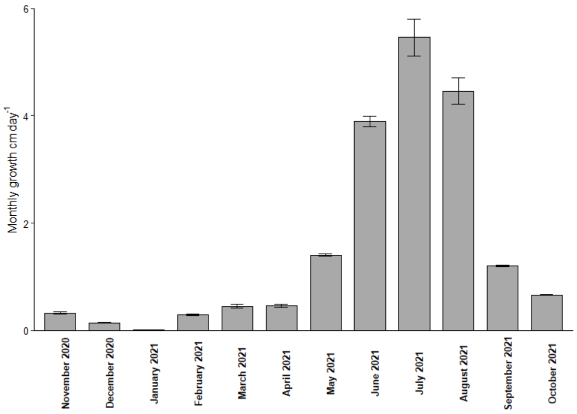


Figure 70: Monthly shoot growth (cm d^{-1}) of *C. nodosa* in 2020/21 at San Nicolò

3.1.6 *R. cirrhosa* at Lio Piccolo

The biomass of *R. cirrhosa* monitored at Lio Piccolo in 2021-22 is shown in **Fig. 71**. The mean biomass of shoots (1,579 g fwt m^{-2}) was extremely higher than that of rhizomes and death parts (300 and 243 g fwt m^{-2}, respectively). However, the total biomass showed highly variable trends throughout the year with a peak in July (4,705 g fwt m^{-2}) and two minimum values in May and September (356 and 402 g fwt m^{-2}, respectively).

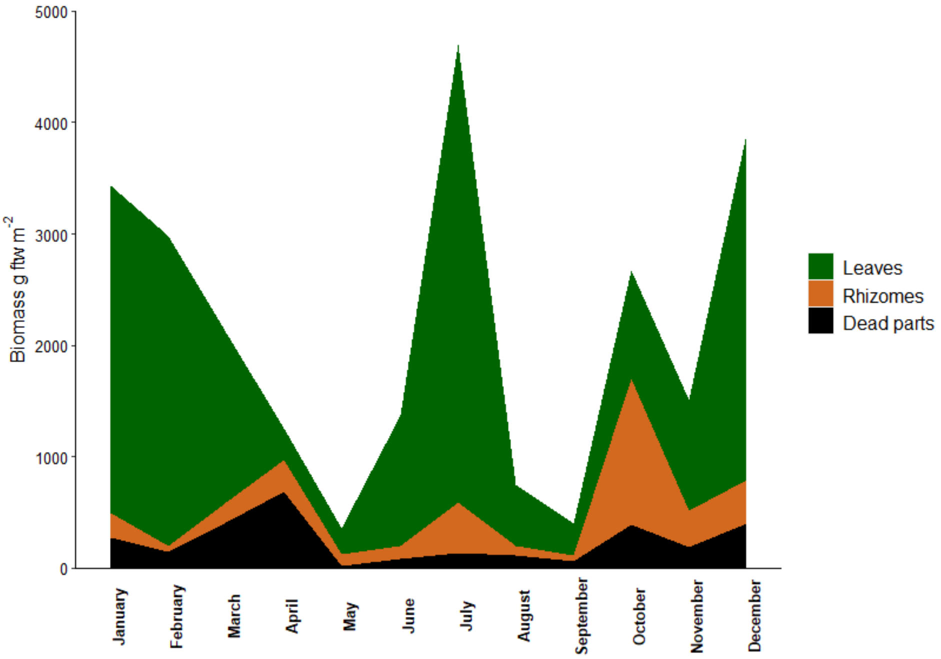


Figure 71: Biomass variation (g fwt m^{-2}) for *R. cirrhosa* in 2021/22

The highest and lowest mean number of shoots were recorded in July (15,758 shoots m^{-2}) and in May (1,440 shoots m^{-2}) respectively, with a similar trend to biomass values (**Fig. 72**).

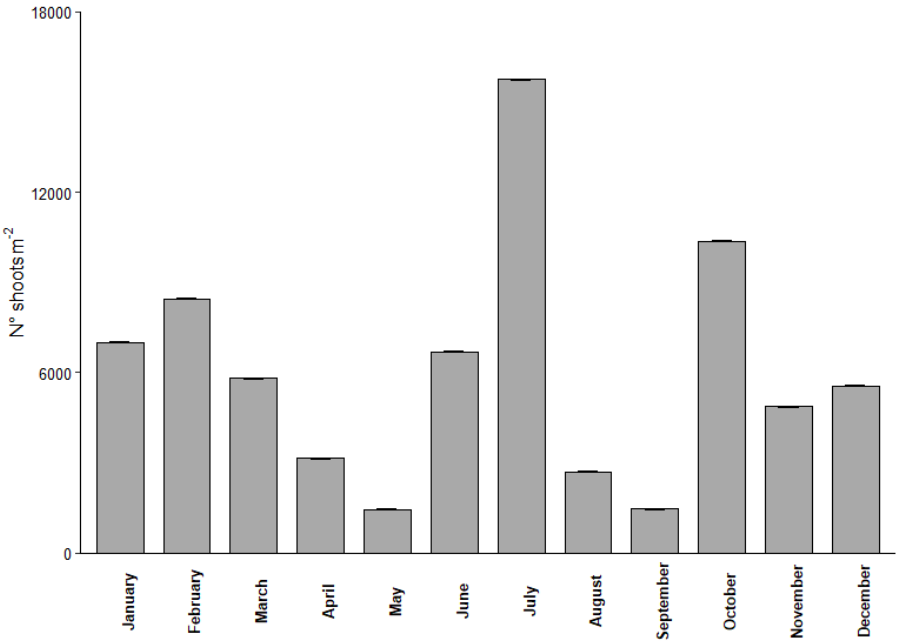


Figure 72: Number of shoots per m^2 for *R. cirrhosa* in 2021/22

The length of the shoots followed the same trend than their number and was the greatest in July (18.8 cm) and the lowest in April (7.89 cm) (**Fig. 73**), with a mean value of 11.2 cm.

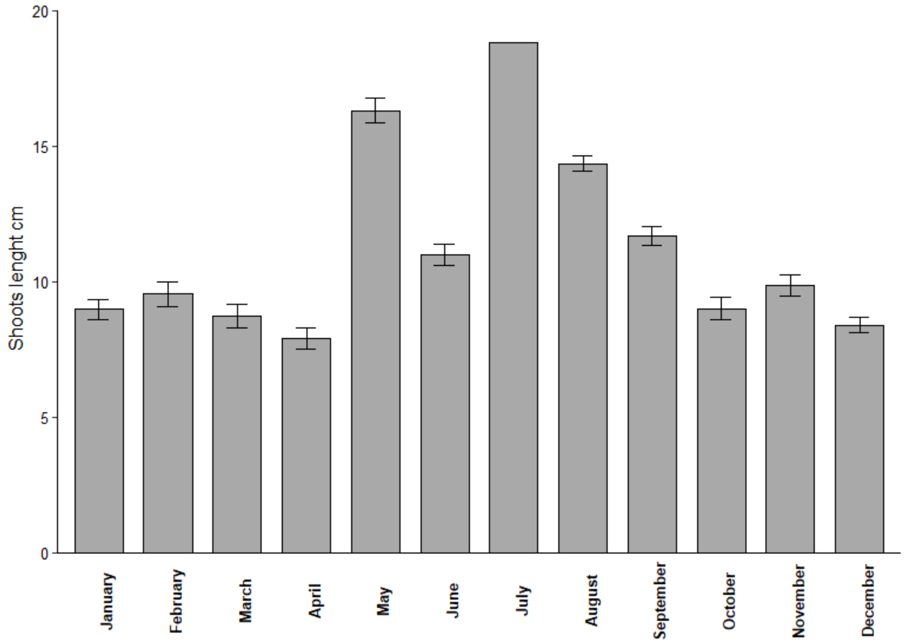


Figure 73: Shoot lengths of *R.cirrhosa* in 2021/22

The number of leaves per shoot peaked in February (5.50) and showed the lowest value in June (2.50), while the mean values was 3.97 (**Fig. 74**).

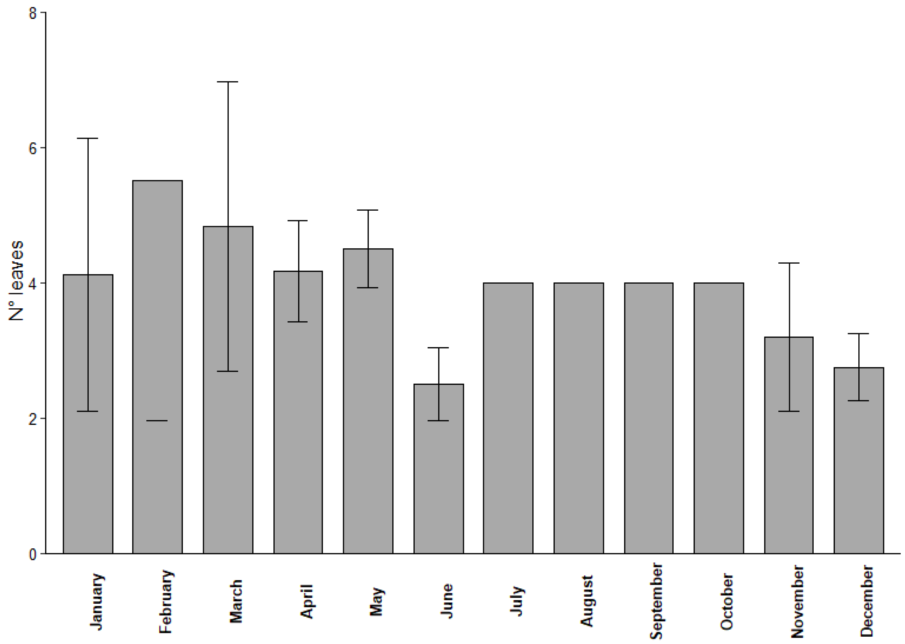


Figure 74: Number of leaves per shoot of *R. cirrhosa* in 2021/22

3.2 NUTRIENT AND CARBON CONTENTS

Total carbon (**Fig. 75**), total nitrogen (**Fig.76**) and total phosphorous (**Fig. 77**) contents in angiosperm tissues showed mean values always lower in rhizomes than in leaves for all species. In fact, the mean global carbon content in 2019 varied from 33.3±2.3 % in leaves and 31.4±4.3 % in rhizomes, while total nitrogen and total phosphorous varied from 2.59±0.52 and 0.17±0.05 % in shoots to 1.75±0.77 and 0.13±0.08 % in rhizomes, respectively.

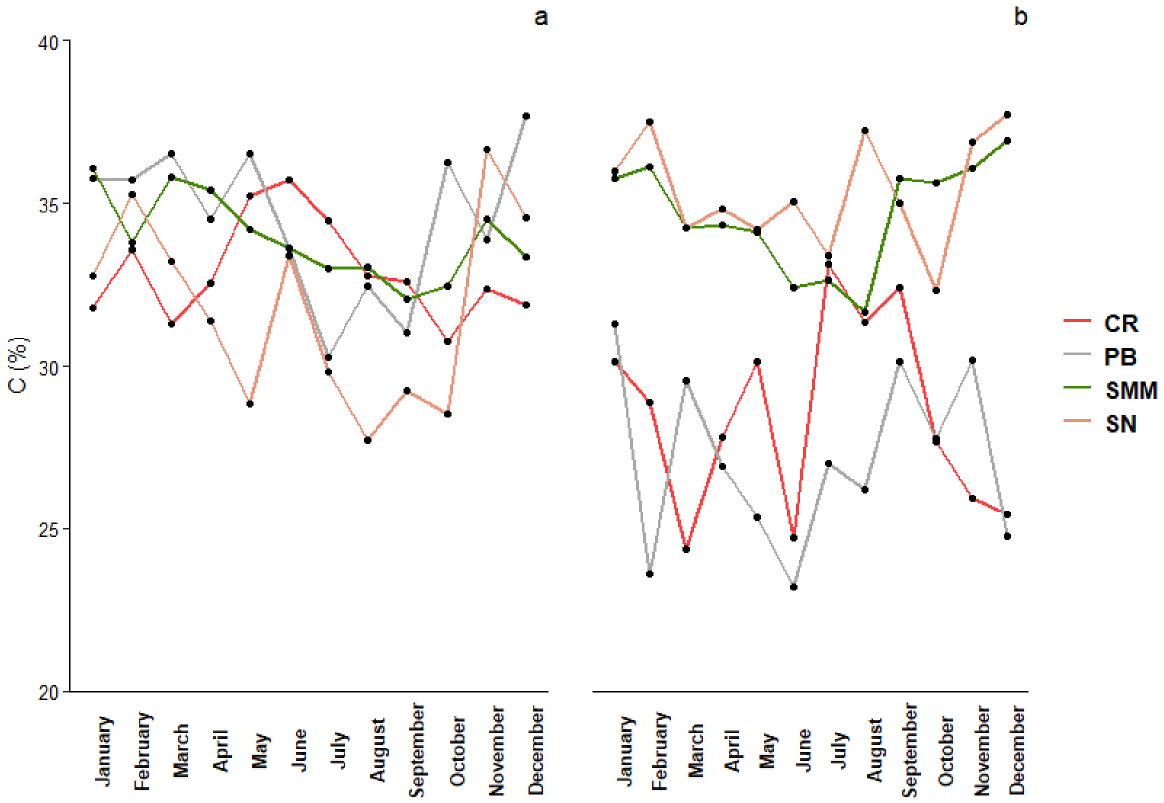


Figure 75: Carbon contents in shoots (a) and rhizomes (b) at Ca' Roman (CR - *Z. marina*), Petta di Bò (PB - *Z. noltei*), Santa Maria del Mare (SMM - *Cymodocea nodosa*) and San Nicolò (SN - *Cymodocea nodosa*) in 2019

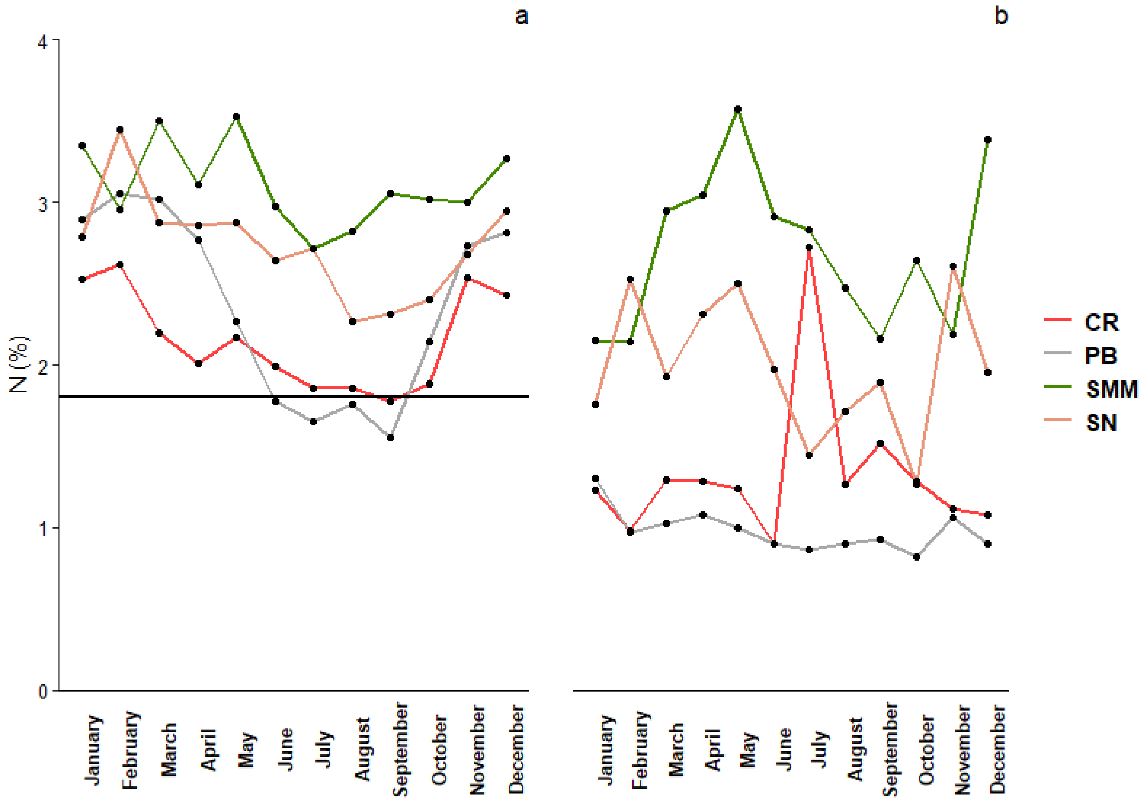


Figure 76: Total nitrogen contents in shoots (a) and rhizomes (b) at Ca' Roman (CR - *Z. marina*), Petta di Bò (PB - *Z. noltei*), Santa Maria del Mare (SMM - *Cymodocea nodosa*) and San Nicolò (SN - *Cymodocea nodosa*) in 2019. The horizontal line represents the limiting value reported in Duarte (1990): i.e. 1.80 %

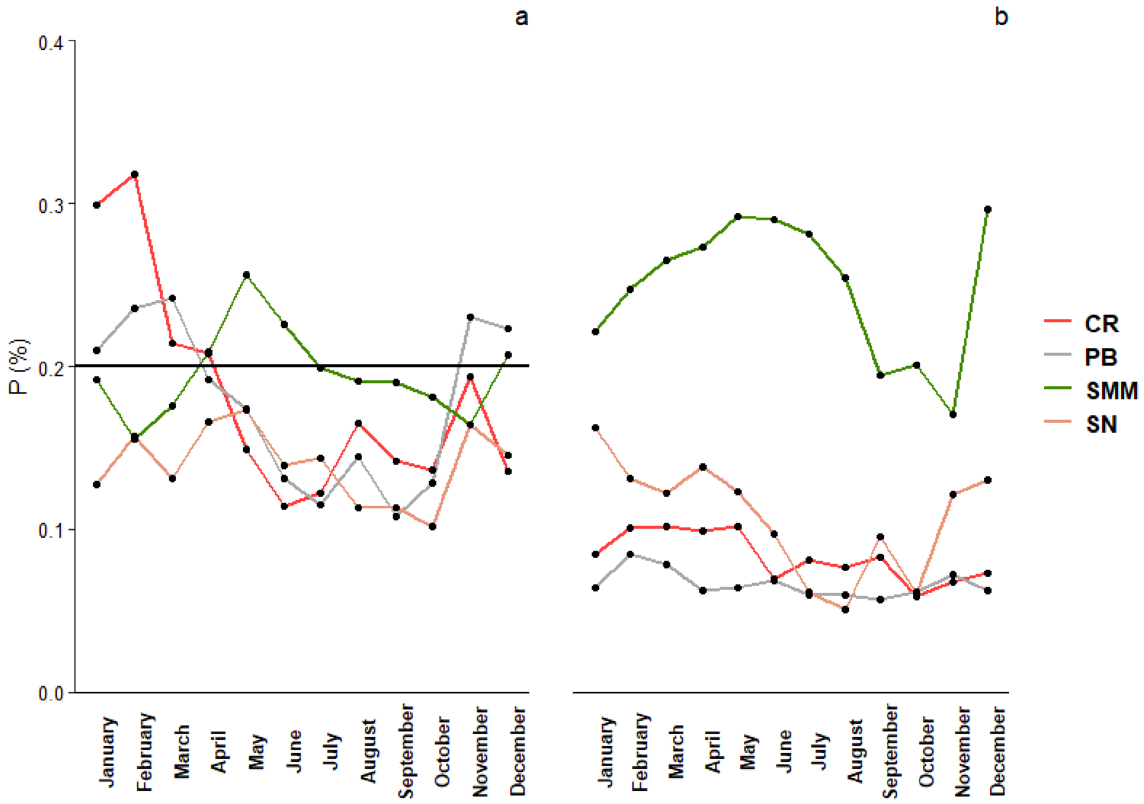


Figure 77: Total phosphorus contents in shoots (a) and rhizomes (b) at Ca' Roman (CR - *Z. marina*), Petta di Bò (PB - *Z. noltei*), Santa Maria del Mare (SMM - *Cymodocea nodosa*) and San Nicolò (SN - *Cymodocea nodosa*). The horizontal line represents the limiting value reported in Duarte (1990): i.e. 0.20 %

Moreover, total nitrogen content in shoots was never below the limiting value reported by Duarte (1990), with the exception of a few cases in *Z. noltei* at Petta di Bò between June and August. However, the mean value (2.37±0.57 %) was higher than 1.80%. In contrast, total phosphorous content was almost always below the value reported by Duarte (1990) with overall means of 0.17±0.05 % for leaves and 0.13±0.08 % for rhizomes.

3.3 BENTHIC CHAMBERS

Water and sediment parameters, including nutrient concentrations, showed high seasonal variability especially at Cavallino-Treporti. Temperature ranged between 10.6°C and 28.8°C, reactive phosphorus between 0.10 µM in spring-summer and 0.65 µM in winter whereas ammonium showed 1.06 µM in autumn and 19.7 µM in winter. Other parameters displayed fewer changes across sampling campaigns with the mean±sd values reported in **Tab. 8**.

Table 8: Station parameters along sampling periods at Cavallino-Treporti expressed as mean±sd

	Mean±SD
Chl-*a* (µg/l)	0.73±0.17
Salinity (psu)	39.0±0.8
TSS (mg/l)	22.1±7.7
Water pH	8.19±0.20
Water Eh (mV)	114±24
Water temperature (°C)	21.6±7.8
Reactive Phosphorous (µM)	0.31±0.27
DIN (µM)	10.3±7.9
Sediment pH	7.78±0.10
Sediment Eh (mV)	-123±53
Sediment Dry Density (g cm^{-3})	1.11±0.04
Sediment Organic Carbon (OC) (%)	1.18±0.02
Sediment fine fraction (<63µm) (%)	22.3±0.3

The net community production (NCP) (**Fig. 78**) had different seasonal patterns according to species characteristics: *Z. marina* NCP decreased at higher temperatures while *Z. noltei* increased until summer. Therefore, the highest values occurred in summer for *Z. noltei* (17.7±2.2 mmol O_2 m^{-2} h^{-1}) and spring (18.1±3.9 mmol O_2 m^{-2} h^{-1}) for *Z. marina*, while the lowest values were recorded in spring (1.37±0.66 mmol O_2 m^{-2} h^{-1}) and autumn (1.74±0.87 mmol O_2 m^{-2} h^{-1}), respectively. At the same time, blanks (i.e. chambers in bare sediment) showed always negative values (mean±sd: -1.85±0.92 mmol O_2 m^{-2} h^{-1}). Water volume in each benthic chamber varied from 12.9 to 19.3 litres, depending on meadow or bare sediment environments.

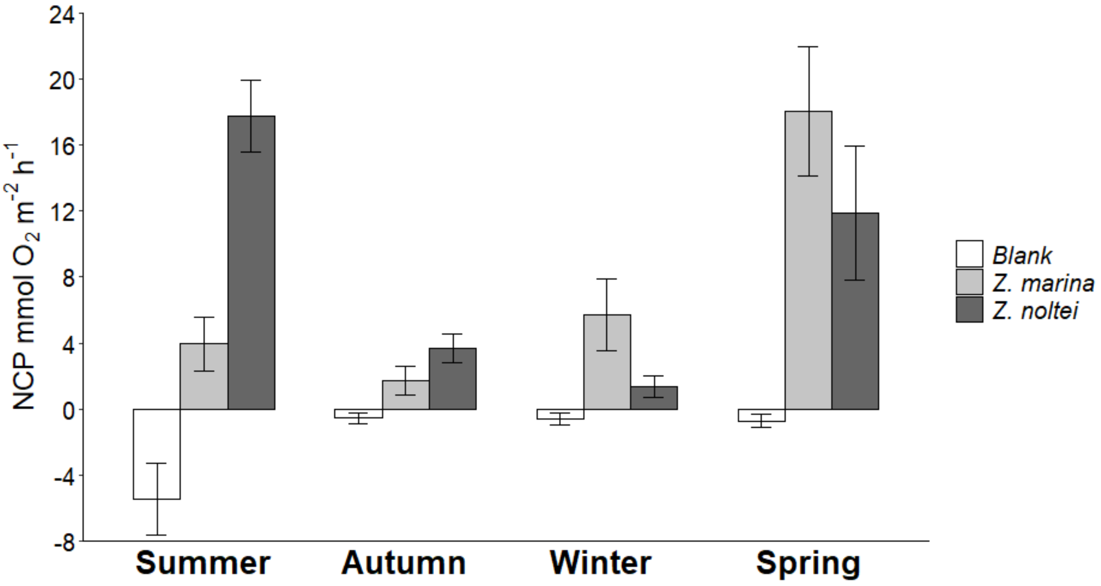


Figure 78: Bar plots showing mean and sd seasonal NCP values of 3 benthic chambers placed in bare sediment (Blank) and seagrass meadows

Larger sizes of leaves and rhizomes of *Z. marina* affected seasonal biomass values (g fwt m^{-2}) with greater values on warmer seasons for leaves (mean±sd: 2475±414 for *Z. marina* and 1179±11 for *Z. noltei*) and fewer variations across sampling campaigns for rhizomes (mean±sd: 1531±755 for *Z. marina* and 1482±673 for *Z. noltei*) (**Tab. 9**).

Table 9: Biomass of leaves and rhizomes of *Z. marina* and *Z. noltei* (g fwt m^{-2}) across sampling campaigns expressed as mean±sd

	Z. marina		***Z. noltei***	
	Leaves	**Rhizomes**	**Leaves**	**Rhizomes**
Summer	2182±636	1095±59	1172±32	1770±86
Autumn	840±10	1379±73	432±34	1084±54
Winter	710±199	1013±64	280±34	791±38
Spring	2768±530	2639±100	1187±151	2282±108

As a result, considering its smaller size, the NCP to leaf biomass ratios (**Fig. 79**) of *Z. noltei* displayed higher values (0.39±0.11 mmol O_2 m^{-2} h^{-1} g^{-1} fwt) than *Z. marina* (0.17±0.0.10 mmol O_2 m^{-2} h^{-1} g^{-1} fwt).

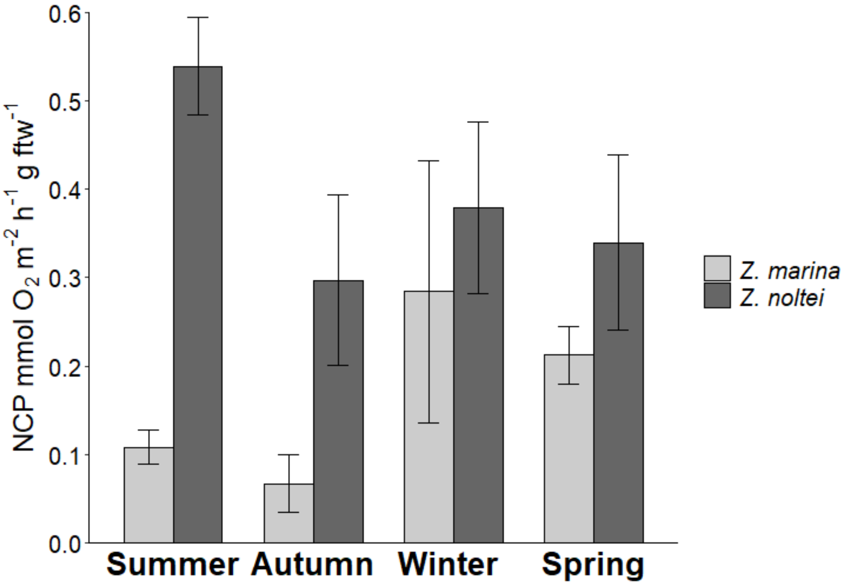


Figure 79: Bar plots showing mean seasonal NCP to leaf biomass ratios of 3 benthic chambers displayed in seagrass meadows

Daily community net production for *Z. marina* (**Fig. 80**) and *Z. noltei* (**Fig. 81**) showed the highest values at 16:30 (13.7±1.6 mmol O_2 m^{-2} h^{-1}) and at 12:55 (12.1±1.8 mmol O_2 m^{-2} h^{-1}), respectively. The lowest values were found at 19:30 and 20:30 for both species (3.07±0.27 and 3.01±0.24 mmol O_2 m^{-2} h^{-1}, respectively). Mean respiration values were: -13.9±1.0 mmol O_2 m^{-2} h^{-1} for *Z. marina* and -2.20±0.19 mmol O_2 m^{-2} h^{-1} for *Z. noltei*. On the other hand, the photosynthetic active radiation (PAR) showed the typical daily pattern with maximum values around midday: 613 μmol m^{-2} s^{-1} at 11:30 for *Z. marina* and 650 μmol m^{-2} s^{-1} at 12:55 for *Z. noltei*. The difference between the two species lies in the different position and depth of the two meadows, as can be seen from the depth values reported in **Tab. 10**.

Table 10: Values of PAR and water depth for *Z. marina* and *Z. noltei* species.

Z. marina			***Z. noltei***		
			Hour	**PAR (μmol m^{-2} s^{-1})**	**Water depth (cm)**
Hour	**PAR (μmol m^{-2} s^{-1})**	**Water depth (cm)**	**06:00**	395	78
06:00	387	55	**07:15**	395	70
07:30	387	62	**09:45**	478	62
09:30	422	78	**11:00**	563	74
11:30	613	92	**12:55**	650	89
13:30	527	112	**14:45**	521	92
16:30	452	97	**17:00**	265	107
19:30	320	77	**19:30**	312	84
20:30	320	58	**20:30**	312	68

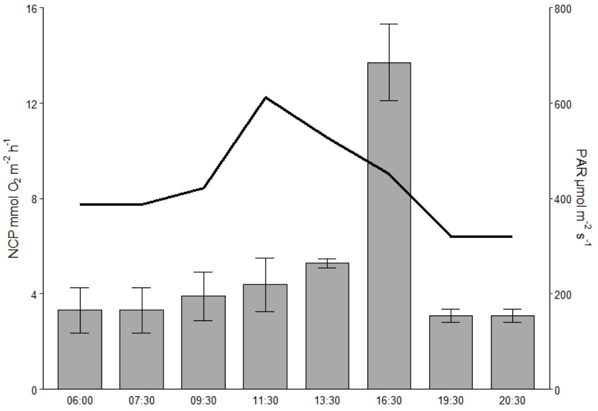


Figure 80: Daily NCP (barplot) and PAR (line chart) for *Z. marina* meadows in the July sampling campaign

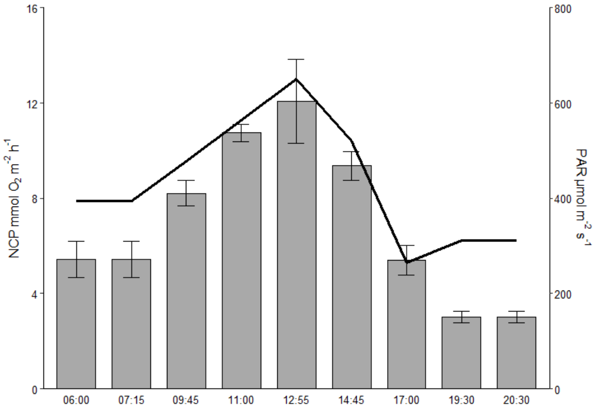


Figure 81: Daily NCP (barplot) and PAR (line chart) for *Z. noltei* meadows in the July sampling campaign

4 DISCUSSIONS

4.1 GROWTH AND PRIMARY PRODUCTION OF AQUATIC ANGIOSPERMS IN THE VENICE LAGOON

The study of growth rates for the evaluation of the primary production of each species was conducted following the methodologies suggested by Short and Duarte (2001). In fact, *C. nodosa*, *Z. marina* and *Z. noltei* are species that continuously produce leaves and are therefore classified by Short and Duarte (2001) as 'leaf replacing form'. For this reason, the authors suggest marking at the level of the leaf sheath in order to estimate the growth of each leaf every 15 days. However, the assessment of rhizome growth is more complex, especially in areas characterised by coarser grain-size as this could lead to rhizome breakage during sampling operations. In addition, smaller species, such as *R. cirrhosa*, are difficult to mark, as the hole itself could lead to tissue necrosis and consequently to limitations in the assessment of growth. For all these reasons, it was decided to evaluate the shoot growth of *C. nodosa*, *Z. marina* and *Z. noltei* by means of the leaf marking technique, while the shoot growth of *R. cirrhosa* and, in general, the rhizome accretions of all species were evaluated as positive inter-monthly biomass differences. The sum of the net primary production (NPP) of shoots and rhizomes and the highest biomass measuring during the year allowed the calculation of the annual production/maximum biomass ratio (P/B ratio) for each species.

These values were then used to calculate the species' contribution to the entire lagoon primary production, taking into account the mapping carried out in 2018 and 2021.

4.1.1 *ZOSTERA MARINA*

Zostera marina is a species that prefers cold water and grows even in winter, while in summer it almost completely stops and may even disappear in areas that are too warm (Sfriso, 2010; Nejrup and Pedersen, 2008). Consequently, its growth follows the phytoecology of the species with a growth in the spring/late spring period and a subsequent decrease in the summer period. Minimum (149 g dwt m^{-2}), maximum (681 g dwt m^{-2}) and mean (311 g dwt m^{-2}) values both in 2019 and 2021 were within the range of other studies. In fact, in a previous study by Olesen and Sand-Jensen (1994) the mean dry total plant biomass was 354 g dwt m^{-2}. Sfriso and Ghetti (1998) in Venice Lagoon found that the total *Z. marina* biomass ranged between a minimum of almost 2,000 g fwt m^{-2} to a maximum of over 6,000 g fwt m^{-2}, accounting for 400-1,200 g dwt m^{-2}. Taking also into account the positive monthly rhizome biomass changes, the NPP was: 12,981 g m^{-2} $year^{-1}$ in 2019 and 20,677 g m^{-2} $year^{-1}$ in 2020/21. The P/B ratio was 2.69 in 2019 and 3.49 in 2020/21. The latter was very similar to the P/B ratio (3.30) found by Sfriso and Ghetti (1998).

4.1.2 *ZOSTERA NOLTEI*

Zostera noltei, which tolerates better higher temperatures (up to 37°C, Massa et al., 2009), showed the peaks in the summer, compensating for the lower biomass and smaller leaf size with more leaf bundles per square metre. Either for *Z. noltei*, the biomass values were within the minimum-maximum range (from almost 1000 to almost 5,000 g ftw m^{-2}) of the study by Sfriso and Ghetti (1998) both in 2019 and 2020/21. Again, NPP and P/B values were determined using the same methods as described in the previous paragraph: 6647 g fwt m^{-2} $year^{-1}$ and 1.38 in 2019 and 8520 g fwt m^{-2} $year^{-1}$ and 1.69 in 2020/21, respectively.

4.1.3 *CYMODOCEA NODOSA*

The biomass at SMM and SN showed similar trends, with peaks in the spring/summer periods. However, significantly higher biomass values were recorded in 2021 at San Nicolò, mainly due to the highest shoot number. However, the values are in accordance with those of Sfriso and Ghetti (1998) that reported values from almost 2,000 g fwt m^{-2} to over 7,000 g fwt m^{-2} and those of Rismondo et al. (1997) that reported values from 2,250 to 9,000 g fwt m^{-}

^{2}. Biomass trends reflected the NPP values, which increases from 12,554 (2019) to 20,114 g fwt m^{-2} year^{-1} (2020/21) at Santa Maria del Mare and from 12,274 (2019) to 19,255 g fwt m^{-2} year^{-1} (2020/21) at San Nicolò. P/B values varied from 1.78 at SMM and 2.74 at SN in 2019 to 3.66 at SMM and 2.35 at SN in 2020/21. The mean P/B ratios calculated as mean value in the two stations (2.29), excluding the value recorded at SMM in 2020/21, was used for estimating the NPP for biomasses higher than 5.63 kg fwt m^{-2}, accounting for prairies with a coverage between 75% and 100%. For lower biomasses was used the mean P/B ratio (3.30) previously recorded by Sfriso and Facca (2007). The ratio found at SMM was too different from all the previous and actual values. For this reason, it was excluded.

4.1.4 *RUPPIA CIRRHOSA*

R. cirrhosa is a species adapted to live in a wide range of salinity, depth, light and temperature conditions (Mannino et al., 2015). *R. cirrhosa* density and biomass have wade ranges of values (from 4,166 to 78,210 shoots m^{-2} and from 12 to 1408 g dwt m^{-2}). This study falls within the same values (min-max: 40.9-740 g dwt) m^{-2}), but it showed higher values that those reported by Cagnoni (1997) (min-max 23-247 g dwt m^{-2}) in the Venice lagoon due to a greater contribution of shoot biomass. Nevertheless, the biomass showed highly variable trends throughout the year probably due to the particular location of the station which is located on the edge of a fishing valley that in May and August was affected by blooms of Ulvaceae that almost completely covered the meadows, leading to death of part of the plants and the reduction of its cover. The positive differences of monthly shoot and rhizome biomass lead to the calculation of the NPP (8605 g fwt m^{-2} year^{-1}) and P/B ratio (1.83). The P/B value is identical to that calculated by Cagnoni (1997).

4.1.5 CALCULATION OF PRIMARY PRODUCTION IN 2018 AND 2019 FOR EACH SPECIES IN VENICE LAGOON

Recent mapping carried out in 2018 and 2021 (Sfriso, 2022) allow to infer the NPP values for the entire Venice lagoon. This allows a comparison with the values of NPP available in literature (Sfriso and Facca, 2007b), related to 2003 and to assess any negative effects on angiosperm NPP following the activation of MOSE gates. Overall, the cover of *Z. marina* in 2021 was 49.4 km^2, 11.2 km^2 higher than in 2018. Taking into account the P/B ratios, the NPP in 2021 was 564 ktonnes fwt against 545 ktonnes fwt in 2018, largely produced in the southern lagoon. The cover of *Z. noltei* increased from 18.1 km^2 in 2018 to 25.7 km^2 in 2021 and the NPP varied from 113 ktonnes fwt in 2018 to 126 ktonnes fwt in 2021. On the other hand, *C. nodosa* covered approx. 32.1 km^2 in 2021, a value very similar to 2018 (32.4 km^2), with the greatest contribution recorded in the southern lagoon (28.7 km^2). As a result, the NPP dropped slightly from 531 to 499 ktonnes fwt. Lastly, *R. cirrhosa* colonises only the northern lagoon with the cover that increased by 71% (6.03 km^2 in 2018 – 10.3 km^2 in 2021) and the NPP that increased by 36% (from 18.0 to 24.5 ktonnes fwt). These data highlight that the angiosperm differences recorded between 2019 (before the closure of the MOSE gates) and in 2020/21 during about ten MOSE closures in the autumn-winter period) have been essentially determined by the different weather conditions at local scale and not by MOSE closures which occurred in periods when the activity of primary producers is very reduced.

Comparing these data with those available in literature for 2003 (Sfriso, 2022), *C. nodosa* cover and NPP increased by 36% and 44%, respectively. *Z. marina* increased by 90% and of 64%, *Z. noltei* by 314% and 408% and *R. cirrhosa* by 71% and 36%, respectively. *Z. noltei* showed the greatest increase as in the past it was strongly affected by clam fishing activities and the eutrophic phenomenon that occurred in summer 2001 with an intense bloom of picocyanobacteria that affected the entire lagoon (Sorokin et al., 2004). *R. cirrhosa*, on the other hand, had completely disappeared from the lagoon by the end of the 1980s (Sfriso, 2008) and was reintroduced both naturally from “Valle Grassabò”, a portion of Venice Lagoon delimited by a system of embankments and located in the north-eastern region of the lagoon, and thanks to Life SERESTO project, which helped to colonise almost 15 km^2 of the northern part of the lagoon with the transplantation of plant sods and rhizomes. In general, the progressive decrease in nutrient concentrations and suspended particles recorded in the water column (Tomio et al., 2020; Sfriso, 2022) and the decrease of total nitrogen, organic phosphorus and organic carbon recorded in sediments (Sfriso et al., 2021c) have favoured the recolonisation of the Venice Lagoon by aquatic angiosperms. This was confirmed by the fact that seagrasses represented the principal primary producer since 2003 (Sfriso and Facca, 2007b) increasing markedly with the decrease of ammonium and nitrate concentrations in the water column (Tomio et al., 2020). Dissolved Inorganic Nitrogen (DIN) concentrations dropped by ca. 64% in 2011-2014 period with low phosphorous concentrations (ca. 0.20 μM) and phytoplankton biomasses and the increase of water transparency (Facca et al., 2014; Aubry et al., 2020). Lower nutrient concentrations triggered an improvement of the ecological status and enhanced the develop of angiosperm meadows and their associated carbon stocks (Sfriso et al., 2020, 2021c). Thus, considering the entire

Venice Lagoon and the summed contributions of the species, the total angiosperms NPP increased from 714 ktonnes fwt in 2003 to 1213 ktonnes fwt in 2021.

4.2 NUTRIENT AND CARBON CONTENTS

Nutrient contents within tissues, especially in leaves, have been studied since the 1980s as they were initially considered a constraint to seagrass growth. In fact, spatial and temporal variations in C:N:P or in C:N ratios are good indicators of seagrass nutritional status (Burkholder et al., 2007). The first study that considered 27 species from 30 different locations was carried out by Duarte (1990), in which median concentration values in leaves for each element were also defined: 33.6±0.3 % for carbon, 1.92±0.05 % for nitrogen and 0.23±0.01 % for phosphorus (Duarte, 1990). The data of this thesis fall within these ranges for carbon (33.3±2.3 %), while nitrogen showed higher mean values (2.59±0.52 %). However, nitrogen is highly variable within species (Burkholder et al., 2007) and both *C. nodosa* and *Z. marina* in Duarte (1990) showed wide ranges of values from over 5.00% to lower than 1.50%. Moreover, the values obtained are in accordance with those measured in a study conducted in Venice Lagoon by Sfriso and Marcomini (1999) where the mean nitrogen content in *Z. marina* leaves was 2.30±0.40 %. In contrast, total phosphorus contents in the leaves showed values below 0.20%, especially in the growing period, suggesting a consumption of nutrients to support growth in accordance with nitrogen contents. However, also phosphorus contents are highly variable within species, e.g. *C. nodosa* ranges between about 0.15 and 2.50% and *Z. marina* between less than 0.20% to almost 0.80% (Duarte, 1990). Nevertheless, the contents and annual trends are in agreement with those in Sfriso and Marcomini (1999)'s study for *Z. marina* (mean: 0.23±0.08 %, min-max: 0.13-0.38).

The mean C:N:P atomic ratios are reported in **Tab. 11** for each species.

Table 11: Mean C:P, N:P and C:N:P atomic ratios for each species

Station	Species	Plant part	C:P	N:P	C:N:P
Ca' Roman	*Z. marina*	Leaves	463	26	436:26:1
		Rhizomes	884	35	884:35:1
Petta di Bò	*Z. noltei*	Leaves	500	29	500:29:1
		Rhizomes	1058	33	1058:33:1
Santa Maria del Mare	*C. nodosa*	Leaves	447	35	447:35:1
		Rhizomes	359	24	359:24:1
San Nicolò	*C. nodosa*	Leaves	587	43	587:43:1
		Rhizomes	844	41	844:41:1

The mean values of C:N:P atomic ratios were highly variable and reflected the nutrient contents within the different parts of the plants, showing higher values in rhizomes. The values of *Z. marina* are in accordance with those reported in the study by Sfriso and Marcomini (1999) (457:24:1 and 843:28:1 for shoots and rhizomes, respectively) and, in general, with those in the study by Atkinson and Smith (1983) (min – max for leaves: 317:16:1 – 1070:29:1; min – max for rhizomes: 388:14:1 – 3550:61:1). However, the values of shoots are in the same range of the mean atomic ratio reported by Duarte (1990) (474:24:1), except for *C. nodosa* at San Nicolò, especially in C:P ratio. The nutrient contents vary greatly not only temporally, but also spatially, even doubling in some cases the C:N and C:P ratios in the same species (Fourqurean et al., 1997). In our case, this can be seen in *C. nodosa* at San Nicolò, which showed higher C:P and N:P ratios in both shoots and rhizomes than at SMM. The two stations have similar but different conditions: SN is located near the mouth of Lido, affected by the Venice effluents and close to the port entrance. This station is more subject to wave motion and resuspension of particulate sediment. Instead, SMM is placed in a sheltered area far by anthropogenic impacts and less affected by ship and pleasure traffic. Therefore, in general, nutrient contents show mean values similar to literature and previous Venice Lagoon papers. However, the spatial variations found for *C. nodosa* deserves further investigation, especially by considering water transparency. In fact, health status, assessed as light availability, can be evaluated by the C:N ratio (Jones and Unsworth, 2015). SN and SMM showed C:N ratios of 13.5 and 12.7, respectively, which are lower than 15.0 a value potentially indicative of light limitation (McMahon et al., 2013). This may possibly be due to self-shading effects of *C. nodosa*, particularly in the growing season, where the longer leaves fold up on the surface of water at low tide, shadowing the entire seabed and the leaves below. The other two species showed mean values higher than 15.0 (*Z. noltei*: 17.0; *Z. marina*: 17.8), suggesting light environment suitable for productive seagrass meadows. However, the introduction of additional parameters for assessing the health status of meadows in Venice Lagoon (e.g. proteins, carbohydrates and lipids contents) could provide very interesting information on the relationships between different species and environments and within the meadows themselves.

Ecosystem's carbon stocks include biomass (both macrophytes and benthic macrofauna) and soil carbon stock (Houghton, 2007, Sfriso et al., 2020). Carbon stored in seagrass leaves is more labile than that in the belowground tissues and sediments due to consumption and decomposition processes (Holmer and Olsen, 2002; Lee et al., 2015) up to 100% within 1 year (Zou et al., 2021). Consequently, since significative values in shoots (mean values: 53.6±34.3 g C m^{-2} for *Z. marina*, 31.3±23.5 g C m^{-2} for *Z. noltei* and 74.2±84.3 g C m^{-2} for *C. nodosa,* respectively) and their great variations in biomass values, we considered the minimum values as the ones that remain stable during the year and that contribute to potential carbon stock. Indeed, leaf biomasses had different trends depending on the species: *Z. marina* almost sextupled (from 59 to 385 g dwt m^{-2}), *Z. noltei* increased more than tenfold (from 19 to 247 g dwt m^{-2}) and *C. nodosa* had the maximum value almost 40 times higher than minimun one (from 36 to 1333 g dwt m^{-2}). On the other hand, rhizomial biomasses showed lower variations with values more than tripled for *Z. marina* (from 78 to 296 g dwt m^{-2}) and for *C. nodosa* (from 191 to 665 g dwt m^{-2}) and more than sextupled for *Z. noltei* (from 55 to 386 g dwt m^{-2}). These high seasonal variations both in the above and belowground biomass are confirmed by a previous study carried out in Venice Lagoon (Sfriso and Ghetti, 1998). Furthermore, belowground portions represent the critical sources of carbon stocks (Zou et al., 2021) with greater contribution of refractory macromolecules (Trevathan-Tackett et al., 2017). In our study, the mean carbon budgets of rhizomes varied from 53.6±34.3 g C m^{-2} for *Z. marina* to 31.3±23.5 g C m^{-2} for *Z. noltei* and 74.2±84.3 g C m^{-2} for *C. nodosa*. All these three values were lower than the global average (252±48 g C m^{-2}) recorded by Fourqurean et al. (2012). This difference could be explained by the nature of sampling environments. In fact, winter intensity and seasonal fluctuation of temperature, the proximity of deep canals and their major wave energy and sediment resuspension could negatively impact on rhizome and sediment carbon reserves (Soissons et al., 2018). The frequent disturbance and exposure of sediment directly to air in case of exceptional low tides might stimulate decomposition of accumulated organic detritus, not letting to settle down (Zou et al., 2021). In fact, organic carbon contents in sediment (C_{org}) in the different stations are lower than global mean (18.0 mg g^{-1} dwt) reported by Zou et al. (2021), but very similar between the different meadows (15.5 mg g^{-1} dwt for *Z. marina*, 8.70 mg g^{-1} dwt for *Z. noltei* and 9.10 mg g^{-1} dwt for *C. nodosa*) and, except for *Z. marina*, to the mean C_{org} value reported in 2018 for the entire Venice Lagoon (11.9 mg g^{-1} dwt, Sfriso et al. (2020)). However, since data of C_{org} contribution of aquatic angiosperm meadow communities for the Venice Lagoon sediments are not available even in the most recent study by Sfriso et al. (2020), C_{org} values recorded in this study in the top-5 cm sediment layer could be used for estimating the minimum carbon contribution of angiosperm communities. We selected to study the top-5 cm sediment due to its crucial role as seat of major sediment disturbance with important consequences in global carbon cycle and so organic carbon burial (van de Velde et al., 2018). Considering *Z. marina*, *Z. noltei* and *C. nodosa* community meadows (Sfriso et al., 2021c): 38.2 km^2, 18.1 km^2 and 32.4 km^2, respectively), the minimum total C_{org} contributions of above and belowground biomasses were respectively 757 and 725 tonnes C for *Z. marina*, 120 and 295 tonnes C for *Z. noltei* and 381 and 2,203 tonnes C for *C. nodosa*. On the other hand, in the surface sediments the concentration of C_{org} was almost 8 times higher (20,007 C tonnes) in the areas colonized by *C. nodosa,* 12 times higher (17,572 C tonnes) in the presence of *Z. marina* and 22 times higher (8,960 C tonnes) in the areas covered by *Z. noltei.* Therefore, the total C_{org} trapped by aquatic angiosperms (sum of minimum annual content in leaves and rhizomes) and surface sediments colonized by these plants was 51,022 C tonnes C.

4.3 BENTHIC CHAMBERS

Net Community Production (NCP) and oxygen/CO_2 fluxes for a given meadow are generally estimated using different techniques (Duarte et al., 2010) based on metabolic approaches (Staehr et al., 2010; Campbell and Fourqurean, 2011; Long et al., 2015), PAM fluorometry (Beer and Björk, 2000; Duarte et al., 2017; George et al., 2020; Purvaja et al., 2020), oxygen/CO_2 variations and the most recent Eddy Covariance technique (Markwitz and Siebicke, 2019; Koopmans et al., 2020), each affected by several biases (Silva et al., 2009). The use of benthic chambers to evaluate O_2/CO_2 fluxes is more practical and direct for estimating photosynthetic rates at community level over a known area (Long et al., 2015; Berger et al., 2020). Recently, Olivé et al. (2016) suggested to use a short time incubation period (1.5-2 hours) to prevent underestimation of NCP up to 44% in respect to longer incubation time (24 h). Olivé et al. (2016), based the study on a single sampling campaign at 4 m depth, therefore not considering seasonal variations and the high variability of temperature of shallow water ecosystems.

In this study, we tested NCP potential of two seagrass meadows in same environmental conditions at peak photosynthesis periods using short incubation times. Sampling campaigns were selected to meet different growth rates for two species according to previous data available for Venice Lagoon (Sfriso and Ghetti, 1998). NCPs of *Z. noltei* (1.37±0.66 - 17.7±2.2 mmol O_2 m^{-2} h^{-1}) and *Z. marina* (1.74±0.87 - 18.1±3.9 mmol O_2 m^{-2} h^{-1}) meadows stand in the same range of previous works (3.69 - 23.1 mmol O_2 m^{-2} h^{-1}, Duarte et al. (2010)). However, although the maximum values were of the same magnitude of the only study following the same incubation period (23.1±2.8 mmol O_2 m^{-2} h^{-1}, Olivé et al., 2016), we also estimated the mean maximum NCP during two minimum production months, which accounted for our very low minimum results. Moreover, between the two species *Z. marina* presented the peak NCP mean value (mean±sd: 8.67±7.55 mmol O_2 m^{-2} h^{-1}), while the mean value was higher for *Z. noltei* (mean±sd: 7.37±7.32 mmol O_2 m^{-2} h^{-1}), confirming its better tolerance to lagoon temperature range (Sfriso et al., 2019). In fact, while photosynthetic capacity and shoot biomass of *Z. noltei* drops over 37°C (Massa et al., 2009), the optimum water temperature for *Z. marina* lies between 10 and 20°C with photosynthetic rate dropping at lower temperature and increasing mortality at higher ones (Nejrup and Pedersen, 2008). However, our results in the Venice Lagoon seemed to suggest that the optimum temperature for *Z. marina* occurs up to 25°C as already recorded by Sfriso et al. (2020, 2021a).

Comparisons between species could be performed not only per unit of area but also per unit of leaf biomass, letting to understand patterns after removing biomass effects. Despite the higher mean leaf biomass of *Z. marina* (319±199 g dwt m^{-2}) than *Z. noltei* (143±89 g dwt m^{-2}), NCP to biomass ratios in each sampling campaign were higher for *Z. noltei* (mean±sd: 1.98±0.11 mmol O_2 m^{-2} h^{-1} g^{-1} dwt) than for *Z. marina* (0.76±0.27 mmol O_2 m^{-2} h^{-1} g^{-1} dwt). These results suggest a major contribution of *Z. noltei* communities to carbon sink potential in accordance with data from Duarte et al. (2010). These authors found that the average NCP of *Z. noltei* from 7 different sampling sites was over 4 times higher than those of *Z. marina* (72.9 in contrast to 17.7 mmol O_2 m^{-2} d^{-1}). Its contribution to carbon biochemical cycle becomes more important considering the effects of Sea Level Rise and deeper waters (Ondiviela et al., 2020). In fact, the cover area of this species could be negatively affected by a rising sea level of 0.63 m with a reduction of the production up to 14.2%, with a consequent loss of carbon storing (Ondiviela et al., 2020).

Oxygen evolution within the benthic chambers is generally considered a proxy for estimating CO_2 capture and for carbon net production with a 1:1 ratio (O_2:CO_2), theoretically ranking between 1.0 and 1.3 depending on physiological state of plant cells (Duarte et al., 2010), despite not general consensus among the scientific community (Gazeau et al., 2005; Ouisse et al., 2014). Our study suggests a mean maximum proxy CO_2 capture of 88.5±87.9 mg C m^{-2} h^{-1} for *Z. marina* community (min and max: 20.9 and 216 mg C m^{-2} h^{-1}) and 104±91 mg C m^{-2} h^{-1} for *Z. noltei* community (min and max: 16.4 and 213 mg C m^{-2} h^{-1}), a greater value than the maximum gross primary production obtained by Stutes et al. (2007) (31.3±16.2 mg C m^{-2} h^{-1}) using 4 h incubation period. This suggests an underestimation of the seagrass potential contribute for carbon sequestration, especially due to longer incubation time (Olivé et al., 2016). As regards the Venice Lagoon, the contribution is even higher considering that bare sediment showed negative values in every sampling campaign for a total NCP of seagrass meadows ranging from 23.8 to 279 mg C m^{-2} h^{-1}. In particular, *Z. marina* varied between 27.5 and 225 mg C m^{-2} h^{-1} (mean: 111$\underline{+}$84 mg C m^{-2} h^{-1}) while *Z. noltei* ranged between 23.8 and 279 mg C m^{-2} h^{-1} (mean: 126$\underline{+}$116 mg C m^{-2} h^{-1}). Therefore, considering the *Z. marina* (37.6 km^2) and *Z. noltei* (18.1 km^2) cover in Venice Lagoon in 2018 (Sfriso et al. (2021b), the maximum carbon sequestration capacities of angiosperm communities varied between 1.03 and 8.49 tonnes C h^{-1} for *Z. marina* (mean: 4.16$\underline{+}$3.17 tonnes C h^{-1}) and between 0.43 and 5.05 tonnes C h^{-1} for *Z. noltei* (mean: 2.28$\underline{+}$2.09 tonnes C h^{-1}). Considering instead seagrass cover in 2021 (49.4 km^2 for *Z. marina* and 25.7 km^2 for *Z. noltei*, Sfriso (2022)), the contribution to carbon sequestration is even higher: 5.47$\underline{+}$4.17 C h^{-1} for *Z. marina* and 3.24$\underline{+}$2.97 C h^{-1} for *Z. noltei*. This is confirmed by the fact that seagrasses are the principal primary producer since 2003 (Sfriso and Facca 2007b) increasing markedly with the decrease of ammonium and nitrate concentrations in water column (Tomio et al., 2020), the decrease of phytoplankton and the increase of water transparency (Facca et al., 2014; Aubry et al., 2020). In fact, aquatic angiosperm meadows have increased their cover area of about 69% (from 55.9 km^2 to 94.7 km^2) between 2003 and 2018 (Sfriso et al., 2021c), also thanks to the contribution of LIFE SeRESTO project (LIFE12 NAT/IT/000331) (Sfriso et al., 2021b,c). Their cover area increased again by 24% between 2018 and 2021 (from 94.7 km^2 to 118 km^2) (Sfriso et al., 2022).

However, gross primary production (GPP), respiration (R) and net community production (NCP) of aquatic angiosperms varies not only seasonally but also daily (Rheuban et al., 2014a,b), driven by light availability (Gacia et al., 2005), temperature (Caffrey, 2004) and water motion (Mass et al., 2010). Thereby, the selection of a single station characterized by the same environmental conditions and the presence of two meadows of *Z. marina* and *Z. noltei* is fundamental in order to investigate the within-day variability in oxygen fluxes and the “hysteretic” pattern in O_2 flux. In fact, Rheuban et al. (2014a), Geertz-Hansen et al. (2011) and Marra (1978) observed that seagrass and marsh ecosystems and phytoplankton cultures have a higher oxygen production in the morning than in the afternoon. However, the study conducted on *Z. marina* by Rheuban et al. (2014a) attributed the “hysteretic” pattern to a variable respiration rate, the release and consumption of dissolved organic carbon (DOC) exudates and/or heat stress. Nevertheless, primary production in other aquatic ecosystems (e.g. phytoplankton and corals) is mainly affected by short-term light history and temperature

(Anthony and Hoegh-Guldberg, 2003; O'Brien et al., 2009). A preliminary study was then conducted in order to estimate the daily contribution of two seagrass meadows to global lagoonal production and to better understand the hysteretic pattern in a shallow water environment characterized by high temperature and irradiance variations due to tidal excursion. The typical hysteretic pattern observed in the studies mentioned above and in the more recent study by Adams et al. (2016) was found only for *Z. noltei* in the selected individual sampling campaign. In fact, the differences in primary production would seem to be more related to the availability of light on the bottom and thus to the combined action of tidal excursions and solar radiation, especially in *Z. noltei* community. *Z. marina* on the other hand, probably has a more delayed primary production within the day due to the decrease in solar irradiation, especially considering *Z. marina*'s low tolerance to high temperatures that in July reached 29.2°C. Repeated sampling campaigns would be appropriate in order to better understand the real factors contributing for this particular pattern and the contribution of temperature, tidal excursion and solar irradiance at canopy level to the primary production of both species. In spite of all this, this study allows to estimate for the first time in Venice Lagoon the contribution to O_2 production by taking into account daily variation and not only net production but also community-level respiration. Hourly production was derived from measurements taken in the benthic chambers (**Fig. 82**), while daily NCP was obtained as the sum of these contributions.

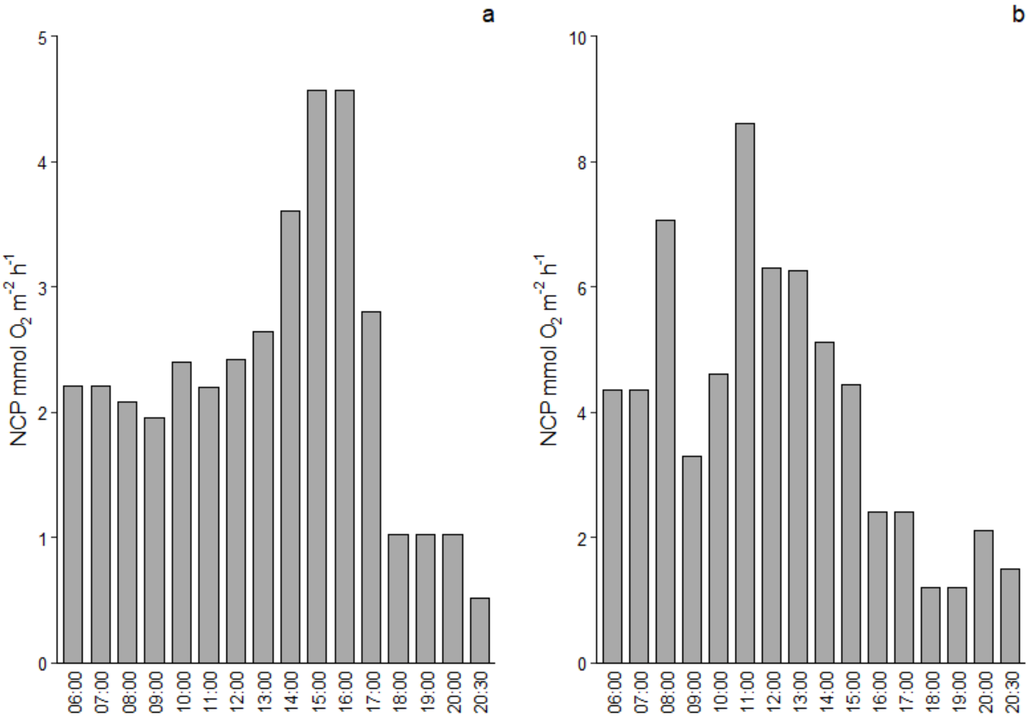


Figure 82: Daily NCP calculated per hour for *Z. marina* (a) and *Z. noltei* (b).

Community respiration (CR) was calculated by multiplying the average respiration of the two replicates by 24 hours. Finally, gross community respiration (GCP) was estimated as the sum of CR and NCP. The values of GCP, CR e NCP obtained for *Z. marina* were 90.0, 52.8 and 37.2 mmol O_2 m^{-2} day^{-1} respectively, while for *Z. noltei* the values were 398.5, 333.4 and 65.1 mmol O_2 m^{-2} day^{-1} respectively. The data obtained are in accordance with those reported in the review made by Duarte et al. (2010) (GCP: $177\underline{+}122$ and $250\underline{+}187$ mmol O_2 m^{-2} day^{-1} for *Z. marina* and *Z. noltei* respectively; CR: $176\underline{+}107$ and $161\underline{+}148$ mmol O_2 m^{-2} day^{-1} for *Z. marina* and *Z. noltei* respectively and NCP: $42.9\underline{+}49.9$ and $127\underline{+}128$ mmol O_2 m^{-2} day^{-1} for *Z. marina* and *Z. noltei* respectively). However, considering the great seasonal variability and in order to obtain reliable estimates of annual primary production and CO_2 sequestration for Venice Lagoon, at least monthly sampling campaigns should be carried out.

5 CONCLUSIONS

The thesis provides an important link between photosynthesis, primary production and carbon stored at the sediment level, updating the NPP of aquatic angiosperms in the last 20 years, estimating for the first time in the Venice Lagoon the CO_2 trapped through photosynthesis and the amount of carbon permanently retained by these plants. Over the past two decades, there has been a progressive improvement in environmental conditions of the Venice Lagoon with a recolonisation by aquatic angiosperms, resulting in a significant increase of their primary production and carbon sequestration. Further studies would be interesting in order to investigate not only the temporal variability of these contributions, but also the spatial variability within the meadows of each individual species. This would allow a better understanding of the environmental factors influencing nutrient and carbon contents and atmospheric CO_2 uptake in order to obtain as complete a picture as possible of their interactions, particularly in areas characterised by high temperature and tidal ranges.

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Estratto per riassunto della tesi di dottorato

Studente: YARI TONIO matricola: 838600

Dottorato: SCIENZE AMBIENTALI

Ciclo: 35°

Titolo della tesi: STUDY OF PRIMARY PRODUCTION OF SEAGRASSES IN VENICE LAGOON

ABSTRACT:

Seagrasses are a group of aquatic angiosperm monocots which adapted to live in marine, lagoonal and coastal environments in totally submerged conditions. Seagrass meadows provide high-value ecosystem services and represent one of the most important primary producers in marine-coastal and lagoonal ecosystems with an average net production of 27.2±5.8 mmol O_2 m^{-2} day^{-1}. Moreover, seagrass meadows are also considered a significant sink for atmospheric CO_2 with a great capacity to sequester and store carbon within their sediment, contributing to the sequestration of about 20% of the global carbon in marine sediments despite occupying only 0.1% of marine surface. The total ecosystem services provided by the presence of seagrass meadows are estimated in \$34,000 ha^{-1} $year^{-1}$. Nevertheless, since they are located in coastal-marine and transitional environments which are some of the most impacted areas by anthropogenic activities, seagrass meadows have declined due to human pressures at a rate of approx. 110 km^2 $year^{-1}$ between 1980 and 2006. The PhD thesis is part of this context and aims to carry out an update of primary production values after almost 20 years since the last ones available in bibliography (2003). The thesis also fits within the Corila Venezia2021 scientific research program which intends to monitor the testing phase of the tidal regulation project known as MOSE (MOdulo Sperimentale Elettromeccanico or Experimental Electromechanical Module). The thesis aimed at obtaining as complete a picture as possible of the primary production of seagrasses and their communities and their contribution to CO_2 capture and carbon sequestration in Venice Lagoon. The Net Primary Production (NPP) of four species (*Zostera marina*, *Zostera noltei*, *Cymodocea nodosa* and *Ruppia cirrhosa*) was calculated by the "leaf-marking" technique and/or the positive changes in monthly leaf and rhizome biomasses. In particular, NPPs of *Z. marina*, *Z. noltei* and *C. nodosa* were calculated by two annual sampling campaigns on a monthly basis in 2019 and 2020/2021 to update NPP combined with the mapping carried out in 2018 and 2021 and to assess possible impacts to seagrass communities from the MOSE project. NPP of *R. cirrhosa* was determined by one annual sampling campaign on a monthly basis in 2021/2022 in order to update its contribution to the global seagrass NPP after 25 years since the last study conducted in Venice Lagoon (1997). Biomasses collected in the 2019 sampling campaign have been analysed to calculate nutrient and carbon concentrations in order to obtain an estimation of carbon sequestration and total phosphorous and nitrogen contents. Moreover, a total of 5 sampling campaigns was carried out in 2019/2020 (August, October, February and June) and 2022 (July) in order to estimate the inter-seasonal and daily primary production of two seagrass communities (*Z. marina* and *Z. noltei*) under the same environmental conditions in one station by variation on oxygen concentrations in benthic chambers using short incubation time (1.5-2 hours). Daily net community productions were calculated by repeated measurements in order to cover the whole photoperiod and at least two measurements of respiration at the end of photoperiod. All these measurements provide an important link between photosynthesis, primary production and carbon stored at the sediment level: a very important factor when taking into account the effects of climate change, its possible repercussions on aquatic and coastal ecosystems, the importance of meadows, the ecosystem services associated with them and their conservation.

ABSTRACT ITALIANO

Le fanerogame sono un gruppo di angiosperme monocotiledoni che si sono adattate a vivere negli ambienti marini, lagunari e costieri in condizioni totalmente sommerse. Le praterie di fanerogame forniscono ecosistemi di alto valore ambientale e rappresentano uno dei più importanti produttori primari negli ambienti marino-costieri e lagunari con una produzione primaria netta stimata in 27.2 ± 5.8 mmol O_2 giorno^{-1}. Le praterie di fanerogame sono anche considerate degli importanti serbatoi per la CO_2 atmosferica con una grande capacità di sequestrare e immagazzinare carbonio all'interno del loro sedimento e contribuendo al sequestro di circa il 20% del carbonio presente nel sedimento marino nonostante ne occupino solamente lo 0.1% della superficie. La somma di tutti i servizi ecosistemici forniti dalle fanerogame è stata stimata in \$34,000 ha^{-1} anno^{-1}. Nonostante ciò, trovandosi nelle aree marine-costiere e nei sistemi lagunari che rappresentano alcune delle aree più impattate, le praterie di fanerogame hanno subito un declino di circa 110 km^2 anno^{-1} tra il 1980 e il 2006 a causa delle attività antropiche. La tesi di dottorato si inserisce all'interno di questo contesto e mira a portare un aggiornamento della produzione primaria in laguna di Venezia dopo quasi 20 anni dall'ultima disponibile in bibliografia (2003). La tesi inoltre è inserita all'interno del programma di ricerca scientifica Corila Venezia2021 che segue il monitoraggio delle fasi di *test* del progetto per la regolazione della marea noto come MOSE (Modulo Sperimentale Elettromeccanico). La tesi mira quindi ad ottenere un quadro più completo possibile sulla produzione primaria delle fanerogame e delle loro comunità e sul loro contributo alla cattura di CO_2 e sul sequestro del carbonio in laguna di Venezia. La Produzione Primaria Netta (PPN) di quattro specie di fanerogame (*Zostera marina*, *Zostera noltei*, *Cymodocea nodosa* e *Ruppia cirrhosa*) è stata calcolata per mezzo della tecnica "*leaf marking*" e/o le variazioni positive delle biomasse mensili di foglie e rizomi. In particolare, le PPN di *Z. marina*, *Z. noltei* e *C. nodosa* sono state calcolate a seguito di due campionamenti annuali a cadenza mensile nel 2019 e nel 2020/2021 al fine di aggiornare la PPN lagunare combinando i dati alle mappature del 2018 e del 2021 e valutare possibili impatti sulle loro comunità dal progetto MOSE. La PPN di *R. cirrhosa* è stata invece determinata in un campionamento annuale a cadenza mensile nel 2021/2022 al fine di stimare il contributo di questa specie alla PPN lagunare globale dopo 25 anni dall'ultimo studio condotto in laguna di Venezia (1997). Le biomasse raccolte nel 2019 sono state analizzate al fine di calcolare i contenuti di nutrienti e carbonio per stimare il carbonio sequestrato e i contenuti di azoto e fosforo totali. Inoltre, sono state effettuate 5 campagne nel 2019/2020 (agosto, ottobre, febbraio e giugno) e nel 2022 (luglio) al fine di stimate la produzione primaria stagionale e giornaliera di due comunità di fanerogame (*Z. marina* e *Z. noltei*) nelle stesse condizioni ambientali in una stazione attraverso misurazioni delle variazioni delle concentrazioni di ossigeno all'interno di camere bentiche usando brevi tempi di incubazione (1.5-2 ore). Le produzioni primarie nette giornaliere delle comunità sono state calcolate attraverso misurazioni ripetute al fine di coprire l'intero fotoperiodo e almeno due misurazioni della respirazione alla fine del fotoperiodo stesso. Tutte queste misurazioni forniscono un importante *link* tra la fotosintesi, la produzione primaria e il carbonio immagazzinato a livello del sedimento: un fattore molto importante se si considerano gli effetti del cambiamento climatico, le possibili ripercussioni sugli ecosistemi acquatici e costieri, l'importanza delle praterie, dei servizi ecosistemici a loro associati e la loro conservazione.

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