University of Zagreb

Faculty of Science
Department of Geology

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Preservation of the endemic alga *Fucus virsoides* J. Agardh: Ecological factors responsible for its regression and extinction

DOCTORAL THESIS

Supervisor:
Ljiljana Iveša, PhD

Zagreb, 2025

Sveučilište u Zagrebu

Prirodoslovno-matematički fakultet
Geološki odsjek

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Očuvanje endemske alge *Fucus virsoides* J. Agardh: ekološki čimbenici odgovorni za njezinu regresiju i izumiranje

DOKTORSKI RAD

Mentorica:
dr. sc. Ljiljana Iveša

Zagreb, 2025

This doctoral thesis was carried out as part of the postgraduate program in Oceanology at the University of Zagreb, Faculty of Science, Department of Geology, under the supervision of Ljiljana Iveša, PhD, scientific advisor. The experimental part of the research was carried out in the Ruđer Bošković Institute, Center for Marine Research, Rovinj. Fieldwork part was conducted along the Istrian coast. The thesis itself was written in Center for Marine Research, Rovinj.

ZAHVALA

Prije svega se želim zahvaliti svojoj dragoj mentorici dr. sc. Ljiljani Iveša na trudu, strpljivosti, pomoći, požrtvovnosti i nemjerljivoj razini dobrote koju mi je pružila.

Zahvaljujem se članovima povjerenstva prof. dr. sc. Petru Kružiću, doc. dr. sc. Maji Mucko te dr.sc. Martinu Pfannkuchenu na savjetima za poboljšanje doktorskog rada. Također se zahvaljujem i prof. dr. sc. Zrinki Ljubešić na konstruktivnom savjetima tijekom formiranja teme i nacrta rada, kao i seminarskih aktivnosti.

Veliko hvala kolegama iz Laboratorija za ekologiju bentosa, posebno dr. sc. Andreji Bilajcu, koji je uvijek spremno uskočio kad je pomoć bila potrebna. Hvala puno i dr. sc. Marseju Markovskom na svoj pomoći, posebno u terenskim aktivnostima. Također sam izrazito zahvalan dr. sc. Mirjani Najdek Dragić, koja je uvijek bila tu za bilo kakav savjet ili pomoć, čak i u mirovini.

Zahvalan sam također svim ostalim kolegama s Centra za istraživanje mora u Rovinju na svakoj potpori koju su mi pružali kad je to bilo potrebno.

Hvala također svim prijateljima, prijateljicama, kolegicama i kolegama s vanjskih institucija i udruga na pomoći i podršci koju su mi pružali.

Za kraj, veliko hvala roditeljima Ivanki i Mariju, braći Mateju i Petru kao i široj obitelju za njihovo strpljenje i potporu.

Hvala van ča ste vajk bili smanon!

THANK YOU NOTE

Additionally, I would like to express huge thanks to Vittoria Ferrari, for being an amazing intern, colleague, and a great friend. Without her help, this achievement would have been a much harder and duller endeavour.

Also, a big thank you to Lilly Bartlakowski who, in her short internship with us has been an amazing addition to our team. I also extend gratitude to dr. Shannen Smith for her help during fieldwork activities.

“If anything can go wrong, it will.”

“If there is a possibility of several things going wrong, the one that will cause the most damage will be the first one to go wrong."

“If anything just cannot go wrong, it will anyway.“

- Murphy's 1st, 2nd & 3rd Laws

“In nature, nothing is ever right. Therefore, if everything is going right ... something is wrong.”

- Addition to Murphy's Laws

“Murphy was an optimist.“

- O'Toole's Commentary on Murphy's Laws

Sveučilište u Zagrebu Doktorski rad
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Jadranski bračić (*Fucus virsoides*, red Fucales) endemska je mediteranska alga trajnica koja isključivo nastanjuje pojas plime i oseke Jadranskog mora, gdje prirodno stvara guste pojaseve ili točkasta naselja od znatne ekološke važnosti. Tijekom posljednjih desetljeća vrsta je doživjela gotovo potpuni kolaps, nestavši s većine jadranskih obala od Italije do Albanije, no uzroci te regresije još uvijek nisu u potpunosti razjašnjeni. U ovom radu istražena je povijesna i recentna rasprostranjenost jadranskog bračića u Istri i susjednim dijelovima sjevernog Jadrana, pri čemu je dokumentiran i sustavan nestanak populacija te njihova zamjena sezonski prisutnim (oportunističkim) vrstama. Analizirana je i struktura populacija, morfologija te utjecaj vanjskih biotičkih čimbenika na proučavane populacije. Mjerenja temperature *in-situ* u naseljima jadranskog bračića pokazala su izrazite i brze promjene uzrokovane izmjenom izloženosti zraku i uronu u more, s najvećim ekstremima zabilježenim tijekom proljetnih danjih oseka. Također je eksperimentalno potvrđeno kako periodička izloženost vrhova talusa povišenim temperaturama zraka od 34°C može uzrokovati trajna oštećenja, gubitak mase te smanjenu fotosintetsku učinkovitost, uz znatno oslabljenu mogućnost oporavka. Na temelju svih tih spoznaja razvijen je i uspješno testiran protokol *ex-situ* uzgoja i restauracije jadranskog bračića. Iako je rani rast talusa spor, juvenilne jedinke presađene u pogodno stanište, uz zaštitu od brstioca, dosežu spolnu zrelost unutar 10 mjeseci, što potvrđuje potencijal metode u budućim konzervacijskim aktivnostima.

(168 stranica, 68 slika, 2 tablice, 189 literaturnih navoda, 6 priloga, jezik izvornika: engleski)

Ključne riječi: *Fucus virsoides*; povijesna distribucija; regresija; struktura zajednice; populacijska struktura; termotolerancija; restauracija

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Rad prihvaćen: 5. 12. 2025.

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Doctoral thesis

Preservation of the endemic alga *Fucus virsoides* J. Agardh: Ecological factors responsible for its regression and extinction

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Fucus virsoides (order Fucales), known also as the Adriatic Fucus, is an endemic Mediterranean perennial that inhabits exclusively the intertidal zone of the Adriatic Sea, where it naturally forms dense belts or patchy stands of significant ecological importance. Over the past decades, populations of *F. virsoides* have undergone almost complete collapse, disappearing from most of the Adriatic coast from Italy to Albania, though the causes of this regression are still uncertain. This study investigated the historical and recent distribution of *F. virsoides* along the Istrian coast and adjacent parts of the northern Adriatic Sea, documenting the systematic decline of populations and their replacement by opportunistic, ephemeral species. Population structure, morphology, and the influence of external biotic factors were also analysed within the study sites. *In-situ* temperature measurements in *Fucus* populations revealed sharp and rapid fluctuations caused by alternating aerial exposure and submersion, with the greatest extremes recorded during spring daytime low tides. Experimental trials further confirmed that periodic exposure of *F. virsoides* apices to the elevated air temperatures of 34°C can cause permanent thallus damage, biomass loss, and reduced photosynthetic efficiency, with markedly weakened recovery potential. Based on all these findings, a protocol for *ex-situ* cultivation and restoration of *F. virsoides* was developed and successfully tested. Although early thallus growth remains slow, juvenile individuals transplanted into suitable habitats, when protected from grazers, can reach reproductive maturity within 10 months, confirming the method's potential for future conservation efforts.

(168 pages, 68 figures, 2 tables, 189 references, 6 appendices, original in English)

Keywords: *Fucus virsoides*; historical distribution; regression; community structure; population structure; thermotolerance; restoration

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Thesis accepted: 5th December 2025.

INFORMATION ABOUT THE SUPERVISOR

Dr. Ljiljana Iveša is a Senior Scientist and Head of the Laboratory for Benthic Ecology at the Ruđer Bošković Institute, Center for Marine Research in Rovinj, Croatia. She holds a PhD in Biology, an M.Sc. in Oceanology, and a B.Sc. in Biology-Ecology from the University of Zagreb. With over two decades of research experience, she has built an extensive career focused on the study of marine benthic communities and the ecology of macroalgae. Since 2018, she has also been an Associate Professor at the University Juraj Dobrila in Pula, contributing significantly to the education of future marine scientists.

Her research expertise encompasses the taxonomy and ecology of seaweeds and seagrasses, with particular emphasis on canopy-forming brown algae (order *Fucales*), restoration of marine forests, non-indigenous species, and coastal habitat ecology. Dr. Iveša has coordinated and participated in numerous international and national scientific projects, including initiatives on biodiversity monitoring and restoration (*REFINE*, *MIRAMAR*, *CAMBioMed*, *HabCYS, BRIGANTINE*). She has authored or co-authored **45 scientific papers**, numerous technical reports, and conference presentations. Her scientific contributions have been recognized with multiple awards from the Ruđer Bošković Institute.

Beyond research, Dr. Iveša is actively involved in the international scientific community, serving as a reviewer for several scientific journals and as a representative in networks such as EuroMarine. She has organized scientific symposia, mentored numerous students at all academic levels, and contributed to the national monitoring and assessment of the ecological status of Croatian coastal waters. Fluent in English, German, and Italian, and an experienced scientific diver, she combines fieldwork expertise with leadership in marine ecological research and education in the Adriatic region.

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1. INTRODUCTION

1.1. Large brown algae - General overview

Forests of large brown algae (generalized as “kelps”) cover vast stretches of the world’s coastlines. When referring to large brown algae, this usually implies the order Laminariales, which includes algae with well differentiated thalli reaching from several to tens of meters in height (but also comprising smaller representatives), but nearly all are characteristic of oceanic coasts and areas where maximum temperatures rarely exceed 20°C (Steneck et al. 2002, Coleman and Wernberg 2017, Wernberg and Filbee-Dexter 2019). Alongside them, up to a few meters in height, are the order Fucales, also a highly developed and differentiated group, inhabiting both oceanic coasts as well as the enclosed seas (Dayton 1985, Steneck et al. 2002, Schiel and Foster 2006). Algae from the order Fucales are distributed from the mediolitoral down to the circalittoral zone and they often form dense “forests” with complex community structures, much like the giant kelps (Giaccone and Bruni 1973). For this reason, they are frequently referred to as “canopy-forming species”, as they effectively create layered communities within the vegetation, similar to terrestrial rainforests. Such “forests” provide rich habitats for numerous species and are vital for the preservation of biodiversity and the ecosystem services they support (Ballesteros et al. 2009, Sales et al. 2012, Cheminée et al. 2013, Thiriet et al. 2016).

Interestingly, although most large brown algae live attached to the seabed, some species can spend part or all of their life floating at the sea surface (e.g., *Sargassum fluitans* (Børgesen) Børgesen*, S. natans* (Linnaeus) Gaillon, *Gongolaria barbata f. aurantia* (Kützing) Falace, Alongi & Kaleb*, Gongolaria barbata* f. *repens* (A.D.Zinova & Kalugina) Sadogurska) (Antolić et al. 2011, Battelli and Catra 2021, Sadogurska et al. 2021). Unfortunately, forests of large brown algae are in regression worldwide, and in some cases have been completely lost, together with the communities they supported (Thibaut et al. 2005, Fujita 2011, Johnson et al. 2011, Ling et al. 2015, Iveša et al. 2016, Eger et al. 2022).

1.2. Large brown algae in the Mediterranean

The Mediterranean Sea hosts about 60 species of large brown algae, primarily from the order Fucales (56 species) and a few relict and non-native species of the order Laminariales (6 species) (Ribera et al. 1992, Iveša et al. 2022, Guiry and Guiry 2024). Mediterranean representatives of the order Fucales include the families Cystoseriaceae, Sargassaceae, and Fucaceae, while the order Laminariales includes only two native, very rare and relict species (Žuljević et al. 2016), together with several non-native species (Ribera et al. 1992). The most diverse group by far are the *Cystoseria sensu lato* (hereafter *Cystoseira s.l.*), which currently comprises of genera *Cystoseira*, *Ericaria* and *Gongolaria* (Ribera et al. 1992, Cormaci et al. 2012, Molinari-Novoa and Guiry 2020, Iveša et al. 2022, Bilajac 2024). Less represented is the genus *Sargassum* with six species (one invasive), and finally the genus *Fucus*, represented by only a single species, *Fucus virsoides* J.Agardh, which is endemic to the Adriatic Sea and considered a glacial relict (Boero et al. 2008).

1.3. Large brown algae in the Adriatic

In the Adriatic Sea, 16 species of *Cystoseira s.l.* have been recorded, along with four[1] species of *Sargassum* (one invasive), and one species each from the genera *Laminaria* (*L. rodriguezii* Bornet) and *Fucus* (*F. virsoides*) (Antolić et al. 2011, Battelli and Catra 2023, Bilajac 2024). In the northern Adriatic specifically, there are 11 species of *Cystoseira s.l.*, four *Sargassum* species (one invasive), and the beforementioned *F. virsoides,* endemic to the Adriatic sea.

Table 1. Overview of large brown algal species occurring in the northern Adriatic (Guiry and Guiry 2024).

Family	Genus	Species
Cystoseiraceae[2]	*Cystoseira*	*Cystoseira compressa* (Esper) Gerloff & Nizamuddin
		Cystoseira pustulata (Ercegovic) Neiva & Serrão
		Cystoseira humilis Schousboe ex Kützing
		Cystoseira foeniculacea (Linnaeus) Greville
	Gongolaria	*Gongolaria barbata* (Stackhouse) Kuntze
		Gongolaria sauvageauana (Hamel) Molinari & Guiry
		Gongolaria montagnei (J.Agardh) Kuntze
	Ericaria	*Ericaria amentacea* (C.Agardh) Molinari & Guiry
		Ericaria corniculata (Turner) Neiva & Serrão
		Ericaria crinita (Duby) Molinari & Guiry
		Ericaria dubia (Valiante) Neiva & Serrão
Sargassaceae	*Sargassum*	*Sargassum vulgare* C.Agardh, nom. illeg.
		Sargassum acinarium (Linnaeus) Setchell
		Sargassum hornschuchii C.Agardh
		Sargassum muticum (Yendo) Fensholt[3]
Fucaceae	*Fucus*	*Fucus virsoides* J.Agardh

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[1] Uncertain due to unclarified taxonomical status of *S. vulgare* (Guiry and Guiry, 2025).
[2] Currently included into family Sargasaceae and no longer used, only stated here for practicality.
[3] Invasive in the Adriatic, but not established along the eastern coast where only floating fragments are found.

1.4. Background information - *Fucus virsoides* J. Agardh (Fucales, Phaeophyceae)

Fucus virsoides, sometimes referred to as the “Adriatic fucus” is a species endemic to the Mediterranean Sea and the only member of its genus (out of approximately a dozen other representatives), that inhabits the coldest part of the Mediterranean: the Adriatic Sea (Ribera et al. 1992, Bianchi and Morri 2000, Bianchi 2007, Guiry and Guiry 2024). It grows in belts and patches along the rocky intertidal zones of the Adriatic (Figure 1), functioning as the ecological equivalent of larger congeners (such as *F. spiralis* Linnaeus*, F. distichus* Linnaeus and *F. vesiculosus* Linnaeus) that form extensive and continuous belts along the oceanic shores of colder seas, such as the Baltic and North Sea (Guiry and Guiry 2024). Occasionally, short-lived patches of *F. vesiculosus* and *F. spiralis* have been reported in the past, notably along the French Riviera (Lamouroux 1805, Naccari 1828, Sancholle 1988), but no long-term colonisation has been reported so far, likely due to the severe seawater and air temperature differences.

Figure 1. *Fucus virsoides* patch photographed at Hotel Delfin site (near Funtana, Istria) during 2021/2022 surveys.

1.5. Description

Fucus virsoides is an herbaceous brown alga found inhabiting the intertidal zone of the Adriatic Sea, reaching up to 20 cm (usually less) in length, sometimes with yellowish or olive-green hues. Linardić (1949) provided a detailed ecological description, classifying it as a mediolitoral alga that occupies both upper and lower mediolitoral zones, making it an "amphibious species".

Like other species in the order Fucales, *F. virsoides* is characterized by a differentiated thallus, in its essence consisting of three main parts (Figure 3):

1. Basal disc or rhizoid
2. Stipe or cauloid
3. Blade or phylloid

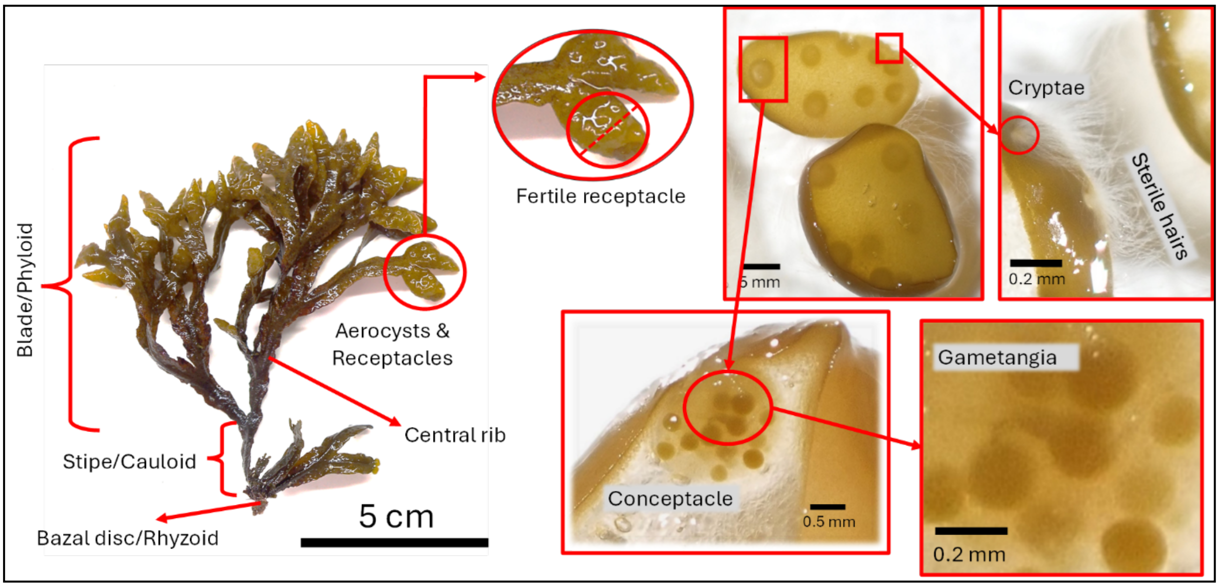

Figure 2. Structure of a *Fucus virsoides* thallus on both macro (left side) and micro scales (right side).

A central rib runs along the centre of each blade, extending to the growing tips, which develop aerocysts and receptacles (Figure 3). While the whole thallus can grow up to 20 cm in height, it more commonly remains under 10 cm. It is important to note that, despite the apparent differentiation of the thallus, brown algae do not have fully differentiated tissues, which, on the other hand, does contribute to their notable regenerative ability. Any damage affecting the central rib leads to branching or "proliferation" of the thallus (Figure 4).

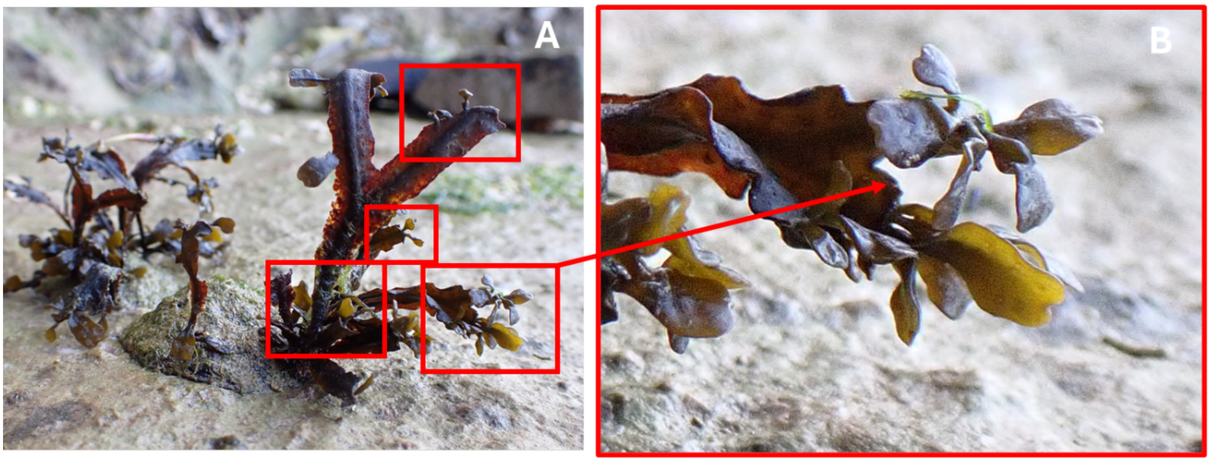

Figure 3. Proliferations as a result of thalli damage in *Fucus virsoides.*

Such proliferations can also grow from the basal disc, though this is less common. Additionally, wounds on the fleshy part of the phylloid can regenerate, either symmetrically or asymmetrically, but this does not significantly affect the thallus's life strategy.

The conceptacles (reproductive structures) are located within the receptacles, which are relatively large compared to related algae like *Cystoseira s.l.* The receptacles are found at the tips of aerocysts, which, in turn, grow at the ends of dichotomously branching phylloids (Figures 2 and 4). However, recent *in-situ* observations show that receptacles can form without any aerocysts. This may be a recent adaptation to external stressors (overgrazing, temperature, etc.) or a missed species trait.

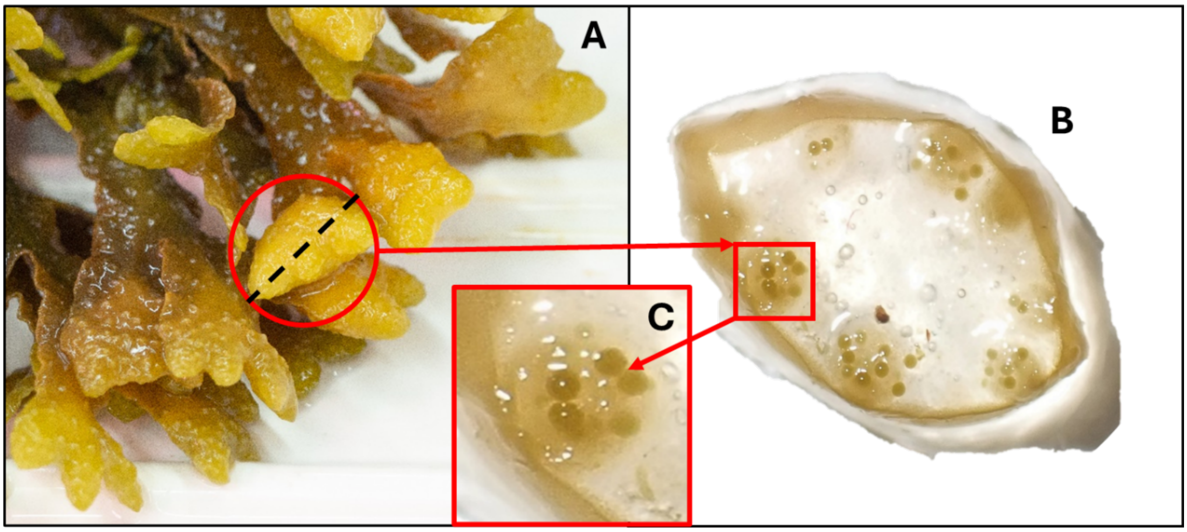

Figure 4. Reproductive structures of *Fucus virsoides*. A) shows receptacles on the top of aerocysts and apices, B) shows a transverse section of a receptacle, where C) conceptacles with gametangia are visible.

The reproductive cells (gametes) are contained within the gametangia; either antheridia (male) and oogonia (female), which are housed in conceptacles (Figures 2 and 4). Similar structures, akin to pores found along the thalli, but without gametangia, are called cryptae (Figure 2). These are characterized by long protruding sterile filaments whose function, believed to be nutrient absorption (Linardić, 1949), is not yet properly understood.

1.6. Nomenclature issues

From a scientific perspective, the nomenclature of this species was questioned when the French phycologist Sauvageau (1908) equated *Fucus virsoides* with the Atlantic species *F. platycarpus* var. *spiralis*. However, he later refuted this claim himself, and *F. virsoides* remained the accepted name (Linardić 1949, Guiry and Guiry 2024). Additionally, throughout the 20th century, several varieties of *F. virsoides* were described, but none were ultimately accepted, and such variation was attributed to the species' morphological plasticity (Schiffner 1916, Forti 1931, Schiffner and Vatova 1938, Linardić 1949, Guiry and Guiry 2024).

1.7. Life cycle

The life cycle of the *Fucus virsoides* can be divided into three stages:

1. Recruit stage - from the moment the zygote "germinates" until the formation of a basic thallus (Figure 5A).

2. Juvenile stage - encompasses the period from the formation of the basic thallus to the development of receptacles (Figure 5B).

3. Adult stage - at this stage, the *F. virsoides* has developed receptacles and is capable of reproduction (Figure 5C).

The development of the thallus, from the beginning of the juvenile stage to the sexually mature individual, takes about one year, during which growth speed may vary depending on the specific habitat's living conditions (Linardić 1949, Gljušćić et al. 2023).

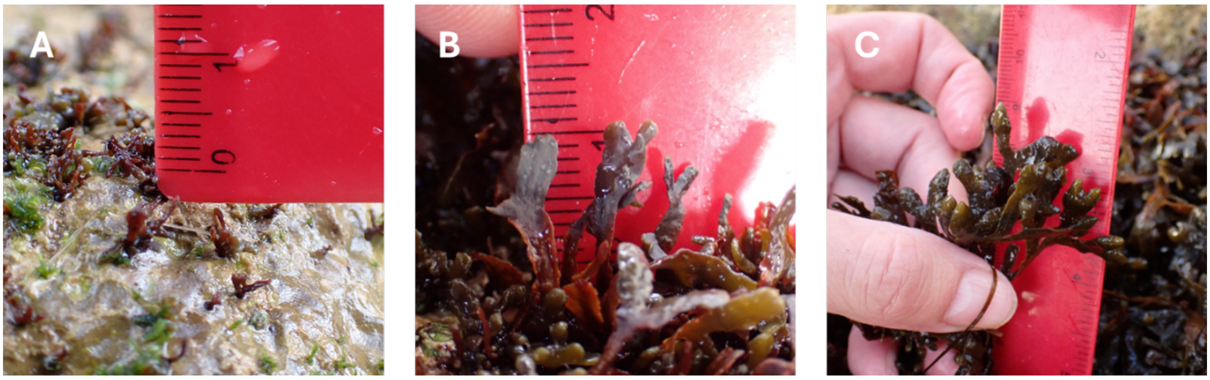

Figure 5. Developmental stages of *Fucus virsoides*: A) recruit, B) juvenile and C) adult.

1.8. Reproductive patterns

The reproductive cycle of *Fucus virsoides* is well-documented and is often compared to records and observations of Atlantic and Baltic *Fucus* species. According to Linardić (1949), the species gradually grows from late autumn to spring, reaching its vegetative peak and becoming sexually mature. Species is a known monoecious, with both male and female gametangia found on the same thallus (Thomé and Migula 1909)[4]. As temperatures rise, the alga gradually shrinks and deteriorates, although Linardić (1949) reports a more constant state of populations found near freshwater sources, attributing that to more constant temperature and reduced salinity. Interestingly, recent observations of populations along the Istrian coast indicate that fertile receptacles can be found in variable abundances throughout the entire year, which may be a recent adaptation to the shifting climate conditions. According to Linardić (1949), fertilization occurs in the water column, although if the reproductive material remains trapped in the protective slime layer for longer periods (e.g., during longer emersion periods), self-fertilisation and recruitment atop the receptacle itself or matron-thallus may occur (Linardić 1949, Gljušćić pers. obs.). The reproductive cells (gametes) are contained within antheridia (male) and oogonia (female), which are housed in conceptacles (Figure 4C).

1.9. Population structure

The population structure of *Fucus virsoides,* akin to most other large brown seaweed, can vary considerably within the studied area. This will depend on the recruitment patterns and phenology of the species, as well as external abiotic and biotic factors. It is also important to note that algae age does not often coincide with their size: small algae can be either young or old and may also delay their reproductive development according to the external factors (Chapman 1995).

Until now, no research into population structure or dynamics has been conducted on *F. virsoides,* although there is considerable information available on the species' phenology (Vatova 1948, Linardić 1949). Presumably, much of the population dynamics of the associated species (*F. spiralis*, *Pelvetia* spp.) can be applied to *F. virsoides* as well, although this needs to be confirmed *in-situ* or experimentally by long-term cohort monitoring. The first attempt to describe this species' population structure is, in fact, presented in this thesis.

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[4] *F. virsoides* (Don.) J. Ag. — *F. vesiculosus* var. Sherardi Turn. Thallus fast bandförmig oder fächerförmig dichotom geteilt, lederig, ohne Blasen, ganzrandig, 10 — 20 cm hoch, 5 — 10 mm breit mit linearen oder etwas keilförmigen, von einer deutlichen Mittelrippe durchzogenen Abschnitten. Fertile Endabschnitte lanzettlich-eirund, gepaart, zuweilen am Grunde zusammenmessend, oft blasig aufgetrieben. Conceptakel gleichzeitig Oogonien und Antheridien enthaltend. — Adriatisches Meer. (Thomé and Migula, 1909).

1.10. Community structure

Normally, *Fucus virsoides* forms a distinct "belt" within the mediolitoral, creating stratified communities (Figure 6). Sometimes, these belts will be “broken” into smaller patches, either due to habitat variations or degradation. These communities consist of densely growing thalli accompanied by various algal species, including those from the genera *Ulva* Linnaeus, *Chaetomorpha* Kützing, *Rivularia* C. Agardh ex Bornet & Flahault, *Gelidium* J. V. Lamouroux, *Gelidiella* Feldmann & G. Hamel, *Catenella* Greville, *Cystoseira s.l.*, *Caulerpa cylindracea* Sonder, *Laurencia* J. V. Lamouroux, and *Ectocarpus* Lyngbye. They also provide habitat for numerous animal species, such as gastropods (*Phorcus turbinatus* (Born, 1778), *Patella caerulea* Linnaeus, 1758, *Melarhaphe neritoides* (Linnaeus, 1758), crabs (*Pachygrapsus marmoratus* (Fabricius, 1787), isopods (*Ligia italica* Fabricius, 1798), barnacles (*Chthamalus* spp.), amphipods, chitons, vagile polychaetes, and bivalves (*Mytilus galloprovincialis* Lamarck, 1819, *Mytilaster minimus* (Poli, 1795), *Ostrea edulis* Linnaeus*, 1758*, *Magallana gigas* (Thunberg, 1793), among others (Figure 6) (Zavodnik 1967, Munda 1972, Čelig 2010, Kučinar 2014, Gljušćić 2016). The diversity and structure of the community will change with the seasons, with different groups exhibiting more dominance over the other (Gljušćić et al. *in prep*.). Presumably, the species diversity within a *Fucus* belt can be at least partially linked to the average cover of the *F. virsoides* thalli, which is linked to the moisture retention, forming a refuge for the smaller, more sensitive species (Pereira et al. 2025).

During low tide, some terrestrial animals, such as flies (Diptera), horseflies (Tabanidae), mosquitoes (Culicidae), mites (Acariformes), and other arachnids, can often be found in these communities, though this aspect remains unexplored (Zavodnik 1967). Birds have also been observed browsing the belts and patches during low tide, likely targeting crustaceans and the attracted insects and other protein-rich food. The presence of insects may be due to the availability of essential minerals, nutrients, or smaller prey species, suggesting intertidal communities may in fact “link” terrestrial and marine ecosystems to a degree. Even though *Fucus* settlements dry out during emersion, the lower layers retain moisture, providing refuge for many species (Migné et al. 2021, Roberts and Bracken 2021).

Such a community structure resembles the "*Fucus* belt", an equivalent of the rich mediolitoral algal habitats found in colder regions such as the Baltic Sea, the North Sea, and oceanic coasts (Chapman 1990).

Figure 6. Layered structure of *Fucus virsoides* canopy with base layer (blue), second layer (green) and main *Fucus*-layer (red).

1.11. Ecophysiology and habitat preferences

Fucus virsoides inhabits the central intertidal zone, preferring relatively sheltered areas such as bays and coves, which influences the variability and structure of its vegetation belt (Linardić 1949, Pignatti and Giaccone 1967, Zavodnik 1967, Munda 1972, Mačić 2006, Verlaque et al. 2019). While it can also occur in more exposed or calmer sites, these conditions strongly affect its abundance, settlement morphology, and thallus structure. Substrate slope and stability (immovability) exert similar influence (Linardić 1949, Munda 1972), with wind and wave exposure and substrate configuration identified as the main distributional drivers (Lipizer et al. 1995, Orlando-Bonaca et al. 2013).

The species can be described as euryvalent, tolerating broad variation in temperature, salinity, humidity, light, and hydrodynamics typically encountered in the mediolitoral zone (Linardić 1949). Linardić (1949) also suggested that high summer air temperatures could be the main limiting factor for its broader distribution, while Vouk (1938) emphasized temperature and salinity as key drivers. Although adapted to an amphibious lifestyle, with alternating exposure to air and water, critical factors such as air temperature, humidity, tidal dynamics, and solar radiation remain insufficiently studied under controlled conditions. Recent climate trends, including heatwaves, storms, and atmospheric extremes, may already pose severe challenges to the species' persistence (Gljušćić et al. 2023, Bilajac et al. 2024).

Seasonal and tidal cycles further shape exposure regimes. For instance, spring daytime low tides expose *F. virsoides* to relatively high air temperatures and cooler seawater, while summer nocturnal low tides produce the opposite effect (Gljušćić et al. 2025). The species tolerates a wide range of temperatures during both immersion and emersion, but damage and physiological stress do eventually occur (Gljušćić et al. 2025). If Linardić's hypothesis is valid, natural tidal rhythms may buffer *F. virsoides* against extreme seasonal conditions by limiting prolonged exposure to high seawater temperatures in summer while allowing greater light and warmth during colder seasons (Linardić 1949, Gljušćić et al. 2025). While plausible, this requires experimental validation.

Photosynthesis, a core physiological process, is highly sensitive to desiccation stress, with significant inhibition during prolonged aerial exposure (Dring and Brown 1982, Lipkin et al. 1993, Blouin et al. 2010). Many intertidal macroalgae, however, exhibit considerable tolerance, maintaining activity until severe water loss occurs (Johnson et al. 1974, Quadir et al. 1979, Oates and Murray 1983, Bidwell and McLachlan 1985, Madsen and Maberly 1990, Bell 1993). This phenomenon was actually studied specifically on *F. virsoides* during the 1970's and 1980's (Gessner and Hammer 1971, Kremer and Munda 1982), and more recent studies confirmed its noteworthy desiccation tolerance, with water loss nevertheless tightly linked to photosynthetic apparatus efficiency, and thus the physiological performance of the thallus itself (Descourvières et al. 2024c).

Despite its physiological resilience, long-term population trends shows a severe decline. Losses around Rovinj and shifts in other fucalean assemblages during the 1960s-1980s and beyond were attributed to pollution (Štirn 1965, Munda 1973, 1979b, 1980c, 1991, 1997). However, rapid regressions persisted even after deindustrialisation and improved water quality, with the species at the time still maintaining presence in some polluted localities (Orlando-Bonaca et al. 2013). In the late 1990s and early 2000s, partial recovery of certain fucalean species was reported, including *F. virsoides* (Hanel 2002, Zavodnik et al. 2002, Iveša and Djakovac 2015). Yet while some taxa later exhibited positive trends until around 2015/2016, *F. virsoides* continued its regression and local extinction across the northern Adriatic (Battelli 2016b, Rindi et al. 2019). In 2023, a species once widespread along the Istrian coast survived only in a few small populations near Funtana, Poreč, Novigrad, and Trget (Gljušćić et al. 2023), and more recently in just two remnant sites: a cohesive stand near Blaz cove (Raša Channel) and a small patch in Lanterna (Gljušćić et al. *in prep*.).

1.12. Spatial distribution

Today, *Fucus virsoides* persists only in small, isolated patches along the eastern Adriatic coast. Historically, however, its range extended along the rocky shoreline from Ancona, Italy, to Durrës, Albania (Figure 7), which marks the southernmost extent of its distribution (Battelli 2016a, Descourvières et al. 2024a, Gljušćić et al. 2025, Kashta 1996, Linardić 1949, Mačić 2006, Munda 1972, Orlando-Bonaca et al. 2013, Rindi et al. 2020, Zavodnik 1967). Although once common and widespread in the Adriatic, the species is now considered functionally extinct due to the low number and size of its already fragmented populations (Estes et al. 1989, Descourvières et al. 2024a).

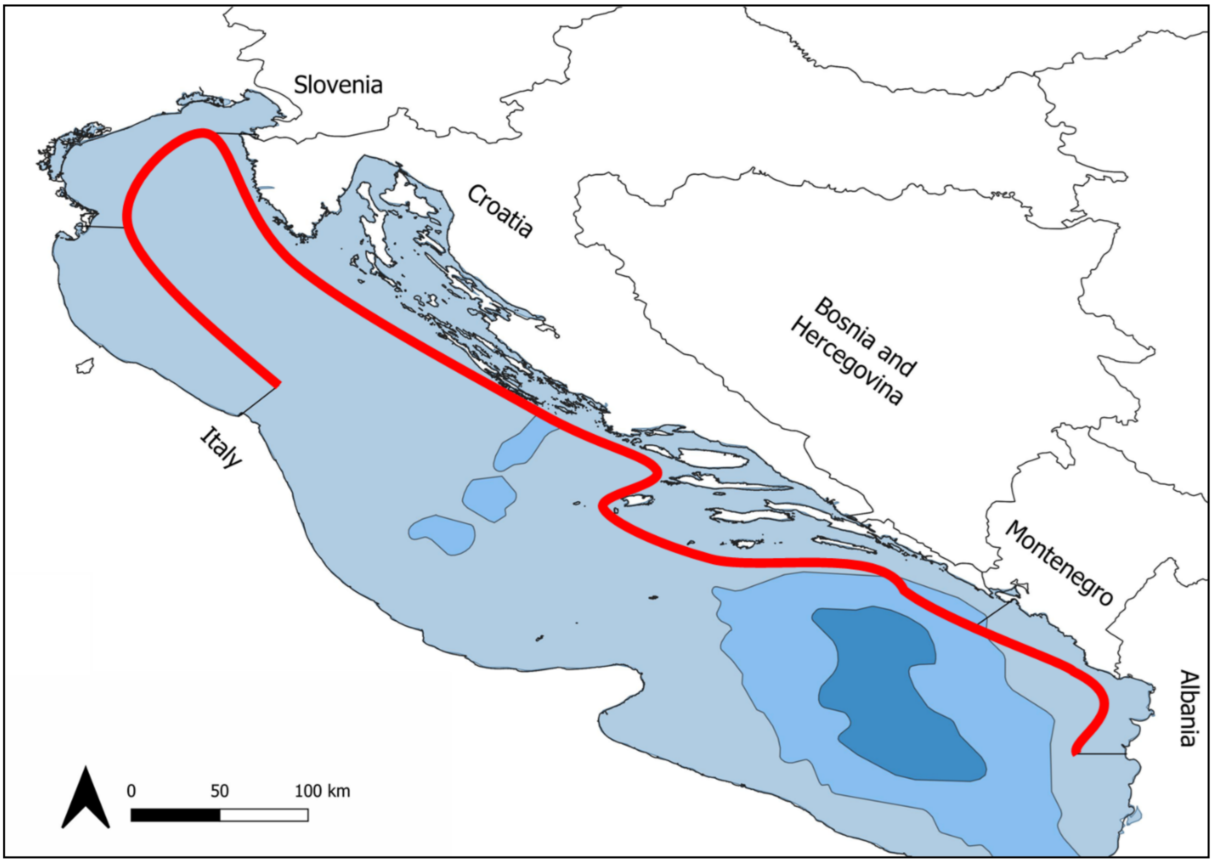

Figure 7. Historical area of presence of *Fucus virsoides* in the Adriatic Sea, with the red line marking its biogeographical range from Ancona, Italy, to Durrës, Albania. Note that *F. virsoides* only inhabits the mediolitoral zone along the rocky littoral coast and islands.

In the past, belts and patches of *Fucus virsoides* supported complex communities, despite the generally harsh conditions of the intertidal zone. Research on these communities was most active in the mid-20th century, with some studies continuing into the 21st century (Linardić 1949, Zavodnik 1967, Munda 1972, 1973, 1990, 1993b, Čelig 2010, Kučinar 2014, Gljušćić 2016).

In the northern Adriatic Sea, investigations were generally limited in spatial scope, often concentrated near the town of Rovinj during the latter half of the 20th century. In nearby Slovenia, with its much shorter coastline, populations of *F. virsoides* have been studied in more detail, particularly regarding habitat preferences, pollution impacts, and distributional controls (Vukovič 1982, Battelli 2002, 2013, 2016b, Rindi and Battelli 2005, Falace et al. 2010, Orlando-Bonaca et al. 2013).

Elsewhere, in the Gulf of Trieste and beyond along the Italian coast, the species has been a subject (either fully or partially) of study since at least the early 20th century (Forti 1931, Schiffner and Vatova 1938, Giaccone and Pignatti 1967, Pignatti and Giaccone 1967, Giaccone 1978, Lipizer et al. 1995, Cormaci et al. 2012, Orlando-Bonaca et al. 2013, Falace et al. 2018, Felline et al. 2019, Rindi et al. 2020, 2024, Kaleb et al. 2022).

Historical records and herbarium collections from the 19th and early 20th centuries show that *F. virsoides* was once abundant throughout the northern Adriatic, particularly along the western Istrian coast and in the Bay of Trieste (Schiffner 1916, Vatova 1928, Linardić 1940, 1949, Battelli 1999, 2016b, Munda 2000, Battelli and Alberti 2003, Rindi et al. 2020, Algae Herbarium Portal 2025). During the 1960s and 1970s, dense populations were reported near Rovinj, with biomasses reaching up to 5 kg/m² (218 g/400 cm²) (Munda 1973). Later assessments in nearby locations revealed lower values, ranging from 2.6-3.5 kg/m² (107-140 g/400 cm²) in 1999, and even further reduced to 0.5-2.5 kg/m² (20-100 g/400 cm²) by 2014 (Zavodnik et al. 2002, Kučinar 2014).

Despite the species previously assumed wide distribution, many coastal sites along the Croatian part of the Istrian peninsula, outside of the Rovinj area, remained unmapped until the early 21st century. Consequently, data on the species' distribution and abundance were largely reliant on outdated literature (Linardić 1949), significantly hindering efforts toward practical conservation and legal protection.

Over the past 30 years, the distribution and abundance of *F. virsoides* have declined significantly. Signs of regression were already mentioned in the 1960s and 1970s, suggesting that biomass levels prior to this period may have been even higher, and that the decline could have begun earlier, possibly coinciding with the onset of coastal industrialization (Štirn 1965, Zavodnik 1967, Munda 1972, 1980c, 1991, Gljušćić et al. 2023, Descourvières et al. 2024a). Unfortunately, literature from the 19th and early 20th centuries, including herbarium records, lacks quantitative or semi-quantitative data. These sources primarily document species presence at specific sites and times (via collection or a note), along with some morphological descriptions

(Schiffner 1916, Vatova 1928, Linardić 1949, Battelli 1999, Munda 2000, Battelli and Alberti 2003, Rindi et al. 2020), making it impossible to reconstruct long-term trends in biomass or standing crop.

Although *F. virsoides* was historically regarded as an "indicator species" sensitive to the trophic state of the habitat, later research has shown that substrate characteristics and exposure to wind and wave action are more critical factors in determining its distribution (Munda 1980a, Kremer and Munda 1982, Lipizer et al. 1995, Orlando-Bonaca et al. 2013). Nonetheless, a potential association with freshwater input cannot be entirely ruled out (Linardić 1949).

The causes behind the ongoing regression of *F. virsoides* populations remain uncertain. Battelli (2016a) outlines possible drivers for decline along the Slovenian coast, but a definitive explanation at the broader Adriatic scale is still lacking, even to this day (Descourvières et al. 2024a). What is clear, however, is that habitat loss due to anthropogenic coastal modification poses one of the most significant threats, not only to *F. virsoides,* but to many coastal terrestrial and marine species (Gljušćić et al. *in prep*.). At the same time, changing climate conditions, affecting both atmospheric and marine environments, cannot be discounted, especially given the species' dependence on both systems (Linardić 1949, Gljušćić et al. 2025).

1.13. Intertidal conditions in the northern Adriatic

In the northern Adriatic Sea, tidal patterns alternate biweekly between "semi-diurnal tides" (two high and two low tides per day) and "diurnal tides" (one high and one low tide per day) (Malačič and Viezzoli 2000, Battelli and Catra 2021). The greatest tidal range within the Adriatic, reaching 1 meter, occurs in the Gulf of Trieste (Vilibić et al. 2017).

The daily timing of the lowest low tides, typically associated with syzygy (new and full moons), shifts with the seasons. During winter and spring, the lowest water levels generally occur during the day or evening, whereas in summer and autumn they tend to occur at night or early morning (Vilibić et al. 2017, Hydrographic Institute of the Republic of Croatia 2025). Understanding the tidal dynamics is crucial for planning, monitoring, sampling and any form of research in the intertidal zone. This is also important for *ex-situ* research approaches, adding to the complexity of each planned or conducted experiment.

Spring conditions, along with occasional early summer mornings, can correspond with particularly harsh environmental stress during low tide. These periods may expose intertidal zones to extreme air temperatures (both high and low), dry air and high solar irradiation. Such conditions can pose significant challenges for intertidal flora, leading to severe water loss and photoinhibition, leading to both morphological and physiological stress to the exposed thalli

(Schonbeck and Norton 1980, Martone et al. 2010, Guenther and Martone 2014, Gljušćić et al. 2023). Species inhabiting these areas have adapted to their environment, though, being very resistant to desiccation, either through physiological means or via intra/interspecific relationships (dense growth patterns and layered canopy formation).

Understanding the full set of conditions that can be encountered in the intertidal zone is very important for describing the complex array of stressors and the mechanisms species inhabiting these areas may use for coping with them.

1.14. Conservation aspects

Along the Istrian coast as well as beyond, *Fucus virsoides* is ecologically effectively extinct because its current abundance no longer allows it to be a significant part of the trophic network (Estes et al. 1989). In a conservation sense, it can also potentially be considered a "plant species with extremely small populations" (PSESP) due to its very small numbers, insufficient for long-term survival in nature, and a negative abundance trend (Ma et al. 2013, Cogoni et al. 2021). Main threats to the species' survival appear to be climate change, which directly and indirectly modifies the biotic and abiotic factors associated with *F. virsoides,* and direct human involvement, through localised pollution (likely not critical anymore), but more so the coastal modification and artificial beach creation, which represents almost total habitat destruction and can be detrimental for the wider benthic communities (Airoldi and Beck 2007, Pitacco et al. 2013, Mamo et al. 2021).

As a consequence of the increasingly negative trend in the abundance of fucalean algae in the Mediterranean, including *F. virsoides,* several restoration methods have been developed (Falace et al. 2006, Cebrian et al. 2021, Kaleb et al. 2022, Gljušćić et al. 2023, Smith et al. 2023), particularly for strengthening weakened populations or reintroducing the species in depopulated areas.

1. Transplantation of adult individuals (Falace et al. 2006, Susini et al. 2007, Perkol-Finkel and Airoldi 2010, Robiveux 2013).
2. *Ex-situ* cultivation and planting (Verdura et al. 2018, De La Fuente et al. 2019, Largo et al. 2020, Orlando-Bonaca et al. 2021, Lokovšek et al. 2024, 2025).
3. *In-situ* manipulation, such as substrate cleaning, predator removal, etc. (Verdura et al. 2018, Piazzi and Ceccherelli 2019, Tamburello et al. 2019, Medrano et al. 2020).

The first method involves transplanting adult individuals from donor populations to weakened habitats or locations where the species has disappeared or has not previously grown. The success of this method depends on the survival of artificially secured individuals and their fitness, or reproductive potential. Additionally, transplantation is more successful with species that have sturdier and more resilient cauloids and the ability to survive in a free-living form, without a holdfast (genera *Gongolaria* and *Ericaria*). This approach is not desirable for *F. virsoides* due to its thin and more sensitive cauloid, as well as a much smaller holdfast, which significantly complicates attachment. Monitoring growth and development during a transplantation experiment on the related species *F. vesiculosus* have been conducted in the Baltic Sea (Kautsky et al. 2019), but the results are not applicable to *F. virsoides* due to differing life strategies and significant differences in ecological factors between the Baltic and the Adriatic, although both areas, at least, share microtidal dynamics.

The second method involves collecting fertile receptacles (see Figure 5) and seeding substrates (tiles, pebbles, rocks, ropes, etc.) with zygotes, and incubating individuals under aquarium conditions until they reach a certain size. Once they reach the desired size, the juveniles are secured to the desired location in the most practical way and, if necessary, protected with cages from herbivores. This approach was used in Gljušćić et al. (2023) and is currently the only successful published example of *ex-situ* cultivation and planting of the *F. virsoides*. The method itself has been adopted from (Orlando-Bonaca et al. 2021) and adapted for large receptacles of the *Fucus* genus. A similar approach has also been independently attempted by Kaleb et al. (2022), albeit with less success.

The third method involves *in-situ* habitat manipulation by modifying biotic or abiotic factors that affect the reproduction or survival of the target species. This approach could be beneficial if one of the stronger factors causing the disappearance of *F. virsoides* is identified (e.g., excessive grazing or presence of invasive species) (Battelli 2016b). Additionally, determining the responses of potential herbivores of the *F. virsoides*, as well as other species, to the presence of their predators opens up the possibility of using certain species as repellents (Pagès et al. 2021).

It is important to note that, unlike the traditional methods used to commercially restore/cultivate kelp in certain parts of the world, such work involving fucalean species is, in a vast majority of cases, still very much experimental, and implemented at a comparatively small scale (Eger et al. 2022, 2024).

1.15. *Ex-situ* cultivation of *Fucus virsoides*

As previously mentioned, the cultivation of large brown algae has become part of numerous research and restoration projects over the past twenty years, all aimed at restoring marine forests across the Mediterranean Sea and beyond (Cebrian et al. 2021, Eger et al. 2022, Orlando-Bonaca et al. 2022). By modifying the cultivation protocols for the genera *Ericaria* and *Gongolaria*, a method of *ex-situ* cultivation for *Fucus virsoides* has recently been developed, which has proven successful on a smaller scale and has been repeated several times outside of experimental frameworks (Gljušćić et al. 2023).

The biggest challenge remains the intensive early cultivation, typically 3-4 weeks for species of *Cystoseira s.l.*, which would significantly reduce the incubation time before planting. Currently, using only natural seawater and basic aquarium equipment, the incubation period to juvenile individuals lasts for months, which is considerably longer than under natural conditions, and sometimes the thalli never reach the juvenile stage, remaining as recruits (Gljušćić et al. 2023). Increasing the early growth rate is crucial for *F. virsoides* cultivation (to be further discussed in this manuscript).

2. LITERATURE OVERVIEW AND PRIOR RESEARCH

Phycological research in the northern Adriatic Sea, particularly in Istria, has a long but fragmented history shaped by the region's complex political changes. The early floristic surveys and species records became more systematic ecological studies and research projects from the late 19th century onwards, often building upon earlier records and studies from the wider Adriatic Sea (Lamouroux 1805, Naccari 1828) and the Mediterranean Sea. While this research was very wide, involving all the algae species (including misrepresented taxa) able to be found at the time (either collected, found washed-up or by the public), large leathery brown seaweed (Fucales), including *Fucus virsoides,* often received more attention.

2.1. Northern Adriatic Sea - Croatian part of the Istrian peninsula

The area that today represents the Croatian coast of the Istrian peninsula became an important area for phycological research already at the turn of the 20th century, which was aided by the opening of the biological station of the Berlin aquarium in Rovinj (later becoming the Center for Marine Research) in 1891. Prominent contributors (both as collectors and phycologists, local and foreign) included Zaratin, Kuckuck, Hansgirg, Hauck, Lucas, de Toni, and later Schiller, Schussnig, Schiffner, Camerloeh, Krumbach, and Vatova (Vatova 1928, 1948, Munda 2000, Battelli and Alberti 2003). While often not directly based in Istria, much of their work has been conducted along the Istrian coastline.

Josip Linardić further advanced knowledge with his doctoral thesis (published posthumously in 1949), which presented data on *F.ucus virsoides* taxonomy, morphology, phenology, physiology and distribution (Linardić 1940, 1949). Together with Vouk (1938), he also investigated habitat preferences, suggesting salinity and average seawater temperature as key distributional limits. Even though based outside of the Istrian region, Linardić provided much of the valuable information about the presence and distribution of *F. virsoides* in Istria and beyond via correspondence with, at the time, Italian and German scientists (Vatova, Schiller and others), but was not at the time able to physically conduct field studies in this area.

From the 1960s onwards, coastal industrialization spurred numerous studies focused on community succession, biomass changes, and ecophysiology of algae, including *F. virsoides*, which was already considered an indicator species (Zavodnik 1967, Munda 1972, 1973, 1977, Zavodnik 1977, Munda 1980a, 1980c, Kremer and Munda 1982, Zavodnik and Juranić 1982, Munda 1990, 1991). These studies provided quality data, including detailed community structure and even algal standing crop estimates for several species, including *F. virsoides*, though most research remained limited to the Rovinj aquatorium (due to practical reasons). Later, from 1990 to 2010's, there was a noticeable gap in the research of *F. virsoides*, although some work involving the species was conducted (Munda 1993a, Munda and Veber 1996, Zavodnik et al. 2002). It was during this period that large-scale regressions of the species were becoming more obvious across the species range, thus prompting the more detailed examinations of the species distributions, but also scaling-back on the sampling due to the ever-decreasing biomass. Along the Croatian part of the Istrian coast, these were conducted via CARLIT monitoring programs, notes by resident scientists and also student theses (Čelig 2010, Kučinar 2014, Gljušćić 2016, Pavičić-Hamer et al. 2016). Most recent conducted research is presented in this thesis.

2.2. Northern Adriatic Sea - Ancona, Venice and Trieste

Early records of *Fucus virsoides* along the Italian Adriatic date back to the early 19th century with notes by Lamouroux (1805), Naccari (1828) and Zanardini (1841) who remarked its Adriatic endemism and distinction from Atlantic and Baltic congeners. Later, the herbarium of Irma Pierpaoli (1925-1951) documented the species along the Conero Riviera, while Sollazzi (1966-1967) recorded its disappearance there (Descourvières et al. 2024a, Rindi et al. 2024). Until the early 2000s, *F. virsoides* also persisted in the Venice Lagoon (where some patches may survive to this day) and coastal waters around Lido and Pellestrina (Descourvières et al. 2024a). The whole regression timeline of *F. virsoides* along the Italian coast between 1941 and 2004 has been comprehensively summarized by Descourvières et al. (2024a).

In the Gulf of Trieste, contributions to *F. virsoides* came from Linardić (1949), Pollesello et al. (1992), Lipizer (2017), Lipizer et al. (1995), Osterc and Stibilj (2008), Falace et al. (2010), Orlando-Bonaca et al. (2013) and Kaleb et al. (2022), reflecting a sustained international research effort spanning nearly a century. Most recent research, involving *F. virsoides* ecophysiology, was conducted during 2022-2024 (Descourvières et al. 2024b, 2024c), and was supplemented by the beforementioned comprehensive, internationally involved, Adriatic-wide examination of the species regression (Descourvières et al. 2024a).

2.3. Northern Adriatic - Slovenian coast

On the Slovenian coast, early phycological contributions, including data on the presence of *Fucus virsoides,* originated from Zaratin, Accurti, and Frater Pius Titius (Battelli 1999, Alberti and Battelli 2002, Battelli and Alberti 2003). In later decades, Matjašič and Štirn (1975) and Vukovič (1982, 1980) investigated intertidal communities including *F. virsoides*. Further research was conducted by Lipizer (2017), Lipizer et al. (1995) and Orlando-Bonaca et al.

(2013), further mapping its distribution in the Bay of Trieste, covering both Slovenian and adjacent Italian shores and investigation the species' habitat preferences. Battelli, together with collaborating scientists, carried out a series of studies targeting the intertidal community (Battelli 2002, 2013, 2016a, 2016b, Rindi and Battelli 2005), which unavoidably involved *F. virsoides* as one of the crucial intertidal species, but also the unfortunate report of its regional extinction from the Slovenian coast in 2016.

2.4. Studies involving morphology, ecophysiology and phenology of *Fucus virsoides*

A very comprehensive and early research conducted by Linardić (1949), which covered the morphology and physiology of the species in great detail, laid the groundwork for further studies. These relatively advanced studies on *Fucus virsoides* were conducted in the region as early as the late 1960's, and continued through the 1970's and 1980's. During this period, phycological research broadened to include analytical and experimental approaches not available before. Stress physiology and ecophysiological responses of *F. virsoides* to desiccation and pollution were investigated by Gessner and Hammer (1971), Kremer and Munda (1982), Müll and Munda (1979) and Munda and Kremer (1977). During the same period, large shifts in coastal community composition, involving replacement of *F. virsoides* in the intertidal, but also other dominant fucalean communities, with more ephemeral species, were noted mostly around Rovinj, but also along the rest of the northern Adriatic, which were linked primarily to pollution (Štirn 1965, Munda 1973, 1980a, 1982, Zavodnik and Juranić 1982, Munda 1991, 1993b). Some of these studies partially involved *F. virsoides,* in addition to the other shallow-water species, further emphasising its common presence as well as importance in the coastal ecosystems at the time. Much later, Lipizer et al. (1995) linked the distribution of *F. virsoides* to substrate type, wind, and wave exposure, complementing, but also, partly refuting the earlier statements. Similar conclusions were drawn by Orlando-Bonaca et al. (2013), although by then regression of the species was already much more pronounced (Battelli 2016b).

More recent ecophysiological studies have examined the effects of pollutants and climate-related stressors, including work by Falace et al. (2018), Felline et al. (2019), Descourvières et al. (2024c, 2024b) and Kaleb et al. (2022) in Trieste, and Gljušćić et al. (2025, this study) in Rovinj. Although *F. virsoides* continues to be of interest for ecological, conservation, and cultivation studies, long-term availability of material is becoming increasingly uncertain (Gljušćić et al., 2023, Descourvières et al., 2024a, Gljušćić et al. *in prep.*).

3. Hypotheses and research goals

Hypotheses for the conducted research were:

1) The overall abundance and settlement size of *Fucus virsoides* along Istrian coast of northern Adriatic Sea follows a negative trend.

2) Population structure (abundance of recruits vs. juveniles vs. adults) in northern Adriatic Sea varies on a spatial and temporal scale.

3) Unusually dry, warm, and sunny weather, if coincided with low tide periods, can have a long-term negative impact on the physiological state of the *F. virsoides* thalli.

4) *In-situ* cultivation and *ex-situ* restoration of *F. virsoides* settlements in northern Adriatic Sea is possible.

The established research goals for this thesis were:

1) Thoroughly map the distribution of *F. virsoides* along the Istrian coast and, if possible, nearby areas.

2) Investigate the community composition and population structure in the residual *F. virsoides* settlements along the Istrian coast.

3) Determine the impact of atmospheric conditions on the physiological state of *F. virsoides* during periods of low water (air exposure *ex-situ* experiments).

4) Develop a method for cultivation and potential restoration of *F. virsoides* settlements.

4. MATERIALS AND METHODS

4.1. Historical and current distribution of *Fucus virsoides*

Data on the presence of *Fucus virsoides* was collected from available sources dating back to the 19th century. This included published scientific literature, herbarium collections and more recent historical overviews containing relevant information. Localities where *F. virsoides* was found or noted in the past were georeferenced to the best possible degree, compiled into table form and converted into a layer using QGis (3.16.10).

Mapping conducted during this research project was conducted mainly during 2021, by foot along the whole western Istrian coast and parts of the eastern coast where the appropriate habitat is present (Figure 8A). After this activity was completed, further monitoring was undertaken via occasional check-ups, and during other specific research activities (such as sampling for receptacles, morphological and physiological studies, etc…) until the species vanished. Position of each settlement was noted and organised into a table; later integrated into a QGis layer.

4.2. Main study site identification

After the mapping of *Fucus virsoides* along the Istrian coast was concluded, the most resilient and representative sites were chosen for further research into the species ecophysiology, morphology, community and population structure. Due to the continuous disappearance of the species during the study, the chosen monitoring sites had to be modified several times. In 2023, four such sites were chosen.

The study site in Lanterna Camping (45.302134° N, 13.587469° E, Figure 8B) is located on the northern part of the western Istrian coast, near the Mirna river mouth (Figure 8B). Here, *F. virsoides* inhabits a shaded area (due to local geomorphology and local terrestrial vegetation cover), growing on a nearly horizontal limestone coastal substrate and is prone to damage from cobles, refuse, and excess sediment coming from the river on the opposite side of the bay. The thalli are also often found covered with discarded *Zostera marina* Linnaeus and *Nanozostera noltei* (Hornemann) Tomlinson & Posluszny leaves, which can help keep more humidity, but also decrease water movement, light availability, and induce necrosis. Part of the population also extended along the vertical parts of the coast on the site.

Site near Hotel Parentium (45.201935° N, 13.588387° E, Figure 8C), in Poreč municipality, is located in the central part of the western Istrian coast and represents an intertidal rockpool approximately 5 x 3 x 0.5m in dimensions, situated on a low, nearly horizontal coastline (Figure 8C). In this rockpool *Fucus* was located around and on the edges. The surrounding subtidal, low intertidal and rockpools host fucalean assemblages dominated by *Ericaria crinita* and *Cystoseira compressa*, with *Gongolaria barbata* and *C. foeniculacea* being present in lower ratios.

Site in Bijela uvala camping resort (45.186492° N, 13.589049° E, Figure 8D) is located a few kilometres south from Hotel Parentium (Figure 8D). Here, *F. virsoides* inhabited a near-horizontal intertidal area, but extended also around a nearby rockpool, partly inhabiting subvertical and vertical surfaces. The area is shaded due to specific orientation and the presence of terrestrial vegetation. The *F. virsoides* thalli in this site were often smothered by marine litter (seagrass, algae, human refuse), but also sometimes by cobbles from nearby artificial beaches during stormy weather conditions. The general area also hosts other fucalean assemblages, both in rockpools, the intertidal and shallow subtidal.

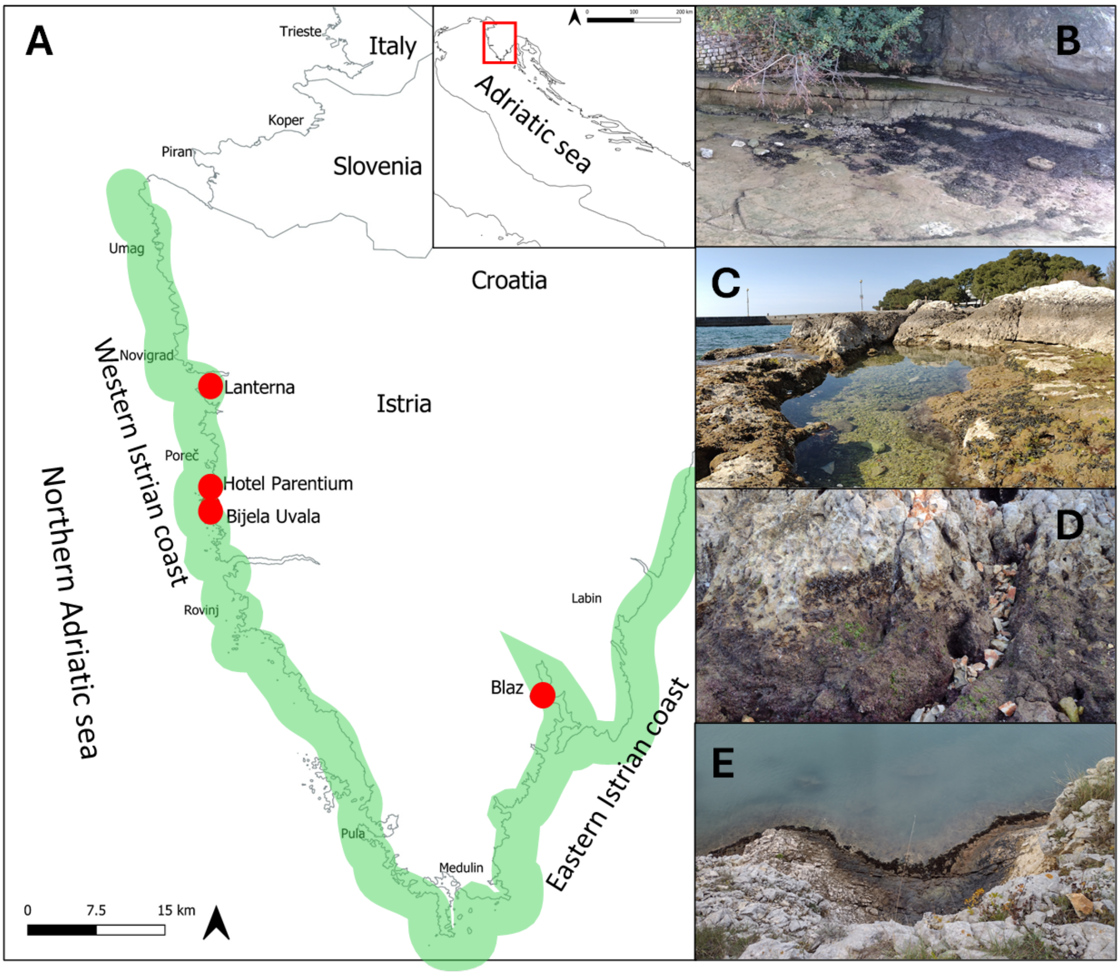

Figure 8. Map of the Istrian coast with the explored area marked in green, main study sites marked in red (A) and the image of the *Fucus virsoides* community at each site: B) Lanterna, C) Hotel Parentium, D) Bijela uvala and E) Blaz.

A locality near Blaz cove (45.000669° N, 14.043643° E, Figure 8E), within Raša Bay, near the village of Trget, on the eastern Istrian coast, hosts the largest remaining *F. virsoides* community on the Istrian coast, extending over 30 meters (with some breaks), but in a narrow belt, up to 50 cm in length (Figure 8E). The area is characterised by near-vertical, steep coastline covered with terrestrial vegetation, reducing the overall sunlight availability and severely limiting accessibility. The seawater in the area has transitional characteristics, its physical and chemical features highly dependent on the local Raša river and spring (terrestrial and underwater) input. The nearby area is utilised for mussel aquaculture as well as fishing. Also, the locality is devoid of any other fucalean species, likely due to less available substrate and very high turbidity, but is instead dominated by dense seagrass meadows (*Zostera* spp.).

4.3. *In-situ* temperature measurements

The intertidal nature of *Fucus virsoides* exposes it to severely and rapidly changing conditions in its habitat, whether periodically or randomly. Hourly temperatures within the *F. virsoides* belts were obtained using HOBO Pendant® Temperature/Light 64K data loggers deployed at four study sites (Figure 9). Loggers were attached to rocks amongst the thalli using drilled stainless steel rings and plastic cable ties and were exchanged monthly for data readout. Additionally, data was also collected from the *ex-situ* restoration experiment site for *F. virsoides* near Rovinj (see Section 4.5).

Among the four main monitored sites, only the site near Blaz (45.000669° N, 14.043643° E) was successfully monitored throughout the entire year. The temperature frequencies recorded in 2024 were analysed using a histogram plot. Furthermore, recorded hourly temperatures data were appended to the predicted daily low water times (adjusted for an approximate one-hour tidal delay) based on data for the city of Rijeka obtained from the "Asterion" webpage (https://www.asterion.info/). Data from Muča site near Rovinj (45.094374° N, 13.632883° E) was also included here, although the measurements were taken earlier, during the *ex-situ* restoration experiment, within the planted settlement (see Sections 4.8. and 5.11.).

4.4. Community structure in *Fucus virsoides* stands

The structure of remnant *Fucus virsoides* communities was assessed at four chosen study sites with the most representative stands: Lanterna, Hotel Parentium, Bijela uvala and Blaz. At each location, five 20 x 20 cm plots (Figure 10) were randomly placed and photographed each month throughout 2024. Photographs were analysed via ImageJ (Rasband 2024) software to quantify the coverage of sessile species.

Figure 9. HOBO Pendant® Temperature/Light 64K data loggers mounted within the monitored *Fucus virsoides* communities for temperature and light measurements in 4 most representative stands: Lanterna (A), Hotel Parentium (B), Bijela uvala (C), and Blaz cove (D).

All identified taxa were categorized into morphofunctional groups following the classification system of Steneck and Dethier (1994), with the addition of a distinct "sessile animal group", and are presented for each site on a monthly basis in Appendix 1. Unicellular algae were included in the "filamentous group" due to their growth patterns. The "leathery group," which consisted solely of *F. virsoides,* was excluded from this representation to avoid the dominance effect (population-level metrics for *F. virsoides* are reported separately). Although data were collected monthly, the community data were presented on a seasonal basis, grouped into three-month periods: Winter (December-February), Spring (March-May), Summer (June-August), and Autumn (September-November), as these seasonal groupings adequately captured patterns of community succession. Thus seasonal average cover for each morphofunctional group was expressed as mean (of all monthly measurements) ± standard error (abb. ± SE). Average taxa richness was likewise assessed on a seasonal basis.

In cases where *F. virsoides* disappeared during the monitoring period, data collection at those plots was discontinued since the studied community has been completely replaced by turf-forming species, which is already well known as a less-complex alternative state consisting of more ephemeral species (Munda 1972, 1980b, 1993a).

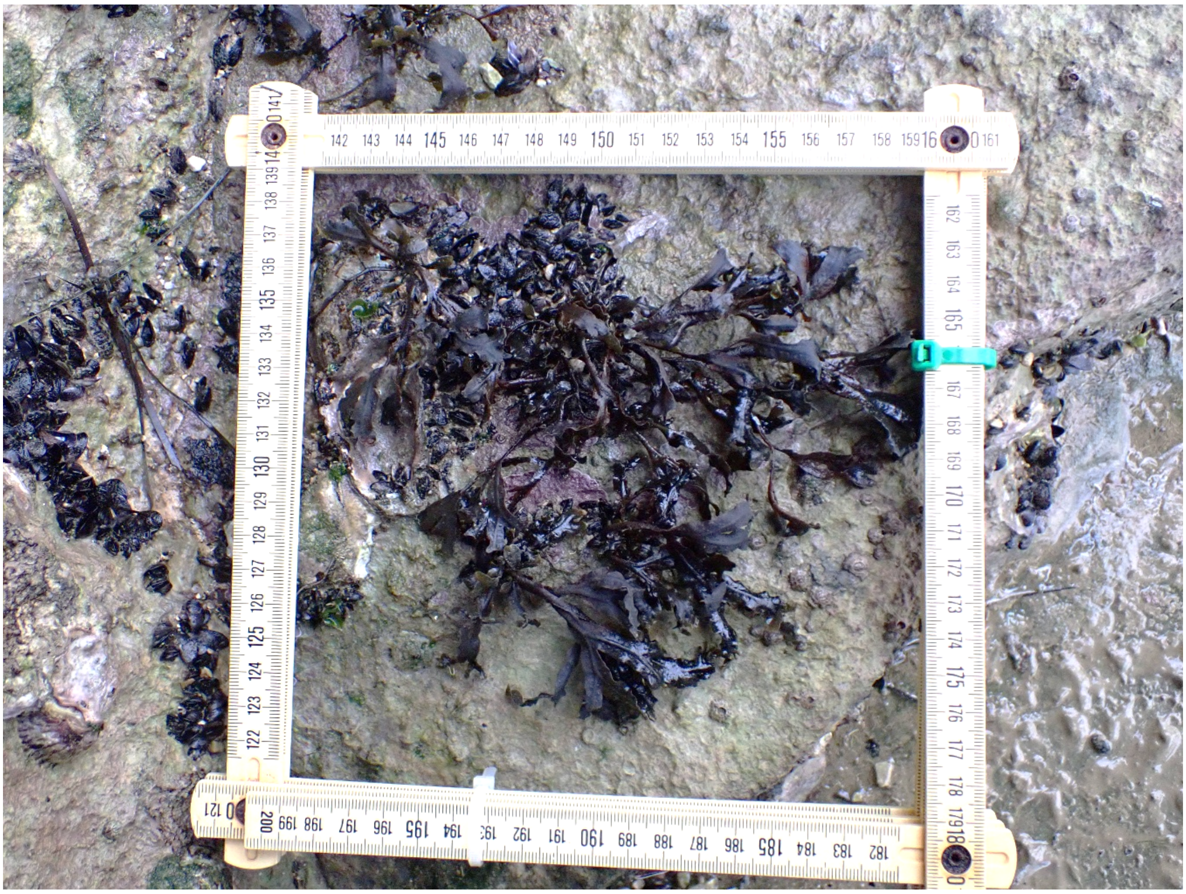

Figure 10. Sample plot (20 x 20 cm) used to asses *Fucus virsoides* community structure, population structure and related metrics.

To analyse seasonal variation in community structure at each site, a Principal Coordinates Analysis (PCoA) and a one-way PERMANOVA (factor: “Season”, 9999 permutations) with pairwise comparisons were performed. Both based on Bray - Curtis dissimilarity matrices. To assess the homogeneity of dispersion among groups, a PERMDISP analysis was also performed using Bray - Curtis dissimilarity and 9999 permutations. PERMDISP results were reported only when statistically significant and indicative of group dispersion heterogeneity, which in turn affects the fidelity of PERMANOVA analysis. Vagile taxa (e.g., gastropods, chitons, crustaceans, and insects) were excluded from the analysis, because their mobility can confound estimates of percent cover. This analysis was conducted via Primer v7 with PERMANOVA+ (Clarke and Gorley 2015, Anderson et al. 2008).

4.5. Population structure of *Fucus virsoides*

The population structure of *Fucus virsoides* was assessed at each site (Lanterna, Hotel Parentium, Bijela uvala, and Blaz cove) using 20 thalli per site, sampled within randomly placed

20 x 20 cm plots used for community assessment. In cases where fewer than 20 individuals were present within a plot, all available thalli were included in the analysis.

Due to the high developmental plasticity of fucalean algae, a small thallus may represent either a juvenile or an adult individual depending on local environmental conditions (Chapman 1995). This means that size structure often does not fit the age structure. Therefore, thallus age class (juvenile or adult) was determined not solely by size (height), but also by examining morphological characteristics, including overall thallus shape, the degree of central rib development, and the presence of aerocysts and reproductive structures (see Figures 2, 4, and 12).

The number of juvenile and adult individuals was expressed as the average count per age class per month (± SE), along with the juvenile to adult ratio. Due to practical reasons (small size, variable numbers and a very clustered distribution within the settlements), recruits were not distinguished separately from juveniles, which were considered to represent the most recent cohort of the population.

It is important to note that recruits observed during *ex-situ* cultivation and those observed *in-situ* can markedly differ due to different growth and development rates stemming from vastly different environments, for example: a 1-month-old lab-cultivated recruit borders 0.1 mm in height, while *in-situ* such recruit may already have a developed thallus shape and reach 0.5 cm, nearing a juvenile stage (Gljušćić et al. 2023; see Figures 5 and 11).

Figure 11. Different developmental stages in cultivated *Fucus virsoides*: A) recruit, B) juvenile and C) adult.

4.6. Morphology, phenology and other biotic metrics among thalli in the study sites

In addition to population structure, morphological variability among *Fucus virsoides* thalli was also evaluated across the study sites. Thallus height was measured using a ruler, and photographic documentation was employed to assist in the measurement process (Figure 12).

Average thallus height and cover percentage of *F. virsoides* were calculated and reported as monthly mean (± SE).

The presence of aerocysts was assessed as the percentage of thalli exhibiting developed aerocysts, while fertility was quantified as the percentage of thalli bearing mature receptacles. Both metrics were calculated as monthly means (± SE) and were compared with monthly grazing pressure, expressed as the average percentage of grazed thalli per month (± SE).

Damaged *F. virsoides* thalli typically undergo regeneration, either through thallus regrowth or the development of proliferations (Figure 3). Regeneration was quantified as the percentage of thalli showing any visible signs of regrowth. Similarly, necrosis was assessed as the percentage of thalli displaying necrotic "tissue". The source of necrosis, however, is very ambiguous and can be attributed to either grazing, environmental damage or seasonal "tissue" die-off in case of receptacles and/or aerocysts (Figure 12). These parameters were also expressed as monthly means (± SE) and analysed in relation to the grazing pressure.

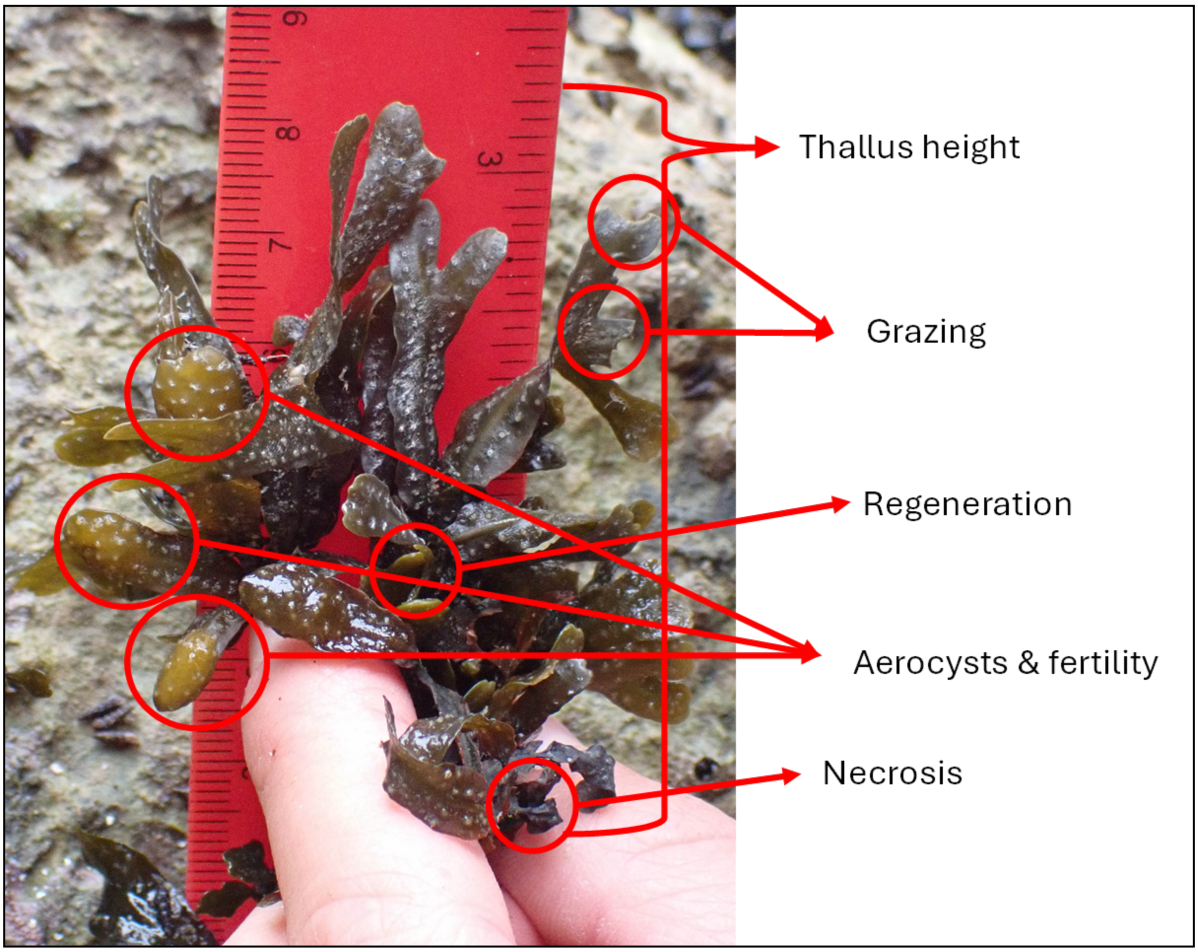

Figure 12. *Fucus virsoides* thalli morphological measurements that were conducted *in-situ* via digital photography and image analysis.

Statistical analysis

To analyse patterns in population-level metrics and thallus characteristics, a Principal coordinates analysis (PCoA) was performed. The analysis included average thallus height, percent cover, grazing pressure, aerocyst presence, fertility, and regeneration. In this case, data were analysed on a monthly basis for each study site, with the addition of a seasonal overview for better clarity (due to variable data availability, not all seasons have the same amount of monthly data). Necrosis was excluded from this specific analysis due to inconsistencies in the dataset. To further explore temporal differences, a one-way PERMANOVA (factor: “Month”) with pairwise comparisons was performed separately for each of the four study sites. Lanterna and Blaz included data from the whole twelve-month sampling period, while Hotel Parentium and Bijela uvala included six months. All analyses were based on the Bray-Curtis dissimilarity index using 9999 permutations with unrestricted permutation of raw data. Statistical confidence interval was 95%, therefore significance was set at $p < 0.05$. Seasonality was not used as statistical factor, but remained as a “grouping variable” for visualisation (each season containing up to 3 months, depending on the study site).

To assess the homogeneity of dispersion among groups, a PERMDISP analysis was also performed using Bray-Curtis dissimilarity and 9999 permutations. PERMDISP results were reported only when statistically significant and indicative of group dispersion heterogeneity, which in turn affects the fidelity of PERMANOVA analysis. These analyses were conducted in Primer v7 with PERMANOVA+ (Anderson et al. 2008, Clarke and Gorley 2015).

4.7. Exposure of *Fucus virsoides* to increased air temperatures: a thermotolerance experiment

To assess the effects of prolonged exposure to different air temperatures, apical fronds (hereafter referred to as "apices") of *Fucus virsoides* were collected from Blaz (as the largest population at the time, Figure 13) and transported to the Center for Marine Research in Rovinj (Ruđer Bošković Institute, Croatia). Samples were stored in seawater maintained at 18-20°C until the start of the experiment. Each apex was taken from a separate individual to avoid sampling bias.

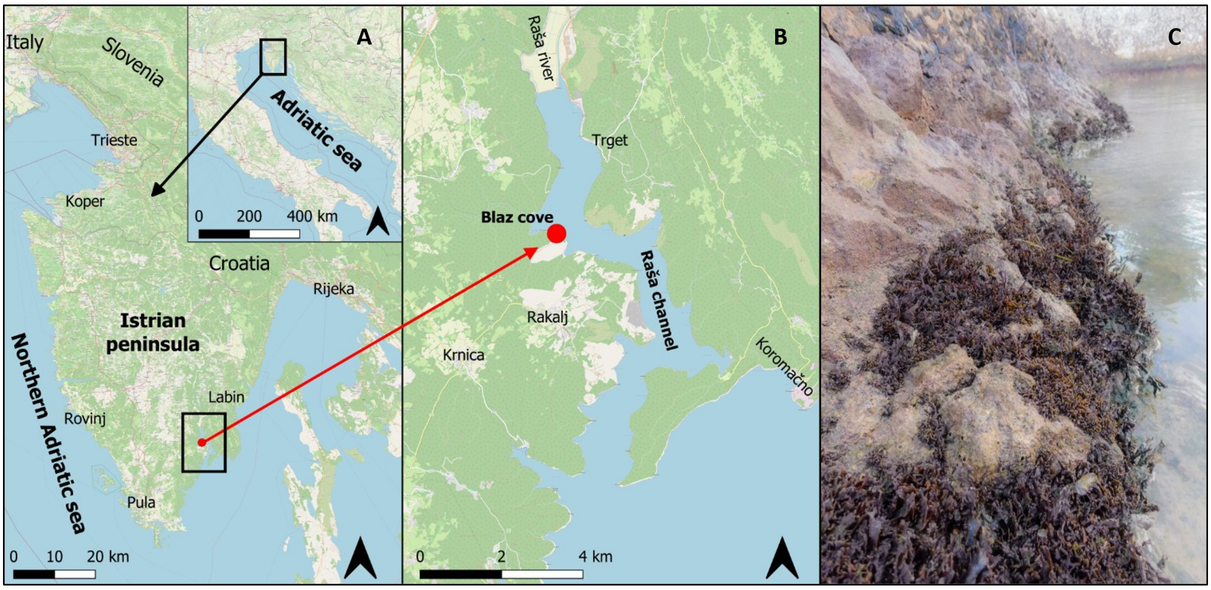

Figure 13. Location of the study site near Blaz cove within the Adriatic (A), Raša channel (B) along the eastern Istrian coast and an image of the *Fucus virsoides* study site during 2024 (C) (from Gljušćić et al. 2025).

For the experimental setup, 15 clay tiles per temperature treatment were prepared, thoroughly washed, and pre-moistened. Tiles were numbered and marked with coloured cable ties corresponding to specific temperature treatments:

- White (14°C, control)
- Blue (20°C)
- Green (25°C)
- Yellow (29°C)
- Red (33°C)

These temperature levels were selected based on the patchy 2021-2024 intertidal temperature measurements from *F. virsoides* sites along the western Istrian coast (Vrsar-Funtana-Poreč-Rovinj), which revealed extreme peaks during spring emersion events (see Sections 4.3. and 5.2.). The control temperature (14°C) reflected both early spring (March-April) seawater conditions and nighttime/shaded microhabitat values recorded by *in-situ* placed data loggers.

Temperature-induced stress has the capacity to disrupt cellular biological processes and affect photosynthetic performance, including the functionality of the photosynthetic apparatus (Davison and Pearson 1996, Crafts-Brandner and Salvucci 2002, Bischof and Rautenberger 2012). Pulse-Amplitude Modulation fluorometry has been identified as a reliable method of measuring the efficiency of the photosystems in their response to internal or external stressors (Hanelt et al. 1993, Beer et al. 2000, Graiff et al. 2015). When conducting measurements under controlled conditions, a reduction in the efficiency of photosystem II within the chloroplasts is the result of stress applied to the monitored photosystem. Measuring the maximum photochemical yield (Fv/Fm) is a well-established method of determining the effects of stressors on the photochemical apparatus of phototrophic species (Schagerl and Möstl 2011, Verdura et al. 2021, Bilajac et al. 2024). In this experiment, Fv/Fm was measured using a PAM fluorometer after 15 minutes of dark adaptation. Photochemical yield was measured with a Heinz Walz GmbH MINI-PAM-II.

Fifteen *F. virsoides* apices were assigned to each treatment group. Baseline measurements (T0) included wet weight, length, maximum photochemical yield (Fv/Fm), and presence of necrosis or regeneration. Each apex (5 apices per box) was gently affixed to a clay tile, and tiles were placed into three plastic boxes. Each box was filled with 1 L of filtered (5 µm) seawater at 14°C, sealed, and left undisturbed until 8:00 a.m. the next day (approx. 18 hours of acclimation; see Figure 14).

Experimental procedure - phase 1: Air exposure

At 8:00 a.m., seawater was drained from the boxes. Apices were gently blotted dry with paper tissues, and a 5 g silica gel pack was added to each sealed box to simulate dry, low-humidity conditions. Temperature and humidity were monitored using a combined hygro-thermometer. Boxes were placed in an incubator (Memmert ICP260) and exposed to their designated treatment temperature for 6 hours (Figure 14).

At 2:00 p.m., post-emersion measurements were taken: wet weight, length, Fv/Fm, necrosis, and regeneration. Apices were photographed using an Olympus TG-6 camera for subsequent analysis, including precise length measurements using ImageJ (Rasband 2024). This procedure was repeated daily for 7 consecutive days.

Experimental procedure - phase 2: Constant Immersion

Following 7 days of air exposure, the apices entered a 7-day constant immersion phase, designed to simulate neap tides when *Fucus virsoides* remains submerged (Figure 15). Samples were kept immersed in 14°C filtered seawater using a Teko TK500 chiller. Daily measurements (wet weight, length, Fv/Fm, necrosis, and regeneration) and photographic documentation were continued throughout this phase. Seawater was changed daily to maintain water quality.

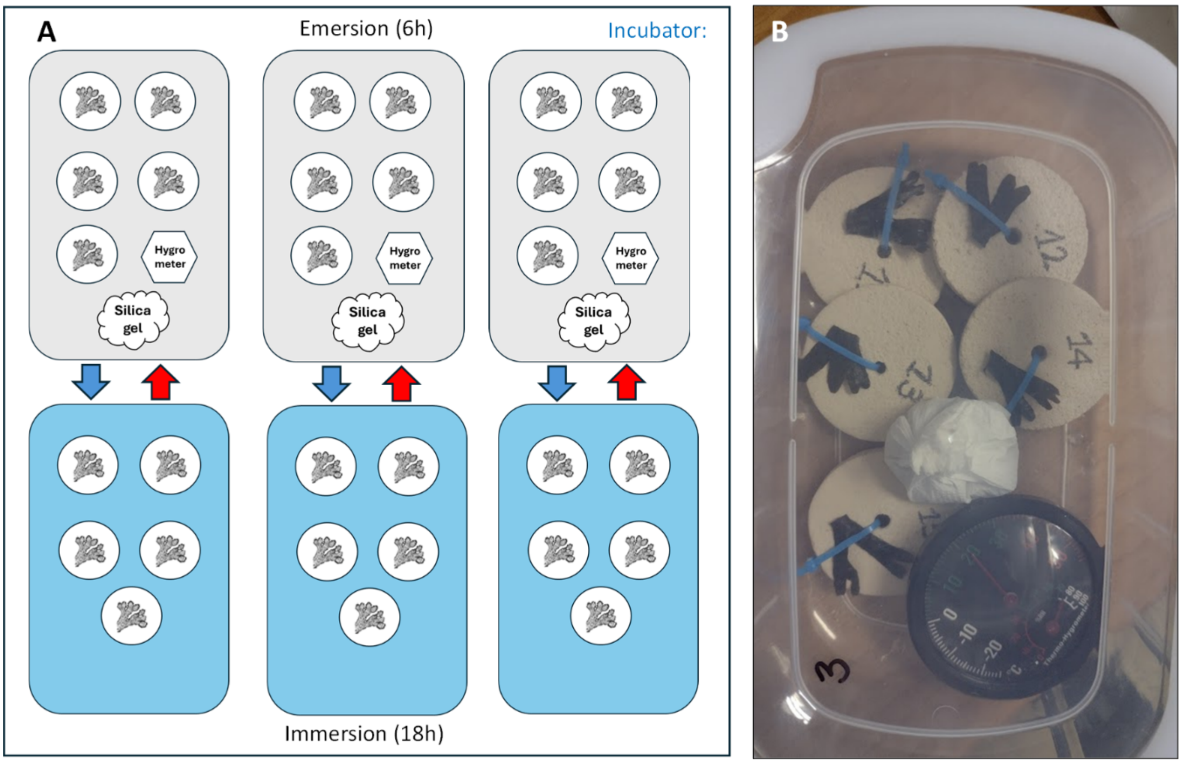

Figure 14. Scheme of the air exposure phase of the experiment (A). *Fucus virsoides* apices attached to clay tiles were placed inside the closed plastic boxes together with a 5g pack of silica gel and a hygrometer (B).

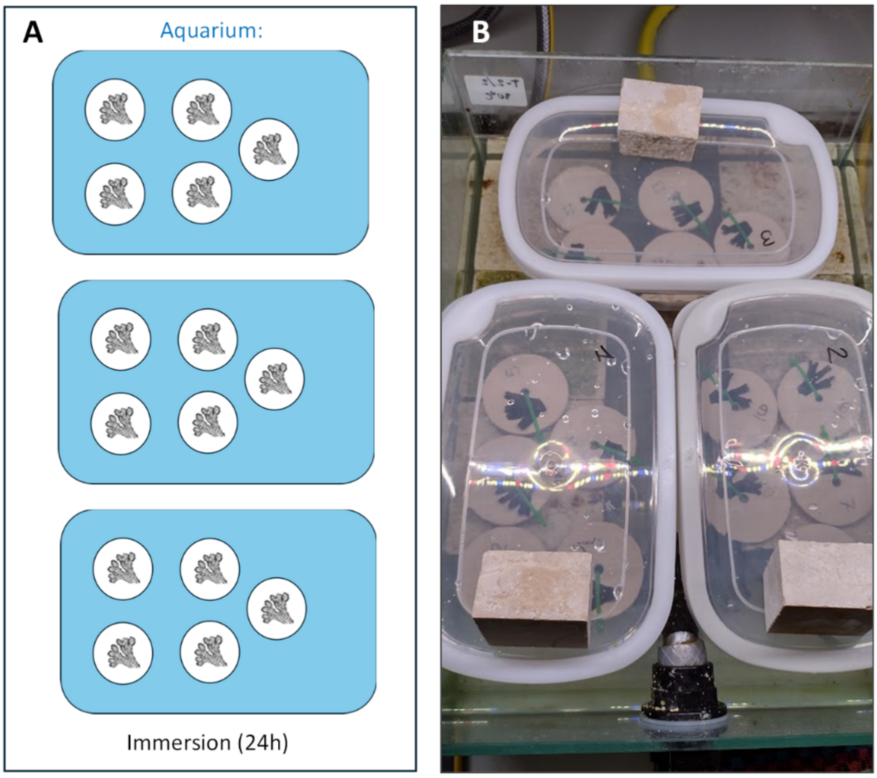

Figure 15. Scheme of the constant immersion phase of the experiment (A). *Fucus virsoides* apices attached to the clay tiles were placed inside the same closed plastic boxes filled with filtered seawater and placed into aquariums with controlled water temperature.

Statistical analysis

Mixed-effects models (MM) were applied to account for both fixed and random effects (Bates et al. 2015, Bolker et al. 2009, Harrison et al. 2018). Linear mixed models (LMM) were used to evaluate temperature effects on wet weight and length, while generalized linear mixed models (GLMM) with Poisson distribution and log-link function were used for Fv/Fm. Measurements of wet weight and length were transformed to percentage change relative to T0.

- Fixed effect: “Temperature” (5 levels: T14, T20, T25, T29, T33)
- Random effects: “Time” (crossed), and “individual apex ID” nested within box (to account for grouped measurements)

Type II Wald χ^2 tests were used to evaluate fixed effects, with Tukey post-hoc comparisons applied to all fitted models.

Statistical analyses were conducted in R (R Core Team 2019) using the lme4 (Bates et al. 2015) and MASS (Venables and Ripley 2002) packages. P-values for statistically significant differences in measured parameters at different temperature levels were obtained via the ‘ANOVA’ function from the CAR package (Fox and Weisberg 2019), and Tukey tests via the ‘glht’ function from MULTCOMP (Hothorn et al. 2008). A significance threshold of $p < 0.05$ was used throughout.

Principal Coordinates Analysis (PCoA) was conducted using Euclidean distances on untransformed data to visualize variation in response variables across treatments and timepoints during both experimental phases. PCoA was carried out using PRIMER v.7 (Clarke and Gorley 2015, Anderson et al. 2008). Additional graphs and visualizations were produced using Grapher 24.2.247.

Environmental and instrumental controls

During the air exposure phase, light intensity inside the incubator was maintained at 70 µmol photons m^{-2} s^{-1} using integrated fluorescent bulbs. During the immersion phase, lighting was provided by LED-GNC Silver Moon Marine aquarium lights. Wet weight was measured using a Mettler Toledo PB 1502-S scale. Length was assessed using ImageJ software, comparing daily apex images to T0 reference images using consistent reference points (Figure 16).

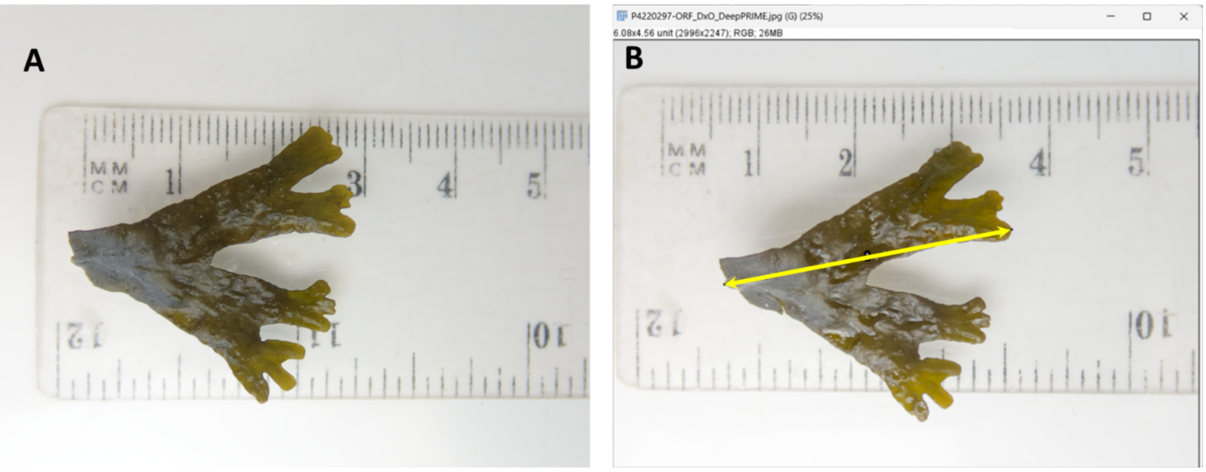

Figure 16. Detailed measurement of *Fucus virsoides* apices changes throughout the experiment. At each measurement period, the new photograph (A) is compared to the reference photograph (B) taken at T0. The yellow line represents the precise measurement conducted in ImageJ software (from Gljušćić et al. 2025).

Assumptions

This thermotolerance experiment was designed based on *in-situ* field observations, under the following assumptions:

1. *Fucus virsoides* may be exposed to air for up to 6 hours during low tide.
2. It can remain immersed for up to 18 hours following low tide, with no second emersion during semi-diurnal cycles.
3. During neap tides, thalli are not exposed to air.
4. Algal body temperature reflects ambient microhabitat conditions, including potential heat from sunlight.

4.8. *Ex-situ* cultivation of *Fucus virsoides* for conservation purposes

The *ex-situ* cultivation and outplanting experiment was conducted during the 2021-2022 period. On 23 April 2021, fertile receptacles of *Fucus virsoides* were hand-collected from a surviving population in Bijela uvala (Figure 8D). Fertility was confirmed *in-situ* via transverse-section of receptacles, with thick conceptacles containing female gametes observed using a macro-capable digital camera (Olympus Tough TG-6; Figure 17). While both gamete types occur in the same receptacle, male gametes are only observable under a microscope and were thus not observed *in-situ*.

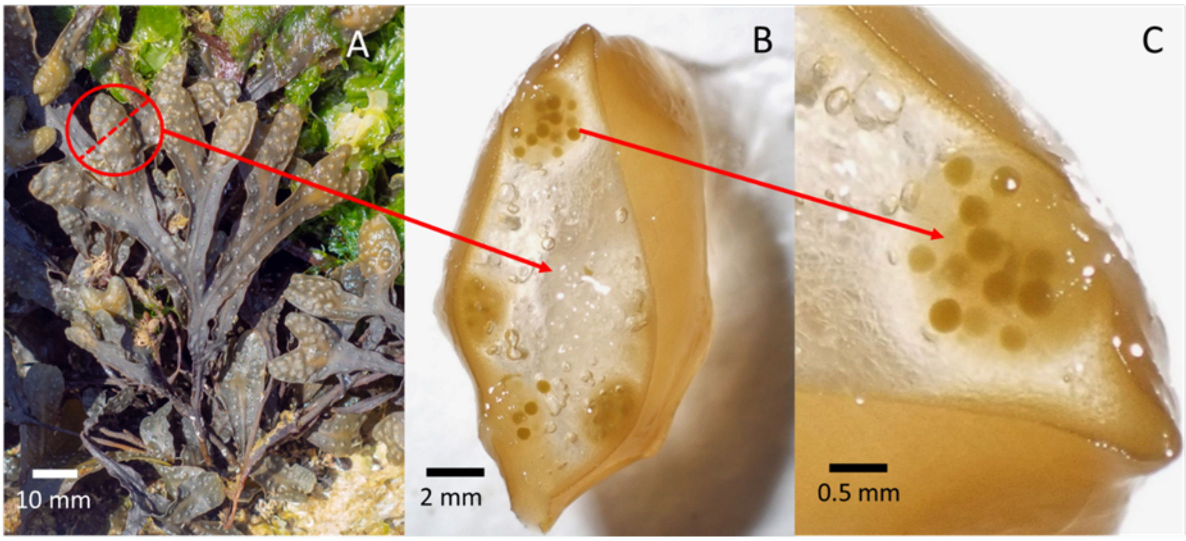

Figure 17. *Fucus virsoides* fertility check: Receptacles (A) are spliced using a sharp object and the presence of conceptacles (B) and gametangia maturity (C) is visually confirmed afterwards (from Gljušćić et al. 2023).

Fertile receptacles (cca. 30), pooled from multiple individuals, were placed in a mesh pouch and floated at the water surface of a 5 L aquarium containing limestone tiles (serving as substrate; Figure 18A). The aquarium was filled with natural seawater, while water movement and aeration was provided via an air pump to promote gamete dispersal and more homogenous zygote settlement on the tiles (Figure 18B). After 24-48 hours, germlings were already observed on the substrate and receptacles were removed.

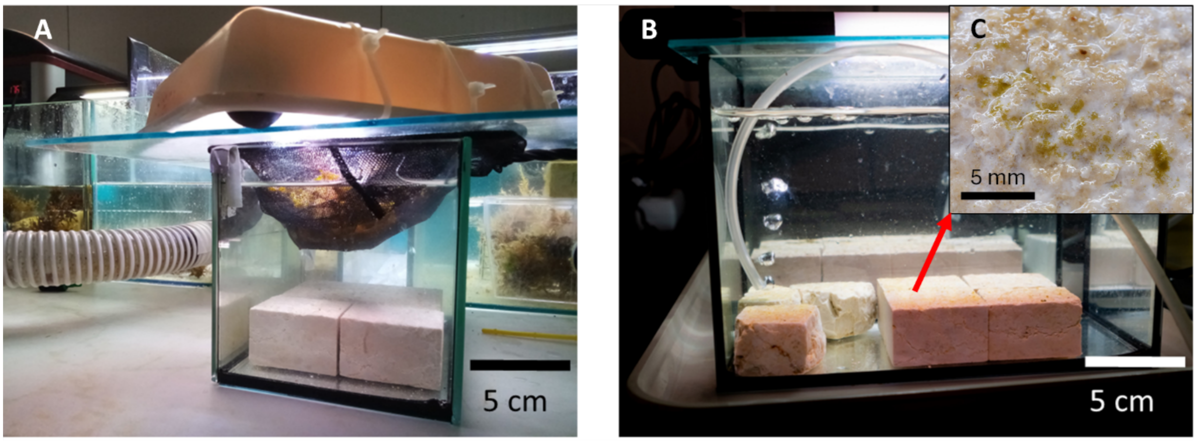

Figure 18. Early phase of *Fucus virsoides* cultivation: substrate seeding from receptacles (A), early cultivation period (B) and magnified view of the early stage embryos (C) (modified from Gljušćić et al. 2023).

After approximately one-week period, seeded tiles with visible germlings were transferred to a larger 24 L closed aquarium system with controlled conditions (16-18°C; LED GNC SilverMoon Marine, 148 µmol photons $m^{-2}s^{-1}$; 12 h light/dark cycle). Weekly full water changes were performed. While macro photography was used in an attempt of early height measurements via ImageJ, initial data proved unreliable due to the small size and visibility of germlings.

In September 2021, once recruits were more prominent and measurable (Figure 19), the tiles were relocated to outdoor open-flow stone basins at the Center for Marine Research courtyard. The basins, supplied with a continuous flow of unfiltered natural seawater, were equipped with fluorescent lighting (Philips Master TL-D 36W/865, 6000 K, 95 µmol photons $m^{-2}s^{-1}$). Over the subsequent two months, thallus height was monitored in 20 randomly selected individuals to determine average size and standard error. ImageJ (Rasband 2024) software was used to acquire measurements from photos taken by the Olympus Tough TG-6 digital camera. Light and temperature were continuously monitored at 1-hour intervals using a HOBO Pendant® Temperature/Light 64K data logger.

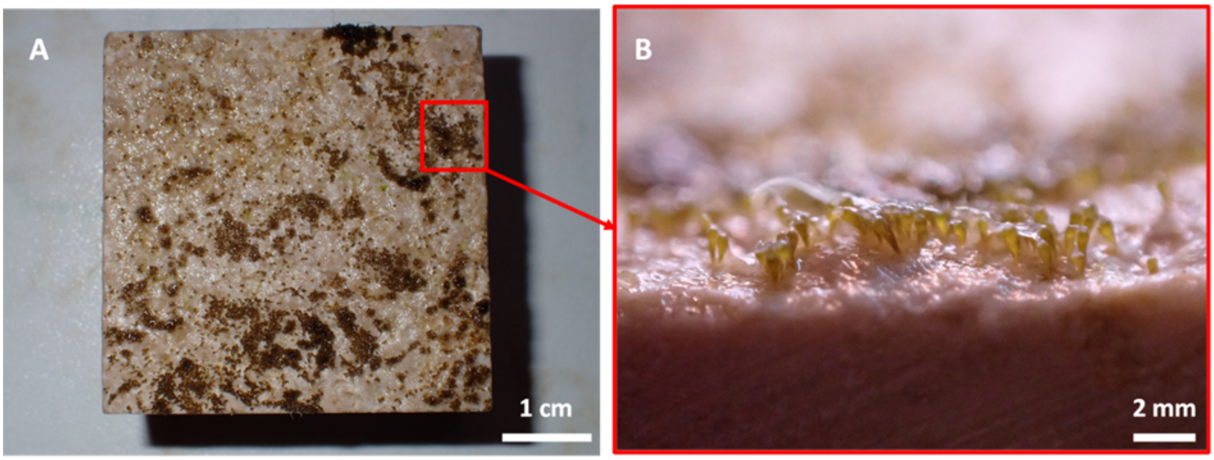

Figure 19. Cultivated *Fucus virsoides* recruits as seen on the limestone tile (A) and a close-up image of the same recruits. Photographed using an Olympus Tough TG-6 digital camera.

Limestone tiles with cultivated *F. virsoides* recruits were outplanted at Muča (Rovinj), a site of previous natural settlement (45.094371° N, 13.632859° E) identified by epoxy markings from 2014 (Figure 20). The tiles with recruits growing on top of them were affixed to the substrate using epoxy (Sub Coat XT Azzuro 2/1, Veneziani) within the previously marked area. Protective mesh cages (12 x 12 x 10 cm, 1 cm mesh size) were installed over each of the two plots (each 100 cm², 4 tiles per plot) to prevent grazing by various herbivores: limpets, gastropods, hermit crabs, *Sarpa salpa*, and sea urchins. Cages were maintained and cleaned periodically to minimize fouling.

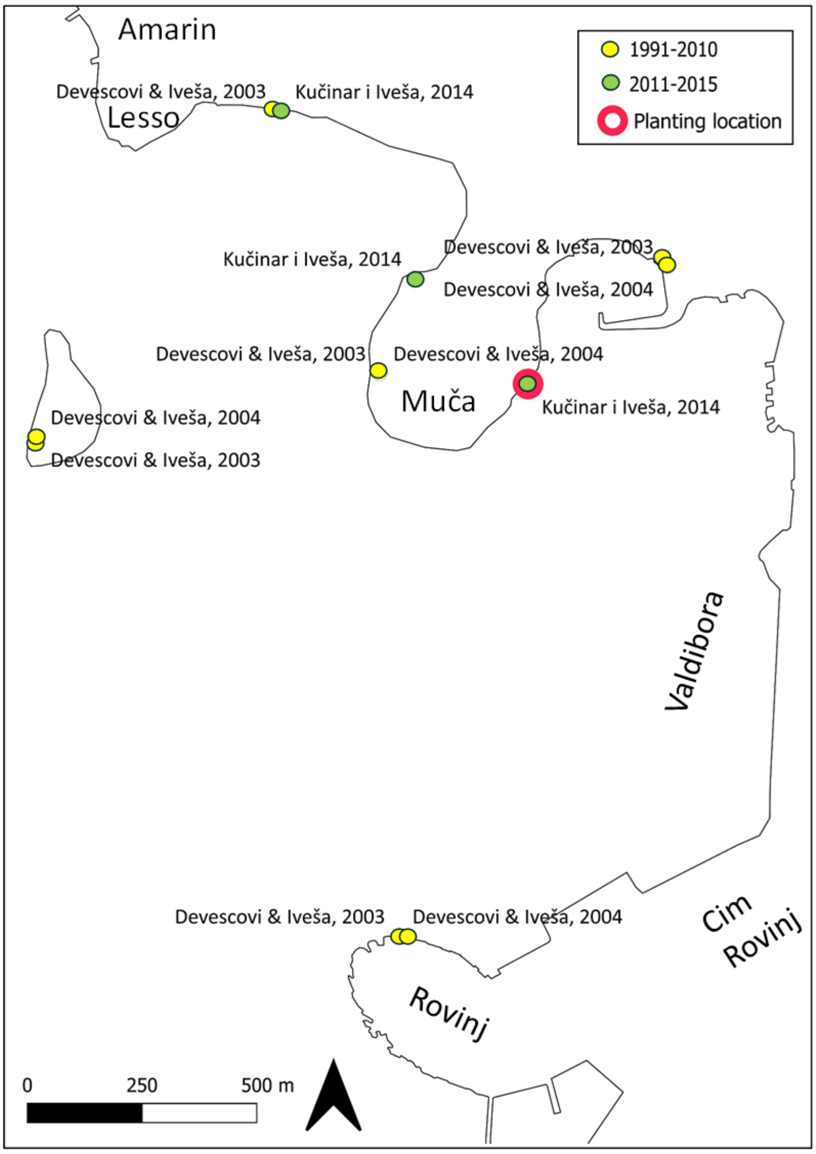

Figure 20. Map of prior recent *Fucus virsoides* presence (yellow for the 1991-2010 period and green for the 2011-2015 period) along the northern part of the Rovinj coast and a selected planting location for the cultivated specimens (marked in red).

Each of the two plots were placed on approximately the upper and lower edges of the intertidal zone (~3 m apart) in order to assess if the positioning of the plots can significantly affect the growth and survivability. Monitoring was conducted monthly over a 12-month period, including percent cover (photography using Olympus Tough TG-6 and image analysis via ImageJ), thallus height (manual measurement), and reproductive phenology (presence of fertile structures). In each plot, 10 randomly selected individuals were measured to determine average height and associated standard error.

Statistical Analysis

Thallus length data were analysed using a two-way ANOVA and tested according to variables “Position” (2 levels: Upper and Lower tidal zone) and “Time” (8 levels: Nov 2021, Jan, Feb, Mar, May, Jul, Aug, Nov 2022). Prior to ANOVA, homogeneity of variance was confirmed using Cochran’s C-test. When significant interactions were detected, post hoc comparisons were made using the Student-Newman-Keuls (SNK) test. Statistical analyses were performed using GMAV-5 for Windows.

5. RESULTS

5.1. Mapping

Along the Istrian coast, most of the older information regarding *Fucus virsoides* presence comes from works conducted near Rovinj, but some older herbarium collections and published literature do mention specific sites and are marked in Figure 21A (Vatova 1948, Linardić 1949, Battelli and Alberti 2003, Algae Herbarium Portal 2025). Data from Linardić (1949) regarding this geographical area comes from secondary sources, which are undated.

Previously compiled historical data on *F. virsoides* suggests a widespread presence during the late 19th and early 20th centuries (Figure 21A), along the rocky coastline of the Adriatic, primarily along the northern part (from Venice to Istria) but also beyond (Linardić 1949, Algae Herbarium Portal 2025). Interestingly, only during the 1990's was the presence of the species confirmed on the southernmost parts of the Adriatic, along the Albanian coast (Kashta 1996), prior limit being considered near Boka Kotorska in Montenegro (Linardić 1949), where the species is supposedly present to this day (Mačić 2006, Descourvières et al. 2024a).

Linardić (1949) provided the distribution data for nearly the whole Adriatic basin. However, the author did not provide the year when, or the type of information provided, which limits its usability of the data; the only certainty being that the data is older than the year 1940. Due to this reason, this specific information was not included in this work (although it is published in Linardić (1949).

Data from the 1950-1990 period comes from published scientific works, but often as secondary information: from samplings and study area descriptions (see Chapter 2 and Section 4.1.). Most of the location data in this period does indeed cluster around the Rovinj area, the likely reason being large abundance and practicality (Figure 21B).

Data from 1991-2010 partially originates from targeted scientific research, but the rest comes from personal observations and notes by resident scientists in the area (Devescovi and Iveša, pers. comm.). Some of this data has been published in later works (Gljušćić et al. 2023, Descourvières et al. 2024a). This data is well dispersed along the western Istrian coast.

During the 2010-2020 period, specific parts of the Istrian coastline were mapped by Čelig (2010), Kučinar (2014) and Gljušćić (2016) as student theses. The northernmost part of the Istrian coastline (Slovenia-Italy) was also comprehensively mapped in this period (Orlando-Bonaca et al. 2013). While together, they seemingly show the persistence of *F. virsoides* along the whole western Istrian coast, the species populations had already started collapsing during the course of these surveys.

Complete western coast and parts of the eastern coast of the Istria were mapped during the 2021-2022 period (Gljušćić et al. 2023), with some more recent data being included in Descourvières et al. (2024a).

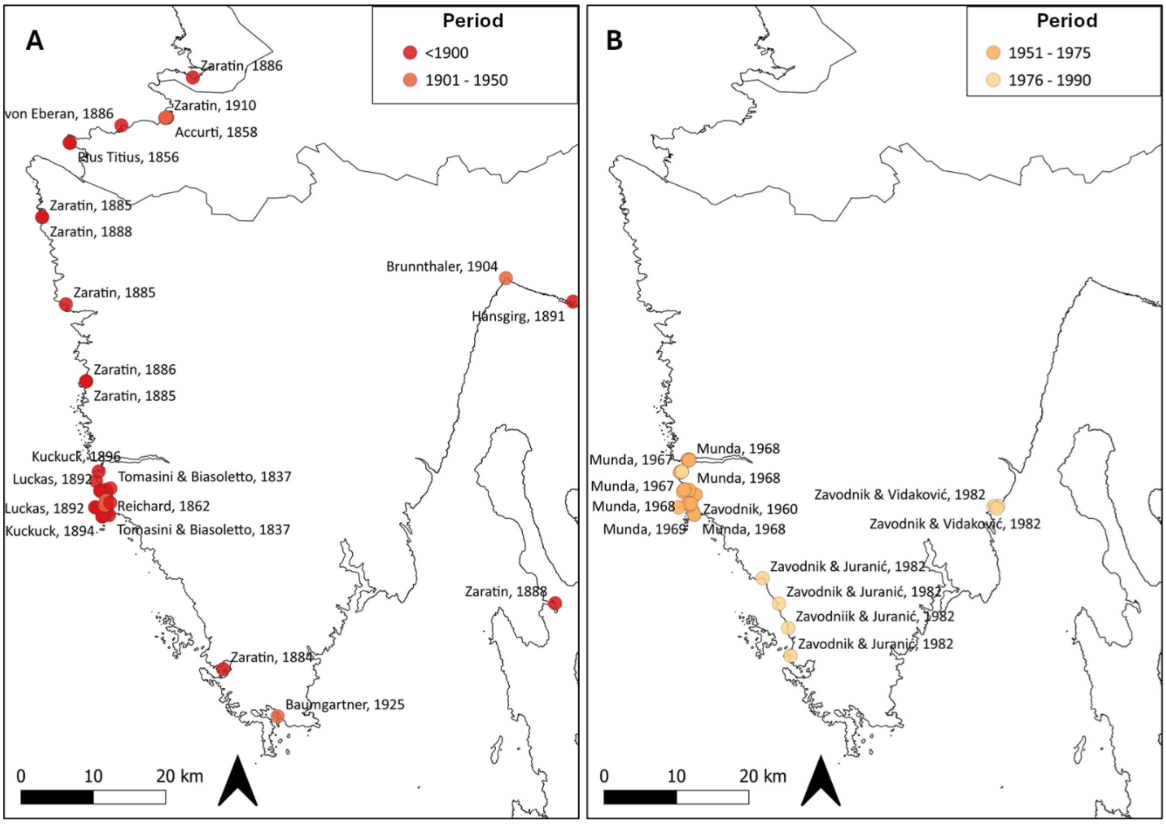

Figure 21. Known presence of *Fucus virsoides* sites along the Istrian coast and nearby areas from <1900 to 1950 (A) and 1951-1990 (B). Color-coded map markings show the period and the data source.

Many of the older (<1900-1975) recorded historical *F. virsoides* sites were indeed located around (or attributed to) the town of Rovinj and partly around the Trieste area (Figure 21), however, this is likely the result of focused research activity along the specific sites and the proximity of research institutions rather than the environmental factors. This is further explained by the regular presence of *F. virsoides* in most towns/settlements along the Istrian coast and beyond, although with fewer records.

More recent records (2010-2016) show the presence to be much more widespread along the western Istrian coast; however, they also point towards a later rapid disappearance, especially along the southern part and the Italian and Slovenian parts of the coast (Figure 22A). Unfortunately, the most recent data from 2025 however, reveals that only a few settlements remain, with one near the town of Cres yet to be confirmed (Figure 22B). At this rate, the species is likely to completely disappear from the Istrian region during the next few years.

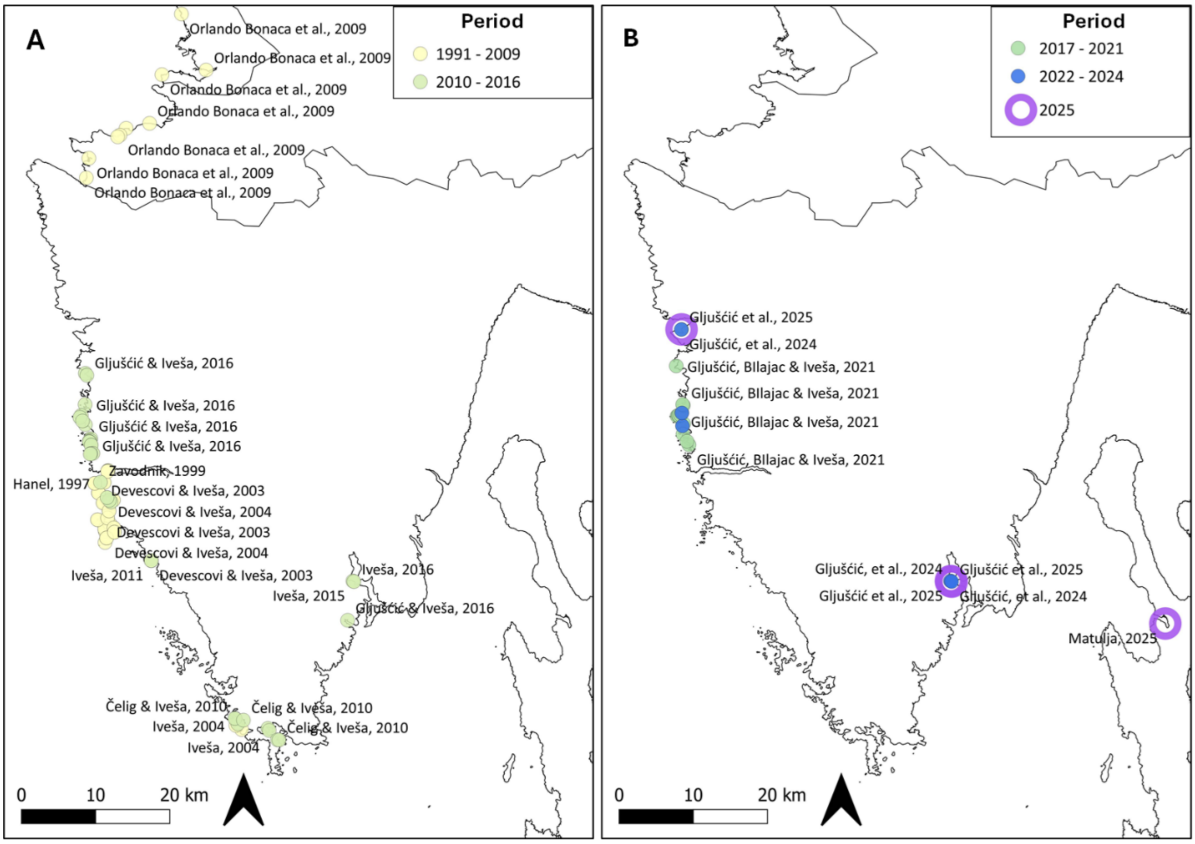

Figure 22. Known presence of *Fucus virsoides* sites along the Istrian coast and nearby areas from 1991-2016 (A) and 2017-2025, including the currently known sites (B). Color-coded map markings show the period and the data source.

5.2. *In-situ* temperature dynamics in the intertidal

While temperature measurements were attempted in multiple *Fucus virsoides* sites and the general intertidal along the western Istrian coast, little consistent data was collected due to the overwhelming losses of data-loggers, either due to dislodgement, leakage, or malfunction. Some temperature data was salvaged, but was only usable for a general overview of intertidal temperature shifts in the intertidal, particularly during winter and spring. In Lanterna, five months of continuous measurements were conducted, but all the loggers placed afterwards were lost faster than the data they collected could be practically read-out (Figure 23A). In Hotel Parentium, nearly 4 months of measurements in total were collected, but logger leakage had disrupted the early measurements (during March 2024, Figure 23B). Measurements in Bijela uvala were conducted in several different periods, from late 2023 to mid-2024. While shorter disturbances (days) did not cause much loss, large gaps during winter and spring (February-March and May) have reduced the usability of the data (Figure 23C). The measurements were stopped after the complete disappearance of *F. virsoides* from the area. Measurements in Muča (near Rovinj) were conducted much earlier, during the 2021-2022 period, and lasted for 7 months in total (Figure 23D). These were partially conducted in tandem with the *ex-situ* restoration experiments (see Section 4.8.), but were discontinued due to logger leakage and several logger losses. These did, however, show very high temperature oscillations during the spring periods, prompting further research into the topic.

Overall, the partial temperature measurements in the intertidal areas where *F. virsoides* was present point towards high variability, which is likely tied to the local topography. The most likely causes are varying exposure to sunlight, as well as different vertical positioning and wind exposure. The overall trend shows that the most intense variations occur during early spring, with warmer air temperatures, but that seawater temperatures still remain low (Figure 23). Unfortunately, due to measurements being disrupted, this information was often too fragmented to be useful. The extreme variations in temperature were best detected in Muča (Figure 23D), with a temperature range from 1.67°C to 32.17°C (± up to 0.2°C measurement error). Temperature variations in the Lanterna site were less intense due to the logger's position within the shaded area, reducing the overall ambient temperatures (Figure 23A).

Temperature measurements in the intertidal were much more successful at the Blaz site, on the eastern Istrian coast, within the Raša bay, likely due to the inaccessibility and isolation of the site. Nearly a full 12-months of hourly temperature data was collected (aside from a short malfunction period during winter). Analyses of temperature occurrence frequency (Figure 24)

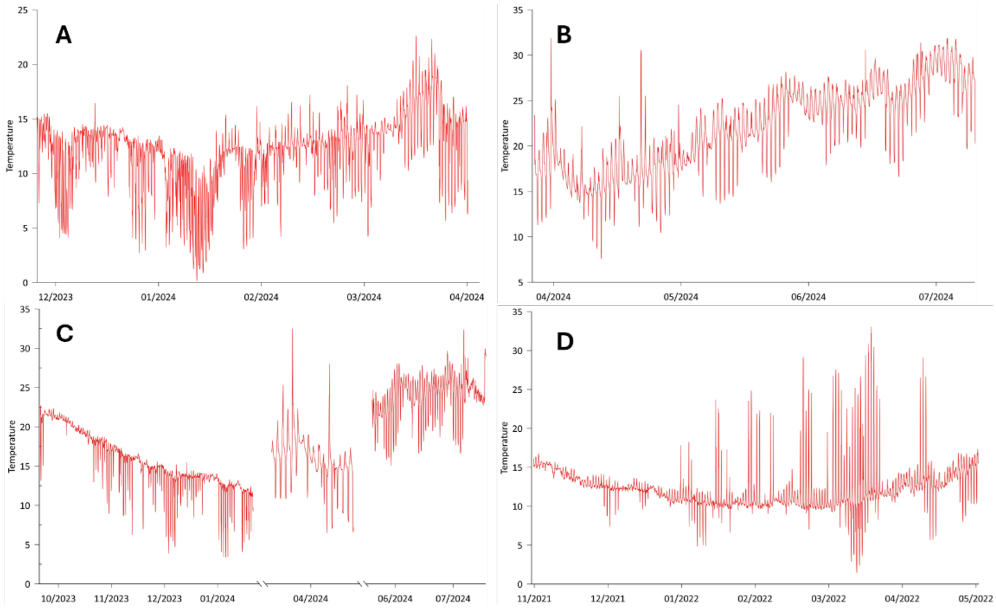

Figure 23. Partial temperature data collected via HOBO Pendant® Temperature/Light 64K data loggers in 4 different *Fucus virsoides* sites along the western Istrian coast at A) Lanterna, B) Hotel Parentium, C) Bijela uvala and D) Muča.

revealed that extremely high temperatures above 30°C during low water periods remain relatively uncommon, typically appearing during late spring and summer (Figure 25). Moderately elevated temperatures between 25°C and 30°C are more common, though occurrences at the higher end of this range are less frequent (Figure 24). These also primarily occur in spring and summer (Figure 25). Mildly elevated temperatures ranging from 20°C to 25°C are more frequent (Figure 24) and span nearly the entire year, except winter (Figure 25). In contrast, lower temperatures around 13°C to 15°C, including values close to the assumed *ex-situ* control condition of 14°C, are highly frequent (Figure 24) and mostly occur in autumn, winter, and spring (Figure 25).

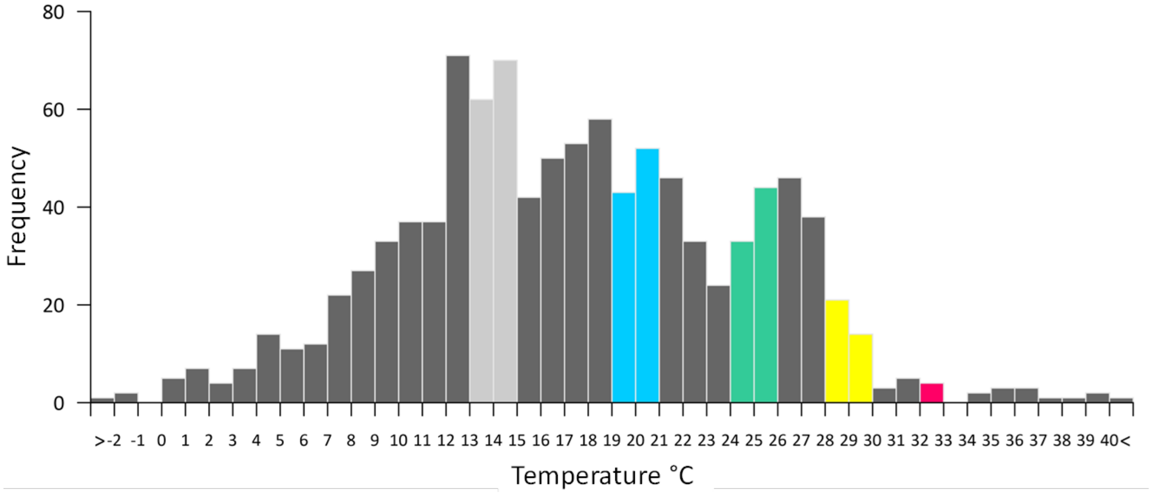

Figure 24. Frequency of hourly temperatures in the monitored *Fucus virsoides* site measured in 2024 during low water periods. The grey (13-15°C), blue (19-21°C), green (24-26°C), yellow (28-30°C) and red (32-34°C) columns correspond to the temperatures used in the experimental treatments, ± 1°C.

The annual overview of intertidal temperature patterns shows that the most extreme fluctuations, involving rapid transitions between very high (> 35°C) and relatively low (~15°C) temperatures, tend to happen during late spring (Figure 25). These fluctuations very likely expose *F. virsoides* to high levels of physiological stress.

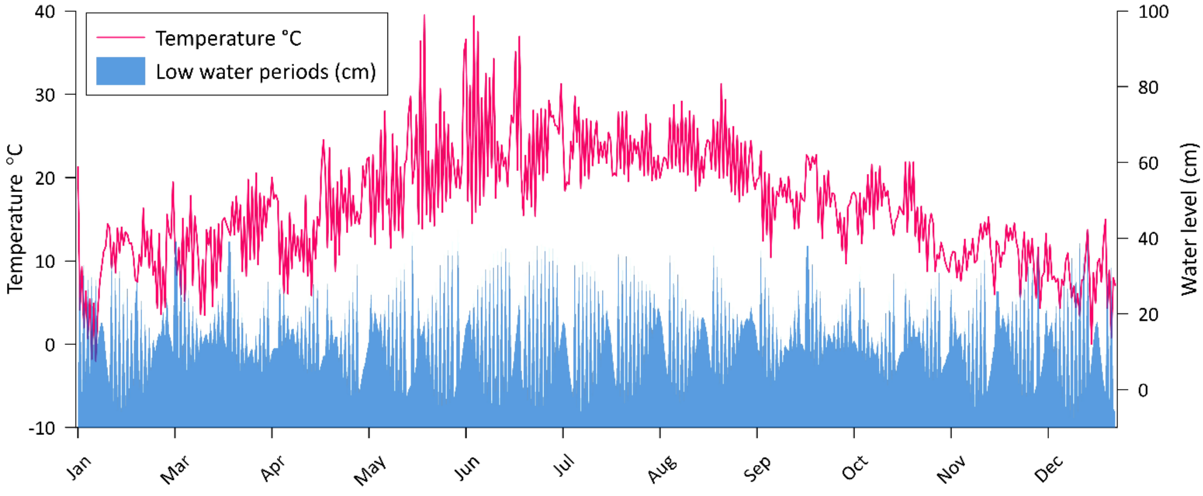

Figure 25. Temperatures recorded in a *Fucus virsoides* site during daily low water periods over the year 2024. The predicted water levels are based on mareographic data for Rijeka, adjusted by +1 hour to account for distance and local geomorphology.

During the summer months, the comparatively milder temperatures recorded during low tide suggest that emersion events mainly occur at night, while immersion happens during daylight hours (Figures 25 and 26). Additionally, periods of reduced temperature variability, usually associated with neap tides, indicate more stable environmental conditions. Notably, there is a lack of even moderately elevated temperatures above 25°C during early autumn (September, Figure 25), a time period generally associated with still moderately high temperatures, implying that thermal stress during this period is minimal and declines further into winter.

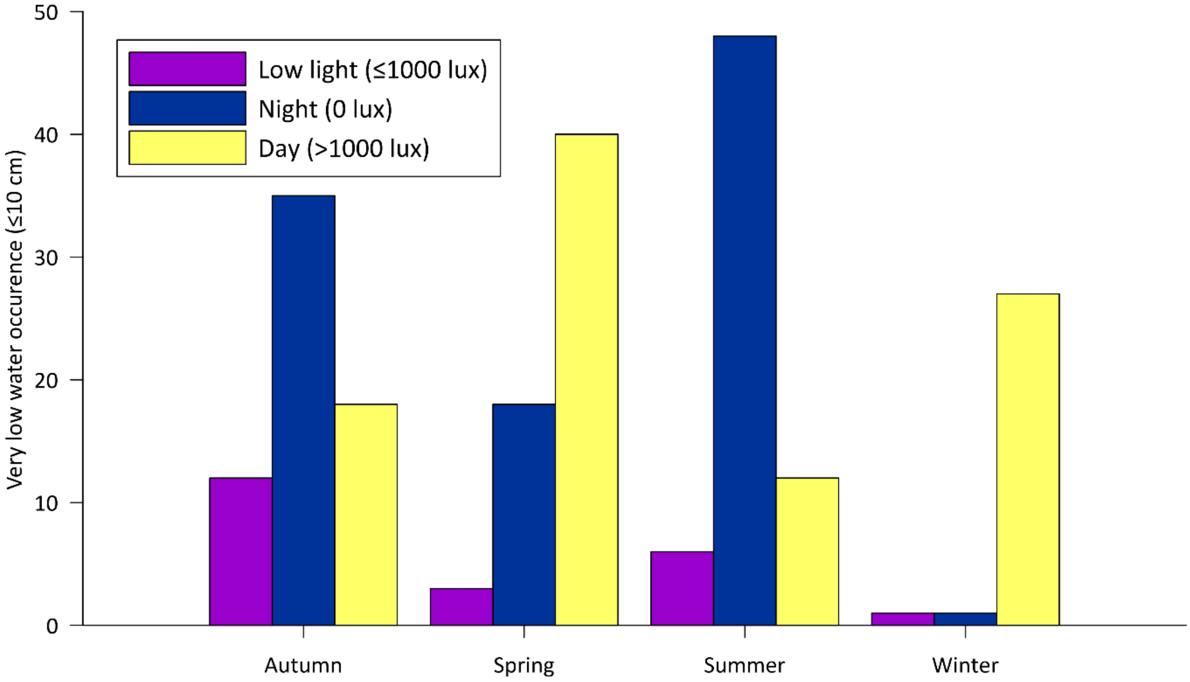

Figure 26. Occurrence of very low water levels (<+10cm) in Blaz according to the period of the day (light availability), and its dependence on the season (from Gljušćić et al. 2025).

Interestingly, during the lowest tide periods in spring (from March 21 to June 21, 2024), temperatures occasionally exceeded 25°C, even during neap tides, indicating more frequent or prolonged emersion than previously assumed (Figure 27).

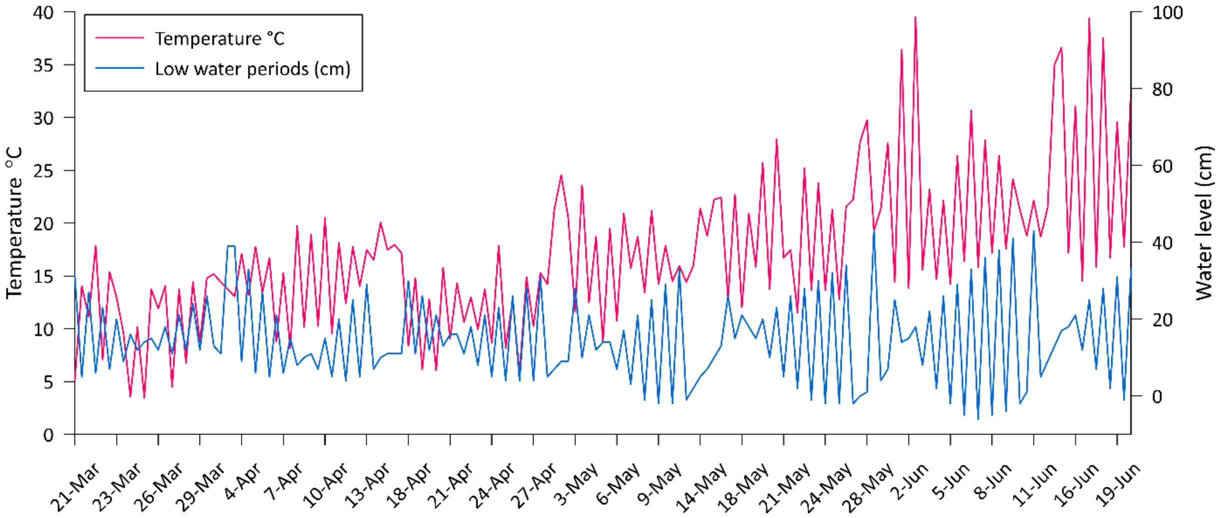

Figure 27. Temperatures recorded in a *Fucus virsoides* site during daily low water periods during the spring of 2024. The predicted water levels are based on mareographic data for Rijeka, adjusted by +1 hour to account for distance and local geomorphology.

Overall species richness

Analysis of remnant *Fucus virsoides* communities indicates that the species sites continue to support a measurable level of biodiversity. However, only two of the four studied sites, Lanterna and Blaz, retained *F. virsoides* populations long enough to allow full-year monitoring. Across all sites, a total of 35 taxa were identified, with marked seasonal and spatial variation in their presence and cover.

5.3. Community structure in *Fucus virsoides* stands

Seasonal variation in species richness differed among the study sites (Figure 28). Bijela uvala consistently supported the highest average number of species, peaking in summer (10 ± 0.3 SE) and spring (9.6 ± 0.4 SE), while winter values were lower (7.6 ± 0.3 SE). The site in Lanterna showed more stable values across seasons, ranging between 7.3 ± 0.3 SE in summer and 8.9 ± 0.4 SE in winter, with a slight increase again in autumn (8.9 ± 0.3 SE). The site in Hotel Parentium, for which only spring and summer measurements were available, exhibited moderate richness (6.6 ± 0.3 SE and 7.5 ± 0.4 SE, respectively). In contrast, Blaz displayed the lowest values overall, with the number of taxa dropping to 2.7 ± 0.2 SE in spring and gradually increasing through summer and autumn (6.8 ± 0.4 SE and 5.1 ± 0.3 SE, respectively).

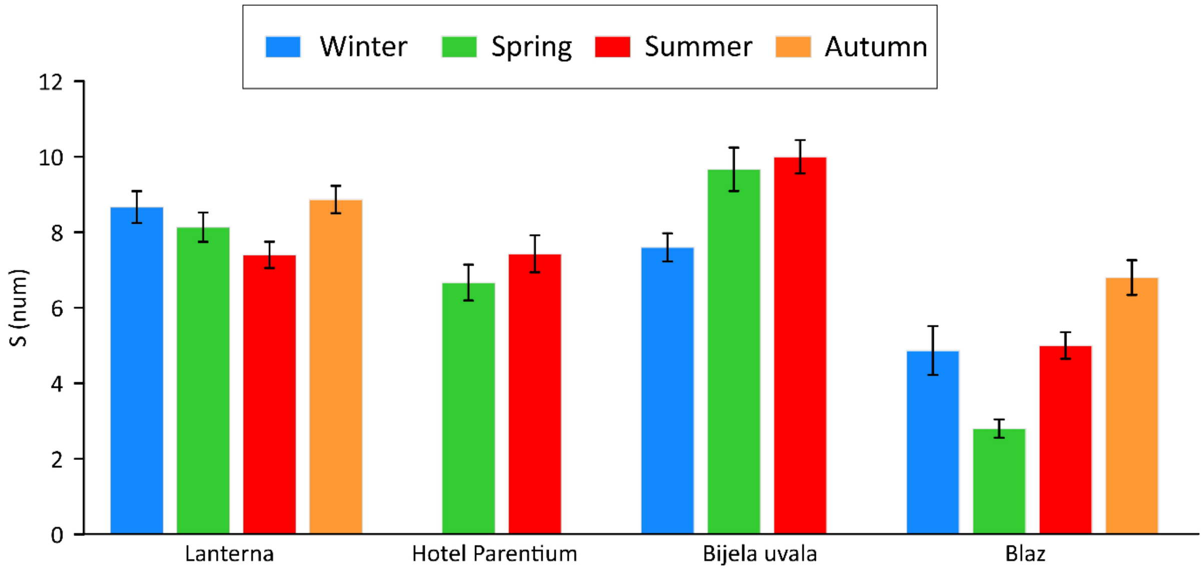

Figure 28. Average number of taxa (± SE) in remnant *Fucus virsoides* communities across the study sites and seasons.

When comparing all the study sites, Blaz exhibited the lowest species richness across all seasons, as well as the lowest total number of taxa (Figure 29). In contrast, Lanterna and Bijela uvala recorded the highest number of taxa, with Hotel Parentium closely following (Figure 29). The main reason for the increased taxa number during the warmer seasons is the appearance of ephemeral, mostly filamentous (*Ceramium*, *Cheatomorpha*, *Cladophora*…) and corticated (*Laurencia*, *Gelidium*, *Osmundea*…) taxa, which replaced the cold-loving foliose taxa (*Ulva*, *Pyropia*…) and also covered-up the lower levels of the community (crustose and articulated calcareous taxa).

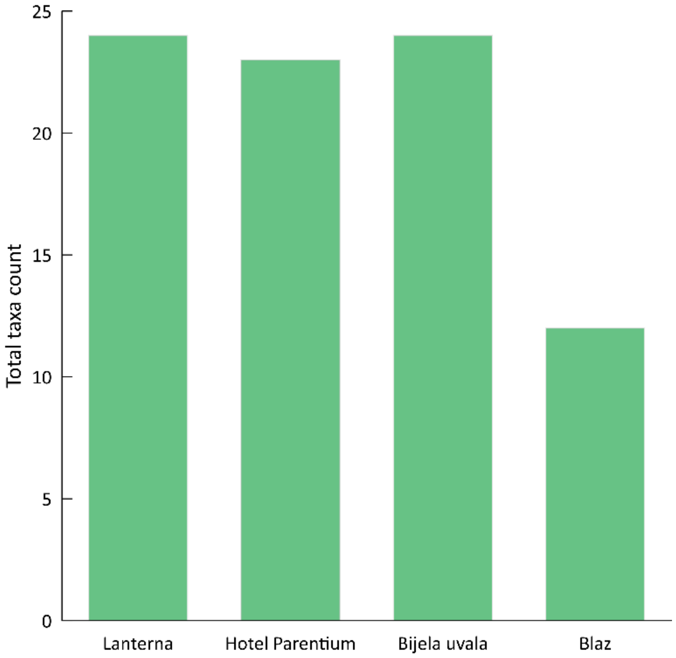

Figure 29. Total number of taxa observed within each study site.

Morphofunctional structure of the studied communities

In Lanterna, corticated algae were dominant in autumn and winter but declined noticeably during warmer seasons (Figure 30). Filamentous algae were present year-round, except for a sharp decline in spring. Foliose algae appeared primarily in colder months, while crustose algae maintained consistently low cover throughout the year. Articulated calcareous algae showed the lowest cover overall. Sessile animals were present in all seasons, though with a notable reduction in winter and substantial variability across the samples.

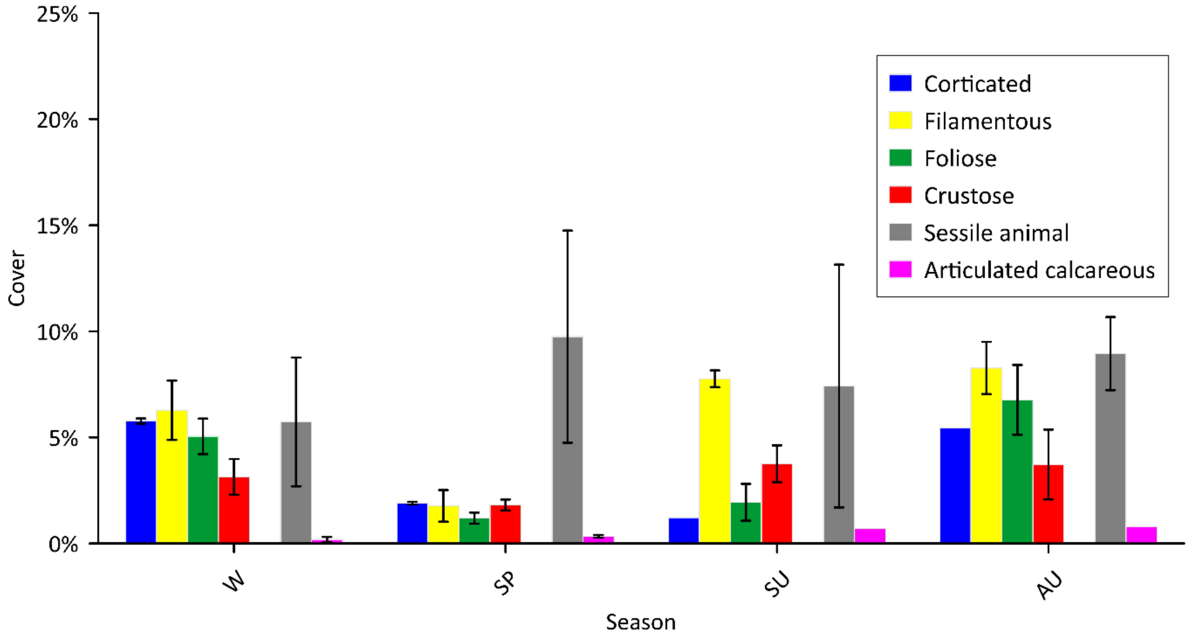

Figure 30. Community composition according to morphofunctional groups in the Lanterna study site. Data is represented as means of percentage cover of all the plots within a season ± SE.

At the Hotel Parentium study site, only spring and summer data were available in this location. During both seasons, filamentous algae consisting mainly of dense turfs of *Polysiphonia* and *Ceramium*, dominated the site. Articulated calcareous algae followed in abundance, while corticated algae (mostly *Laurencia obtusa*) were present in lower densities (Figure 31). Other groups were minimally represented. The sharp decline of *Fucus virsoides* during summer coincided with a rapid community shift towards ephemeral turfs, making it unclear whether such community structure represented a stable pattern or an exception

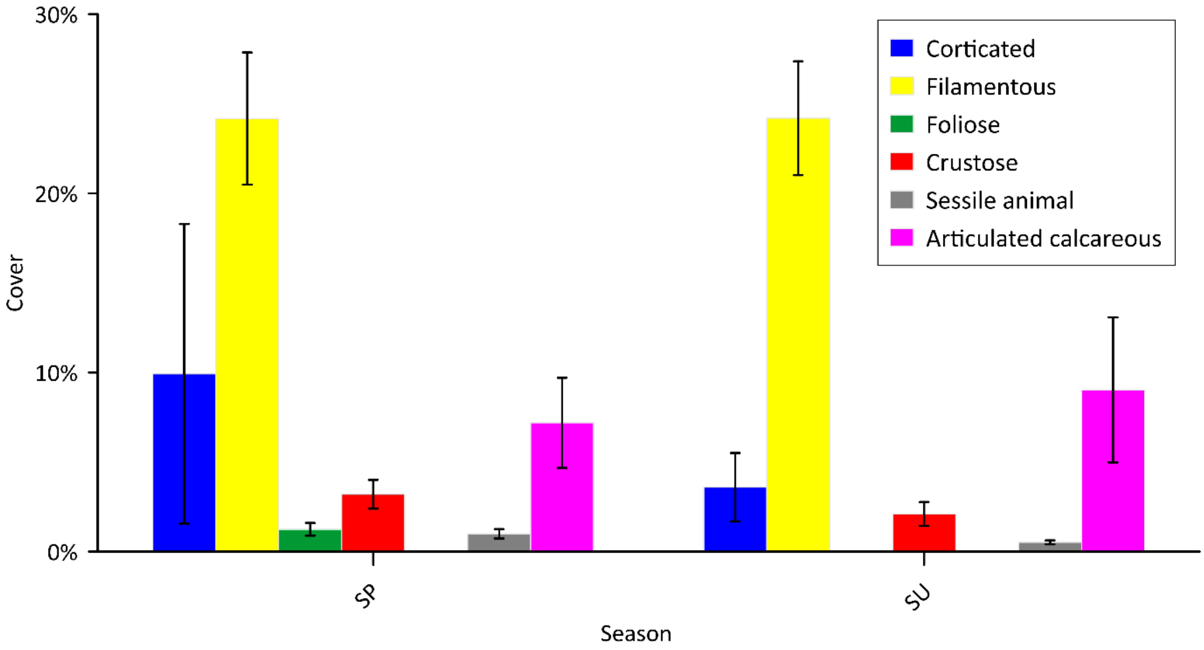

Figure 31. Community composition according to morphofunctional groups in the Hotel Parentium study site Data is represented as means of percentage cover of all the plots within a season ± SE.

In the Bijela uvala study site, which was monitored over three seasons (six months), corticated algae were dominant in winter and spring but declined in summer (Figure 32). Filamentous algae maintained moderate cover with a reduction in spring, while crustose algae slightly increased toward summer. Foliose algae and sessile animals remained rare, although foliose algae increased slightly in winter. Articulated calcareous algae were inconsistently present, remaining low in spring and summer. Monitoring in summer was discontinued after the *F. virsoides* population completely disappeared due to a combination of overgrazing, competition and stochastic events.

At the study site near Blaz, filamentous algae peaked in autumn and winter but showed variability in spring (Figure 33). Foliose algae were also most abundant during winter and spring, reflecting their preference for cooler temperatures and increased freshwater input. Sessile animals maintained relatively stable cover, with periodic overgrowth by ephemeral species like *Ulva* and *Pyropia*. Corticated and crustose algae were infrequent and inconsistently distributed across samples. This site displayed a distinct community structure, likely shaped by local geomorphology and locally strong freshwater inflow.

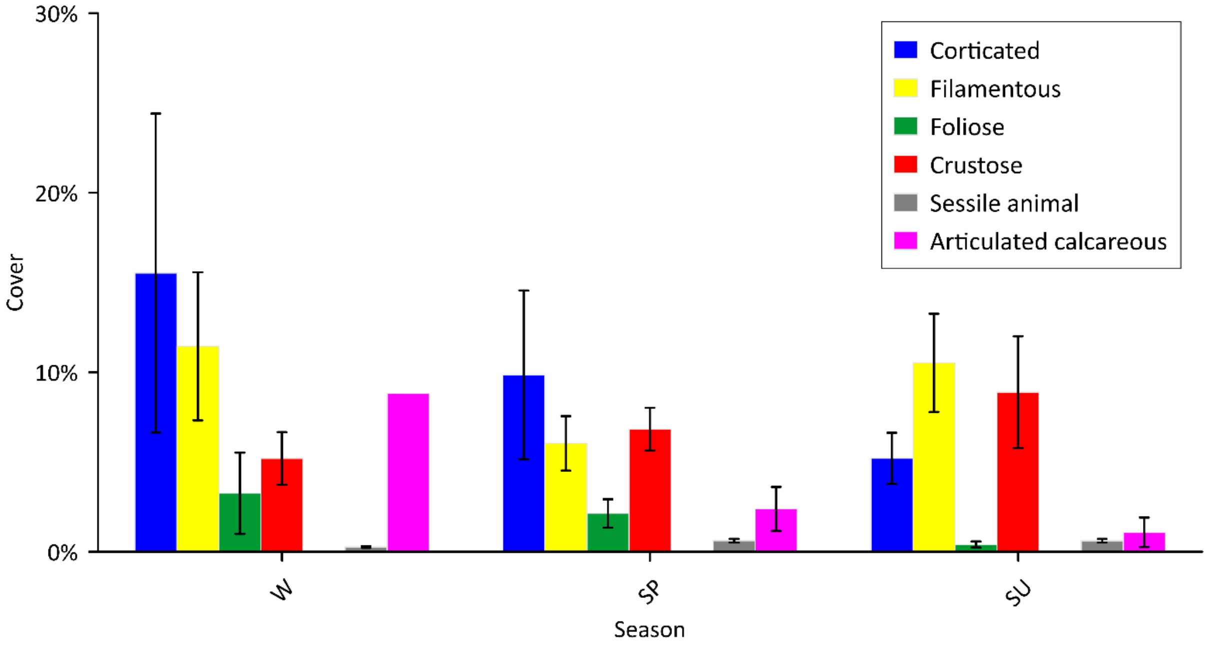

Figure 32. Community composition according to morphofunctional groups in the Bijela uvala study site. Data is represented as means of percentage cover of all the plots within a season ± SE.

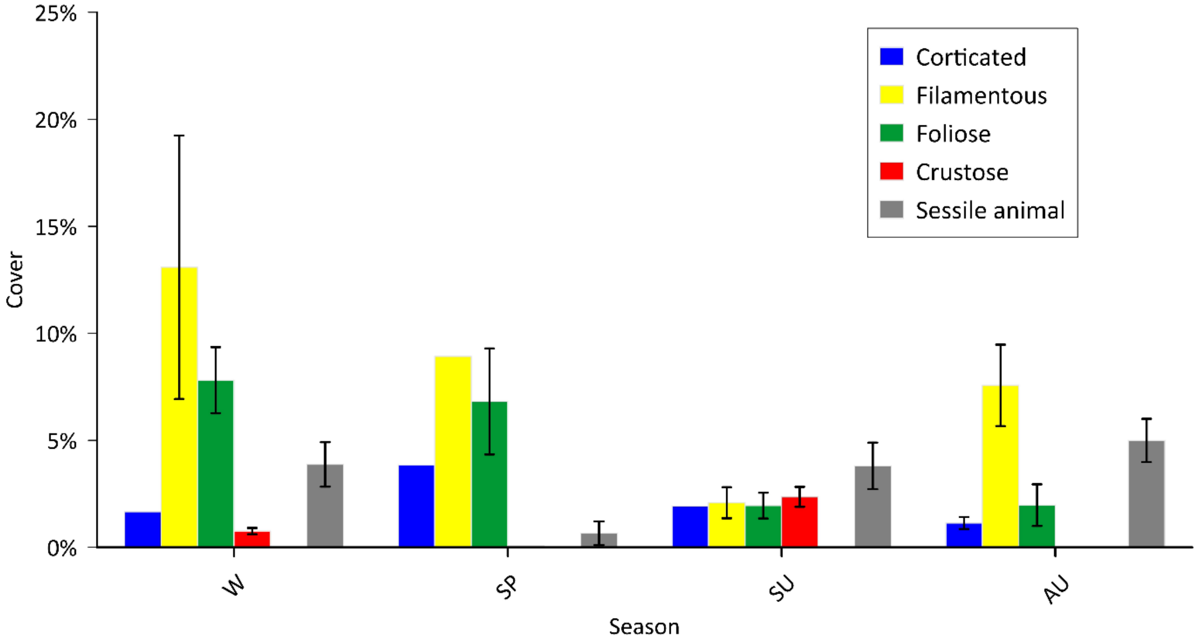

Figure 33. Community composition according to morphofunctional groups in the Blaz study site. Data is represented as means of percentage cover of all the plots within a season ± SE.

5.4. PCoA and PERMANOVA analysis of *Fucus virsoides* associated community structure

Principal coordinate (PCoA) and PERMANOVA analyses, based on morphofunctional groups found within the *Fucus virsoides* sites revealed varying degrees of seasonal community shifts across the four study sites.

At the study site Lanterna, winter samples clustered on the negative side of the PCO1 axis, while spring and summer samples shifted positively, indicating pronounced seasonal changes. Autumn samples were more transitional. PCO1 explained 31.4% of total variation, driven primarily by corticated algae (-0.653), foliose algae (-0.634), and sessile animals (0.596). PCO2 (20.6%) was influenced mainly by filamentous algae (0.590) and sessile animals (0.574). These results are represented in Figure 34. PERMANOVA analysis (p = 0.0001) revealed statistically significant differences between the seasons. Pairwise comparison further identified statistically significant differences between winter and spring (p = 0.0012), winter and summer (p = 0.0021), spring and autumn (p = 0.0001) as well as summer and autumn (p = 0.0009). PERMANOVA, PERMDISP and pairwise comparison results for Lanterna are shown in Appendix 2.

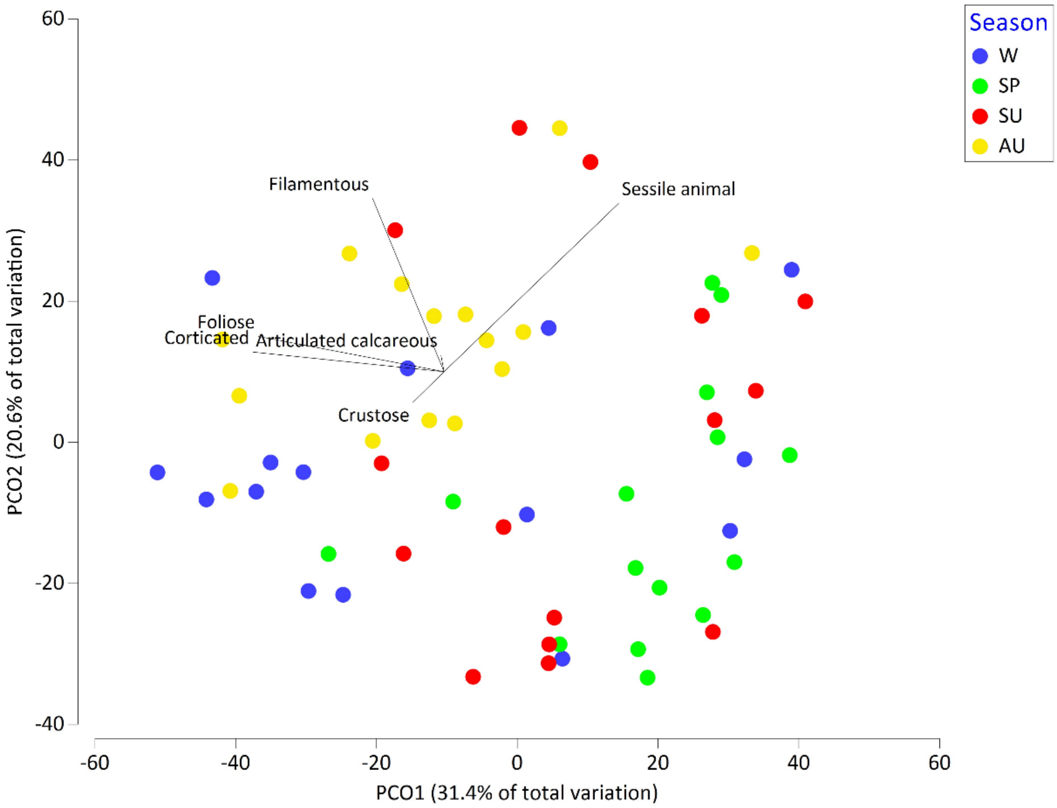

Figure 34. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of community composition based on morphofunctional group structure at the Lanterna study site.

At the Hotel Parentium study site, spring samples were scattered, while summer samples clustered tightly on the positive side of PCO1, reflecting the sharp compositional shift. PCO1 accounted for 48.2% of the variation, largely due to filamentous algae (0.938), with contributions from crustose (0.395) and foliose algae (0.343). PCO2 (18.2%) was influenced by corticated (-0.484) and articulated calcareous (0.353) algae. These results correspond with the collapse of the *Fucus virsoides* population during late spring/summer (Figure 35). PERMANOVA analysis (p = 0.0076) again revealed statistically significant differences between the seasons. Pairwise comparison confirmed statistically significant differences between spring and summer (p = 0.0083), which were the only seasons in this dataset. Importantly, PERMDISP analysis of the data dispersal revealed statistically significant results (p = 0.0001) indicating heterogeneity of multivariate spread, which reduces the fidelity of the PERMANOVA results for this site. PERMANOVA, PERMDISP and pairwise comparison results for Hotel Parentium site are shown in Appendix 3.

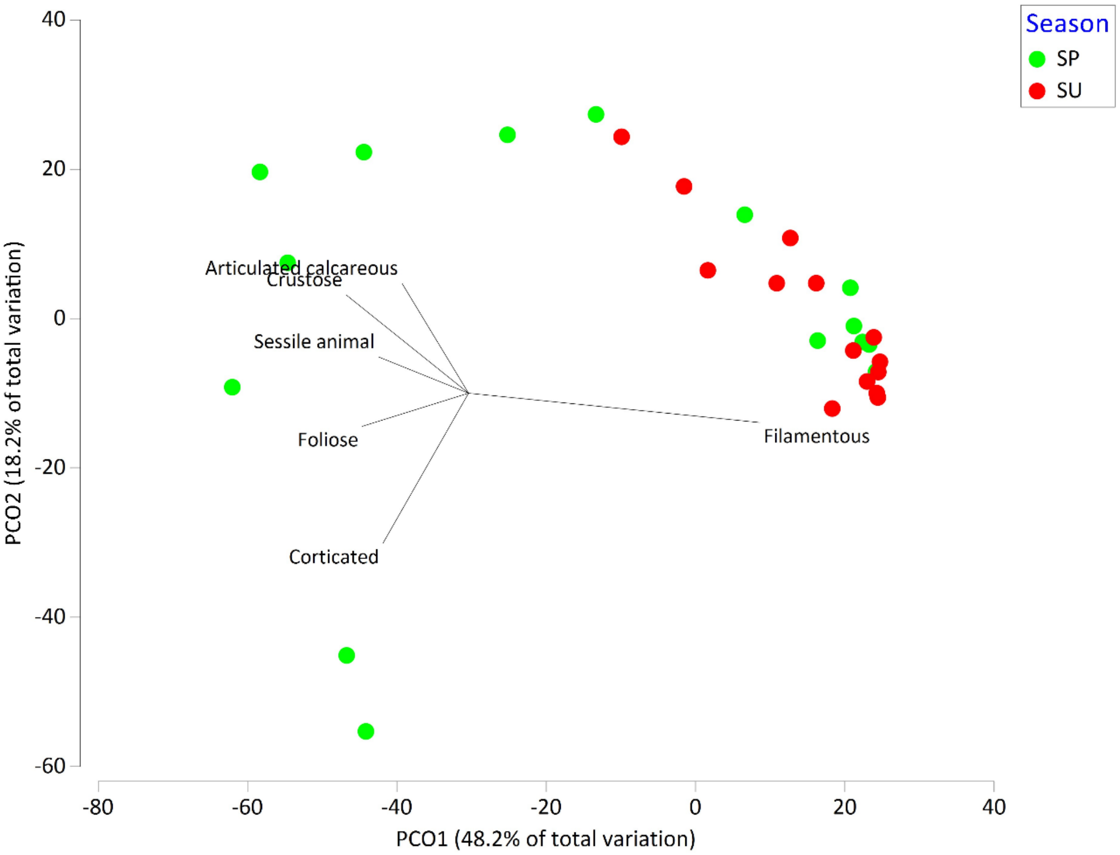

Figure 35. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of community composition based on morphofunctional group structure at the Hotel Parentium study site.

In the Bijela uvala study site, some winter and spring samples were slightly distinct from the more tightly clustered remaining samples (including the summer). PCO1 (38.5%) was mainly influenced by filamentous algae (0.925), with smaller contributions from articulated calcareous

(0.431) and crustose algae (-0.415). PCO2 (25%) was driven predominantly by corticated algae (-0.863), underscoring their role in seasonal community differences. These results are represented in Figure 36. However, PERMANOVA analysis of Bijela uvala dataset did not find any statistically significant differences between the seasons. PERMANOVA, PERMDISP and pairwise comparison results for Bijela uvala are shown in Appendix 4.

At the study site in Blaz Cove, summer and autumn samples grouped on the negative side of PCO1, while winter and spring samples were more dispersed but generally positive leaning. This pattern highlights a clear seasonal distinction between warmer and colder periods. PCO1 (37.2%) was most influenced by sessile animals (-0.735), crustose algae (-0.489), and filamentous algae (-0.397). PCO2 (25.5%) was mainly driven by foliose algae (0.794), with additional input from filamentous algae (0.320). These results are represented in Figure 37. PERMANOVA analysis revealed statistically significant differences between the seasons ($p = 0.0001$). Pairwise comparison further pointed out significant differences between all the seasons ($p < 0.05$; see Appendix 5 for PERMANOVA, PERMDISP and pairwise comparison results).

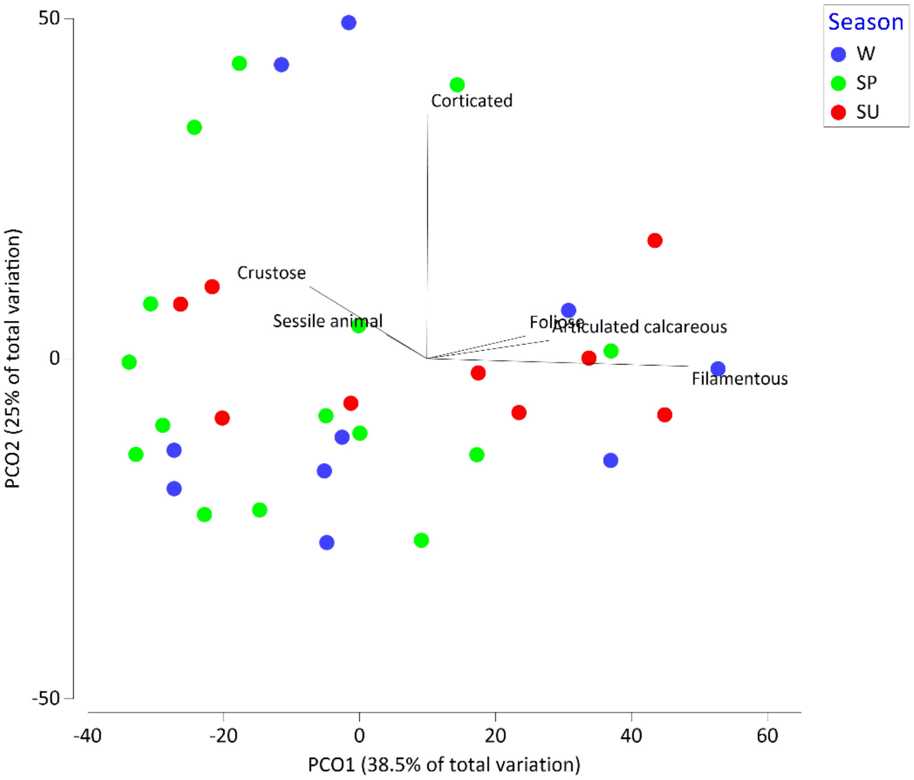

Figure 36. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of community composition based on morphofunctional group structure at the Bijela uvala study site

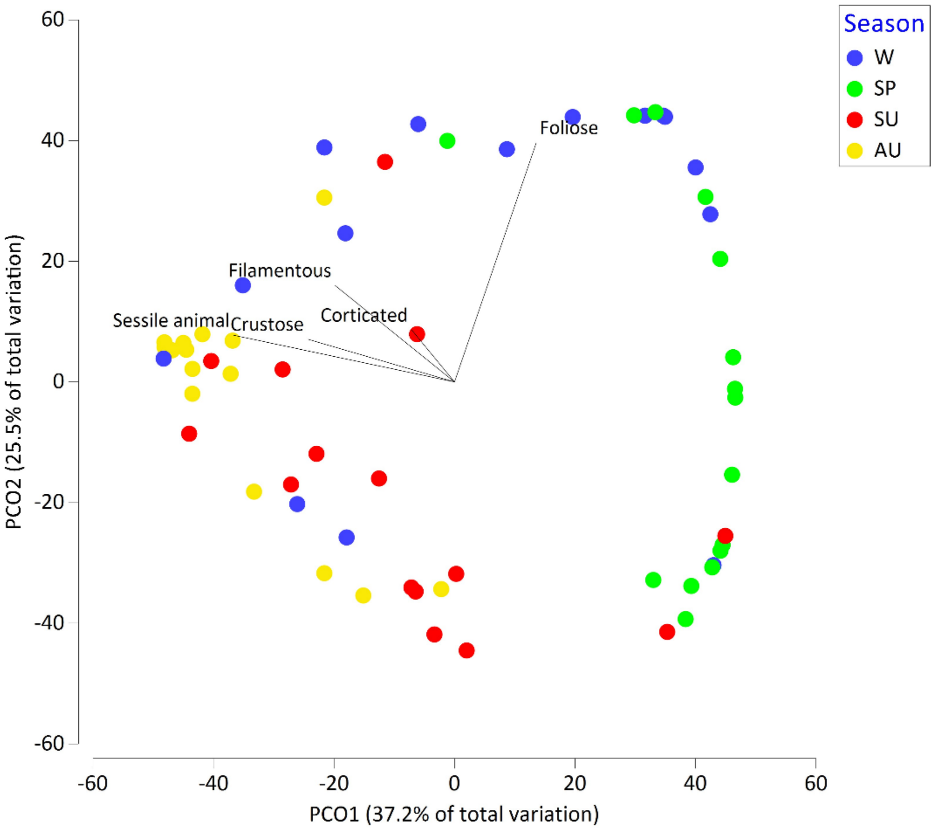

Figure 37. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of community composition based on morphofunctional group structure at the Blaz study site.

5.5. Population structure of *Fucus virsoides* stands

The demographic composition of *Fucus virsoides* thalli exhibited pronounced variability, primarily driven by intensive grazing activity but also stochastic events. These disturbances disproportionately affected older, larger thalli, leading to a population shift favouring juveniles and underdeveloped/overgrazed adults over mature individuals.

At Lanterna adult thalli dominated the population throughout the year. Nonetheless, increases in the juvenile to adult (j/a) ratio were noted in January (0.4), March (0.28), November (0.51), and December (0.49), although the elevated values in the latter months are likely skewed due to a reduced number of remaining individuals (Figure 38).

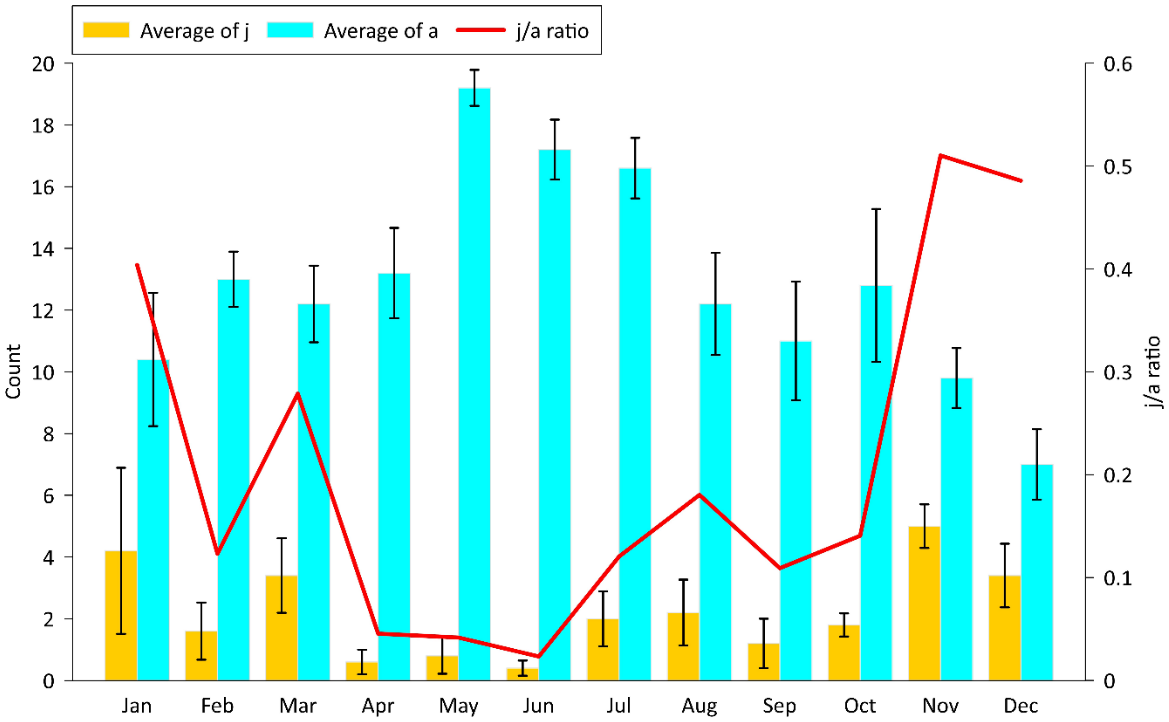

Figure 38. Monthly average number of adults and juvenile *Fucus virsoides* thalli and their juvenile to adult (j/a) ratio in the Lanterna study site. Data are represented as average count per plot per month ± SE.

In Hotel Parentium, the j/a ratio ranged from 0.67 in March to 0.41 in May, followed by a sharp rise to 2.0 in June and 1.65 in July (Figure 39). This increases coincided with intensive *Sarpa salpa* grazing, which caused extensive thallus damage, but also fouling. By August, the ratio had dropped to 0.5, and later *F. virsoides* had vanished from the site.

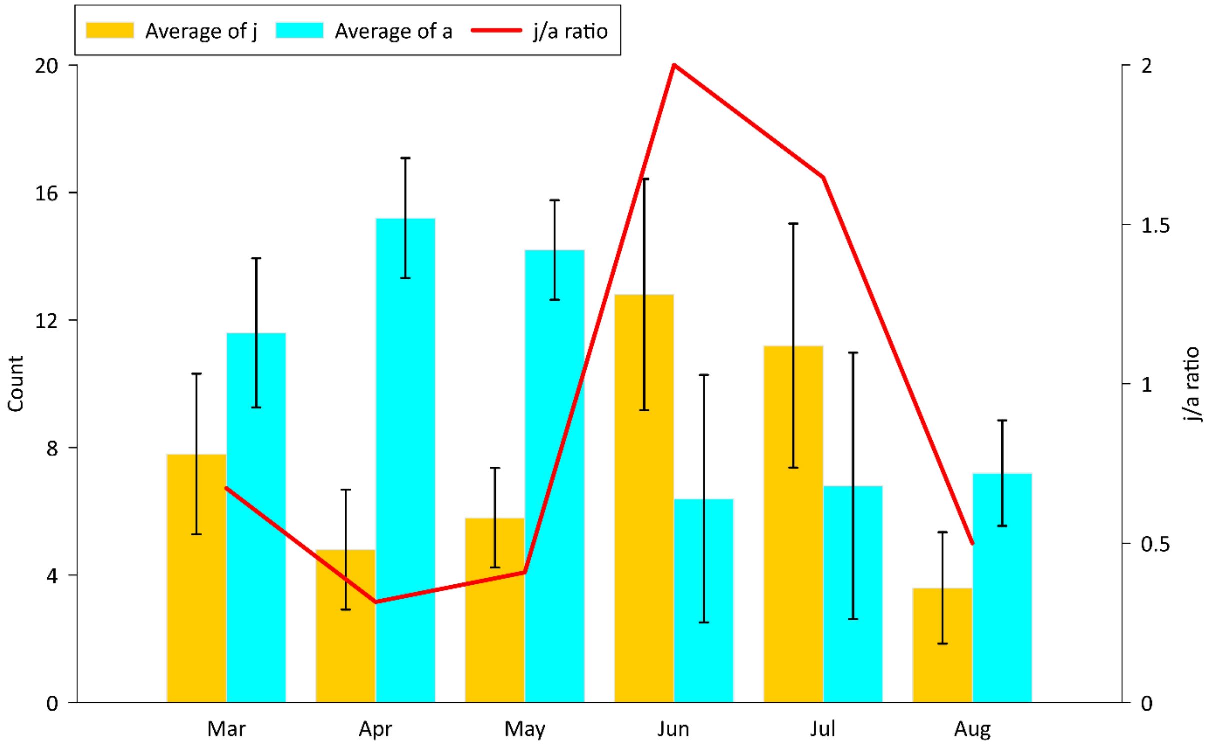

Figure 39. Monthly average number of adults and juvenile *Fucus virsoides* thalli and their juvenile to adult (j/a) ratio in Hotel Parentium study site. Data are represented as average count per plot per month ± SE.

Bijela uvala showed a similar trajectory, with a decline in j/a ratio from 0.56 in January to 0.2 in April, pointing to the strong dominance of adults (Figure 40). A dramatic spike occurred in June (12.86), corresponding to severe damage from both *S. salpa* grazing and pebble movement. In the aftermath, the population, now comprised mostly of juveniles and a few degraded adults, failed to recover.

At Blaz, the j/a ratio remained low (0.22-0.28) from January to May, indicating a population strongly dominated by adults (Figure 41). An increase of up to 0.45 was observed in June, continuing with minor fluctuations through September. Later in the year, the ratio peaked at 1.56 in December, driven by new recruits and heavy grazing pressure. However, field observations suggest some regenerating adults highly resembled juveniles, owing to their severely grazed thalli, particularly in densely packed patches. This may have affected the quality of the collected data, since the difference between the two was oftentimes barely noticeable (except under high magnification and very close inspection).

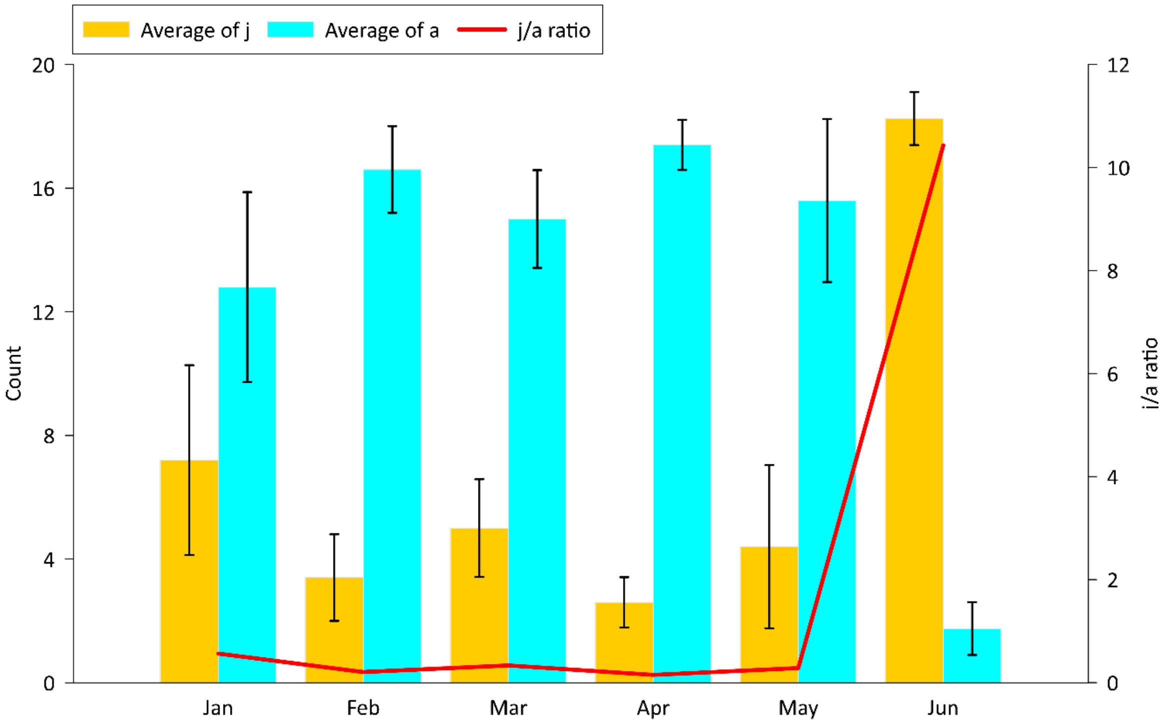

Figure 40. Monthly average number of adults and juvenile *Fucus virsoides* thalli and their juvenile to adult (j/a) ratio in the Bijela uvala study site. Data are represented as average count per plot per month ± SE.

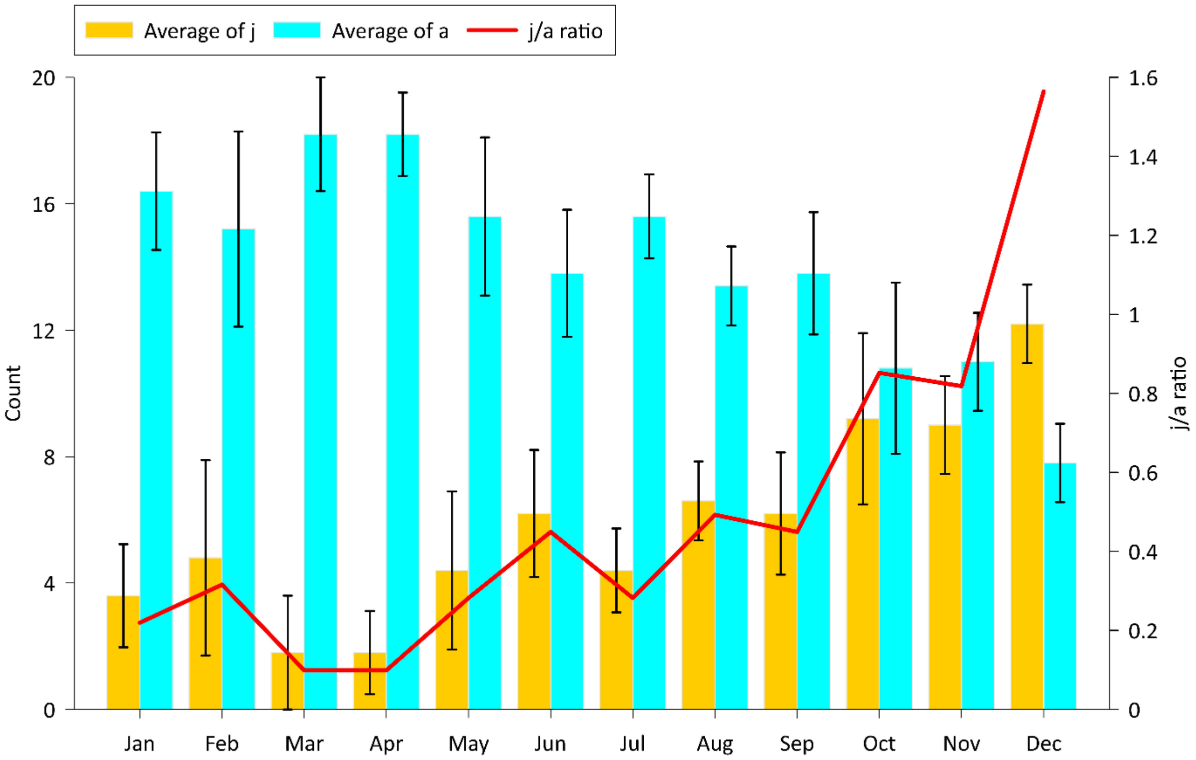

Figure 41. Monthly average number of adults and juvenile *Fucus virsoides* thalli and their juvenile to adult (j/a) ratio in the Blaz study site. Data are represented as average count per plot per month ± SE.

5.6. Morphological variability among study sites

Thallus size and cover

The average height and percentage cover of *Fucus virsoides* varied seasonally and spatially across the study sites. At Lanterna, thallus height showed somewhat clear seasonal patterns (Figure 42), peaking in June (7.1 ± 0.2 cm) before a steady decline towards December. *F. virsoides* cover increased steadily from January to May, peaking at 73 ± 8%, before declining to 20 ± 3% in December. These dynamics closely followed the grazing patterns, mainly from *S. salpa* during high tides (according to bite marks).

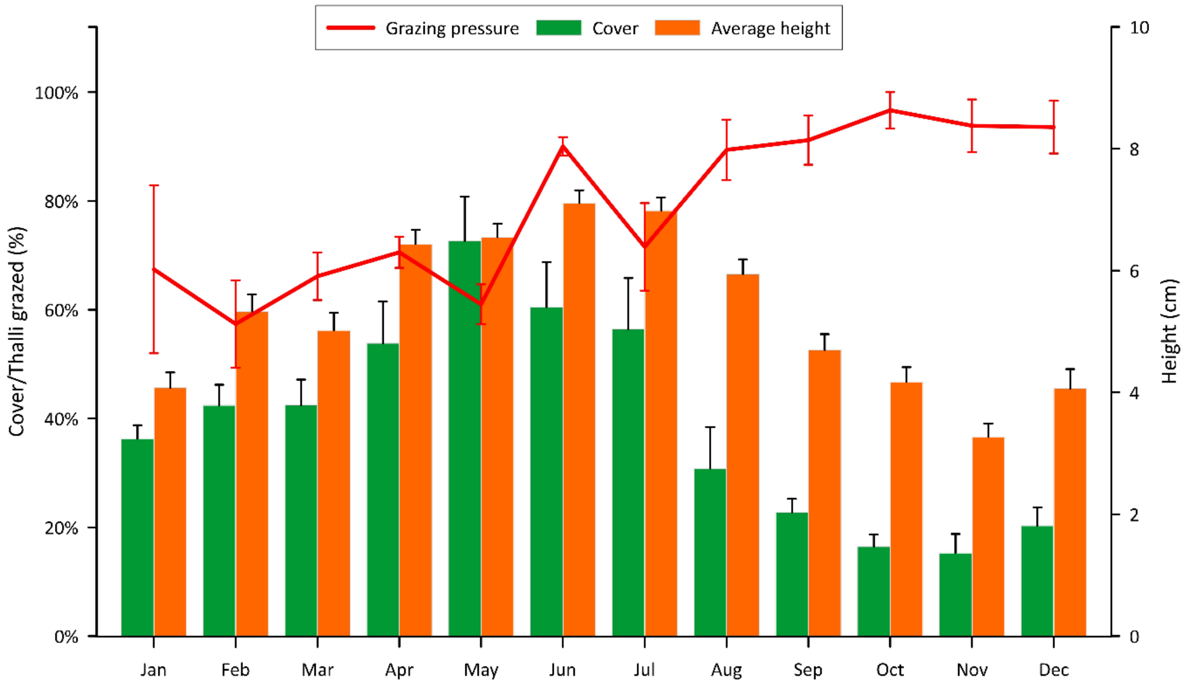

Figure 42. Monthly average height and percentage cover in relation to the grazing pressure in the Lanterna study site. Data is represented as average ± SE.

In Hotel Parentium, thalli were of a consistently smaller size , with the highest average height recorded in March (2.5 ± 0.11 cm) (Figure 43). Continuous grazing and fouling reduced the size until complete disappearance by August. Cover peaked modestly in April (37 ± 3%) and dropped to 14 ± 3% in August. The collapse of the population was attributed primarily to grazing, with fouling by ephemeral species accelerating the decline.

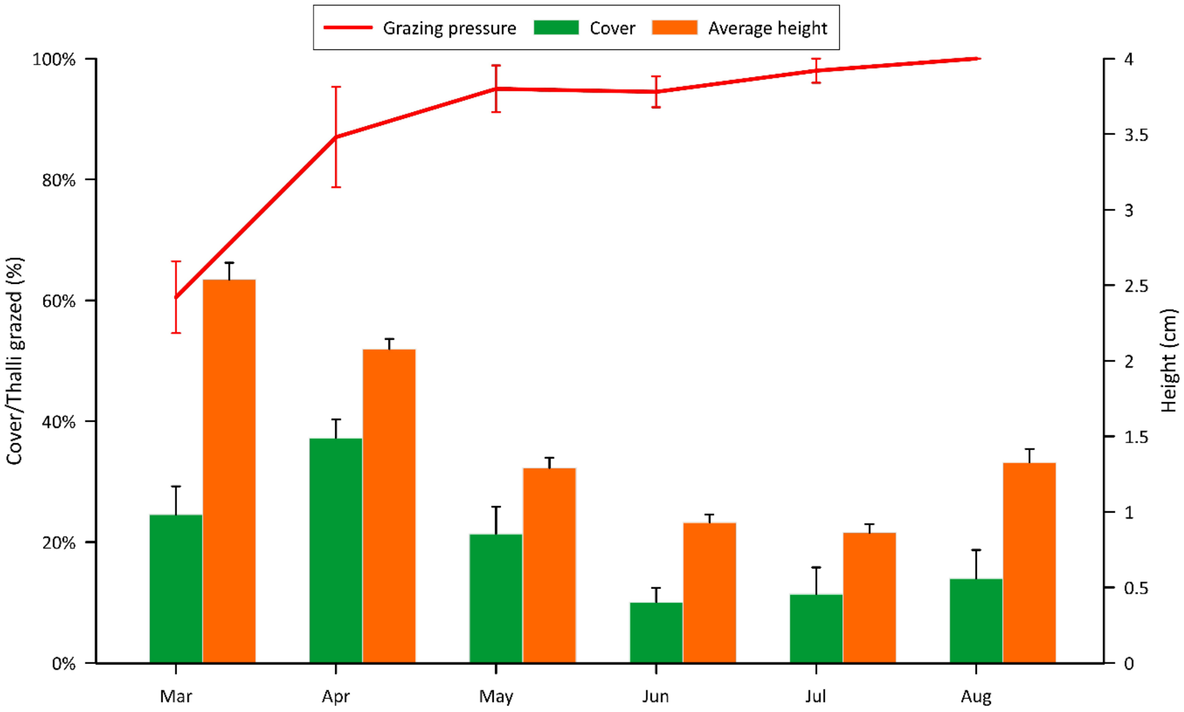

Figure 43. Monthly average height and percentage cover in relation to the grazing pressure in the Hotel Parentium study site. Data is represented as average ± SE.

In Bijela uvala, average thallus height increased until April (3.2 ± 0.12 cm) before a sudden decline in May (1.34 ± 0.07 cm) due to mass pebble displacement and subsequent *S. salpa* grazing (Figure 44). This led to the population's collapse. Cover peaked in April (67 ± 4%) and dropped rapidly thereafter. By July, no individuals remained detectable.

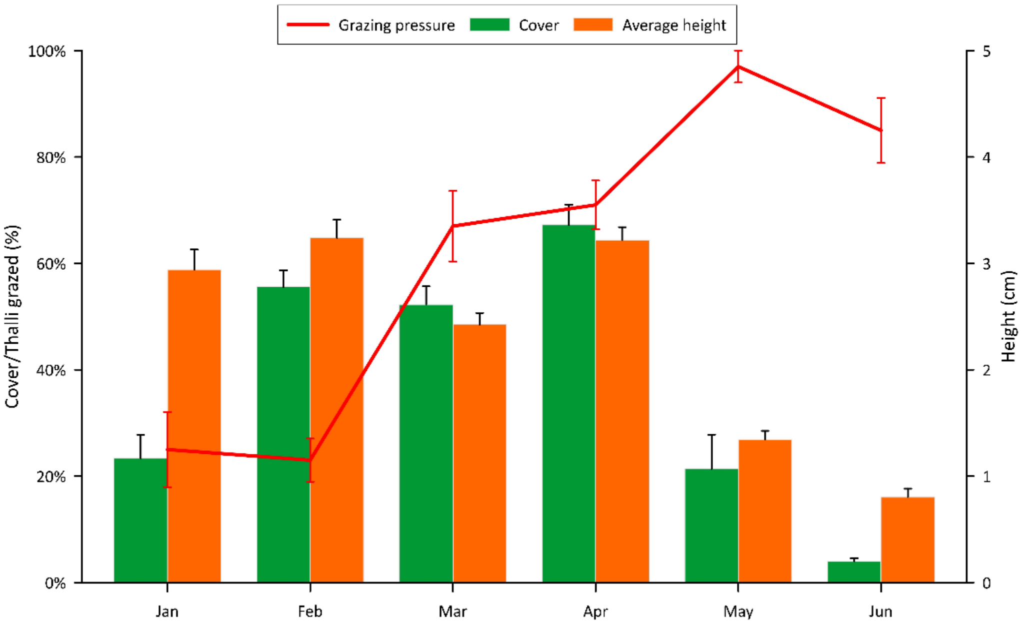

Figure 44. Monthly average height and percentage cover in relation to the grazing pressure in the Bijela uvala study site. Data is represented as average ± SE.

Blaz supported the most robust *F. virsoides* population. Average thallus height decreased from 5.04 ± 0.19 cm in April to 2.27 ± 0.2 cm in September, concurrent with intense grazing (Figure 45). Cover remained high for most of the year, peaking at 97 ± 0.5% in May before dropping sharply in October (48 ± 9%). Partial recovery was observed in November and December. Average cover trend was closely tied to grazing activity, with decreases following periods of high herbivory pressure and subsequent recovery when grazing lessened (Figure 45).

Figure 45. Monthly average height and percentage cover in relation to the grazing pressure in the Blaz study site. Data is represented as average ± SE.

Aerocyst and fertility dynamics

Fertility in *Fucus virsoides* is typically associated with aerocyst development, as receptacles form atop aerocysts. At Lanterna, no aerocysts were present in January, though small receptacles were detected (13 ± 0%; Figure 46), which in itself is an anomaly. Aerocyst presence increased through February - May (peak 28 ± 7%), aligning with maximal fertility, and then declined toward year's end, following the increase in grazing pressure, following an increase in grazing pressure. December also showed increased fertility, but this is due to very small remaining sample size that increases the values,

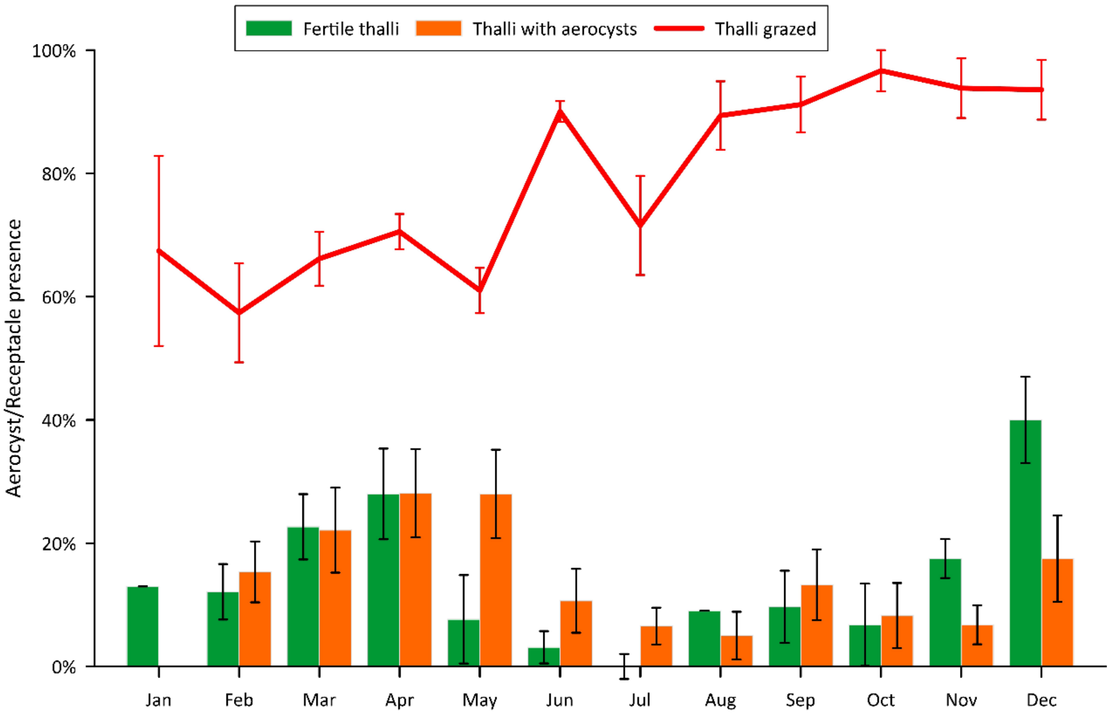

Figure 46. Monthly presence of aerocysts and percentage of fertile *Fucus virsoides* thalli, in relation to the grazing pressure in the Lanterna study site. Data are presented as average ± SE.

In Hotel Parentium, aerocysts and fertility peaked in March (22 ± 5%; Figure 47), then sharply declined due to grazing and structural damage (Figure 47). After April however, both aerocysts and fertility reduced greatly due to intense grazing and thallus damage.

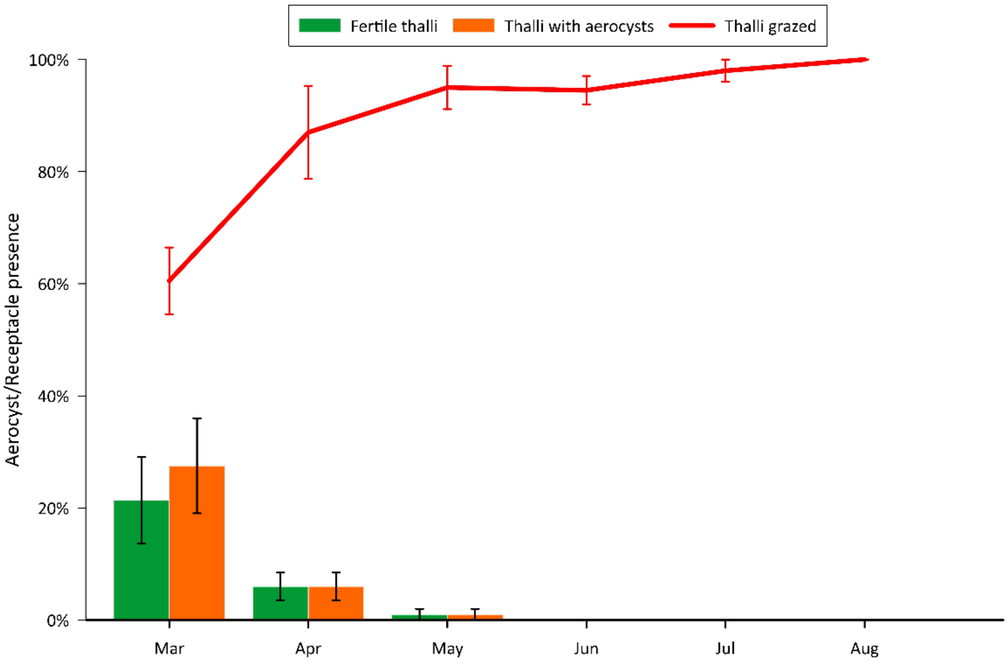

Figure 47. Monthly presence of aerocysts and percentage of fertile *Fucus virsoides* thalli, in relation to the grazing pressure in the Hotel Parentium study site. Data are presented as average ± SE.

At Bijela uvala, aerocyst presence was minimal: 1 ± 1% in January, 14 ± 6% in February, and 0% by May (Figure 48). Fertility followed suit, declining from 10 ± 4% in February to 5 ± 3% in April. No fertility was observed beyond this point due to severe grazing and damage to *F. virsoides* thalli.

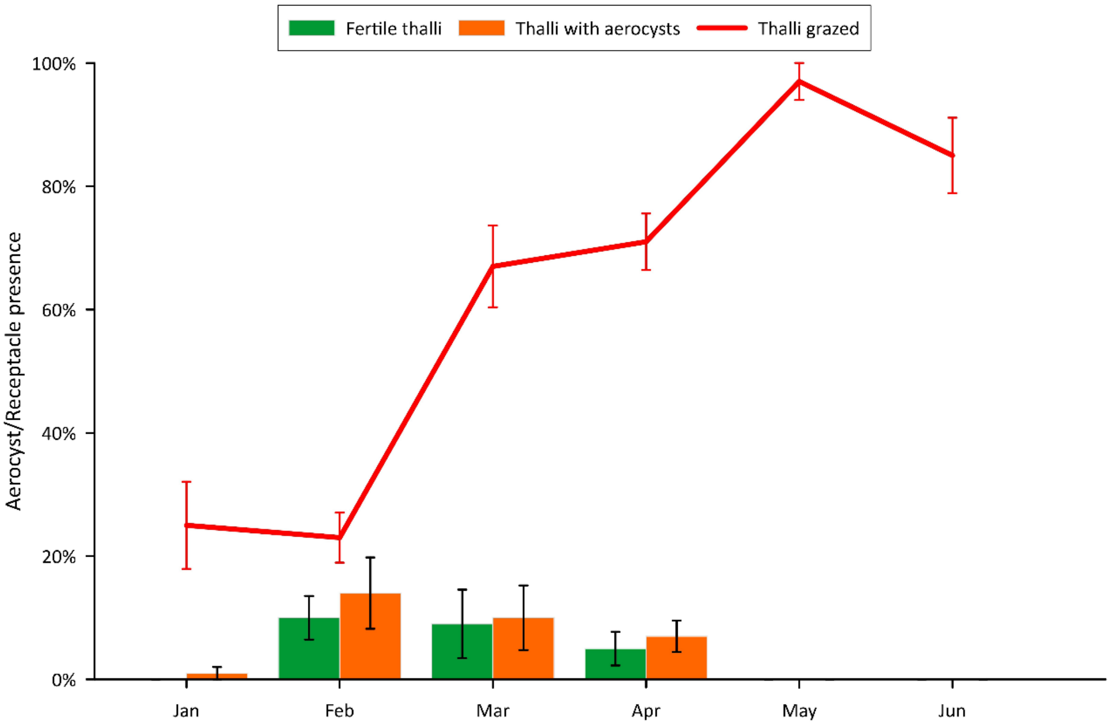

Figure 48. Monthly presence of aerocysts and percentage of fertile *Fucus virsoides* thalli, in relation to the grazing pressure in the Bijela uvala study site. Data are presented as average ± SE.

In Blaz, aerocyst presence remained low (max 4 ± 1%) with peak fertility (9 ± 4%) in February. As in Lanterna, a certain quantity of receptacles was found without any formed aerocysts, which may represent a local adaptation or a stress response. A sudden spike occurred in August, with aerocyst reaching (35 ± 6%) and fertility (25 ± 6%), which is an unusual reproductive period for this coldwater species (Figure 49). In September, aerocysts were still present (15 ± 7%) and a small portion of thalli remained fertile (5 ± 3%), although the population was heavily grazed at that time. No fertile individuals or a significant amount of formed aerocysts were observed afterwards, likely due to ongoing intense grazing.

Figure 49. Monthly presence of aerocysts and percentage of fertile *Fucus virsoides* thalli, in relation to grazing pressure in the Blaz study site. Data are presented as average ± SE.

5.7. Grazing pressure, regeneration, and necrosis

In Lanterna grazing pressure was lowest in February (57 ± 8%), only slightly below January, and increased steadily throughout the year. It reached 90 ± 2% in June and remained above 90% from September to December. Regeneration rates stayed stable between 40-50% for most of the year, with pronounced peaks in July and August (79 ± 8%) and again in December (77 ± 8%), but dropped below 40% in October. Necrosis levels were generally stable around 20%, except for a sharp spike in November (73 ± 11%), likely linked to increase marine litter and seagrass (*Zostera* sp.) accumulation, before decreasing in December (37 ± 10%). Dynamics of all three metrics are represented in Figure 50.

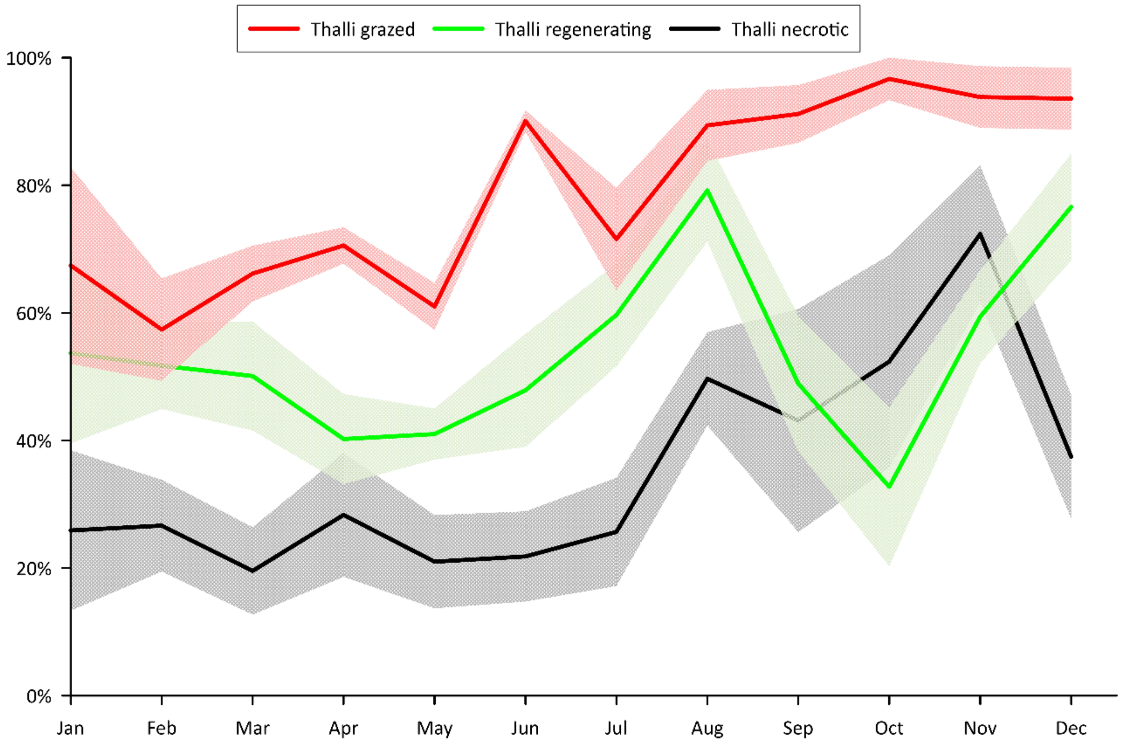

Figure 50. Monthly levels of grazing pressure, regeneration and necrosis at the Lanterna study site. Data is represented as average ± SE.

In Hotel Parentium, at the start of the monitoring in March, 61 ± 6% of thalli showed grazing marks, and 48 ± 9% showed signs of regeneration (Figure 51). Grazing intensity increased rapidly, exceeding 80% in April and reaching 90-100% from May through August, when the population had already collapsed. Regeneration was low in April (21 ± 15%) but increased dramatically in May (53 ± 18%). Following a drop in June, nearly all surviving thalli were regenerating in July (95 ± 3%). However, regeneration stopped completely in August, owing to, presumably, the poor physiological state of the thalli. The necrosis levels have been slowly increasing from March towards June, but peaked at 80-100% only during July and August, just before the complete collapse.

In Bijela uvala, grazing, regeneration and necrosis levels were low (< 25%) during the colder months (Figure 52). In March and April, grazing increased to 67 ± 7% and 71 ± 5%, while regeneration and necrosis levels remained below 30%. A sharp rise in both grazing and regeneration occurred in May (97 ± 3% and 96 ± 4%, respectively) and June (85 ± 6% and 84 ± 4%, respectively), following an intense grazing by *S. salpa*, after which *F. virsoides* vanished completely. Necrosis levels never reached highly notable levels since the thalli did not survive long enough for them to be recorded (Figure 52).

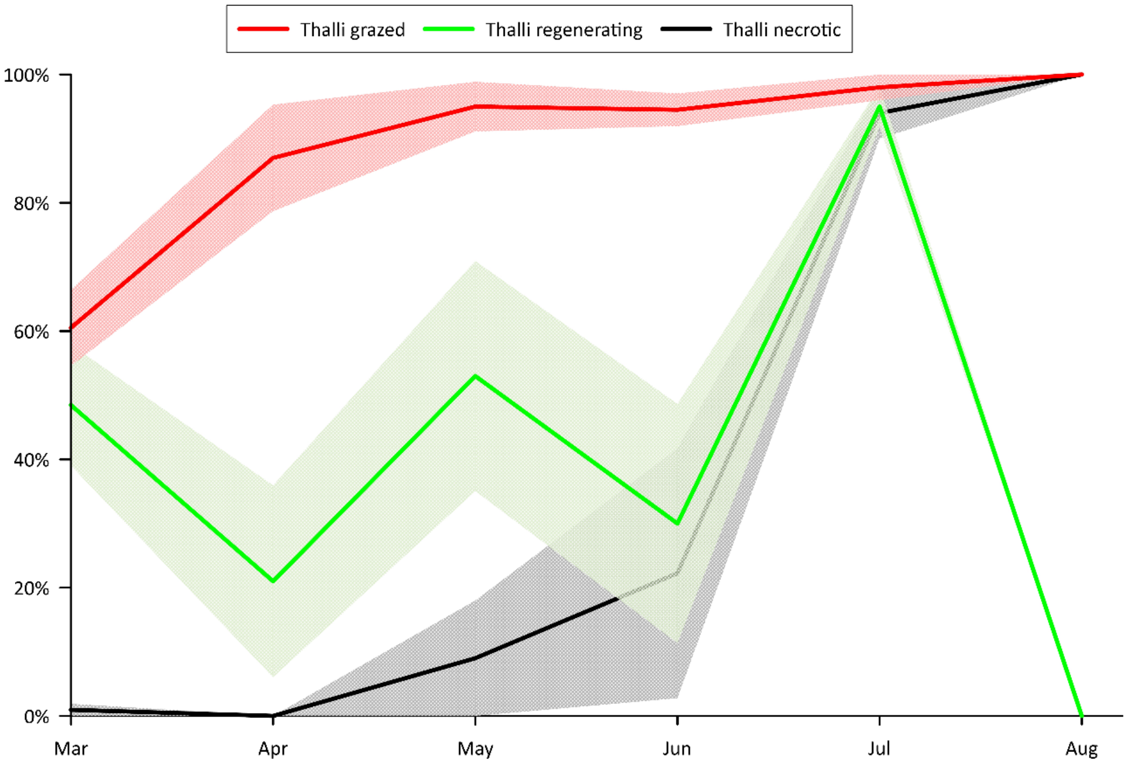

Figure 51. Monthly levels of grazing pressure, regeneration and necrosis at the Hotel Parentium study site. Data is represented as average ± SE.

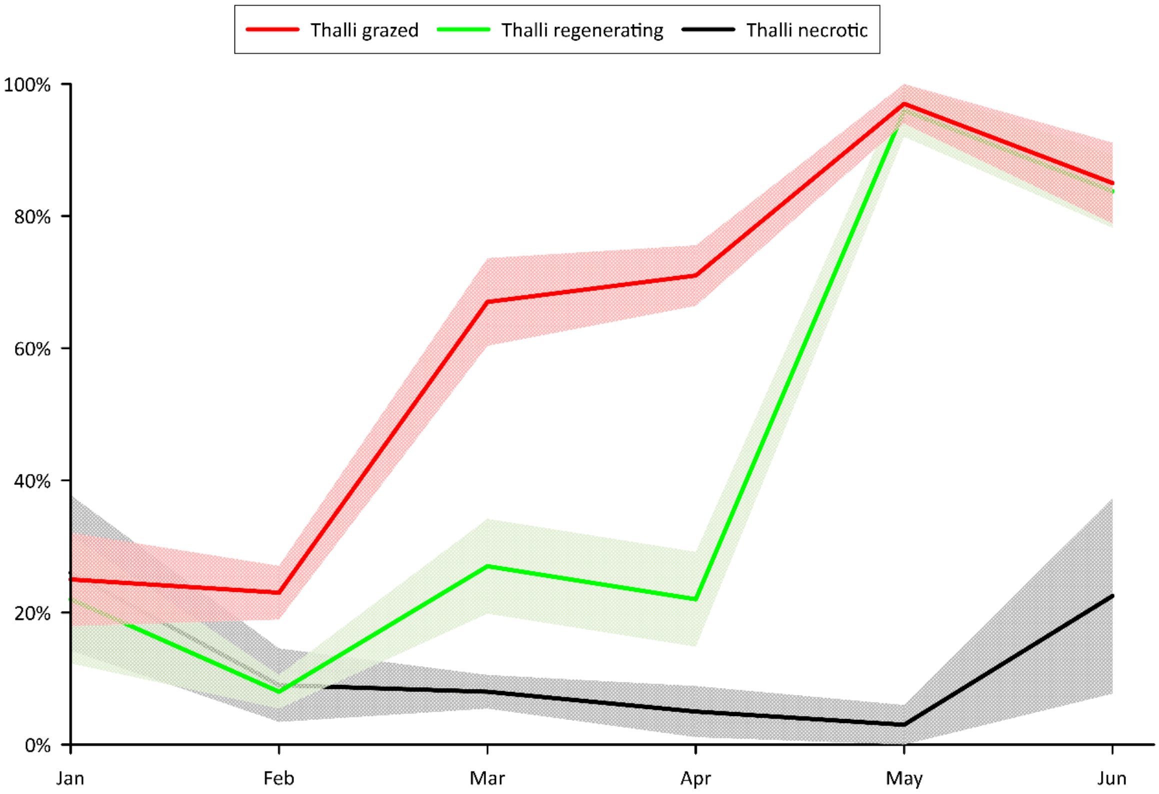

Figure 52. Monthly levels of grazing pressure, regeneration and necrosis at Bijela uvala study site. Data is represented as average ± SE.

In Blaz Cove, in January, grazing and regeneration rates were both high (66 ± 6% and 67 ± 9%) but declined in April to 27 ± 7% and 12 ± 3%, respectively. Grazing increased again in May (63 ± 14%), reaching its maximum in October and November (93±3% and 88 ± 6%, respectively). Regeneration responded with a moderate increase in July and August (46 ± 6% and 57 ± 10%, respectively) but remained generally low (12-33% ± SE) through the year. Grazing pressure decreased in December while regeneration increased (36 ± 13% and 34 ± 9%, respectively), reflecting recovery following the earlier damage to thalli. Necrosis remained low throughout the year, suggesting high recovery capacity of the thalli (Figure 53).

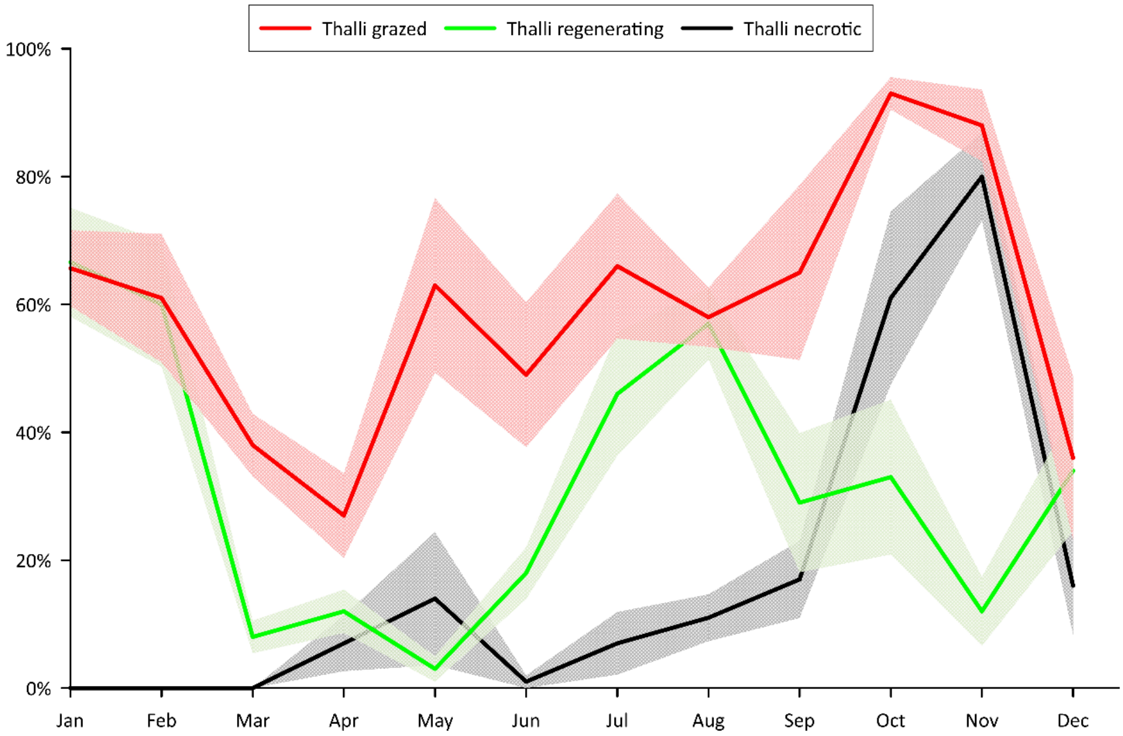

Figure 53. Monthly levels of grazing pressure, regeneration and necrosis at the Blaz study site. Data is represented as average ± SE.

Overall, across all the study sites, an increase in grazing pressure was closely related to the aerocyst and receptacle development, especially at Blaz (see Figures 45, 49 and 53) and somewhat less so in Lanterna (see Figures 42, 46 and 50), suggesting preferential grazing of adult and fertile thalli.

5.8. PCoA analysis of *Fucus virsoides* morphological and population metrics

The PCoA plot revealed pronounced but varying seasonal clustering across sites. In Lanterna, winter and autumn datapoints were somewhat separated from the spring and summer, suggesting an influence from the seasonal changes (Figure 54). Variations along the PCO1 axis (69.1% of total variation) was driven primarily by average thallus height (0.982) and average cover (0.632), with aerocysts presence (0.473) contributing moderately. Along the PCO2 axis (17.8% of total variation), differences were occurring primarily according to the grazing pressure (-0.857), fertility (-0.771), and less so the average cover (0.587).

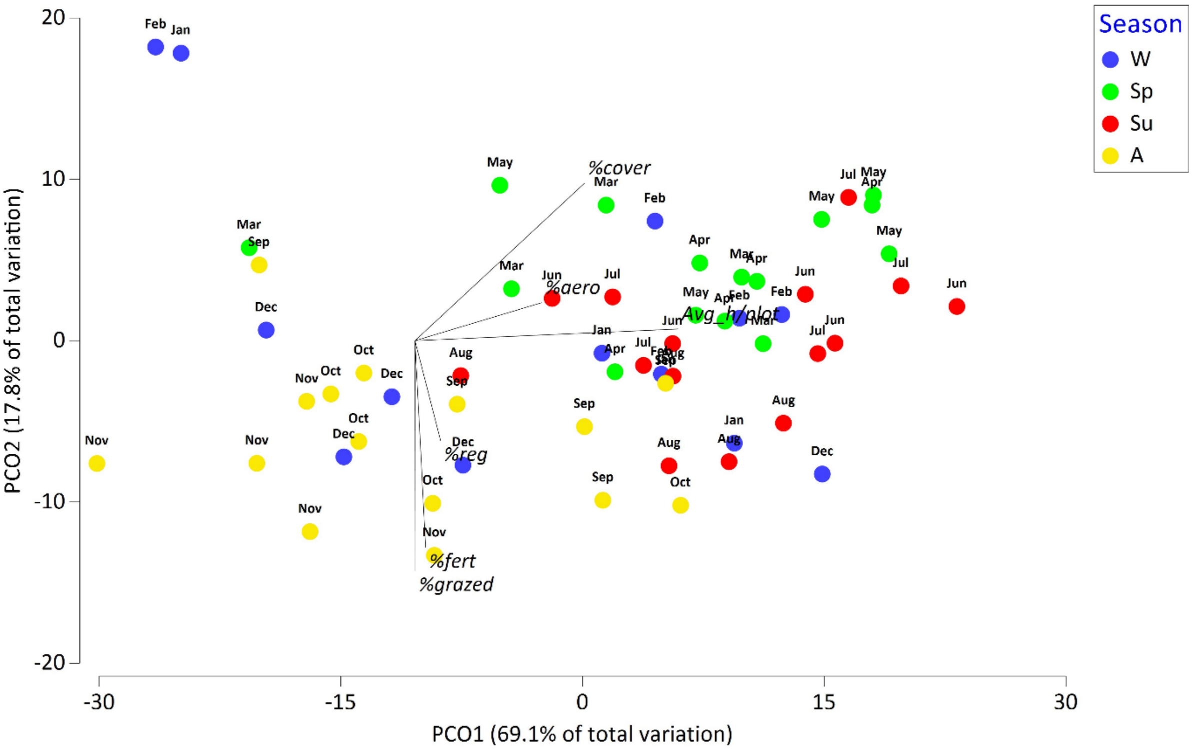

Figure 54. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of *Fucus virsoides* population traits within the Lanterna study site on a monthly basis. Included variables: Average height (Avg_h/plot), average *Fucus virsoides* cover (%cover), presence of aerocysts (%aero), fertility levels (%fert), grazing levels (%grazed), and regeneration levels (%reg). Specific months are shown above the datapoints as abbreviations. Seasons are denoted as W (winter), Sp (spring), Su (summer) and Au (autumn) for better clarity.

In Hotel Parentium, the datapoints from the two available seasons (spring and summer) showed a clear separation from one another, with a visible "May-June" transition (Figure 55). PCO1 axis (62% of total variation) was influenced by average height (0.910), average cover (0.760), fertility (-0.705), grazing (-0.664) and aerocyst (0.603). PCO2 axis (27% of total variation) are driven by regeneration levels (-0.804) and less so by thallus fertility (0.416).

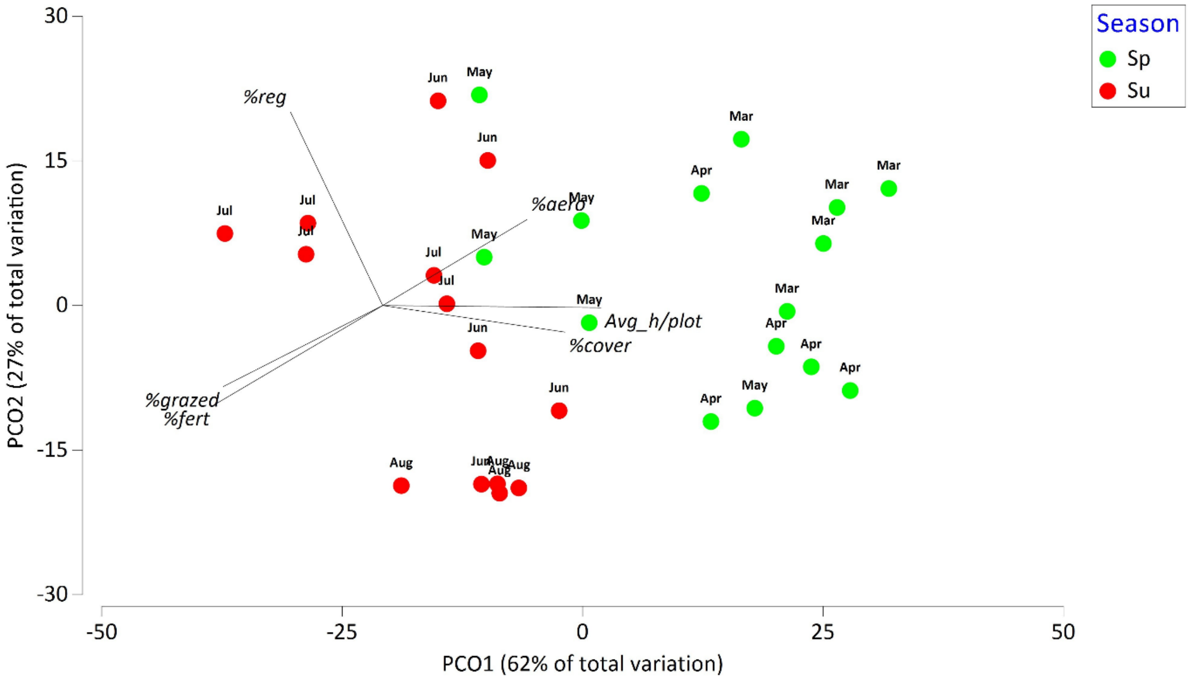

Figure 55. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of *Fucus virsoides* population traits within the Hotel Parentium study site on a monthly basis. Included variables: Average height (Avg_h/plot), average *F. virsoides* cover (%cover), presence of aerocysts (%aero), fertility levels (%fert), grazing levels (%grazed), and regeneration levels (%reg). Specific months are shown above the datapoints as abbreviations. Seasons are denoted as W (winter), Sp (spring), Su (summer) and Au (autumn) for better clarity.

In Bijela uvala, a clear separation of spring and early summer datapoints is evident along the PCO1 axis (Figure 56), reflecting major changes in population due to stochastic events such as sediment movement and intense grazing, both of which led to the disappearance of *Fucus virsoides*. Variations along the PCO1 axis (80.5% of total variation) were driven by average height (0.902), grazing pressure (-0.773), average cover (0.716), and regeneration (-0.899). Variations along the PCO2 axis (13.6% of total variation) were less notable.

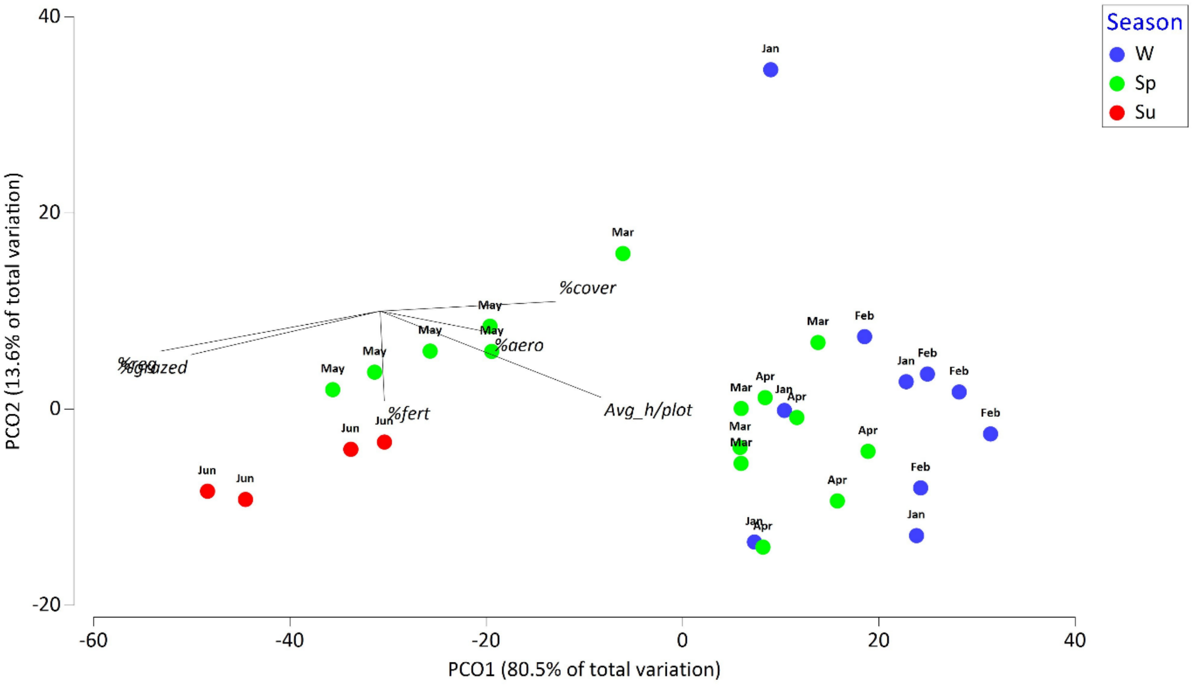

Figure 56. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of *Fucus virsoides* population traits within the Bijela uvala study site on a monthly basis. Included variables: Average height (Avg_h/plot), average *F. virsoides* cover (%cover), presence of aerocysts (%aero), fertility levels (%fert), grazing levels (%grazed), and regeneration levels (%reg). Specific months are shown above the datapoints as abbreviations. Seasons are denoted as W (winter), Sp (spring), Su (summer) and Au (autumn

In Blaz, data was more tightly clustered, with slight seasonal structuring. Spring-summer datapoints aligned towards the positive PCO1, and autumn-winter datapoints towards the negative PCO1. There is no clear distinction between the specific months within each season, though, with the slight exception in winter months, where December is positioned more closely to the other autumn months (Figure 57). Variations along the PCO1 axis (59.9% of total variation) were driven primarily by average height (0.952), average cover (0.696) and less so fertility (-0.541), which spiked during August, continuing slightly into September. All of these parameters experienced a dramatic decline due to grazing in early autumn, which likely strongly influenced the data distribution. On the other hand, variations along the PCO2 axis (19.4% of total variation) were associated with grazing pressure (0.746), which spiked in early autumn, regeneration levels (0.611) and, less so the average cover (-0.407).

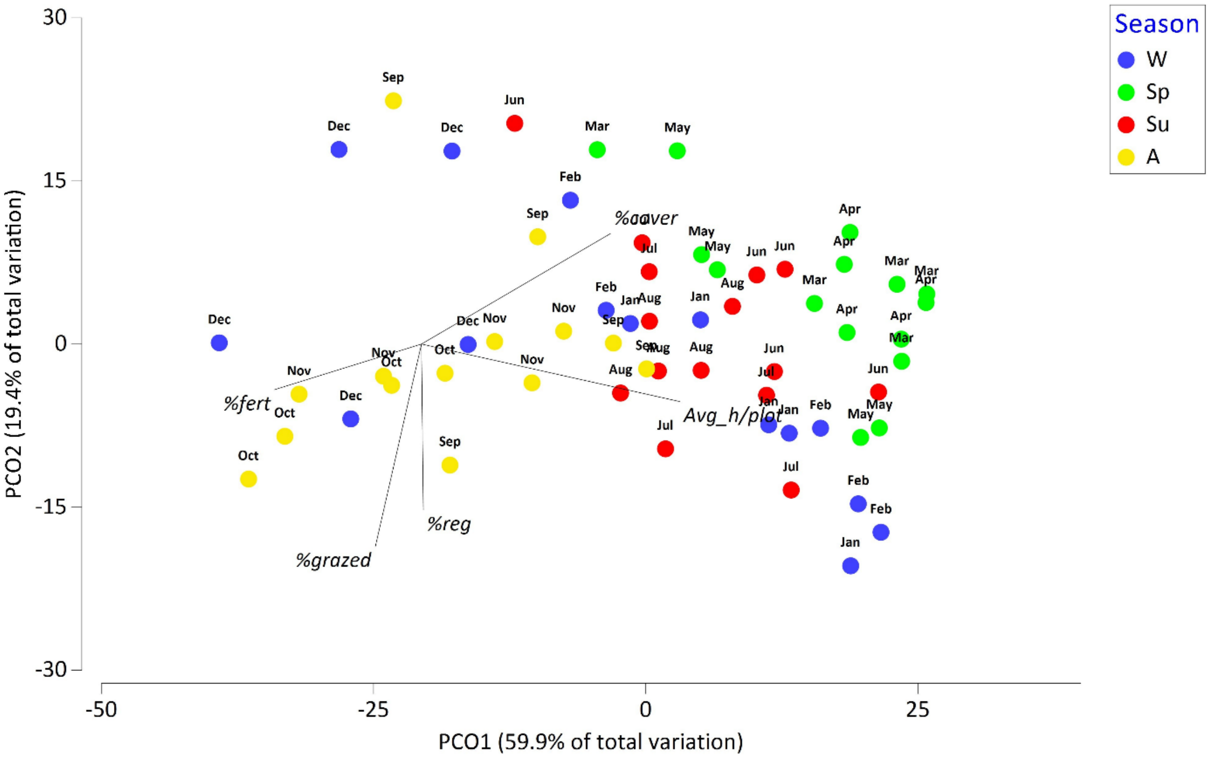

Figure 57. Principal coordinates analysis (based on Bray-Curtis dissimilarity) of *Fucus virsoides* population traits within the Blaz study site on a monthly basis. Included variables: Average height (Avg_h/plot), average *F. virsoides* cover (%cover), presence of aerocysts (%aero), fertility levels (%fert), grazing levels (%grazed), and regeneration levels (%reg). Specific months are shown above the datapoints as abbreviations. Seasons are denoted as W (winter), Sp (spring), Su (summer) and Au (autumn) for better clarity.

5.9. One-way PERMANOVA results of *Fucus virsoides* morphological and population metrics analysis

PERMANOVA analysis revealed significant temporal differences in *Fucus virsoides* population structure in Lanterna (Pseudo-F = 3.4712; P = 0.0001). However, the pairwise comparisons showed limited month to month variation overall, with many comparisons not being statistically significant (p > 0.05, Appendix 6). Notable differences emerged between spring-summer and spring-late autumn, particularly between April vs. November (t = 4.7545; p = 0.0076) and May vs. November (t = 4.5621; p = 0.0082). This suggests a seasonal shift in thallus traits, primarily driven by increasing grazing pressure later in the year. Results of this analysis are represented in Appendix 6.

Furthermore, PERMANOVA also revealed significant temporal differences in community structure at Hotel Parentium (Pseudo-F = 13.292; P = 0.0001). Most pairwise comparisons were significant, especially during the spring and summer months. The strongest differences were between April and July (t = 8.07, p = 0.0092) and between March and July (t = 7.35, p = 0.0099), reflecting the collapse of the population due to overgrazing and necrosis. May and June did not statistically differ from each other (t = 1.0331, p = 0.4068, Appendix 7), however, both were significantly different from March and April, pointing towards the observed signs of decline. These findings highlight a major shift in measured population metrics and assemblage structure from spring to summer, driven by strong grazing and massive necrosis. Importantly, PERMDISP results revealed significant differences in dispersion between temporal groups (F: 5.231, p = 0.0089, Appendix 4), indicating heterogeneity of multivariate spread, which reduces the fidelity of the PERMANOVA results for this study site. The results of this analysis are represented in Appendix 7.

At Bijela uvala, PERMANOVA revealed significant temporal differences (Pseudo-F = 17.81; P = 0.0001). Pairwise comparisons point towards differences between winter-spring months (January-March) and spring months (May-June), with the most pronounced dissimilarities occurring between February and May (t = 8.686, p = 0.0067) and between April and May (t = 7.9074, p = 0.0081). These results reflect the stochastic event involving sediment shift and overgrazing, which disrupted the population during spring. Results of this analysis are represented in Appendix 8.

PERMANOVA also showed significant monthly differences at Blaz (Pseudo-F = 7.2377; P = 0.0001). Pairwise comparisons revealed that the strongest differences occurred between early-year months (January to April) and late spring to early summer (May to June). The highest dissimilarities were between February and May (t = 8.69, p = 0.0067), April and May (t = 7.91, p = 0.0081), and February and June (t = 7.86, p = 0.0082). These shifts align with seasonal transitions and a peak in vegetative traits during spring. The results of this analysis are represented in Appendix 9.

5.10. Effects of prolonged exposure to increased air temperatures during emersion

Effects on morphology and physiology

During the experiment, no visible signs of necrosis were observed in thalli subjected to T-20, T-25, T-29, or C-14 treatments during either phase, aside from the loss of naturally occurring sterile hairs. However, in both phases, a necrotic odour typical of exposed fucalean algae was noticeable in the T-29 and T-33 treatments. In the T-33 treatment, physical necrosis of the thalli was evident during both experimental phases, with some minor indications of tissue recovery during the constant immersion phase. Across all treatments and phases, apical growth was evident, with visible increases in length. All of these changes are summarised in Figure 58.

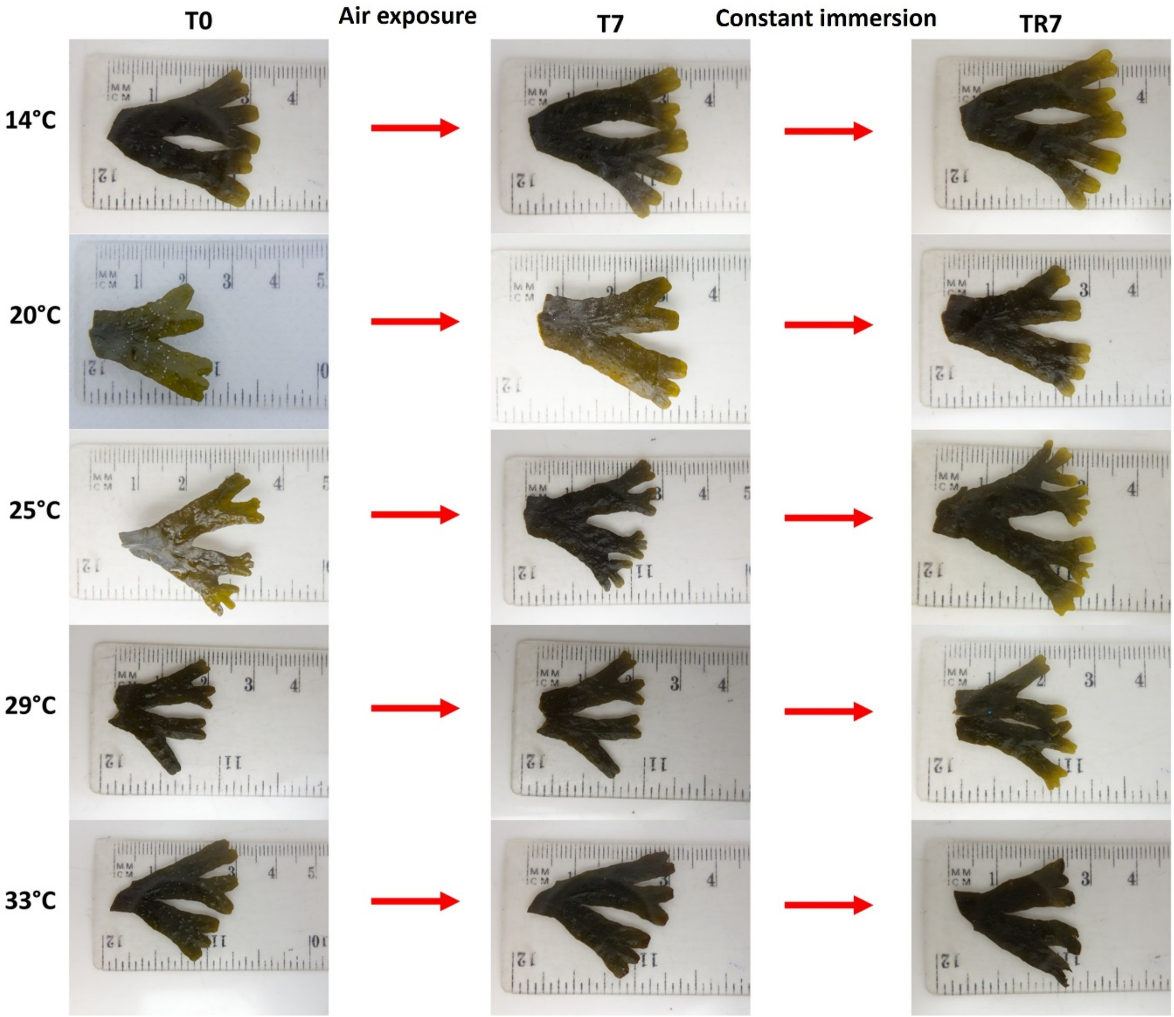

Figure 58. Examples of physical changes in *Fucus virsoides* apices throughout the experiment, shown at the start of the experiment (T0), at the end of the air exposure phase (T7) and at the end of the constant immersion phase (TR7) (from Gljušćić et al. 2025).

Changes in wet weight of the apices (Figure 59) were minimal in the T-20, T-25, and T-29 treatments when compared to the control (C-14), with a gradual increase observed throughout the experiment. In contrast, the T-33 treatment consistently showed a decline in wet weight, indicating progressive deterioration. A similar pattern was seen in apex length (Figure 60): all treatments except T-33 showed slight increases over time, whereas T-33 resulted in a marked reduction.

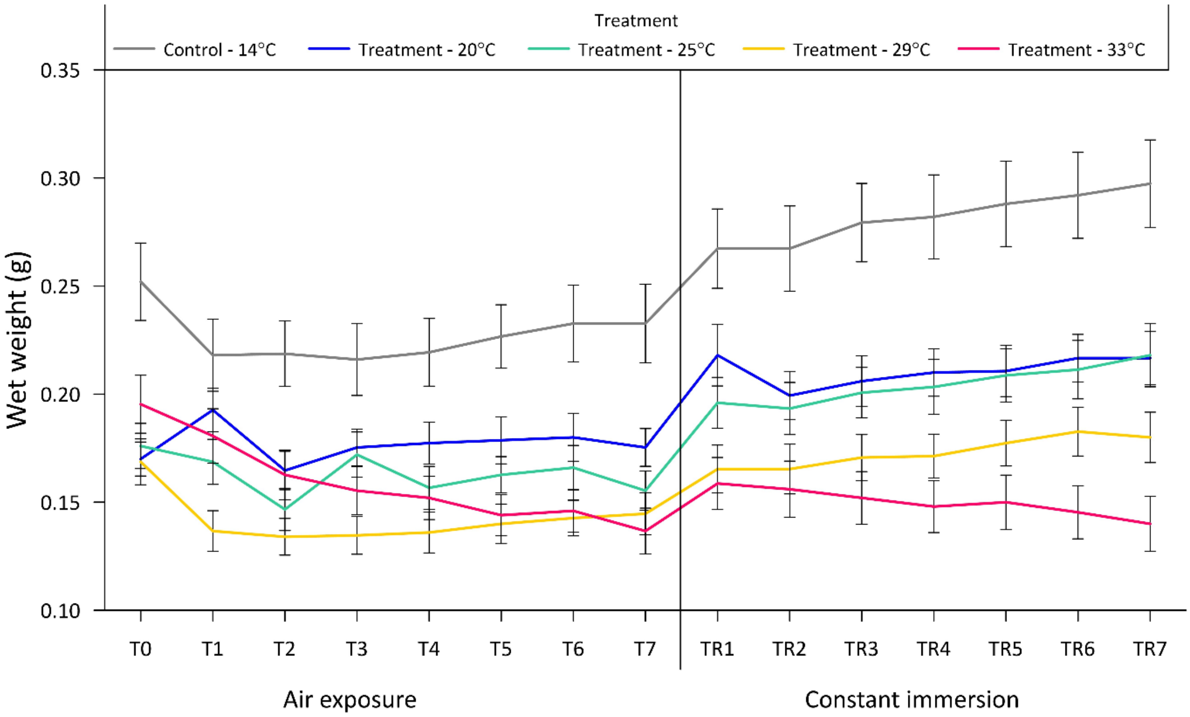

Figure 59. Changes in the wet weight of *Fucus virsoides* apices during the air exposure and constant immersion phases for the 20°C (blue), 25°C (green), 29°C (yellow) and 33°C (red) treatments compared with those for the control treatment at 14°C (grey). The data are presented as the means ± SE for 15 apices.

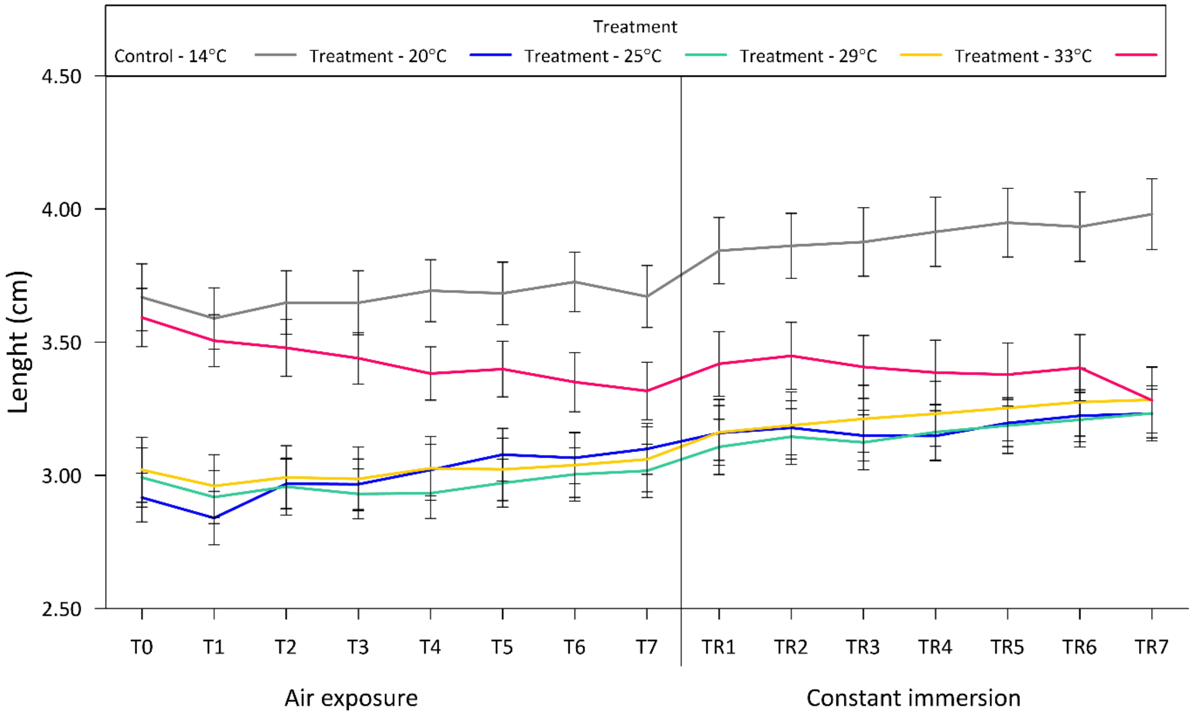

Figure 60. Changes in the length of *Fucus virsoides* apices during the air exposure and constant immersion phases for the 20°C (blue), 25°C (green), 29°C (yellow) and 33°C (red) treatments compared with those for the control treatment at 14°C (grey). The data are presented as the means ± SE for 15 apices.

Maximum photochemical yield (Fv/Fm) remained relatively stable over time in T-20, T-25, T-29, and C-14 treatments, but a substantial decline was evident in T-33 (Figure 61). Some recovery in Fv/Fm was noted during the constant immersion phase for T-33, though it remained significantly lower than the others. Comparisons of Fv/Fm across treatments revealed negligible differences between T-20, T-25, T-29, and C-14.

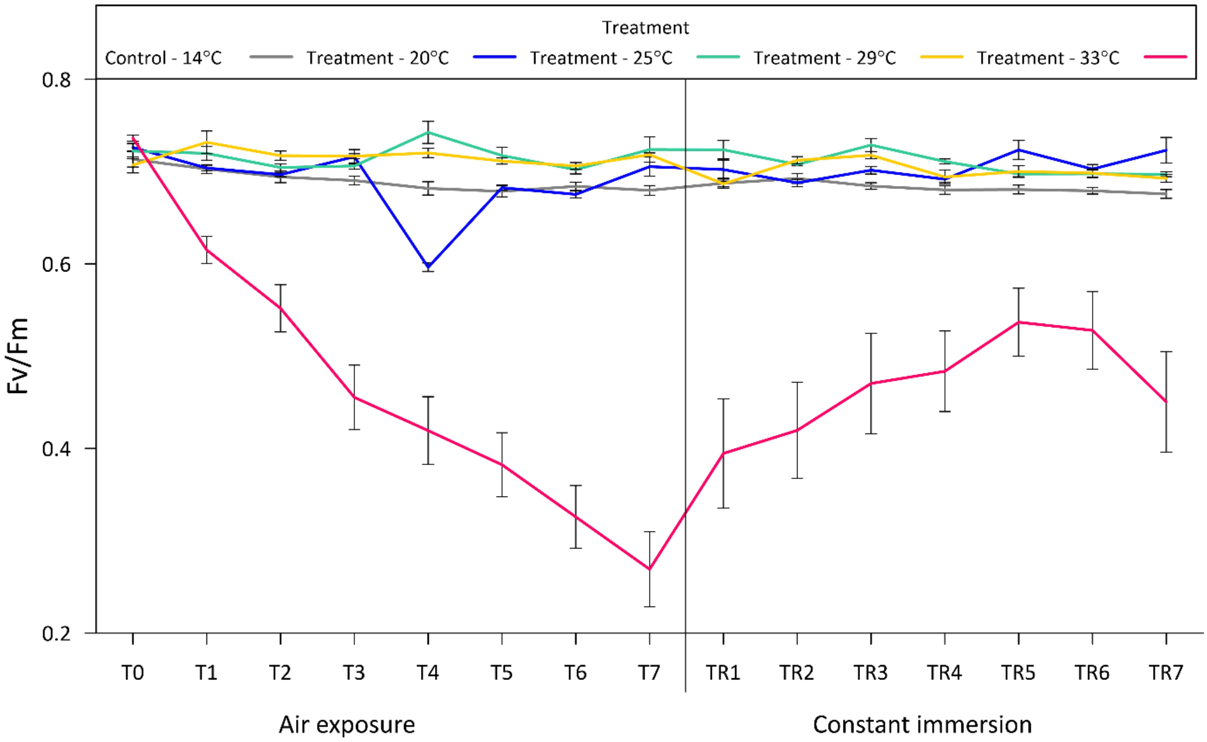

Figure 61. Changes in the maximum photochemical yield (Fv/Fm) of *Fucus virsoides* apices during the air exposure and constant immersion phases for the 20°C (blue), 25°C (green), 29°C (yellow) and 33°C (red) treatments compared with those for the control treatment at 14°C (grey). The data are presented as the means ± SE for 15 apices.

LMM & GLMM analysis results - Air exposure phase

Linear Mixed Model (LMM) analysis of wet weight percentage change revealed highly significant differences among treatments. Tukey post-hoc tests confirmed strong significance between most treatment pairs, though the comparison between T-29 and C-14 showed only marginal significance. No significant differences were observed between T-25 and C-14, or between T-33 and T-29. Similarly, for length percentage change, the LMM identified statistically significant differences between treatments, though no significant differences were detected between T-25 vs. C-14, T-29 vs. C-14, and T-29 vs. T-25. Generalized Linear Mixed Model (GLMM) analysis of Fv/Fm values revealed strong treatment effects, driven primarily by the sharp decline in the T-33 group. No significant differences were found among the remaining treatments. Full results of this analysis are presented in Appendix 10.

LMM & GLMM analysis results - Constant immersion phase

During the constant immersion phase, LMM results showed similar trends, with wet weight, length, and Fv/Fm all displaying significant differences among treatments. Tukey post-hoc analysis again found significant differences in wet weight percentage change for most treatment comparisons, except for T-29 vs. C-14, which was marginally significant. No significant differences were found between T-25 vs. C-14 or T-25 vs. T-20. The same statistical pattern applied to apex length, where most treatment comparisons were significantly different except for T-29 vs. C-14 and the T-25-related comparisons. GLMM results for Fv/Fm mirrored those of the air exposure phase, with T-33 significantly differing from all other treatments and no other treatment showing significant separation from the control. Full statistical results are provided in Appendix 10.

PCoA analysis

Principal coordinate analysis of the air exposure phase data revealed a clear separation of T-33 samples from those of other treatments, including the C-14 control. No distinct clustering was found among T-20, T-25, T-29, or C-14. Most variance was explained by the PCO1 axis, accounting for 92.4% of the total variation (Figure 62A). Overlayed vector analysis showed that both wet weight and apex length were strongly negatively associated with this axis, while Fv/Fm had a minor positive contribution. For the constant immersion phase, a comparable pattern was observed. Again, T-33 data points separated strongly along the PCO1 axis, which explained 93.4% of the variation, indicating that severe damage from earlier exposure limited recovery capacity (Figure 62B). Wet weight and apex length were strongly associated with PCO1, whereas Fv/Fm remained only weakly influential.

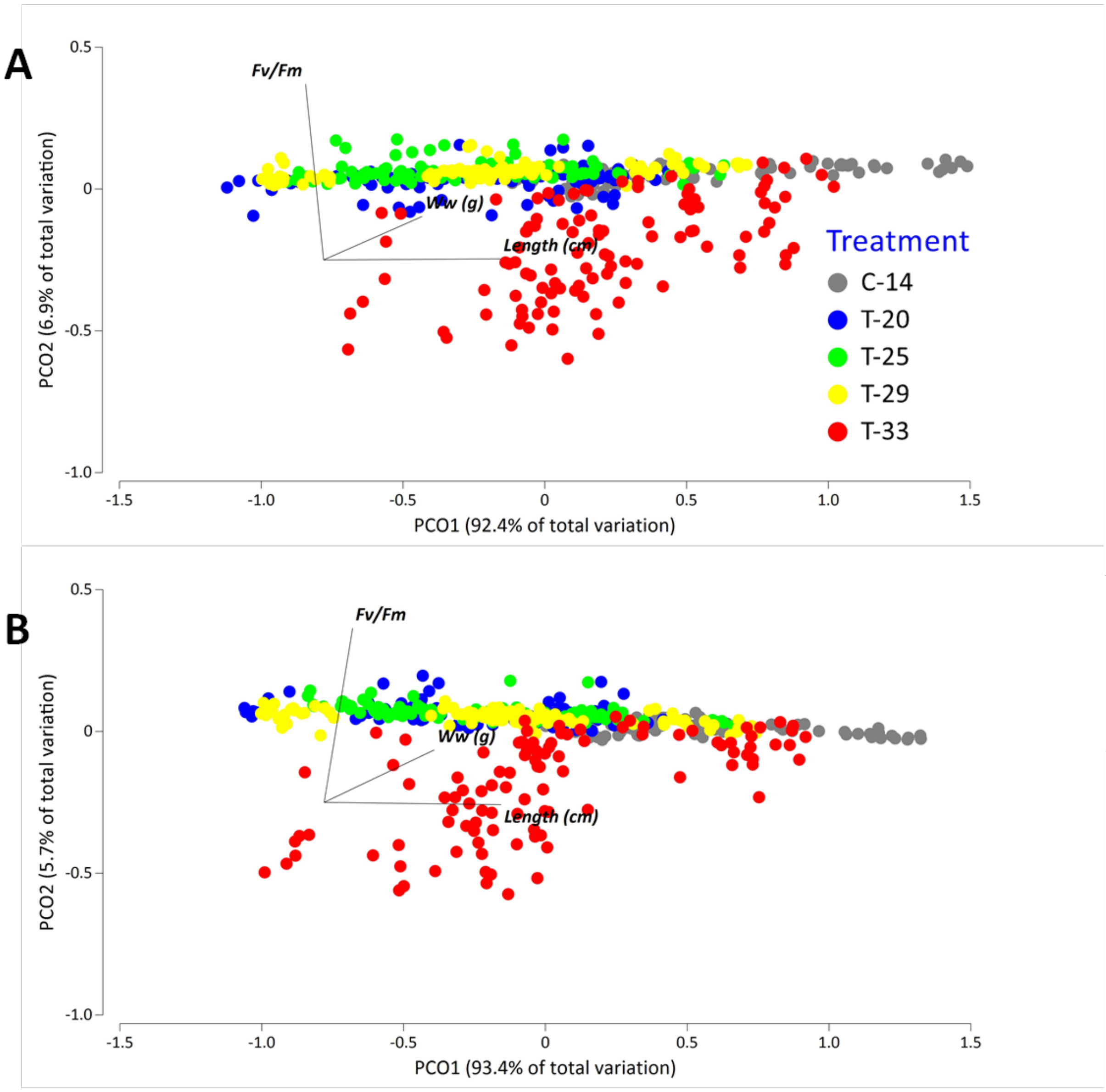

Figure 62. Principal coordinates analysis (PCoA) plot (based on the Euclidean distance) of wet weight, length and Fv/Fm measurements during the air exposure phase (A) and constant immersion phase (B) of the experiment

5.11. *Ex-situ* cultivation of *Fucus virsoides* for conservation purposes

Early growth

Settled germlings of *Fucus virsoides* became visible only a few hours after the seeding process commenced (Figure 63). A total of eight stone fragments, covering an approximate surface area of 200 cm², were successfully seeded and retained viable recruits up to the planting phase. The remaining stones did not support successful recruitment, primarily due to insufficient initial seeding density, which allowed fouling organisms to dominate before the recruits could grow to a sustainable size.

For the first four months following seeding (from May to September), the recruits exhibited virtually no growth and remained too small for precise measurement (Figure 64A, B). However, after being transferred to an outdoor system in September 2021, where their average initial size was 0.228 ± 0.016 cm, an unexpected increase in size was recorded (Figure 64C). By November 2021, just before planting, their average size had increased to 0.437 ± 0.036 cm, indicating a shift in growth conditions that facilitated development (Figure 64D).

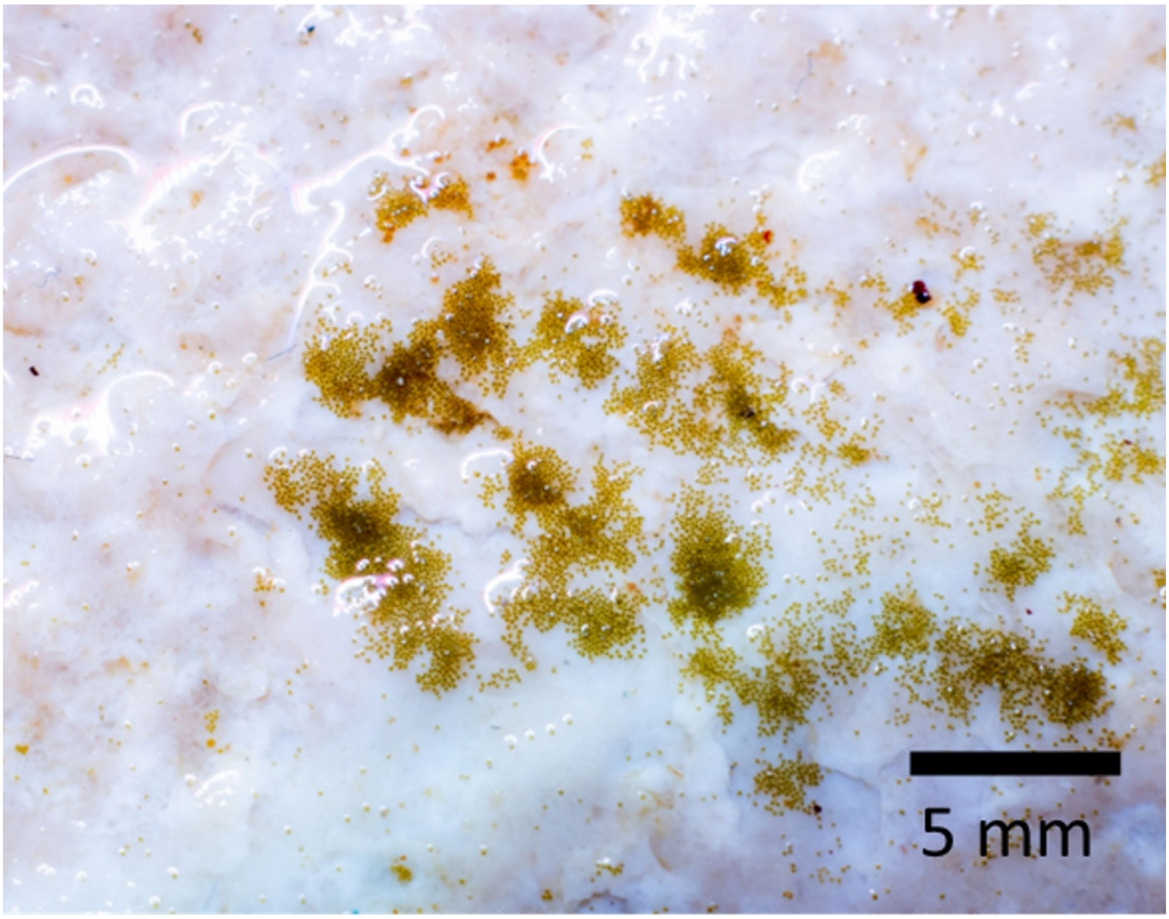

Figure 63. Pre-recruit sized *Fucus virsoides* embryos (from Gljušćić et al. 2023).

Post-planting growth

Following transplantation in November 2021 to designated positions in the field, growth rates increased considerably. The whole growth process of the planted thalli is summarized in Figure 65. At the lower position, thalli reached an average height of 1.470 ± 0.159 cm after two months, 3.520 ± 0.193 cm after five months, and 5.540 ± 0.135 cm after seven months. By the ninth month post-planting, average height had increased to 8.420 ± 0.283 cm, with individuals developing fertile receptacles, suggesting successful maturation (Figure 65D).

Growth at the upper position followed a similar trend, reaching 1.908 ± 0.105 cm after two months, 3.250 ± 0.282 cm after five months, and 6.800 ± 0.902 cm after seven months. By the ninth month, algae at this position had reached 7.020 ± 0.305 cm. In August 2022, ten months after planting, growth at the lower position plateaued at 8.000 ± 0.301 cm, while thalli at the upper position continued to increase slightly, reaching 7.700 ± 0.397 cm. However, by November 2022, one year after planting, a reduction in average thallus size was observed at both positions, which is expected for the autumn period (Figure 65F).

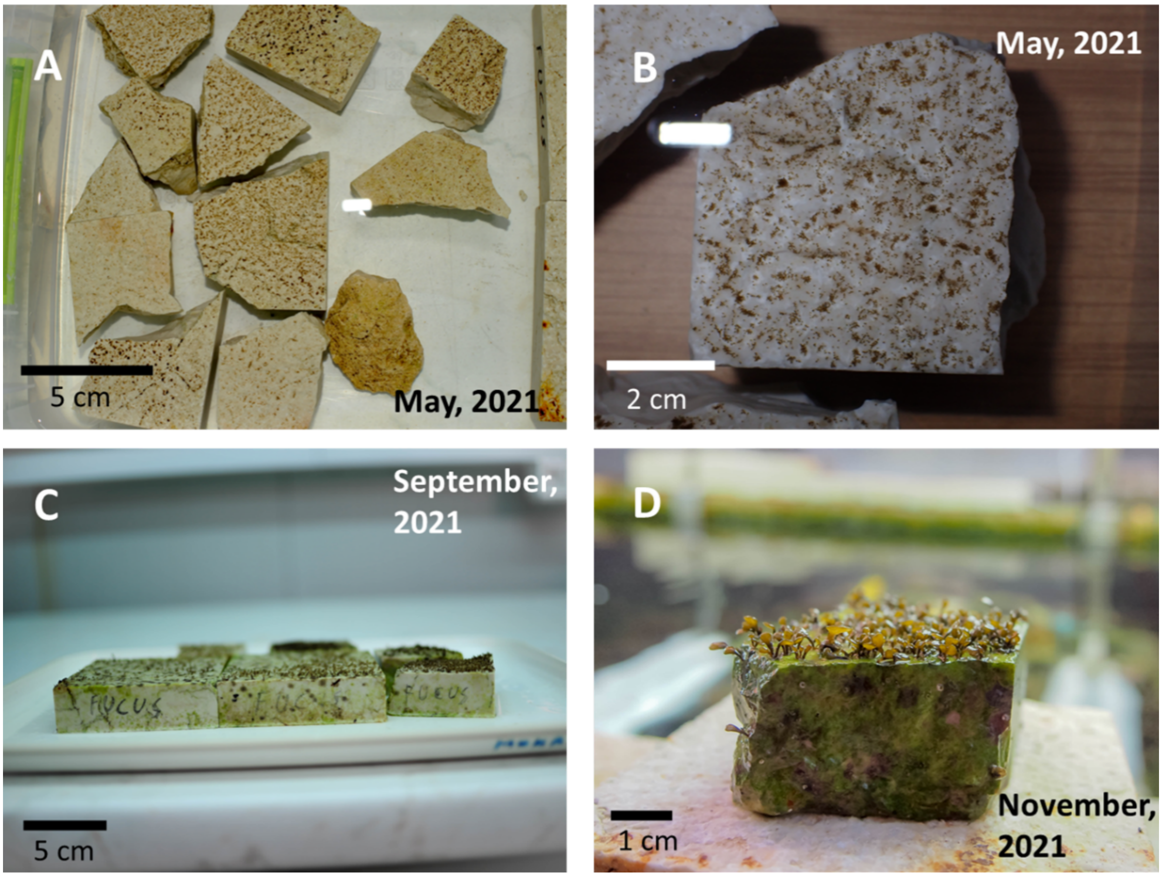

Figure 64. Early growth of *Fucus virsoides* recruits from May to November 2021 (from Gljušćić et al. 2023).

On the upper position, thalli averaged 7.060 cm (±0.412 SE), while at the lower position, a more substantial decline was recorded, with average size reduced to 3.840 cm (±0.753 SE). These size changes across the entire observation period are illustrated in Figure 66.

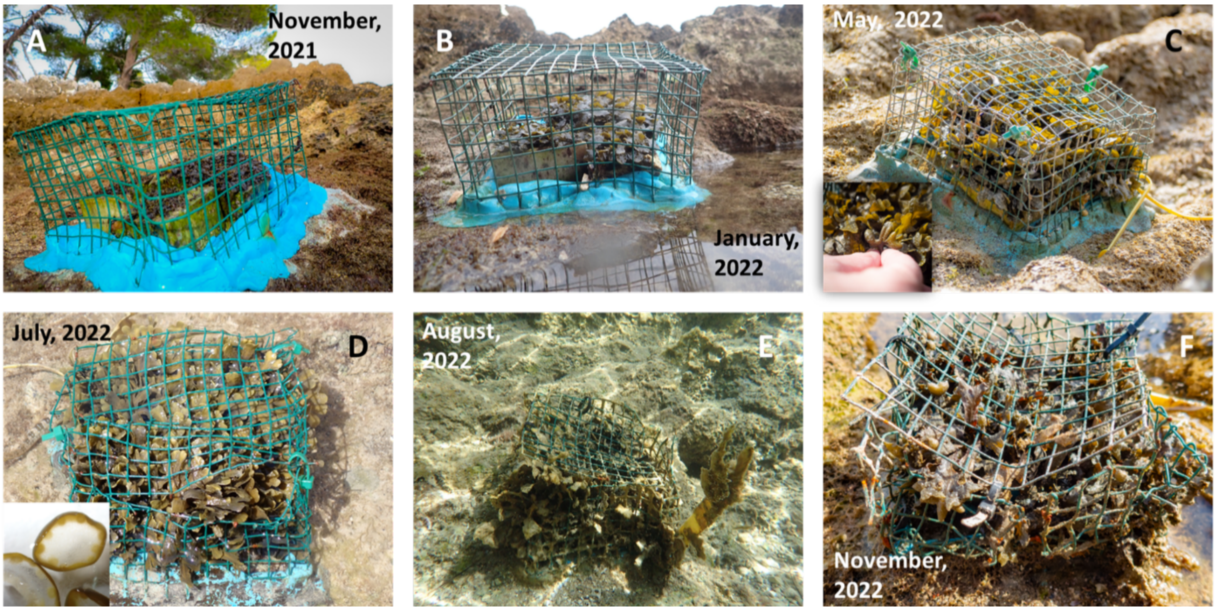

Figure 65. Post-planting growth of *Fucus virsoides* in Muča-Rovinj over a 1-year period (from Gljušćić et al. 2023).

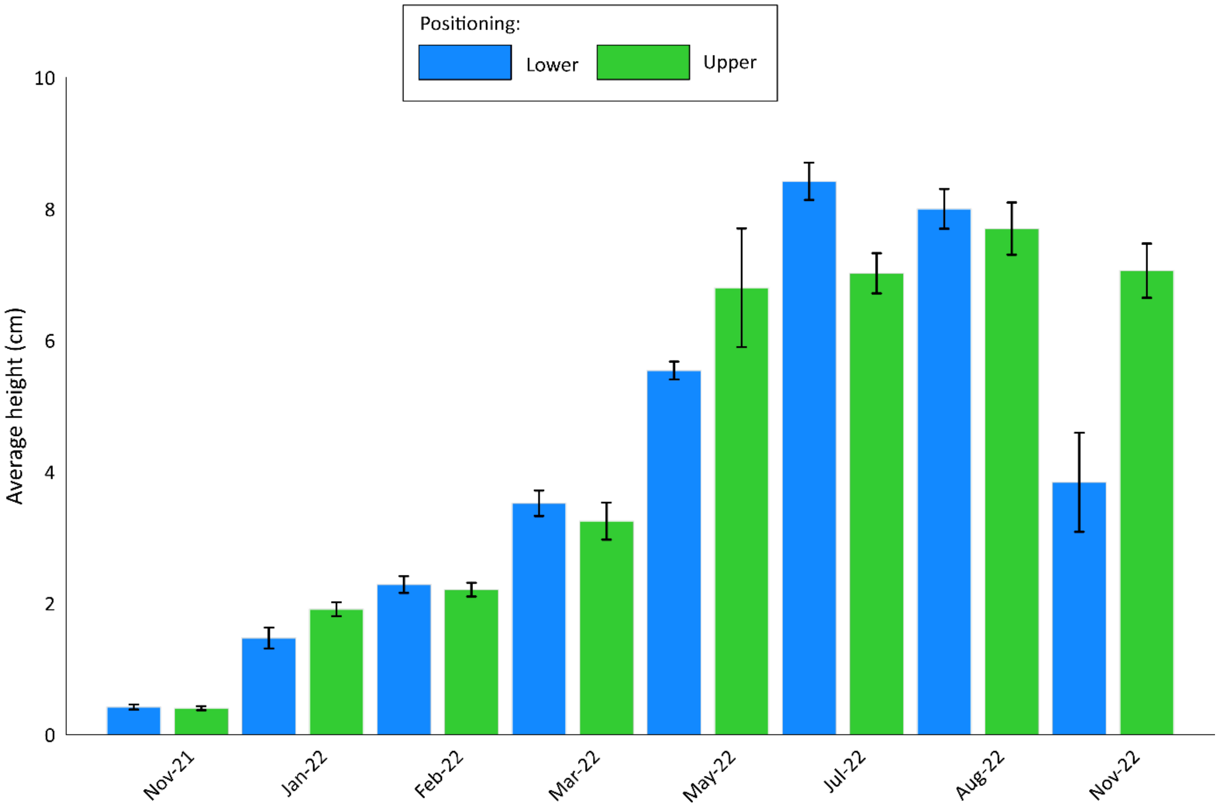

Figure 66. Growth of planted *Fucus virsoides* over 1 year period. Each measurement represents an average of 10 measured thalli. Data are presented as mean ± SE. Colours represent lower (blue) and upper (green) positions for plots.

In late August 2022, the protective cage at the lower position was destroyed by unknown causes, leaving the fully grown, fertile thalli exposed to grazing. As a result, most of the algal fronds were consumed, with only the holdfasts remaining (Figure 67). This event explains the significant drop in average thallus height recorded at the lower position in November 2022 (Figure 66). Despite the damage, some surviving individuals within the impacted area were still found to be fertile, suggesting partial resilience among the exposed specimens.

Figure 67. Destroyed anti-grazer cage with consumed *Fucus virsoides* within. Note that the thalli were grazed down to the basal discs (from Gljušćić et al. 2023).

Statistical analysis results

A Two-way ANOVA followed by the Student-Newman-Keuls (SNK) test for the “Position x Time” interaction revealed that thallus length was significantly greater at the lower position compared to the upper one in May 2022 (seven months post planting) and again in November 2022 (one year post planting). In contrast, in July 2022 (eight months post planting), the thallus length was higher at the upper position.

At all other measured time points, no significant differences in thallus length were found between the two positions. The apparent reversal in November 2022, where thalli at the upper position were longer than those at the lower, can be directly attributed to the destruction of the cage and subsequent overgrazing at the lower site following the August measurement. These results are summarized in Table 2.

Table 2. Two-way ANOVA testing the effects of two positions of *Fucus virsoides* in the intertidal (upper and lower) on thallus growth. Factors: “Position” (fixed, 2 levels - Upper and Lower), “Time” (random, 8 levels - November 2021, January 2022, February 2022, March 2022, May 22, July 2022, August 2022, November 2022). Number of replicates per each combination of factor levels n=10. Total number of replicates N=160. Statistically significant values are marked in **bold.**

Source	df	MS	F	p
Position	1	2.4337	0.38	0.5556
Time	7	160.2287	104.77	**0.0000**
Position x Time	7	6.3555	4.16	**0.0003**
Residual	144	1.5293		
Cochran’s test: 0.33, $p < 0.05$				
SNK test for the interaction Position x Time:				
November 2021: Upper = Lower		May 2022: Upper > Lower		
January 2022: Upper = Lower		July 2022: Upper < Lower		
February 2022: Upper = Lower		August 2022: Upper = Lower		
March 2022: Upper = Lower		November 2022: Upper > Lower		

6. DISCUSSION

6.1. Historical and current distribution of *Fucus virsoides*

After conducting an intense literature review, unsurprisingly*, Fucus virsoides* was found to have been widespread along the rocky Adriatic coast. Herbarium specimens and brief literature records were found to be located at most coastal towns along the Istrian coast and beyond; smaller villages and localities were only mentioned during the latter part of the 20th century. However, no abundance data or location description were given in a vast majority of cases (until the 1960's period), providing no other insight except the general area.

Ecological studies during the second half of the 20th century often mentioned *F. virsoides* as an important part of the vertical species composition in the coastal communities along the rocky Adriatic; also providing distribution information, although unintentionally, since the species was still widespread along most of the rocky coast and considered "common". The more recent 2000-2025 period involved several student theses where *F. virsoides* sites were mapped along parts of the Istrian coast, although in much greater detail, providing population sizes, morphology data and detailed location information (Čelig 2010, Kučinar 2014, Gljušćić 2016). Later scientific works during this period also provided compiled data on the wider distribution, population sizes and general state of the each *F. virsoides* community, while also providing ecophysiological and environmental data, in an effort to understand why the species is in the process of extinction and if the species can somehow be saved (Kaleb et al. 2022, Gljušćić et al. 2023, Descourvières et al. 2024c, 2024b).

Although some decline of *F. virsoides* has been reported since the mid-20th century (Zavodnik 1967, Munda 1972, 1973, 1980a, Battelli 2016b, Rindi et al. 2019, 2020, Gljušćić et al. 2023), pronounced community shifts became truly evident between 2010 and 2016 (Falace et al. 2010, Orlando-Bonaca et al. 2013, Battelli 2016b, Gljušćić et al. 2023). The Adriatic Sea, long considered a climatic refuge for *F. virsoides* due to its relatively cold waters, especially on its northern part, has since seen a dramatic reduction in the species' distribution, most likely driven by a combination of anthropogenic pressures (habitat loss, pollution, overgrazing) and the accelerating impacts of climate change (Boero et al. 2008, Gljušćić et al. 2023, Descourvières et al. 2024a). Current presence of *F. virsoides* along the Istrian coast, namely the remnant settlements in Lanterna and Blaz, given the rapid changes in the environmental conditions and the increased risk of stochastic events (natural or anthropogenic disturbances), is unlikely to last long term (Figure 22B).

6.2. *In-situ* intertidal temperature dynamics

The main problem with the *in-situ* temperature measurements inside the intertidal zone was the loss and failure of data loggers, which resulted in fragmented data, largely reducing the data usability. The regular (biweekly/monthly) readouts turned out to be less frequent than the loss of the loggers. The causes of this include seawater penetration due to thermal expansion, fouling (encrusting algae), breakage of cable ties holding the loggers, as well as obvious intentional removal (stealing). In the end, the only study site that was monitored for a full year was Blaz, most likely due to the sheer inaccessibility of the site (no proper path leads to the site). While the losses due to material degradation in cable ties may be mitigated (attachment of loggers via steel screws), intentional removal represents a more complicated problem, only mitigated by inaccessibility of the loggers or concealment of the loggers, which limits the available commercially available options.

The variations in the measured temperatures in the Blaz, even when considering the exposure of the logger to sunlight and the high measurement frequency, indicated the frequent emersion/immersion of the data logger and the nearby *Fucus virsoides* thalli (Figure 23), especially in spring (Figures 25 and 27). Solar protection was not used in this study, assuming the *F. virsoides* thalli at the site would be exposed to the same amount of sunlight as the logger, mitigation of which would notably change the results. These extreme variations are likely due to a combination of tidal dynamics, atmospheric forcing (pressure and wind effects), waves and variable exposure to sunlight (due to geomorphology and the terrestrial vegetation canopy), but the physical placement of each logger (relative to other loggers and position within the fucus-patch/belt) also cannot be ruled out (given the variations in size and dispersal of each studied *F. virsoides* population).

While not consistent with the experimental results due to the difference in exposure to specific temperatures during similar timeframes (low- or high-water level periods), this study provides insight into the instability and complexity of the habitat inhabited by *F. virsoides,* in addition to the actual resilience of the species to acute and extended thermal shocks during both the natural and simulated emersion periods.

Moreover, overlaying hourly temperature data with actual hourly water level measurements (either from a specialised data logger or corrected measurements from the nearest mareographic station) viewed over short increments could shed more light on this complex dynamic.

Use of specific loggers able to detect immersion/emersion or the water level would likely increase the quality of the collected data, possibly providing more insights into the dynamics of abiotic conditions within the intertidal zone.

6.3. Variations in community composition

The remaining *Fucus virsoides* sites examined in this study were located in distinct micro-localities, each characterized by unique geomorphological features such as rockpool slope, orientation, and levels of shading, often not present in other sites. Despite these small-scale differences, broader environmental parameters, including sea and air temperatures, salinity, and general water quality, remained relatively consistent across sites, with the exception of study site at Blaz, which has increased freshwater input. Unfortunately, monitoring had to be discontinued at two of the four study sites following the complete collapse of their *F. virsoides* populations, which were replaced by uniform, turf-dominated communities; rendering any further research irrelevant.

Analysis of community structure across sites revealed significant temporal and spatial variation. These differences were largely driven by fluctuations in the presence of sessile invertebrates (particularly mussels and barnacles) and the coverage of ephemeral algal species. For certain groups, such as crustose algae, actual cover likely remained stable over time due to their perennial nature and low growth rates; however, their relative cover appeared to vary as a function of dominance by other, more dynamic species. Site-specific environmental conditions played a crucial role in shaping community composition, with the contrast between the more distant locations, Blaz and Lanterna, being especially pronounced.

Notably, the sites at Hotel Parentium and Bijela uvala experienced visible degradation and homogenization over time, presumably due to intense grazing pressure, preventing the *F. virsoides* population from recovering and turf-species likely taking the advantage of the situation. The grazing not only negatively affected key population metrics for *F. virsoides,* such as cover and average height, but also likely contributed to broader shifts in community composition. The decline of *F. virsoides* created ecological space for ephemeral and opportunistic species to increase in abundance, further reinforcing the turf-dominated state.

Among all the study sites, Blaz exhibited the lowest taxonomic diversity. Interestingly, this was not reflected in a lower total cover; on the contrary, Blaz had by far the highest coverage. This paradox may be explained by the site's unique position near transitional waters at the mouth of the Raša River, where large fluctuations in salinity, temperature, and nutrient availability likely suppress certain ephemeral species that are more sensitive to such instability. Moreover, the dense occupancy of available space within the intertidal belt may have limited opportunities for other species to establish, maintaining high competitiveness for *F. virsoides* and limiting overall biodiversity.

The Bijela uvala and Hotel Parentium sites provided a clear example of how *F. virsoides* populations can rapidly collapse and be succeeded by more seasonal, turf-forming species that are normally found only in association with *F. virsoides* . While stochastic disturbances, such as pebble and cobble movement, played a role at Bijela uvala, both sites ultimately saw collapse due to excessive grazing pressure, which disrupted thallus development and inhibited future recruitment.

At the Lanterna site, signs of regression also emerged during the latter part of the study period. While the exact cause was not identified, a rise in grazing activity was noted at the time. Although the community shift here was not as severe as at the other degraded sites, it still involved a decline in *F. virsoides* cover, a slight increase in ephemeral species, and increased visibility of bare substrate and crustose algal layers, indicating early-stage community change.

6.4. Variations in morphology, population structure, and biotic interactions

At the Lanterna site, an apparent increase in certain population metrics toward the end of the year can be attributed to a sharp decline in sample size. By the final months, only a few individual thalli remained, primarily larger ones that had survived the increasing grazing pressure. This led to a statistical inflation of most measured parameters, skewing the results. This pattern contrasts with observations from other sites, where larger and adult specimens were typically the first to disappear under grazing stress. In Hotel Parentium, the steady decrease in average thallus size closely followed the escalation of grazing pressure over the months. This trend was reflected in a decreasing juvenile to adult (j/a) ratio, likely due to selective grazing by *Sarpa salpa*, which tends to avoid juvenile plants, and a reduction in overall *Fucus virsoides* cover. However, the eventual collapse of the population cannot be attributed to grazing alone. The remaining thalli, mostly juvenile and/or physically small, were sparsely distributed, making them highly vulnerable to desiccation and overgrowth by turf species, which ultimately outcompeted them. Additionally, high necrosis levels observed in the final months indicate a compromised physiological state among the surviving individuals. At Blaz, the decline in average size and cover during autumn was again due to intense *S. salpa* grazing. Despite the damage, cover remained relatively high owing to a flush of recruits and small thalli growing between and beneath grazed individuals. This suggested two important dynamics: (i) successful recruitment had occurred shortly before or during the grazing period, likely facilitated by a well-seeded local area; and (ii) grazers targeted larger thalli, allowing smaller individuals to survive in the understory and later grow rapidly. It became increasingly difficult to distinguish between true juveniles and heavily grazed adults trimmed down to similar sizes.

Principal coordinate (PCoA) and PERMANOVA analyses of morphological and population metrics revealed apparent seasonal or quasi-seasonal changes. However, in sites like Hotel Parentium and Bijela uvala, these results seem to reflect abrupt changes in the final months of the study rather than gradual seasonal dynamics. The strong impact of grazing, either directly on thalli or indirectly through habitat modification, appears to have overridden other underlying population patterns at all sites.

Population monitoring challenges

Recruitment success and early survival are critical in the life cycle of fucalean algae. As Schiel and Foster (2006) highlighted, the highest mortality typically occurs at the earliest life stages. In long-term studies, population dynamics are ideally assessed by monitoring cohorts over time (Schiel 1985, Choi and Norton 2005, Viana et al. 2015). However, for *Fucus virsoides* along the Istrian coast, and more broadly in the northern Adriatic, this approach is unfeasible due to the uncertain long-term persistence of remnant populations. While semi-annual CARLIT assessments of dominant communities are conducted along the Croatian coast, and all discovered *F. virsoides* stands are duly noted, the long-term survival of each of the *Fucus virsoides* stands, as well as the species itself, is increasingly precarious (Gljušćić et al. 2023, Descourvières et al. 2024a).

If additional persistent populations could be located elsewhere in the Adriatic, similar to the one near Blaz Cove during 2024 and early 2025, cohort-based studies could be a viable option, offering better insight into population trends. In the meantime, insights from restoration and *ex-situ* cultivation experiments provide some valuable alternatives. Although early survival and growth can be artificially enhanced under controlled conditions, competition for space following planting is often intense, and few thalli survive to adulthood, mirroring natural selection in the wild. However, while inherently positive, the mere presence of recruits does not guarantee successful development or future reproduction. Thus, recruitment metrics alone should be interpreted with caution, especially in highly disturbed environments like those of the northern Adriatic.

Density dependence and canopy effects

Density-dependent processes in fucalean species are complex, exerting both positive and negative influences across different life stages and species (Chapman 1995, Schiel and Foster 2006). For example, *Fucus distichus*, a congenial intertidal species, exhibits both positive and negative density dependant effects on survival, depending on the developmental stage of the thalli (Ang and De Wreede 1992). *F. virsoides,* which experiences wide temperature fluctuations, both submerged and when exposed to air, may respond similarly, though other variations in abiotic factors further complicate these dynamics.

Linardić (1949) noted that denser *F. virsoides* patches appeared healthier (i.e., with less necrosis), likely due to better moisture retention during emersion. Today, however, most of this structural complexity has been lost, further reducing the survivability of the species.

Canopy structure may also influence survival. Like other congeneric species, *F. virsoides* canopies are layered, potentially providing refuge from desiccation for smaller individuals and supporting associated biodiversity (Munda 1972). In healthy stands, upper thalli are more exposed to stress, while lower layers retain moisture and shelter developing individuals. Unfortunately, the rarity of healthy or near-pristine *F. virsoides* populations makes such hypotheses difficult to test *in-situ*, though similar studies may be feasible with related species elsewhere.

Top-down imaging was used during this study to collect information on the community composition. While non-destructive, the data in this case depends on the canopy positioning and structure during emersion periods at specific times (larger thalli can be flipped randomly and/or cover much of the plot area), which controls the visible biota within the plot. Using destructive methods (such as plot removal for later detailed examination) or non-destructive, but more intense, direct *in-situ* data collection, could bring better results, but both options are limited either by available material or time (tidal changes, light availability).

6.5. Insights: Seasonal patterns and growth dynamics in relation to grazing pressure

Although *Fucus virsoides* is a perennial species, it exhibits seasonal peaks in growth and reproductive development. Spring, and occasionally warm winter periods, are characterized by increased biomass, size, and development of aerocysts and receptacles (Vatova 1948, Linardić 1949, Gljušćić et al. 2023, Descourvières et al. 2024c). In this study, vegetative peaks were mostly recorded around April and May. While apical dieback and necrosis during summer and autumn are typical, these phenomena were relatively minor, except at Hotel Parentium. There, collapse was driven by a combination of intense grazing, declining physiological health, and overgrowth by turf species.

Considering the results, grazing by *Sarpa salpa* appears to have played a central role in limiting thallus development. The species appeared to selectively feed on *F. virsoides* even in the presence of other available macroalgae (e.g., *Cystoseira s.l.*), as best observed in Bijela uvala. At Blaz, fertile thalli emerged in the July-August period but were afterwards rapidly and nearly completely eradicated by grazing, with plants trimmed close to their holdfasts. However, this opened space for pre-existing recruits and fragments to grow rapidly, suggesting canopy removal can sometimes trigger compensatory growth. A similar occurrence was observed during July 2025, however, the thalli were trimmed down even before any recruitment could have occurred, suggesting little regrowth will occur. In Bijela uvala, post-disturbance grazing following a stochastic event led to the complete extirpation of the population, which might otherwise have recovered. This aligns with findings from other systems. For example, in Mediterranean rockpools, *Cystoseira* recruitment increased under grazer exclusion only when the adult canopy was removed (Cecchi and Cinelli 1992). Similar effects were observed in kelp forests (Reed and Foster 1984). In contrast, *Pelvetia helvetica* recruits in intertidal zones appear to require canopy cover to retain moisture in order to survive (Brawley and Johnson 1991).

Can grazer activity drive population turnover in Fucus virsoides?

In this study, extensive canopy loss at Blaz, which was triggered by increased grazing, coincided with a rapid increase in juvenile growth. The shaded microhabitat and cooler autumn conditions likely helped minimize desiccation intensity after canopy removal, potentially enabling this surge, although, regenerating thalli in the immediate vicinity may have also played a role (density dependence). These dynamics suggest that canopy removal, whether from grazing or physical disturbance, can release a hidden cohort of recruits (Schiel and Foster 2006), provided environmental conditions are favourable, which can help the population turnover rates, but with the inherit risks due to overgrazing and stochasticity. On the other hand, for this mechanism to activate, there would need to be a ready stock of recruits or juveniles, in a physiologically healthy state, already present under the canopy. Long-term grazing pressure within the fertile period or intense grazing upon the embryos by small grazers (Gastropods) may completely negate this mechanism.

6.6. Field notes: Developmental anomalies

As previously noted, *Fucus virsoides* typically develops receptacles during the colder months, particularly in spring (Vatova 1948, Linardić 1949), a pattern consistent with most other cold-water fucalean species. The normally gradual increase in seawater temperature from winter to late spring may be the trigger of reproductive activity, which could also be replicated under *ex-situ* conditions for cultivation purposes. However, we have observed that receptacle formation occurs year-round, albeit in varying and limited quantities, at several *F. virsoides* sites. The most notable case of developmental anomalies was found in Blaz during August 2024, just before the intense grazing outbreak. Other cases were noted in Lanterna during 2024, where fertile receptacles could be found year-round, albeit in low abundances. The underlying cause of this atypical pattern, while potentially linked to temperature shifts, remains unknown, and could just as easily, considering the lack of information, be a natural occurrence.

6.7. Potential causes of *Fucus virsoides* collapse

While historically, the largest threat to *Fucus virsoides* has been severe pollution and habitat loss (Štirn 1965, Munda 1980c, 1980a, 1997, Airoldi and Beck 2007, Falace et al. 2010, Perkol-Finkel et al. 2012), the recent regressions to small, isolated sites are more likely the result of larger-scale changes to the Adriatic ecosystem (Boero et al. 2008, Descourvières et al. 2024a). Certain populations have been lost due to direct anthropogenic means, such as habitat modification (artificial beach creation and nourishment, coastal infrastructure construction), however, this does not explain the collapse of more isolated populations and the sheer abruptness of the collapses. More likely, these can be attributed to climate change, increasing sea temperatures and more frequent heatwaves, which have negative consequences both to submerged and littoral coastal communities (Straub et al. 2019, Gljušćić et al. 2023). On top of that, population performance and vulnerability to a severe climatic events have been found to be strongly related to latitudinal patterns in genetic diversity, with low genetically diverse populations suffering the most (Wernberg et al. 2018). This mechanism could easily be well underway in *F. virsodies*, although research data is still lacking. Given the severe fragmentation of the *F. virsoides* populations, researching relations between genetic structure and fitness of individuals in different populations could be a worthwhile endeavour, potentially providing data relevant beyond the species in focus. Also, changes in the freshwater input regimes may have played a role, especially if the freshwater input is tied to reduced average seawater temperatures in small localities where *F. virsoides* would normally grow (semi-enclosed rocky bays and shores, with low coastline, horizontal-subvertical coastline, local shading, some wind/wave exposure and freshwater input).

Overgrazing and stochasticity

Historically, *Fucus virsoides,* like other fucaleans, served as a key food source for several herbivores, notably *Paracentrotus lividus*, *Patella* spp., *Phorcus* spp., and *Sarpa salpa* (Battelli 2016a, Gianni et al. 2018, Orlando-Bonaca et al. 2021, Gljušćić et al. 2023). Over the past decade, *S. salpa* has become increasingly abundant in the Adriatic, likely due at least in part to its low commercial value (Gianni et al. 2017), though a lack of larger predatory fish in shallow areas may also play a role, allowing for the *S. salpa* to reach larger sizes, which changes their grazing behaviour (Buñuel et al. 2020). This species is a dominant Mediterranean and Adriatic herbivore frequently observed grazing in intertidal zones (Antolić et al. 1994, Vergés et al. 2009). While grazing plays an important role in structuring intertidal communities, rare or critically endangered populations (PSESPs) such as *F. virsoides* are particularly vulnerable to overgrazing, which may prevent recovery or even lead to local extirpation (Sala et al. 1998, Iveša et al. 2016, Cogoni et al. 2021). While this alone may not fully account for the widespread decline of fucalean assemblages in the Mediterranean, its intense and selective grazing, especially on nutrient-rich fucalean algae, appears to significantly accelerate their collapse. This grazing pressure is especially damaging when it occurs before the release of reproductive material, or rather, when thalli contain the highest nutritive value to the grazers. In the northern Adriatic, this was observed across several species, including *F. virsoides, Ericaria crinita*, and *Gongolaria barbata*. Although *S. salpa* can only access intertidal stands like *F. virsoides* during high tides, its gregarious feeding can lead to complete local extinction or severe degradation within days (Figure 68). By contrast, *P. lividus*, though capable of grazing *F. virsoides,* is less likely to take advantage of high-water levels due to its slower mobility.

Figure 68. Grazing marks on *Fucus virsoides* thallus, presumably caused by *Sarpa salpa.*

Interestingly, grazer-mediated propagule dispersal remains understudied but plausible. All Adriatic fucaleans are monoecious, with both male and female gametes produced in separate conceptacles on the same thallus. Fragments of fertile receptacles, whether ingested and excreted or lost during sloppy feeding, may carry viable gametes or zygotes embedded in mucous layers. This can potentially increase the dispersal, either pre- or post-fertilisation. Preliminary trials suggest successful recruitment is possible from *S. salpa* faeces after feeding on fertile *E. crinita*, though further research is needed. A similar concept was described by Veenhof et al. (2022) for gastropod-mediated kelp dispersal. A rigorously controlled study, with appropriate permits, could yield valuable insights into the dual role of *S. salpa* as both a grazer and a potential dispersal vector.

The risk of local extinction increases significantly as population fragmentation and abundance decline. In Bijela uvala, a combination of overgrazing by *S. salpa* and a stochastic event, specifically, sediment transport caused by a weather disturbance, led to the total collapse of this *F. virsoides* population. Movement of sediment (cobbles, pebbles, and coarse sand) can cause significant physical damage to fucalean assemblages, typically destroying larger specimens while sparing smaller thalli in crevices (pers. obs.). These crevices, while not effective protection against small grazers (Jernakoff 1983), may be sufficient to deter *S. salpa*, preventing complete consumption. Similar impacts were observed in the restoration trials, where underwater installations and planted thalli were damaged.

6.8. Exposure to increased air temperatures

Results from thermotolerance trials indicate that moderate air temperatures (20-29°C) during emersion are not significantly harmful to *Fucus virsoides*. However, exposure to 33°C caused substantial and potentially long-term damage to thalli, as evidenced by reductions in wet weight, length, and photochemical yield. Both statistical analyses and PCoA plots suggest that high air temperatures (33°C) can impair morphology and physiology.

Thermotolerance experiment limitations

This study did not assess several field-relevant factors that could affect *Fucus virsoides*, such as: 1) the effects of repeated direct sunlight exposure (variable intensity and spectrum), 2) the influence of specific moisture levels (but see Descourvières et al. 2024c) and 3) light intensity effects under laboratory conditions. Environmental variables such as air and sea temperatures, salinity, pH, humidity, wind exposure, and coastal geomorphology can all impact species persistence (Lipizer et al. 1995, Orlando-Bonaca et al. 2013, Kaleb et al. 2022, Gljušćić et al. 2023). While individual factors or interactions can be studied in isolation, reproducing their combined effects in any conceived way *ex-situ* will be challenging, especially given the limited availability of *F. virsoides* specimens.

Comparative insights: Fucus virsoides vs. Gongolaria barbata

To contextualize our findings, we compared them with results from a thermotolerance experiment on *Gongolaria barbata*, a shallow-water brown alga from the Istrian coast (Bilajac et al. 2024). Despite differing in morphology, life history, and habitat, both species showed clear thresholds for thermal stress, which was unexpected given the general plasticity of these species. However, their strategies do diverge significantly: *G. barbata*, a subtidal species, exhibits strong seasonal dynamics, including a summer aestivation phase during which the thallus reduces to a persistent cauloid. Growth resumes in autumn from adventive branches (Iveša et al. 2022, Bilajac et al. 2024). *Fucus virsoides,* by contrast, shows continuous growth with moderate seasonal variation. Growth slows in late summer and autumn but never ceases entirely (Linardić 1949, Gljušćić et al. 2023). As a true intertidal species, *F. virsoides* naturally endures greater environmental variability, alternating between immersion and emersion, depending on tides, seasons and atmospheric/seawater conditions. This may offer certain adaptive advantages over fully subtidal species, like potential cooling during summer immersion or enhanced photosynthesis from light exposure during winter emersion. The contrasting strategies, namely dormancy in *G. barbata* vs. environmental tolerance in *F. virsoides,* highlight different evolutionary pathways for coping with thermal stress. Future experiments should investigate whether *F. virsoides* can indeed avoid heatwaves via tidal submersion or capitalize on winter warming through increased emersion.

Photosynthetic activity - Fv/Fm values fluctuations

Photosynthesis in algae behaves in the same way as in terrestrial plants; efficiency of the apparatus increases as the light intensity increases, typically during the morning hours, after which it starts to drop as there is an excess of available light; a dynamic that naturally varies with geographic position and season (Hanelt et al. 1993). The high level of efficiency will remain more consistent if the photosynthetic apparatus is not oversaturated, although this does not necessarily guarantee optimal production (in case of constant undersaturation) and will result in less production (as observed during fucalean algae cultivation trials). Oftentimes, low water levels further coincide with some light level limitations: occurring during early morning or late evening, depending on the season, additionally affecting the overall photosynthetic activity.

Photosynthetic activity will also reduce with the reduction of water content in the algae when emersed during the low water levels (Flores-Molina et al. 2014, Descourvières et al. 2024c). Varying levels of *Fucus virsoides* thalli desiccation encountered during the fieldwork have also shown that maximum photochemical yield (Fv/Fm) can vary notably depending on the vertical positioning of each measured thallus, resulting in high levels of inconsistency across the samples. This can also depend on the positioning of thalli within the canopy itself (lower levels keep moisture better), placement within the belt/patch (thalli closer to the sea are more often splashed/moisturised), as well as which part of the thalli is measured (dryer parts are less photosynthetically active). A lower level of tissue differentiation in algae (although less so in fucalean species) does, in this case represent a survival advantage, since all parts of the thallus can conduct photosynthesis to a notable degree.

Due to these reasons, the collected data on the photosynthetic activity variations across the seasons was not included in this work, as the protocol did not account for the water content of the assessed thalli or the physical state of the thalli. Fv/Fm measurements themselves, thus could not differentiate the effects of physical thalli damage (such as necrosis of the tissue) from the effects of the water content loss.

6.9. *Ex-situ* cultivation and restoration challenges

Salinity has long been recognized as an important factor in the distribution of *Fucus virsoides*. Early studies by Vouk (1938) and Linardić (1949) highlighted its role, and more recent work by Orlando-Bonaca et al. (2013) demonstrated a correlation between species abundance along the Slovenian and Italian coasts of the Gulf of Trieste and the presence of freshwater inputs or fluctuating salinity. This conclusion is consistent with both historical and more recent distribution data (Linardić 1949, Munda 1972, Zavodnik et al. 2002, Descourvières et al. 2024a). Other members of the genus *Fucus* typically occur in areas of lower salinity than *F. virsoides,* although this difference may reflect geographic isolation and subsequent speciation rather than direct physiological constraints (Cánovas et al. 2011). During the *ex-situ* cultivation experiments, salinity was controlled only by regular water changes and was not a limiting factor for growth. However, the full effect of salinity fluctuations on growth and fitness remains to be addressed through dedicated experiments.

During the *ex-situ* phase of the experiment, the air conditioning unit used for temperature regulation had malfunctions and was not able to properly keep the temperature constant within the laboratory. The temperature varied between 16-18°C due to this reason, although the effects from this were considered negligible (considering the temperature variations in its natural environment).

Observations during one of the unpublished (scrapped) experiments, where the effects of simulated tidal dynamics on the growth rate of *F. virsoides* recruits were tested, showed that an uncontrolled increase in salinity levels occurring due to evaporation may have a detrimental effect on the recruits, although the effect of the desiccation itself could not be excluded. Also, when the reduction of seawater salinity (to 30) was conducted during stock cultivation, no noticeable changes in the development were observed, raising even more questions about the cultivation of this species and its ecophysiological preferences.

F. virsoides generally inhabits semi-exposed or semi-sheltered mid-intertidal areas with gently sloping coastlines (Zavodnik 1967, Munda 1972, 1979a, 1980a, Zavodnik and Juranić 1982, Zavodnik et al. 2002). Its abundance and distribution have been linked to substrate stability and wave exposure, as well as wind exposure (Vukovič 1982, Lipizer et al. 1995, Rindi and Battelli 2005, Orlando-Bonaca et al. 2013). While the alga can attach to any fixed solid surface, firmer substrates, such as cut limestone tiles, have proven to be the most effective substrate type for recruitment of *F. virsoides* . Often used clay tiles also perform well, but observations have shown that the surface layer of these tiles is not as persistent, leading to weaker attachment by algae and loss of recruits over time.

The vicinity of mobile substrate (such as pebbles, cobbles, boulders or sand) has also proven to be threatening to the presence of most fucalean algae (either planted or naturally occurring), as the substrate transport is easily able to erode most, if not all of the thalli present in the area. This must be taken into account when planning any conservation or restoration activity.

Although traditionally regarded as a photophilic species due to its intertidal distribution (Linardić 1949), *F. virsoides* may be more accurately described as "tolerant of strong sunlight exposure" during emersion rather than being able to actively exploiting high irradiance. While potentially self-evident, as the photosystem can quickly get overwhelmed by the excess light, this phenomenon is easily detected via PAM measurements of the effective photochemical yield Y(II) *in-situ*. Exposure to direct sunlight also results in exposure to UV radiation, which is normally blocked by immersion (Hanžek 2014), but the complete role of this spectrum requires more research. During the experimental cultivation, growth was slow during the first five months under LED lighting but accelerated markedly once specimens were transferred to outdoor tanks with natural seawater, ambient temperatures, and fluorescent tube lighting. While this shift cannot be attributed solely to light conditions, it raises the possibility that the LED spectra or intensities used were suboptimal compared to fluorescent illumination, which has been standard in other *ex-situ* studies. Even during later cultivation trials, experimenting with various light sources and intensities, this problem still persists, suggesting a key issue is still not understood. Despite that, slow early growth may be mitigated by faster *in-situ* post-planting growth and utilisation of robust anti-grazer protection, which is currently the only viable option.

During the post-planting phase of the *ex-situ* restoration experiment, no reduction in cover was observed between November and late August, with plots quickly becoming fully overgrown by *F. virsoides* thalli extending through the protective cage meshes (Figure 65E, F). Overcrowding of the substrate prevented any meaningful quantitative assessments beyond the second measurement. Such thalli density showed that the simple anti-grazing cages can be highly effective, though they require frequent maintenance due to wave action, mobile stones, and trampling. The only significant reduction in cover occurred when one cage was destroyed, allowing grazers (presumably *Sarpa salpa,* according to observed bite marks) to consume nearly all thalli inside (Figure 67). Protective measures are therefore crucial, but for larger-scale restoration, simpler methods of grazer exclusion will be necessary, or planting may need to be optimised by selecting tidal heights or positions less accessible to macro-grazers. Additionally, rockpools above mid-tide level may serve as artificial refugia where fucalean algae have often been observed "retreating" into along the eastern Adriatic. Although not the typical habitat of *F. virsoides,* such refugia could help establish long-term populations in areas where grazing pressure is otherwise prohibitive.

The final problem for the cultivation and restoration of *F. virsoides,* even disregarding the apparent inability of the species to cope with rapid climatic and environmental changes affecting the Adriatic, is the currently low availability of material to run any kind of experiments. As of mid-2025, only 2 small patches remain along the Istrian coast, severely limiting the source of reproductive material. Locating a better source of material (reports of several sites in Novigrad sea - central Adriatic; Šarić 2023) will be crucial for any future restoration attempts or *ex-situ* research, although locally adapted populations may not be suited for geographically too distant reintroduction.

7. CONCLUSIONS

Based upon the results of the conducted in-depth studies of the remaining *Fucus virsoides* stands along the Istrian coastline, the following conclusions can be made:

1) Compiled historical and recent data on the presence and distribution of *F. virsoides* along the Adriatic coast over the last 200 years, with the specific focus on the northern Adriatic, shows that the species regression likely began around the 1960-1970 period, despite the earlier signs along the Italian coast. This was, at least at that time, likely driven by rapid industrialisation and urbanisation of the coastline, which led to coastal habitat loss and modification as well as pollution, thus prompting the contemporary phycologists to link the two. The decline became much more evident during the 2010's, when *F. virsoides* stands started to disappear rapidly throughout the Adriatic coast, although this was well-documented only in a few areas. This secondary regression was likely triggered by long-term shifts in the Adriatic coastal ecosystem, involving changes to temperature, salinity, as well as biotic factor regimes (grazing, reproductive patterns, metabolism); in effect, making the Adriatic rocky coast unfit for this species.

   The species persists in small pockets (Descourvières et al. 2024a) across the Adriatic, but in the opinion of the author, it is essentially ecologically extinct as it no longer plays any noticeable role in the coastal ecosystems like it did in the past (Estes et al. 1989).
2) In contrast to the assumptions, the temperature values, water level variations, and their relationships reflect an unpredictable environment in the study area, with some emerging patterns that warrant further research. The results of temperature monitoring in the intertidal point towards a chaotic environment characterised by rapid temperature shifts, irregular immersion/emersion periods, as well as irregular desiccation/moisturisation dynamics. Most of these can be linked to the tidal dynamics, but also residual (atmospheric) effects on the sea level and surface conditions.
3) The findings of this study indicate that *Fucus virsoides* stands along the Istrian coast are undergoing a collapse, rapidly being replaced by ephemeral turf species. This shift appears to be the result of the low competitive ability of *F. virsoides* compared to "turf" algae, combined with intense grazing pressure that reduces cover, fitness, and reproductive output of the thalli. The communities themselves, at the time of study, were still dominated by *F. virsoides,* although the average cover trends of this dominant species showed a reduction over time (attributed to grazing). Increased grazing pressure likely led to the lower competitiveness of *F. virsoides,* which was in some cases

completely replaced by more opportunistic taxa (seasonal filamentous and corticated algae). Increased grazing activity likely obscured many site-specific community and population features, as well as the expected natural seasonal dynamics (often similar to the related fucalean species).

4) The grazing pressure, notably by *Sarpa salpa*, is strongly affecting the population structures (increasing the ratio of juveniles versus the adults), reducing the average size and cover, but more importantly, degrading the natural reproduction patterns of *Fucus virsoides* by targeting adult, fertile thalli. The full implications of this relation (density dependence, grazer-facilitated dispersal, population turnover) are yet to be studied, but not all should be considered outright negative, and could be applied to other canopy forming species. Of all the studied sites, the stand near Blaz shows some potential to persist in the short term and could serve as a reference or donor site for conservation efforts. However, with mounting grazing pressure from *S. salpa* (which, in reality, affects all fucalean species in the region), its long-term survival is increasingly doubtful. Effective preservation of *F. virsoides* will likely require permanent, field-based grazer exclusion measures (e.g., cages or refugia) or the establishment of *ex-situ* cultivated stocks for restoration.
5) The results of the thermotolerance experiment suggest that *Fucus virsoides* can be vulnerable to increased air temperatures during warm and dry weather conditions, when these conditions coincide with extended periods of air exposure. While *F. virsoides* is still generally resilient to acute stress, the increasing temperatures, shifting extremes, instabilities resulting from climate change, atmospheric and marine heatwaves, and limited geographical distribution appear to be pushing the tolerance limits of this species. These results may also suggest that *F. virsoides* has, in a sense, adapted to the yearly shifts in tidal dynamics by attuning the growth patterns with the complex abiotic conditions of the intertidal, encountered in different seasons (light availability, air/seawater temperature variations). However, more targeted research is needed to confirm this statement.
6) Although *Fucus virsoides* remains on the verge of extinction along the Istrian coast, this study demonstrated that *ex-situ* cultivation and small-scale planting of the species is feasible using relatively simple methods. Success was largely attributable to the unexpectedly rapid post-planting growth and resilience of the established thalli. Early growth period (recruit-stage) remains the weak-point of this method, with further research needed to determine if enhancing the growth rate is feasible.

While growth performance did show a difference with position within the intertidal zone, these differences are unlikely to pose a major limitation for future restoration efforts. Continued research into the ecological interactions of *F. virsoides* within restored habitats will be essential to refine best practices and develop scalable restoration approaches aimed at re-establishing stable populations in the future.

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9. APPENDICES

Appendix 1. Compiled community composition data in *Fucus virsoides* sites collected during 2024, including sampling location, sampling month, plot number (replicate), taxonomy, morphofunctional group and specific taxa cover. Also, the percent cover of abiotic area (sediment, bare rock etc…) is included.

Sampling location	Sampling month	Plot number	Taxa	Upper taxa	Morphofunctional group	Taxa cover (%)
Blaz	January	1	*Fucus virsoides*	Phaeophyta	Leathery	74.05%
Blaz	January	1	*Ulva* sp.	Chlorophyta	Foliose	11.70%
Blaz	January	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.22%
Blaz	January	1	*Neopyropia leucostycta*	Rhodophyta	Foliose	0.79%
Blaz	January	1	Bare rock	Abiota	N/A	10.24%
Blaz	January	2	*Ulva* sp.	Chlorophyta	Foliose	15.19%
Blaz	January	2	*Fucus virsoides*	Phaeophyta	Leathery	84.81%
Blaz	January	3	*Ulva* sp.	Chlorophyta	Foliose	0.93%
Blaz	January	3	*Fucus virsoides*	Phaeophyta	Leathery	99.07%
Blaz	January	4	*Fucus virsoides*	Phaeophyta	Leathery	58.46%
Blaz	January	4	*Ulva* sp.	Chlorophyta	Foliose	21.14%
Blaz	January	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	17.41%
Blaz	January	4	*Neopyropia leucostycta*	Rhodophyta	Foliose	0.79%
Blaz	January	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.20%
Blaz	January	5	*Enteromorpha* sp.	Chlorophyta	Foliose	7.03%
Blaz	January	5	*Fucus virsoides*	Phaeophyta	Leathery	92.97%
Blaz	February	1	*Ulva* sp.	Chlorophyta	Foliose	9.29%
Blaz	February	1	*Fucus virsoides*	Phaeophyta	Leathery	90.71%
Blaz	February	2	*Enteromorpha* sp.	Chlorophyta	Foliose	15.61%
Blaz	February	2	Bare rock	Abiota	N/A	1.31%
Blaz	February	2	*Fucus virsoides*	Phaeophyta	Leathery	83.08%
Blaz	February	3	*Enteromorpha* sp.	Chlorophyta	Foliose	19.52%
Blaz	February	3	Bare rock	Abiota	N/A	3.40%
Blaz	February	3	*Fucus virsoides*	Phaeophyta	Leathery	76.98%
Blaz	February	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.10%

Blaz	February	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	2.26%
Blaz	February	4	*Ulva* sp.	Chlorophyta	Foliose	5.72%
Blaz	February	4	*Enteromorpha* sp.	Chlorophyta	Foliose	13.63%
Blaz	February	4	*Fucus virsoides*	Phaeophyta	Leathery	81.45%
Blaz	February	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.66%
Blaz	February	5	*Enteromorpha* sp.	Chlorophyta	Foliose	0.62%
Blaz	February	5	*Fucus virsoides*	Phaeophyta	Leathery	92.57%
Blaz	February	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	6.72%
Blaz	February	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.08%
Blaz	March	1	*Enteromorpha* sp.	Chlorophyta	Foliose	17.62%
Blaz	March	1	*Fucus virsoides*	Phaeophyta	Leathery	82.38%
Blaz	March	2	*Enteromorpha* sp.	Chlorophyta	Foliose	2.94%
Blaz	March	2	*Fucus virsoides*	Phaeophyta	Leathery	97.06%
Blaz	March	3	*Enteromorpha* sp.	Chlorophyta	Foliose	24.04%
Blaz	March	3	Bare rock	Abiota	N/A	2.18%
Blaz	March	3	*Fucus virsoides*	Phaeophyta	Leathery	73.78%
Blaz	March	4	*Enteromorpha* sp.	Chlorophyta	Foliose	5.55%
Blaz	March	4	Bare rock	Abiota	N/A	0.30%
Blaz	March	4	*Fucus virsoides*	Phaeophyta	Leathery	94.15%
Blaz	March	5	*Enteromorpha* sp.	Chlorophyta	Foliose	0.64%
Blaz	March	5	*Fucus virsoides*	Phaeophyta	Leathery	99.36%
Blaz	April	1	*Enteromorpha* sp.	Chlorophyta	Foliose	7.75%
Blaz	April	1	*Fucus virsoides*	Phaeophyta	Leathery	92.25%
Blaz	April	2	*Enteromorpha* sp.	Chlorophyta	Foliose	3.43%
Blaz	April	2	*Fucus virsoides*	Phaeophyta	Leathery	96.57%
Blaz	April	3	*Ulva* sp.	Chlorophyta	Foliose	31.14%
Blaz	April	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	8.92%
Blaz	April	3	*Gelidium* sp.	Rhodophyta	Corticated	3.85%
Blaz	April	3	*Fucus virsoides*	Phaeophyta	Leathery	58.18%
Blaz	April	3	*Chthamalus* sp.	Crustacea	Sessile animal	1.76%
Blaz	April	4	*Ulva* sp.	Chlorophyta	Foliose	0.38%

Blaz	April	4	*Fucus virsoides*	Phaeophyta	Leathery	99.62%
Blaz	April	5	*Ulva* sp.	Chlorophyta	Foliose	2.81%
Blaz	April	5	*Fucus virsoides*	Phaeophyta	Leathery	97.19%
Blaz	May	1	Bare rock	Abiota	N/A	1.38%
Blaz	May	1	*Ulva* sp.	Chlorophyta	Foliose	1.94%
Blaz	May	1	*Fucus virsoides*	Phaeophyta	Leathery	96.65%
Blaz	May	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.03%
Blaz	May	2	Bare rock	Abiota	N/A	3.46%
Blaz	May	2	*Ulva* sp.	Chlorophyta	Foliose	0.87%
Blaz	May	2	*Fucus virsoides*	Phaeophyta	Leathery	95.49%
Blaz	May	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.19%
Blaz	May	3	*Ulva* sp.	Chlorophyta	Foliose	1.14%
Blaz	May	3	Bare rock	Abiota	N/A	0.64%
Blaz	May	3	*Fucus virsoides*	Phaeophyta	Leathery	98.22%
Blaz	May	4	*Ulva* sp.	Chlorophyta	Foliose	1.08%
Blaz	May	4	Bare rock	Abiota	N/A	1.30%
Blaz	May	4	*Fucus virsoides*	Phaeophyta	Leathery	97.62%
Blaz	May	5	Bare rock	Abiota	N/A	2.25%
Blaz	May	5	*Ulva* sp.	Chlorophyta	Foliose	0.91%
Blaz	May	5	*Fucus virsoides*	Phaeophyta	Leathery	96.84%
Blaz	June	1	Bare rock	Abiota	N/A	5.19%
Blaz	June	1	*Ulva* sp.	Chlorophyta	Foliose	0.13%
Blaz	June	1	*Fucus virsoides*	Phaeophyta	Leathery	93.50%
Blaz	June	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	1.12%
Blaz	June	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.06%
Blaz	June	2	Bare rock	Abiota	N/A	7.68%
Blaz	June	2	*Ulva* sp.	Chlorophyta	Foliose	1.24%
Blaz	June	2	*Fucus virsoides*	Phaeophyta	Leathery	91.09%
Blaz	June	3	Bare rock	Abiota	N/A	0.77%
Blaz	June	3	*Ulva* sp.	Chlorophyta	Foliose	0.67%
Blaz	June	3	*Fucus virsoides*	Phaeophyta	Leathery	95.35%

Blaz	June	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	3.20%
Blaz	June	4	Bare rock	Abiota	N/A	2.34%
Blaz	June	4	*Ulva* sp.	Chlorophyta	Foliose	4.43%
Blaz	June	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	6.91%
Blaz	June	4	*Fucus virsoides*	Phaeophyta	Leathery	86.32%
Blaz	June	5	Bare rock	Abiota	N/A	8.74%
Blaz	June	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.32%
Blaz	June	5	*Fucus virsoides*	Phaeophyta	Leathery	90.87%
Blaz	June	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.07%
Blaz	July	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	0.73%
Blaz	July	1	*Ulva* sp.	Chlorophyta	Foliose	0.65%
Blaz	July	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	4.34%
Blaz	July	1	Bare rock	Abiota	N/A	5.09%
Blaz	July	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	1.77%
Blaz	July	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.34%
Blaz	July	1	*Fucus virsoides*	Phaeophyta	Leathery	87.09%
Blaz	July	2	Bare rock	Abiota	N/A	21.01%
Blaz	July	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.70%
Blaz	July	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	0.24%
Blaz	July	2	*Fucus virsoides*	Phaeophyta	Leathery	78.06%
Blaz	July	3	Bare rock	Abiota	N/A	6.20%
Blaz	July	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	0.61%
Blaz	July	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	11.70%
Blaz	July	3	*Fucus virsoides*	Phaeophyta	Leathery	81.49%
Blaz	July	4	*Ulva* sp.	Chlorophyta	Foliose	2.08%
Blaz	July	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.45%
Blaz	July	4	Bare rock	Abiota	N/A	1.86%
Blaz	July	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	15.10%
Blaz	July	4	*Fucus virsoides*	Phaeophyta	Leathery	79.51%
Blaz	July	5	Bare rock	Abiota	N/A	5.09%
Blaz	July	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	5.73%

Blaz	July	5	*Enteromorpha* sp.	Chlorophyta	Foliose	5.26%
Blaz	July	5	*Ulva* sp.	Chlorophyta	Foliose	6.92%
Blaz	July	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	5.80%
Blaz	July	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.36%
Blaz	July	5	*Fucus virsoides*	Phaeophyta	Leathery	70.84%
Blaz	August	1	Bare rock	Abiota	N/A	3.53%
Blaz	August	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.08%
Blaz	August	1	*Enteromorpha* sp.	Chlorophyta	Foliose	0.29%
Blaz	August	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	1.28%
Blaz	August	1	*Fucus virsoides*	Phaeophyta	Leathery	94.82%
Blaz	August	2	Bare rock	Abiota	N/A	10.12%
Blaz	August	2	*Enteromorpha* sp.	Chlorophyta	Foliose	0.62%
Blaz	August	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.16%
Blaz	August	2	*Fucus virsoides*	Phaeophyta	Leathery	89.10%
Blaz	August	3	Bare rock	Abiota	N/A	13.95%
Blaz	August	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	5.89%
Blaz	August	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	0.90%
Blaz	August	3	*Ulva* sp.	Chlorophyta	Foliose	0.90%
Blaz	August	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	14.02%
Blaz	August	3	*Chthamalus* sp.	Crustacea	Sessile animal	1.16%
Blaz	August	3	*Fucus virsoides*	Phaeophyta	Leathery	64.08%
Blaz	August	4	Bare rock	Abiota	N/A	0.77%
Blaz	August	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.30%
Blaz	August	4	*Ulva* sp.	Chlorophyta	Foliose	0.79%
Blaz	August	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	7.65%
Blaz	August	4	*Fucus virsoides*	Phaeophyta	Leathery	90.49%
Blaz	August	5	Bare rock	Abiota	N/A	8.99%
Blaz	August	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.65%
Blaz	August	5	*Ulva* sp.	Chlorophyta	Foliose	1.36%
Blaz	August	5	*Gelidium* sp.	Rhodophyta	Corticated	1.92%
Blaz	August	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.35%

Blaz	August	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.03%
Blaz	August	5	*Fucus virsoides*	Phaeophyta	Leathery	82.70%
Blaz	September	1	Bare rock	Abiota	N/A	22.03%
Blaz	September	1	*Ulva* sp.	Chlorophyta	Foliose	0.33%
Blaz	September	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.82%
Blaz	September	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	10.79%
Blaz	September	1	*Chthamalus* sp.	Crustacea	Sessile animal	1.67%
Blaz	September	1	*Fucus virsoides*	Phaeophyta	Leathery	61.36%
Blaz	September	2	Bare rock	Abiota	N/A	6.29%
Blaz	September	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.42%
Blaz	September	2	*Chthamalus* sp.	Crustacea	Sessile animal	1.20%
Blaz	September	2	*Fucus virsoides*	Phaeophyta	Leathery	92.09%
Blaz	September	3	Bare rock	Abiota	N/A	33.39%
Blaz	September	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.09%
Blaz	September	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	23.51%
Blaz	September	3	*Chthamalus* sp.	Crustacea	Sessile animal	6.74%
Blaz	September	3	*Fucus virsoides*	Phaeophyta	Leathery	33.26%
Blaz	September	4	Bare rock	Abiota	N/A	3.80%
Blaz	September	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.31%
Blaz	September	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.23%
Blaz	September	4	*Fucus virsoides*	Phaeophyta	Leathery	95.66%
Blaz	September	5	Bare rock	Abiota	N/A	7.70%
Blaz	September	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	1.68%
Blaz	September	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.78%
Blaz	September	5	*Fucus virsoides*	Phaeophyta	Leathery	89.85%
Blaz	October	1	Bare rock	Abiota	N/A	20.50%
Blaz	October	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	6.04%
Blaz	October	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.11%
Blaz	October	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	7.25%
Blaz	October	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	3.85%
Blaz	October	1	*Chthamalus* sp.	Crustacea	Sessile animal	1.30%

Blaz	October	1	*Fucus virsoides*	Phaeophyta	Leathery	58.95%
Blaz	October	2	Bare rock	Abiota	N/A	13.23%
Blaz	October	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.58%
Blaz	October	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.06%
Blaz	October	2	*Ulva* sp.	Chlorophyta	Foliose	0.17%
Blaz	October	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	7.12%
Blaz	October	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	10.29%
Blaz	October	2	*Chthamalus* sp.	Crustacea	Sessile animal	2.79%
Blaz	October	2	*Fucus virsoides*	Phaeophyta	Leathery	60.76%
Blaz	October	3	Bare rock	Abiota	N/A	36.29%
Blaz	October	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.38%
Blaz	October	3	*Ulva* sp.	Chlorophyta	Foliose	0.27%
Blaz	October	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.67%
Blaz	October	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.59%
Blaz	October	3	*Chthamalus* sp.	Crustacea	Sessile animal	2.77%
Blaz	October	3	*Fucus virsoides*	Phaeophyta	Leathery	56.03%
Blaz	October	4	Bare rock	Abiota	N/A	22.99%
Blaz	October	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.06%
Blaz	October	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.44%
Blaz	October	4	*Enteromorpha* sp.	Chlorophyta	Foliose	1.32%
Blaz	October	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	11.13%
Blaz	October	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.31%
Blaz	October	4	*Chthamalus* sp.	Crustacea	Sessile animal	2.40%
Blaz	October	4	*Fucus virsoides*	Phaeophyta	Leathery	54.35%
Blaz	October	5	Bare rock	Abiota	N/A	11.26%
Blaz	October	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.62%
Blaz	October	5	*Ulva* sp.	Chlorophyta	Foliose	5.86%
Blaz	October	5	*Enteromorpha* sp.	Chlorophyta	Foliose	6.88%
Blaz	October	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	37.94%
Blaz	October	5	*Gelidium* sp.	Rhodophyta	Corticated	1.42%
Blaz	October	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	18.54%

Blaz	October	5	*Chthamalus* sp.	Crustacea	Sessile animal	2.40%
Blaz	October	5	*Fucus virsoides*	Phaeophyta	Leathery	12.08%
Blaz	November	1	Bare rock	Abiota	N/A	8.15%
Blaz	November	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.82%
Blaz	November	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	7.20%
Blaz	November	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	13.36%
Blaz	November	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.58%
Blaz	November	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.95%
Blaz	November	1	*Fucus virsoides*	Phaeophyta	Leathery	64.94%
Blaz	November	2	Bare rock	Abiota	N/A	7.84%
Blaz	November	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.14%
Blaz	November	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	12.31%
Blaz	November	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	6.59%
Blaz	November	2	*Chthamalus* sp.	Crustacea	Sessile animal	4.19%
Blaz	November	2	*Fucus virsoides*	Phaeophyta	Leathery	89.55%
Blaz	November	3	Bare rock	Abiota	N/A	6.32%
Blaz	November	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.85%
Blaz	November	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.00%
Blaz	November	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	9.56%
Blaz	November	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	10.78%
Blaz	November	3	*Chthamalus* sp.	Crustacea	Sessile animal	2.13%
Blaz	November	3	*Fucus virsoides*	Phaeophyta	Leathery	66.35%
Blaz	November	4	Bare rock	Abiota	N/A	15.02%
Blaz	November	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.65%
Blaz	November	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	2.07%
Blaz	November	4	*Ulva* sp.	Chlorophyta	Foliose	0.50%
Blaz	November	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	7.07%
Blaz	November	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.82%
Blaz	November	4	*Chthamalus* sp.	Crustacea	Sessile animal	3.23%
Blaz	November	4	*Fucus virsoides*	Phaeophyta	Leathery	66.64%
Blaz	November	5	Bare rock	Abiota	N/A	19.98%

Blaz	November	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.53%
Blaz	November	5	*Chaetomorpha* sp.	Chlorophyta	Filamentous	6.43%
Blaz	November	5	*Ulva* sp.	Chlorophyta	Foliose	0.46%
Blaz	November	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	5.10%
Blaz	November	5	*Gelidium* sp.	Rhodophyta	Corticated	0.85%
Blaz	November	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	12.41%
Blaz	November	5	*Chthamalus* sp.	Crustacea	Sessile animal	1.55%
Blaz	November	5	*Fucus virsoides*	Phaeophyta	Leathery	52.69%
Blaz	December	1	Bare rock	Abiota	N/A	1.65%
Blaz	December	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.80%
Blaz	December	1	*Enteromorpha* sp.	Chlorophyta	Foliose	9.71%
Blaz	December	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	65.10%
Blaz	December	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	9.33%
Blaz	December	1	*Chthamalus* sp.	Crustacea	Sessile animal	1.08%
Blaz	December	1	*Fucus virsoides*	Phaeophyta	Leathery	12.33%
Blaz	December	2	Bare rock	Abiota	N/A	3.53%
Blaz	December	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.06%
Blaz	December	2	*Ulva* sp.	Chlorophyta	Foliose	2.80%
Blaz	December	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	17.99%
Blaz	December	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	10.28%
Blaz	December	2	*Chthamalus* sp.	Crustacea	Sessile animal	3.93%
Blaz	December	2	*Fucus virsoides*	Phaeophyta	Leathery	60.42%
Blaz	December	3	Bare rock	Abiota	N/A	6.17%
Blaz	December	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.36%
Blaz	December	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.58%
Blaz	December	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.71%
Blaz	December	3	*Ulva* sp.	Chlorophyta	Foliose	0.11%
Blaz	December	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.51%
Blaz	December	3	*Fucus virsoides*	Phaeophyta	Leathery	90.12%
Blaz	December	4	Bare rock	Abiota	N/A	4.66%
Blaz	December	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.82%

Blaz	December	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.16%
Blaz	December	4	*Ulva* sp.	Chlorophyta	Foliose	6.83%
Blaz	December	4	*enteromorpha* sp.	Chlorophyta	Foliose	5.36%
Blaz	December	4	*Neopyropia leucostycta*	Rhodophyta	Foliose	1.61%
Blaz	December	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	13.91%
Blaz	December	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	9.45%
Blaz	December	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.93%
Blaz	December	4	*Fucus virsoides*	Phaeophyta	Leathery	55.26%
Blaz	December	5	Bare rock	Abiota	N/A	20.66%
Blaz	December	5	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.93%
Blaz	December	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	6.31%
Blaz	December	5	*Gelidium* sp.	Rhodophyta	Corticated	1.66%
Blaz	December	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	9.74%
Blaz	December	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.41%
Blaz	December	5	*Fucus virsoides*	Phaeophyta	Leathery	59.28%
BU	January	1	Bare rock	Abiota	N/A	4.54%
BU	January	1	*Ulva* sp.	Chlorophyta	Foliose	1.14%
BU	January	1	*Cladophora* sp.	Chlorophyta	Filamentous	7.47%
BU	January	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.59%
BU	January	1	*Gelidium* sp.	Rhodophyta	Corticated	59.11%
BU	January	1	*Fucus virsoides*	Phaeophyta	Leathery	25.14%
BU	January	2	Bare rock	Abiota	N/A	10.24%
BU	January	2	*Ulva* sp.	Chlorophyta	Foliose	1.24%
BU	January	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	8.00%
BU	January	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	11.45%
BU	January	2	*Gelidium* sp.	Rhodophyta	Corticated	38.39%
BU	January	2	*Fucus virsoides*	Phaeophyta	Leathery	30.43%
BU	January	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.26%
BU	January	3	Bare rock	Abiota	N/A	9.05%
BU	January	3	*Ulva* sp.	Chlorophyta	Foliose	1.49%
BU	January	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.86%

BU	January	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	12.01%
BU	January	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	49.49%
BU	January	3	*Gelidium* sp.	Rhodophyta	Corticated	4.50%
BU	January	3	*Fucus virsoides*	Phaeophyta	Leathery	20.87%
BU	January	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.34%
BU	January	4	Bare rock	Abiota	N/A	4.65%
BU	January	4	*Ulva* sp.	Chlorophyta	Foliose	19.07%
BU	January	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.81%
BU	January	4	*Corallina* sp.	Rhodophyta	Articulated calcareous	8.82%
BU	January	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	58.71%
BU	January	4	*Fucus virsoides*	Phaeophyta	Leathery	7.67%
BU	January	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.27%
BU	January	5	Bare rock	Abiota	N/A	28.17%
BU	January	5	*Ulva* sp.	Chlorophyta	Foliose	1.11%
BU	January	5	*Cladophora* sp.	Chlorophyta	Filamentous	0.81%
BU	January	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.61%
BU	January	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	34.38%
BU	January	5	*Fucus virsoides*	Phaeophyta	Leathery	32.63%
BU	January	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.24%
BU	January	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.06%
BU	February	1	Bare rock	Abiota	N/A	23.68%
BU	February	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	10.54%
BU	February	1	*Gelidium* sp.	Rhodophyta	Corticated	1.66%
BU	February	1	*Halopteris scoparia*	Phaeophyta	Corticated	2.79%
BU	February	1	*Fucus virsoides*	Phaeophyta	Leathery	64.12%
BU	February	2	Bare rock	Abiota	N/A	44.26%
BU	February	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.71%
BU	February	2	*Ulva* sp.	Chlorophyta	Foliose	0.72%
BU	February	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.79%
BU	February	2	*Ceramium* sp.	Rhodophyta	Filamentous	1.82%
BU	February	2	*Laurencia obtusa*	Rhodophyta	Corticated	0.78%

BU	February	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.04%
BU	February	2	*Fucus virsoides*	Phaeophyta	Leathery	48.89%
BU	February	3	Bare rock	Abiota	N/A	36.15%
BU	February	3	*Ulva* sp.	Chlorophyta	Foliose	1.15%
BU	February	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	7.41%
BU	February	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.31%
BU	February	3	*Ceramium* sp.	Rhodophyta	Filamentous	2.04%
BU	February	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.99%
BU	February	3	*Fucus virsoides*	Phaeophyta	Leathery	50.72%
BU	February	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.24%
BU	February	4	Bare rock	Abiota	N/A	15.88%
BU	February	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	12.33%
BU	February	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	8.21%
BU	February	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.06%
BU	February	4	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	1.09%
BU	February	4	*Fucus virsoides*	Phaeophyta	Leathery	62.08%
BU	February	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.44%
BU	February	5	Bare rock	Abiota	N/A	40.07%
BU	February	5	*Gelidium* sp.	Rhodophyta	Corticated	1.46%
BU	February	5	*Cladophora* sp.	Chlorophyta	Filamentous	1.07%
BU	February	5	*Ulva* sp.	Chlorophyta	Foliose	0.17%
BU	February	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	6.01%
BU	February	5	*Fucus virsoides*	Phaeophyta	Leathery	52.13%
BU	February	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	5.24%
BU	February	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.54%
BU	March	1	Bare rock	Abiota	N/A	24.54%
BU	March	1	*Ulva* sp.	Chlorophyta	Foliose	0.24%
BU	March	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	25.51%
BU	March	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	6.90%
BU	March	1	*Gelidium* sp.	Rhodophyta	Corticated	0.07%
BU	March	1	*Fucus virsoides*	Phaeophyta	Leathery	42.73%

BU	March	2	Bare rock	Abiota	N/A	8.00%
BU	March	2	*Ulva* sp.	Chlorophyta	Foliose	6.33%
BU	March	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	12.66%
BU	March	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	5.05%
BU	March	2	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.84%
BU	March	2	*Gelidium* sp.	Rhodophyta	Corticated	1.98%
BU	March	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.80%
BU	March	2	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.19%
BU	March	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.31%
BU	March	2	*Fucus virsoides*	Phaeophyta	Leathery	64.03%
BU	March	3	Bare rock	Abiota	N/A	7.51%
BU	March	3	*Ulva* sp.	Chlorophyta	Foliose	0.42%
BU	March	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	3.92%
BU	March	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	7.06%
BU	March	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.33%
BU	March	3	*Gelidium* sp.	Rhodophyta	Corticated	29.47%
BU	March	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.16%
BU	March	3	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.10%
BU	March	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.24%
BU	March	3	*Fucus virsoides*	Phaeophyta	Leathery	50.60%
BU	March	4	Bare rock	Abiota	N/A	37.75%
BU	March	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	2.21%
BU	March	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.12%
BU	March	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.91%
BU	March	4	*Gelidium* sp.	Rhodophyta	Corticated	0.10%
BU	March	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.78%
BU	March	4	*Fucus virsoides*	Phaeophyta	Leathery	52.02%
BU	March	4	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.35%
BU	March	5	Bare rock	Abiota	N/A	17.92%
BU	March	5	*Chaetomorpha* sp.	Chlorophyta	Filamentous	13.96%
BU	March	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	10.93%

BU	March	5	*Ulva* sp.	Chlorophyta	Foliose	0.69%
BU	March	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.72%
BU	March	5	*Gelidium* sp.	Rhodophyta	Corticated	1.41%
BU	March	5	*Chthamalus* sp.	Crustacea	Sessile animal	1.44%
BU	March	5	*Fucus virsoides*	Phaeophyta	Leathery	51.94%
BU	April	1	Bare rock	Abiota	N/A	16.32%
BU	April	1	*Cladophora* sp.	Chlorophyta	Filamentous	2.20%
BU	April	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	6.30%
BU	April	1	*Ulva* sp.	Chlorophyta	Foliose	0.75%
BU	April	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.00%
BU	April	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.07%
BU	April	1	*Fucus virsoides*	Phaeophyta	Leathery	73.36%
BU	April	2	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.71%
BU	April	2	Bare rock	Abiota	N/A	26.56%
BU	April	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	13.58%
BU	April	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.04%
BU	April	2	*Ulva* sp.	Chlorophyta	Foliose	0.75%
BU	April	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.63%
BU	April	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.10%
BU	April	2	*Fucus virsoides*	Phaeophyta	Leathery	55.63%
BU	April	3	Bare rock	Abiota	N/A	13.07%
BU	April	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	7.99%
BU	April	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.15%
BU	April	3	*Ulva* sp.	Chlorophyta	Foliose	0.74%
BU	April	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.97%
BU	April	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.36%
BU	April	3	*Fucus virsoides*	Phaeophyta	Leathery	72.72%
BU	April	4	Bare rock	Abiota	N/A	21.77%
BU	April	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	3.06%
BU	April	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	9.29%
BU	April	4	*Gelidium* sp.	Rhodophyta	Corticated	0.80%

BU	April	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.00%
BU	April	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.76%
BU	April	4	*Fucus virsoides*	Phaeophyta	Leathery	60.69%
BU	April	4	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.54%
BU	April	5	Bare rock	Abiota	N/A	0.80%
BU	April	5	*Chaetomorpha* sp.	Chlorophyta	Filamentous	7.35%
BU	April	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.08%
BU	April	5	*Ulva* sp.	Chlorophyta	Foliose	8.00%
BU	April	5	*Gelidium* sp.	Rhodophyta	Corticated	5.46%
BU	April	5	*Corallina* sp.	Rhodophyta	Articulated calcareous	4.17%
BU	April	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.26%
BU	April	5	*Fucus virsoides*	Phaeophyta	Leathery	73.89%
BU	May	1	Bare rock	Abiota	N/A	24.72%
BU	May	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	2.51%
BU	May	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	13.19%
BU	May	1	*Ulva* sp.	Chlorophyta	Foliose	0.85%
BU	May	1	*Gelidium* sp.	Rhodophyta	Corticated	16.53%
BU	May	1	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.09%
BU	May	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.85%
BU	May	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.10%
BU	May	1	*Fucus virsoides*	Phaeophyta	Leathery	40.79%
BU	May	1	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.37%
BU	May	2	Bare rock	Abiota	N/A	8.41%
BU	May	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	17.14%
BU	May	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.08%
BU	May	2	*Ulva* sp.	Chlorophyta	Foliose	5.25%
BU	May	2	*Gelidium* sp.	Rhodophyta	Corticated	53.55%
BU	May	2	*Corallina* sp.	Rhodophyta	Articulated calcareous	2.05%
BU	May	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.52%
BU	May	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.45%
BU	May	2	*Fucus virsoides*	Phaeophyta	Leathery	7.55%

BU	May	2	*Mytilaster minimus*	Bivalvia	Sessile animal	1.63%
BU	May	2	*Spirorbis* sp.	Polychaeta	Sessile animal	0.33%
BU	May	3	Bare rock	Abiota	N/A	42.35%
BU	May	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	0.87%
BU	May	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	15.73%
BU	May	3	*Ulva* sp.	Chlorophyta	Foliose	1.47%
BU	May	3	*Gelidium* sp.	Rhodophyta	Corticated	2.71%
BU	May	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.27%
BU	May	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	2.47%
BU	May	3	*Chthamalus* sp.	Crustacea	Sessile animal	1.88%
BU	May	3	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.62%
BU	May	3	*Fucus virsoides*	Phaeophyta	Leathery	31.62%
BU	May	4	Bare rock	Abiota	N/A	33.91%
BU	May	4	*Cladophora* sp.	Chlorophyta	Filamentous	5.27%
BU	May	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.18%
BU	May	4	*Ulva* sp.	Chlorophyta	Foliose	0.16%
BU	May	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	34.65%
BU	May	4	*Gelidium* sp.	Rhodophyta	Corticated	5.20%
BU	May	4	*Corallina* sp.	Rhodophyta	Articulated calcareous	8.97%
BU	May	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.25%
BU	May	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.45%
BU	May	4	*Mytilaster minimus*	Bivalvia	Sessile animal	1.76%
BU	May	4	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.69%
BU	May	4	*Fucus virsoides*	Phaeophyta	Leathery	9.62%
BU	May	5	Bare rock	Abiota	N/A	63.80%
BU	May	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	12.40%
BU	May	5	*Chaetomorpha* sp.	Chlorophyta	Filamentous	0.28%
BU	May	5	*Gelidium* sp.	Rhodophyta	Corticated	0.98%
BU	May	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.57%
BU	May	5	*Chthamalus* sp.	Crustacea	Sessile animal	1.32%
BU	May	5	*Mytilaster minimus*	Bivalvia	Sessile animal	0.28%

BU	May	5	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.71%
BU	May	5	*Fucus virsoides*	Phaeophyta	Leathery	17.28%
BU	June	1	Bare rock	Abiota	N/A	36.72%
BU	June	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	26.49%
BU	June	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.36%
BU	June	1	*Cladophora* sp.	Chlorophyta	Filamentous	27.60%
BU	June	1	*Ulva* sp.	Chlorophyta	Foliose	0.85%
BU	June	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.19%
BU	June	1	*Fucus virsoides*	Phaeophyta	Leathery	4.17%
BU	June	2	Bare rock	Abiota	N/A	71.90%
BU	June	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.18%
BU	June	2	*Cladophora* sp.	Chlorophyta	Filamentous	3.16%
BU	June	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	6.29%
BU	June	2	*Gelidium* sp.	Rhodophyta	Corticated	0.60%
BU	June	2	*Corallina* sp.	Rhodophyta	Articulated calcareous	1.91%
BU	June	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	2.62%
BU	June	2	*Ulva* sp.	Chlorophyta	Foliose	0.26%
BU	June	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.78%
BU	June	2	*Fucus virsoides*	Phaeophyta	Leathery	4.58%
BU	June	2	*Laurencia obtusa*	Rhodophyta	Corticated	4.72%
BU	June	3	Bare rock	Abiota	N/A	66.11%
BU	June	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.49%
BU	June	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	7.50%
BU	June	3	*Gelidium* sp.	Rhodophyta	Corticated	6.86%
BU	June	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.26%
BU	June	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.30%
BU	June	3	*Ulva* sp.	Chlorophyta	Foliose	0.46%
BU	June	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.25%
BU	June	3	*Fucus virsoides*	Phaeophyta	Leathery	2.35%
BU	June	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	10.06%
BU	June	4	Bare rock	Abiota	N/A	74.84%

BU	June	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	6.98%
BU	June	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	4.23%
BU	June	4	*Gelidium* sp.	Rhodophyta	Corticated	2.59%
BU	June	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	4.19%
BU	June	4	*Chthamalus* sp.	Crustacea	Sessile animal	1.07%
BU	June	4	*Spirobranchus triqueter*	Polychaeta	Sessile animal	1.04%
BU	June	4	*Fucus virsoides*	Phaeophyta	Leathery	4.86%
BU	July	1	Bare rock	Abiota	N/A	67.32%
BU	July	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	15.08%
BU	July	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	0.83%
BU	July	1	*Gelidium* sp.	Rhodophyta	Corticated	6.71%
BU	July	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	6.58%
BU	July	1	*Chthamalus* sp.	Crustacea	Sessile animal	1.00%
BU	July	1	*Fucus virsoides*	Phaeophyta	Leathery	2.13%
BU	July	1	*Spirobranchus triqueter*	Polychaeta	Sessile animal	0.35%
BU	July	2	Bare rock	Abiota	N/A	41.73%
BU	July	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	5.13%
BU	July	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	38.94%
BU	July	2	*Cladophora* sp.	Chlorophyta	Filamentous	0.16%
BU	July	2	*Ulva* sp.	Chlorophyta	Foliose	0.06%
BU	July	2	*Gelidium* sp.	Rhodophyta	Corticated	5.09%
BU	July	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	4.04%
BU	July	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.75%
BU	July	2	*Fucus virsoides*	Phaeophyta	Leathery	4.09%
BU	July	3	Bare rock	Abiota	N/A	17.97%
BU	July	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.77%
BU	July	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	3.33%
BU	July	3	*Cladophora* sp.	Chlorophyta	Filamentous	9.52%
BU	July	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	51.71%
BU	July	3	*Gelidium* sp.	Rhodophyta	Corticated	13.42%
BU	July	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.21%

BU	July	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.33%
BU	July	3	*Fucus virsoides*	Phaeophyta	Leathery	0.80%
BU	July	4	Bare rock	Abiota	N/A	57.59%
BU	July	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	31.23%
BU	July	4	*Cladophora* sp.	Chlorophyta	Filamentous	0.06%
BU	July	4	*Gelidium* sp.	Rhodophyta	Corticated	1.68%
BU	July	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	4.90%
BU	July	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.24%
BU	July	4	*Fucus virsoides*	Phaeophyta	Leathery	4.31%
BU	July	5	Bare rock	Abiota	N/A	54.99%
BU	July	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	9.79%
BU	July	5	*Cladophora* sp.	Chlorophyta	Filamentous	8.39%
BU	July	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	24.69%
BU	July	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.75%
BU	July	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.80%
BU	July	5	*Fucus virsoides*	Phaeophyta	Leathery	0.60%
HPAR	March	1	*Fucus virsoides*	Phaeophyta	Leathery	17.99%
HPAR	March	1	*Ulva* sp.	Chlorophyta	Foliose	2.41%
HPAR	March	1	*Laurencia obtusa*	Rhodophyta	Corticated	76.79%
HPAR	March	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.00%
HPAR	March	1	*Mytilaster minimus*	Bivalvia	Sessile animal	0.91%
HPAR	March	1	Bare rock	Abiota	N/A	0.10%
HPAR	March	2	*Fucus virsoides*	Phaeophyta	Leathery	26.56%
HPAR	March	2	*Laurencia obtusa*	Rhodophyta	Corticated	1.00%
HPAR	March	2	*Gelidium* sp.	Rhodophyta	Corticated	0.90%
HPAR	March	2	*Cladophora* sp.	Chlorophyta	Filamentous	29.69%
HPAR	March	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	29.66%
HPAR	March	3	*Fucus virsoides*	Phaeophyta	Leathery	14.14%
HPAR	March	3	*Cladophora* sp.	Chlorophyta	Filamentous	27.87%
HPAR	March	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	41.81%
HPAR	March	3	*Gelidium* sp.	Rhodophyta	Corticated	1.05%

HPAR	March	3	Bare rock	Abiota	N/A	15.12%
HPAR	March	4	*Fucus virsoides*	Phaeophyta	Leathery	41.17%
HPAR	March	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.95%
HPAR	March	4	*Ulva* sp.	Chlorophyta	Foliose	0.48%
HPAR	March	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	8.51%
HPAR	March	4	Bare rock	Abiota	N/A	46.89%
HPAR	March	5	*Fucus virsoides*	Phaeophyta	Leathery	22.99%
HPAR	March	5	*Mytilaster minimus*	Bivalvia	Sessile animal	0.13%
HPAR	March	5	Bare rock	Abiota	N/A	13.68%
HPAR	March	5	*Mixed turf (Cladophora* spp. + *Polysiphonia* spp.*)*	N/A	Filamentous	63.20%
HPAR	April	1	*Fucus virsoides*	Phaeophyta	Leathery	37.33%
HPAR	April	1	*Ulva* sp.	Chlorophyta	Foliose	2.52%
HPAR	April	1	*Mytilaster minimus*	Bivalvia	Sessile animal	0.71%
HPAR	April	1	*Ceramium* sp.	Rhodophyta	Filamentous	2.41%
HPAR	April	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	34.46%
HPAR	April	1	Bare rock	Abiota	N/A	22.56%
HPAR	April	2	*Fucus virsoides*	Phaeophyta	Leathery	42.14%
HPAR	April	2	*Cladophora* sp.	Chlorophyta	Filamentous	22.22%
HPAR	April	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	31.78%
HPAR	April	2	Bare rock	Abiota	N/A	2.96%
HPAR	April	2	*Ceramium* sp.	Rhodophyta	Filamentous	0.89%
HPAR	April	3	*Fucus virsoides*	Phaeophyta	Leathery	30.40%
HPAR	April	3	*Cladophora* sp.	Chlorophyta	Filamentous	13.26%
HPAR	April	3	*Gelidium* sp.	Rhodophyta	Corticated	2.15%
HPAR	April	3	Bare rock	Abiota	N/A	5.06%
HPAR	April	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	49.13%
HPAR	April	4	*Fucus virsoides*	Phaeophyta	Leathery	30.73%
HPAR	April	4	*Mixed turf (Cladophora* spp. + *Polysiphonia* spp.*)*	N/A	Filamentous	3.86%
HPAR	April	4	*Ulva* sp.	Chlorophyta	Foliose	0.12%
HPAR	April	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	21.92%
HPAR	April	4	*Corallina* sp.	Rhodophyta	Articulated calcareous	6.65%

HPAR	April	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.91%
HPAR	April	4	*Mytilaster minimus*	Bivalvia	Sessile animal	0.55%
HPAR	April	4	Bare rock	Abiota	N/A	25.21%
HPAR	April	5	*Fucus virsoides*	Phaeophyta	Leathery	45.64%
HPAR	April	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	5.14%
HPAR	April	5	*Ulva* sp.	Chlorophyta	Foliose	0.90%
HPAR	April	5	*Corallina* sp.	Rhodophyta	Articulated calcareous	3.01%
HPAR	April	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.01%
HPAR	April	5	*Mytilaster minimus*	Bivalvia	Sessile animal	0.60%
HPAR	April	5	Bare rock	Abiota	N/A	41.70%
HPAR	May	1	*Fucus virsoides*	Phaeophyta	Leathery	11.87%
HPAR	May	1	Bare rock	Abiota	N/A	8.45%
HPAR	May	1	*Ulva* sp.	Chlorophyta	Foliose	1.53%
HPAR	May	1	*Laurencia obtusa*	Rhodophyta	Corticated	1.98%
HPAR	May	1	*Mytilaster minimus*	Bivalvia	Sessile animal	3.69%
HPAR	May	1	*Corallina* sp.	Rhodophyta	Articulated calcareous	3.05%
HPAR	May	1	*Cladophora* sp.	Chlorophyta	Filamentous	30.00%
HPAR	May	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	39.43%
HPAR	May	2	*Fucus virsoides*	Phaeophyta	Leathery	18.10%
HPAR	May	2	*Cladophora* sp.	Chlorophyta	Filamentous	27.35%
HPAR	May	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	52.21%
HPAR	May	2	Bare rock	Abiota	N/A	1.37%
HPAR	May	2	*Laurencia obtusa*	Rhodophyta	Corticated	0.97%
HPAR	May	3	*Fucus virsoides*	Phaeophyta	Leathery	14.69%
HPAR	May	3	Bare rock	Abiota	N/A	34.32%
HPAR	May	3	*Ballanus* sp.	Crustacea	Sessile animal	0.57%
HPAR	May	3	*Rivularia atra*	Cyanophyta	Incrusting	0.57%
HPAR	May	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.57%
HPAR	May	3	*Laurencia obtusa*	Rhodophyta	Corticated	1.42%
HPAR	May	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	6.25%
HPAR	May	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	16.74%

HPAR	May	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	14.20%
HPAR	May	3	*Cladophora* sp.	Chlorophyta	Filamentous	5.11%
HPAR	May	4	*Fucus virsoides*	Phaeophyta	Leathery	25.55%
HPAR	May	4	Bare rock	Abiota	N/A	38.22%
HPAR	May	4	*Corallina* sp.	Rhodophyta	Articulated calcareous	6.50%
HPAR	May	4	*Ulva* sp.	Chlorophyta	Foliose	0.76%
HPAR	May	4	*Mytilaster minimus*	Bivalvia	Sessile animal	0.92%
HPAR	May	4	*Cladophora* sp.	Chlorophyta	Filamentous	1.80%
HPAR	May	4	*Gelidium* sp.	Rhodophyta	Corticated	3.06%
HPAR	May	5	*Fucus virsoides*	Phaeophyta	Leathery	36.65%
HPAR	May	5	*Ostrea edulis*	Bivalvia	Sessile animal	1.48%
HPAR	May	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.89%
HPAR	May	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.44%
HPAR	May	5	Bare rock	Abiota	N/A	56.55%
HPAR	June	1	*Fucus virsoides*	Phaeophyta	Leathery	3.60%
HPAR	June	1	*Cladophora* sp.	Chlorophyta	Filamentous	17.23%
HPAR	June	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	25.15%
HPAR	June	1	*Padina pavonica*	Phaeophyta	Leathery	1.10%
HPAR	June	1	Bare rock	Abiota	N/A	8.18%
HPAR	June	2	*Fucus virsoides*	Phaeophyta	Leathery	7.93%
HPAR	June	2	*Mytilaster minimus*	Bivalvia	Sessile animal	0.89%
HPAR	June	2	*Cladophora* sp.	Chlorophyta	Filamentous	29.40%
HPAR	June	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	27.41%
HPAR	June	2	*Gelidium* sp.	Rhodophyta	Corticated	0.89%
HPAR	June	2	*Padina pavonica*	Phaeophyta	Leathery	0.89%
HPAR	June	3	*Fucus virsoides*	Phaeophyta	Leathery	15.33%
HPAR	June	3	*Cladophora* sp.	Chlorophyta	Filamentous	13.08%
HPAR	June	3	Bare rock	Abiota	N/A	3.76%
HPAR	June	3	*Osmundea pinnatifida*	Rhodophyta	Corticated	0.58%
HPAR	June	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	67.24%
HPAR	June	4	*Fucus virsoides*	Phaeophyta	Leathery	7.75%

HPAR	June	4	Bare rock	Abiota	N/A	15.60%
HPAR	June	4	*Osmundea pinnatifida*	Rhodophyta	Corticated	2.23%
HPAR	June	4	*Cladophora* sp.	Chlorophyta	Filamentous	0.57%
HPAR	June	4	*Ballanus* sp.	Crustacea	Sessile animal	0.61%
HPAR	June	4	*Rivularia atra*	Cyanophyta	Incrusting	0.61%
HPAR	June	4	*Mytilaster minimus*	Bivalvia	Sessile animal	0.61%
HPAR	June	4	*Corallina* sp.	Rhodophyta	Articulated calcareous	15.13%
HPAR	June	4	*Gelidium* sp.	Rhodophyta	Corticated	4.54%
HPAR	June	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	5.00%
HPAR	June	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	47.36%
HPAR	June	5	*Fucus virsoides*	Phaeophyta	Leathery	15.77%
HPAR	June	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	22.52%
HPAR	June	5	*Cladophora* sp.	Chlorophyta	Filamentous	0.58%
HPAR	June	5	*Osmundea pinnatifida*	Rhodophyta	Corticated	0.58%
HPAR	June	5	*Rivularia atra*	Cyanophyta	Incrusting	0.58%
HPAR	June	5	*Mytilaster minimus*	Bivalvia	Sessile animal	0.89%
HPAR	June	5	Bare rock	Abiota	N/A	59.08%
HPAR	July	1	Bare rock	Abiota	N/A	8.42%
HPAR	July	1	*Fucus virsoides*	Phaeophyta	Leathery	0.95%
HPAR	July	1	*Cladophora* sp.	Chlorophyta	Filamentous	31.28%
HPAR	July	1	*Lithophaga lithophaga*	Bivalvia	Sessile animal	0.14%
HPAR	July	1	*Mytilaster minimus*	Bivalvia	Sessile animal	0.28%
HPAR	July	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	58.93%
HPAR	July	2	Bare rock	Abiota	N/A	1.11%
HPAR	July	2	*Fucus virsoides*	Phaeophyta	Leathery	6.42%
HPAR	July	2	*Cladophora* sp.	Chlorophyta	Filamentous	34.17%
HPAR	July	2	*Chthamalus* sp.	Crustacea	Sessile animal	0.14%
HPAR	July	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.95%
HPAR	July	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.14%
HPAR	July	2	*Rivularia atra*	Cyanophyta	Incrusting	0.05%
HPAR	July	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	57.02%

HPAR	July	3	Bare rock	Abiota	N/A	14.25%
HPAR	July	3	*Fucus virsoides*	Phaeophyta	Leathery	6.24%
HPAR	July	3	*Cladophora* sp.	Chlorophyta	Filamentous	19.60%
HPAR	July	3	*Padina pavonica*	Phaeophyta	Leathery	0.14%
HPAR	July	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.37%
HPAR	July	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	1.37%
HPAR	July	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	57.03%
HPAR	July	4	*Fucus virsoides*	Phaeophyta	Leathery	19.14%
HPAR	July	4	*Cladophora* sp.	Chlorophyta	Filamentous	11.29%
HPAR	July	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	41.51%
HPAR	July	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.45%
HPAR	July	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.45%
HPAR	July	4	*Mytilaster minimus*	Bivalvia	Sessile animal	0.58%
HPAR	July	4	Bare rock	Abiota	N/A	24.57%
HPAR	July	5	*Fucus virsoides*	Phaeophyta	Leathery	24.30%
HPAR	July	5	*Cladophora* sp.	Chlorophyta	Filamentous	15.23%
HPAR	July	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	18.47%
HPAR	July	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	6.74%
HPAR	July	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.33%
HPAR	July	5	*Rivularia atra*	Cyanophyta	Incrusting	1.67%
HPAR	July	5	Bare rock	Abiota	N/A	33.26%
HPAR	August	1	*Fucus virsoides*	Phaeophyta	Leathery	14.47%
HPAR	August	1	*Cladophora* sp.	Chlorophyta	Filamentous	5.77%
HPAR	August	1	*Ostrea edulis*	Bivalvia	Sessile animal	0.28%
HPAR	August	1	Bare rock	Abiota	N/A	5.88%
HPAR	August	1	*Gelidium* sp.	Rhodophyta	Corticated	14.59%
HPAR	August	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	41.05%
HPAR	August	1	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	15.84%
HPAR	August	2	*Fucus virsoides*	Phaeophyta	Leathery	10.62%
HPAR	August	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	33.50%
HPAR	August	2	*Gelidium* sp.	Rhodophyta	Corticated	1.76%

HPAR	August	2	*Cladophora* sp.	Chlorophyta	Filamentous	14.10%
HPAR	August	2	*Rivularia atra*	Cyanophyta	Incrusting	1.76%
HPAR	August	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.76%
HPAR	August	2	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	12.34%
HPAR	August	2	*Corallina* sp.	Rhodophyta	Articulated calcareous	10.58%
HPAR	August	2	Bare rock	Abiota	N/A	13.57%
HPAR	August	3	Bare rock	Abiota	N/A	23.10%
HPAR	August	3	*Fucus virsoides*	Phaeophyta	Leathery	4.32%
HPAR	August	3	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	17.78%
HPAR	August	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	27.65%
HPAR	August	3	*Cladophora* sp.	Chlorophyta	Filamentous	13.62%
HPAR	August	4	*Fucus virsoides*	Phaeophyta	Leathery	26.60%
HPAR	August	4	*Chthamalus* sp.	Crustacea	Sessile animal	1.33%
HPAR	August	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	1.86%
HPAR	August	4	*Cladophora* sp.	Chlorophyta	Filamentous	1.86%
HPAR	August	4	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	39.66%
HPAR	August	4	Bare rock	Abiota	N/A	28.69%
Lanterna	January	1	*Fucus virsoides*	Phaeophyta	Leathery	27.93%
Lanterna	January	1	*Chthamalus* sp.	Crustacea	Sessile animal	0.22%
Lanterna	January	1	*Enteromorpha* sp.	Chlorophyta	Foliose	7.25%
Lanterna	January	1	*Gelidium* sp.	Rhodophyta	Corticated	14.04%
Lanterna	January	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.19%
Lanterna	January	1	*Rivularia atra*	Cyanophyta	Incrusting	0.03%
Lanterna	January	1	Bare rock	Abiota	N/A	48.35%
Lanterna	January	2	*Fucus virsoides*	Phaeophyta	Leathery	43.32%
Lanterna	January	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	23.72%
Lanterna	January	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	0.68%
Lanterna	January	2	*Enteromorpha* sp.	Chlorophyta	Foliose	9.77%
Lanterna	January	2	*Ulva* sp.	Chlorophyta	Foliose	0.84%
Lanterna	January	2	*Rivularia atra*	Cyanophyta	Incrusting	0.03%
Lanterna	January	2	Bare rock	Abiota	N/A	21.63%

Lanterna	January	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	37.46%
Lanterna	January	3	*Fucus virsoides*	Phaeophyta	Leathery	38.04%
Lanterna	January	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.48%
Lanterna	January	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	0.33%
Lanterna	January	3	*Ulva* sp.	Chlorophyta	Foliose	0.15%
Lanterna	January	3	Bare rock	Abiota	N/A	22.53%
Lanterna	January	4	*Fucus virsoides*	Phaeophyta	Leathery	36.78%
Lanterna	January	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	7.04%
Lanterna	January	4	*Ulva* sp.	Chlorophyta	Foliose	1.25%
Lanterna	January	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	1.01%
Lanterna	January	4	*Rivularia atra*	Cyanophyta	Incrusting	0.09%
Lanterna	January	4	*Enteromorpha* sp.	Chlorophyta	Foliose	1.92%
Lanterna	January	4	*Gelidium* sp.	Rhodophyta	Corticated	6.59%
Lanterna	January	4	*Spirorbis* sp.	Polychaeta	Sessile animal	0.03%
Lanterna	January	4	Bare rock	Abiota	N/A	45.29%
Lanterna	January	5	*Fucus virsoides*	Phaeophyta	Leathery	35.39%
Lanterna	January	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	12.79%
Lanterna	January	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.92%
Lanterna	January	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.61%
Lanterna	January	5	*Ulva* sp.	Chlorophyta	Foliose	0.60%
Lanterna	January	5	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.06%
Lanterna	January	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	0.09%
Lanterna	January	5	*Cladophora* sp.	Chlorophyta	Filamentous	0.12%
Lanterna	January	5	*Rivularia atra*	Cyanophyta	Incrusting	0.09%
Lanterna	January	5	Bare rock	Abiota	N/A	45.34%
Lanterna	February	1	*Fucus virsoides*	Phaeophyta	Leathery	40.97%
Lanterna	February	1	*Enteromorpha* sp.	Chlorophyta	Foliose	3.44%
Lanterna	February	1	*Ulva* sp.	Chlorophyta	Foliose	3.18%
Lanterna	February	1	*Gelidium* sp.	Rhodophyta	Corticated	11.11%
Lanterna	February	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.15%
Lanterna	February	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	3.75%

Lanterna	February	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.12%
Lanterna	February	1	Bare rock	Abiota	N/A	34.29%
Lanterna	February	1	*Ulva* sp.	Chlorophyta	Foliose	12.71%
Lanterna	February	2	*Fucus virsoides*	Phaeophyta	Leathery	48.32%
Lanterna	February	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	10.94%
Lanterna	February	2	*Enteromorpha* sp.	Chlorophyta	Foliose	2.08%
Lanterna	February	2	*Spirorbis* sp.	Polychaeta	Sessile animal	0.03%
Lanterna	February	2	*Gelidium* sp.	Rhodophyta	Corticated	4.79%
Lanterna	February	2	*Cladophora* sp.	Chlorophyta	Filamentous	0.66%
Lanterna	February	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.30%
Lanterna	February	2	Bare rock	Abiota	N/A	32.88%
Lanterna	February	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	8.86%
Lanterna	February	3	*Fucus virsoides*	Phaeophyta	Leathery	40.20%
Lanterna	February	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	11.21%
Lanterna	February	3	*Ulva* sp.	Chlorophyta	Foliose	1.77%
Lanterna	February	3	*Enteromorpha* sp.	Chlorophyta	Foliose	5.20%
Lanterna	February	3	*Cladophora* sp.	Chlorophyta	Filamentous	0.91%
Lanterna	February	3	*Spirorbis* sp.	Polychaeta	Sessile animal	0.61%
Lanterna	February	3	*Rivularia atra*	Cyanophyta	Incrusting	0.30%
Lanterna	February	3	Bare rock	Abiota	N/A	30.94%
Lanterna	February	4	*Fucus virsoides*	Phaeophyta	Leathery	30.44%
Lanterna	February	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	8.97%
Lanterna	February	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.77%
Lanterna	February	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	1.14%
Lanterna	February	4	*Chthamalus* sp.	Crustacea	Sessile animal	1.55%
Lanterna	February	4	*Gelidium* sp.	Rhodophyta	Corticated	0.37%
Lanterna	February	4	*Spirorbis* sp.	Polychaeta	Sessile animal	0.06%
Lanterna	February	4	Bare rock	Abiota	N/A	54.70%
Lanterna	February	5	*Fucus virsoides*	Phaeophyta	Leathery	52.27%
Lanterna	February	5	*Gelidium* sp.	Rhodophyta	Corticated	1.33%
Lanterna	February	5	*Enteromorpha* sp.	Chlorophyta	Foliose	2.64%

Lanterna	February	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.73%
Lanterna	February	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	5.23%
Lanterna	February	5	*Cladophora* sp.	Chlorophyta	Filamentous	1.24%
Lanterna	February	5	*Spirorbis* sp.	Polychaeta	Sessile animal	0.03%
Lanterna	February	5	Bare rock	Abiota	N/A	35.49%
Lanterna	March	1	*Fucus virsoides*	Phaeophyta	Leathery	43.72%
Lanterna	March	1	*Ulva* sp.	Chlorophyta	Foliose	4.07%
Lanterna	March	1	*Cladophora* sp.	Chlorophyta	Filamentous	0.98%
Lanterna	March	1	*Gelidium* sp.	Rhodophyta	Corticated	2.87%
Lanterna	March	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	1.96%
Lanterna	March	1	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	6.32%
Lanterna	March	1	Bare rock	Abiota	N/A	40.08%
Lanterna	March	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	48.16%
Lanterna	March	2	*Ulva* sp.	Chlorophyta	Foliose	2.18%
Lanterna	March	2	*Cladophora* sp.	Chlorophyta	Filamentous	1.18%
Lanterna	March	2	*Ralfsia verrucosa*	Phaeophyta	Incrusting	2.35%
Lanterna	March	2	*Fucus virsoides*	Phaeophyta	Leathery	24.52%
Lanterna	March	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.05%
Lanterna	March	2	Bare rock	Abiota	N/A	20.55%
Lanterna	March	3	*Ulva* sp.	Chlorophyta	Foliose	0.96%
Lanterna	March	3	*Enteromorpha* sp.	Chlorophyta	Foliose	2.29%
Lanterna	March	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	18.56%
Lanterna	March	3	*Fucus virsoides*	Phaeophyta	Leathery	51.25%
Lanterna	March	3	*Cladophora* sp.	Chlorophyta	Filamentous	1.53%
Lanterna	March	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.31%
Lanterna	March	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.35%
Lanterna	March	3	Bare rock	Abiota	N/A	23.76%
Lanterna	March	4	*Fucus virsoides*	Phaeophyta	Leathery	48.25%
Lanterna	March	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	15.68%
Lanterna	March	4	*Ulva* sp.	Chlorophyta	Foliose	2.08%
Lanterna	March	4	*Enteromorpha* sp.	Chlorophyta	Foliose	0.24%

Lanterna	March	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.43%
Lanterna	March	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.76%
Lanterna	March	4	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.20%
Lanterna	March	4	*Spirorbis* sp.	Polychaeta	Sessile animal	0.03%
Lanterna	March	4	Bare rock	Abiota	N/A	30.33%
Lanterna	March	5	*Fucus virsoides*	Phaeophyta	Leathery	44.62%
Lanterna	March	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	8.13%
Lanterna	March	5	*Ulva* sp.	Chlorophyta	Foliose	0.94%
Lanterna	March	5	*Enteromorpha* sp.	Chlorophyta	Foliose	1.00%
Lanterna	March	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.94%
Lanterna	March	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.98%
Lanterna	March	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.11%
Lanterna	March	5	Bare rock	Abiota	N/A	38.28%
Lanterna	April	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	7.33%
Lanterna	April	1	*Ulva* sp.	Chlorophyta	Foliose	1.14%
Lanterna	April	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.88%
Lanterna	April	1	Bare rock	Abiota	N/A	17.38%
Lanterna	April	1	*Cladophora* sp.	Chlorophyta	Filamentous	0.28%
Lanterna	April	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.57%
Lanterna	April	1	*Fucus virsoides*	Phaeophyta	Leathery	72.42%
Lanterna	April	2	*Fucus virsoides*	Phaeophyta	Leathery	53.93%
Lanterna	April	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	9.41%
Lanterna	April	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	7.86%
Lanterna	April	2	*Ulva* sp.	Chlorophyta	Foliose	0.30%
Lanterna	April	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.30%
Lanterna	April	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	30.63%
Lanterna	April	3	*Gelidium* sp.	Rhodophyta	Corticated	3.46%
Lanterna	April	3	*Fucus virsoides*	Phaeophyta	Leathery	29.58%
Lanterna	April	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.43%
Lanterna	April	3	*Ulva* sp.	Chlorophyta	Foliose	0.52%
Lanterna	April	3	*Spirorbis* sp.	Polychaeta	Sessile animal	0.06%

Lanterna	April	3	Bare rock	Abiota	N/A	34.32%
Lanterna	April	4	Bare rock	Abiota	N/A	17.78%
Lanterna	April	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	13.13%
Lanterna	April	4	*Cladophora* sp.	Chlorophyta	Filamentous	0.51%
Lanterna	April	4	*Ulva* sp.	Chlorophyta	Foliose	0.28%
Lanterna	April	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.42%
Lanterna	April	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.70%
Lanterna	April	4	*Fucus virsoides*	Phaeophyta	Leathery	67.17%
Lanterna	April	5	*Fucus virsoides*	Phaeophyta	Leathery	46.11%
Lanterna	April	5	*Cladophora* sp.	Chlorophyta	Filamentous	0.57%
Lanterna	April	5	*Ulva* sp.	Chlorophyta	Foliose	0.37%
Lanterna	April	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.42%
Lanterna	April	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	2.92%
Lanterna	April	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.84%
Lanterna	April	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.07%
Lanterna	April	5	Bare rock	Abiota	N/A	43.70%
Lanterna	May	1	*Fucus virsoides*	Phaeophyta	Leathery	72.00%
Lanterna	May	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	4.61%
Lanterna	May	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.78%
Lanterna	May	1	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.34%
Lanterna	May	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.41%
Lanterna	May	1	Bare rock	Abiota	N/A	19.87%
Lanterna	May	2	Bare rock	Abiota	N/A	3.33%
Lanterna	May	2	*Ulva* sp.	Chlorophyta	Foliose	0.33%
Lanterna	May	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	9.03%
Lanterna	May	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.11%
Lanterna	May	2	*Cladophora* sp.	Chlorophyta	Filamentous	0.90%
Lanterna	May	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.66%
Lanterna	May	2	*Fucus virsoides*	Phaeophyta	Leathery	84.64%
Lanterna	May	3	Bare rock	Abiota	N/A	2.69%
Lanterna	May	3	Sediment	Abiota	N/A	5.47%

Lanterna	May	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.51%
Lanterna	May	3	*Gelidium* sp.	Rhodophyta	Corticated	0.85%
Lanterna	May	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.21%
Lanterna	May	3	*Fucus virsoides*	Phaeophyta	Leathery	90.27%
Lanterna	May	4	*Fucus virsoides*	Phaeophyta	Leathery	73.11%
Lanterna	May	4	*Ulva* sp.	Chlorophyta	Foliose	1.08%
Lanterna	May	4	*Gelidium* sp.	Rhodophyta	Corticated	0.42%
Lanterna	May	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.53%
Lanterna	May	4	*Cladophora* sp.	Chlorophyta	Filamentous	0.31%
Lanterna	May	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.84%
Lanterna	May	4	Bare rock	Abiota	N/A	19.70%
Lanterna	May	5	*Fucus virsoides*	Phaeophyta	Leathery	43.32%
Lanterna	May	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	10.31%
Lanterna	May	5	*Ulva* sp.	Chlorophyta	Foliose	1.35%
Lanterna	May	5	*Cladophora* sp.	Chlorophyta	Filamentous	0.58%
Lanterna	May	5	*Chthamalus* sp.	Crustacea	Sessile animal	0.56%
Lanterna	May	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.67%
Lanterna	May	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	5.71%
Lanterna	May	5	Bare rock	Abiota	N/A	35.50%
Lanterna	June	1	*Fucus virsoides*	Phaeophyta	Leathery	42.83%
Lanterna	June	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	15.55%
Lanterna	June	1	*Cladophora* sp.	Chlorophyta	Filamentous	1.41%
Lanterna	June	1	*Gelidium* sp.	Rhodophyta	Corticated	0.49%
Lanterna	June	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.49%
Lanterna	June	1	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	3.38%
Lanterna	June	1	Bare rock	Abiota	N/A	34.86%
Lanterna	June	2	Bare rock	Abiota	N/A	2.64%
Lanterna	June	2	*Cladophora* sp.	Chlorophyta	Filamentous	0.48%
Lanterna	June	2	*Ulva* sp.	Chlorophyta	Foliose	0.54%
Lanterna	June	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	6.03%
Lanterna	June	2	*Fucus virsoides*	Phaeophyta	Leathery	90.31%

Lanterna	June	3	*Fucus virsoides*	Phaeophyta	Leathery	60.31%
Lanterna	June	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	23.83%
Lanterna	June	3	*Gelidium* sp.	Rhodophyta	Corticated	0.63%
Lanterna	June	3	*Cladophora* sp.	Chlorophyta	Filamentous	0.94%
Lanterna	June	3	Bare rock	Abiota	N/A	14.29%
Lanterna	June	4	*Fucus virsoides*	Phaeophyta	Leathery	61.39%
Lanterna	June	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	3.86%
Lanterna	June	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	6.26%
Lanterna	June	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.59%
Lanterna	June	4	*Cladophora* sp.	Chlorophyta	Filamentous	0.58%
Lanterna	June	4	*Spirorbis* sp.	Polychaeta	Sessile animal	0.03%
Lanterna	June	4	Bare rock	Abiota	N/A	24.28%
Lanterna	June	5	*Fucus virsoides*	Phaeophyta	Leathery	47.62%
Lanterna	June	5	*Ostrea edulis*	Bivalvia	Sessile animal	1.96%
Lanterna	June	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.83%
Lanterna	June	5	*Ulva* sp.	Chlorophyta	Foliose	1.39%
Lanterna	June	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	2.19%
Lanterna	June	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.42%
Lanterna	June	5	*Cladophora* sp.	Chlorophyta	Filamentous	3.68%
Lanterna	June	5	Bare rock	Abiota	N/A	38.92%
Lanterna	July	1	*Fucus virsoides*	Phaeophyta	Leathery	77.99%
Lanterna	July	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.25%
Lanterna	July	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.55%
Lanterna	July	1	*Cladophora* sp.	Chlorophyta	Filamentous	4.54%
Lanterna	July	1	*Spirorbis* sp.	Polychaeta	Sessile animal	0.30%
Lanterna	July	1	*Ulva* sp.	Chlorophyta	Foliose	0.31%
Lanterna	July	1	Bare rock	Abiota	N/A	13.06%
Lanterna	July	2	Bare rock	Abiota	N/A	8.38%
Lanterna	July	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	1.96%
Lanterna	July	2	*Ostrea edulis*	Bivalvia	Sessile animal	1.56%
Lanterna	July	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	14.92%

Lanterna	July	2	*Cladophora* sp.	Chlorophyta	Filamentous	1.53%
Lanterna	July	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.61%
Lanterna	July	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.31%
Lanterna	July	2	*Fucus virsoides*	Phaeophyta	Leathery	70.72%
Lanterna	July	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	27.90%
Lanterna	July	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.99%
Lanterna	July	3	*Ulva* sp.	Chlorophyta	Foliose	0.15%
Lanterna	July	3	*Gelidium* sp.	Rhodophyta	Corticated	2.37%
Lanterna	July	3	*Cladophora* sp.	Chlorophyta	Filamentous	4.45%
Lanterna	July	3	Bare rock	Abiota	N/A	10.38%
Lanterna	July	3	*Fucus virsoides*	Phaeophyta	Leathery	53.77%
Lanterna	July	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	27.64%
Lanterna	July	4	*Fucus virsoides*	Phaeophyta	Leathery	23.52%
Lanterna	July	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	18.17%
Lanterna	July	4	*Cladophora* sp.	Chlorophyta	Filamentous	3.07%
Lanterna	July	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.98%
Lanterna	July	4	Bare rock	Abiota	N/A	26.62%
Lanterna	July	5	*Fucus virsoides*	Phaeophyta	Leathery	56.18%
Lanterna	July	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	2.58%
Lanterna	July	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.22%
Lanterna	July	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.27%
Lanterna	July	5	*Gelidium* sp.	Rhodophyta	Corticated	0.63%
Lanterna	July	5	*Ulva* sp.	Chlorophyta	Foliose	2.99%
Lanterna	July	5	*Cladophora* sp.	Chlorophyta	Filamentous	0.63%
Lanterna	July	5	*Spirorbis* sp.	Polychaeta	Sessile animal	0.32%
Lanterna	July	5	Bare rock	Abiota	N/A	32.18%
Lanterna	August	1	*Fucus virsoides*	Phaeophyta	Leathery	6.61%
Lanterna	August	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	20.80%
Lanterna	August	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	3.20%
Lanterna	August	1	*Cladophora* sp.	Chlorophyta	Filamentous	1.87%
Lanterna	August	1	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	53.33%

Lanterna	August	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	5.33%
Lanterna	August	2	*Fucus virsoides*	Phaeophyta	Leathery	21.15%
Lanterna	August	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	4.75%
Lanterna	August	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	17.89%
Lanterna	August	2	*Enteromorpha* sp.	Chlorophyta	Foliose	2.85%
Lanterna	August	2	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	53.36%
Lanterna	August	3	*Fucus virsoides*	Phaeophyta	Leathery	45.67%
Lanterna	August	3	*Cladophora* sp.	Chlorophyta	Filamentous	5.05%
Lanterna	August	3	*Ulva* sp.	Chlorophyta	Foliose	0.47%
Lanterna	August	3	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.70%
Lanterna	August	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	8.63%
Lanterna	August	3	*Spirorbis* sp.	Polychaeta	Sessile animal	1.17%
Lanterna	August	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.52%
Lanterna	August	3	Bare rock	Abiota	N/A	34.78%
Lanterna	August	4	*Fucus virsoides*	Phaeophyta	Leathery	33.99%
Lanterna	August	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	18.18%
Lanterna	August	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.97%
Lanterna	August	4	*Ulva* sp.	Chlorophyta	Foliose	0.52%
Lanterna	August	4	*Rivularia atra*	Cyanophyta	Incrusting	0.03%
Lanterna	August	4	*Cladophora* sp.	Chlorophyta	Filamentous	1.31%
Lanterna	August	4	*Spirorbis* sp.	Polychaeta	Sessile animal	0.78%
Lanterna	August	4	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	6.53%
Lanterna	August	4	Bare rock	Abiota	N/A	33.68%
Lanterna	August	5	*Fucus virsoides*	Phaeophyta	Leathery	46.63%
Lanterna	August	5	*Ulva* sp.	Chlorophyta	Foliose	8.27%
Lanterna	August	5	*Cladophora* sp.	Chlorophyta	Filamentous	1.77%
Lanterna	August	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	6.02%
Lanterna	August	5	*Gelidium* sp.	Rhodophyta	Corticated	1.97%
Lanterna	August	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.45%
Lanterna	August	5	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.22%
Lanterna	August	5	*Bacillariophyta indet.*	Bacilariophyta	Filamentous	8.36%

Lanterna	August	5	Bare rock	Abiota	N/A	24.32%
Lanterna	September	1	*Fucus virsoides*	Phaeophyta	Leathery	19.59%
Lanterna	September	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	20.51%
Lanterna	September	1	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.79%
Lanterna	September	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	3.97%
Lanterna	September	1	*Spirorbis* sp.	Polychaeta	Sessile animal	2.94%
Lanterna	September	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	5.23%
Lanterna	September	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	2.05%
Lanterna	September	1	*Cladophora* sp.	Chlorophyta	Filamentous	44.91%
Lanterna	September	2	*Ulva* sp.	Chlorophyta	Foliose	25.18%
Lanterna	September	2	*Fucus virsoides*	Phaeophyta	Leathery	27.38%
Lanterna	September	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	17.84%
Lanterna	September	2	*Gelidium* sp.	Rhodophyta	Corticated	4.33%
Lanterna	September	2	*Cladophora* sp.	Chlorophyta	Filamentous	3.21%
Lanterna	September	2	Bare rock	Abiota	N/A	22.06%
Lanterna	September	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	52.65%
Lanterna	September	3	*Fucus virsoides*	Phaeophyta	Leathery	16.14%
Lanterna	September	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.18%
Lanterna	September	3	*Ulva* sp.	Chlorophyta	Foliose	0.75%
Lanterna	September	3	*Cladophora* sp.	Chlorophyta	Filamentous	0.41%
Lanterna	September	3	*Chthamalus* sp.	Crustacea	Sessile animal	0.54%
Lanterna	September	3	*Ostrea edulis*	Bivalvia	Sessile animal	1.75%
Lanterna	September	3	Bare rock	Abiota	N/A	26.58%
Lanterna	September	4	*Fucus virsoides*	Phaeophyta	Leathery	21.26%
Lanterna	September	4	*Ralfsia verrucosa*	Phaeophyta	Incrusting	9.73%
Lanterna	September	4	*Polysiphonia* spp.	Rhodophyta	Filamentous	14.18%
Lanterna	September	4	*Gelidium* sp.	Rhodophyta	Corticated	0.91%
Lanterna	September	4	*Cladophora* sp.	Chlorophyta	Filamentous	3.03%
Lanterna	September	4	*Chthamalus* sp.	Crustacea	Sessile animal	0.61%
Lanterna	September	4	*Ulva* sp.	Chlorophyta	Foliose	1.49%
Lanterna	September	4	*Enteromorpha* sp.	Chlorophyta	Foliose	0.30%

Lanterna	September	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	10.22%
Lanterna	September	4	Bare rock	Abiota	N/A	38.27%
Lanterna	September	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	16.13%
Lanterna	September	5	*Fucus virsoides*	Phaeophyta	Leathery	29.40%
Lanterna	September	5	*Polysiphonia* spp.	Rhodophyta	Filamentous	2.87%
Lanterna	September	5	*Gelidium* sp.	Rhodophyta	Corticated	0.90%
Lanterna	September	5	*Ulva* sp.	Chlorophyta	Foliose	10.96%
Lanterna	September	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	0.54%
Lanterna	September	5	*Mytilaster minimus*	Bivalvia	Sessile animal	0.60%
Lanterna	September	5	*Spirorbis* sp.	Polychaeta	Sessile animal	1.50%
Lanterna	September	5	*Enteromorpha* sp.	Chlorophyta	Foliose	0.60%
Lanterna	September	5	*Cladophora* sp.	Chlorophyta	Filamentous	3.59%
Lanterna	September	5	Bare rock	Abiota	N/A	32.91%
Lanterna	October	1	*Fucus virsoides*	Phaeophyta	Leathery	15.89%
Lanterna	October	1	*Enteromorpha* sp.	Chlorophyta	Foliose	5.31%
Lanterna	October	1	*Gelidium* sp.	Rhodophyta	Corticated	7.09%
Lanterna	October	1	*Cladophora* sp.	Chlorophyta	Filamentous	6.68%
Lanterna	October	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	12.36%
Lanterna	October	1	Bare rock	Abiota	N/A	18.60%
Lanterna	October	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	7.20%
Lanterna	October	2	*Fucus virsoides*	Phaeophyta	Leathery	21.49%
Lanterna	October	2	*Cladophora* sp.	Chlorophyta	Filamentous	8.40%
Lanterna	October	2	*Ulva* sp.	Chlorophyta	Foliose	1.95%
Lanterna	October	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	8.11%
Lanterna	October	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	15.71%
Lanterna	October	2	*Gelidium* sp.	Rhodophyta	Corticated	1.59%
Lanterna	October	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	8.55%
Lanterna	October	2	*Cyanophyta indet.*	Cyanophyta	Filamentous	3.67%
Lanterna	October	2	Bare rock	Abiota	N/A	19.85%
Lanterna	October	3	*Fucus virsoides*	Phaeophyta	Leathery	17.38%
Lanterna	October	3	*Enteromorpha* sp.	Chlorophyta	Foliose	12.80%

Lanterna	October	3	*Ralfsia verrucosa*	Phaeophyta	Incrusting	5.28%
Lanterna	October	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	8.69%
Lanterna	October	3	*Cladophora* sp.	Chlorophyta	Filamentous	8.10%
Lanterna	October	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.43%
Lanterna	October	3	*Ostrea edulis*	Bivalvia	Sessile animal	8.70%
Lanterna	October	3	Bare rock	Abiota	N/A	37.62%
Lanterna	October	4	*Fucus virsoides*	Phaeophyta	Leathery	19.24%
Lanterna	October	4	*Ulva* sp.	Chlorophyta	Foliose	7.40%
Lanterna	October	4	*Cladophora* sp.	Chlorophyta	Filamentous	4.04%
Lanterna	October	4	*Gelidium* sp.	Rhodophyta	Corticated	8.60%
Lanterna	October	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.28%
Lanterna	October	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	1.77%
Lanterna	October	4	Bare rock	Abiota	N/A	15.01%
Lanterna	October	5	*Gelidium* sp.	Rhodophyta	Corticated	10.81%
Lanterna	October	5	*Fucus virsoides*	Phaeophyta	Leathery	8.31%
Lanterna	October	5	*Cladophora* sp.	Chlorophyta	Filamentous	40.78%
Lanterna	October	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	5.38%
Lanterna	October	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.66%
Lanterna	October	5	Bare rock	Abiota	N/A	18.21%
Lanterna	November	1	*Fucus virsoides*	Phaeophyta	Leathery	4.68%
Lanterna	November	1	*Chaetomorpha* sp.	Chlorophyta	Filamentous	5.69%
Lanterna	November	1	*Enteromorpha* sp.	Chlorophyta	Foliose	2.39%
Lanterna	November	1	*Ulva* sp.	Chlorophyta	Foliose	1.60%
Lanterna	November	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	6.11%
Lanterna	November	1	*Cyanophyta indet.*	Cyanophyta	Filamentous	11.56%
Lanterna	November	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.08%
Lanterna	November	1	*Rivularia atra*	Cyanophyta	Incrusting	0.31%
Lanterna	November	1	Bare rock	Abiota	N/A	64.57%
Lanterna	November	2	*Fucus virsoides*	Phaeophyta	Leathery	24.65%
Lanterna	November	2	*Ulva* sp.	Chlorophyta	Foliose	8.05%
Lanterna	November	2	*Enteromorpha* sp.	Chlorophyta	Foliose	5.65%

Lanterna	November	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	6.09%
Lanterna	November	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	7.69%
Lanterna	November	2	*Gelidium* sp.	Rhodophyta	Corticated	3.08%
Lanterna	November	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	3.08%
Lanterna	November	2	Bare rock	Abiota	N/A	41.73%
Lanterna	November	3	*Fucus virsoides*	Phaeophyta	Leathery	15.58%
Lanterna	November	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	4.26%
Lanterna	November	3	*Enteromorpha* sp.	Chlorophyta	Foliose	8.15%
Lanterna	November	3	*Ulva* sp.	Chlorophyta	Foliose	3.48%
Lanterna	November	3	*Gelidium* sp.	Rhodophyta	Corticated	12.95%
Lanterna	November	3	*Cyanophyta indet.*	Cyanophyta	Filamentous	1.52%
Lanterna	November	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	3.04%
Lanterna	November	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	4.55%
Lanterna	November	4	*Enteromorpha* sp.	Chlorophyta	Foliose	24.79%
Lanterna	November	4	*Fucus virsoides*	Phaeophyta	Leathery	20.28%
Lanterna	November	4	*Ulva* sp.	Chlorophyta	Foliose	1.50%
Lanterna	November	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	9.01%
Lanterna	November	4	*Gelidium* sp.	Rhodophyta	Corticated	6.37%
Lanterna	November	4	*Ceramium* sp.	Rhodophyta	Filamentous	1.50%
Lanterna	November	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	0.90%
Lanterna	November	4	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.50%
Lanterna	November	4	Bare rock	Abiota	N/A	31.15%
Lanterna	November	5	*Fucus virsoides*	Phaeophyta	Leathery	11.28%
Lanterna	November	5	*Enteromorpha* sp.	Chlorophyta	Foliose	11.60%
Lanterna	November	5	*Ostrea edulis*	Bivalvia	Sessile animal	6.95%
Lanterna	November	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.02%
Lanterna	November	5	*Ulva* sp.	Chlorophyta	Foliose	1.45%
Lanterna	November	5	*Ralfsia verrucosa*	Phaeophyta	Incrusting	5.82%
Lanterna	November	5	*Gelidium* sp.	Rhodophyta	Corticated	3.33%
Lanterna	November	5	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	5.30%
Lanterna	November	5	Bare rock	Abiota	N/A	52.27%

Lanterna	December	1	*Fucus virsoides*	Phaeophyta	Leathery	24.96%
Lanterna	December	1	*Polysiphonia* spp.	Rhodophyta	Filamentous	18.55%
Lanterna	December	1	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	11.50%
Lanterna	December	1	*Mesophyllum* sp.	Rhodophyta	Incrusting	2.95%
Lanterna	December	1	*Ralfsia verrucosa*	Phaeophyta	Incrusting	3.24%
Lanterna	December	1	Bare rock	Abiota	N/A	38.79%
Lanterna	December	2	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	12.52%
Lanterna	December	2	*Enteromorpha* sp.	Chlorophyta	Foliose	7.58%
Lanterna	December	2	*Fucus virsoides*	Phaeophyta	Leathery	12.75%
Lanterna	December	2	*Ulva* sp.	Chlorophyta	Foliose	3.37%
Lanterna	December	2	*Polysiphonia* spp.	Rhodophyta	Filamentous	8.09%
Lanterna	December	2	*Gelidium* sp.	Rhodophyta	Corticated	4.49%
Lanterna	December	2	*Chaetomorpha* sp.	Chlorophyta	Filamentous	2.10%
Lanterna	December	2	Mixed turf *(Cladophora* spp. + *Polysiphonia* spp.)	N/a	Filamentous	36.23%
Lanterna	December	2	*Laurencia obtusa*	Rhodophyta	Corticated	0.90%
Lanterna	December	2	*Mesophyllum* sp.	Rhodophyta	Incrusting	4.49%
Lanterna	December	2	Bare rock	Abiota	N/A	4.07%
Lanterna	December	3	Bare rock	Abiota	N/A	18.47%
Lanterna	December	3	*Ulva* sp.	Chlorophyta	Foliose	8.91%
Lanterna	December	3	*Enteromorpha* sp.	Chlorophyta	Foliose	9.34%
Lanterna	December	3	*Polysiphonia* spp.	Rhodophyta	Filamentous	3.44%
Lanterna	December	3	*Chaetomorpha* sp.	Chlorophyta	Filamentous	6.09%
Lanterna	December	3	*Fucus virsoides*	Phaeophyta	Leathery	25.53%
Lanterna	December	3	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.13%
Lanterna	December	3	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	2.74%
Lanterna	December	3	Bare rock	Abiota	N/A	22.36%
Lanterna	December	4	*Chaetomorpha* sp.	Chlorophyta	Filamentous	4.76%
Lanterna	December	4	*Enteromorpha* sp.	Chlorophyta	Foliose	9.82%
Lanterna	December	4	*Ulva* sp.	Chlorophyta	Foliose	2.30%
Lanterna	December	4	*Fucus virsoides*	Phaeophyta	Leathery	26.70%
Lanterna	December	4	*Mytilus galloprovincialis*	Bivalvia	Sessile animal	5.63%

Lanterna	December	4	*Gelidium* sp.	Rhodophyta	Corticated	7.26%
Lanterna	December	4	Bare rock	Abiota	N/A	36.36%
Lanterna	December	4	*Corallina* sp.	Rhodophyta	Articulated calcareous	0.31%
Lanterna	December	4	*Cyanophyta indet.*	Cyanophyta	Filamentous	2.15%
Lanterna	December	5	*Ulva* sp.	Chlorophyta	Foliose	4.95%
Lanterna	December	5	*Enteromorpha* sp.	Chlorophyta	Foliose	12.04%
Lanterna	December	5	*Mesophyllum* sp.	Rhodophyta	Incrusting	3.11%
Lanterna	December	5	*Fucus virsoides*	Phaeophyta	Leathery	11.54%
Lanterna	December	5	*Gelidium* sp.	Rhodophyta	Corticated	6.81%
Lanterna	December	5	Bare rock	Abiota	N/A	61.55%

Appendix 2. Results of one-way PERMANOVA (factor: Season) analysis of community structure in *Fucus virsoides* stands based on morphofunctional groups, PERMDISP test for homogeneity and Pairwise tests for Lanterna study site. Statistically significant results ($P < 0.05$) are marked in **bold**

PERMANOVA table of results - Lanterna						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Season	3	21514	7171.3	4.0374	**0.0001**	9917
Res	56	99467	1776.2			
Total	59	1.21E+05				
PERMDISP results - Lanterna - Deviations from centroid						
F	1.0509					
Df1	3					
Df2	56					
P(perm)	0.4782					
PAIR-WISE TESTS - Factor: Season						
Groups	t	P(perm)	Unique perms			
W, SP	2.1918	**0.0012**	9941			
W, SU	2.072	**0.0021**	9956			
W, AU	1.3741	0.1171	9956			
SP, SU	1.3241	0.1064	9938			
SP, AU	2.7542	**0.0001**	9932			
SU, AU	2.0496	**0.0009**	9940			
Average Similarity between/within groups	W	SP	SU	AU		
W	39.167					
SP	34.294	45.599				
SU	33.447	41.949	41.687			
AU	42.632	34.194	38.736	49.687		

Appendix 3. Results of one-way PERMANOVA (factor: Season) analysis of community structure in *Fucus virsoides* stands based on morphofunctional groups, PERMDISP test for homogeneity and Pairwise tests for Hotel Parentium study site. Statistically significant results ($P < 0.05$) are marked in **bold**

PERMANOVA table of results - Hotel Parentium						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Season	1	6340.9	6340.9	3.7792	**0.0076**	9932
Res	27	45302	1677.9			
Total	28	51643				
PERMDISP results - Hotel Parentium - Deviations from centroid						
F	31.105					
Df1	1					
Df2	27					
P(perm)	**0.0001**					
PAIR-WISE TESTS - Factor: Season						
Groups	t	P(perm)	Unique perms			
SP, SU	1.944	**0.0083**	9941			
Average Similarity between/within groups	SP	SU				
SP	32.272					
SU	47.363	73.276				

Appendix 4. Results of one-way PERMANOVA (factor: Season) analysis of community structure in *Fucus virsoides* stands based on morphofunctional groups, PERMDISP test for homogeneity and Pairwise tests for Bijela uvala study site. Statistically significant results ($P < 0.05$) are marked in **bold**

PERMANOVA table of results - Bijela uvala						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Season	2	4330.4	2165.2	1.2799	0.2538	9934
Res	31	52442	1691.7			
Total	33	56772				
PERMDISP results - Bijela uvala - Deviations from centroid						
F	1.8523					
Df1	2					
Df2	31					
P(perm)	0.2338					
PAIR-WISE TESTS - Factor: Season						
Groups	t	P(perm)	Unique perms			
W, SP	0.99061	0.4151	9914			
W, SU	0.96897	0.4316	9437			
SP, SU	1.3981	0.0995	9920			
Average Similarity between/within groups	W	SP	SU			
W	38.072					
SP	42.581	45.833				
SU	44.543	45.529	50.551			

Appendix 5. Results of one-way PERMANOVA (factor: Season) analysis of community structure in *Fucus virsoides* stands based on morphofunctional groups, PERMDISP test for homogeneity and Pairwise tests for Blaz study site. Statistically significant results ($P < 0.05$) are marked in **bold**

PERMANOVA table of results - Blaz						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Season	3	58261	19420	8.468	**0.0001**	9923
Res	56	128430	2293.4			
Total	59	186690				
PERMDISP results - Blaz - Deviations from centroid						
F	292					
Df1	3					
Df2	56					
P(perm)	0.3651					
PAIR-WISE TESTS - Factor: Season						
Groups	t	P(perm)	Unique perms			
W, SP	2.4746	**0.0016**	9945			
W, SU	2.292	**0.0006**	9945			
W, AU	2.8037	**0.0002**	9944			
SP, SU	3.004	**0.0001**	9955			
SP, AU	4.5517	**0.0001**	9930			
SU, AU	1.9345	**0.009**	9937			
Average Similarity between/within groups	W	SP	SU	AU		
W	33.988					
SP	25.486	41.724				
SU	21.347	17.565	31.202			
AU	22.847	4.0109	30.628	44.417		

Appendix 6. Results of one-way PERMANOVA (factor: Month) analysis of morphological features and population metrics, PERMDISP test for homogeneity and Pairwise tests Lanterna study site. Statistically significant results ($P < 0.05$) are marked in **bold**.

PERMANOVA table of results - Lanterna						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Month	11	7360.8	669.16	3.4712	**0.0001**	9914
Res	48	9253.3	192.78			
Total	59	16614				

PERMDISP results - Lanterna - Deviations from centroid	
F	1.772
Df1	11
Df2	48
P(perm)	0.2868

PAIR-WISE TESTS – Factor: Month			
Groups	t	P(perm)	Unique perms
Jan, Feb	0.74706	0.4458	126
Jan, Mar	0.67817	0.568	126
Jan, Apr	1.616	0.1321	126
Jan, May	1.6743	0.137	126
Jan, Jun	1.7919	0.0969	126
Jan, Jul	1.7168	0.1097	126
Jan, Aug	1.5042	0.1827	126
Jan, Sep	0.91649	0.3752	126
Jan, Oct	1.1146	0.3208	126
Jan, Nov	1.456	0.1471	126
Jan, Dec	1.0131	0.3554	126
Feb, Mar	0.34143	0.8155	126

Feb, Apr	1.0388	0.3491	126
Feb, May	1.1207	0.3356	126
Feb, Jun	1.3983	0.158	126
Feb, Jul	1.2296	0.2151	126
Feb, Aug	1.1429	0.2801	126
Feb, Sep	1.1072	0.3337	126
Feb, Oct	1.7687	0.063	125
Feb, Nov	2.5596	**0.0254**	126
Feb, Dec	1.483	0.1428	126
Mar, Apr	1.2881	0.1515	126
Mar, May	1.4177	0.1563	126
Mar, Jun	1.617	0.1046	126
Mar, Jul	1.5489	0.1043	126
Mar, Aug	1.2231	0.2321	126
Mar, Sep	0.86719	0.4958	126
Mar, Oct	1.7196	0.0788	126
Mar, Nov	2.6933	**0.0267**	126
Mar, Dec	1.3625	0.1574	126
Apr, May	0.71028	0.7237	126
Apr, Jun	1.0628	0.339	126
Apr, Jul	0.89779	0.452	126
Apr, Aug	1.3078	0.2015	126
Apr, Sep	2.0571	**0.016**	126
Apr, Oct	3.2551	**0.0147**	126
Apr, Nov	4.7545	**0.0076**	126

Apr, Dec	2.7062	**0.0307**	126
May, Jun	1.0404	0.3513	126
May, Jul	0.88391	0.5395	126
May, Aug	1.7602	0.0656	126
May, Sep	2.2925	**0.0158**	126
May, Oct	3.2435	**0.0148**	126
May, Nov	4.5621	**0.0082**	126
May, Dec	2.7719	**0.024**	126
Jun, Jul	0.45777	0.8141	126
Jun, Aug	1.4328	0.1413	126
Jun, Sep	2.1549	**0.0401**	126
Jun, Oct	3.0015	**0.0161**	126
Jun, Nov	4.2462	**0.0073**	126
Jun, Dec	2.5736	**0.0229**	126
Jul, Aug	1.2568	0.1967	126
Jul, Sep	2.1921	**0.0231**	126
Jul, Oct	3.1291	**0.0065**	126
Jul, Nov	4.3404	**0.0087**	126
Jul, Dec	2.5818	**0.0292**	126
Aug, Sep	1.3805	0.1608	126
Aug, Oct	2.1434	**0.0206**	126
Aug, Nov	3.241	**0.0062**	126
Aug, Dec	1.6034	0.1622	126
Sep, Oct	0.73521	0.6653	126
Sep, Nov	1.9469	**0.0464**	126

Sep, Dec	0.81916	0.5704	126
Oct, Nov	1.4672	0.1227	126
Oct, Dec	0.96552	0.4377	126
Nov, Dec	1.4625	0.0837	126

Average Similarity between/within groups	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	71.797											
Feb	77.069	79.477										
Mar	77.034	82.351	80.51									
Apr	76.347	84.836	84.523	89.297								
May	73.706	82.225	82.132	87.921	85.857							
Jun	73.762	80.662	80.354	86.233	85.092	84.74						
Jul	74.299	81.752	80.746	86.861	85.579	86.59	84.549					
Aug	77.474	82.644	82.414	86.501	82.71	84.187	84.837	87.123				
Sep	77.086	79.628	81.591	81.454	77.48	78.486	78.374	83.434	82.312			
Oct	74.918	75.432	78.079	75.948	72.814	73.967	73.233	79.871	84.03	84.747		
Nov	72.137	69.887	72.381	67.457	64.435	65.939	65.686	74.109	79.121	83.038	84.956	
Dec	75.056	76.13	78.713	76.208	73.767	74.821	74.743	81.034	82.502	83.781	82.178	81.974

Appendix 7. Results of one-way PERMANOVA (factor: Month) analysis of morphological features and population metrics, PERMDISP test for homogeneity and Pairwise tests Bijela uvala study site. Statistically significant results ($P < 0.05$) are marked in **bold**.

PERMANOVA table of results - Bijela uvala

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Month	5	15739	3147.7	17.81	**0.0001**	9947
Res	23	4065	176.74			
Total	28	19804				

PERMDISP results - Bijela uvala - Deviations from centroid

F	2.2073
Df1	5
Df2	23
P(perm)	0.251

PAIR-WISE TESTS - Factor: Month

Groups	t	P(perm)	Unique perms
Jan, Feb	1.2317	0.197	126
Jan, Mar	1.5844	0.0951	126
Jan, Apr	1.7925	**0.0138**	126
Jan, May	4.0878	**0.0085**	126
Jan, Jun	4.3197	**0.0079**	126
Feb, Mar	2.4642	**0.0086**	126
Feb, Apr	1.9156	**0.0324**	126
Feb, May	8.686	**0.0067**	126
Feb, Jun	7.8572	**0.0082**	126
Mar, Apr	1.7964	**0.0399**	126

Mar, May	4.9751	**0.0074**	126
Mar, Jun	5.0501	**0.0068**	126
Apr, May	7.9074	**0.0081**	126
Apr, Jun	6.901	**0.0083**	126
May, Jun	2.0757	**0.0234**	126

Average Similarity between/within groups	Jan	Feb	Mar	Apr	May	Jun
Jan	71.714					
Feb	76.129	85.542				
Mar	73.549	78.419	84.245			
Apr	73.617	83.753	83.67	88.698		
May	53.944	47.841	66.133	58.916	89.784	
Jun	41.869	33.495	53.079	46.254	79.798	80.609

Appendix 8. Results of one-way PERMANOVA (factor: Month) analysis of morphological features and population metrics, PERMDISP test for homogeneity and Pairwise tests for Hotel Parentium study site. Statistically significant results (P < 0.05) are marked in **bold**.

PERMANOVA table of results - Hotel Parentium						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Month	5	12284	2456.9	13.292	**0.0001**	9940
Res	23	4251.4	184.85			
Total	28	16536				

PERMDISP results - Hotel Parentium - Deviations from centroid	
F	5.231
Df1	5
Df2	23

P(perm)		**0.0089**	*Homogeneity assumption not met			
PAIR-WISE TESTS - Factor: Month						
Groups	t	P(perm)	Unique perms			
Mar, Apr	2.2949	**0.0167**	126			
Mar, May	2.8214	**0.0086**	126			
Mar, Jun	3.8685	**0.007**	126			
Mar, Jul	7.3506	**0.0099**	126			
Mar, Aug	6.6875	**0.008**	126			
Apr, May	2.3654	**0.0328**	126			
Apr, Jun	3.1349	**0.0074**	126			
Apr, Jul	8.0684	**0.0092**	126			
Apr, Aug	6.0068	**0.0094**	126			
May, Jun	1.0331	0.4068	126			
May, Jul	3.0685	**0.0073**	126			
May, Aug	2.8914	**0.0151**	126			
Jun, Jul	2.7011	**0.0082**	126			
Jun, Aug	2.6216	**0.0232**	126			
Jul, Aug	5.207	**0.0085**	126			
Average Similarity between/within groups	Mar	Apr	May	Jun	Jul	Aug
Mar	83.492					
Apr	79.362	86.128				
May	66.818	73.474	75.201			
Jun	55.089	63.85	74.687	73.811		
Jul	50.51	53.458	69.527	69.485	89.775	
Aug	54.904	66.449	68.867	71.185	76.592	94.82

Appendix 9. Results of one-way PERMANOVA (factor: Month) analysis of morphological features and population metrics, PERMDISP test for homogeneity and Pairwise tests Blaz study site. Statistically significant results (P < 0.05) are marked in **bold**.

PERMANOVA table of results - Blaz						
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
Month	11	20635	1875.9	7.2377	**0.0001**	9918
Res	48	12441	259.18			
Total	59	33075				

PERMDISP results - Blaz - Deviations from centroid	
F	1.9362
Df1	11
Df2	48
P(perm)	0.3228

PAIR-WISE TESTS - Factor: Month			
Groups	t	P(perm)	Unique perms
Jan, Feb	0.51809	0.6415	126
Jan, Mar	1.5366	0.1317	126
Jan, Apr	2.2337	**0.0227**	126
Jan, May	1.5143	0.1512	126
Jan, Jun	1.215	0.2708	126
Jan, Jul	0.82088	0.4505	126
Jan, Aug	1.9888	**0.0387**	126
Jan, Sep	2.1623	**0.016**	126
Jan, Oct	3.9197	**0.0071**	126
Jan, Nov	4.324	**0.0088**	125

Jan, Dec	3.082	**0.0087**	126
Feb, Mar	1.1047	0.2555	126
Feb, Apr	1.598	0.1009	126
Feb, May	1.3222	0.2032	126
Feb, Jun	0.99379	0.3396	126
Feb, Jul	0.83736	0.4241	126
Feb, Aug	1.5617	0.1409	126
Feb, Sep	1.8001	0.0727	126
Feb, Oct	3.3862	**0.0067**	126
Feb, Nov	3.34	**0.0092**	126
Feb, Dec	2.7106	**0.0067**	126
Mar, Apr	0.85744	0.5214	126
Mar, May	0.74598	0.5349	126
Mar, Jun	0.84066	0.4421	126
Mar, Jul	1.5965	0.1124	126
Mar, Aug	3.0727	**0.0086**	126
Mar, Sep	2.436	**0.0164**	126
Mar, Oct	4.6091	**0.0091**	126
Mar, Nov	4.3959	**0.008**	126
Mar, Dec	3.3761	**0.0083**	126
Apr, May	1.4331	0.1687	126
Apr, Jun	1.4337	0.1087	126
Apr, Jul	2.5573	**0.0163**	126
Apr, Aug	5.1595	**0.0074**	126
Apr, Sep	3.1748	**0.0072**	126

Apr, Oct	5.6556	**0.0068**	125
Apr, Nov	6.2857	**0.0068**	126
Apr, Dec	4.0236	**0.0074**	126
May, Jun	0.79692	0.4813	126
May, Jul	1.2756	0.221	126
May, Aug	2.3616	**0.0112**	126
May, Sep	1.9162	**0.0142**	126
May, Oct	3.9265	**0.0095**	126
May, Nov	3.4163	**0.0094**	126
May, Dec	3.2273	**0.008**	126
Jun, Jul	0.99272	0.3688	126
Jun, Aug	1.8624	**0.0253**	126
Jun, Sep	1.6301	0.0874	126
Jun, Oct	3.7054	**0.008**	126
Jun, Nov	3.3993	**0.0076**	126
Jun, Dec	2.7377	**0.0152**	126
Jul, Aug	1.5101	0.0788	126
Jul, Sep	1.7056	0.0577	126
Jul, Oct	3.5888	**0.0072**	126
Jul, Nov	3.6658	**0.0076**	126
Jul, Dec	2.8009	**0.0083**	126
Aug, Sep	1.5202	0.0623	126
Aug, Oct	4.1564	**0.0078**	126
Aug, Nov	5.0208	**0.0084**	126
Aug, Dec	3.0027	**0.0076**	126

Sep, Oct	1.9709	**0.0147**	126
Sep, Nov	1.7004	**0.0392**	126
Sep, Dec	1.5245	0.0891	126
Oct, Nov	1.6659	0.0663	126
Oct, Dec	1.7564	**0.0317**	126
Nov, Dec	2.4562	**0.0066**	126

Average Similarity between/within groups	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	83.982											
Feb	81.446	76.264										
Mar	79.605	78.108	82.629									
Apr	80.35	77.863	86.516	88.292								
May	79.46	76.121	81.848	81.796	80.698							
Jun	80.576	77.015	81.201	81.898	80.541	79.028						
Jul	84.98	80.01	79.114	78.792	80.546	81.025	83.555					
Aug	83.914	78.267	74.038	73.913	78.27	78.905	85.15	91.78				
Sep	70.663	68.567	65.352	63.014	70.063	70.673	73.954	78.235	72.25			
Oct	54.818	53.103	46.133	43.406	52.48	52.528	58.314	58.483	65.585	76.02		
Nov	64.382	62.837	60.051	56.787	66.942	64.436	69.071	68.849	73.082	77.527	84.221	
Dec	56.963	56.325	51.896	48.939	53.547	57.57	60.119	61.563	66.941	65.169	64.72	67.85

Appendix 10. Results of LMM and GLMM analysis of response variables (change in wet weight, change in length and maximum photochemical yield) for both phases of the experiment. Wald χ2 test was used for analyses of deviance for each fitted model used to test the impact of different treatments on morphological and physiological characteristics of *Fucus virsoides*, across the two phases of the experiment. Tukey's post-hoc test was used for the pairwise comparisons between different levels of the fixed factor. "LMM" stands for "Linear mixed model, "GLMM stands" for "Generalised linear mixed mode". "AE stands for "Air exposure phase", and CI stands for "Constant immersion phase". "Ww_c" stands for "wet weight percentage change", "L_c" stands for "length percentage change" and "Fv/Fm" stands for "maximum photochemical yield". Statistically significant differences ($p < 0.05$) are marked in **bold** letters (from Gljušćić et al. 2025).

Test	Phase	Resp.	χ2	Df	p	PW	Est.	STE	z	Pr(>|z|)
LMM	AE	Ww_c	158.94	4	<2.2 x 10^{-16}	T20 - C14	0.159	0.022	7.139	**<0.001**
						T25 - C14	0.033	0.022	1.492	0.568
						T29 - C14	-0.063	0.022	-2.822	**0.038**
						T33 - C14	-0.096	0.022	-4.331	**<0.001**
						T25 - T20	-0.125	0.022	-5.647	**<0.001**
						T29 - T20	-0.221	0.022	-9.961	**<0.001**
						T33 - T20	-0.255	0.022	-11.469	**<0.001**
						T29 - T25	-0.096	0.022	-4.314	**<0.001**
						T33 - T25	-0.129	0.022	-5.823	**<0.001**
						T33 - T29	-0.034	0.022	-1.508	0.557
LMM	AE	L_c	177.55	4	<2.2 x 10^{-16}	T20 - C14	0.030	0.006	4.870	**<0.001**
						T25 - C14	-0.008	0.006	-1.304	0.689
						T29 - C14	-0.003	0.006	-0.408	0.994
						T33 - C14	-0.051	0.006	-8.271	**<0.001**
						T25 - T20	-0.038	0.006	-6.174	**<0.001**
						T29 - T20	-0.032	0.006	-5.279	**<0.001**
						T33 - T20	-0.081	0.006	-13.142	**<0.001**
						T29 - T25	0.006	0.006	0.896	0.899
						T33 - T25	-0.043	0.006	-6.968	**<0.001**
						T33 - T29	-0.048	0.006	-7.863	**<0.001**
GLMM	AE	Fv/Fm	326.8	4	<2.2 x 10^{-16}	T20 - C14	-0.004	0.029	-0.129	1
						T25 - C14	0.038	0.029	1.304	0.689
						T29 - C14	0.037	0.029	1.249	0.722
						T33 - C14	-0.401	0.029	-13.638	**<0.001**
						T25 - T20	0.042	0.029	1.433	0.606
						T29 - T20	0.040	0.029	1.379	0.641
						T33 - T20	-0.397	0.029	-13.509	**<0.001**
						T29 - T25	-0.002	0.029	-0.054	1
						T33 - T25	-0.439	0.029	-14.941	**<0.001**
						T33 - T29	-0.437	0.029	-14.887	**<0.001**
LMM	CI	Ww_c	289.76	4	<2.2 x 10^{-16}	T20 - C14	0.113	0.030	3.739	**0.002**
						T25 - C14	0.043	0.030	1.432	0.607
						T29 - C14	-0.091	0.030	-3.028	**0.021**
						T33 - C14	-0.354	0.030	-11.754	**< 0.001**
						T25 - T20	-0.069	0.030	-2.307	0.143
						T29 - T20	-0.204	0.030	-6.767	**< 0.001**

						T33 - T20	-0.466	0.030	-15.493	**< 0.001**
						T29 - T25	-0.134	0.030	-4.460	**< 0.001**
						T33 - T25	-0.397	0.030	-13.186	**< 0.001**
						T33 - T29	-0.263	0.030	-8.726	**< 0.001**
LMM	CI	L_c	325.97	4	$<2.2 \times 10^{-16}$	T20 - C14	0.026	0.009	2.793	**0.002**
						T25 - C14	-0.005	0.009	-0.538	0.607
						T29 - C14	0.004	0.009	0.428	**0.021**
						T33 - C14	-0.124	0.009	-13.317	**< 0.001**
						T25 - T20	-0.031	0.009	-3.331	0.143
						T29 - T20	-0.022	0.009	-2.365	**< 0.001**
						T33 - T20	-0.150	0.009	-16.109	**< 0.001**
						T29 - T25	0.009	0.009	0.966	**< 0.001**
						T33 - T25	-0.119	0.009	-12.779	**< 0.001**
						T33 - T29	-0.128	0.009	-13.744	**< 0.001**
GLMM	CI	Fv/Fm	96.472	4	$<2.2 \times 10^{-16}$	T20 - C14	0.031	0.059	0.533	0.984
						T25 - C14	0.038	0.059	0.638	0.969
						T29 - C14	0.025	0.059	0.428	0.993
						T33 - C14	-0.435	0.059	-7.353	**<0.001**
						T25 - T20	0.006	0.059	0.106	1
						T29 - T20	-0.006	0.059	-0.105	1
						T33 - T20	-0.466	0.059	-7.885	**<0.001**
						T29 - T25	-0.012	0.059	-0.211	1
						T33 - T25	-0.473	0.059	-7.991	**<0.001**
						T33 - T29	-0.460	0.059	-7.780	**<0.001**

10. CURRICULUM VITAE

Edi Gljušćić was born on 8th of October, 1994, in Pula, Croatia. He attended and finished high school in Pazin and, in the year 2012, began his Bachelor's degree studies in Marine sciences at the Juraj Dobrila University of Pula. Afterwards, he continued on his Master's degree studies in Nature conservation at the Faculty of Mathematics, Natural Sciences and Information Technologies in Koper, Slovenia. In 2019, he obtained the Master's degree in Nature conservation.

During his student days, Edi was active in the BIODIVA student organisation, focusing on biology and nature conservation. He was also involved in minor research and monitoring activities, fieldwork assistance and biodiversity data collection (Entomology, Ornithology, Herpetology), which to some degree continues to this day.

From 2019 to late 2020, Edi was employed as an Educator in Kamenjak public institution, where his previously gained knowledge and experience was applied.

Since January 2021, Edi has been employed as an assistant (PhD student) in the Laboratory for Benthic Ecology, within the Center for Marine Research of the Ruđer Bošković Institute in Rovinj. Since then he authored and coauthored 10 scientific papers as well as 15 conference presentations and posters.

10.1. List of scientific publications (first author, corresponding author or coauthor)

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