NOTE

Temporal stability in macroalgal assemblage standing stock despite high species turnover

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ABSTRACT: Species populations are variable in time and space as a response to biotic and/or environmental conditions. However, ecological stability is regarded as an important asset of diversity in natural communities. Here, we followed seasonal variation in a mid-shore rocky intertidal algal-dominated assemblage at 2 sites in the Azores for 1 yr. The assemblage went through significant taxa turnover as a response to the seasonal loss of its dominant species. Yet, assemblage aggregate biomass (assemblage standing stock) remained remarkably stable through the study period. A diverse mixture of algae comprising 77 taxa, including species with contrasting life histories, was found, although only a handful of species appeared to be responsible for ensuring assemblage stability. This study highlights the role of taxa diversity and their compensatory dynamics in maintaining temporal stability in these assemblages. Future direct tests should be done through manipulative experiments to understand the mechanisms underlying community stability in this system.

KEY WORDS: Rocky intertidal · Macroalgae · *Osmundea pinnatifida* · Biomass · Temporal variability

INTRODUCTION

Populations can be highly variable through time in natural ecosystems as a response to interspecific competition and fluctuation in environmental conditions. Ecological stability is an important feature of natural ecosystems and there is an increasing body of literature investigating the factors that underpin stability of biological communities (e.g. Cottingham et al. 2001, Ives & Carpenter 2007, Bulleri et al. 2012), including a debate about the concept itself and its multiple components such as variability, resistance, resilience, persistence and robustness (e.g. O'Gorman & Emmerson 2009, Donohue et al. 2013).

Assemblages of organisms, in general, and macroalgae in particular, show a diversity of life cycles that evolved in line with environmental heterogeneity. These include differences in growth strategies, timing of colonisation, reproductive mode, dispersal ability, or grazing defence mechanisms (Hurd et al. 2014). This array of traits allows species to exploit environmental heterogeneity, which is a fundamental underlying assumption of the concept of the 'insurance' hypothesis (Yachi & Loreau 1999). This concept predicts that diverse communities are more stable because (1) the differential responses of species may buffer the effects of environmental fluctuations, contributing to maintain community properties relatively stable in spite of species variability and (2) the sum of several randomly or independently varying populations is less variable than the average population, known as the portfolio-effect (Doak et al. 1998, Tilman et al. 1998, Tilman 1999).

There is a plethora of studies investigating seasonal and temporal patterns of macroalgal distribution and replacements (e.g. Hawkins 1981, Underwood & Chapman 1998). For instance, Underwood & Jernakoff (1984) experimentally show that distribution and abundance of macroalgae in the rocky intertidal of New South Wales (Australia) are determined by complex interactions between abiotic (tidal height, wave exposure, season and wetness) and biotic (grazing by gastropods) processes. Fewer studies, however, have tracked aggregate community or ecosystem properties over time and how seasonal species replacements or variation in a single population influence these properties (but see Mrowicki et al. 2016). Macroalgae are important primary producers and some species are ecologically and functionally structuring species (Mann 1973, Graham 2004), offering habitat, food and refuge to a diverse assemblage of animals (e.g. Hurd et al. 2014) and delivering important ecosystem services (Smale et al. 2013).

Macroalgal standing stock is widely used as a crude measure of macroalgal primary production (Bruno et al. 2005, 2006), and species functional contribution (e.g. gross community productivity, nutrient uptake) was found to be proportional to their contribution to community biomass across 2 contrasting ecosystems (salt marsh plants and macroalgal turfs) (Davies et al. 2011). In this study we tracked the seasonal change in species mass and replacements over 1 yr in a mid-shore macroalgal assemblage and examined its influence on the aggregate assemblage biomass. We hypothesised that although assemblage structure (species abundances and identities) would be temporally variable according to environmental heterogeneity (e.g. Underwood & Jernakoff 1984, Underwood & Chapman 1998), compensatory dynamics in the diverse algal assemblages would lead to temporal stability in assemblage aggregate biomass. That is, we predicted that if compensatory dynamics are occurring in this system, subordinate species, or some of these, will increase in mass to the extent that they offset the loss in mass of the dominant species. This in turn, will dampen the aggregate assemblage mass from significant variations in time.

MATERIALS AND METHODS

Study sites and community

The study was performed at the mid-intertidal zone at 2 rocky sites on the south coast of São Miguel,

Azores: Pranchinha (Site 1; 37° 44′ 30″ N, 25° 38′ 57″ W) and Lagoa (Site 2; 37° 44′ 32″ N, 25° 35′ 16″ W). Both sites are similarly exposed to wave-action, made of gently sloping volcanic bedrock and support similar assemblages of the fauna and flora typical of Azorean shores (Martins et al. 2008). The dominant algal species on both sites is *Osmundea pinnatifida* (Hudson) Stackhouse, 1809. *O. pinnatifida* can form extensive turfs on bedrock on exposed to moderately exposed shores along European coasts (Maggs & Hommersand 1993). In the Azores, in general, and in our study sites in particular, *O. pinnatifida* also forms extensive turfs that dominate in terms of biomass during most of the colder months (authors′ pers. obs.). Although perennial, this species has a marked seasonal variation in size with larger plants and higher biomass values recorded from late summer to early spring (Neto 1997). This also occurs in the British Isles, where fronds are severely bleached and damaged in early summer, when low spring tides and high air temperature occur simultaneously (Prathep et al. 2003). After this bleaching event, fronds are virtually absent until late summer, when they regrow. This study uses the temporal variability in *O. pinnatifida* biomass and associated flora as a model system to investigate how seasonal changes in species abundances influence assemblage standing stock.

Experimental design

Prior to the start of the experiment, a total of 30 patches measuring 10 × 10 cm were marked at mid shore level on each site using screws inserted in holes drilled in 2 opposing corners of the quadrats. Patches were established haphazardly along the shore with the proviso that they were > 90 % covered by *O. pinnatifida*. This criterion was intended to reduce variability among all quadrats, thus ensuring that variation in the cover of *O. pinnatifida* at the outset of the experiment did not influence response variables in quadrats sampled at different times of the year (see below). At the start of the experiment in March 2013 (T0) and on 5 subsequent occasions (T1 to T5) roughly every 2 mo thereafter until March 2014, 5 patches were randomly selected on each site. These were completely scraped clean of all macroscopic biota. The material was stored in labelled zipped bags and brought to the laboratory where samples were frozen until inspection.

In the lab, samples were defrosted, sorted, all the algae identified to the lowest taxonomic level possi-

ble, dried at 60°C until achieving a constant biomass (after 48 h) and weighed separately.

The level of replication of the study was based on previous knowledge of the system (showing that variation in species abundances at the scale of sites ranges between 0 and 18% at this shore height, whilst variation at the scale of quadrats accounts for >45% of total variation; Martins et al. 2008) and the need to balance sampling costs (e.g. time to sample processing) and statistical power to detect changes.

Data analysis

A 2-way fully crossed model analysis of variance (ANOVA) with Time (random, 6 levels) and Site (random, 2 levels) was used to investigate spatial and temporal patterns of variability in the abundance of *O. pinnatifida* (both absolute and relative abundances) and assemblage standing stock (the sum of the mass of all species). Prior to analysis, data were checked for heterogeneity of variances using Cochran's test and transformations were applied where necessary (Underwood 1997).

To investigate temporal and spatial changes in the structure of macroalgal assemblages we ran the same design using the multivariate analogue PERMANOVA (Anderson 2001). These were run on 2 different similarity matrices: Bray-Curtis on untransformed data and Jaccard. When calculated on untransformed data, Bray-Curtis gives more weight to changes in species abundances, whereas Jaccard does not take into account the species relative abundances and is based on changes in species composition. The combined use of these 2 measures of similarity allows the assessment of the importance of changes in species abundances relative to changes in composition. Non-metric multidimensional scaling (NMDS) was used to visualize multivariate results. Similarity of percentages (SIMPER) was used to identify the taxa contributing to similarities among samples for each time using a cut-off level of 90%.

Mean squares were used to calculate the components of variation associated with each term in the analyses above (ANOVA and PERMANOVA). Negative estimates of variation were set to zero, the corresponding factor was removed from the model and the estimates were re-calculated for the remaining factors following the procedure described by Fletcher & Underwood (2002). Estimates of variation were calculated on the untransformed data and reported as percentages for comparability.

RESULTS

A total of 77 taxa, comprising 46 Rhodophyta, 20 Chlorophyta, 6 Heterokontophyta (Phaeophyceae) and 5 Cyanophyta were identified (see Appendix 1).

At the start of the experiment, and in accordance with our visual selection of experimental patches, *Osmundea pinnatifida* was the single most abundant species in the assemblage with an average of 2.95 ± 0.17 g per patch (100 cm^2) of algal dry biomass, corresponding to 76% of the community standing stock. The abundance (both absolute and relative) of *O. pinnatifida* varied throughout the year as predicted by its annual life cycle, with the species dying-off (mostly via bleaching) during late summer and recovering from autumn onwards (Fig. 1). Its lowest mass was recorded in September (0.28 ± 0.03 g per patch of alga dry biomass) when it corresponded only
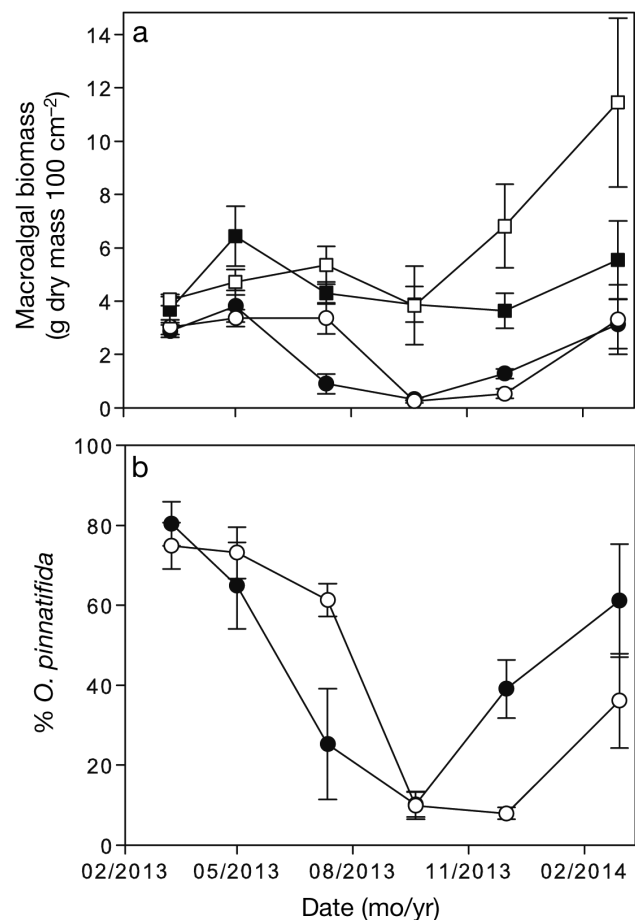

Fig. 1. (a) Absolute biomass of (circles) *Osmundea pinnatifida* and (squares) the entire macroalgal assemblage in the mid-intertidal zone at 2 rocky sites in the Azores over a 1 yr period. (b) The corresponding relative biomass of *O. pinnatifida*. Values are mean ± SE, n = 5. Filled symbols: Site 1; open symbols: Site 2

to 7% of the assemblage standing stock. This pattern was generally similar in the 2 sites (Fig. 1), although there was a significant Time × Site interaction (Table 1). Inspection of Student-Newman-Keuls *a posteriori* tests (not shown) and Fig. 1 showed that this result arose because the seasonal loss and subsequent recover of *O. pinnatifida* occurred slightly earlier in the year at Site 1 than at Site 2. The reason why this happened is elusive but probably reflected the interplay between large-scale (e.g. sea surface temperature) and local-scale (e.g. substratum topography) processes. Analysis of the components of variation (Table 1) showed that the largest sources of variation were indeed associated with Time but also with smaller-scale spatial variation among replicate quadrats.

Despite significant temporal variation in the mass of its initial dominant element, *O. pinnatifida*, the standing stock of the entire assemblage (*O. pinnatifida* included) remained remarkably stable over the entire period of the study, showing no significant temporal or spatial variation (Fig. 1, Table 1). Unlike the pattern observed for *O. pinnatifida*, the largest source of variation in assemblage standing stock was among replicate quadrats (Table 1). Time had a minor influence supporting the result that assemblage standing stock remained relatively stable throughout the year.

Multivariate analysis showed that the response of the assemblage after excluding *O. pinnatifida* significantly varied among some times at some sites (Time × Site interaction) both in

abundance (Bray-Curtis) and composition (Jaccard) (Fig. 2, Table 2). Inspection of the NMDS (Fig. 2) showed that the assemblages tended to diverge between T2 and T3 (July and September) when *O. pinnatida* was at lowest abundance and converging towards initial conditions (T0) thereafter. Inspection of the components of variation showed that, in both cases (Jaccard and Bray-Curtis) the largest source of variation was amongst replicates (Table 2), suggest-
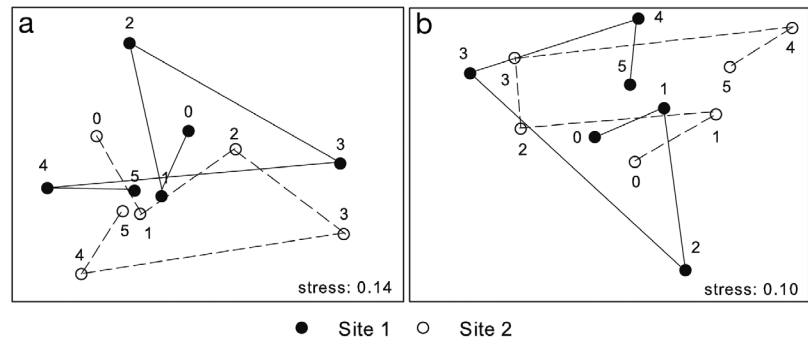

Fig. 2. Non-metric multidimensional scaling (NMDS) showing variation in assemblage structure of macroalgae on rocky sites in the Azores over a 1 yr period, based on (a) abundances (Bray-Curtis) and (b) composition (Jaccard). Lines indicate the successional paths of the assemblages, at times T0 (initial conditions in March 2013), T1 (May 2013), T2 (July 2013), T3 (September 2013), T4 (December 2013) and T5 (March 2014). Filled symbols: Site 1; open symbols: Site 2

Table 2. Results of PERMANOVA of temporal variation in assemblage structure of macroalgae at 2 sites based on composition (Jaccard) and abundances (Bray-Curtis) and the corresponding components of variation. *p < 0.05, **p < 0.01, ***p < 0.001

Source	df	Jaccard MS	Jaccard F	Jaccard % var	Bray-Curtis MS	Bray-Curtis F	Bray-Curtis % var
Time	5	10126.0	2.52**	20	13198.0	2.06*	16
Site	1	7614.6	1.89	4	10173.0	1.59	3
Time × Site	5	4020.3	2.13***	14	6409.8	2.42***	18
Residual	48	1884.6		62	2650.8		63

Table 1. Analysis of temporal variation in biomass of macroalgae in the mid-intertidal zone at 2 rocky sites in the Azores over a 1-yr period, showing results of ANOVA for the absolute and relative abundance of *Osmundea pinnatifida* and for assemblage standing stock, and the corresponding components of variation. *p < 0.05,** p < 0.01, ***p < 0.001

Source	df	*O. pinnatifida* (absolute) MS	*O. pinnatifida* (absolute) F	*O. pinnatifida* (absolute) % var	*O. pinnatifida* (relative) MS	*O. pinnatifida* (relative) F	*O. pinnatifida* (relative) % var	Assemblage MS	Assemblage F	Assemblage % var
Time	5	0.0989	5.35*	43	6676.87	4.54	48	0.42	1.73	9
Site	1	0.0004	0.02	0	131.13	0.09	0	0.37	1.52	4
Time × Site	5	0.0185	6.37***	11	1470.23	4.18**	20	0.25	1.69	16
Residual	48	0.0029		44	351.84		32	1.14		71
Transformation		$x^{0.1}$			None			Ln($x + 1$)		
Cochran's test		$C = 0.24$			$C = 0.24$			$C = 0.27$		

ing that responses of the assemblage to the loss of *O. pinnatida* were driven by processes occurring at small spatial scales (e.g. competition).

Analysis of SIMPER showed that *O. pinnatifida* was the single most representative taxa of samples at the start of the experiment (Table 3). As time elapsed, its dominant role in the assemblage was gradually replaced by the appearance of several other turf-forming algal species of which *Ellisolandia elongata* was the most dominant one. At T3 (September 2013), when the biomass of *O. pinnatifida* attained its lowest mean abundance, a total of 5 other species (*E. elongata*, *Gelidium pusillum*, *Gymnogongrus griffithsiae*, *Endarachne binghamiae* and *Fucus spiralis*) were necessary to compensate for its loss. After T3, however, these species were gradually replaced by *O. pinnatifida* that tended to become the dominant species in the assemblage again.

DISCUSSION

Results showed that in the diverse assemblages of species, the aggregate assemblage standing stock remained stable despite significant temporal taxa turnover and loss of dominant species. Stability in assemblage standing stock was likely the result of asynchronous (or compensatory) responses of species to temporal changes in environmental conditions (Micheli et al. 1999, Cottingham et al. 2001). Interestingly, a mixture of species was needed to achieve stability and buffer assemblage standing stock against seasonal loss of its dominant species, thereby emphasising the relative importance of richness for community stability.

The assemblage of species that compensated for the loss of *Osmundea pinnatifida* during its die-off comprised species with variable life-histories such as slow-growing and persistent ones (*Ellisolandia elongata* and *Fucus spiralis*) as well as short-lived upright forms (e.g. *Endarachne binghamiae*), highlighting the role of diversity in species trait for community stability (Griffin & Silliman 2011). Many of the species that compensated the loss of *O. pinnatifida* were turf-forming algae (as is also *O. pinnatifida*), which have the ability to quickly secure space via rapid lateral vegetative growth (see Airoldi 1998 for review), hence explaining the fast response of the assemblage observed. Moreover, some of these species (e.g. *E. elongata*, *F. spiralis*) are protected either chemically (e.g. phenols) or physically (e.g. calcareous structures) so that temporal variability in their abundance is unlikely to be related to the activity of grazers, as is commonly found for ephemerals (e.g. Lubchenco & Cubit 1980, O'Connor et al. 2013). Instead, both *E. elongata* and *F. spiralis* are generally dominant forms occurring mostly at lower and upper shore levels, respectively (Martins et al. 2008). At mid-shore levels, where the study was done, these 2 species are usually less abundant and may thus be excluded during most of the year by direct competition with *O. pinnatifida*, which is probably better adapted to local environmental conditions. This suggests that temporal variability in the strength of species interactions, mediated by fluctuations in the abundance of the superior competitor, may be an important factor underpinning community stability. This result is also supported by the work of Griffin et al. (2008) and Maggi et al. (2011), who found that changes in species abundance or densities mediated competitive interactions and thus affected the functioning of the ecosystem.

While our study was not designed to experimentally test the effects of richness on assemblage stability there are a few key points worth highlighting: (1) the studied assemblage was a rather diverse one with a total of 77 taxa, and (2) only a handful of species

Table 3. SIMPER results identifying the taxa that most contributed to similarity among pooled samples of macroalgae from 2 rocky sites in the mid-intertidal zone in the Azores (n = 10), for each sampling time (T0 to T5) over a 1-yr period, showing mean biomass (B) and the percent contribution to similarity among samples

Taxon	T0 March 2013		T1 May 2013		T2 July 2013		T3 September 2013		T4 December 2013		T5 March 2014	
	B	%	B	%	B	%	B	%	B	%	B	%
Osmundea pinnatifida	2.95	92	3.59	89	2.13	75	0.28	26	0.90	41	3.22	81
Ellisolandia elongata	–	–	0.99	7	0.48	6	1.30	44	2.82	38	2.97	13
Caulacanthus ustulatus	–	–	–	–	0.22	10	–	–	–	–	–	–
Gelidium pusillum	–	–	–	–	–	–	0.19	8	0.56	12	–	–
Gymnogongrus griffithsiae	–	–	–	–	–	–	0.24	5	–	–	–	–
Endarachne binghamiae	–	–	–	–	–	–	0.12	5	–	–	–	–
Fucus spiralis	–	–	–	–	–	–	0.12	5	–	–	–	–

was apparently responsible for the observed stability. While the role of all those rare taxa for assemblage stability remains unclear, our results suggests that some species identity may be more important than richness per se for assemblage stability, at least over short experimental durations (e.g. a year) at environmentally similar sites to that studied here. While the community stability debate has been primarily centred on the diversity-stability relationships (Griffin et al. 2009), there is now ample evidence that species identity is an important aspect in the context of diversity–ecosystem functioning links (e.g. O'Connor & Crowe 2005, Bruno et al. 2005, 2006) and that, in particular, functional groups are more important than richness in determining some ecosystem proprieties (resistance to invasion) in macroalgal assemblages (Arenas et al. 2006).

In summary, this study highlights the role of taxa diversity and their compensatory dynamics in maintaining seasonal stability in these assemblages. More direct tests of the factors underlying community stability via experimental manipulations should be done in the future. It is important to note that this was a short, limited and exploratory observational study. It would also be important to investigate whether the stability in the aggregate assemblage biomass here found would still be consistent in the longer term (e.g. the last sampling point in Fig. 1 suggests that assemblage biomass might have undergone a significant variation), whether this is a specific attribute of this model system or a general attribute of intertidal systems and other marine ecosystems, as well as explicitly test some of the ideas here developed via properly designed experimental manipulations.

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Appendix 1. Taxa (77 in total) identified during the present investigation

RHODOPHYTA
Asparagopsis armata Harvey 1855
Aglaothamnion sp. Feldmann-Mazoye 1941
Ahnfeltiopsis sp. P.C.Silva & DeCew 1992
Anotrichium sp. Nägeli 1862
Anotrichium tenue (C.Agardh) Nägeli 1862
Antithamnion sp. Nägeli 1847
Boergeseniella fruticulosa (Wulfen) Kylin 1956
Bonnemaisonia sp. C.Agardh, 1822
Bonnemaisonia hamifera Hariot 1891
Callithamnion sp. Lyngbye 1819
Caulacanthus ustulatus (Mertens ex Turner) Kützing 1843
Centroceras clavulatum (C.Agardh) Montagne 1846
Ceramium atrorubescens Kylin 1938
Ceramium circinatum (Kützing) J.Agardh 1851
Ceramium diaphanum (Lightfoot) Roth 1806
Ceramium flaccidum (Harvey ex Kützing) Ardissone 1871
Ceramium rubrum C.Agardh 1811
Ceramium tenerrimum (G.Martens) Okamura 1921
Chondracanthus acicularis (Roth) Fredericq 1993
Chondria dasyphylla (Woodward) C.Agardh 1817
Chondria sp. C.Agardh 1817
Calcareous crust
Ctenosiphonia hypnoides (Welwitsch ex J.Agardh) Falkenberg 1897
Dipterosiphonia rigens (Shousboe ex C.Agardh) Falkenberg 1901
Ellisolandia elongata (J.Ellis & Solander) K.R.Hind & G.W.Saunders 2013
Gastroclonium reflexum (Chauvin) Kützing 1849
Gelidium microdon Kützing 1849
Gelidium pusillum (Stackhouse) Le Jolis 1863
Gelidium spinosum (S.G.Gmelin) P.C.Silva 1996
Gymnogongrus griffithsiae (Turner) Martius 1833
*Gymnogongru*s *crenulatus* (Turner) J.Agardh 1851
*Hypoglossum hypoglossoide*s (Stackhouse) F.S.Collins & Hervey 1917
Jania sp. J.V.Lamouroux 1812
Laurencia sp. J.V.Lamouroux 1813
Lophosiphonia cristata Falkenberg 1901
Lophosiphonia reptabunda (Suhr) Kylin 1956
Osmundea pinnatifida (Hudson) Stackhouse 1809
Plocamium cartilagineum (Linnaeus) P.S.Dixon 1967
Polysiphonia sertularioides (Grateloup) J.Agardh 1863
Polysiphonia denudata (Dillwyn) Greville ex Harvey 1833
Polysiphonia sp. Greville 1823

Porphyra sp. C.Agardh 1824
Pterocladiella capillacea (S.G.Gmelin) Santelices & Hommersand 1997
Sphondylothamnion multifidum (Hudson) Nägeli 1862
Spyridia sp. Harvey in W.J.Hooker 1833
Symphyocladia marchantioides (Harvey) Falkenberg 1897

CHLOROPHYTA
Bryopsis cupressina J.V.Lamouroux 1809
Bryopsis hypnoides J.V.Lamouroux
Chaetomorpha linum (O.F.Müller) Kützing
Chaetomorpha mediterranea (Kützing) Kützing
Chaetomorpha pachynema (Montagne) Kützing 1847
Cladophora albida (Nees) Kutzing 1843
Chaetomorpha antennina (Bory de Saint-Vincent) Kützing
Cladophora coelothrix Kützing 1843
Cladophora conferta P.L.Crouan & H.M.Crouan in Schramm & Mazé 1865
Cladophora sp. Kützing, 1843
Cladophora membranacea (Hofman Bang ex C.Agardh) Kützing 1843
Cladophora prolifera (Roth) Kützing 1843
Cladophora sericea (Hudson) Kützing 1843
Cladophoropsis membranacea (Hofman Bang ex C.Agardh) Børgesen 1905
Codium sp. Stackhouse 1797
Ulva compressa Linnaeus 1753
Ulva multiramosa Taskin 2012
Ulva muscoides Clemente 1807
Ulva prolifera O.F.Müller 1778
Ulva rigida C.Agardh 1823

HETEROKONTOPHYTA (PHAEOPHYCEAE)
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier 1851
Dictyota sp. J.V.Lamouroux 1809
Fucus spiralis Linnaeus 1753
Halopteris filicina (Grateloup) Kützing 1843
Halopteris scoparia (Linnaeus) Sauvageau 1904
Sphacelaria sp. Lyngbye in Hornemann 1818

CYANOPHYTA
Calothrix crustacea Schousboe ex Thuret 1876
Lyngbya sp. C.Agardh ex Gomont 1892
Oscillatoria sp. Vaucher ex Gomont 1892
Oscillatoria submembranacea Ardissone & Strafforello ex Gomont 1892
Schizothrix sp. Kützing ex Gomont 1892