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A new proposal for zonation of the midlittoral in the Bay of Koper (Gulf of Trieste, northern Adriatic) based on macroalgal communities

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The zonation of midlittoral mainly based on macroalgal communities was studied at six sites of the Bay of Koper (Slovenian south-east part of the Gulf of Trieste) in spring (April) and autumn (November) 2010. The study, using the random selection method, involved different types of substrate (limestone, marl and sandstone). It was surveyed from the upper midlittoral to the infralittoral fringe (from the mean higher high water to the mean lower low water), the upper limit of the occurrence of the brown macroalgae Cystoseira compressa*. The zonation of the midlittoral zone was divided into three horizons (upper, middle and lower) by biotic (leader species) and abiotic (sea level) criteria. By using multivariate technique the main dissimilarity was found between the macroalgal communities of the upper and lower horizon. The species that most contributed to this difference was* Blidingia minima*. The main differences in species composition in different substrates were found between limestone and marl. The species* Chaetomorpha linum *mainly characterized such differences, while the species* Fucus virsoides *was the main contributor to dissimilarity among the middle horizons on limestone and sandstone.*

Key words: midlittoral zonation, macroalgae, substrates, Slovenian coast, Gulf of Trieste

INTRODUCTION

The general scheme of vertical zonation of organisms of marine hard substrate in the uppermost zones, as suggested by many authors (STEPHENSON & STEPHENSON, 1949, 1972; LEWIS, 1964, 1972; BALLESTEROS & ROMERO, 1988), in principle, corresponds to the scheme of the Mediterranean (PÉRÈS & PICARD, 1964; PÉRÈS, 1967; COPPEJANS, 1974; BELLAN-SANTINI *et al.*, 1994, 2002) and the Adriatic Sea (PÉRÈS & GAMULIN-BRIDA,1973; BAKRAN-PETRICIOLI, 2007, 2011). They comprehend supralittoral and midlittoral zones affected by waves, submitted to sea level variations caused by wind, atmospheric pressure and tides.

Slightly different is the division of the midlittoral into smaller parts (e.g. horizons). In the Mediterranean (including the middle and southern Adriatic Sea), the midlittoral was divided into the upper midlittoral that is moisturized by waves and splashing, and the lower midlittoral, which is under direct influence of waves and fluctuations in sea level (PÉRÈS & PICARD, 1964; PÉRÈS & GAMULIN-BRIDA, 1973; COPPEJANS, 1974; BELLAN-SANTINI *et al.*, 2002). This scheme was accepted also in Slovenia (LIPEJ *et al.*, 2000; LIPEJ *et al.*, 2004), although the vertical distribution of organisms, especially algae, of the midlittoral zone of the Gulf of Trieste received comparatively little attention.

Some authors (GIACCONE *et al*., 1993; CORMACI *et al*., 2003) divided the midlittoral zone into the upper horizon (above the mean water level) and the lower horizon (below the mean water level). In the northern Adriatic, especially in the Gulf of Trieste, the amplitude of the tide is higher than in the rest of the Mediterranean and Adriatic (PÉRÈS & GAMULIN-BRIDA, 1973; CORMACI *et al*., 2003; MALAČIČ *et al*., 2000). We can, therefore, expect that the vertical distribution of organisms in the midlittoral zone of the Slovenian coast, as part of the Gulf of Trieste, is different from the general scheme described for the Mediterranean, southern and central Adriatic coast, as suggested by BATTELLI (2002) and BATTELLI & DOLENC ORBANIĆ (2009).

The present paper represents a further contribution to the description of the zonation of the midlittoral macroalgal communities of the Gulf of Trieste, focused on three different types of hard substrate in the Bay of Koper. The study aims at evaluating the importance of the tide levels and the type of substrate in determining the vertical distribution of macroalgae. The main aims of our study were: a) to present a new and detailed characterization of the midlittoral zonation inside the generally accepted zonation pattern of the midlittoral zone for the Mediterranean; b) to establish if there is a relationship between position and extension of algal horizons on different types of substrate (limestone, marl, and sandstone) and tidal range and c) to determine which species most contribute to the differences in species composition in different horizons and types of substrates.

MATERIAL AND METHODS

Study area

The Slovenian trait of coast of the Gulf of Trieste extends for approximately 46 km in the southern part of the Gulf. It mostly faces north and is mainly influenced by wind blowing from north-northeast (popularly called “burja“ in Slovene; “bora“ in Italian and “bura” in Croatian). Sea surface temperature normally ranges between 8 °C in winter and 25 °C in summer (MALAČIČ *et al*., 2006). Hydrographic characteristics of the Bay of Koper are similar to the general characteristics of the Gulf of Trieste. Tides are mixed. Approximately every 15 days alternating half-day (two high tides and two low tides in a day) and daily tidal type (one high tide and one low tide per day). The mean sea level is 217 cm (baseline measurements of the sea level are Mareographic zero at the tide gauge station in Koper; data are available on the website of the Ministry of the Environment and Spatial Planning (MPO), Slovenian Environment Agency (ARSO): (www.arso.gov.si/water/sea). The average tidal amplitude is 67 cm, with high water reaching the maximum of 240–260 cm (25–45 cm above the mean sea level), low water is 180–200 cm (15 to 30 cm below the mean sea level). The lowest low water occurs during the period from December to February (about 160 cm), the highest high in the autumn months (370 cm) (MALAČIČ *et al*., 2000).

The rocky substratum of the Slovenian coast consists mainly of Eocene flysch layers with alternating solid sandstone and soft marl (OGORELEC *et al*., 1997); while in Izola (Simon bay) the coast is formed of limestone (PAVLOVEC, 1985). These three types of substrate that occur in close proximity provide a useful occasion to test the influence of the substrate to determine the species composition of macroalgal communities.

Description of the sampling sites

The study was conducted at six sites on three different types of rocky substrates (limestone, marl, and sandstone) located in separate parts of the coast. All sites will be hereafter indicated, from the names of the substrata, as Sand1 and Sand2 on sandstone, Marl1 and Marl2 on marl and Lim1 and Lim2 on limestone. Three sites (Marl1, Marl2 and Sand1) are located at Cape Debeli rtič, on the north-western side of the Bay of Koper, and three sites (Lim1, Lim2 and Sand2) on the south-western side of the Bay of Koper, near Izola (Fig. 1). The sites located at Debeli rtič consist of rocky platforms with a horizontal extent of about 500 m, exposed to wave action generated by winds blowing from northwest to northeast. The substratum of sites

Marl1 and Marl2 consists of marl and is formed of large steps with a smooth surface. The substratum of the site Sand1 consists of sandstone and is characterized by the presence of boulders of different sizes with rough surface.

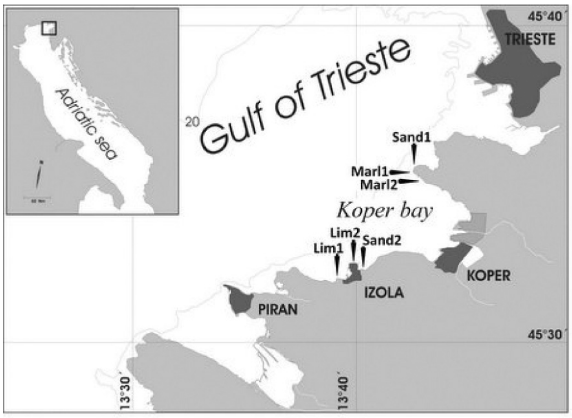

Fig. 1. The study area in the Bay of Koper, showing the sampling sites.

Two sites (Lim1 and Lim2) situated in St Simon Bay (Izola) are approximately 4 km from the sites Marl1, Marl2 and Sand1. They have a horizontal extent of about 250 m and consist of limestone with alveolines and nummulites (PAVLOVEC, 1985). The site Sand2, on sandstone, is located in the Viližan Bay near Izola and consists of different size boulders with rough surface.

Sampling design and collection of data

The study was conducted from the upper limit of the midlittoral to the infralittoral fringe (from the mean higher high water to the mean lower low water). Samples were collected by scraping off square surfaces of 100 cm^2 (10 × 10 cm). The material was preserved in 75% alcohol in seawater and examined microscopically for identification at the best possible level of taxonomic resolution. Algal nomenclature follows GUIRY & GUIRY (2015).

Samples were collected in two periods: in spring (April) and in autumn (November) 2010, in order to get different seasonal aspects of the vegetation. At each site three replicates were taken on each sampling period. A total of 108 samples were collected: 18 at each site, 36 per each type of substrate.

Analysis of data

The data collected were then analyzed using multivariate techniques. Non-parametric multivariate analyses were carried out using the species number. The PRIMER-5 package (CLARKE & GORLEY, 2001) was used. Matrices of similarity comparing average samples for each combination of horizon and substrate were calculated using the Bray Curtis index of similarity on untransformed data. Two-way crossed analysis of similarities (ANOSIM) and multiple pairwise comparisons were used to test for differences in communities among horizons and substrates. When ANOSIM detected a high dissimilarity between horizons and substrates, analysis of species contribution to similarity (SIMPER) was carried out to detect which species most contributed to the dissimilarity.

RESULTS

Pattern of zonation of the midlittoral zone

The vertical distribution of benthic macroorganisms in the uppermost zones was distinctly visible and identifiable at all six studied sites. On the basis of the zonation of the most abundant and leading organisms, we found, and thereby confirmed, the presence of three generally recognized zones: supralittoral, midlittoral and infralittoral zone.

More specifically, we wanted to define the zonation of the midlittoral zone, because, on the basis of observational evidence, we were inclined to consider its zonation different from that already described for the Adriatic and Mediterranean Sea. We have also found differences in the occurrence or absence of certain macroalgae in certain sites of the midlittoral due to differences in the type of substrate (Table 1).

For the investigated sites we proposed a new pattern of zonation of the midlittoral zone that differs from that generally accepted for the Mediterranean. Our pattern of zonation is supported by the fact that the mean tide amplitude in the Gulf of Trieste is greater (about 90 cm) than in the Mediterranean and middle and south

Adriatic Sea (only about 30 cm) (MORRI *et al.*, 2003).

We defined the midlittoral zone as the area between the mean higher high water and mean lower low water. The borders of the midlittoral zone of the researched area are between +46 cm and -44 cm with the average width of approximately 90 cm (Fig. 2). We set the lower limit of the occurrence of barnacles *Chthamalus depressus* for the upper limit of this zone, and the upper limit of the occurrence of the brown macroalga *Cystoseira compressa* for the lower limit.

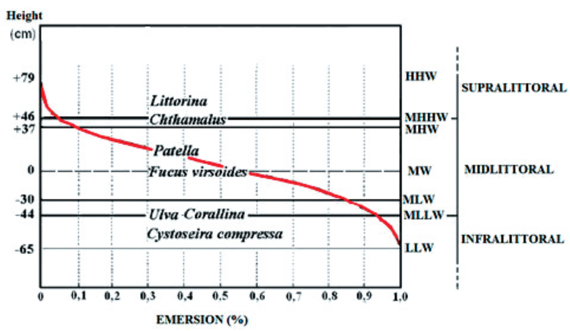

Fig. 2. Schematic presentation of zonation of the midlittoral zone of the Bay of Koper with average sea levels over the period 1961–2008. Source of data: MOP, ARSO, 2011; analysis of data: Harpha Sea, d.o.o. 2011. HHW – Higher High water; MHHW – Mean Higher High Water; MHW – Mean High Water; MW – Mean Water; MLW – Mean Low Water; MLLW – Mean Lower Low Water; LLW – Lower Low Water.

The organisms within the boundaries of midlittoral zone of the investigated sites were the most frequently distributed in mosaic or in bands. The zonation of the organisms was clearly identifiable on both limestone and sandstone substrates, but more difficult to determine on marl. Nevertheless, at all six investigated sites, three distinct horizons were clearly identified, although a high degree of overlap was noted in some instances (Fig. 3).

The identified three distinct horizons are:

<u>The upper horizon</u>: is located between mean higher high water and mean high water level (from +46 to +37 cm) (Fig. 2), although it varies from about 10 cm and 20 cm in height, depending on the exposure of the coast to waves. We defined it as an area that on the upper side borders with the supralittoral zone corresponding

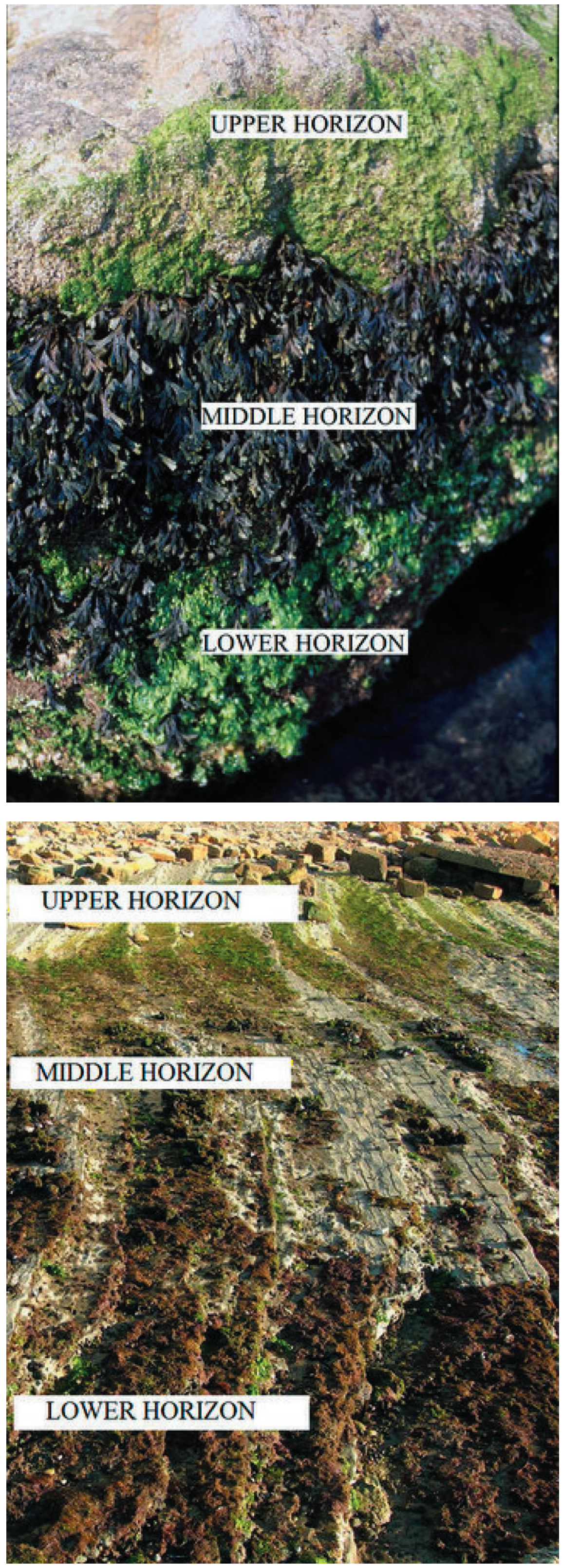

Fig. 3. Example of zonation of the midlittoral zone: (A) at site Lim1 on limestone (vertical slop) and (B) at site Marl1 on marl (gently slop). Both in spring.

to the lower limit of the occurrence of the barnacle *Chthamalus depressus*. We set the lower limit of the occurrence of the red alga *Bangia fuscopurpurea*, the green algae *Ulothrix implexa* and *Blidingia minima* and the beginning of the occurrence of brown alga *Ralfsia verrucosa* as the lower limit of the horizon. On limestone and sandstone the lower limit of this horizon coincides also with the beginning of the occurrence of the brown alga *Fucus virsoides*.

Concerning the sessile animal components, the upper horizon was densely populated in all sites by the barnacle *Chthamalus montagui*. Within the community of barnacles, especially in summertime, there were many colonies of cyanobacteria, with the dominant species *Calothrix crustacea*, which creates dark green coating bulbous forms with a few millimetres to a few centimetres in diameter. In this horizon green algae were also frequent. Among them the species of genera *Cladophora, Chaetomorpha* and *Ulva* with the species *U. compressa* dominate, while rarer was the red alga *Nemalion elminthoides*.

During winter and springtime a thin layer of macroalgae was present, composed of the dominant species *B. fuscopurpurea* and *U. implexa*, which—particularly on rocks with gentler slope—extend upward sand cover the lower limit of the supralittoral zone. The period from late autumn until the end of springtime was characterized by the occurrence of the red alga *Pyropia leucosticta* that occupied the entire midlittoral zone.

This horizon, at the sites on limestone (Lim1, Lim2) and sandstone (Sand1, Sand2), was mainly characterized by the presence of the red alga *Catenella caespitosa*, absent on marl. This alga thrives only in shadowy areas and develops mainly in cracks, crevices and inside rocks. The substrate of marl was characterized by the occurrence of red alga *Gymnogongrus griffithsiae* that in this horizon, did not occur either on limestone or sandstone (Table 1).

Table 1. List of macroalgal species occurring at different types of substrate and horizons of the midlittoral zone: upper (○), middle (□), lower (■). (Gr = green, Rd = red and Br = brown algae).

Substrate	Limestone			Marl			Sandstone		
Horizon	Up	Mid	Low	Up	Mid	Low	Up	Mid	Low
Species									
(Gr) *Chaetomorpha linum* (O. F. Müller) Kützing	○	□	■	○	□	■	○	□	■
(Gr) *Cladophora dalmatica* Kützing	○	□	■	○	□	■	○	□	■
(Rd) *Pyropia leucosticta* (Thuret) Neefus *et* J. Brodie	○	□	■	○	□	■	○	□	■
(Gr) *Ulva compressa* Linnaeus	○	□	■	○	□	■	○	□	■
(Rd) *Neogoniolithon brassica-florida* (Harvey) Setchell *et* L.R. Mason	○	□	■	○	□	■	○	□	■
(Rd) *Phymatolithon lenormandii* (Areschoug) W. H. Adey	○	□	■	○	□	■	○	□	■
(Gr) *Ulva laetevirens* Areschoug	○	□	■	○	□	■	○	□	■
(Gr) *Cladophora albida* (Nees) Kützing		□	■	○	□	■	○	□	■
(Gr) *Cladophora laetevirens* (Dillwyn) Kützing		□	■	○	□	■	○	□	■
(Br) *Ectocarpus siliculosus* (Dillwyn) Lyngbye	○	□	■		□	■	○	□	■
(Rd) *Stylonema alsidii* (Zanardini) K. M. Drew	○	□	■		□	■	○	□	■
(Gr) *Ulva clathrata* (Roth) C. Agardh		□	■	○	□	■	○	□	■
(Gr) *Ulva prolifera* O. F. Müller		□	■	○	□	■	○	□	■
(Rd) *Polysiphonia scopulorum* Harvey		□	■	○	□		○	□	■
(Rd) *Neosiphonia sertularioides* (Grateloup) K.W. Nam *et* P.J. Kang		□	■	○	□		○	□	■
(Rd) *Ceramium ciliatum* (J. Ellis) Ducluzeau		□	■	○	□	■		□	■
(Gr) *Cladophora coelothrix* Kützing		□	■		□	■	○	□	■
(Rd) *Gymnogongrus griffithsiae* (Turner) Martius		□	■	○	□	■		□	■

(Rd) *Titanoderma pustulatum* (J. V. Lamouroux) Nägeli		□	■	○	□	■		□	■
(Rd) *Antithamnion cruciatum* (C. Agardh) Nägeli		□	■		□	■		□	■
(Rd) *Aglaothamnion tripinnatum* (C. Agardh) Feldmann-Mazoyer		□	■		□	■		□	■
(Gr) *Bryopsis plumosa* (Hudson) C. Agardh		□	■		□	■		□	■
(Rd) *Caulacanthus ustulatus* (Turner) Kützing		□	■		□	■		□	■
(Rd) *Ceramium siliquosum* (Kützing) Maggs *et* Hommersand		□	■		□	■		□	■
(Rd) *Gayliella mazoyerae* T.O. Cho, Fredericq *et* Hommersand		□	■		□	■		□	■
(Rd) *Ceramium tenerrimum* (G. Martens) Okamura		□	■		□	■		□	■
(Rd) *Chondracanthus acicularis* (Roth) Fredericq		□	■		□	■		□	■
(Rd) *Palisada perforata* (Bory) K.W. Nam		□	■		□	■		□	■
(Rd) *Crouania attenuata* (C. Agardh) J. Agardh		□	■		□	■		□	■
(Rd) *Gastroclonium clavatum* (Roth) Ardissone		□	■		□	■		□	■
(Rd) *Gelidium* sp. J. V. Lamouroux		□	■		□	■		□	■
(Br) *Halopteris filicina* (Grateloup) Kützing		□	■		□	■		□	■
(Rd) *Hildenbrandia rubra* (Sommerfelt) Meneghini		□	■		□	■		□	■
(Rd) *Hydrolithon farinosum* (J. V. Lamouroux) Penrose *et* Y. M. Chamberlain		□	■		□	■		□	■
(Rd) *Lophosiphonia obscura* (C. Agardh) Falkenberg		□	■		□	■		□	■
(Rd) *Nemalion elminthoides* (Velley) Batters	○	□		○	□		○	□	
(Rd) *Pneophyllum fragile* Kützing		□	■		□	■		□	■
(Rd) *Polysiphonia opaca* (C. Agardh) Moris *et* De Notaris		□	■		□	■		□	■
(Br) *Ralfsia verrucosa* (Areschoug) Areschoug		□	■		□	■		□	■
(Br) *Sphacelaria cirrosa* (Roth) C. Agardh		□	■		□	■		□	■
(Gr) *Ulothrix implexa* (Kützing) Kützing	○	□		○	□		○	□	
(Rd) *Chondria coerulescens* (J. Agardh) Falkenberg		□	■			■		□	■
(Rd) *Compsothamnion thuyoides* (J. E. Smith) Nägeli		□	■			■		□	■
(Rd) *Polysiphonia polyspora* (C. Agardh) Montagne		□	■		□	■		□	
(Gr) *Chaetomorpha ligustica* (Kützing) Kützing	○			○	□		○	□	
(Rd) *Spyridia filamentosa* (Wulfen) Harvey			■		□	■			■
(Gr) *Bryopsis hypnoides* J. V. Lamouroux			■		□	■			■
(Rd) *Callithamnion corymbosum* (J. E. Smith) Lyngbye			■			■		□	■
(Rd) *Catenella caespitosa* (Withering) L. M. Irvine	○	□					○	□	
(Rd) *Pterocladiella melanoidea* (Schousboe ex Bornet) Santelices *et* Hommersand		□	■					□	■
(Rd) *Pterosiphonia pennata* (C. Agardh) Sauvageau		□	■					□	■
(Rd) *Pterothamnion plumula* (J. Ellis) Nägeli			■			■		□	■
(Rd) *Bangia fuscopurpurea* (Dillwyn) Lyngbye	○			○			○		
(Gr) *Blidingia minima* (Nägeli ex Kützing) Kylin	○			○			○		
(Gr) *Cladophora prolifera* (Roth) Kützing			■			■			■
(Br) *Scytosiphon lomentaria (*Lyngbye) Link			■			■			■
(Rd) *Ellisolandia elongata* (J. Ellis *et* Solander) K. Hind *et* G.W. Saunders			■						■
(Rd) *Corallina officinalis* Linnaeus			■						■
(Br) *Fucus virsoides* C. Agardh		□						□	
(Rd) *Lomentaria clavellosa* (Turner) Gaillon			■						■
Q (by horizon)	17	48	54	21	44	46	22	51	52
Q (total)		60			53			60	

Middle horizon: it extends between the mean high water and mean low water, for about 67 cm in height (from +37 cm to -30 cm) (Fig. 2). In this horizon the upper and the lower limits coincide with the limits of the occurrence of the species *Fucus virsoides*, which densely inhabits large parts of this horizon on limestone and sandstone, while it is absent on marl (Fig. 3). So, for the biotic upper limit of this horizon on marl, the onset of the brown crustose algae *Ralfsia verrucosa* was chosen, and for the lower limit, the onset of the green alga *Cladophora prolifera*.

Among animal components the barnacle *Chthamalus montagui*, snails of the genus *Phorcus*, the mussel *Mytilus galloprovincialis* (forming dense aggregates), the red sea anemone *Actinia equina* and the striated one *A. cari*, dominated. All the investigated substrates, especially in the upper part of this horizon (above the level of mean water), were characterized by the presence of the snails of the genus *Patella*, among which *P. coerulea* was the most common.

In general, the middle horizon at all the substrates was fully densely populated by cushions of macroalgae, among which species of genera *Ulva, Gelidium, Polysiphonia, Ceramium* and *Cladophora*, the species *Gymnogongrus griffithsiae* and *Caulacanthus ustulatus* dominated. The surface of the substrate was characterized by the presence of the red alga *Hildenbrandia rubra*, the brown alga *R. verrucosa* and Corallinacean species *Neogoniolithon brassica-florida* and *Phymatolithon lenormandii* (Table 1).

Lower horizon: it is situated between the mean low water and mean lower low water, for about 20 cm in height (between -30 cm and -44 cm) (Fig. 2). It was easier to define the upper limit of this horizon on limestone and sandstone because it corresponds to the lower limit of the occurrence of *F. virsoides* and the onset of *Corallina officinalis*, *Ellisolandia elongata* and *Cladophora prolifera*. On marl, we set the upper limit of this horizon at the beginning of the occurrence of the alga *C. prolifera*. The lower limit of this horizon, on all the substrates, was represented by the beginning of the occurrence of brown alga *Cystoseira compressa*, which also characterized the infralittoral fringe (Fig. 2).

At all sites of this horizon, the species of the genera *Ulva, Polysiphonia, Lophosiphonia, Ceramium, Cladophora, Gelidium*, the species *Gymnogongrus griffithsiae* and *Caulacanthus ustulatus* were the most common macroalgae. The surfaces of the substrate were dominated by the red alga *Hildenbrandia rubra* (typical of shaded area), the brown alga *Ralfsia verrucosa* and the Corallinacean species *Neogoniolithon brassica-florida* and *Phymatolithon lenormandii*.

Among the animals, in addition to mussels, this horizon was dominated by the barnacle *Chthamalus stellatus*. Abundant were also the snails of the genera *Phorcus*. The sites on marl (Marl1, Marl2) were characterized by the presence of the endolithic shell *Pholas dactylus*, which in this substrate can thrive since marl is a rock softer than limestone and sandstone.

Species composition of macroalgal communities and their distribution

Overall in the midlittoral zone of the investigated sites 60 macroalgal species were identified: 7 of them were exclusive on both limestone and sandstone and 53 were common on the three types of substrates (Table 1). A major difference in the number of species was found among horizons: the smallest number (26) was recorded in the upper horizon, while it was significantly greater in the middle and in the lower horizon (51 and 54, respectively). Red algae were the most numerous with 39 species, while considerably lower was the number of green and brown algae (15 and 6 species, respectively).

Only 7 species were present in all the investigated horizons, namely: the green algae *Chaetomorpha linum, Ulva compressa* and *Cladophora dalmatica*, and the red algae *Pyropia leucosticta, Neogoniolithon brassica-florida* and *Phymatolithon lenormandii*. The red alga *Bangia fuscopurpurea* and the green *Blidingia minima* were the only species that occurred in the upper horizon on all three substrates. In addition to them, in that horizon, *Ulothrix implexa* occurred, which also extends along the middle horizon. The communities of the upper and the middle horizons on limestone and sandstone were characterized by the presence of the red alga *Catenella caespitosa*. The rest of the collected species were more frequent in the communities of the middle and the lower horizons (Table 1).

The investigated macroalgal communities are characterized by a moderate dissimilarity in species composition with regards to horizons and substrates, as highlighted by the multivariate ANOSIM analysis. As shown in Fig. 4, algal communities are clearly separated into two clusters: on the right side the samples of the upper horizons are grouped, on the left side those of the middle and the lower horizons. The specimens of the middle and the lower horizons on sandstone and limestone are more closely together, while the samples of the middle and the lower horizons on marl are well separated from each other.

The differences in species composition of the algal communities of the midlittoral zone with regards to horizons and substrates are indicated by the R values of the global test for horizons and substrates (Table 2). The R value is more significant among horizons (R = 0.699***) than among different types of substrates (R = 0.040 ns). The main differences are found between the upper and the lower horizons (R = 0.956***). Considering the substrates, the dissimilarity of macroalgal communities was statistically significant only between limestone and marl (R = 0.137*) (Table 2).

Furthermore we wanted to determine which species contribute the most to the differences among horizons and among substrates. Taking into account only the dissimilarity among horizons, major differences are found between the communities of the upper and the lower horizons (74.62%; Table 3). The species that contributed the most to this difference are: *Blidingia minima*, *Gelidium* spp. and *Ceramium* spp. (Table 3). *Fucus virsoides* contributes the most to the differences between the communities of the middle and lower horizons on sandstone and limestone, since in the middle horizon it occurs only on limestone and on sandstone (Tables 3 and 5).

The principle difference among communities on different substrates is found between limestone and marl (Table 2). The species *Chaetomorpha linum*, which was more abundant on marl and *Ectocarpus siliculosus*, which was more abundant on limestone, mainly characterized this difference (Table 3).

We have also compared the differences in species composition between the communities of the macroalgae of different horizons on the same substrate. The ANOSIM analysis detected in general a higher difference between upper and lower horizon on limestone and the lower differences between the middle and lower horizon on sandstone (Table 4).

Regarding the contribution of species to the dissimilarities between the same substrate and different horizons, the SIMPER analysis (Table 5) detected in general a higher difference between upper and lower horizon on limestone and on marl, while on sandstone a higher dissimilarity was found between upper and middle horizons. There were many species (for example: *Blidingia minima, Ceramium* spp. and

Table 2. Results of the two-way crossed ANOSIM on the effect of horizons and substrates on the species composition of macroalgal communities of the midlittoral zone. Marl = marl, Sand = sandstone, Lim = limestone; Up = upper, Mid = middle and Low = lower

Global test for horizons: R = 0.699***		Global test for substrate: R = 0.040 ns	
Pairwise test for horizons:		Pairwise test for substrates:	
Horizons	R	Substrate	R
Up-Low	0.956***	Lim-Marl	0.137*
Up-Mid	0.881***	Marl-Sand	ns
Mid-Low	0.279***	Lim-Sand	ns

* = P < 0.05; ** = P < 0.01; *** = P < 0.001; ns = statistically not significant

Table 3. Results of SIMPER analysis on the contribution of the species (%) to dissimilarity between pairs of horizons and pairs of substrates. The average dissimilarity between each pairs is reported in parentheses.

Up-Low (74.62 %)		Up-Mid (69.29 %)		Mid-Low (49.15 %)	
Taxon	%	Taxon	%	Taxon	%
Blidingia minima	5.87	*Gelidium* spp.	6.31	*Fucus virsoides*	4.08
Gelidium spp.	5.37	*Blidingia minima*	6.31	*Antithamnion cruciatum*	3.65
Ceramium spp.	5.18	*Lophosiphonia obscura*	4.42	*Lophosiphonia obscura*	3.50
Ulva laetevirens	4.10	*Ceramium* spp.	4.33	*Polysiphonia opaca*	3.39
Chondracanthus acicularis	3.98	*Polysiphonia opaca*	4.13	*Ralfsia verrucosa*	3.33
Gymnogongrus griffithsiae	3.87	*Fucus virsoides*	3.97	*Ectocarpus siliculosus*	3,24
Lim-Marl (60.57 %)		Lim-Sand (58.37 %)		Marl-Sand (57.41 %)	
Taxon	%	Taxon	%	Taxon	%
Chaetomorpha linum	4.85	*Chaetomorpha linum*	3.86	*Polysiphonia opaca*	4.10
Ectocarpus siliculosus	4.26	*Cladophora* spp.	3.46	*Ectocarpus siliculosus*	4.06
Polysiphonia opaca	3.55	*Ulva laetevirens*	3.39	*Gymnogongrus griffithsiae*	4.01
Ceramium spp.	3.40	*Gelidium* spp.	3.34	*Ceramium* spp.	3.89
Gymnogongrus griffithsiae	3.38	*Chondracanthus acicularis*	3.34	*Cladophora* spp.	3.83
Ulva laetevirens	3.28	*Catenella caespitosa*	3.33	*Gelidium* spp.	3.60

Table 4. Results of the two-way crossed ANOSIM on the effect of the combination same substrate-different horizon on the species composition of macroalgal communities of the midlittoral zone

Global test for substrate-horizon: R = 0.718***

Pairwise test for substrate-horizon:

Substrate-horizon	R
LimUp-LimLow	1.000**
LimUp-LimMid	0.930**
LimMid-LimLow	0.698**
SandUp-SandLow	0.968**
SandUp-SandMid	0.922**
SandMid-SandLow	0.406*
MarlUp-MarlLow	0.896**
MarlUp-MarlMid	0.804**
MarlMid-MarlLow	ns

* = P < 0.05; ** = P < 0.01; *** = P < 0.001;
ns = statistically not significant

Fig. 4. Non-metric multidimensional scaling (MDS) ordination plot for combination substrate-horizon. Marl = marl, Sand = sandstone, Lim = limestone; Up = upper, Mid = middle and Low = lower

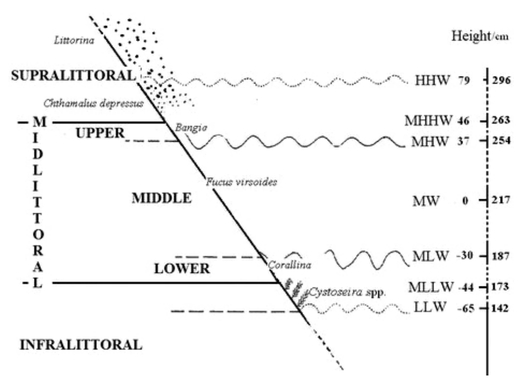

Fig. 5. Similarity dendrogram showing the relationship among macrobenthic algal samples from different horizons of the midlittoral zone on different substrates. Marl = marl, Sand = sandstone, Lim = limestone; Up = upper, Mid = middle and Low = lower. Cluster analysis obtained using presence/absence data based on Bray Curtis similarity and elaborated through complete linkage option

Gelidium spp.) that significantly contributed to the dissimilarities between the upper and the lower horizons on all the investigated substrates (Table 5), mainly because among the cited species *B. minima* was the only one present in the upper horizon (Table 1).

Table 5. Results of SIMPER analysis on contribution of species (%) to dissimilarity between pairs of the same substrates and different horizons of the midlittoral zone. The average dissimilarity between each pair is reported in parentheses.

LimUp-LimLow (76.88 %)		LimUp-LimMid (69.35 %)		LimMid-LimLow (46.92 %)	
Taxon	%	Taxon	%	Taxon	%
Gymnogongrus griffithsiae	6.66	*Blidingia minima*	6.73	*Fucus virsoides*	7.61
Ulva laetevirens	6.66	*Fucus virsoides*	6.73	*Ulva compressa*	6.28
Blidingia minima	6.66	*Gelidium* spp.	6.73	*Corallina officinalis*	5.82
Ceramium spp.	6.66	*Chondracanthus acicularis*	5.46	*Ulva laetevirens*	5.00
Gelidium spp.	6.66	*Ceramium* spp.	5.18	*Neogoniolithon brassica- florida*	4.32
Ulva compressa	5.57	*Cladophora* spp.	4.39	*Catenella ceaspitosa*	4.32
SandUp-SandLow (62.96 %)		SandUp-SandMid (67.42 %)		SandMid-SandLow (43.69 %)	
Taxon	%	Taxon	%	Taxon	%
Blidingia minima	7.65	*Blidingia minima*	6.93	*Fucus virsoides*	8.49
Ceramium spp.	7.65	*Fucus virsoides*	6.93	*Ectocarpus siliculosus*	5.00
Gelidium spp.	7.65	*Gelidium* spp.	6.93	*Catenella caespitosa*	4.84
Ulva laetevirens	6.21	*Lophosiphonia obscura*	5.34	*Cladophora prolifera*	4.79
Chondracanthus acicularis	6.12	*Ulva laetevirens*	4.63	*Polysiphonia opaca*	4.46
Caulacanthus ustulatus	4.93	*Caulacanthus ustulatus*	4.32	*Ralfsia verrucosa*	4.39
MarlUp-MarlLow (63.09 %)		MarlUp-MarlMid (55.52 %)			
Taxon	%	Taxon	%		
Blidingia minima	7.85	*Polysiphonia opaca*	8.52		
Gelidium spp.	7.85	*Blidingia minima*	8.52		
Ceramium spp.	6.64	*Gelidium* spp.	8.52		
Polysiphonia opaca	6.27	*Ceramium* spp.	7.19		
Ulva laetevirens	5.22	*Lophosiphonia obscura*	6.52		
Bangia fuscopurpurea	4.52	*Ulva laetevirens*	5.87		

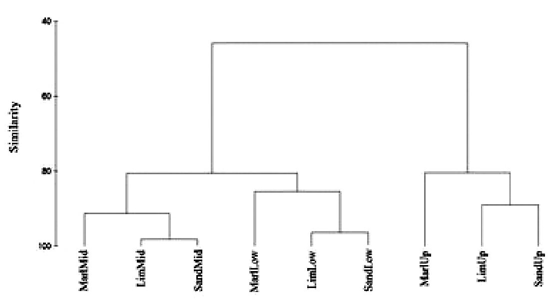

Fig.6. Proposed scheme of zonation in the research area (Koper Bay). Biotic and abiotic limits of the horizons and leader species are presented.

The differences between the upper and the middle horizon on limestone and on sandstone were primarily determined by *B. minima* and *Fucus virsoides*, as one of the species that occurs only in the middle horizons. As observable in Table 5, *F. virsoides* was the main contributor to the differences between the middle and the lower horizon on limestone and on sandstone, too. On marl, *Polysiphonia opaca, B. minima,* and *Gelidium* spp. mainly contributed to the dissimilarity between the communities of the upper and the middle horizons.

Our field observations supported by the results of the statistical analysis indicate the possibility of a new proposal for zonation of the midlittoral zone of the Bay of Koper (Gulf of Trieste) as shown in Fig. 5.

DISCUSSION

The overall pattern of zonation of the midlittoral zone found in the investigated area is slightly different from that of the Mediterranean (PÉRÈS & PICARD,1964; BELLAN-SANTINI *et al*., 1994; 2002) and other parts of the Adriatic Sea (in particular the central and southern Adriatic) (PÉRÈS & GAMULIN-BRIDA,1973; TORUNSKI, 1979; BAKRAN-PETRICIOLI, 2007, 2011). The observed differences can be attributed to higher amplitude of tides in the northern Adriatic (mean amplitude of about 90 cm) than in the central and southern part of the Adriatic and the Mediterranean Sea (mean amplitude 20-30 cm) (PÉRÈS & GAMULIN-BRIDA,1973; MORRI *et al*., 2003; BAKRAN-PETRICIOLI, 2007, 2011). Many studies (e.g. SCHÖNBECK & NORTON, 1978, 1980; DRUEHL & GREEN, 1982) have demonstrated that the tide was one of the fundamental factors that significantly affect the vertical distribution of the macroalgal communities of the midlittoral zone. In addition to the abiotic criterion, e.g. the height of sea level, which defines the limits of horizons, we especially used leader species, like many authors before us (STEPHENSON & STEPHENSON, 1949, 1972; LEWIS, 1964, 1972; PÉRÈS & PICARD, 1964; PÉRÈS & GAMULIN-BRIDA, 1973; BELLAN-SANTINI *et al*., 1994, 2002).

We set the lower limit of the occurrence of barnacle *Chthamalus depressus* and snail *Melarhaphe neritoides*, which are present at the level of the mean higher high water (about 45 cm from the mean sea water) as the upper limit of the midlittoral, which was in accordance with the generally accepted scheme of bionomic definition of the midlittoral for the Mediterranean (PÉRÈS & PICARD, 1964; PÉRÈS, 1967; COPPEJANS, 1974, UNEPRAC-SPA, 1998). In this case, the upper biotic and abiotic limits of the midlittoral zone coincide (Fig. 2). We set the upper limit of the occurrence of stands of brown algae of the genus *Cystoseira*—in accordance with what proposed by many authors for the Mediterranean (PÉRÈS & PICARD, 1964; COPPEJANS, 1974; BELLAN-SANTINI *et al*., 1994; MORRI *et al*, 2003) (Fig. 2)—as the lower biotic limit of this zone. Some variations, however, did occur. Several researchers of the eastern Adriatic coast (e.g., ERCEGOVIĆ, 1932; PÉRÈS & GAMULIN-BRIDA, 1973; GRUBELIĆ, 1992; BAKRAN-PETRICIOLI, 2007) divided the supralittoral zone in the upper and lower part and added the lower part of the upper supralittoral to midlittoral. As leader species for this part they choose the snails *Patella lusitanica* and *Phorcus turbinatus*, the barnacle *Chthamalus stellatus* and the red alga *Catenella caespitosa*. During our study we found that all these species occur in the middle horizon of the midlittoral zone; only *C. caespitosa* extends to the upper horizon. The barnacle *C. stellatus*, for example, does not occur, or occurs very rarely, in the upper horizon of the midlittoral zone, while is dominant in the lower horizon in the Mediterranean, according to CRISP *et al*. (1981) and BATTELLI & DOLENC ORBANIĆ (2009) for the Slovenian coast.

In the adopted scheme of the vertical zonation of the midlittoral zone for the Mediterranean (UNEP RAC-SPA, 1998), the upper midlittoral (which is moisturized by the waves spraying and fluctuations of the sea level as a result of changing air pressure, which extends between the mean higher high water and the mean high water), corresponds to the upper horizon in our scheme (Fig. 2). Lower midlittoral (which is under the direct influence of waves and tidal fluctuation, which extends between the mean high water and the mean low water), corresponds to the middle horizon in our scheme. Midlittoral fringe of the general scheme corresponds to the lower horizon in our scheme.

PIGNATTI (1962), who studied the communities of the Venetian coast, placed the entire midlittoral zone (as Littoral) between the mean high water and the lowest low water (approximately from +30 to -100 cm). The author divided this zone into the upper horizon (from +30 to -30 cm) and the lower horizon (from -30 to -100 cm). After this division the upper horizon corresponds to the zone between mean high water and mean low water, which we defined as the middle horizon of the midlittoral zone, while the lower horizon coincides with our lower horizon.

GIACCONE *et al*. (1993) and CORMACI *et al*. (2003) divided the midlittoral of the Mediterranean into the upper midlittoral, located above the mean water level, and into the lower midlittoral, located below the mean water level. Similarly, BENAC *et al.* (2004) and BAKRAN-PETRICIOLI (2007), separated the midlittoral zone of the Eastern Adriatic in the upper part, the so called white zone (according to SCHNEIDER, 1976), situated above the mean water level and in the lower part or green zone (after TORUNSKI, 1979), situated below the mean water level. The white zone is so called because, due to the occurrence of endolitic Cyanobacteria (among them the predominant species is *Mastigocoleus testarum*) and intensive grazing by gastropods (especially *Patella* spp.), it is a bit brighter. The lower zone is slightly green colored, because it is affected by a significantly lower grazing pressure that allows a more pronounced colonization and growth of algae.

Our division of midlittoral zone into three horizons (upper, middle and lower), primarily takes into account the tidal levels, as abiotic criterion, and the upper and the lower limits of occurrence of the leading species, as biotic criterion. According to this, we are inclined to consider the midlittoral as a zone that is under the direct influence of fluctuation of the sea levels as a result of tides. This is supported by the fact that approximately at the level of the mean higher high water the barnacle *Chthamalus montagui* occurs (a species that occurs throughout the midlittoral zone) and in accordance with abiotic limits represented by the mean lower low water. From autumn to springtime the presence of the alga *Pyropia leucosticta*, which occupies the whole midlittoral (Table 1) was characteristic in all the investigated area. So this species could be classified as one of the leading midlittoral species that well defines the borders of this zone. The division of the midlittoral zone into three distinct horizons was supported also by the fact that, within the borders of this zone, the vertical distribution of organisms was clear at all the investigated sites on limestone, sandstone and marl, although on marl the zonation was slightly less identifiable due to the absence of some of the leading species (*Fucus virsoides* and *C. caespitosa*) (Table 1).

In general, we define the lower limit of the upper horizon as the lower limit of occurrence of red alga *Bangia fuscopurpurea* and the green *Blidingia minima* (in our scheme both are leading species of the upper midlittoral horizon) and the beginning of the occurrence of the brown alga *Ralfsia verrucosa*. We chose the beginning of the occurrence of the green alga *Cladophora prolifera* (leading species of the lower midlittoral horizon) as lower limit of the middle horizon. On limestone and sandstone, in addition to *C. prolifera*, this limit is indicated by the beginning of the occurrence of the species of the genus *Corallina*, which on marl does not occur. The abundance of species of the genus *Corallina* in the lower horizon, agrees with observations by many authors for the Mediterranean (PIGNATTI, 1962; GIACCONE, 1970; BOUDOURESQUE, 1971; BALLESTEROS *et al.*, 1984). On limestone and sandstone, the upper and lower limits of the middle horizon are represented by the limits of the occurrence of the leader species for the middle horizon, *F. virsoides*.

The division of the midlittoral zone into three horizons was described by ZAVODNIK (1967) during the study on the community with *Fucus virsoides* in the vicinity of Rovinj. His work represents the first example of zonation of the midlittoral zone into three horizons for the northern Adriatic. But it is important to notice that this division was done only on the basis of animal components of the midlittoral zone. It differs from ours in the height of single horizons. The height of the middle and the upper horizon was 15 cm, the lower 10 cm. The differences in the height of the horizons are due to the smaller amplitude of the tides in the area of Rovinj in comparison with the Gulf of Trieste, which is about 50 cm (MUNDA, 1972).

The abiotic factors (tides, geological type of substrates) act in combination with biotic ones (grazing, intra-and interspecific competition, colonization) and can influence zonation patterns as well as species composition of algal communities in the midlittoral zone (HAWKINS *et al.*, 1992; DUGGINS & DETHIER, 1985; BOAVENTURA *et al.*, 2002). On the basis of field observational evidence, we are inclined to consider grazing, especially by snails of the genus *Patella*, one of the most important biotic factors in determining the vertical distribution of the organisms of the midlittoral zone. In all investigated sites we have noticed that particularly in the upper part of the middle horizon (between the mean water and the mean high water) a belt of limpets occurs. Characteristic for limpets is that, as consequence of their movement and the use of their radula, they "clean up" large areas of substrates and thus have a significant impact on the composition and distribution of algal communities, especially in the middle horizon of the midlittoral.

Along the Bay of Koper limpets can frequently be seen grazing the upper middle horizon above the *Fucus virsoides* stand. Often, however, limpets clean up the entire middle horizon, where the community with *F. virsoides* occurs. Such a distribution of the limpets is in accordance with the scheme of the zonation of organisms on the coast of the Gulf of Trieste (TORUNSKI, 1979).

Often, the surfaces of the rocks between the mean sea water and mean high water, remain without vegetation, only limpets and rare populations of barnacles are present. Our considerations on the effects of grazers on macroalgal communities are based only on field observational evidence, which is supported by the results of many studies (LEWIS, 1964; HAWKINS *et al*., 1992; DUGGINS & DETHIER, 1985; BOAVENTURA *et al*., 2002; MALM & KAUTSKY, 2003; JONSSON *et al*., 2006) on the impact of grazers on the macroalgal communities. Experimentally, it has been demonstrated that the attachment and survival of young thalli of the species of the genus *Fucus* depends on the number of limpets. In fact, after their removal, the abundance of stands of these species increased significantly (WORM & CHAPMAN, 1998; WORM & LOTZE, 2006, SOUTHWARD, 1964).

On the other hand, the absence of grazers allows the colonization and development of the cushion layer of algae, which inhibits the introduction of sessile organisms, such as limpets, barnacles and other cirripedia, which densely populate mainly the upper horizon, wherein the cushion layer of algae is less developed (DAYTON, 1971; SOUTHWARD, 1964; UNDERWOOD, 1980; HAWKINS, 1983).

On the basis of the results of the multivariate analysis, we are inclined to consider that the sea levels are mainly characterized by the dissimilarities of macroalgal communities among the horizons rather than by the type of the investigated substrates. The results of ANOSIM analysis showed greater differences between the algal communities of the upper and the lower as well as of the upper and the middle horizons. Among the communities of the middle and lower horizons the differences were smaller. This can be explained by a significantly greater difference in the time of immersion and emersion of the algal stands between the upper and lower horizon than among the other horizons. This is in accordance with many studies that have shown that the relationship between emersion and immersion has significant impact on the zonation of the communities that occur in the midlittoral zone. DRUEHL & GREEN (1982), for example, have experimentally demonstrated that the emersion time for some midlittoral species of the genus *Fucus* is even necessary to survive in this area. SCHÖNBECK & NORTON (1978, 1980) studied the factors that affect the upper and lower limits of occurrence of some species of the genus *Fucus*, and found that adult thalli of *F. spiralis* die if they are exposed for longer warmer period. We observed, for example, that in the warmer summer months thalli of *Fucus virsoides*, especially the tops of the stems, in the upper limit of the horizon, fell apart.

Regarding the substrates, we observed that macroalgal communities are distributed mainly in relation to the exposure of emersion and immersion, rather than to the geological type of substrates. In fact, statistically significant differences in species composition of macroalgal communities were found only between the communities on limestone and on marl (Table 2). In accordance with these results we can assert that the type of substrate only partially affects the differences of the algal communities among the horizons and only supports a greater influence of the tidal fluctuation on dissimilarities of the communities among different horizons. On the other hand we found the greatest differences among different horizons on the same substrate especially between the upper and the lower.

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Novi prijedlog za podjelu mediolitoralnog pojasa na zone u Koparskom zaljevu (Tršćanski zaljev, sjeverni Jadran) koji se temelji na zajednicama makroalgi

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SAŽETAK

Podjela tj. zonacija mediolitoralnog pojasa pretežito se temelji na istraživanjima zajednica makroalgi na šest postaja u zaljevu Koper (slovenski jugoistočni dio tršćanskog zaljeva) provedenih u proljeće (travanj) i jesen (studeni) 2010. godine. Studija provedena metodom slučajnog odabira, uključuje različite vrste podloga (vapnenac, lapor i pješčenjak). Uzorkovano je područje od gornjeg mediolitoralnog pojasa do ruba infralitorala (između srednje gornje razine plime do srednje donje razine oseke), te gornje granice prisustva smeđe alge *cystoseira Compressa.*

Zonacijom je mediolitoral podijeljen u tri sloja (viši, srednji i niži) prema biotičkim (vodeće vrste) i abiotičkim kriterijima (razina mora). Primjenom multivarijatne tehnike glavna različitost je ustanovljena između zajednica makroalgi gornjeg i donjeg sloja. Vrsta koja je najviše doprinijela ovakvoj različitosti je *Blidingia minima.* Glavne razlike u sastavu vrsta u različitim podlogama su pronađene između vapnenca i lapora. Vrsta *Chaetomorpha linum* uglavnom karakterizira takve razlike, dok je vrsta *Fucus virsoides* bila glavni pridonositelj različitosti među srednjim slojem na vapnencu i pješčenjaku.

Ključne riječi: podjela mediolitoralnog pojasa, makroalge, podloge, slovenska obala, tršćanski zaljev

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