

# The vertical structure of the vegetative canopy of the brown algae *Cystoseira* (Black Sea)

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**Abstract** In the coastal ecosystems of the Black Sea, macrophytobenthos and, in particular, the association of *Cystoseira crinite*, *C. barbata*, *Cladostephus verticillatus*, and *Corallina mediterranea*, with its thick vegetative canopy (VC), is the key contributor to primary production (PP). Though the vertical structure of the canopy, formed by the algal association, is of principal importance to the PP level, this subject has been long-neglected by researchers. The goal of our work was to compare vertical structures of the vegetative canopy of *Cystoseira* brown algae under diverse hydrodynamical conditions of the Crimean Peninsula coast. Samples were collected using the 50 cm×50 cm counting frame at eight stations positioned in shallow (55–60 cm deep) sites of Sevastopol Bay (Crimean Peninsula). Dry weight biomass of the VC was determined for all algae assemblage and for each algal species individually, per horizontal surface unit, at each height (Z). The study shows that: 1) the VC is characterized by unimodal vertical distribution of biomass, with maximum estimate in the lower part, where the biomass increases to 85% of the total biomass; 2) a series of single-peaked curves reliably describes the unimodal distribution of the biomass; thalli of different age groups are found along the canopy profile; and 3) algae found in epiphytic synusia prefer inhabiting the upper part of the VC. The role of environmental factors (seawater turbulence and solar radiation) is discussed in reference to the formation of the vertical structure, made up of the associations of the brown algae *Cystoseira*.

**Keyword:** vertical structure of the canopy; phytobenthos; phytocenosis; *Cystoseira*; epiphyte; biomass; multicellular algae; Black Sea

## 1 INTRODUCTION

Macrophytes growing in shallow littoral areas of the sea play an important role in primary-production formation (Thomaz and Cunha, 2010) and in sustaining the stable structure of the marine ecosystem (Warfe and Barmuta, 2004). Large macrophytes can produce a vegetative canopy (Kalugina-Gutnik, 1975) and be habitat-formers (Thomaz and Cunha, 2010; Stiers et al., 2011; Prazukin, 2015). They can also have an effect on the diversity, abundance, and functioning of micro and macrofauna (Lucena-Moya and Duggan, 2011; Schultz and Dibble, 2012; Habib and Yousuf, 2015) and micro and macroalgae in the phytocenosis (Stiers et al., 2011; Prazukin, 2015).

Vegetative canopy (VC), in its turn, is a subject worthy of special consideration. Its complexly

arranged vertical structure is optimally adjusted to the received solar irradiance. Differences in the efficiency of solar energy conversion by different plant communities depend on both their photosynthetic capability and on the canopy structure. Many works have acknowledged the importance of the structure of terrestrial plant communities (Tooming, 1984; Forseth and Teramura, 1986; Sassenrath-Cole, 1995), but investigations on aquatic plant communities are rare (Binzer and Sand-Jensen, 2002; Middelboe and Binzer, 2004).

In the Black Sea, littoral habitats situated along the coastal line of the Crimean Peninsula and the Caucasus are formed predominantly by the brown

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algae *Cystoseira*, in particular *Cystoseira crinita* (Desf.) Bory, 1832 and *C. barbata* (Good. et Wood.) Ag., 1821 (Kalugina-Gutnik, 1975). These large multicellular algae are considered ecosystem architects, but little is known about the intricate vertical profile of their canopy.

The goal of our work was to compare vertical structures of the vegetative canopy of *Cystoseira* brown algae (*C. crinita* and *C. barbata*) and its epiphytes under the diverse hydrodynamic conditions of the Crimean Peninsula coast.

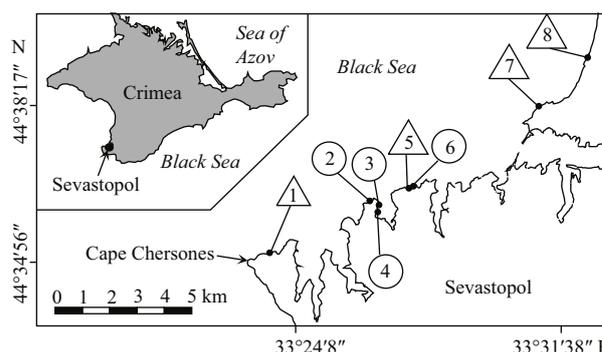
Our working hypothesis was that the bay geography (i.e., the water mass movement) can cause a pronounced impact on taxonomic composition and the vertical structure of the vegetative canopy.

## 2 MATERIAL AND METHOD

Observations were conducted along the shoreline of Sevastopol Bay in shallow waters (depth ranging from 55 to 60 cm), with high hydrodynamic activity favoring the development of the stratified bushy phytocenoses with a rich, well-formed canopy. Two groups of stations (4 locations each) with contrasting geography and water mobility (Fig.1) were selected. Water mobility was measured by means of the gypsum-plaster ball technique (Muus, 1968), modified by S. A. Kovardakov (Kovardakov et al., 1985; Khailov et al., 1988) according to the gypsum dissolution rate from the ball surface, that reflect body contact with water (CBW, g CaSO<sub>4</sub>/(h·cm<sup>2</sup>)). In accordance with data acquired (Zavalko and Khailov, 1985), water mobility at the shallow-water coastal areas of Sevastopol with a depth of 0–1 m varied within the range of 0.11–0.13 g CaSO<sub>4</sub>/(h·cm<sup>2</sup>) for areas protected from direct wave action (stations 2, 3, 4, and 6) and 0.20–0.24 g CaSO<sub>4</sub>/(h·cm<sup>2</sup>) for areas not protected from wave action (stations 1, 5, 7, and 8) (Fig.1).

Despite the absence of direct sources of pollution, the drastic rise of recreational nutrient load in the summer months seriously decreased marine environmental quality at stations 2–6, and 8 (Kovardakov et al., 1985) and, to a lesser degree, at stations 1 and 7, located near Cape Chersones and Cape Tolsty, respectively. Station 6 was situated directly in the interspace between concrete blocks of the pier constructed at the city beach in Victory Park.

According to the classification of Black Sea benthic vegetation (Kalugina-Gutnik, 1975), the studied phytocenosis is referred to as the *Cystoseira crinita*, *Cystoseira barbata*, *Cladostephus verticillatus*,



**Fig.1 Stations 1–8 in the seawater areas of Sevastopol (Black Sea)**

There are two types of areas: open sea (triangles) and areas protected from wave action (circles).

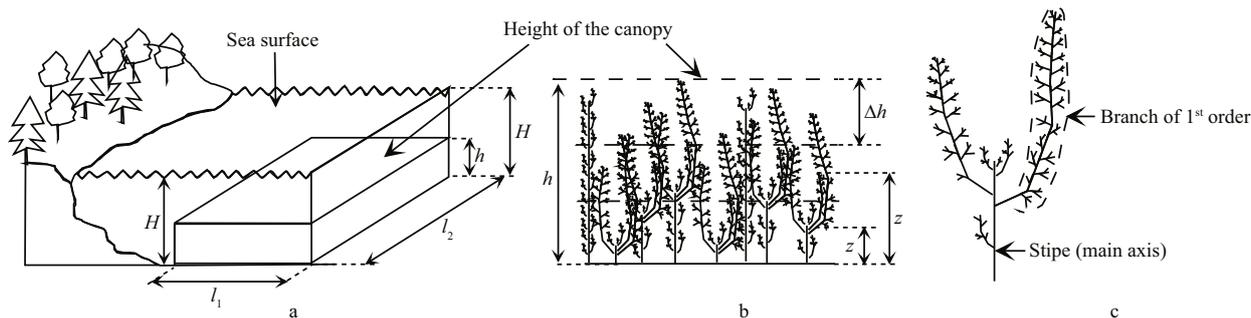
*Corallina mediterranea* association. *Cystoseira crinita* and *Cystoseira barbata* are morphologically similar to a large extent (Kalugina-Gutnik, 1975; Khailov and Parchevskiy, 1983; Kovardakov et al., 1985; Khailov et al., 1992). There is an important difference in the structure of the stipes and in the size of the body of algae. *Cystoseira crinita* has a thin elastic stipe and a small body size. *C. barbata* has a thick and not very flexible stipe and a relatively large body size.

Our investigation focused in particular on the vertical structure (VS) of this association in the upper part of its vegetative canopy.

The 50 cm×50 cm counting frame was used for gathering macroalgae from the middle part of the vegetative canopy at 8 stations, in July 2013. These macroalgae grow on hard substrates of a relatively flat seabed (Fig.2a); the procedure conformed to the routine method (Kalugina-Gutnik, 1975).

The *C. crinita* and *C. barbata* samples (105–237 specimens) collected at each site (i.e., 420 to 948 specimens/m<sup>2</sup>) were divided into size groups, depending on the length of the stipe in 5 cm intervals. The age ( $T$ , year) of thalli in both *Cystoseira* species was determined from their stipe length (Khailov and Parchevskiy, 1983):  $T=0.132+0.35L_0$ , where  $L_0$  is the stipe length (cm) (Fig.2c). The step between the middle intervals of the age groups was 1.75 years.

While studying the VS of the algal canopy, the method of stratified clipping (Myneni et al., 1989) was applied. Erect thalli of *C. barbata* and *C. crinita*, together with their epiphytes, were cut into equal vertical layers with the step  $\Delta h=5$  cm (Fig.2b). As all thalli of the same age (age groups,  $T$ , yr) were dissected, the resulting pieces were combined in layers. The layers were assembled together one after another, desiccated, and weighed to determine their



**Fig.2** Fragment of an algal canopy formed in the shallow (depth,  $H=55-60$  cm) open-sea habitats (a); vegetative canopy divided by horizons, with the interval  $\Delta h=5$  cm (b); the erect thallus (stipe and its branches) (c)

$h, l_1, l_2$ : linear parameter;  $Z$ : the distance from the base to the center of any layer (horizon) of the canopy.

dry mass ( $W_{\text{DRY}(Z)}$ ). For each layer of the canopy, morphological elements (stipes, branches of 1<sup>st</sup> order from thalli of age  $T$ , thalli of epiphytes) were correspondingly grouped and their dry weight per unit of the sea-bed surface ( $S_0$ ) was calculated by equation  $((W/S_0)_Z = W_{\text{DRY}(Z)}/S_0)$ , where  $S_0$  is the sea-bed area, and  $Z$  is the distance from the base of the vegetative canopy to each horizontal-layer center.

Vertical profile of the canopy is described by the vertical profiles of  $Z$ :

- 1) Dry mass of all algae collectively and of each participating species (per unit of the canopy's horizontal surface) at height  $Z$  is  $W/S_0(Z)$ ;
- 2) Dry mass of the morphological elements of algal thalli of different ages ( $T$ ) (per unit of the canopy's horizontal surface) at height  $Z$  is  $W_T/S_0(Z)$ .

### 2.1 Statistical analyses

The two-sided, independent-sample  $t$ -tests were applied to check whether there is a significant difference of biomass between the two groups of stations, for each alga (*C. crinita*, *C. barbata*, and epiphytes).  $T$ -tests were also applied to compare the biomass profile between the lower and upper halves. For even point numbers in a profile, the points were divided into two equal halves; otherwise the central point of the profile was ignored. Correlation analysis was performed for a pair of variables characterizing the algal biomass (*C. crinita* and *C. barbata*). A logarithmic transformation,  $\log(x+0.01)$ , was applied to normalize the data and perform a Pearson correlation. The IBM SPSS Statistics program, version 21, was used for all statistical analyses (Norussis, 1999).

## 3 RESULT

The main results of our observations were provided

through comparison of two groups of stations:

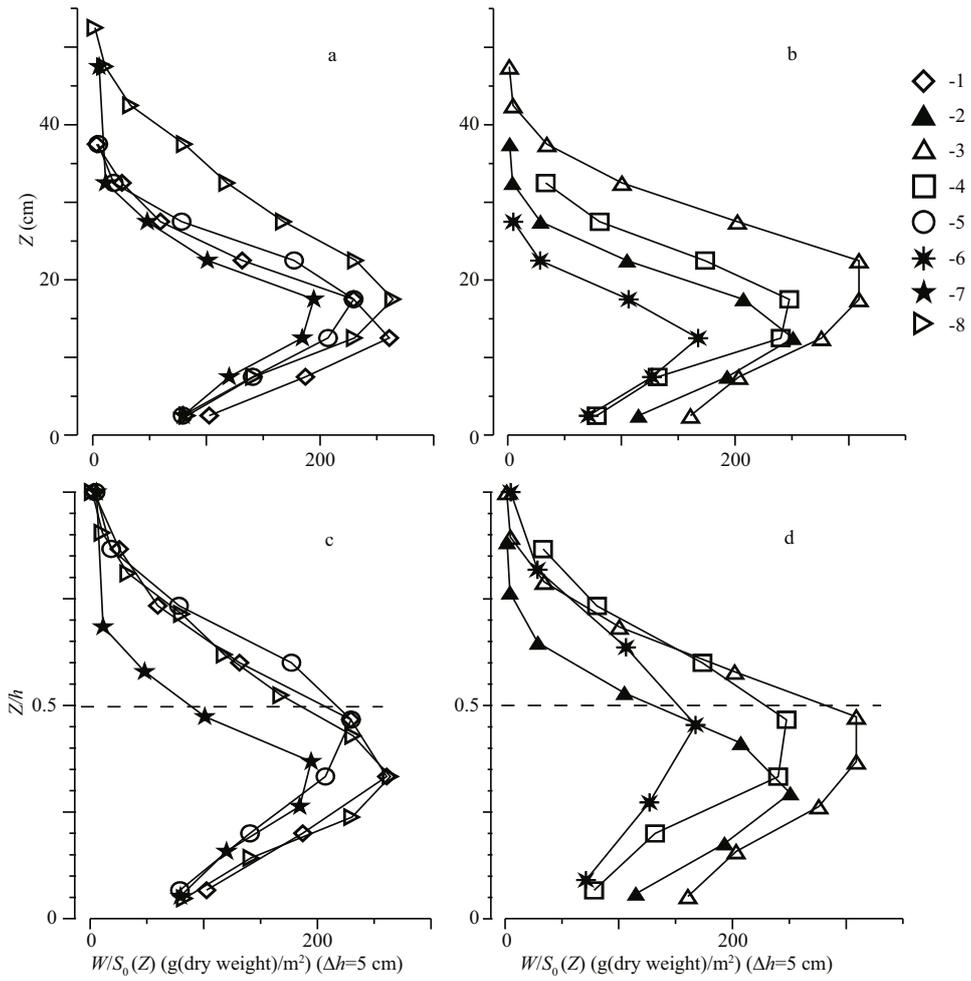
**The 1<sup>st</sup> group** (Figs.3a & c, 4a, 5) characterizes the VS of the canopy, with the erect thalli of *C. crinita* and the epiphytes mostly forming in the coastal areas facing the open sea (stations 1, 5, 7, and 8). The diagram illustrates the unequal distribution of  $W/S_0(Z)$  along the vertical profile, when the largest part of the biomass (some 80% of the total, thalli and epiphytes together) is in the lower part of the canopy (Fig.4a). The maximum values calculated for  $W/S_0(Z)$  ranged from 194 to 264 g dry/m<sup>2</sup> (Fig.3a, c).

The distribution of the dry biomass, contributed by branches of a separate age group ( $T$ ), is usually described by unimodal symmetrical or asymmetrical curves. As the age of the thalli increases, the biomass of their branches often increases to the maximum near the canopy top. It is worth noting that the values of  $W_T/S_0(Z)$  calculated for thalli older than 5 years (more frequently, 9 years) are distributed relatively evenly.

Conversely, the total biomass of the stipes (main axes) of the erect thalli of all age groups increases downward to 74%–85% in the lower horizons of the canopy.

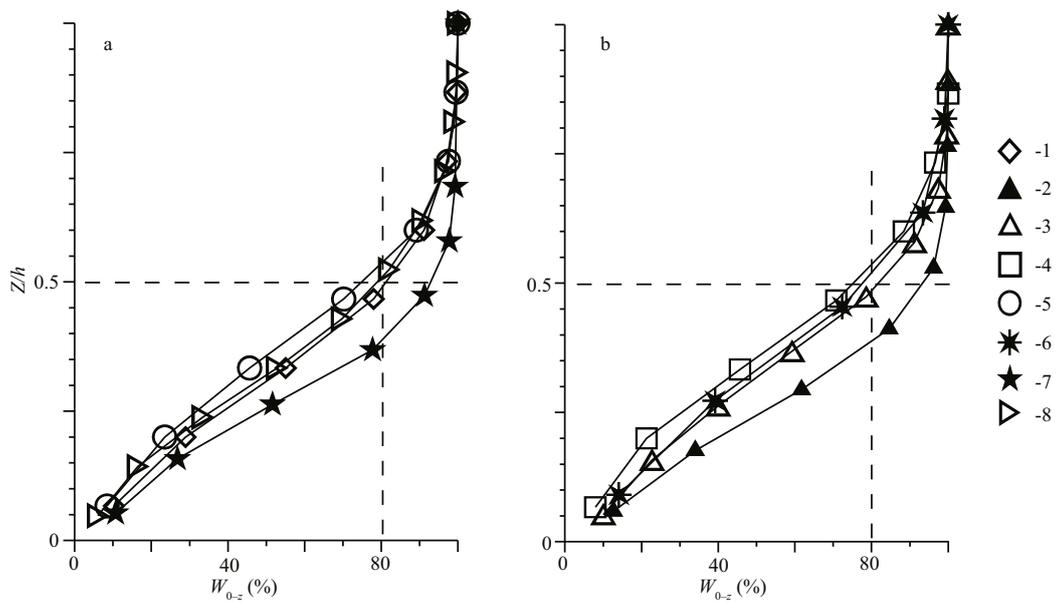
Each layer of the canopy is characterized by an individual ratio between biomasses generated by the thalli of different age groups; hence, the different solar energy uptake (Fig.5a–d). At stations 1, 5, and 7, cenopopulations of *C. crinita* consist of 7 age groups, and the canopies have identical heights of 37 cm each. At station 8, where the canopy is made up of 10 age groups, the height is 52 cm.

**The 2<sup>nd</sup> group** (Figs.3b & d, 4b, 6) represent the architecture that the erect algae *C. barbata* and *C. crinita* with their epiphytes usually have in the sheltered coastal habitats (stations 2, 3, 4, and 6). Like *C. crinita* with their epiphytes, *C. barbata* with *C. crinita* and their epiphytes make up the canopy characterized by the unimodal distribution of  $W/S_0(Z)$

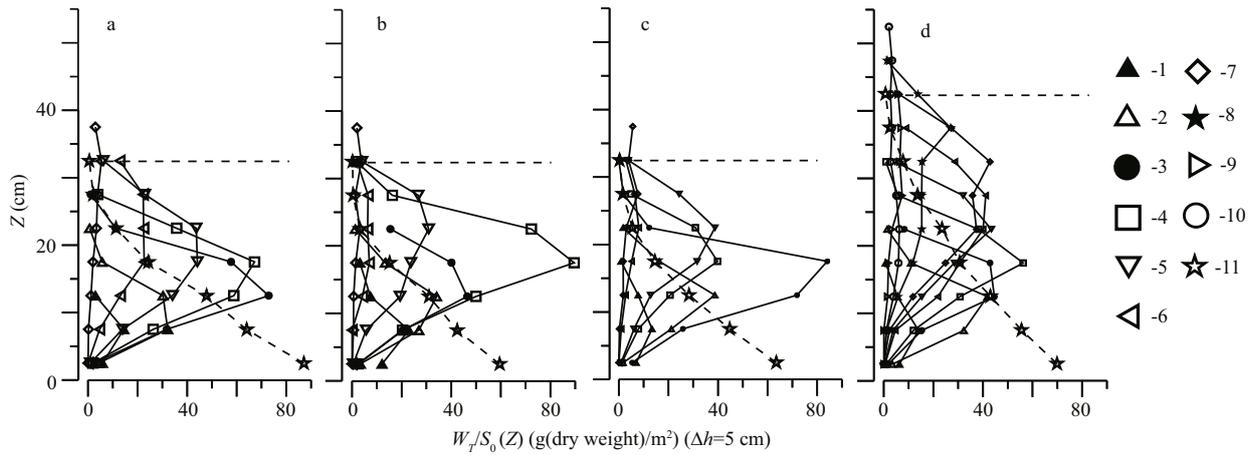


**Fig.3** Vertical distribution of dry weight biomass  $W/S_0(Z)$  in the vegetative canopies of the erect thalli of *C. crinita* and their epiphytes (a, c) and the thalli of *C. crinita*+*C. barbata* and their epiphytes (b, d) near Sevastopol

Symbols correspond to stations 1–8. On plates c and d,  $Z$  is normalized to the maximal height ( $h$ ).

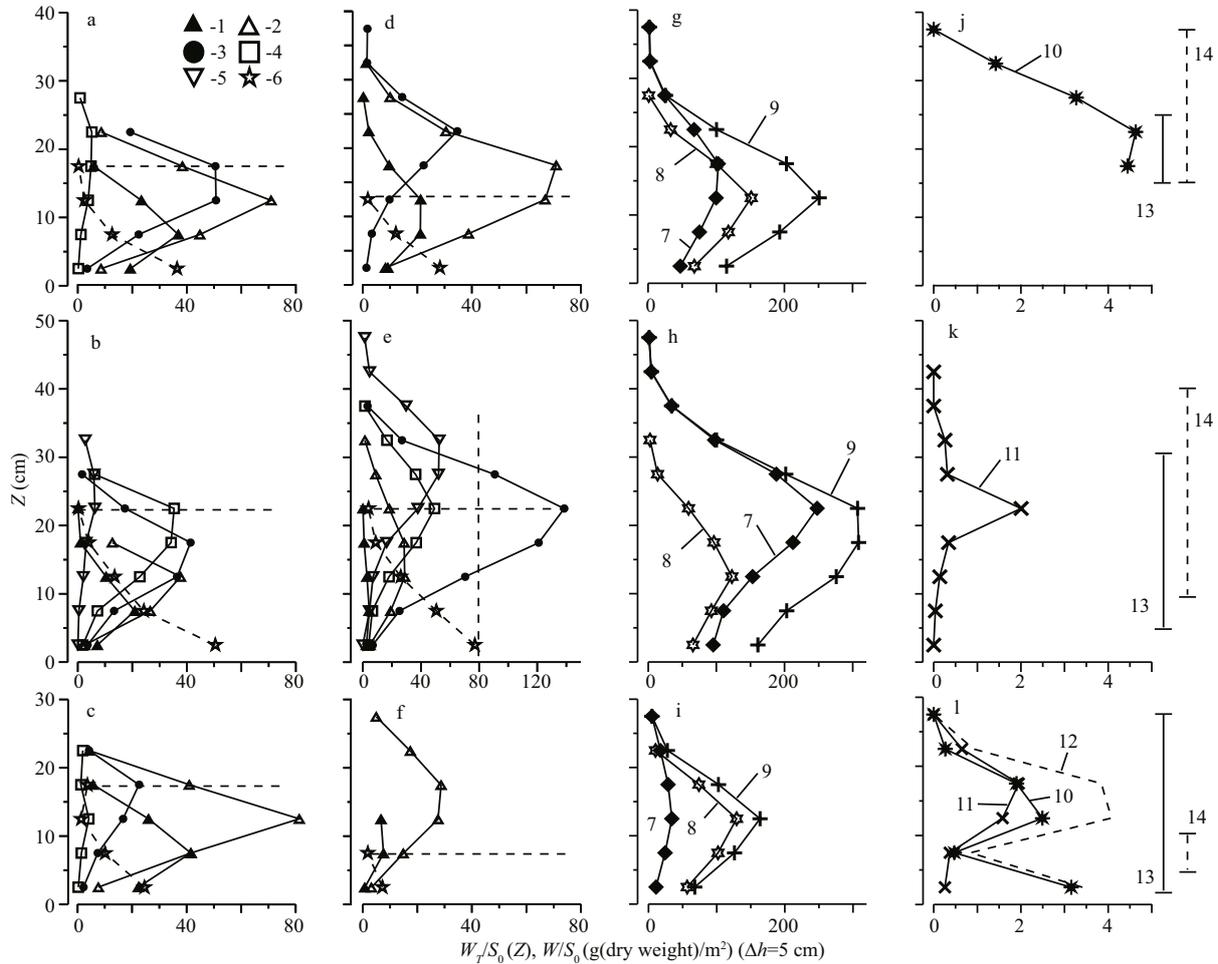


**Fig.4** The total (cumulative) mass ( $W_{0-z}$ , %), depending on the relative height ( $Z/h$ ) of the vegetative canopies; the erect thalli of algae *C. crinita* and their epiphytes (a) and *C. crinita*+*C. barbata* with their epiphytes (b), at stations 1–8



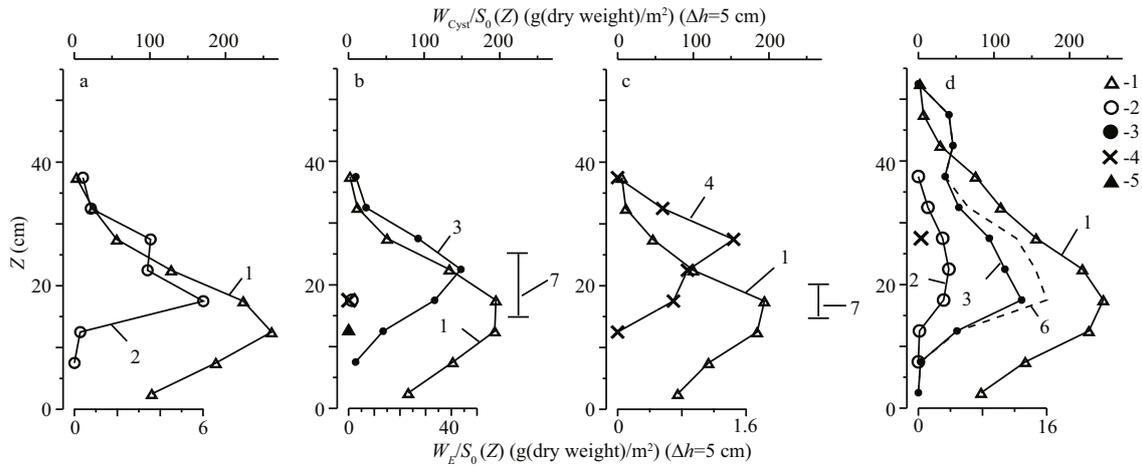
**Fig.5** Vertical distribution of the total dry weight biomass ( $W_T/S_0(Z)$ ), with branches on the erect algae *C. crinita* of all age groups (1–10) and the erect stipes (11) at stations 1 (a), 5 (b), 7 (c), and 8 (d)

Dashed lines mark the upper limit that the erect stipes can reach. Dashed line marks the upper limit that the stipes (main axes) can reach. Age groups (yr): 1) <1.9; 2) 1.9≤3.7; 3) 3.7≤5.4; 4) 5.4≤7.2; 5) 7.2≤8.9; 6) 8.9≤10.7; 7) 10.7≤12.5; 8) 12.5≤17.2; 9) 17.2≤16; and 10) 16≤17.7.



**Fig.6** Total dry weight biomass ( $W_T/S_0$ ) that the branches (age groups 1–5) of *C. crinita* (a, b, c) and *C. barbata* (d, e, f), and all erect stipes of each algal species (6) (a–f), the erect thalli of the *C. crinita* (8) with *C. barbata* (7) individually and jointly (9) (g, h, i), and epiphytes (j, k, l) have in different horizons of the canopy (standing axis, Z): stations 2 (plates a, d, g, j), 3 (b, e, h, k), 6 (c, f, i, l)

Note the x-axis scale difference between the plates. Dashed line marks the upper limit that the stipes (main axes) can reach. Age groups (yr) of the erect thalli: 1) <1.9; 2) 1.9≤3.7; 3) 3.7≤5.4; 4) 5.4≤7.2; 5) 7.2≤8.9. Epiphytes on the two algae: 10) *P. subulifera*; 11) *C. sericea*; and 12) *P. subulifera*+*C. sericea* jointly. The vertical stick shows the range of *K. virgatula* occurrence on the *C. crinita* (13) and *C. barbata* (14).



**Fig.7 Vertical distribution of the dry biomass of the erect algae *C. crinita* (1,  $W_c/S_0$ ) and several epiphytes (species N2–6,  $W_e/S_0$ ) in the vegetative canopies at stations 1 (a), 5 (b), 7 (c), and 8 (d)**

Standing axis shows the range limit of *K. virgatula* occurrence on *C. crinita* (7). Species are: 2: *L. coronopus*; 3: *P. subulifera*; 4: *C. sericea*; 5: *Grateloupia dichotoma* J. Ag.; 6: joint weight of *L. coronopus*+*P. subulifera*.

(Fig.3d). The largest biomass was seen in the lower part of the canopy; the estimates increased toward the mid-zone, representing up to 80% of the total biomass (Fig.4b).

At station 6, the vegetative canopy is mainly made up of *C. crinita* (Fig.6i), and at station 3: *C. barbata* (Fig.6h). At station 2, these two algae have nearly equal shares of the total biomass. Maximums of  $W/S_0(Z)$  diverge for these two species, as seen in Fig.6g and h. Sometimes the *C. crinita* does not grow to the full height of the canopy with *C. barbata*. In such a case, most of the branches spread within the height range of their thalli (Figs.5 and 6). Unlike *C. crinita*, the *C. barbata* reaches the total height of the canopy; their tops form the upper margin of the canopy. For this species, some branches grow no higher than the apex of the thallus, while other branches go far beyond this limit (Fig.6d, e, f). At station 6, where the recreation nutrients load is enormous, *C. barbata* is characterized by a substantially lower number of age groups; hence, the canopy there is shorter than at all the other stations.

Special attention (Figs.6j–l, 7, 8) was given to the interplay between two ecological groups: macro-epiphytes and their hosts. The counting of the epiphytes included only macro-epiphytes that contributed most to the biomass of the vegetative canopy. *Kylinia virgatula* (Harvey) Papenfuss 1947, found in small quantities on the stipes and apical parts of branches of the *Cystoseira* at several stations, was not included in the count.

Macro-epiphytes dominated by biomass in the epiphytic synusia of phytocenoses, differ from each

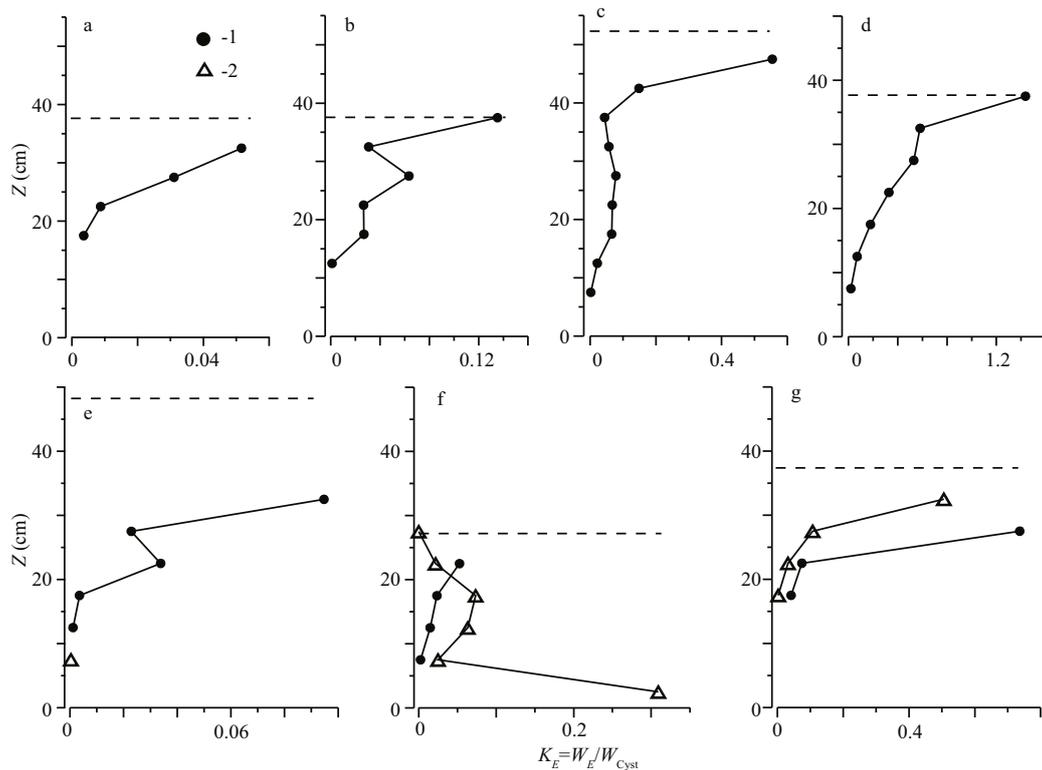
other and depend on the examined locations. At station 1, it is *Laurencia coronopus* J. Ag., at stations 2 and 5: *Polysiphonia subulifera* (C. Ag.) Harv., and at stations 3 and 7: *Cladophora sericea* (Huds.) Kütz. At stations 6 and 8, the two key components were *P. subulifera* with *C. sericea*, and *P. subulifera* with *L. coronopus*, respectively.

The biomass distribution generated by macro-epiphytes at different horizons of the canopy's vertical profile— $W/S_0(Z)$ —the *C. crinita* and *C. barbata*, seemed to be unimodal. The peak of the macro-epiphytes biomass was mostly positioned over the peak of  $W/S_0(Z)$  of the host algae (Figs.6j, 6k, 7). Biomass of the macro-epiphytes measured at different layers, though slightly increasing towards the top of the canopy, was negligible when compared with the biomass of their hosts ( $W_{epi}/W_{Cys}$ ) (Fig.8). Even in summer (July), the share of epiphytes in the total phytocenosis biomass at the coastal areas under examination was negligible, 0.19%–14.1%.

In Figs.6j, k, l, and 7, vertical lines show the height range of *K. virgatula* in the canopy's profile. Depending on the special features of each species of *Cystoseira*, the presence of this epiphyte in the canopy can be mostly confined to the central part (Fig.7b, c), or conspicuously increase, taking up large spaces within the canopy (Fig.6j, k, l).

### 3.1 Results of statistical analyses

The independent-samples t-test has demonstrated a significant difference between the two groups of stations (the open sea and inshore stations) of *C. crinita* biomass ( $P=0.001$ ;  $n=8$ ). Significant



**Fig.8 Total weights of the epiphytes compared with the total weights of the thalli of the hosts ( $W_E/W_C$ ), *C. crinita* (1) and *C. barbata* (2), in different horizons of the canopy**

Stations 7 (a), 1 (b), 8 (c), 5 (d), 3 (e), 6 (f), and 2 (g).

difference between the two groups of stations was found also for the *C. barbata* biomass ( $P=0.036$ ;  $n=8$ ). Correlation analysis showed a strong negative correlation ( $R=-0.79$ ;  $P=0.02$ ;  $n=8$ ) for biomasses of the two species of *Cystoseira*. Significant difference between the two groups of stations was found for the biomass sum in the upper and lower halves of the vertical profile ( $t$ -test;  $P=0.002$ ;  $n=8$ ).

#### 4 DISCUSSION

The water turbulence in the shallow coastal areas is the principal factor in the formation of the age structure of the brown algae *Cystoseira* populations, of the species composition of phytocenoses, and, eventually, the architecture of the vegetative canopy. Other factors influencing the VS of the canopy are solar radiation and the anthropogenic impact.

Though the canopy in one phytocenosis group has evident distinctions from the canopy of the other group; their architecture develops according to the general rules discussed below. We interpret the optimal architecture of the canopy as the structure supporting maximal photosynthetic production of the phytocenosis under adequate conditions. Hence, in nature, any vegetative canopy has its VS optimally adjusted to the

habitat conditions, in particular, to the energy flux.

Some terrestrial agrophysiologists (Tooming, 1984; Forseth and Teramura, 1986; Karmanova et al., 1987; Myneni et al., 1989; Sassenrath-Cole, 1995, and—in aquatic phytocenoses—Zavalko and Kovalchuk, 1994; Binzer and Sand-Jensen, 2002; Middelboe and Binzer, 2004) assume that the VS of a vegetative canopy is formed to have production stabilized within the limits of external gradients, and water stratification amplifies this stabilization (Tooming, 1984; Myneni et al., 1989). An appropriate example is the upper part of the associations of brown algae *Cystoseira*, with their own multi-layer vertical structure composed of thalli of different ages) and their epiphytic synusiae.

Our results indicate that in the canopy profile, each age group of thalli was represented by its own layer, where biomass of the age group was maximal. Thalli of other age groups usually overlapped with these horizons.. When two species of *Cystoseira* share the same habitat, their biomass maximums [ $W/S_0(z)$ ] in the canopy profile usually diverge. Results of our study and other works (Zavalko and Kovalchuk, 1994) give evidence that epiphytic synusiae were seen mainly in the top part of the vegetative canopy.

An earlier investigation showed that this spatial preference depends on the light level (Zavalko and Kovalchuk, 1994). In the well-illuminated 0.5 m layer, maximal biomass depths of algal thalli and their epiphytes can coincide. The discrepancy begins from a depth of 1.5–2 m (Zavalko and Kovalchuk, 1994), where the distribution of  $W/S_0(Z)$  values becomes more even.

The series of unimodal curves, the peaks of which usually diverge, also applies to terrestrial phytocenoses. It is suitable for the vertical distribution of the biomass and the assimilating surface area of plants, for all species participating in canopy formation (Karmanova et al., 1987). Moreover, any of the contributing species maximally increases its assimilating surface area at the horizon, where the irradiance level corresponds to the maximal gas exchange adopted for this species (Tooming, 1984; Myneni et al., 1989). In our case, this notion is true for algal branches of thalli of different age groups and for species of epiphytic synusiae. This spatial organization allows terrestrial phytocenoses to assimilate light with maximal efficiency (Tooming, 1984; Forseth and Teramura, 1986; Myneni et al., 1989; Sassenrath-Cole, 1995), and works in aquatic phytocenoses as well (Binzer and Sand-Jensen, 2002; Middelboe and Binzer, 2004).

The adaptation potentialities of the canopy in the *Cystoseira* phytocenoses are apparently due to its multivariant, stratified structure, with the spatially interplaying morphological elements of young and old thalli, and the special arrangement that epiphytic species have within their synusia and on the host algae.

## 5 CONCLUSION

1) In the associations of the brown algae *Cystoseira*, the canopy is characterized by unimodal distribution of the biomass along the vertical profile. The lower part contributes a significantly higher amount (75%–85%) of the total dry biomass than the upper part of the profile.

2) The biomass distribution contributed by thalli of each age group to different horizons of the algal canopy is described by a series of unimodal curves. The discordant peaks presumably suggest some orderliness that allows the *Cystoseira* plants, in cooperation with the algae of other groups, to regulate the production characteristics over the larger portion of the vertical profile.

3) The epiphytic synusia species dwell mostly in the upper part of the canopy and form an individual

epiphytic layer. The biomass of epiphytes in the total phytocenosis at the coastal areas under examination was negligible.

4) A statistically significant difference was found between the two groups of stations (the open sea and the inshore stations) for each macrophyte (*C. crinita* and *C. barbata*) biomass.

5) Correlation analysis showed significant negative correlation of biomasses of the two species of *Cystoseira*. For that reason, we think that the environmental factors [bay geography (first of all, its hydrodynamics)] caused a pronounced impact on the macrophyte taxonomic composition.

## 6 DATA AVAILABILITY STATEMENT

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

## 7 ACKNOWLEDGMENT

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