The decadal changes in the *Ahnfeltia* bed in the Peter the Great Bay (Sea of Japan): possible causes

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Abstract The decadal changes (from 1992 to 2005) of a community of unattached red algae in the Sea of Japan dominated by *Ahnfeltia tobuchiensis* were studied for the first time. The most important changes were an increase in species richness and significant changes in the stock of dominant species in the *Ahnfeltia* bed accompanied by a drastic decrease in the stock and biomass of the cold-temperate-water species *Chondrus armatus*, which coincided with a significant increase in the stock and biomass of *Ahnfeltiopsis flabelliformis*, an alga with warm-temperate-water affinity, while the stock and biomass of *A. tobuchiensis* did not change considerably. These changes led to the alteration of the algal community. The association co-dominated by *A. tobuchiensis* and *C. armatus* was noted in 1992, and by 2005, this association was replaced by the *A. tobuchiensis* and *A. flabelliformis* co-dominated association. Possible causes for these changes are discussed. It was concluded that warmer waters may be the basic environmental stress factor playing the central role in changing the community structure of the studied *Ahnfeltia* bed.

Keywords *Ahnfeltia tobuchiensis* · Peter the Great Bay · Sea of Japan · Macrophyte benthic communities · Unattached seaweeds

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Introduction

Ahnfeltia tobuchiensis (Kanno et Matsubara) Makienko is one of the most commercially important seaweed producing high-quality agar. This alga forms extensive beds which are used as a sole source of raw material for agar production in the Russian Far East as well as in northern Japan (Cherbadgy and Popova 1998). This phycocolloid is used mainly as a gelling and thickening agent in food industries (Sukhoverkhov et al. 2000). Besides their economic value, *Ahnfeltia* beds have significant ecological importance. They serve as food and habitat for numerous benthic organisms including commercially valuable species such as scallops, sea cucumbers, and fish (Ivanova et al. 1994). So knowledge of *Ahnfeltia* community dynamics and the main environmental factors influencing community stability and succession can be important not only for understanding how the community is functioning but also for enhancing our ability to predict changes in the resources of the commercial algae and animals associated with *Ahnfeltia* beds.

Ahnfeltia beds are truly unique; they are distributed in the cold-temperate coastal zones of Asia Pacific only: in Peter the Great Bay (Sea of Japan), in Busse lagoon (Sakhalin Island), in the Bay of Izmena (Kunashir Island), and on the northern coast of Hokkaido Island (Makienko 1980). *Ahnfeltia* beds were found on sandy and sandy-muddy bottoms at depths between 5 and 20 m, where it forms a 0.15–1.0 m thick carpet, or stratum, on the seafloor. *Ahnfeltia* beds represent specific biocoenotic communities which include dozens of macrophyte species and have a complicated structure. These beds are invariably, for a hundred years, present at the same locations where circular currents and bottom morphology prevent the algae from drifting away (Titlyanov et al. 1993). *Ahnfeltia* communities are formed by red annual and perennial unattached seaweeds, and their epiphytes (Titlyanova 1980). Only perennial long-lived (up to 10 years) species such as

A. tobuchiensis and *Chondrus armatus* dominate in such communities. These algae are sterile and reproduce only vegetatively, mainly by fragmentation. Due to low growth rate of the main species (less than 21–26 % of algal biomass per year), the ratios of dominant algae in a community are not susceptible to either seasonal or interannual changes if environmental conditions are stable. Minor species also have no effect on the seasonal variations of a community's structure and biomass.

The proportion of *A. tobuchiensis* in a community differs slightly depending on the locality, but usually 50–100 % of the biomass is made up by this species. In general, the proportion of other species is usually low, less than 5 % (Ivanova et al. 1994; Skriptsova and Nabivailo 2009). However, there are *Ahnfeltia* beds co-dominated by *A. tobuchiensis* and other species such as *C. armatus*, *Ptilota filicina*, and *Sargassum pallidum* (Sukhoveeva et al. 1985). For example, the biomass of *C. armatus* can reach 22.6 % of the community biomass in some parts of the *Ahnfeltia* bed in the Bay of Izmena and even 50–80 % at some stations (Ivanova et al. 1994). In Baklan Bay (southern part of Peter the Great Bay), a community co-dominated by *A. tobuchiensis* and *P. filicina* is formed. The biomass of the latter species at some parts of the bed can reach 80–90 % (Sukhoveeva et al. 1985).

The population density and proportion of the dominant red algal species are not distributed uniformly but vary spatially. For example, the maximal accumulation of *C. armatus* in the *Ahnfeltia* bed located in the Bay of Izmena is concentrated in the south-eastern marginal part of the bed, and the alga occurred only sporadically in the other parts of the bed (Ivanova et al. 1994; Cherbadgy and Popova 1998). The total biomass of the bed and the area occupied by the algal stratum may vary insignificantly from season to season and from year to year (Titlyanov et al. 1993). It was shown that the northern and western boundaries of the *Ahnfeltia* bed in the Strait of Stark (Peter the Great Bay) can move between 50–100 and 150–250 m from summer to late autumn. The most obvious impact on the bed area is a change in the configuration and total stock of the algae due to strong storms induced by typhoons. Although they can conduce to the periodical turning of the stratum or its parts, the bed structure is generally strongly temporally stable because *Ahnfeltia* beds are mostly climax communities composed of the species best adapted to average conditions in the area. The community usually returned to its prior state within a year after a disturbance.

The *Ahnfeltia* beds in Peter the Great Bay were monitored by phycologists in the late twentieth century. The studies have detected general modification and regression of all *Ahnfeltia* beds in Peter the Great Bay during the last century due to extensive commercial harvesting (Kulepanov et al. 1999). However, since 1992, the harvesting of *Ahnfeltia* from the native beds in Peter the Great Bay has ceased (Kulepanov et al. 1999). Therefore, any change in the communities which could be found must be attributed to the impact of environmental changes or the natural succession of the communities. Early studies have suggested that abiotic environmental factors, such as temperature, light, and nutritive conditions as well as biotic interactions, are considered as the main factors regulating the dynamics of the major community-forming species in the *Ahnfeltia* beds (Titlyanov et al. 1993; Nabivailo et al. 2014).

The objectives of this study are (1) to assess the current state of the *Ahnfeltia* beds in Amursky Bay, (2) to compare it with historical records, (3) to try to relate the evolution of this algal community to environmental changes, and (4) to provide a baseline for further monitoring of this community.

Materials and methods

The studied *Ahnfeltia* beds are located in Amursky Bay near Mt. Stolovaya (between the mouth of the Barabashevka River and Peschanyi Peninsula, from 43° 06′ N, 131° 38′ E to 43° 10′ N, 131° 45′ E) (Fig. 1a). The previous data on the species composition, biomass, and distribution of the dominant species were obtained in the summer of 1992 (own unpublished data). This survey revealed two large accumulations of unattached algae at depths of 4 to 9 m: the southern bed located alongside the Barabashevka's mouth and the northern bed located opposite Mt. Stolovaya (Fig. 2a, b).

Sampling was done in the *Ahnfeltia* bed by SCUBA-diving in summer, 1991 at 27 stations and in summer, 1992 and 2005 within the network of 147 sampling stations including those surveyed in 1991 (Fig. 1b). The distance between stations was about two cables (382 m). The positioning of a vessel relative to a station was carried out by use of a GPS navigation device.

The methods of sampling were similar in all undertaken studies. Three quadrats (0.25 m^2) were randomly placed over the bottom at each sampling station in 2005, and only one quadrat was collected in both 1991 and 1992. Within each quadrat, all visible plants were collected by hand, placed into a mesh, and transported to the laboratory for further processing. At the laboratory, the samples were sorted by species, which were identified based on Perestenko's identification keys (1980, 1994). The algae collected in 1992 were identified by T.V. Titlyanova, and the seaweeds collected in 2005, by T.V. Titlyanova and A.V. Skriptsova. The plants were weighed with a digital scale (±0.1 g). The additional collection was done in 2002. Ten quadrats were randomly collected in different parts of the northern bed. These data were not used in the analysis because the coordinates of these sampling locations did not overlap with the coordinates of stations sampled in 1991/92 and 2005. In 2002, the percentage of *A. tobuchiensis* in the sample ranged from 60 to 80 % (more than 2 kg m^{-2} on average), the percentage of the second dominant species, *Ahnfeltiopsis flabelliformis*, was 5–40 % of the total algae biomass (about 1 kg m^2 in average) at all locations. *C. armatus* was not found in the whole set of samples.
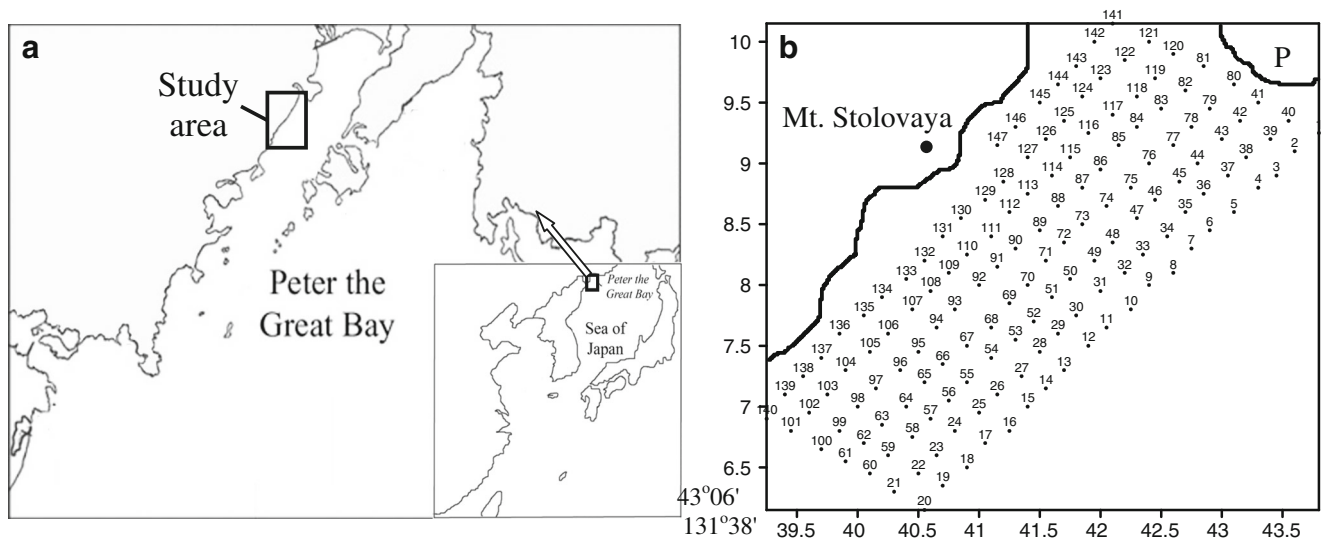
Fig. 1 Location of study area in Peter the Great Bay, Sea of Japan (**a**) and position of the sampling stations in the Amursky Bay (**b**). *P* Peschaniy peninsula. *Arabic numbers* are numbers of sampling stations

From the data obtained, the following bed areas were defined: (1) "pure" *Ahnfeltia* areas are those dominated by only *A. tobuchiensis* with the biomass of attendant species less than 5 % of the community biomass in the sample; and (2) "mixed" areas, named after the co-occurring dominant species, are comprised of two species, with the biomass of each species varying between 20 and 80 % of the community biomass.

Data analysis

To analyze relative similarity of the algal associations and species lists for different years, the data were visualized in a two-dimensional non-metric multidimensional scale (n-MDS) ordination plot based on Bray-Curtis similarity matrix calculated for standardized biomass data or presence/absence data for species lists. Resulting maximum percentage similarity lines were obtained from a group average dendrogram and overlaid on the n-MDS plot. The significance of the resulting groups was tested using the one-way analysis of similarities (ANOSIM). The null hypothesis states that the mean of differences between groups is zero. All analyses were carried out using the software package PRIMER 6.0. The diagrams of algae distribution were prepared using Surfer 7.0 (GoldenSoftware).

Results

Changes of the floristic composition of the *Ahnfeltia* bed

Significant changes in the floristic composition of seaweeds were observed in the *A. tobuchiensis* beds in Amursky Bay over the last 13 years (Table 1). A total of 20 species of macrophytes were found in 1992 (2 species of Chlorophyta, 4 species of Phaeophyceae, and 14 species of Rhodophyta). In 2005, 35 algal species were recorded (2 species of Chlorophyta, 7 species of Phaeophyceae, and 26 species of Rhodophyta). Fifteen species were found in both collections. Additional species (those present in the latest study but not in the earlier) are small epiphytic algae with finely-branched or delicate foliaceous thalli. However, five species were large frondose seaweeds, such as *Chorda filum*, *S. pallidum*, *Stephanocystis crassipes*, and *Desmarestia kurilensis*. It should be noted that all additional species were detected in the northern bed only. The collections of 1992 and 2005 from the northern bed had a similarity of 65.3 %. Both collections from the southern bed were more similar to each other with a similarity of 88.8 % (Fig. 3). The similarity between total species lists of 1992 and 2005 was 64 %.

Changes in the stock and biomass of the dominant species

The total stock of the macrophytobenthos in both *Ahnfeltia* beds decreased from 17,100 t in 1992 to 14,650 t in 2005, although the patterns of changes in various parts of the bed were different. The stock decreased in the southern bed (from 12,600 to 9850 t), while in the northern one, the seaweed resources did not change significantly (4500 t in 1992 and 4800 t in 2005). The stratum thickness was higher in 2005 as compare with 1992 (Fig. 2a, b).

Three algal species had the highest biomass in the *Ahnfeltia* beds (*A. tobuchiensis*, *A. flabelliformis*, and *C. armatus*). These species constitute more than 90 % of the total biomass of macrophytobenthos. Significant changes in the biomass of this species have been found in the study area over the last 13 years. The total *A. tobuchiensis* biomass slightly decreased from 1992 to
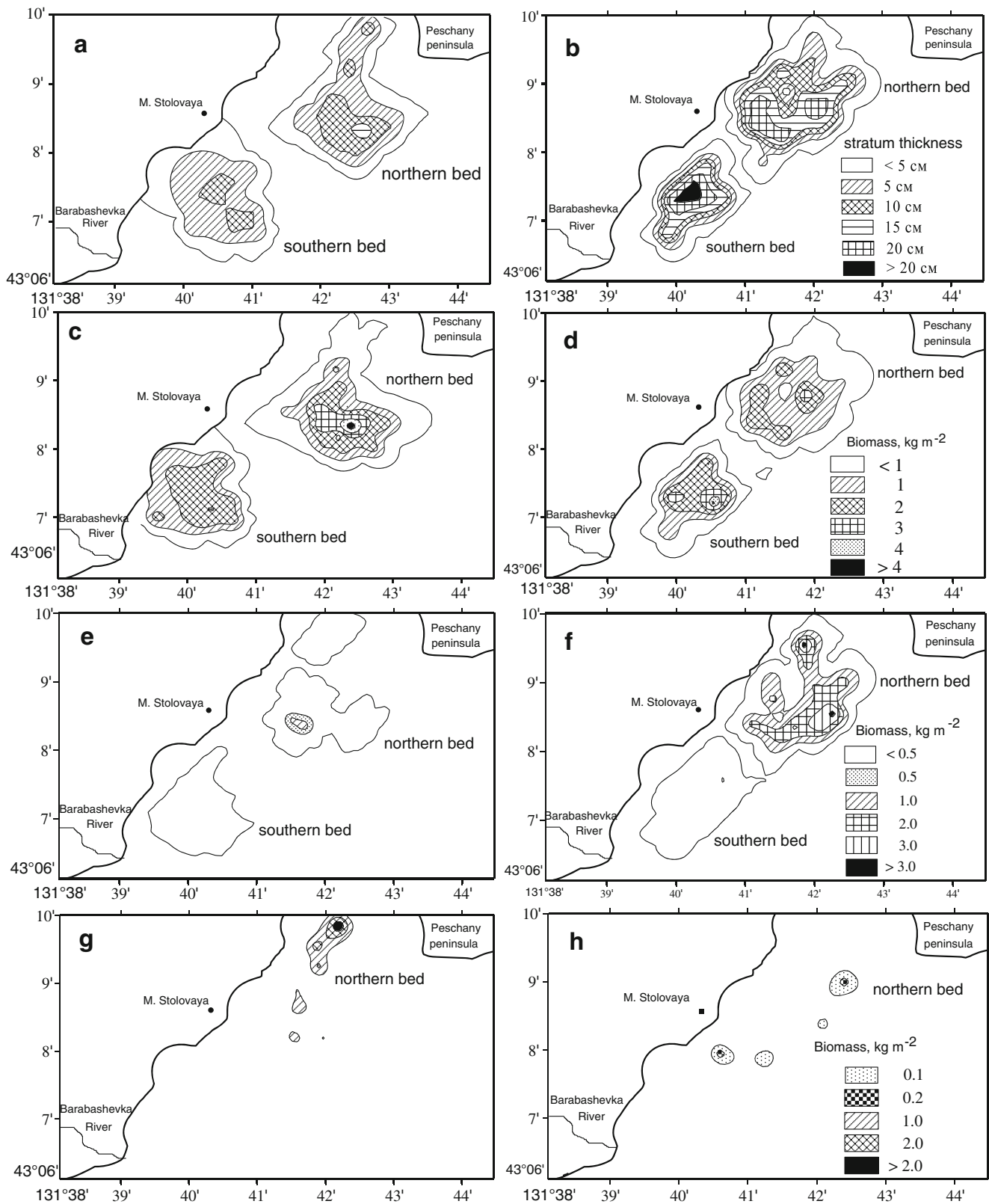
Fig. 2 Stratum thickness and biomass of dominant species in the *Ahnfeltia* bed in 1992 (**a**, **c**, **e**, and **g**) and 2005 (**b**, **d**, **f**, and **h**). **a**, **b** Stratum thickness, **c**, **d** biomass of *Ahnfeltia tobuchiensis*, **e**, **f** biomass of *Ahnfeltiopsis flabelliformis*, and **g**, **h** biomass of *Chondrus armatus*

Table 1 Area of the studied *Ahnfeltia* beds and the stock of dominant species in 1992 and 2005

	Area of *Ahnfeltia* beds (km²)		Stock of the *Ahnfeltia* beds (t)		Stock of *Ahnfeltia tobuchiensis* (t)		Stock of *Chondrus armatus* (t)		Stock of *Ahnfeltiopsis flabelliformis* biomass (t)	
Years	1992	2005	1992	2005	1992	2005	1992	2005	1992	2005
Northern bed	4.8	3.8	12,600	9850	8500	6050	3500	180	575	3050
Southern bed	2.2	1.8	4500	4800	4500	4600	0	15	0	76
Total	7.0	5.6	17,100	14,650	13,000	10,650	3500	195	575	3126

2005. This reduction occurs mainly due to stock decline in the northern bed, while the *A. tobuchiensis* stock in the southern bed was unaltered. The stock of *A. flabelliformis* increased by five times during the study period. The stock of *C. armatus* decreased by 20 times (Table 2).

A. tobuchiensis was a dominant species in both beds in the 1990s and in 2005. Its biomass per square meter was almost constant over the last 13 years (Fig. 2a, b). Major variations in the areas occupied by species and their biomasses were found for *A. flabelliformis* and *C. armatus*. The biomass of *A. flabelliformis*, occurring in the northern bed only, increased by 2–4 times (from 0.1–0.8 kg m^{-2} in 1992 to 0.2–3.5 kg m^{-2} in 2005). The area of the algae accumulations also significantly expanded (Fig. 2e, f). The proportion of this species in the community increased from 4 to 15 % of the community biomass in 1992 to 10–60 % in 2005. The biomass of *C. armatus* decreased from 0.5–3.6 to 0.05–0.2 kg m^{-2} during the same period, coinciding with reduction in the area of the alga accumulation (Fig. 2g, h). The algal proportion in the community decreased from 20 to 50 % of the community biomass in 1992 to 0.1–4 % in 2005.

The MDS ordination plot graphically represents the variation in the *Ahnfeltia* bed over time. Five clusters based on the dominant species biomass were separated (Fig. 4a). The overlay of the MSD plot with the cluster dendrogram similarity lines indicated the respective maximum boundary values for discrimination of clusters. The maximum relative similarity of all clusters was only 15.8 % (Bray-Curtis similarity). The clusters formed by the *C. armatus* or *A. flabelliformis* dominated stations were less similar to all the other (17.3 %). The collections of 1991–1992 and 2005 from the northern bed were separated at a similarity level of 58.4 %. The collections from the southern bed were more similar to each other with an 80 % similarity. The obtained clusters are strongly determined by the biomasses of *A. tobuchiensis*, *A. flabelliformis*, and *C. armatus* (Fig. 4b–d, respectively). There were no significant differences between the samples of 1991 and 1992 (Global R: 0.093, significance level: 1.6 %, no. of permutations: 999, no. of permuted R statistics greater than or equal to Global R: 15, for the results of the pair-wise test see

Fig. 3 Two-dimensional non-metric multidimensional scaling ordination (n-MDS) of similarities in species composition for different time periods
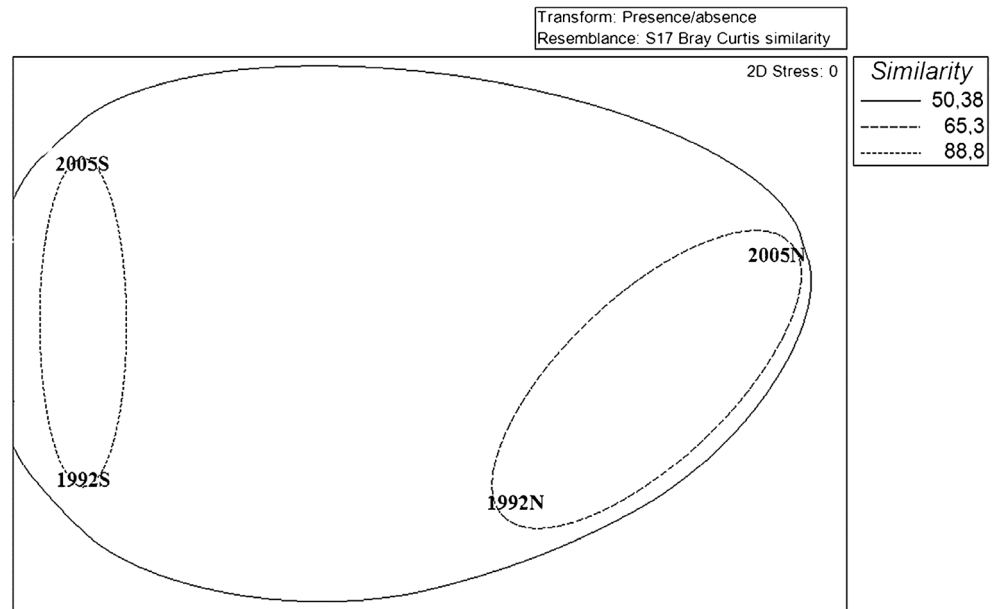
Table 2 Species list of macrophytes recorded in the *Ahnfeltia* bed in 1992 and 2005

Species	1992	2005
Chlorophyta		
Chaetomorpha linum (Müller) Kützing	+	+
Cladophora stimpsonii Harvey	+	
Rhodophyta		
Ahnfeltia tobuchiensis (Kanno et Matsubara) Makienko	d	d
Ahnfeltiopsis flabelliformis (Harvey) Masuda	+++	d
Antithamnion densum (Suhr) Howe	+	+
Bossiella compressa Kloczcova	+	+
Branchioglossum nanum Inagaki*		+
Callophyllis rhynchocarpa Ruprecht		+
Ceramium japonicum Okamura		+
Ceramium cimbricum Petersen		+
Chondrus armatus (Harvey) Okamura	d	++
Coccotylus orientalis (Zinova et Makienko) Perestenko	++	++
Heterosiphonia japonica Yendo		+
Hollenbergia subulata (Harvey) Wollaston	+	
Janczewskia morimotoi Tokida*		+
Laurencia nipponica Yamada	++	++
Masudaphycus irregulare (Yamada) Lindstrom		+
Neorhodomela munita (Perestenko) Masuda	++	++
Neosiphonia japonica (Harvey) Kim et Lee	+	+
Neosiphonia yendoi (Segi) Kim et Lee		+
Nienburgella angusta (A.D. Zinova) Perestenko	+	++
Palmaria stenogona Perestenko		+
Ptilota filicina J. Agardh	+++	+++
Sparlingia pertusa (Postels et Ruprecht) Saunders, Strachan et Kraft	+	+
Stylonema alsidii (Zanardini) Drew		+
Symphyocladia latiuscula (Harvey) Yamada		+
Tichocarpus crinitus (Gmelin) Ruprecht	+	+
Phaeophyceae		
Chorda filum (Linnaeus) Stackhouse		+
Stephanocystis crassipes (Mertens et Turner) C. Agardh		+
Desmarestia kurilensis Yamada*		+
Saccharina cichorioides (Miyabe) Lane, Mayes, Druehl et Saunders	+	+
Sargassum pallidum (Turner) C. Agardh		+
Scytosiphon lomentaria (Lyngbye) Link	+	
Sphacelaria plumosa Lyngbye	+	+

(+) rare species found only in few samples; (++) common species with a biomass less than 10 g m^{-2} (less than 1 % of the total biomass of macrophytobenthos in the bed); (+++) common species with a biomass less that 10 % of the total biomass of macrophytobenthos in the bed; (d) dominant species with a biomass exceeding 20 % of the total biomass of macrophytobenthos in the bed; (*) new species for the *Ahnfeltia* beds

Table 3). No correlation between depth and species distribution in the northern bed was found.

Thus, a total of three areas were described in the studied *Ahnfeltia* beds in the 1990s and in 2005. These were (1) "pure" *Ahnfeltia* areas in the southern bed in both sampling periods and in the south-eastern part of the northern bed in 1992, (2) "mixed" *A. tobuchiensis* and *A. flabelliformis* area in the northern bed in 2005, and (3) "mixed" *A. tobuchiensis* and *C. armatus* area mainly in the southern and western parts of the northern bed in the 1990s (Fig. 5).

Discussion

The results of the present research revealed a community alteration in the *Ahnfeltia* bed in Amursky Bay since 1992. The most important changes are (1) the increase in species richness and (2) the significant changes in the stock of the dominant species in the bed, i.e., the drastic decrease in the biomass of *C. armatus* and the simultaneous significant increase in the biomass of *A. flabelliformis*, while the biomass of *A. tobuchiensis* did not change considerably from 1992 to 2005. These changes led to the alteration of the community structure in the northern bed. Here, the association co-dominated by *A. tobuchiensis* and *C. armatus* was recorded in 1992, and by 2005, this association was succeeded by the *A. tobuchiensis* and *A. flabelliformis* co-dominated association.

Although in the present study the number of species differed significantly between the collections made in 1992 and 2005, the floristic similarity value of both collections was high (Bray-Curtis similarity 64 %). New for the community records are generally rare in the beds and may be absent from the transects. It should be noted that all the species collected in 2005 as well as in 1992 are common in Peter the Great Bay (Perestenko 1980), and most of them were previously recorded in the other *Ahnfeltia* beds of the bay (Titlyanova 1980). Therefore, the differences found in the species compositions of the tested *Ahnfeltia* beds between 1992 and 2005 are strongly believed to be rather caused by higher sampling efforts in 2005, during which three parallel samplings were carried out at each station than the influx of biota from the surrounding coast.

The most obvious change was found in the community structure of the northern bed, where *C. armatus* was replaced by *A. flabelliformis*. It must be taken into consideration that under a long-term study of marine communities, the measured differences between two distant samplings may be a short-term process, such as seasonal or interannual fluctuations in the community, instead of long-term trends. The seasonal changes of dominant species biomass in the studied *Ahnfeltia* beds can be repudiated because the samplings were done at the same time (in July). Moreover, it was shown that the community is just slightly variable between seasons and

Fig. 4 Two-dimensional non-metric multidimensional scaling ordination (n-MDS) of similarities of community (**a**) and biomass of *Ahnfeltia tobuchiensis* (**b**), *Ahnfeltiopsis flabelliformis* (**c**), and *Chondrus armatus* (**d**) for different time periods. *N5* northern bed 2005, *N92* northern bed 1992, *N91* northern bed 1991, *S5* southern bed 2005, *S92* southern bed 1992, *S91* southern bed 1991. In **b**–**d**, the algae biomass (kg m⁻²) is given
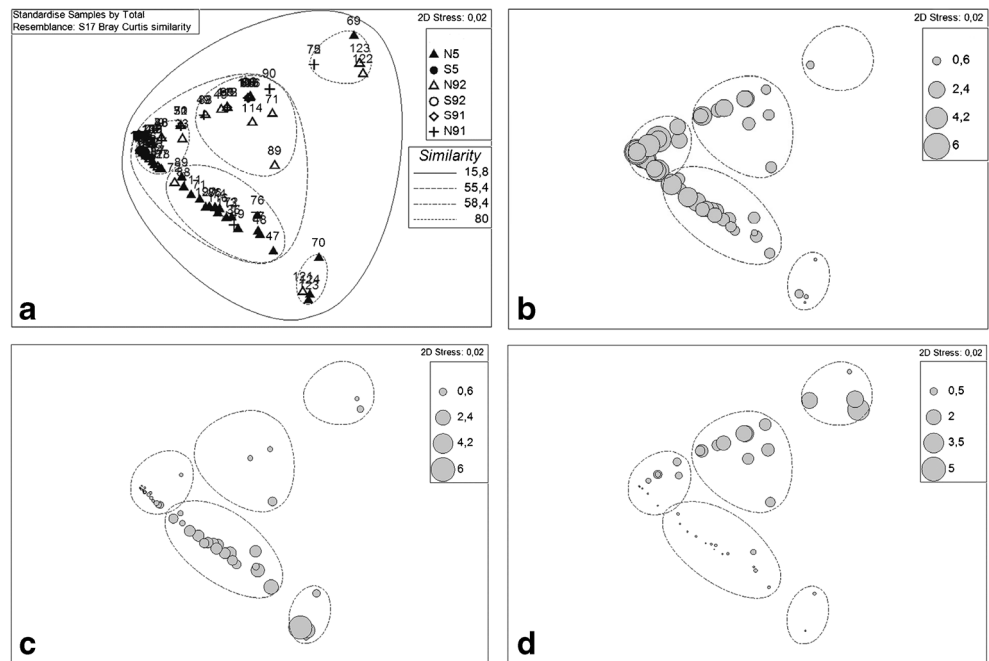
years due to slow growth and failing of seaweeds senescence after reproduction. A reinvestigation of the same station during 1991 and 1992 did not show any changes in the proportions of the dominant species from 1991 to 1992. In stark contrast, the decadal (13-year) pattern of change recorded at the 37 stations located in the northern bed and resurveyed in 1991, 1992, and 2005 is similar to the widespread changes in the proportion of the dominant species. This confirms the data obtained from the whole station set. Moreover, an additional survey done in 2002 revealed that *C. armatus* almost disappeared in the northern bed and the coenotic role of *A. flabelliformis* increased, i.e., its percentage rose from 4 to 15 % of the total community biomass in 1992 to 5–40 % in 2002 (data of 2002 are not shown). So this result suggests that the observed *Ahnfeltia* bed changes over 13 years may not represent short-term fluctuations in the biomass of species. The gradual substitution of *C. armatus* by *A. flabelliformis* in the northern bed has been observed since 2002 at least.

The revealed alterations in the *Ahnfeltia* bed community structure may be the result of environmental changes in Peter the Great Bay, namely water quality change, water warming, physical disturbance by strong storms, or dramatic reduction in community disturbance due to ceased harvesting of seaweeds from the bed. However, they may not be responsible for the observed community alterations to the same degree.

For example, strong storms can occasionally disrupt *Ahnfeltia* beds (Titlyanov et al. 1993). During strong waves, powerful near-bottom currents are formed that conduce to loosening and moving of an algal stratum, its peripheral parts breaking into fragments that can be stranded (Titlyanov et al. 1993). Big accumulations of wrack algae after strong storms confirm the disruption of *Ahnfeltia* strata (Kulepanov et al. 1999). Moreover, storms can induce periodical turning of an algal stratum or its parts (Titlyanova 1980). Consequently, the algae that occur chiefly on the surface of a stratum are removed to the lower layer. Here, the algae are practically subjected to total darkness, hence only the species resistant to extremely low light intensity can occupy this niche. As it was earlier shown, these species are *A. tobuchiensis* and

Table 3 Results of the pair-wise test of one-way ANOSIM test

Groups	Sample *R*	No. of possible permutations	No. of actual permutations	No. of permutated *R*≥sample *R*	Significance level, %
N91, N92	−0.007	Very large	999	417	41.8
S91, S92	−0.008	Very large	999	735	73.6

Groups is the same in Fig. 5

N northern bed, *S* southern bed, 91 and 92—years of collection

Fig. 5 Distribution of the "pure" and "mixed" *Ahnfeltia tobuchiensis* areas in the beds in 1992 (**a**) and 2005 (**b**). *A* "pure" *A. tobuchiensis* areas, *AG* "mixed" *A. tobuchiensis* and *Ahnfeltiopsis flabelliformis* areas, *AC* "mixed" *A. tobuchiensis* and *Chondrus armatus* areas
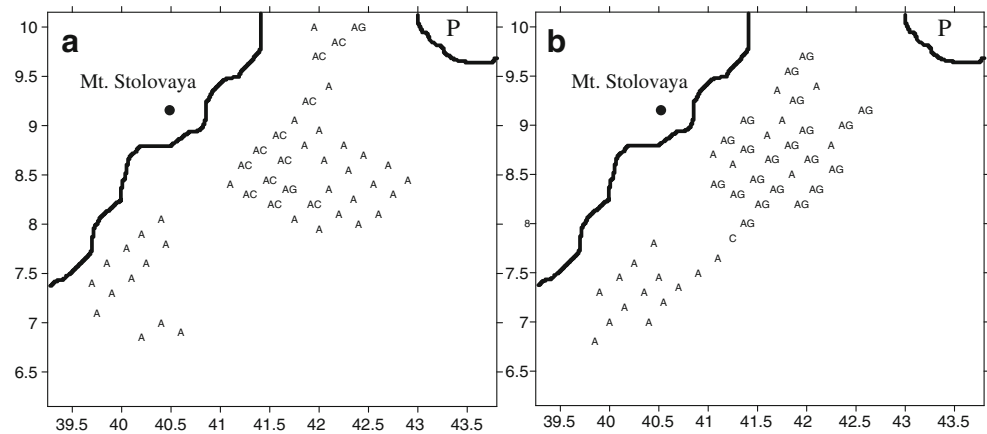
A. flabelliformis, while *C. armatus* inhabiting the bed's surface is less tolerant to low light (Varfolomeeva et al. 1994). Therefore, if *C. armatus* happens to get under the bed, it dies because of light deficiency. Individual fragments of the alga are source for *C. armatus* stock restoration. So the stratum turning can lead to the temporary modification of the community structure. Usually, in favorable environmental conditions, the community returns to its prior state within the year after disturbance. So, we strongly suppose that turning of the studied stratum by strong waves cannot be responsible in itself for decadal community changes.

The cessation of the *Ahnfeltia* bed exploitation could cause the alteration of the community structure. Dragging, similarly to storm disturbance, results in the break and overturn of parts of the bed (Titlyanov et al. 1993). Certainly, the stratum becomes stable when harvesting stops, and it might cause gradual structural changes in the community. In case of stratum stabilization, photophilous species, such as *C. armatus*, stay on the bed surface under the most favorable light conditions that allow this species to grow fast and enlarge its biomass if other environmental conditions do not limit the algal growth. Conversely, our data showed significant reduction in the biomass of this species in the study area. Similar catastrophic reduction (by 20 times) in *C. armatus* stock occurred in Ismena Bay from 1991 to 2008 (own unpublished data). The elimination of *C. armatus* from the studied bed could be explained by its competitive supplantation by the dominant species *A. tobuchiensis*. However, our experiments did not show inhibitive effect of *A. tobuchiensis* on the photosynthetic rates and growth of *C. armatus* at least in a short time period (about 3 weeks) (Nabivailo et al. 2014). A significant increase in the stock and biomass of *A. flabelliformis* in the studied bed cannot also be explained by harvesting termination. This species is physiologically similar to *A. tobuchiensis*: both species have similar requirements in light and nutrients and show similar growth rates in the same growth conditions (Nabivailo et al. 2014). One of the possible explanations of the increase in *A. flabelliformis* stock is the influx of spores or seedlings from the surrounding coasts which resupply the population of the

alga in the bed. However, it was shown that *A. flabelliformis* found within the *Ahnfeltia* bed is genetically distant from the one growing in the nearest water area (Shibneva and Zaslavskaya 2012) and the latter cannot be a source for the algal population increment in the studied community.

So we strongly suggest that both storm disturbance and harvesting cessation cannot be responsible for the observed community alteration in themselves; however, they might be a trigger of the succession maintained by environmental changes. In general, secondary succession does not return the ecosystem to its historic state if environmental conditions change. A new-forming community will be best adapted to average conditions in the area and will reach a new stable equilibrium. It is considered that in general, long-term alterations in stable macroalgal communities are caused by unidirectional varying long-affected factors. Nutrients, water temperature, and light levels are the major factors regulating the dynamics of macroalgal communities at local scale.

Deterioration of the water quality due to eutrophication or increase of pollution is considered as one of the basic reasons of the decadal and interdecadal changes of seaweed communities (Eriksson et al. 2002). However, it should be noted that, though the coastal ecosystem of Amursky Bay is subject to considerable anthropogenic stress since mid-twentieth century, no marked increase in nutrient concentrations or other polluting agents due to coastal run-off has been observed in the bay in the last two decades, and some reports even revealed its stabilization or decrease (Ogorodnikova 2001; Belan et al. 2007). The decrease in anthropogenic pressure on Amursky Bay during the last decades led to some improvement in the state of the ecosystem and its biodiversity (Belan et al. 2007). Moreover, it did not show any significant changes in nutrient concentrations in the studied area from 1986 to 2005 (Moshchenko et al. 2011). So, the changes detected in the *Ahnfeltia* bed do not seem to be explained by either a nutrient supply increase or rise of pollution in this area.

The next possible cause of the changes found in the *Ahnfeltia* bed may be water warming during the past two decades. In Amursky Bay, the annual sea surface temperature
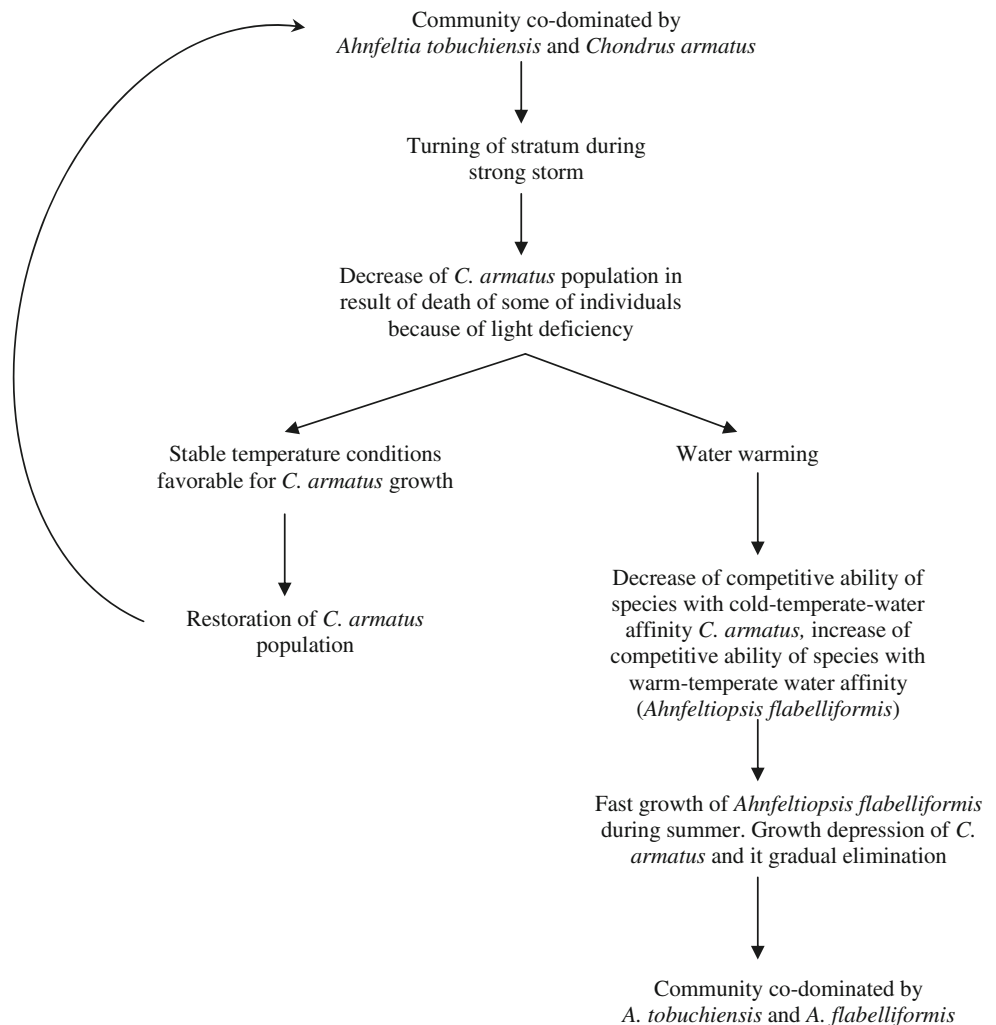
(SST) has increased by 1.7 °C during the last 50 years (Gayko 2005; Moshchenko et al. 2011). The heating caused dramatic changes in seasonal extreme temperatures. Gayko showed that before 1988, the temperatures varied little around the long-term average annual level, but since 1989, positive annual SST anomalies increased to 1–1.4 °C over the normal SST.

These changes could more likely cause the decadal change in the biomass of community-forming species in the studied *Ahnfeltia* beds. We found significant decrease in *C. armatus* biomass and increase in *A. flabelliformis* biomass with relatively small change in the biomass of *A. tobuchiensis* from 1990s to 2005. These alterations can be explained by the prediction of Harley et al. (2006): "species living near their range boundaries are exhibited to thermal stress, and their distribution and abundance may shift when environmental conditions are more favorable." As a consequence, the abundance of southern species should increase and the abundance of northern species should decrease in response to water warming, especially at the edge of their geographic range (Sagarin et al. 1999; Harley et al. 2006). Analysis of latitudinal

distribution of species dominating in the studied *Ahnfeltia* beds revealed that *C. armatus* is a boreal species with cold-temperate-water affinity. It is an endemic of the Sea of Japan. Here, it occurs along the continental coast and at the west coast of Sakhalin Island, as well as at Honshu Island and at the Southern Kuril Islands. Peter the Great Bay is close to the southern margin of *C. armatus* range. On the contrary, *A. flabelliformis* is a warm-temperate species with tropical and subtropical to temperate distribution. In the northern hemisphere, it occurs mainly in Vietnam, Philippines, Taiwan, Hawaii, China, and along the continental and insular coasts of the Sea of Japan (Guiry and Guiry 2013). Peter the Great Bay is the northern margin of its distribution. *A. tobuchiensis* occurs only in Peter the Great Bay, Aniva Bay (south of Sakhalin Island), at Honshu and Kunashir islands, and is therefore a species with temperate-water affinity. Therefore, our findings strongly support the hypothesis that the increase in water temperature observed during past decades can cause changes in the *Ahnfeltia* bed community.

Fig. 6 The hypothetical scenario explained the evolution of the studied *Ahnfeltia* bed community from 1992 to 2005

Community co-dominated by *Ahnfeltia tobuchiensis* and *Chondrus armatus*

Turning of stratum during strong storm

Decrease of *C. armatus* population in result of death of some of individuals because of light deficiency

Stable temperature conditions favorable for *C. armatus* growth

Water warming

Restoration of *C. armatus* population

Decrease of competitive ability of species with cold-temperate-water affinity *C. armatus*, increase of competitive ability of species with warm-temperate water affinity (*Ahnfeltiopsis flabelliformis*)

Fast growth of *Ahnfeltiopsis flabelliformis* during summer. Growth depression of *C. armatus* and it gradual elimination

Community co-dominated by *A. tobuchiensis* and *A. flabelliformis*

It should be noted that changes in the abundance of algae with warm-water and cold-water affinity are well-documented in the temperate zone of the oceans. These include an increase in the abundance of "southern species" in subtidal algal communities in Norway (Husa et al. 2008), a drastic decrease in the abundance of relatively cold-water species such as *Saccharina japonica*, *Kjellmaniella crassifolia*, and *Costaria costata*, and an increase in the biomass of warmer-water species *Undaria pinnatifida*, *Undaria peterseniana*, and *Ecklonia stolonifera* along with an SST rise of 1 °C near northern Honshu Island, Japan (Kirihara et al. 2006). Similarly, a decline of the *Ecklonia cava* population associated with an increase in seawater temperature was observed in southern Japan (Serisawa et al. 2004; Tanaka et al. 2012). Similarly, temperate species such as *Sargassum micracanthum* and *Sargassum okamurae* that dominated during the 1970s in *Isoyake* areas (Japan) have been decreasing, and the subtropical species *Sargassum duplicatum* has become a major component of the flora since the 1990s (Nagai et al. 2011).

So we assume that water warming may be the most possible environmental stress factor playing a central role in changing the community structure of the studied *Ahnfeltia* beds. However, biotic interactions cannot be excluded from consideration. As it was shown before, environmental changes may strongly alter interspecific interactions in algal communities. For example, an increase in light intensity and nutrient accessibility significantly enhanced the competitive ability of *A. tobuchiensis*, *C. armatus*, and *A. flabelliformis* and decreased the negative influence of *A. tobuchiensis* on attendant species (Nabivailo et al. 2014). So it can be suggested that water warming of only a few degrees could have an effect on community competition, altering the competitive ability of relative warm-temperate-water and cold-temperate-water competitors, and therefore affecting community composition. Our preliminary data also support this assumption. It was shown that *C. armatus* is more sensitive to elevated temperature than *A. tobuchiensis* and *A. flabelliformis*. Both the photosynthetic rate and growth rate of *C. armatus* were depressed under 15 °C, whereas in *A. flabelliformis*, these parameters increased with temperature increase from 5 to 15 °C. At low temperature (5–10 °C), the growth rates of *C. armatus* were twice as high compared to *A. flabelliformis*, whereas at 15 °C, the growth rate of *A. flabelliformis* was 1.8 times higher (own unpublished data). This data suggest that the competitive ability and productivity of *A. flabelliformis* increase and of *C. armatus* decrease with water warming. The temperature above 12 °C is an average summer-autumn temperature in Peter the Great Bay. Rising water temperature in warm period of a year allows *A. flabelliformis* to grow actively for a longer period and suppresses the growth of *C. armatus*. This may apparently allow *A. flabelliformis* to gradually replace *C. armatus* in the bed, and the latter wins in the competition for light and nutrients. However, this hypothesis requires experimental confirmation.

Summing up, probably the main factor that caused the alteration of the *Ahnfeltia* bed community located in Amursky Bay is water warming. The hypothetical scenario explaining the evolution of the *Ahnfeltia* bed communities from 1992 to 2005 is given at Fig. 6.

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