



Article The Holocene History of the Diatom Community in a Small Water Body on Shemya Island (Aleutian Arc, USA): The Influence of Global and Local Environmental Changes

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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Abstract: A diatom analysis of a peat deposit from Shemya Island (Aleutian Arc, USA) is performed, and the dynamics of the diatom community are described. According to the radiocarbon dating, the formation of the deposit began 9300 cal. years BP. Principal component analysis made it possible to relate the dynamics of the diatom community to certain environmental conditions and the factors that influenced the coastal ecosystems during its formation. The following factors (predictors) were considered: the influence of age, zoo- and anthropogenic effects, and changes in climatic conditions. Sea level change was the main driver of the diatom community in the studied water body having a continuous direct and indirect influence on the studied small water body, i.e., by bird colony formation and more humid and coastal conditions. Since 3000-2000 cal. years BP, the anthropogenic factor (hunting depression of the bird colony) also became significant. During the whole water body lifetime and following peat formation, the diatom community was influenced by groups of factors: global factors (e.g., sea level rise) caused gradual change of local factors, which resulted in smooth shifts in community. In contrast, local factor influence (bird colony rise and fall due to human activity) caused abrupt and transient shifts. We can hypothesize that the relatively stable global environmental conditions in the Late Holocene were an auspicious background to see abrupt changes due to influence of the zoogenic and anthropogenic factors. We believe that further works on the material from other islands will make it possible to form a general picture of changes in the diatom communities in the Holocene and interpret it in connection with climatic changes in the region.

Keywords: diatoms; diatom analysis; principal component analysis (PCA); climate reconstruction; Aleutian Islands; Shemya Island; Holocene

1. Introduction

A great number of palaeoecological publications of the two last decades have been focused on the whole Holocene period with special attention to human-induced transformations of ecosystems in the second half of the Holocene [1–5]. The Aleutian Arc is an area where such studies have intensified over the past two decades on several large and small islands [6–10]. The terrestrial communities of the Aleutian Islands represent a good model for palaeoecological reconstructions for several important reasons.

First of all, the Islands were all formed by volcanic and tectonic activity [11,12]. Terrestrial and freshwater communities of each island have originated by colonization from the continent or from the adjacent islands and are simplified as compared to the mainland communities [13,14] as commonly occurs in relatively small islands [15]. The sea level in the region has been rising during the Holocene, and we expect its strong influence on the

island communities. Volcanic eruptions during different periods of the Holocene also had a significant impact on the flora and fauna of these islands, and their influence was recorded even in localities distant from eruption sites [16–18]. Volcanic activity was more intense in the eastern part of the Aleutian Arc, while more western islands were less vulnerable to its impact [11]. Finally, climatic changes in the region strongly influenced the biota through changes in the annual temperature and humidity, storm activity, snow cover in winter, etc. [19,20].

Along with global factors (volcanism, sea level, and climate changes), local biotic factors have strongly influenced the flora and fauna of the Aleutian Islands. Except for a few islands closest to Alaska and Kamchatka, the Aleutians are lacking top terrestrial mammal predators [21–23], which favored colonization of islands by seabirds forming great coastal colonies [22,24]. In turn, the activity of birds (active guano deposition) influenced the chemical composition of soil and water, and the structure of islands' flora [8,25–28]. Since the beginning of the Early Holocene, the Aleutian Islands began to be colonized by ancient Aleuts, whose activities influenced the local flora and fauna, but not so crucially as people colonization in Europe [29]. Humans colonized different islands at different times from the East, and the seabirds were among their main prey [10,22,30].

Thus, the terrestrial and aquatic biota of each island was influenced by a specific combination of local and global environmental factors, and a comparison of different islands can be helpful for understanding the influence of environmental changes in the Holocene on island biota.

A relatively small island of the Aleutian Arc, Shemya Island, where several archeological sites were detected [31], has attracted the attention of the investigators of the terrestrial communities and their dynamics during the Holocene. Savinetsky et al. [8] analyzed a peat deposit located at the sea shore of this island. They revealed a significant $\delta^{15}N$ enrichment of layers formed at 4700–2800 years BP due to a high seabird guano deposition (due to global sea level rise and seashore approaching to the water body that produced peat). Then, a sharp decline in $\delta^{15}N$ coincided with the first appearance of human settlement on the island and reflected a drastic reduction in seabird abundance. Therefore, the terrestrial fauna of Shemya Island was greatly influenced by a combination of factors specific for this island due to its small size and position in the Aleutian Arc.

In contrast to terrestrial communities, the Holocene history of the freshwater communities in the Aleutians is poorly studied [32]. The remains of several invertebrate (Cladocera, Copepoda, Ostracoda, Rotifera) and algal (cyanobacteria, diatoms) groups are well preserved in the lake sediments and can be used efficiently to reconstruct the Holocene history. In particular, diatom analysis is widely recognized as a useful tool to indicate past environmental changes and to study the effects of environmental factors on the dynamics of the water-body communities. Diatoms, modern and fossil, are ideal proxies allowing assembly of training and calibration sets for different geographical regions and a wide range of purposes [5,33–37]. The diatoms of the Aleutian Islands are poorly studied, although some studies have been conducted on the diatoms of Adak Island [32,38] or the Carlisle Islands [39]. Species composition of Bering Island (Commander Islands) water bodies was also investigated [40]. Fossil diatoms of the Shemya peat deposit were studied previously in a taxonomic aspect [41,42], but no studies on diatom (or any other freshwater) community dynamics in the Holocene on the small Shemya Island have been conducted up to date.

This work is aimed to elucidate the dynamics of the diatom community of a small water body located in Shemya Island during the Holocene and to identify the main global and local factors driving these changes.

2. Materials and Methods

2.1. Study Area and Sampling

Shemya Island is a relatively small (its total area does not exceed 15.3 km²) island in the Near Islands group of the western part of the Aleutian-Commander Islands chain (Figure 1). Unlike most other islands of the Aleutian Arc, it has no volcanoes. In 1999, a peat deposit with a total depth of 385 cm (lab name "McDonald Point") was sampled from the ledge protruding into the sea near Fox Beach in the southeast end of the island (52°42′19″ N, 174°09′11″ E) by a joint expedition of the IEE RAS (A.B. Savinetsky, N.K. Kiseleva, B.F. Khasanov) and the US Western Aleutians Archaeological and Paleobiological Project (WAAPP) [6]. The samples were collected from 76 layers (each with thickness of 3–5 cm).



Figure 1. The general view of the Aleutian Islands (**a**), group of the Near Islands (**b**), Shemya Island (**c**) with McDonald point peat location (marked by black dot).

The lithological description of the deposit, results of the calibrated radiocarbon dating, and data on $\delta^{15}N$ (sometimes with gaps) have been published by Savinetsky et al. [8,43] and Smyshlyaeva et al. [27] (see Table S1). Additional information about layers age and "Bchron" package calculations can be found in Table S2 [44,45]. According to the radiocarbon dating, the formation of the deposit began at 9300 cal. years BP. The age of the layers was estimated using previous radiocarbon dating data [8], and, as expected, showed a strong and reliable correlation with the layer depth (r = 0.97, p < 0.000001, N = 16). Some layers were represented by sand masses with little organic matter and no data on the nitrogen content were available for them.

Based on previous studies [8,25,28], we assumed that $\delta^{15}N$ (a difference in ‰ in the ${}^{15}N/{}^{14}N$ rate from that in atmospheric N₂) reflects the strength of the zoogenic effect associated with the abundance of avian guano inputted into the soil. The degree of peat decomposition was calculated by Kiseleva et al. [46]. The degree of decomposition of organic material is supposed to reflect climatic patterns—its high values indicate warmer conditions [46–48], but this correlation could be complicated by different factors [49], especially for volcanic islands. We tested the possibility of its application as an additional proxy in the diatom-based reconstruction.

2.2. Diatom Analysis

The samples were treated in the laboratory following the hot peroxide method described by Kelly et al. [50]. Permanent slides were made using aniline-formaldehyde mount medium (n = 1.67-1.68). The slides were examined under high-power light microscopes Leica 2500 and Leica DM500 at 1000× magnification and under scanning electron microscopy using a Jeol JSM-6380 microscope. For the scanning electron microscopy investigation, drops of cleaned material were air-dried on pieces of aluminium foil, mounted on brass stubs with double sided carbon tape, and coated with Au-Pd in a Giko IB-3 ion coater.

In total, 80 taxa and variations of diatoms were recorded (Table S3). The diatoms were classified into ecological groups according to Van Dam et al. [51], Lange-Bertalot et al. [52], Spaulding et al. [53], and Guiry and Guiry [54]. Proper diatom taxon names were verified according to Guiry and Guiry [54]. Light microscope (LM) and scanning electron microscope (SEM) images of dominant species are represented in Figure 2.

The composition of the diatom community and the abundance of different species for each layer were estimated from the number of valves counted in five slides. For some layers, we counted less than 300 valves in the five slides [34]. In these cases, if neighboring poor layers were similar in their species composition and belonged to similar stratigraphic layers according to Savinetsky et al. [8], we merged them with each other to have 300 or more valves for each of the resulting combined layers. Especially poor (="empty") layers (usually associated with mostly sand intercalations) were excluded from the analysis. After merging neighboring valve-poor layers and excluding "empty" layers with no diatoms found, 16 combined layers were included in the analysis (Table S1). For each combined layer, δ^{15} N and degree of decomposition of plant material were calculated as the average of estimates for all initial layers. The mean age of each combined layer was determined according to Table S2.

Most of the diatom species found here are widely distributed taxa, which allowed us to use the data on their ecological preferences known from previous studies [51,52,54–56]. The taxa included in the analysis were selected and grouped according to the following scheme: (1) abundant indicator species with specific ecology were included as separate taxa; (2) ecologically similar species from the same genera were combined at the genera level and in one case (close genera *Staurosira* and *Staurosirella*) in an artificial supra-genera group; and (3) rare taxonomic groups for which <30 valves were detected over the entire deposit were excluded from the analysis. As a result, 17 groups of taxa (6 individual species, 10 genera-level groups, and 1 supra-generic group were used for the analysis (Table 1, Figure 2)). Unfortunately, different taxa in these groups have mainly different trophic preferences (see [51]), and such data could not be used in the analysis of trophic conditions in the water body.

Tilia 2.6.1 and Tilia-Graph software [57] were used to plot a diagram of the layer-bylayer distribution of the taxa of the diatoms and to perform the stratigraphically constrained incremental sum of squares cluster analysis (CONISS) to identify the stages of the diatom community dynamics. The stratigraphic zones were visually identified using the results from CONISS [58].

Taxonomic Groups		Ecological Characteristics		
Combined Groups	Taxa Included in the Combined Groups	Ecological Group	Habitat	Water Patterns
Aulacoseira spp.	Aulacoseira canadensis, Aulacoseira crassipunctata, Aulacoseira italica	Freshwater	Benthic, planktonic	Slightly acidic waters
Cavinula spp.	Cavinula cocconeiformis, Cavinula cocconeiformis f. elliptica, Cavinula davisiae	Freshwater, terrestrial	Benthic	Oligotrophic, slightly acidic waters with a low conductivity
Chamaepinnularia spp.	Chamaepinnularia krookii, Chamaepinnularia krookiiformis,	Freshwater, brackish, terrestrial	Benthic	
Cocconeis spp.	Cocconeis cf. californica, Cocconeis cf. islandica, Cocconeis cf. scutellum, Cocconeis costata, Cocconeis nacentula s 1	Marine/freshwater	Epiphytic	
Diadesmis + Humidophila	Diadesmis mochalovae, Humidophila laevissima,	Freshwater, terrestrial	Benthic	
Diploneis spp.	Diploneis krammeri, Diploneis ovalis, Dinloneis vseudovalis	Freshwater, terrestrial	Benthic	Low alkalinity, slightly acid waters
Encyonema spp.	Encyonema silesiacum, Encyonema minutum	Freshwater, marine, terrestrial	Benthic	Circumneutral waters
Luticola spp.	Luticola arctica, Luticola cf. mutica Discutaria anta dii	Freshwater, terrestrial	Benthic	
Pinnularia spp.1	Pinnularia arkaai, Pinnularia intermedia, Pinnularia lagerstedtii, Pinnularia regudoparza	Freshwater, terrestrial	Benthic	Slightly acidic, oligotrophyc, low conductivity waters
Pinnularia spp.2	Pinnularia inconstans, Pinnularia cf. islandica	Freshwater	Benthic	
Staurosira spp. + Staurosirella spp.	Staurosira construens, Staurosira construens var. exigua, Staurosira construens var. venter, Staurosirella lapponica, Staurosirella martyi, Staurosirella minuta	Freshwater	Benthic, planktonic, epiphytic	
Individual species				
·	Eunotia cf. bidens Eunotia curtagrunowii Pinnularia borealis Pinnularia lata	Freshwater Freshwater, terrestrial Freshwater, terrestrial Freshwater, terrestrial	Benthic, epiphytic Benthic Benthic Benthic	Acid waters with a low conductivity Cold, acidic waters with low conductivity Cold, oligotrophic waters Cold, oligotrophic waters
	Kextowea navicularis Stauroforma exiguiformis	Freshwater Freshwater	Benthic Epiphytic	Circumneutral waters

Table 1. Species and taxonomic groups of diatoms and their ecological preferences (according to [51,54,55,59–61]) included in the analysis.



Figure 2. LM and SEM images of dominant species in the peat deposit from McDonald Point, Shemya Island: (a1) Aulacoseira crassipunctata; (a2,3) Aulacoseira canadensis; (a4) Aulacoseira crassipunctata SEM; (b1) Cavinula davisiae; (b2) Cavinula cocconeiformis; (b3) Cavinula cocconeiformis f. elliptica; (c1) Humidophila laevissima; (c2) Diadesmis mochalovae; (d) Encyonema silesiacum; (e) Luticola arctica; (f1) Staurosirella lapponica; (f2) Staurosirella martyi; (f3) Staurosirella minuta; (g1) Eunotia cf. bidens; (g2,3) Eunotia curtagrunowii; (h1,2) Stauroforma exiguiformis; (i1) Staurosira construens var. venter; (i2) Staurosira construens; (i3) Staurosira construens var. exigua; (j1,2) Pinnularia pseudoparva; (j3) Pinnularia intermedia; (j4,5) Pinnularia borealis; (j6) Pinnularia arkadii; (j7) Pinnularia inconstans; (j8) Pinnularia lata. Scale bar = 10 μm for all, except (a4). For (a4), scale bar = 5 μm.

To describe the dynamics of the diatom community, we assessed the taxonomic diversity and relative abundances of the 17 taxonomic groups included in the analysis for each of the 16 layers. As a measure of taxonomic diversity, we used Shannon's diversity index, (H') [62]. We assessed the relative abundances of taxonomic groups as the number of valves of each group divided by the total number of valves of all taxa found in the layer. The latter varied slightly (from 300 to 306), which made it possible to obtain adequate comparable estimates of the relative abundances of taxa in different layers. To reduce the dimensionality of correlated measures of the relative abundances of 17 taxa, we used a principal component analysis. The first three components, which explained 65.8% of the total variation in taxa abundances, and Shannon's H' were all normally distributed (Shapiro-Wilk test: p > 0.05) and used in GLMs (generalized linear models) as dependent variables to assess the effects of the (1) age of the layer, (2) nitrogen content, and (3) decomposition rate (factors) on their variation. Accordingly, we constructed three models with a full set of four dependent variables and one factor in each.

Statistical analyses were performed using Statistica 12 software, version 12.5.192.7 (TIBCO[®] (StatSoft[®])) [63] and the free software environment R, version 3.6.2, using the vegan, rioja, and ggplot2 packages [64–66].

3. Results

3.1. Environmental Factor Dynamics

The decomposition rate was fluctuated strongly through the time (from 4 to 60%). Decomposition rate values, fluctuated in the range of 4–25.7%, before Zones changing, reached a maximum at approximately 265 cm (~4800 cal. years BP) (Figure 3a). Then, the decomposition rate declined, not reaching its minimum values, but stopping at 20–31%. No data were available on decomposition rate in the two uppermost layers (0–6 cm).

Table 2. Factor loadings (based on variable-component correlations) for the first three components.Bold type indicates cases of moderate or strong correlations.

Taxa	PC1	PC2	PC3
Aulacoseira spp.	0.11	0.36	-0.11
Cavinula spp.	0.32	0.83	0.27
Chamaepinnularia spp.	-0.69	-0.15	0.56
Cocconeis spp.	-0.85	-0.05	0.37
Diadesmis + Humidophila	0.51	-0.58	0.39
Diploneis spp.	-0.53	-0.08	-0.31
Encyonema spp.	0.28	0.84	0.19
Eunotia cf. bidens	0.29	-0.35	-0.31
Eunotia curtagrunowii	0.54	-0.61	0.32
Luticola spp.	-0.70	-0.13	0.58
Pinnularia borealis	0.58	-0.68	0.02
Pinnularia lata	0.34	-0.41	-0.30
<i>Pinnularia</i> spp.1	-0.86	-0.16	-0.12
Pinnularia spp.2	-0.32	-0.04	-0.68
Rexlowea navicularis	-0.65	-0.11	-0.23
Stauroforma exiguiformis	0.29	0.90	0.20
Staurosira + Staurosirella	0.13	-0.31	0.77



Figure 3. Dynamics of environmental conditions: decomposition rate (**a**), δN^{15} (**b**), and diatom community parameters: first three principal components (**c**–**e**) and Shannon Index (**f**). PC1 is associated with cold-water and terrestrial diatoms, PC2 with benthic and epiphytic diatoms, and PC3 with taxa inhabiting moist soil and mosses (see Tables 1 and 2). Dashed line marks the border between Zone 1 and Zone 2 (at 265 cm), while areas of gray color mark layers of sandy content with no diatom valves found.

The δ^{15} N (Figure 3b) began to accumulate in the peatland soil at ~8800 cal. years BP (~350 cm) and, with accelerating pace, reached high values at ~4800 cal. years BP (~270 cm), and a peak of concentration at ~3900–3800 cal. years BP (235–245 cm, Figure 3b). Then, it rapidly declined (by more than three times by 2000 cal. years BP) and continued to decrease gradually to nearly zero by the present time. No data on the nitrogen content were available for some layers—they were represented by continuous sandy layers, with extremely low concentrations of organic matter (layers 285–296, 300–305, 305–310 cm).

3.2. Diatom Community Dynamics

Based on the diatom analysis and CONISS clustering, we identified two zones with three subzones in each zone that were strongly different in the species composition (Figure 4). Four intervals with sand layers contained no or single diatom valves: 6–65 cm (40–680 cal. years BP), 75–144 cm (690–2000 cal. years BP), 164–235 cm (2200–3900 cal. years BP), and 245–265 cm (4000–4800 cal. years BP).

Zone 1 covered 120 cm (9500–4500 cal. years BP) and was divided into three subzones (1a, 1b, and 1c). The dominant taxa in this zone were *Aulacoseira* species, *Diadesmis* + *Humidophila*, *Eunotia* species, *Pinnularia borealis*, *Pinnularia lata*, and species of the genera *Staurosira* and *Staurosirella*.

Subzone 1a (385–350 cm, ~9500–8800 cal. years BP) was characterized by the presence of *Pinnularia lata* and *Eunotia* cf. *bidens* with their abundances decreased towards the subzone top. The presence of *Eunotia curtagrunowii*, *Pinnularia borealis*, *Stauroforma exiguiformis* and species of *Diadesmis* + *Humidophila* was also noted.

An abundance of *Pinnularia borealis* and *Eunotia curtagrunowii* increased in Subzone 1b (350–318 cm, ~8800–7400 cal. years BP). Epiphytic forms, represented by *Cavinula*, *Staurosira*, and *Staurosirella* species, with *Stauroforma exuguiformis* as dominant, appeared. An abundance of epiphytic taxa decreased towards the top of the subzone, while an abundance of *Diadesmis* + *Humidophila*, preferring terrestrial habitats, increased, reaching its maximum. The valves of *Eunotia* cf. *bidens*, presented in the underlying layers, disappeared in this zone, while *Aulacoseira* spp. was observed sporadically.



Figure 4. Stratigraphic profiles based on diatom analysis (relative abundance, %) and CONISS clustering results. Dashed line marks boundary between Zone 1 and Zone 2 (at 265 cm), areas of gray color mark layers of sand with no diatom valves found. Five or less valves in a layer are marked with dots, while the more abundant valves are marked with bars.

In Subzone 1c (318–265 cm, ~7400–4800 cal. years BP), the number of *Aulacoseira* valves increased noticeably. At the same time, the core of the diatom community was formed by *Stauroforma exiguiformis, Cavinula* (mainly *C. cocconeiformis* f. *elliptica* and *C. davisiae*), and *Encyonema* (*E. silesiacum* and *E. minutum*) species. *Diadesmis* + *Humidophila, Eunotia curtagrunowii*, and *Pinnularia borealis* completely disappeared. A complex of species from the genus *Pinnularia* (including mainly *P. intermedia, P. incostans*, and *P. arkadii*) appeared at the top of this zone.

The interval between Zones 1 and 2 (265–245 cm, ~4800–4000 cal. years BP) was represented by a layer of sand where the diatom valves were absent or sporadically recorded.

Zone 2 covered 245 cm (~4000 cal. years BP to present). The dominant taxa of Zone 2 were represented by two ecologically different species complexes of the genus *Pinnularia*.

In Subzone 2a (245–235 cm, ~4000–3900 cal. years BP), a dramatic change in the species composition and structure of the diatom complex was observed. All usual species of the underlying layers disappeared here. *Pinnularia* cf. *islandica*, *Pinnularia incostans*, and *Pinnularia intermedia* became the obvious dominants.

In the interval between Subzones 2a and 2b (235–164 cm, ~3900–2000 years BP), diatom valves were absent or represented by single fragments.

Subzone 2b (164–65 cm, ~2000–680 cal. years BP) contained an interval without any valves (75–144 cm, ~1700–690 cal. years BP). The similarity of the species composition in the layers above (65–75 cm, ~700–650 cal. years BP) and below (144–164 cm) allowed us to combine them into a single zone. The zone was characterized by the dominance of *Pinnularia* cf. *islandica*, *P. viridiformis*, and *P. inconstans*. Their abundance began to decrease from the base to the top of this subzone. At the same time, *Rexlowea navicularis*, whose valves were found only in this subzone, and representatives of the genus *Diploneis* (*D. krammeri*, *D. ovalis*) were among the dominants.

The interval of 65–6 cm (~650–41 cal. years BP) was represented by a thick layer of sand without diatom valves.

Subzone 2c (6–0 cm, ~41 cal. years BP–present time) was characterized by an increased species number and the presence of *Pinnularia lagerstedtii* among the dominants. In addition, species of the genus *Chamaepinnularia* (*C. krookii* and *C. krookiiformis*), inhabiting moist and aerated habitats, and species of the genus *Luticola* (*L. arctica* and *L.* cf. *mutica*), were present

only in this subzone, where they reached a high abundance. The presence of *Staurosira* and *Staurosirella* spp. was also noticeable in this subzone.

Shannon's diversity index (H') varied strongly with the layer age, from 0.57 to 1.73 (Figure 3f), showing no linear time trend ($R^2 = 0.02$, $F_{1,14} = 0.3$, p = 0.6). The diversity was the highest at the lowest and uppermost layers (H' = 1.30-1.50 for 350–385 cm, ~8700–9500 cal. years BP, and H' = 1.36-1.74 for 0–6 cm, ~25 cal. years BP–present, respectively). The lowest diversities were recorded at 285–310 cm (5600–6600 BP) and 235–245 cm (3800–3900 cal. years BP). The latest minimum of the diatom diversity coincided in time with the maximum of δ^{15} N. In general, the Shannon's H' was negatively related to δ^{15} N ($R^2 = 0.52$, slope = -0.72 ± 0.21 , $F_{1,11} = 11.9$, p < 0.01), but was not related to decomposition rate ($R^2 = 0.14$, $F_{1,9} = 1.43$, p = 0.26).

3.3. Principal Component Analysis

The first three principal components (PC) explained 65.8% of the total variation in initial variables reflecting the relative abundances of 17 diatom groups and individual taxa. Analysis of the loadings of each taxon to each PC (Table 2) allowed us to interpret their ecological meaning.

PC1 (27% of the total variance) (Figures 3c and 5a,b) reflected an increase in the abundances of the cold-water taxa living in aerated water with low pH and conductivity (*Eunotia*, see Table 2 and Table S3) and terrestrial (=soil) species (*Pinnularia borealis* and *P. lata*). Among the acidophiles, these are *Eunotia curtagrunowii*, *Pinnularia borealis*, and *P. lata*, cold-water terrestrial species that also need silica available in the environment to form their frustules. In addition, PC1 was associated with an increase in abundance of *Diadesmis* + *Humidophila*, also preferring moist soils, but negatively associated with epiphytic *Cocconeis*, *Chamaepinnularia*, and *Pinnularia lagerstedtii*. PC1 was strongly and positively correlated with the layer age (i.e., showed a significant negative linear time trend, $R^2 = 0.94$, $F_{1,14} = 220.8$, slope = 0.97 ± 0.07 , p < 0.000001), weakly negatively and non-significantly correlated with decomposition rate ($R^2 = 0.27$, $F_{1,9} = 3.26$, p = 0.1), and varied independently of δ^{15} N ($R^2 = 0.04$, $F_{1,11} = 0.4$, p = 0.5).

PC2 (23.4% of the total variance) (Figure 3d) was associated with an increase in abundances of benthic and epiphytic species (*Cavinula* spp., *Encyonema* spp., and *Stauroforma exiguiformis*, Table 1). The latter is absent in dystrophic habitats and environments strongly acidified by inorganic acids. PC2 also reflected the decline of cold-water and acidophilic taxa (*Eunotia curtagrunowii* and *Pinnularia borealis*). PC2 did not show a linear time trend ($R^2 = 0.01$, $F_{1,14} = 0.1$, p = 0.7; Figure 3d), peaking at 5000–7000 cal. years BP, and ambient significantly increased with increasing $\delta^{15}N$ ($R^2 = 0.27$, $F_{1,11} = 4.0$, slope = 0.52 ± 0.26 , p = 0.07), but varied independently of the decomposition rate ($R^2 = 0.0004$, $F_{1,9} = 0.0003$, p = 0.95).

PC3 (15.3% of the total variance) (Figure 3e) reflected an increase in abundances of *Chamaepinnularia* spp., *Luticola* spp., *Staurosira* spp., and *Staurosurella* spp.—the taxa inhabiting moist soil and mosses. It did not show a linear time trend ($R^2 = 0.0001$, $F_{1,14} = 0.002$, p = 0.97), peaking at 6000–8000 cal. years BP and at the present time, and ambient significantly decreased with an increase in δ^{15} N ($R^2 = 0.29$, $F_{1,11} = 4.5$, slope = -0.54 ± 0.25 , p = 0.057) and was strongly and negatively related to the decomposition rate ($R^2 = 0.41$, $F_{1,9} = 6.2$, slope = 0.64 ± 0.26 , p = 0.03).



Figure 5. Regressions of the first three components on δ^{15} N (**a**) and decomposition rate (**b**). Dashed lines show significant and close to significant relationships.

4. Discussion

4.1. Diatom Community Dynamics: Environmental Effects

Short paleoreconstruction based on the diatom analysis is represented in Appendix A. PC1 associated with the diatoms of aerated waters with a low pH and conductivity, and with terrestrial taxa, is the only PC that shows a significant negative linear time trend (Figure 3c). These ecological groups were most abundant in the lowest time Zone 1 and then disappeared. This may reflect a general trend in the abiotic changes, in particular the growing influence of the coastal conditions (i.e., the microclimate), as a result of a gradual advance of the coast towards the water body due to the global sea level rise in the Holocene [12]. Landward shift of the coastline should lead to a more humid and milder microclimate as compared to severe and drier conditions at the earlier phases of the water body development when the sea level was lower. But note that PC1 is non-significantly related to decomposition rate (Figure 5a), a possible indicator of warmer conditions [46] (Figure 4). The local trend of PC1 was apparently caused by the global effect of the gradual sea level rise in the Holocene on all coastal ecosystems, not just individual water bodies. In

particular, the observed shift in diatom zones is consistent with vegetation transformations and the humidification of local conditions reported in other studies [27].

PC2 indicates an abrupt rise of benthic and epiphytic diatoms ~7000 cal. years BP (Figure 3d) which coincides in time with an abrupt shift in community structure at the upper Zone 1 (the transition from Subzone 1b to Subzone 1c, Figure 4). Then, its abundance sharply declined at ~5000 cal. years BP, at the next abrupt transition of diatom community from Zone 1 to Zone 2, which suggests that the period of its peak values (~7000–5000 cal. years BP) was the time of maximum development of the pool when it was relatively deep and had a well-developed macrophyte zone.

Macrophytes may also indicate an input of nutrients (including nitrogen) required for their growth. Moreover, "benthic and epiphytic" PC2 demonstrates positive (close to significant) correlation with $\delta^{15}N$ (Figure 5a), and its rise roughly coincides with the beginning of active nitrogen accumulation, an indicator of seabird impact (Figure 3b). Thus, the development of epiphytic assemblages may indicate the introduction of additional organic material into the ecosystem by seabirds and, consequently, the development of higher plants due to a strong increase in the nutrient inflow. In parallel, the excessive nitrogen inflow depressed the community and reduced the diatom diversity as indicated by the negative correlation between δ^{15} N and Shannon's index. Diversity was lowest during the peak of nitrogen inflow, the "benthic and epiphytic period" of community history (7000–4000 cal. years BP), and high before and after this period (Figure 3). The growing influence of the seabird colony on the diatom community after 7000 cal. years BP may be related to the coastline advance towards the pool as the sea level rose [8]. In turn, the decrease of the seabird impact (after 4000 cal. years BP) may be attributed to the decline of the seabird colony due to the colonization of the island by Aleuts [8]. Thus, the "benthic and epiphytic period" of the diatom community history may be the result of a combination of abiotic, zoogenic, and anthropogenic effects.

PC3 (Figure 3e), associated with an abundance of diatoms inhabiting moist soil and mosses, may inversely reflect the pool depth. High values at the bottom of the column may indicate a shallow water body if not just moist soil, while the following decrease after 7000 cal. years BP, in parallel with an abrupt increase of "benthic-epiphytic" PC2, suggests the development of the pool.

"Moss" PC3 is the only component showing a negative relationship with δ^{15} N (Figure 5a)—its minimum coincides with the peak of the organic inflow as indicated by an increase in δ^{15} N enrichment (Figure 5a). On the other hand, PC3 is negatively related to the decomposition rate, which could depend on the temperature (Figure 5b). The increase of the decomposition rate can be explained by a shift to more coastal (mild) conditions in the vicinity of the water body. In addition, PC3 is associated with an increase in the abundance of epiphytic taxa. Decline of epiphytic and soil diatoms after 6000 cal. years BP and their low abundances in Zone 2 can also indicate wetter conditions due to a shift of the coastline towards land, unfavorable for soil- and moss-living diatoms.

4.2. Environmental Factors as Drivers of Gradual and Abrupt Changes in Diatom Community Y

The presence of thick layers of sand could be, theoretically, a trace of tsunamis, which are quite frequent in the Aleutian region [67,68]. However, we found only two valves of truly marine species (*Arachnodiscus* sp. and *Cocconeis* cf. *scutellum* in layer 210–215 cm) in the entire deposit. Such a small number of marine valves allows us to exclude the possible influence of tsunamis on diatom community dynamics. Volcanic ash or other traces of volcanic activity were not found in the studied peat deposit [8,27,43] and, thus, volcanism also did not affect local diatom communities.

The abundance of cold-water diatoms, dominant taxa in the lower Zone 1, had been decreasing during the Holocene (Figures 3c and 4). This is in agreement with the gradual decline of dry dwarf shrub tundra communities at the same point in Shemya Island in the Holocene, indicating the transition from severe to more mild and humid coastal conditions [27]. This local climatic trend which could be proposed based on our diatom

analysis contradicts the global trend of cooling after 4000 BP as the Neoglacial period started [32,69] and can be explained by the growing ocean-coast effect on the local diatom community due to the sea level rise. Humidification of local conditions is also supported by the gradual decline in terrestrial soil-living taxa. Thus, the continuous rise of the ocean level produced a stronger effect on the local microclimate than the global climate changes.

Together with the direct influence on the microclimate and hence the diatom community, the sea level rise had a significant indirect impact on the pool environment. The sea level rise began around 6000 cal. years BP, leading to the flooding of the old shoreline, and forced seabirds to move inland for nesting. This influence was not linear—at first, the δ^{15} N level had been increasing gradually, but then, at about 4500 cal. years BP it rose sharply, which corresponds to a global sea level rise that reached the present values around 5000–4000 cal. years BP [12,70,71]. The zoogenic factor explains the development of higher plants with additional nitrogen inflow as fertilizer, and, consequently, the abundance of epiphytic diatom species in 6000–4000 cal. years BP.

Soils on the islands are known to be exposed to colonial seabirds and have high levels of NO₃, NH₄⁺, and total nitrogen (N) abundance [25,72]. The massive introduction of organic agents (by the influx of water, animals, and mammals) leads to the eutrophication of the water bodies, which is confirmed for other regions [73–75]. In our case, the eutrophication was not so obvious, because the observed diatom species mostly prefer oligotrophic to dystrophic water (*Pinnularia borealis, Pinnularia intermedia, Pinnularia lagerstedtii, Pinnularia lata, Cavinula* spp.). This means that the water body was located out of the bird colony itself, although it received a high input of organic matter. On the other hand, too high concentrations of the nutrients (hyper-eutrophication) can inhibit the growth and development of the diatoms and all vegetation in general [76,77].

The effect of an increase of the organic matter inflow on the diatom community of the pool is clearly detectable. In particular, we found a positive relationship between δ^{15} N and the "benthic-epiphytic" component (PC2), and a negative one with the Shannon's index. A rather sharp decline in the diversity index during the period between ~4000 and ~2000 cal. years BP (154–242 cm) is associated with the peak of nutrients introduced, presumably, with the guano of birds nesting close to the peat deposits (see Figure 3b). After that, diatom diversity again increased as the bird colony on Shemya Island was depressed by human hunting [8]. Therefore, after colonization of the island at about 3000 cal. years BP, humans became one of the main drivers of changes in the coastal environment and fauna, even indirectly influencing the diatoms. The vegetation communities of the Shemya coast also radically changed with the high guano input and after the reduction of avian influence [27]. Thus, combined effects of zoogenic and anthropogenic factors can cause abrupt changes in the coastal ecosystems.

Zone 1 and Zone 2 in diatom community history represent two basically different types of communities. They are separated by 20 cm of layers with high sand content (about 400 years) with no diatoms, suggesting that at the transition point between two regimes (c.a. 4500 cal. years BP), the pool had dried out, and the newly formed pool community was not related by origin to the former, primary community. This abrupt transition in community structure coincided with the peaks of decomposition rate and $\delta^{15}N^5$ (Figure 3a,b), and sharp decline in diatom diversity (Figure 3f). These synchronized abrupt shifts in community and environmental parameters suggest that, at the transition point between the Zone 1 and Zone 2, the properties of the water body have changed drastically due to the regime shift.

Moreover, patterns of community dynamics in the lower Zone 1 and upper Zone 2 differ strongly in terms of the amplitude of fluctuations and graduality. In the continuous Zone 1, not disrupted by sand-filled layers with no diatoms, we observed abrupt rapid threshold-type shifts in community composition (e.g., between Subzones 1b and 1c), strong fluctuations of the Shannon index, and all three principal components. In contrast, in Zone 2, the community changed gradually without sharp transitions from one state to another. The interrelatedness of successive communities and the continuity of community

dynamics was maintained despite long (6000–1000 years, Figure 4) intervals with pure sand with no diatoms, suggesting that the pool was dried out several times during this period. This difference in dynamic patterns between lower and upper zones may be explained by the more stable climatic conditions and sea level in the second half of Holocene compared to the first half, when they had changed significantly and sometimes fluctuated [69,78,79]. These changes might cause rapid shifts in ecosystem states, indicated by several "tipping points" (as per Gladwell [80]; see also [81,82]) in diatom community dynamics observed in the Early Holocene (between Subzones 1a and 1b, 1b and 1c, and Figures 3 and 4) and at the transition point between Zone 1 and Zone 2. We can also hypothesize that the relatively stable global environmental conditions were an auspicious background to see abrupt changes due to influence of the zoogenic and, then, anthropogenic factors.

5. Conclusions

Sea level change was the main driver of the diatom community producing direct (i.e., climatic) and indirect (i.e., zoogenic) influences on the studied small water body. After 3000–2000 cal. years BP, the anthropogenic factor (hunting depression of the bird colony) also became significant. During the entire water body history, the diatom community was influenced by groups of factors: global factors (e.g., sea level rise) caused gradual change of local factors, which resulted in smooth shifts in community. In contrast, local factor influence (bird colony rise and fall due to human activity) caused abrupt and transient shifts. We can hypothesize that relatively stable global environmental conditions in the Late Holocene were an auspicious background to see abrupt changes caused by zoogenic and anthropogenic factors.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/ 10.3390/w13213134/s1, Table S1. Information for the combined layers of McDonald Point peat deposition included in the analysis, Table S2: Information for the layers age carried out using the Bchron package for R environment, Table S3: Species found with their ecological preferences.

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Appendix A

Paleoreconstruction Based on the Diatom Analysis

Based on our diatom analysis and taking into consideration earlier obtained data on abiotic factors, we can reconstruct the history of the studied water body during the Holocene.

Zone 1 (~9500 cal. years BP to -4700 cal. years BP). At this time, earlier stages of a pool formation and then its subsequent filling by water with a gradual depth increasing took place. During all this time, the pool was fresh, with a low conductivity and low pH. The earlier Holocene was a relatively warm period, but the winters were cooler than now [69]. This fact alone explains the abundance of several cold-tolerant taxa in Zone 1.

The diatom community of Subzone 1a indicates a weak acidification of the water body, and, apparently, very earlier stages of its formation since dominant species in the community are usually characteristic of moist soils and very shallow waters (Table 1). *Pinnularia borealis* is a cold- and desiccation-resistant species that can withstand temperatures down to -20 °C [83]. *Pinnularia lata* is an indicator species of siliceous waters; its abundance can mean a high availability of biogenic silica [59]. The presence of few valves of the genus *Aulacoseira* (mainly *A. canadensis* and *A. crassipunctata*), which are planktonic forms, may indicate an increase in pool depth. In general, beginning of the freshwater sedimentogenesis took place at this time.

Aulacoseira spp. valves in Subzone 1b are rare, which is most likely associated with the cessation of the depth increasing. An increase of the epiphytic form abundances and a great abundance of *Eunotia*, as well as a decrease of terrestrial diatom abundances, are evidence of waterlogging beginning as well as of a pH lowering in the pool. The diatom assemblage of Subzone 1b corresponds to an initial stage of the bog development.

A noticeable increase of *Aulacoseira* abundance in Subzone 1c indicates a rise of the water level. Since this genus occurs throughout the entire subzone with a strong abundance which increases towards its top, the water body level can be considered as constantly increasing. In general, only centric diatoms are well-represented in the diatom communities of sphagnum bogs [84]; however, in very shallow bog basins (with depth of 5–10 cm²), centric diatoms are not present [85]. Interestingly, Heart Lake from Adak Island (located 635 km west of Shemya Island) was also characterized by the dominance of planktonic forms (*Aulacoseira subarctica, Cyclotella* spp.) in the period from 9300 to 4400 BP [32]. The authors proposed that it was warmer than now at 9600 BP. They also hypothesized possible strong winds which promoted the mixing of water masses and explain the presence of a large amount of biogenic silicon in the environment.

Staurosira exiguiformis was among the dominants at that time. This is a widespread freshwater benthic cosmopolitan species which also prefers near-neutral waters with a low nutrient content [86]. The water level in the pool was increased at that time, the pH value also increased, and the level of humic acids fell. The observed species of the genus *Cavinula* prefer oligotrophic or dystrophic near-neutral or slightly acidic waters with a low conductivity [87]. An increase of *Encyonema* species abundances is an indicator of depth increasing, as well as of the presence of possible weak water flows [88]. *P. intermedia* is widespread both in swampy water bodies and in sediments of shallow lakes and rivers; it prefers slightly acidified waters (optimal pH = 6.6–7) with a low conductivity [89].

The transition to Zone 2 is marked lithologically by a layer of sand and can be characterized by the absence of any diatom valves. This sand mass was probably transferred by wind from the ocean shore, as, due to the sea level rise, the peat bog became closer to the edge of the island and could be strongly affected by the ocean. Moreover, the beginning of the Neoglacial was characteristic of the winter storm intensification [69]. Most likely, due to the abundant sand drift, this pool was completely filled by sand and dried up, and a newly appeared water body with its diatom community has no continuity with the pool which existed there during Phase 1. A new water body was formed in changed climatic conditions as a cooler Neoglacial climatic phase began. For example, according to the study of the pollen spectra of the peat bog from another island of the Aleutian Arc, Carlisle Island, some changes in the pollen spectra after 4500 cal. years BP reflected an increase in humidity and the climate cooling [26].

Zone 2 (-4700 cal. years BP-present). Zone 2 corresponds to the formation of a peatland with a change of its water chemistry towards near-neutral conditions.

The absolute dominants of the Subzone 2a (*Pinnularia cf. islandica, Pinnularia incostans, Pinnularia intermedia*) are freshwater benthic species, so they could not be introduced with sea sand. They form the core of the diatom community in the new reservoir.

The species composition of Subzone 2b is similar to that of Subzone 2a, but freshwater species preferring waters with moderate conductivity also appear (*Diploneis krammeri*, *D. ovalis*), which could indicate an increase in the ocean influence on the water body, i.e., due to salty water splashes.

Subzone 2c is characterized by the presence of the northern alpine aerophile *Pinnularia lagerstedtii*, which often inhabits wet mosses and the soil surface. *P. lagerstedtii* is a terrestrial species preferring near-neutral or acid waters [90]. *Luticola* cf. *mutica* is a terrestrial species, which indicates the development of soil processes in the surrounding area. An increase in the number of valves of the species *Staurosira* and *Staurosirella* may indicate the development of water macrophyte vegetation.

Thus, we can assume that after disappearance of the pool existing at the time of Zone 1, active waterlogging began, accompanied by some peat-forming processes. At the final stage of its development, the water body was represented by a medium-sized boggy swamp with well-developed vegetation and well-moistened adjacent soil. The water varied from acid (at the very beginning) to slightly acidic (at the end of existence), and the conductivity remained low throughout the entire time.

References

- 1. Mackel, R.; Schneider, R.; Seidel, J. Anthropogenic impact on the landscape of southern Badenia (Germany) during the holocenedocumented by colluvial and alluvial sediments. *Archaeometry* **2003**, *45*, 487–501. [CrossRef]
- Van Bellen, S.; Garneau, M.; Booth, R.K. Holocene carbon accumulation rates from three ombrotrophic peatlands in boreal Quebec, Canada: Impact of climate-driven ecohydrological change. *Holocene* 2011, 21, 1217–1231. [CrossRef]
- Anderson, T.W.; Lewis, C.F.M. A new water-level history for Lake Ontario basin: Evidence for a climate-driven early Holocene lowstand. J. Paleolimnol. 2012, 47, 513–530. [CrossRef]
- García-Alix, A.; Jimenez-Espejo, F.J.; Lozano, J.A.; Jiménez-Moreno, G.; Martinez-Ruiz, F.; García Sanjuán, L.; Aranda Jiménez, G.; García Alfonso, E.; Ruiz-Puertas, G.; Anderson, R.S. Anthropogenic impact and lead pollution throughout the Holocene in Southern Iberia. *Sci. Total Environ.* 2013, 449, 451–460. [CrossRef] [PubMed]
- 5. Barrow, J.L.; Jeziorski, A.; Rühland, K.M.; Hadley, K.R.; Smol, J.P. Diatoms indicate that calcium decline, not acidification, explains recent cladoceran assemblage changes in south-central Ontario softwater lakes. J. Paleolimnol. 2014, 52, 61–75. [CrossRef]
- 6. Corbett, D.G.; West, D.L.; Lefèvre, C. (Eds.) *The People at the End of the World: The Western Aleutians Project and the Archaeology of Shemya Island*; Alaska Anthropological Association: Anchorage, AK, USA, 2010; ISBN 1890396087.
- Savinetsky, A.B.; Kiseleva, N.K.; Khassanov, B.F. Dynamics of sea mammal and bird populations of the Bering Sea region over the last several millennia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 2004, 209, 335–352. [CrossRef]
- 8. Savinetsky, A.B.; Khasanov, B.F.; West, D.L.; Kiseleva, N.K.; Krylovich, O.A. Nitrogen Isotope Composition of Peat Samples as a Proxy for Determining Human Colonization of Islands. *Arct. Anthropol.* **2014**, *51*, 78–85. [CrossRef]
- Hatfield, V.L.; Nicolaysen, K.; WEST, D.L.; Krylovich, O.A.; Bruner, K.M.; Savinetsky, A.B.; Vasyukov, D.D.; MacInnes, B.T.; Khasanov, B.F.; Persico, L.; et al. Human resilience and resettlement among the Islands of Four Mountains, Aleutians, Alaska. *Quat. Res.* 2019, 91, 917–933. [CrossRef]
- 10. Krylovich, O.A.; Vasyukov, D.D.; Khasanov, B.F.; Hatfield, V.; West, D.; Savinetsky, A.A. Hunter-gatherers subsistence and impact on fauna in the Islands of Four Mountains, Eastern Aleutians, Alaska, over 3000 yr. *Quat. Res.* **2019**, *91*, 983–1002. [CrossRef]
- 11. Coats, R.R. *Volcanic Activity in the Aleutian Arc: Contributions to General Geology;* United States Government Printing Office: Washington, DC, USA, 1950.
- 12. Black, R.F. Isostatic, tectonic, and eustatic movements of sea level in the Aleutian Islands, Alaska. In *Earth Rheology, Isostasy and Eustacy*; Moerner, N.-A., Ed.; John Wiley & Sons: Chichester, UK, 1980; pp. 231–248.
- 13. Murie, O.J. Fauna of the Aleutian Islands and Alaska Peninsula; North American Fauna 61–63, 1959. Available online: http://pubs.er.usgs.gov/publication/naf61A (accessed on 30 September 2021).
- 14. Garroutte, M.; Huettmann, F.; Webb, C.O.; Ickert-Bond, S.M. Biogeographic and anthropogenic correlates of Aleutian Islands plant diversity: A machine-learning approach. *J. Syst. Evol.* **2018**, *56*, 476–497. [CrossRef]
- 15. MacArthur, R.H.; Wilson, E.O. *The Theory of Island Biogeography*; Princeton University Press: Princeton, NJ, USA, 2001; ISBN 9780691088365.

- 16. Edwards, K.J.; Dugmore, A.J.; Blackford, J.J. Vegetational response to tephra deposition and land-use change in Iceland: A modern analogue and multiple working hypothesis approach to tephropalynology. *Polar Rec.* **2004**, *40*, 113–120. [CrossRef]
- 17. Hotes, S.; Grootjans, A.P.; Takahashi, H.; Ekschmitt, K.; Poschlod, P. Resilience and alternative equilibria in a mire plant community after experimental disturbance by volcanic ash. *Oikos* 2010, *119*, 952–963. [CrossRef]
- McConnell, J.R.; Sigl, M.; Plunkett, G.; Burke, A.; Kim, W.M.; Raible, C.C.; Wilson, A.I.; Manning, J.G.; Ludlow, F.; Chellman, N.J.; et al. Extreme climate after massive eruption of Alaska's Okmok volcano in 43 BCE and effects on the late Roman Republic and Ptolemaic Kingdom. *Proc. Natl. Acad. Sci. USA* 2020, *117*, 15443–15449. [CrossRef] [PubMed]
- 19. Hulten, E. Flora of Alaska and Neighboring Territories: A Manual of the Vascular Plants; Stanford University Press: Stanford, UK, 1968; ISBN 9780804706438.
- 20. Heusser, C.J. Late Quaternary vegetation of the Aleutian Islands, southwestern Alaska. Can. J. Bot. 1990, 68, 1320–1326. [CrossRef]
- West, D.; Crawford, M.; Savinetsky, A.B. Genetics, prehistory and the colonisation of the Aleutian Islands. *Earth Environ. Sci. Trans. R. Soc. Edinb.* 2007, 98, 47–57. [CrossRef]
- Crockford, S.J. Archaeozoology of Adak Island: 6000 Years of Subsistence History in the Central Aleutians. In *The People Before: The Geology, Paleoecology and Archaeology of Adak Island, Alaska*; West, D., Hatfield, V., Wilmerding, E., Lefèvre, C., Gualtieri, L., Eds.; Archaeopress: Oxford, UK, 2012; pp. 107–143. ISBN 9781407309057.
- 23. Vasyukov, D.D.; Krylovich, O.A.; West, D.L.; Hatfield, V.; Savinetsky, A.B. Ancient canids of the Aleutian Islands (new archaeological discoveries from the Islands of Four Mountains). *Quat. Res.* **2019**, *91*, 1028–1044. [CrossRef]
- 24. Byrd, V.G.; Renner, H.M.; Renner, M. Distribution patterns and population trends of breeding seabirds in the Aleutian Islands. *Fish. Oceanogr.* **2005**, *14*, 139–159. [CrossRef]
- 25. Maron, J.L.; Estes, J.A.; Croll, D.A.; Danner, E.M.; Elmendorf, S.C.; Buckelew, S.L. An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. *Ecol. Monogr.* **2006**, *76*, 3–24. [CrossRef]
- Kuzmicheva, E.A.; Smyshlyaeva, O.I.; Vasyukov, D.D.; Khasanov, B.F.; Krylovich, O.A.; Okuno, M.; West, D.L.; Hatfield, V.L.; Savinetsky, A.B. A 7300-yr-old environmental history of seabird, human, and volcano impacts on Carlisle Island (the Islands of Four Mountains, eastern Aleutians, Alaska). *Quat. Res.* 2019, *91*, 934–952. [CrossRef]
- Smyshlyaeva, O.I.; Severova, E.E.; Krylovich, O.A.; Kuzmicheva, E.A.; Savinetsky, A.B.; Dixie, W.; Hatfield, V. Ornithogenic vegetation: How significant has the seabird influence been on the Aleutian Island vegetation during the Holocene? *Ecol. Evol.* 2021, *11*, 14088–14100. [CrossRef]
- Croll, D.A.; Maron, J.L.; Estes, J.A.; Danner, E.M.; Byrd, G.V. Introduced predators transform subarctic islands from grassland to tundra. *Science* 2005, 307, 1959–1961. [CrossRef]
- 29. Davis, R.S.; Knecht, R.A. Continuity and change in the eastern Aleutian archaeological sequence. *Hum. Biol.* **2010**, *82*, 507–524. [CrossRef]
- Causey, D.; Corbett, D.G.; Lefevre, C.; West, D.L.; Savinetsky, A.B.; Kiseleva, N.K.; Khassanov, B.F. The palaeoenvironment of humans and marine birds of the Aleutian Islands: Three millennia of change. *Fish. Oceanogr.* 2005, 14, 259–276. [CrossRef]
- Lefèvre, C.; Corbett, D.G. Appendix G: WAAPP Radiocarbon Dates. In *The People at the End of the World: The Western Aleutians* Project and the Archaeology of Shemya Island; Corbett, D.G., West, D.L., Lefèvre, C., Eds.; Alaska Anthropological Association: Anchorage, AK, USA, 2010; pp. 243–257. ISBN 1890396087.
- Bailey, H.L.; Kaufman, D.S.; Sloane, H.J.; Hubbard, A.L.; Henderson, A.C.; Leng, M.J.; Meyer, H.; Welker, J.M. Holocene atmospheric circulation in the central North Pacific: A new terrestrial diatom and δ18O dataset from the Aleutian Islands. *Quat. Sci. Rev.* 2018, 194, 27–38. [CrossRef]
- 33. Smol, J.P. Diatoms and Lake Acidity: Reconstructing pH from Siliceous Algal Remains in Lake Sediments; Springer: Dordrecht, The Netherlands, 1986; ISBN 978-90-6193-536-0.
- Battarbee, R.W. Diatom analysis. In *Handbook of Holocene Palaeoecology and Palaeohydrology*; Berglund, B.E., Ralska-Jasiewiczowa, M., Eds.; Wiley: Chichester, UK, 1986; ISBN 9780471906919.
- 35. Vos, P.C.; de Wolf, H. Diatoms as a tool for reconstructing sedimentary environments in coastal wetlands; methodological aspects. *Hydrobiologia* **1993**, *269*, 285–296. [CrossRef]
- 36. Reid, M.A.; Tibby, J.C.; Penny, D.; Gell, P.A. The use of diatoms to assess past and present water quality. *Aust. J. Ecol.* **1995**, 20, 57–64. [CrossRef]
- 37. Pandey, L.K.; Bergey, E.A.; Lyu, J.; Park, J.; Choi, S.; Lee, H.; Depuydt, S.; Oh, Y.-T.; Lee, S.-M.; Han, T. The use of diatoms in ecotoxicology and bioassessment: Insights, advances and challenges. *Water Res.* **2017**, *118*, 39–58. [CrossRef] [PubMed]
- 38. Hein, M. Flora of Adak Island, Alaska: Bacillariophyceae (Diatoms); J.Cramer: Berlin, Stuttgart, 1990; ISBN 978-3443570125.
- Neplyukhina, A.A.; Chudaev, D.A.; Gololobova, M.A. Diatomovie vodorosly torfyanogo otlojenia ostrova Karlayl (Aleutskye ostrova, S.Sh.A) (in russian). In *Materialy V Vserossiyskoy Naychnoy Konferencii s Mezjdunarodnym Uchastiem «Dinamika Ecosistem v Golocene»* (k 100-Letiy L.G. Dinesmana); Savinetsky, A.B., Ed.; Media-PRESS: Moskva, Russia, 2019; pp. 235–236. ISBN 978-5-901003-57-2.
- 40. Potapova, M. Diatoms of Bering Island, Kamchatka, Russia. Nova Hedwig. 2014, 143, 63–102.
- Neplyukhina, A.A.; Chudaev, D.A.; Krylovich, O.A.; Gololobova, M.A. Diatoms of the Peatbog Sediments from Shemya Island (Aleutian Islands, United States). *Mosc. Univ. Biol. Sci. Bull.* 2018, 73, 76–81. [CrossRef]
- 42. Neplyukhina, A.A.; Chudaev, D.A.; Gololobova, M.A. *Pinnularia arkadii* sp. nov., a new diatom (Naviculales, Bacillariophyceae) from Shemya Island, Alaska, USA. *Nov. Sist. Nizshikh Rastenii* **2018**, *52*, 83–89. [CrossRef]

- 43. Savinetsky, A.B.; Kiseleva, N.K.; Khassanov, B.F. Paleoenvironment—Holocene deposits from Shemya Island. In *The People at the End of the World: The Western Aleutians Project and the Archaeology of Shemya Island*; Corbett, D.G., West, D.L., Lefèvre, C., Eds.; Alaska Anthropological Association: Anchorage, AK, USA, 2010; ISBN 1890396087.
- 44. Parnell, A. Bchron: Radiocarbon Dating, Age-Depth Modelling, Relative Sea Level Rate Estimation, and Non-Parametric Phase Modelling: R package version 4.1.1. Available online: https://CRAN.R-project.org/package=Bchron (accessed on 30 September 2021).
- 45. Haslett, J.; Parnell, A. A simple monotone process with application to radiocarbon-dated depth chronologies. J. R. Stat. Soc. Ser. C Appl. Stat. 2008, 57, 399–418. [CrossRef]
- 46. Kiseleva, N.K.; Savinetsky, A.B.; Khassanov, B.F. Development of Natural Processes over the Holocene in Aleutian Islands. *Izv. AN Seriya Geogr.* **2002**, *1*, 97–103.
- 47. Gorham, E. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecol. Appl.* **1991**, *1*, 182–195. [CrossRef] [PubMed]
- 48. Ise, T.; Dunn, A.L.; Wofsy, S.C.; Moorcroft, P.R. High sensitivity of peat decomposition to climate change through water-table feedback. *Nat. Geosci.* 2008, 1, 763–766. [CrossRef]
- 49. Biester, H.; Knorr, K.-H.; Schellekens, J.; Basler, A.; Hermanns, Y.-M. Comparison of different methods to determine the degree of peat decomposition in peat bogs. *Biogeosciences* **2014**, *11*, 2691–2707. [CrossRef]
- 50. Kelly, M.G.; Adams, C.; Graves, A.C. *The Trophic Diatom Index: A User's Manual*; Revised Edition; WRC: Swindon, UK, 2001; ISBN 1-857-05597-7.
- Dam, H.; Mertens, A.; Sinkeldam, J. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. *Neth. J. Aquat. Ecol.* 1994, 28, 117–133. [CrossRef]
- 52. Lange-Bertalot, H. (Ed.) Diatoms of Europe; A.R.G. Gantner Verlag (Koeltz Scientific Books): Königstein, Germany, 2000.
- Spaulding, S.A.; Bishop, I.W.; Edlund, M.B.; Lee, S.; Fure, P.; Jovanovska, E.; Potapova, M. Diatoms of North America. Available online: https://diatoms.org (accessed on 27 April 2021).
- 54. Guiry, M.D.; Guiry, G. AlgaeBase: World-Wide Electronic Publication. Available online: http://www.algaebase.org (accessed on 27 April 2021).
- 55. Lange-Bertalot, H.; Bak, M.; Witkowski, A. Eunotia and Some Related Genera. In *Süßwasserflora von Mitteleuropa*; Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D., Eds.; Spektrum Akademischer Verlag: Stuttgart, Germany, 2007.
- 56. Lange-Bertalot, H. Navicula Sensu Stricto, 10 Genera Separated from Navicula Sensu Lato, Frustulia. In *Diatoms of Europe*; Lange-Bertalot, H., Ed.; A.R.G. Gantner Verlag (Koeltz Scientific Books): Königstein, Germany, 2000.
- 57. Grimm, E.C. Tilia (software): Version 2.6.1. Available online: https://www.tiliait.com/download/ (accessed on 12 June 2021).
- 58. Grimm, E.C. CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Comput. Geosci.* **1987**, *13*, 13–35. [CrossRef]
- Schaumburg, J.; Schranz, C.; Stelzer, D.; Hofmann, G.; Gutowski, A.; Foerster, J. Instruction Protocol for the ecological Assessment of Running Waters for Implementation of the EC Water Framework Directive: Macrophytes and Phytobenthos. 2006. Available online: http://www.planktonforum.eu/fileadmin/_migrated/content_uploads/PHYLIB_instruction_protocol_running_waters_ 01_2006__Schaumburg_etal_2006_.pdf (accessed on 12 June 2021).
- 60. Spaulding, S.; Edlund, M. Staurosira. In Diatoms of North America. Available online: https://diatoms.org/genera/staurosira (accessed on 13 May 2021).
- 61. Spaulding, S.; Edlund, M. Chamaepinnularia. In Diatoms of North America. Available online: https://diatoms.org/genera/ chamaepinnularia (accessed on 13 May 2021).
- 62. Shannon, C.E. A mathematical theory of communication. Bell Syst. Tech. J. 1948, 27, 379–423. [CrossRef]
- 63. TIBCO Software Inc. TIBCO Statistica, v. 12.5.192.7. Available online: https://www.tibco.com/products/tibco-statistica (accessed on 30 September 2021).
- 64. Juggins, S. Rioja: Analysis of Quaternary Science Data.: R Package Version 0.9-26. Available online: https://cran.r-project.org/package=rioja (accessed on 12 June 2021).
- Jari, O.; Guillaume, B.F.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; et al. Vegan: Community Ecology Package: R Package Version 2.5-7. Available online: https://CRAN.R-project.org/ package=vegan (accessed on 12 June 2021).
- 66. Wickham, H. ggplot2: Elegant Graphics for Data Analysis; Springer International Publishing: Cham, Switzerland, 2016; ISBN 978-3-319-24275-0.
- 67. Mann, D.H.; Crowell, A.L.; Hamilton, T.D.; Finney, B.P. Holocene Geologic and Climatic History around the Gulf of Alaska. *Arct. Anthropol.* **1998**, *35*, 112–131.
- Nelson, A.R.; Briggs, R.W.; Dura, T.; Engelhart, S.E.; Gelfenbaum, G.; Bradley, L.-A.; Forman, S.L.; Vane, C.H.; Kelley, K.A. Tsunami recurrence in the eastern Alaska-Aleutian arc: A Holocene stratigraphic record from Chirikof Island, Alaska. *Geosphere* 2015, 11, 1172–1203. [CrossRef]
- 69. Kaufman, D.S.; Axford, Y.L.; Henderson, A.C.; McKay, N.P.; Oswald, W.W.; Saenger, C.; Anderson, R.S.; Bailey, H.L.; Clegg, B.; Gajewski, K.; et al. Holocene climate changes in eastern Beringia (NW North America)—A systematic review of multi-proxy evidence. *Quat. Sci. Rev.* 2016, 147, 312–339. [CrossRef]
- 70. Kaplin, P.A. Osnovnye Etapy Razvitiya Beregovoi Zony v Golotsene[Main Stages of Development of Coastal Area in the Holocene]. *Geogr. Investig. Quat. Period* **1982**, 87–96.

- 71. Kaplin, P.A.; Leont'ev', O.K.; Luk'yanova, S.A.; Nikiforov, L.G. Berega [Shores]; Mysl': Moscow, Russia, 1991.
- 72. Caut, S.; Angulo, E.; Pisanu, B.; Ruffino, L.; Faulquier, L.; Lorvelec, O.; Chapuis, J.-L.; Pascal, M.; Vidal, E.; Courchamp, F. Seabird modulations of isotopic nitrogen on islands. *PLoS ONE* **2012**, *7*, e39125. [CrossRef]
- 73. González-Bergonzoni, I.; Johansen, K.L.; Mosbech, A.; Landkildehus, F.; Jeppesen, E.; Davidson, T.A. Small birds, big effects: The little auk (Alle alle) transforms high Arctic ecosystems. *Proc. Biol. Sci.* **2017**, *284*. [CrossRef]
- 74. Manny, B.A.; Johnson, W.C.; Wetzel, R.G. Nutrient additions by waterfowl to lakes and reservoirs: Predicting their effects on productivity and water quality. *Hydrobiologia* **1994**, 279-280, 121–132. [CrossRef]
- 75. Otero, X.L.; de La Peña-Lastra, S.; Pérez-Alberti, A.; Ferreira, T.O.; Huerta-Diaz, M.A. Seabird colonies as important global drivers in the nitrogen and phosphorus cycles. *Nat. Commun.* **2018**, *9*, 246. [CrossRef] [PubMed]
- 76. Ganning, B.; Wulff, F.; Ganning, B. The Effects of Bird Droppings on Chemical and Biological Dynamics in Brackish Water Rockpools. *Oikos* 1969, 20, 274. [CrossRef]
- 77. Mulder, C.P.H.; Anderson, W.B.; Towns, D.R.; Bellingham, P.J. Seabird Islands; Oxford University Press: Oxford, UK, 2011; ISBN 9780199735693.
- 78. Manley, W.F. Postglacial Flooding of the Bering land Bridge: A Geospatial Animation: INSTAAR, Vol. 1. Available online: http://instaar.colorado.edu/QGISL/bering_land_bridge (accessed on 12 June 2021).
- 79. Smith, D.E.; Harrison, S.; Firth, C.R.; Jordan, J.T. The early Holocene sea level rise. Quat. Sci. Rev. 2011, 30, 1846–1860. [CrossRef]
- 80. Gladwell, M. The Tipping Point: How Little Things Can Make a Big Difference; Little: Boston, MA, USA, 2000; ISBN 9780316316965.
- 81. Dakos, V.; Matthews, B.; Hendry, A.P.; Levine, J.; Loeuille, N.; Norberg, J.; Nosil, P.; Scheffer, M.; De Meester, L. Ecosystem tipping points in an evolving world. *Nat. Ecol. Evol.* **2019**, *3*, 355–362. [CrossRef]
- 82. Dudney, J.; Suding, K.N. The elusive search for tipping points. Nat. Ecol. Evol. 2020, 4, 1449–1450. [CrossRef]
- 83. Souffreau, C.; Vanormelingen, P.; Verleyen, E.; Sabbe, K.; Vyverman, W. Tolerance of benthic diatoms from temperate aquatic and terrestrial habitats to experimental desiccation and temperature stress. *Phycologia* **2010**, *49*, 309–324. [CrossRef]
- 84. Kulikovskiy, M.S. The species composition and distribution of diatom algae in sphagnum bogs in European Russia: The Polistovo-Lovatskii land tract. *Inland Water Biol.* **2009**, *2*, 135–143. [CrossRef]
- 85. Cantonati, M.; Lange-Bertalot, H.; Decet, F.; Gabrieli, J. Diatoms in very-shallow pools of the site of community importance Danta di Cadore Mires (south-eastern Alps), and the potential contribution of these habitats to diatom biodiversity conservation. *Nova Hedwig.* **2011**, *93*, 475–507. [CrossRef]
- 86. Gottschalk, S.; Kahlert, M. Shifts in taxonomical and guild composition of littoral diatom assemblages along environmental gradients. *Hydrobiologia* **2012**, *694*, 41–56. [CrossRef]
- 87. Cvetkoska, A.; Levkov, Z.; Hamilton, P.B.; Potapova, M. The biogeographic distribution of Cavinula (Bacillariophyceae) in North America with the descriptions of two new species. *Phytotaxa* **2014**, *184*, 181. [CrossRef]
- Barinova, S.S.; Niyatbekov, T. Bioindication of aquatic habitats with diatom algae in the Pamir Mountains, Tajikistan. *MOJES* 2018, 3, 117–120. [CrossRef]
- Antoniades, D.; Douglas, M.S.V.; Smol, J.P. benthic diatom autecology and inference model development from the Canadian High Arctic archipelago. J. Phycol. 2005, 41, 30–45. [CrossRef]
- 90. Foets, J.; Stanek-Tarkowska, J.; Teuling, A.J.; van de Vijver, B.; Wetzel, C.E.; Pfister, L. Autecology of terrestrial diatoms under anthropic disturbance and across climate zones. *Ecol. Indic.* **2021**, *122*, 107248. [CrossRef]