Accounting for Uncertainties in Biodiversity Estimations: A New Methodology and Its Application to the Mesopelagic Sound Scattering Layer of the High Arctic

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Measures of biological diversity (biodiversity) are important for monitoring the state of ecosystems. Several indices and methods are used to describe biodiversity from field observations. Marine faunal biodiversity is often quantified based on analysis of samples collected using a trawl during research surveys. To monitor spatial and temporal changes in biodiversity between surveys, samples are generally collected from a series of stations. Inference regarding changes in biodiversity must account for uncertainties in the estimation of the values for the different biodiversity indices used. Estimation for a single station is affected by spatial-temporal variation in the species composition in the area and by uncertainty due to the finite sample size taken by the trawl. Therefore, variation between stations needs to be accounted for when estimating uncertainty for values of different indices during a survey as total or as mean for the survey. Herein, we present a method based on nested bootstrapping that accounts for uncertainties in the estimation of various indices and which can be used to infer changes in biodiversity. Application of this methodology is demonstrated using data collected in the mesopelagic sound scattering layer in the high Arctic.

Keywords: uncertainty, sound scattering layer, mesopelagic, bootstrapping, biodiversity indices, Arctic

INTRODUCTION

Loss of biological diversity (biodiversity) negatively affects ecosystem functioning and may ultimately lead to ecosystem collapse (Bland et al., 2018). Several examples in the literature describe and use different indices to quantify species biodiversity in marine ecosystems (Whittaker, 1972; Chao, 2005; Gamfeldt et al., 2014). These indices also allow to detect changes due to, for example, climate change, ocean warming, acidification, loss of habitat and to assess the impact that fisheries have on marine ecosystems (Kaiser et al., 2011).

As biodiversity is a multidimensional concept that includes estimates of both species' richness and evenness, a single measure of biodiversity is often not sufficient (Daly et al., 2018) and several biodiversity indices are often used. However, using variation in biodiversity indices to infer

changes in an ecosystem raises the following questions: (i) How certain are we that changes in biodiversity indices reflect changes in community biodiversity? (ii) Could differences observed in the biodiversity indices be coincidental? (iii) How reliable are biodiversity indices estimated from experimental sampling? To answer these questions, realistic uncertainty limits around biodiversity indices are needed. Furthermore, to be able to monitor spatial or temporal changes in biodiversity, the uncertainties of differences in index values need to be quantified. Survey trawls are one of the methods used to sample data on species biodiversity (Geoffroy et al., 2019). However, the estimation of biodiversity indices based on a single survey trawl haul is affected by spatial-temporal variation in species composition within the area and by uncertainty related to the finite sample size taken by the sampling trawl. Therefore, for a series of sampling hauls (stations) during a survey, the variation between hauls needs to be accounted for when estimating uncertainty of the value for the different indices. This can be done for the survey area as total or as mean for the stations sampled within.

In this study, we present a method based on a nested bootstrapping technique to account for uncertainties when estimating various biodiversity indices. This type of bootstrapping-based method has previously been used to estimate uncertainties (within- and between-station variability) in relation to fishing gear size selectivity studies (Millar, 1993; Herrmann et al., 2017; Larsen et al., 2017, 2018). Our purpose is to adopt this kind of method for assessing uncertainty in biodiversity studies which are subjected to multilevel sources of uncertainties. Further, this novel approach can be used to infer changes in biodiversity. Specifically, we applied this approach to survey trawl data collected in the Arctic ecoregion as a case study of mesopelagic biodiversity with the purpose to investigate and demonstrate the advantages of this new method.

Mesopelagic macrozooplankton and small pelagic fish occupy the zone extending from 200 to 1000 m below the surface of the ocean. These organisms form a sound scattering layer (SSL), which appears on acoustic echograms as echoes that are higher than background noise in the water column (Proud et al., 2015). SSLs were firstly observed and described in the late 1940s (Dietz, 1948) and further explored during the 1960s (Barham, 1966). Mesopelagic SSLs are ubiquitous in the world's oceans (Irigoien et al., 2014; Proud et al., 2018). However, several knowledge gaps persist regarding the role of these species in the ecosystem and their contribution to biodiversity (St. John et al., 2016; Hidalgo and Browman, 2019).

MATERIALS AND METHODS

Survey Data for Estimation of Biodiversity in the Sound Scattering Layer of the High Arctic

The data used in this study were collected by Geoffroy et al. (2019) onboard the research vessel "Helmer Hanssen" (63.8 m, 4080 HP) in the northern Barents Sea, north of Svalbard, during three trials conducted from 14 to 16 January 2016 (cruise 1), 28 to 29 August 2016 (cruise 2), and 11 to 14 January 2017 (cruise 3). Bottom depth ranged from < 50 m close to shore to ~2000 m at the end of the transects. The SSLs were located between 200 and 700 m in August 2016 and from 50 to 500 m in January 2016 and 2017 (Geoffroy et al., 2019). The samples were collected using a Harstad pelagic trawl within the SSL to ground truth the acoustic signal. The mesh size of the inner liner of the trawl's codend was 10 mm. The Harstad trawl had an opening of 18.28×18.28 m with an actual height of 9–11 m and width of 10–12 m at the towing speed of 3 knots (Geoffroy et al., 2019). The towing time was kept between 20 and 80 min (**Supplementary Material 1**). The catch of the codend was sorted on board, and all organisms were identified to the lowest possible level (species or genus). However, due to time constraints, number of individuals of highly abundant species was estimated from the number in a subsample and then raised to the total number from weight of the subsample to the total weight (**Table 1**).

Therefore, in this study, we used a dataset consisting of 44 marine faunal species from the Arctic mesopelagic SSL belonging to 9 classes, 21 orders, and 32 families to estimate biodiversity indices. The maximum number of species ($n = 33$) was recorded during cruise 3. Due to the selectivity of the 10 mm mesh size codend of the Harstad trawl, the samples of the mesopelagic SSL might exclude some of the smaller organisms, such as small euphausiids, thus the dataset does not include the whole community of the mesopelagic SSL.

Description of Biodiversity Indices

Several indices are usually applied when assessing biodiversity (Daly et al., 2018), as restricting the analysis to a single biodiversity index can be uninformative and lead to biased conclusions. The diversity indices estimated in this study were richness (Daly et al., 2018), Shannon (1948; Simpson (1949), Margalef (1958); Menhinick (1964), and Pielou (1966) indices. The value for each of those indices was estimated for each trawl station. For trawl station j, the processed sample consisted of count numbers n_{ij} for each species S_i, where i is the species index (species ID) that was predefined. We describe below how the value for each of the biodiversity indices was estimated for a single trawl station j from count numbers $n_{1j} \ldots n_{ij} \ldots n_{Qj}$, where there are Q species in the list.

Indices of Species Richness

The richness biodiversity index accounts for the absolute number of species within the sample (Daly et al., 2018). This index does not account for species abundance distribution, thus less abundant species and highly abundant ones have equal weight. The richness was estimated as follows:

$$R_j = \sum_{i=1}^{Q} e\left(n_{ij}\right)$$
$$where$$
$$e\left(n\right) = \begin{cases} 0 \ \forall \ n < 1 \\ 1 \ \forall \ n \geq 1 \end{cases} \quad (1)$$

Margalef (Eq. 2) and Menhinick (Eq. 3) indices also measure species richness but account for a relationship

TABLE 1 | List of species and number of individuals sampled during the three experiments.

			Number of sampled individuals		
Species ID	Species	Common name	Cruise 1 (3 stations)	Cruise 2 (6 stations)	Cruise 3 (6 stations)
1	*Acanthostepheia malmgreni* (Goës, 1866)		0	0	13
2	*Arctozenus risso* (Bonaparte, 1840)	Spotted barracudina	0	13	0
3	*Aglantha digitale* (Müller, 1776)		0	28	0
4	*Anarhichas lupus* Linnaeus, 1758	Atlantic wolffish	0	14	0
5	*Beroe cucumis* Fabricius, 1780	Comb jelly	0	1	3*
6	*Boreogadus saida* (Lepechin, 1774)	Polar cod	23	191	64
7	*Clione limacina* (Phipps, 1774)	Sea butterfly	0	14	115
8	–	Comb jelly	14	0	0
9	*Cyanea capillata* (Linnaeus, 1758)	Lion's mane jellyfish	40*	67*	40*
10	*Euchirella maxima* (Wolfenden, 1905)		0	0	2
11	*Gadus morhua* (Linnaeus, 1758)	Atlantic cod	1	19	2
12	*Gammarus wilkitzkii* Birula, 1897		0	0	21
13	*Gonatus fabricii* (Lichtenstein, 1818)	Armhook squid	4	59	11
14	*Icelus bicornis* (Reinhardt, 1840)	Twohorn sculpin	0	57	1
15	–	Unidentified isopod	2	0	0
16	*Lebbeus polaris* (Sabine, 1824)	Polar shrimp	1	0	13
17	*Leptagonus decagonus* (Bloch and Schneider, 1801)	Atlantic poacher	0	2	0
18	*Leptoclinus maculatus* (Fries, 1838)	Daubed shanny	31	1096	776
19	*Liparis* spp.	Snailfish	0	11	11
20	*Mallotus villosus* (Müller, 1776)	Capelin	23	0	79
21	*Meganyctiphanes norvegica* (M. Sars, 1857)	Northern krill	609	16342	710*
22	*Melanogrammus aeglefinus* (Linnaeus, 1758)	Haddock	2	45	2
23	*Mertensia ovum* (Fabricius, 1780)	Arctic comb jelly	0	41	44*
24	*Myctophidae* sp.	Lantern fish	16	161	28
25	*Onisimus* sp.		0	0	4
26	*Pasiphaea* sp.	Glass shrimp	0	7	0
27	*Pandalus borealis* Krøyer, 1838	Deep-water shrimp	10	1	199
28	*Pasiphaea multidenta* Esmark 1866	Glass shrimp	2	0	0
29	*Reinhardtius hippoglossoides* (Walbaum, 1792)	Greenland halibut	0	68	1
30	*Sebastes* spp.	Redfish	1270	150	1021
31	*Eusergestes arcticus* (Krøyer, 1855)		0	0	3
32	–	Siphonophore	1	0	0
33	*Themisto abyssorum* (Boeck, 1871)		184	924	364
34	*Themisto libellula* (Lichtenstein in Mandt, 1822)		245*	77050	2081
35	*Thysanoessa* spp. [mainly *T. inermis* (Krøyer, 1846)]	Krill	3910*	79443	21778
36	*Triglops murrayi* Günther, 1888	Moustache sculpin	0	2	0
37	*Catablema multicirratum* Kishinouye, 1910		0	14	0
38	*Clupea harengus* Linnaeus, 1758	Atlantic herring	0	0	30
39	*Periphylla periphylla* (Péron and Lesueur, 1810)		0	0	1
40	*Apherusa glacialis* (Hansen, 1888)		0	0	8
41	*Hyperia galba* (Montagu, 1813)		0	0	5
42	–	Unidentified decapod	0	0	5
43	*Anonyx* sp.		0	0	2
44	*Sabinea septemcarinata* (Sabine, 1824)	Sevenline shrimp	0	0	9

Represents values that were estimated from weight of the sorted species.

between the number of species and the number of individuals:

$$MA_j = \frac{R_j - 1.0}{ln\left(\sum_{i=1}^{Q} n_{ij}\right)} \quad (2)$$

$$ME_j = \frac{R_j}{\sqrt{\left(\sum_{i=1}^{Q} n_{ij}\right)}} \quad (3)$$

Index of Entropy

The Shannon index is a measure of the entropy or disorder of the community of the sample. The Shannon index is sensitive to species richness because it depends on number of species that are sampled (Daly et al., 2018). The value of the Shannon index is zero when there is only one species in a sample, and it increases with each added species. It generally varies between 1.3 and 3.5, but in some cases it can exceed 4.0 (Kanieski et al., 2018). Thus,

the lower the value of the Shannon index, the lower the diversity. The Shannon index was estimated by:

$$H_j = -\sum_{i=1}^{Q} ln\left(\left(\frac{n_{ij}}{n_j}\right)^{\frac{n_{ij}}{n_j}}\right)$$

$$where$$

$$n_j = \sum_{i=1}^{Q} n_{ij} \tag{4}$$

Index of Species Evenness

Pielou's evenness index measures how evenly the number of individuals are distributed among the species. Species evenness in the biodiversity context is the evenness of a community's species abundance distribution. A community is perfectly even if every species is present in equal proportions and uneven if one species dominates the abundance distribution. The Shannon index is the basis for calculating the Pielou's index, which was estimated using the following equation:

$$J_j = \frac{-H_j}{ln\left(R_j\right)} \tag{5}$$

Pielou's evenness is the most widely used evenness index in the ecological literature (Daly et al., 2018). The value of Pielou's evenness index ranges from 0 to 1, with a value of 1 indicating that all species are equally abundant (Kanieski et al., 2018).

Index of Species Dominance

Indices of dominance express whether one or more species are more abundant than others in the sampled area. Therefore, these indices account for the dominance of some species within the sampled community and do not qualify as indicators of diversity or richness (Kanieski et al., 2018). The Simpson index represents the probability that two individuals randomly taken from the population represent the same species. High values of the Simpson index (range: 0–1) indicate higher dominance of one or a few species, thus implying lower species diversity. The index can be estimated by:

$$SI_j = \sum_{i=1}^{Q} \left(\frac{n_{ij}}{n_j}\right)^2$$

$$where$$

$$n_j = \sum_{i=1}^{Q} n_{ij} \tag{6}$$

Dominance Pattern

Apart from reducing the biodiversity data to one summary statistic such as a biodiversity index, dominance curves are often used to quantify information about the pattern of relative species abundances for a given sampling station and can be estimated as follows (Warwick et al., 2008):

$$d_{ij} = \frac{n_{ij}}{\sum_{i=1}^{Q} n_{ij}} \tag{7}$$

Cumulative dominance curves are often used to represent species dominance patterns:

$$D_{Ij} = \frac{\sum_{i=1}^{I} n_{ij}}{\sum_{i=1}^{Q} n_{ij}}$$

$$with$$

$$1 \leq I \leq Q \tag{8}$$

where I is the species ID summed up to in the nominator.

Generally, dominance curves are based on ranking of species in a sample in decreasing order of their abundance (Clarke, 1990). This implies that the species ranking could potentially vary among stations. The advantage of this is that by comparing the steepness of the curves, one obtain an overview on how many species are dominant and the distribution of their relative dominance. However, a more detailed picture in comparison of dominance curves among different stations can be obtained if the species ranking remains fixed according to the species ID (**Table 1**). In the latter case, the dominance curves will have horizontal parts where specific species are not present in the sample. We propose to have both options available dependent on the objective of the specific research.

Estimating Uncertainty for Biodiversity Measures at the Station Level

The number of individuals of all species identified in the sample from trawl station j was defined as n_j:

$$n_j = \sum_{i=1}^{Q} n_{ij} \tag{9}$$

Because n_j is a finite number, a resampling method with replacement (Chernick, 2007) was used to estimate the uncertainty around the value. Obviously, the resulting count numbers n_{ij} for the individual species varied from one such resampling to another. By performing 1000 resampling, we obtained a population of data for each n_{ij}. After applying equations (1)–(8), we obtained a bootstrap population of 1000 values for each indicator measure, which we used to obtain Efron percentile 95% confidence bands (Efron, 1982) for each indicator measure for each trawl station j. This application of the bootstrap procedure can be viewed as a method for estimating precision using confidence intervals obtained based on creating new datasets from the original dataset by the resampling in each bootstrap iteration and calculating indicator values for each of them (Rowland et al., 2021). This procedure enables estimation of the uncertainty at a station level for each biodiversity index induced by the limited sample size at station level without having to make any prior assumptions regarding the distributions in the samples. This is a well-established procedure for estimation of uncertainty at single sample level such as a station and is being applied in several other branches of science (Manly, 1997; Chernick, 2007). The analysis was conducted using the software tool SELNET (Herrmann et al., 2012), which implements the described method.

Inferring Difference in Biodiversity Between Stations

The difference Δr in a biodiversity index r between the stations x and y was estimated by:

$$\Delta r = r_y - r_x \tag{10}$$

The 95% confidence intervals (CIs) for Δr were obtained based on the two bootstrap population results for r_x and r_y, respectively, as described above. As they were obtained

independently of each other, a new bootstrap population of results for Δr was created using:

$$\Delta r_i = r_{y_i} - r_{x_i} \quad i \in [1 \ldots 1000] \tag{11}$$

where i denotes the bootstrap repetition index. As resampling was random and independent between the two bootstrap populations of results, it is valid to generate the bootstrap population of results for Δr based on (11) using the two independently generated bootstrap files (Moore et al., 2003). Based on the bootstrap population of results for Δr, we were able to obtain Efron percentile 95% confidence bands (Efron, 1982). To determine whether the difference between indices is significant, we compared the overlap among the confidence intervals. If the value 0.0 was not within the obtained confidence bands, then the indicator values for stations x and y differed significantly. In general, the confidence limits for Δr cannot exceed what is spanned by r_x and r_y together and will often be smaller (Larsen et al., 2018). Therefore, using this approach will increase the power of making inference compared to the simple strategy based on the search for non-overlapping confidence limits between the two confidence bands for r_x and r_y.

Estimating Mean Biodiversity and Uncertainty for Mean Biodiversity Based on a Group of Stations

First, to estimate the mean value r_{mean} for a biodiversity index r based on a group of trawl stations K (i.e., trawl stations within each cruise), a bootstrap population of results was obtained for it for each trawl station j following the procedure described in section "Estimating Uncertainty for Biodiversity Measures at the Station Level." The bootstrap population of results was obtained independent for each trawl station. Second, a bootstrap population of results was obtained for r_{mean} by for each of the 1000 bootstrap iterations i independent to form a mean based on resampling K stations with replacement between the K stations available in an outer resampling loop. The mean was then calculated based on the values for r for the stations selected for the specific bootstrap iteration i. This procedure was applied for each of the biodiversity indices described by equations (1)–(8) to provide a bootstrap population of results with 1000 values for the mean value based on the K stations considered. Efron 95% percentile confidence bands were then obtained for the mean values for the biodiversity indices based on this bootstrap population for the mean values.

Estimating Total Biodiversity and Uncertainty for Total Biodiversity Based on a Group of Stations

Section "Estimating Uncertainty for Biodiversity Measures at the Station Level" described how the biodiversity measures were estimated with uncertainties for a single trawl station J. Section "Estimating Mean Biodiversity and Uncertainty for Mean Biodiversity Based on a Group of Stations" described how the mean value with uncertainties can be obtained based on a group of K stations. However, sometimes one would more

be interested in estimating the total biodiversity in an area covered based on the K trawl stations rather than estimating the mean based on the stations. To estimate the total value for the biodiversity indices for a group of trawl stations (i.e., trawl stations within each cruise), n_{ij} in equations (1)–(8) were replaced with n_i which is given by:

$$n_i = \sum_{j=1}^{K} n_{ij} \tag{12}$$

where the summation was considered over a group of K stations.

To account for variation between stations when estimating the uncertainties in the total biodiversity, another resampling loop around the one described for single station analysis was applied. This outer resampling loop resampled with replacement K stations over the K stations considered. For each station selected, the inner resampling was conducted accounting for the finite sample size for the specific station according to the resampling procedure described in section "Estimating Uncertainty for Biodiversity Measures at the Station Level." This nested resampling technique was applied 1000 times, leading to 1000 sets of n_i data. We applied equations (1)–(8) to these data to obtain a population of results for the total value of biodiversity indicators to estimate Efron 95% percentile confidence bands for this estimation based on the group of stations within the area considered. The same approach used to compare biodiversity estimates between two stations (section "Inferring Difference in Biodiversity Between Stations") was applied to compare biodiversity estimates between the groups of stations. The nested bootstrapping technique described here are similar in structure to the well-established method applied for fishing gear size selectivity for estimating the uncertainty (Wileman et al., 1996) when aggregating data over multiple trawl stations (Millar, 1993) except for the structure in the inner resampling which follows the procedure outlined in Larsen et al. (2017). However, its application and adaption to provide realistic uncertainty estimates for overall (total) species biodiversity based on a group of stations is new. With its resampling procedure, the method accounts for both the additional uncertainty induced by variation in sample composition between stations and the uncertainty on station level (section "Estimating Uncertainty for Biodiversity Measures at the Station Level") caused by the finite sample size in the individual samples.

Figure 1 presents a conceptual diagram on the methodological details of the nested bootstrapping approach described above for estimation of total biodiversity.

RESULTS

Indices of Species Richness

Species richness varied between stations within each cruise (**Figure 2**). Further, it showed a significant pairwise difference between the cruises regarding total values (**Figure 3**) and between some of the stations within the cruises (**Supplementary Material 2**). Total values for species richness differed significantly [pairwise difference (delta)] between cruise 1 and cruises 2 and 3, but the difference between cruises 2 and 3 was not significant
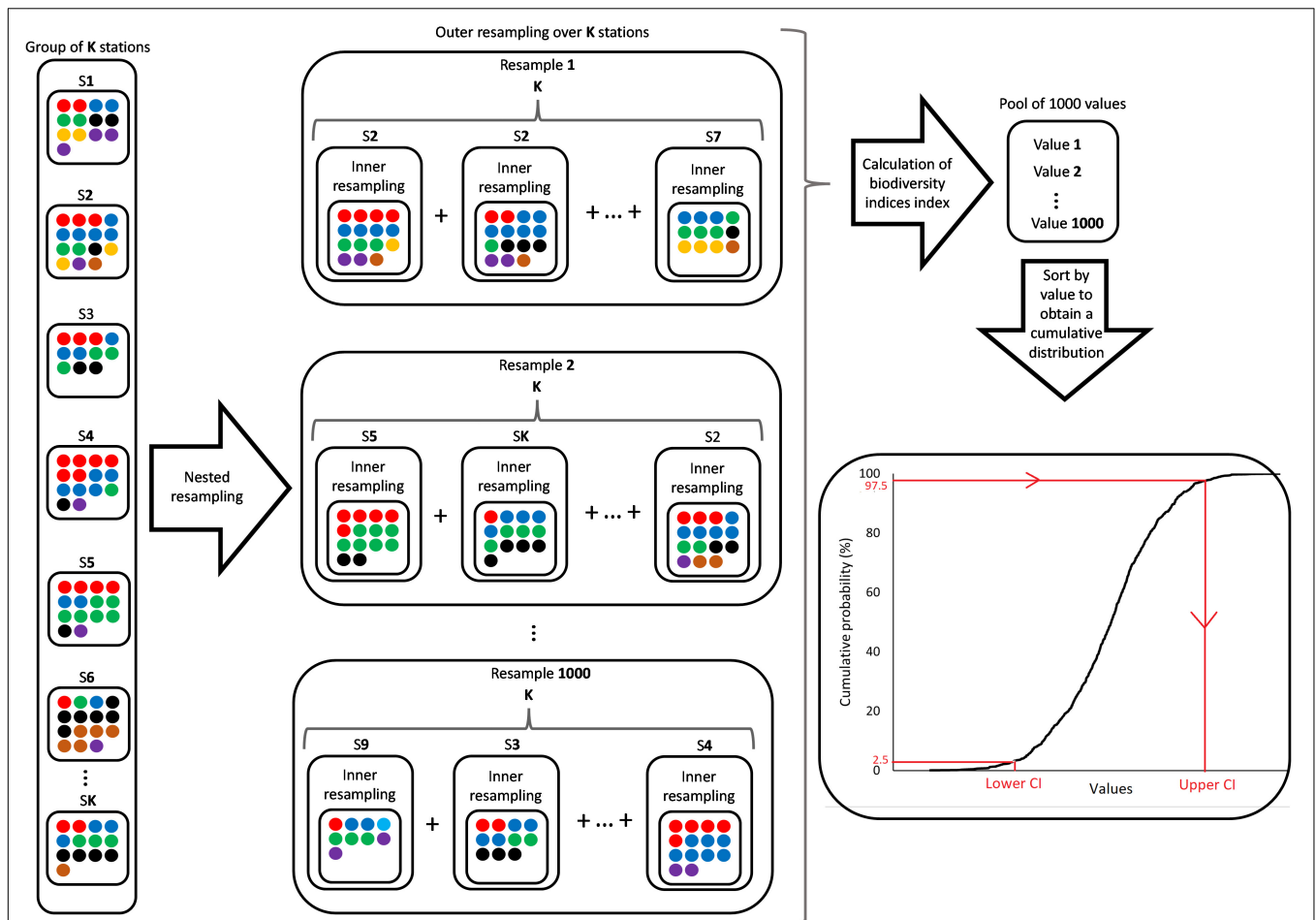
FIGURE 1 | Conceptual diagram on the methodological details of the nested bootstrapping approach applied to estimate uncertainties for the biodiversity indices. Stations S1 to SK have different number of species and number of individuals within each which is represented by colored circles where specific colors represent specific species. The nested bootstrapping consists of an outer resampling loop where the K stations are resampled. The data for each station selected in the outer loop is then resampled in the inner loop. This leads to variation in the composition of numbers of individuals for the same station depictured by the color mixtures for the resampled station data. The inner resampled data belonging to the same outer resampling iteration are summed to produce a pooled population symbolized by the "+." The obtained data from each pooled population are then used separately to calculate a value for each of the biodiversity indices. Lower and upper confidence limits for each diversity index is subsequently obtained from the cumulative distribution of values. Specifically, the value for the index that corresponds to the 2.5 and 97.5 percentiles represents respectively, lower and upper confidence limits, and thereby forms a 95% percentile confidence interval for the specific index.
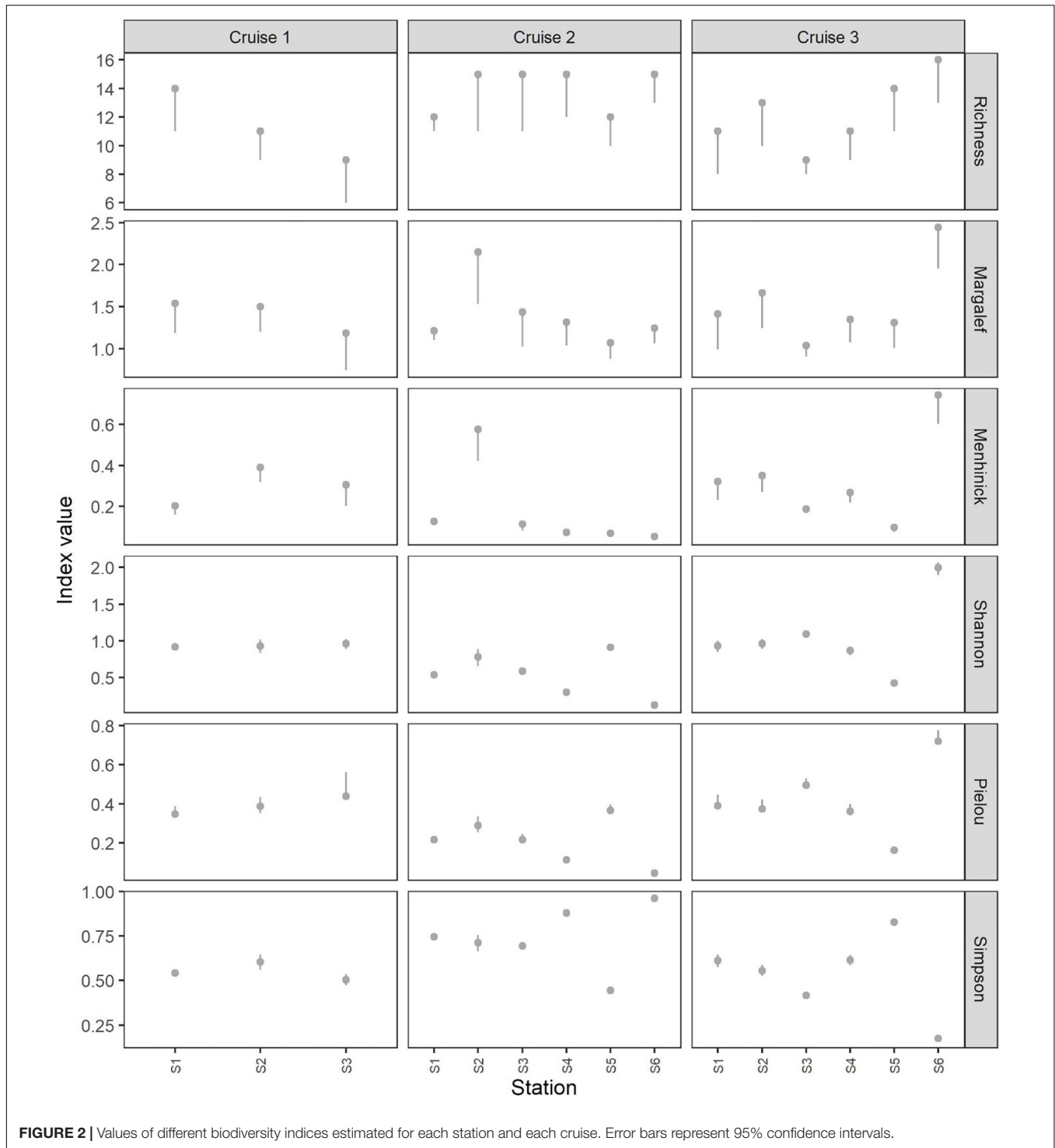
(**Figure 3**). For mean values, there were no significant differences between cruises. Note that the species richness for a station and for a group of stations as total contrary to mean values will have one-sided percentile confidence bands since resampled data cannot contain more species than found in the original sample. This pattern is clear from the results obtained (**Figure 2**). Contrary, the difference (delta) in species richness will have two-sided percentile confidence bands (**Figure 3**).

The Margalef and Menhinick indices explain the relationship between the number of species and the number of individuals within each species. Both indices have no upper limit, thus they can be compared between the stations and cruises. In some cases, the values did not display a significant difference in species richness but did differ significantly in terms of the number of individuals within each species (e.g., stations 2 and 3 of cruise 2; **Figure 2**). Overall, the indices were low (between 1.0 and 1.5 for

the Margalef index and between 0.0 and 0.4 for the Menhinick index) compared with two stations displaying higher diversity within each cruise (i.e., station 2 of cruise 2 and station 6 of cruise 3 for both Margalef and Menhinick indices) (**Figure 2**). At the cruise level, total values for both Margalef and Menhinick indices indicated higher diversity for cruise 3 compared with cruises 1 and 2, but the difference in the Menhinick index between cruise 3 and cruise 1 was not statistically significant (**Figure 3**). Mean values for those indices did not display any significant differences between cruises (**Figure 3**).

Index of Entropy
The Shannon index considers not only species richness but also species evenness; therefore, high species richness does not always mirror higher values of the Shannon index (values for stations 2–4 of cruise 2) and vice versa (station 3 of cruise 3) (**Figure 2**).

FIGURE 2 | Values of different biodiversity indices estimated for each station and each cruise. Error bars represent 95% confidence intervals.

The variation in Shannon index values between cruises ranged from close to 0.0 at station 6 of cruise 2 to 2.0 at station 6 during cruise 3. There was no significant difference in the Shannon index between cruises regarding total values (**Figure 3**). Mean values for Shannon index differed significantly between cruise 2 and cruises 1 and 3, but the difference between cruises 1 and 3 was not significant (**Figure 3**). However, differences in the Shannon index between stations during cruises 2 and 3 were statistically significant (**Supplementary Material 2**).

Index of Species Evenness
No pairwise difference in the Pielou index was observed when the total values were compared between the three cruises (**Figure 3**). Mean values for Pielou index differed significantly
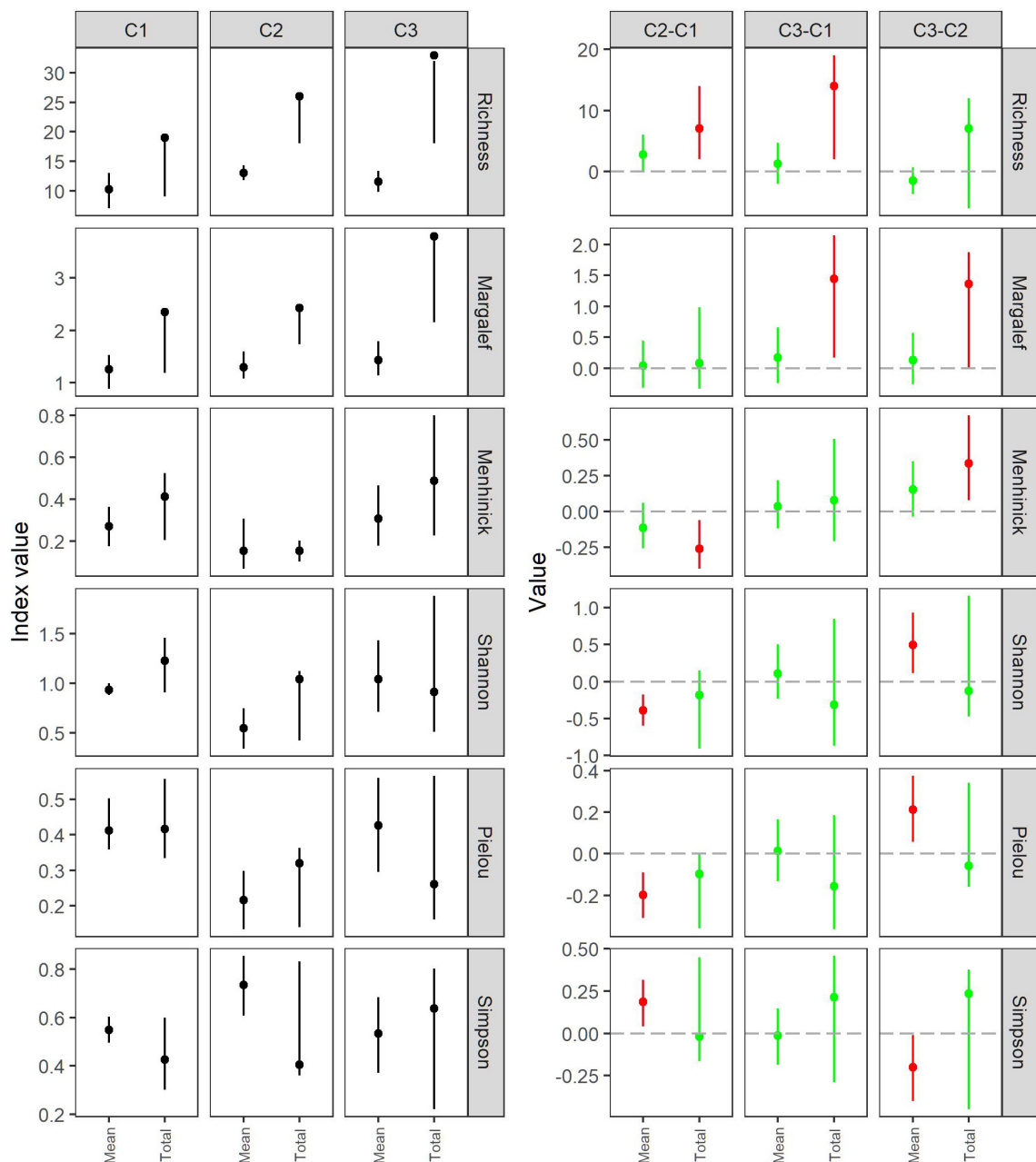
FIGURE 3 | Mean and total values for different biodiversity indices estimated for each cruise **(left)** and pairwise difference in biodiversity index values (deltas) between cruises **(right)**. Error bars represent 95% confidence intervals (CI). Red circles and corresponding CI highlights significant difference between the two stations, whereas green circles and their CIs represent stations without significant difference in biodiversity index values.

between cruise 2 and cruises 1 and 3, but the difference between cruises 1 and 3 was not significant (**Figure 3**). However, the species evenness during each cruise showed significant pairwise differences between stations, with few exceptions (**Supplementary Material 2**).

Index of Species Dominance

There were significant differences in values of the Simpson index between stations during each cruise, indicating that one or few

species were more abundant than the others. The Simpson index exceeded 0.50 at most stations (**Figure 2**), with exceptions of station 3 of cruise 1, station 5 of cruise 2, and stations 3 and 5 of cruise 3. The dominance index values generally mirrored the values of the Pielou index (higher species dominance of one or few species implies a lower evenness within the sample). In several cases, however, there was a significant difference in species dominance but not in species evenness (pairwise difference between stations 4 and 2 of cruise 3) and vice versa (pairwise

difference between stations 2 and 1 of cruise 2) (**Supplementary Material 2**). In most cases, both the Simpson and Pielou indices exhibited a significant difference in the delta plots, indicating dominance by one or a few species in the sample at the station level. Similar to the Pielou index, the Simpson index did not show significant pairwise difference in the total index values between the cruises (**Figure 3**). However, the mean values for Simpson index differed significantly between cruise 2 and cruises

1 and 3, while the difference between cruises 1 and 3 was not significant (**Figure 3**).

Dominance Pattern

Overall, *T. inermis* (ID 35) was the single species dominating the samples collected during cruises 1 and 2, while *T. libellula* (ID 34) was also dominant during cruise 3 (43.82% with CI:10.83%–90.71%) (**Table 2**). Most species were recorded from only a few

TABLE 2 | Species dominance values d_{ij} according to Eq. (8) for each cruise. Values in parentheses represent 95% confidence intervals.

Species ID	Species	Cruise 1	Cruise 2	Cruise 3
1	*Acanthostepheia malmgreni*	–	–	0.05 (0–0.51)
2	*Actozenus risso*	–	0.01 (0–0.02)	–
3	*Aglanta digitale*	–	0.02 (0–0.05)	–
4	*Anarhichas lupus*	–	0.01 (0–0.04)	–
5	*Boreo cucumis*	–	–	0.01 (0–0.11)
6	*Boreogadus saida*	0.36 (0.08–0.57)	0.11 (0.04–0.35)	0.23 (0.01–1.68)
7	*Clione limacina*	–	0.01 (0–0.03)	0.42 (0.21–0.89)
8	Unidentified ctenophores	0.22 (0–1.62)	–	–
9	*Cyanea capillata*	0.63 (0–1.98)	0.04 (0–0.09)	0.15 (0–1.26)
10	*Euchirella maxima*	–	–	0.01 (0–0.07)
11	*Gadus morhua*	0.02 (0–0.15)	0.01 (0–0.04)	0.01 (0–0.09)
12	*Gammarus wiltikii*	–	–	0.08 (0–0.53)
13	*Gonatus fabricii*	0.06 (0–0.29)	0.03 (0.01–0.12)	0.04 (0–0.27)
14	*Icelus bicornis*	–	0.03 (0–0.06)	0 (0–0.05)
15	Unidentified isopod	0.03 (0–0.15)	–	–
16	*Lebbeus polaris*	0.02 (0–0.05)	–	0.05 (0–0.52)
17	*Leptoagonus decagonus*	–	0 (0–0.01)	–
18	*Leptoclinus maculatus*	0.49 (0–0.69)	0.62 (0.01–3.31)	2.83 (0.96–6.44)
19	*Liparis* spp.	–	0.01 (0–0.01)	0.04 (0–0.1)
20	*Mallotus villosus*	0.36 (0–0.55)	–	0.29 (0–2.9)
21	*Meganyctiphanes norvegica*	9.53 (0–76.59)	9.29 (0.52–30.38)	2.59 (0–19.71)
22	*Melanogrammus aegelfinus*	0.03 (0–0.29)	0.03 (0–0.11)	0.01 (0–0.09)
23	*Mertensia ovum*	–	0.02 (0–0.13)	0.16 (0–1.21)
24	*Myctophidae* sp.	0.25 (0.08–1.1)	0.09 (0.01–0.25)	0.1 (0–0.69)
25	*Onisimus* sp.	–	–	0.01 (0–0.08)
26	*Pasiphaea* spp.	–	0 (0–0.01)	–
27	*Pandalus borealis*	0.16 (0–0.28)	–	0.73 (0.05–6.02)
28	*Pasiphaea multidenta*	0.03 (0–0.29)	–	–
29	*Reinhardtius hippoglossoides*	–	0.04 (0.01–0.12)	0 (0–0.01)
30	*Sebastes* spp.	19.88 (9.42–22.71)	0.09 (0.01–0.22)	3.72 (1.51–4.3)
31	*Sergestes arcticus*	–	–	0.01 (0–0.09)
32	*Siphonophore*	0.02 (0–0.05)	–	–
33	*Themisto abyssorum*	2.88 (2.45–4.24)	0.53 (0–0.97)	1.33 (0.18–7)
34	*Themisto libellula*	3.84 (3.26–5.66)	43.82 (10.83–90.71)	7.58 (1.89–39.67)
35	Mainly *Thysanoessa inermis*	61.21 (0–70.77)	45.18 (1.51–84.99)	79.35 (22.18–89.35)
36	*Triglops murrayi*	–	0 (0–0.01)	–
37	*Catablema multicirratum*	–	0.01 (0–0.02)	–
38	*Clupea harrengus*	–	–	0.11 (0–0.98)
39	*Periphylla*	–	–	0 (0–0.01)
40	*Apherusa* sp.	–	–	0.03 (0–0.05)
41	*Hyperia galba*	–	–	0.02 (0–0.03)
42	Unidentified decapod	–	–	0.02 (0–0.21)
43	*Anonyx* sp.	–	–	0.01 (0–0.08)
44	*Sabinea septemcarinata*	–	–	0.03 (0–0.33)

stations during one of the three cruises. A total of 81.82% of the species were recorded in only one or two cruises across the whole study, and 54.55% of the species were recorded during only one of the cruises. Lanternfish (*Myctophidae* sp.) (ID 24) did not dominate the samples in any of the cruises, but they were recorded during all three of them, with species dominance values between 0.09 (CI: 0.01–0.25) in cruise 2 and 0.25 (0.08–1.1) in cruise 1.

At the station level, organism abundance was dominated by a few species: euphausiids (*Meganyctiphanes norvegica*) (ID 21) and *Thysanoessa inermis* (ID 35), the amphipod *Themisto libellula*, (ID 34) and daubed shanny (*Leptoclinus maculatus*) (ID 18) (**Supplementary Materials 3–5**). During cruise 1, krill (*M. norvegica*) (ID 21) constituted 76.8% (CI: 73.77–79.70%) of the assemblage at station 2, while *T. inermis* (ID 35) accounted for 66.97% (CI: 63.63–70.09%) to 70.42% (CI: 69.13–71.73%) of all samples (**Supplementary Material 3**). Cruise 2, which was conducted in summer, showed a different pattern compared with cruises 1 and 3, which were conducted in winter. During cruise 2, *T. libellula* (ID 34) dominated at five of the six stations, accounting for 78% (CI: 50.22–51.41%) up to 93.68% (CI: 93.45–93.91%) of the mesopelagic community, whereas station 6 was dominated by krill *T. inermis* (ID 35) (98.00% with CI: 97.9–98.09%) (**Supplementary Material 4**). During cruise 3, *T. inermis* (ID 35) dominated the community at five out of six stations [55.85% (CI: 53.79–57.86%) to 90.77% (CI: 90.36%–91.17%)] (**Supplementary Material 5**).
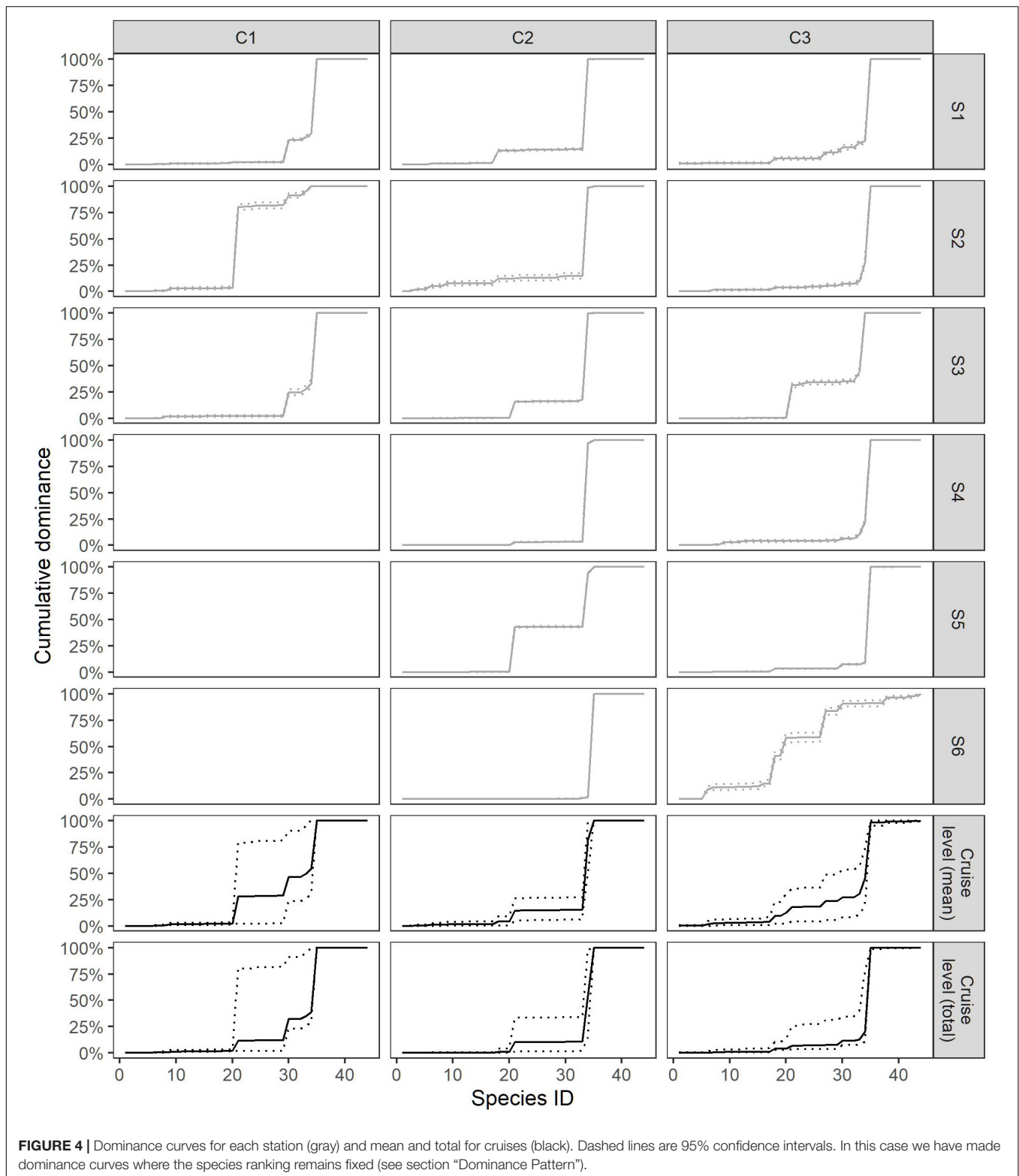
Figure 4 shows dominance curves for the cumulative dominance values as estimated by Equation (8) for each station within each cruise and as mean and total for the cruises. Note that the species ranking remains fixed. Differences in dominance indicate the dissimilarity among stations sampled in winter (January 2016 and 2017) and summer (August 2016). However, the values within the dominance curves for some stations were larger than in the others for particular species but less so for the others. For example, at stations 3 and 6 of cruise 3, species *L. maculatus* (ID 18) and *M. norvegica* (ID 21) were more dominant compared with other stations within the same cruise, which was shown by the incline of the dominance curves for those species. *T. libellula* (ID 34) and *M. norvegica* (ID 21) strongly dominated the samples collected in August (cruise 2). In winter, a higher abundance of *Thysanoessa* spp. (ID 35) was noted (cruises 1 and 3). Redfish species (*Sebastes* spp.) (ID 30) were more abundant during cruise 1 compared with cruises 2 and 3, and the species was significantly more dominant in cruise 3 compared with cruise 1 (**Table 2**). The horizontal parts in **Figure 4** shows specific species that were not represented in the sample of particular station or groups of stations.

The pairwise difference in dominance (delta) curves show the difference in species dominance between cruises (**Figure 5**) and between different stations (**Supplementary Materials 6–8**). Between cruise differences in species dominance (**Figure 5**) included increased dominance of redfish (ID30) in cruise 1 compared with the other cruises. Cruise 2 showed increased dominance of *T. libellula* (ID 34) but lower dominance of *T. inermis* (ID 35) relative to the cruises conducted in winter (**Figure 5**).

Cruise 1 shows a high dominance of *M. norvegica* (ID 21) and a lower dominance of redfish (*Sebastes* spp.) (ID 30) at station 2. Additionally, stations 1 and 3 showed a significantly higher dominance of *T. inermis* (ID 35) compared with station 2 (**Supplementary Material 6**). The differences in station level in cruise 2 were mainly associated with the abundance of *L. maculatus* (ID 18), *M. norvegica* (ID 21), *T. inermis* (ID 35), and *T. libellula* (ID 34). For example, relative to the other stations, station 5 displayed greater dominance of *M. norvegica* (ID 21), followed by insignificant changes in dominance of the following species (flat curve), which was followed by a decrease in dominance of *T. libellula* (ID 34) compared with other stations within the cruise. Station 6, however, had a high dominance of *T. inermis* (ID 35) [98.00% (CI: 97.90–98.09%)] but a significantly lower dominance of *T. libellula* (ID 34) [0.84% (0.78–0.91%)] compared with the other station in cruise 2 (**Supplementary Material 7**). In cruise 3, station 6 showed increased dominance of *L. maculatus*, capelin (*Mallotus villosus*) (ID 20), and deep-water shrimp (*Pandalus borealis*) (ID 27) compared with the other stations within the cruise. Both stations 3 and 6 displayed a lower dominance of *T. inermis* (ID 35) compared with the other stations. Between cruise differences in species dominance (**Figure 5**) included increased dominance of redfish in cruise 1 compared with the other cruises. Cruise 2 showed increased dominance of *T. libellula* (ID 34) but lower dominance of *T. inermis* (ID 35) relative to the cruises conducted in winter (**Supplementary Material 8**).
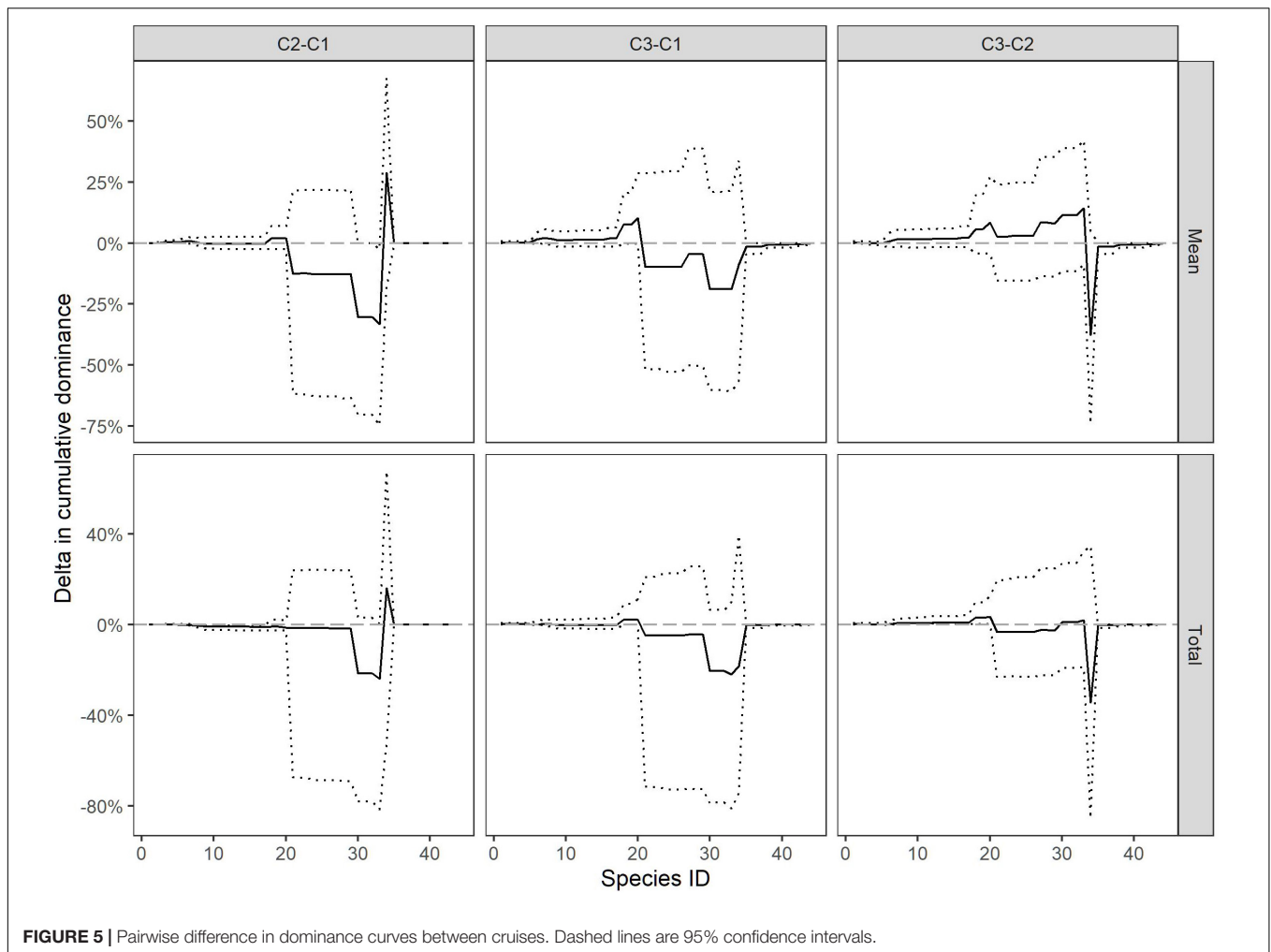
DISCUSSION

In this study, we adapted a method based on a nested bootstrapping technique that enables us to account for uncertainties when estimating various biodiversity indices resulting from sampling at the station level and at the cruise level as mean and as total (between-station variation) (**Figure 1**). This method is applicable when sampling is affected by spatial-temporal variation in the species composition in the study area (station level) and by uncertainty due to the finite sample size taken by the trawl (variation between stations; Fryer, 1991). This method has been widely used to estimate uncertainties (within- and between-station variability) in fishing gear size selectivity studies (Millar, 1993; Herrmann et al., 2017). Herein we have demonstrated that it can also be applied to biodiversity studies that are subject to multilevel sources of uncertainties. The increased power in making inference at a station level or between groups of stations when the delta approach based on the bootstrap calculus [Equations (10)-(11)] is applied, is demonstrated in **Figure 3** where richness is being compared between cruises. If the simple approach of looking for non-overlapping confidence bands is applied, no significant difference between cruises 1–2 and 1–3 could be detected. Contrary, when the delta approach is used, we are able to detect a significant difference in both cases. These examples demonstrate the usefulness of the bootstrap with the delta approach to increase the power in making inference.

FIGURE 4 | Dominance curves for each station (gray) and mean and total for cruises (black). Dashed lines are 95% confidence intervals. In this case we have made dominance curves where the species ranking remains fixed (see section "Dominance Pattern").

However, while bootstrapping is a powerful technique to obtain realistic estimates for uncertainties even for complex sampling designs, like, for example, estimates on group level (several stations) without requiring several assumptions to be fulfilled, it, of course, cannot account for species that are not present in any of the samples. In species biodiversity analysis this can be a challenge with species of low abundancy. This is a special challenge regarding the species richness (see section "Indices of

FIGURE 5 | Pairwise difference in dominance curves between cruises. Dashed lines are 95% confidence intervals.

Species Richness") and can cause limitations in studies where the species composition is subjected to under-sampling on species. Thus, the result is affected by the sampling effort. However, this should not be considered as a shortcoming of the statistical analysis method applied, in our case the nested bootstrapping presented in this study. Instead, it should be considered more as a shortcoming or challenge regarding sampling methodology and effort. Further, sampling is also affected by net avoidance, gear selectivity and body composition of the organisms (fragile organisms are known to break and extrude through nets).

We applied our methodology to data collected from the mesopelagic SSL in the high Arctic. In this case study, samples were collected in a similar area during summer and winter periods of 2016–2017, thus covering two different seasons. Smaller organisms, such as small euphausiids, were likely undersampled because we used a 10 mm mesh size codend in the Harstad trawl. Eriksen et al. (2016) estimated that most of the euphausiids larger than 15 mm in length would be retained while most of the individuals smaller than 10 mm in length would be lost when using the Harstad trawl. Sampling biases differ among net catches, optical observations, and acoustic sampling, and they have been well reported for macrozooplankton and

micronekton (Kaartvedt et al., 2012; Kloser et al., 2016; Hosia et al., 2017). Hence, we cannot be certain that trawling will retain all mesopelagic organisms in the water column or if the proportions are representative of the SSL. However, this bias would have been consistent among cruises, and our aim was to demonstrate the use of our method on the biodiversity estimation of the sampling catch of the mesoplegaic SSL and not that of the complete mesopelagic community.

Our results showed how applying bootstrapping method provided useful information regarding uncertainty of different indicator values and allowed to estimate if the differences among biodiversity indices between the samplings are significant. Values of the biodiversity indices as total differed among the three cruises, with cruise 1 exhibiting significantly less species richness. This can be explained by the smaller number of species collected due to fewer stations sampled during this cruise (three hauls conducted on cruise 1 compared with six hauls during cruises 2 and 3). The Margalef and Menhinick indices showed the same pattern, as they also consider species richness. Lower diversity associated with some of the stations, as described by the Shannon, Margalef, and Menhinick indices, were likely due to fewer number of species. However, the total value of the

Menhinick index did not differ significantly between cruises 1 and 3. The Menhinick index values exhibited smaller variation compared with the Margalef index, which explains the differences in the Margalef and Menhinick in total indices values between cruises 1 and 2 (**Figure 3**; Cozolli et al., 2017). Other indices (Shannon index, Pielou index, and Simpson index) did not differ significantly in the pairwise comparison of the three cruises. There was significant variation in Pielou index at a station level within each of the cruises, which could have been affected by changes in species distribution throughout the sampling.

The nested bootstrapping method provided CIs for our biodiversity index values, thereby accounting for the uncertainty in the estimation resulting from variation between stations and cruises (**Figure 1**). Therefore, the method allows estimating uncertainties when extrapolating about a population from a limited size of samples. To the best of our knowledge, this is the first time this bootstrap scheme has been adapted and incorporated into biodiversity analysis. However, the method has a broad scope of applicability and importance to address questions regarding biodiversity estimates, especially since biodiversity indices are estimated using limited data sets to draw broader conclusions (Rowland et al., 2021).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

BH, KC, JB, and EG contributed to conception and design of this study and wrote the first draft of the manuscript. MG, MD, and JB collected the data used in this study. KC organized the data. BH, KC, and JB performed the statistical analysis. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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