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The Effect of Short-Term Upwelling Events on Fish Assemblages at the South-Eastern Coast of the Baltic Sea

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Abstract: Multiple stressors, such as overfishing, pollution, climate change, biological invasions etc., are affecting fish communities, and thus can have versatile effects on marine ecosystems and socio-economic activities as well. Understanding the changes in the fish community structure is ecologically and economically important, yet a very complex issue, requiring comprehensive analysis of multiple factors. The role of regional oceanographic variability, namely, coastal upwelling, is often neglected when it comes to the analysis of fish assemblages. In this perspective, we were aiming, for the first time in the Baltic Sea, to assess the upwelling influence on fish communities and fish community-based ecological indices used under Marine Strategy Framework Directive. The study covered a long-term period (2000–2019) for upwelling identified by satellite data analysis and fish gillnet surveys, performed in three distinct locations in the coastal waters of the SE Baltic Sea. Overall, our study revealed that temporal dynamics of fish abundance and community composition were associated with the presence of coastal upwelling. The study outcomes suggest that the fish community was more diverse and a higher number of some fish species was observed before upwelling. During upwelling, there was more evident dominance of 1–2 main marine fish species. Through the changes in fish abundance and species composition upwelling was also responsible for the changes in fish community structure-based indices for marine environment status, i.e., in the majority of the cases a decrease in Trophic, Piscivorous Fish, and Diversity indices were observed. Our study demonstrates that upwelling can affect both, the quantitative and qualitative characteristics of coastal fish communities, therefore, it is important to consider this when predicting shifts in the distribution of fish stocks or assessing environmental status indicators, especially under changing climate. We believe that our approach adds novel information to the study of coastal ecosystems of the Baltic Sea and is important for better management of socio-economic activities in the coastal zone.

Keywords: upwelling; SST; fish community; ecological indices; good environmental status (GES); marine ecosystems

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1. Introduction

Many coastal regions support rich marine ecosystems and are important areas for economic activities, including fisheries [1] which is one of the most important services derived from coastal and marine ecosystems [2]. However, the variability of environmental factors such as water temperature, salinity, and availability of food might significantly influence the abundance, distribution, and species composition of fish [3,4] and may also significantly affect the growth of marine species [5]. In turn, these parameters are to a great extent influenced by coastal upwelling, which brings cold nutrient-rich waters to the surface making upwelling sites of particularly high productivity [6]. Eastern ocean boundaries are some of the most productive areas on the Earth supporting major fisheries as a result of wind-driven coastal upwelling systems [7]. In these systems, coastal upwelling is regulated by Ekman dynamics, where winds blowing alongshore towards the equator transport surface waters offshore, causing them to be replaced by cold and nutrient-rich waters from depth, thus increasing phytoplankton production [8]. Besides the aforementioned major upwelling systems, there are other important upwelling regions in the Global Ocean. For example, the production and its variability over coastal upwelling systems located at the western Arabian Sea, Sri Lanka Dome, and the Java and Sumatra coast is a key concern for the fishing sector and are important for the Indian Ocean rim countries [9]. Seasonal upwelling systems observed in the Pacific Ocean East Asian marginal seas have become increasingly important because the potential changes in the upwelling may have a dramatic ecosystem, socioeconomic, and even climate impacts [10]. However, less attention has been paid to the short-term upwelling events that are also relatively frequently observed in the enclosed or semi-enclosed seas such as the Mediterranean Sea [11,12], Black Sea [13,14] or the Baltic Sea [15–18].

In particular, upwelling is a typical phenomenon of the Baltic Sea [16,17]. Here, the extensive coastlines oriented in many directions mean that winds from any direction blowing parallel to some section of the coast can cause local coastal upwelling [19,20]. It was found that coastal upwelling is rather frequently observed at the SE Baltic coast, occurring about four times per warm (April-September) season and covering about 16% of it. The typical upwelling-induced sea surface temperature (SST) drop here is about 2–6 °C with the maximal values reaching up to 10–14 °C, suggesting that the water is being uplifted from the bottom layers, where they are generally nutrient-rich and relatively cold even during summer months [17]. In addition, satellite-based analysis of chlorophyll-a (Chl-a) variability in the coastal zone of the SE Baltic Sea revealed that Chl-a concentration in the upwelling zone is, on average, 40–50% lower than in the ambient waters due to lateral offshore transport of warm and productive coastal waters [18]. In turn, through the changes in thermal balance and nutrient conditions, coastal upwelling significantly influences the coastal ecosystems of the Baltic Sea [18,21,22].

The environmental effects of the Baltic Sea upwelling have received considerable attention in a relation to changes in nutrient concentrations [23] and primary production [18,22,24]. However, the possible upwelling impacts on higher trophic levels, such as coastal fish communities, have not yet been assessed in the region, although fishery dynamics might be influenced in a complex way by the changes in biophysical environments [25]. Upwelling-induced rapid decrease in water temperature could be an important factor for ecosystem processes from phytoplankton and cyanobacteria to upper trophic levels. It is well known and documented that fish have a fast and direct response to suddenly changing temperatures as water temperature controls and limits all physiological and behavioral parameters of ectotherms [26]. Therefore, rapid decreases in water temperature may result in a number of physiological, behavioral, and fitness consequences for fish [27,28]. Variations in upwelling intensity can influence the spawning behavior, larval survival, and even recruitment success of some species [29].

Baltic coastal waters are intensively used by nine nations for regionally important commercial fishery [30]. At the same time, the coastal zone is precisely the place where the wind-induced upwelling develops, thus it has a direct influence on coastal areas that are the key spawning and feeding habitats for many marine species, such as flounder (*Platichtys flesus*), Baltic herring (*Clupea harengus membras*), turbot (*Scophthalmus maximus*) and a number of non-commercial species. The coastal zone is also an important area for freshwater fish species, such as percids (Percidae) and cyprinids (Cyprinidae) [31]. Coastal fish communities are of high ecological and socio-economic importance in the Baltic Sea, both for ecosystem functioning and for recreational and small-scale coastal commercial fishery activities [31], however, they are influenced by a multitude of impacting pressures [32]. We hypothesize that by the presence of upwelling, through the suddenly decreased temperatures, the activity and, in turn, catchability of fish may decrease, at the same time affecting the efficiency of passive fishing gears, such as nets or traps.

In addition, the potential impact of upwelling on coastal fish assemblages (diversity, community structure, and separate coastal species appearance and abundance) may have other overlooked aspects. For example, fish community-based ecological indices are used to evaluate marine environment status according to HELCOM and Marine Strategy Framework Directive (MSFD, 2008/56/EC) [33]. In turn, if fish community surveys are performed under monitoring programs with temporally limited sampling and the evaluation of environmental status coincides with upwelling-impacted fish community, this potentially may lead to misinterpretation of good environmental status (GES). Therefore, our aim was to better understand the importance of coastal upwelling on fish communities, fishing stocks, and fish community indices-based environmental monitoring reliability. For this, coastal fishing efficiency due to short-term upwelling events was analyzed by coupling long-term (2000–2019) satellite SST data and fish communities' data originating from gill-net fishery monitoring activities. We hypothesize, that even though Baltic Sea upwelling is a short-term phenomenon with more of a sporadic nature, it can still influence coastal fish communities and, therefore, should be taken into account when evaluating the overall status of the environment.

2. Materials and Methods

2.1. Study Site

The Baltic Sea is an enclosed, brackish, shallow sea with limited water exchange, strong seasonality, and stratification [34,35]. Our study area covers part of the South Eastern (SE) Baltic Sea region and is representing the Lithuanian Baltic Sea coastal waters (Figure 1). The coastal area of the SE Baltic Sea is relatively shallow, up to 20 m in depth. The lowest water temperatures here are observed in winter months (in January and February the average water temperature is around 2 °C), while in summer months, e.g., July and August, the average water temperature is around 18–19 °C (see, e.g., [36]). The salinity in the coastal zone is varying around 6–7, while in the Curonian Lagoon plume-affected waters it can drop down drastically to being nearly fresh water (0–3) [37]. The coastline itself is relatively straight and oriented in such a way that coastal upwellings are rather frequently observed in the region under northerly and north-easterly winds [16,17,19], especially during the warm season, when the vertical temperature stratification is strongest. In addition, a shallow, highly eutrophic, and mainly freshwater basin—the Curonian Lagoon that has a connection to the sea through the narrow (0.4–1.1 km) Klaipeda Strait at the northern end of the Lagoon, and is situated here. Apart from the episodic formation of upwelling fronts, the Curonian Lagoon coastal plume, containing highly productive lagoon waters, is another common dynamic feature along the Lithuanian coast [36,38].

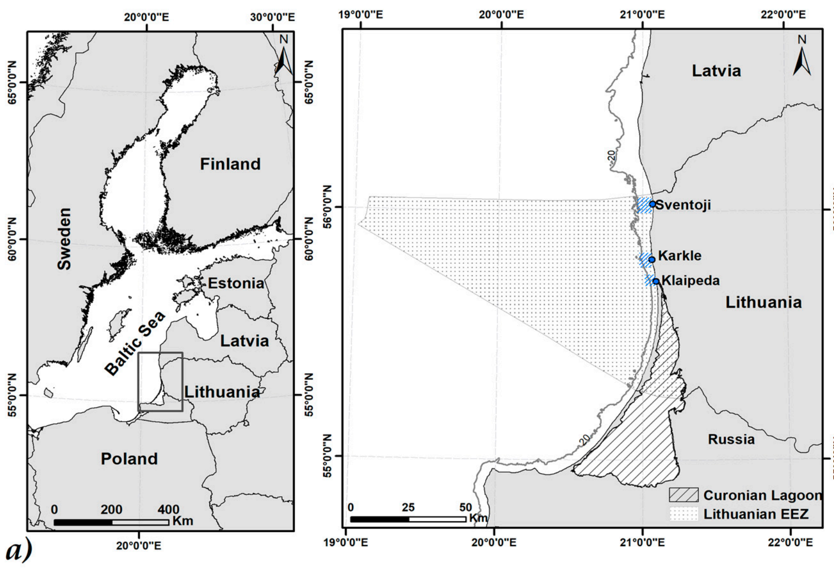

Figure 1. *Cont.*

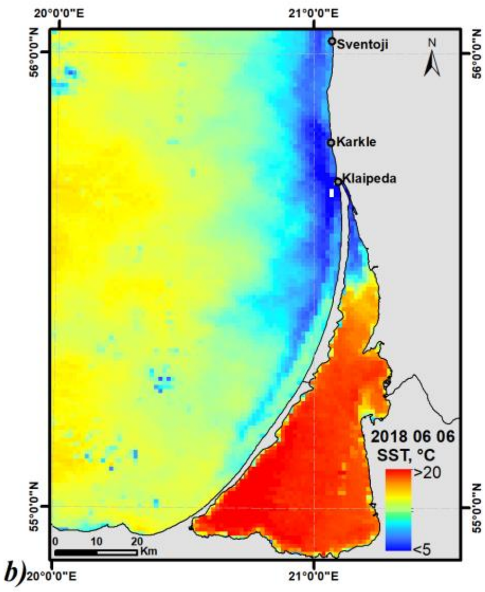

Figure 1. (**a**) Study area and sampling locations (marked as blue) at the coastal zone, which corresponds with the 20 m isobath. (**b**) An example of strong coastal upwelling in June 2018 on the Lithuanian Baltic coast, showing the spatial distribution of sea surface temperature from MODIS SST data.

The three sites alongside Lithuania's seashore were studied in this survey, representing spatial replicates that are also characterized by different bottom types, i.e., Klaipeda at the end of Curonian Spit, which is predominated by the bare sand seabed, and Karkle and Sventoji (Figure 1) that contain diverse bottom types, including stones, gravel, coarse, medium, and fine sands with patches of macroalgae [37].

2.2. Upwelling Statistics

To understand the upwelling influence on fish assemblages we focus on the warm period (April-September), when upwelling is most pronounced in terms of SST changes. Upwellings were identified based on the methodology used in the previous research works [15,39], i.e., 2 °C threshold was used (temperature drop ≥2 °C relative to ambient waters) to identify coastal upwelling events in satellite SST images and exclude other processes with temperature changes not associated with coastal upwelling, e.g., diurnal temperature changes. More details are provided in the study of [18]. For upwelling identification and evaluation of upwelling-related SST drop, level-2 SST data were extracted from daily MODIS Terra/Aqua SST products for the period of 2000–2019 that have been obtained from the NASA OceanColor website (http://oceancolor.gsfc.nasa.gov/, accessed on 1 September 2021). During the study period, 80 upwelling events were identified in the SE Baltic Sea coast for the April-September months. According to a detailed study of the SE Baltic Sea upwelling conducted by authors of [18], upwelling in this region is typically observed four times per warm period with a peak in July. The typical upwelling-induced temperature drop is 2–6 °C (can reach up to 10–14 °C during extreme cases) with an average SST drop in spring around 3.5 °C, while in summer and early autumn, it is 5.3 °C. The cross-shore extent of the SE Baltic Sea upwelling is about 10–20 km, with the along-shore length ranging from 50 to 400 km. All estimated upwelling events were compared with the dates of all available coastal fishery campaigns, and 36 upwelling events that coincided with the dates of fishing before and during the same upwelling event were chosen for more detailed analysis.

2.3. Coastal Fish Communities Monitoring Data

Fish catch (FC) data from 2000–2019 April-September were collected during the monitoring of coastal fish communities in three locations alongside Lithuania's seashore: Klaipeda, Karkle, and Sventoji (see Figure 1). Coastal monitoring was performed at random dates under suitable hydrometeorological conditions but kept once-per-month frequency for considerable temporal coverage. The fishing was performed according to HELCOM guidelines for coastal fish monitoring sampling methods [40] using a consistent set of multi-mesh (14–17.5–20–30–40–45–50–55–60–70 mm) gill nets, usually set for 24 h (always covering the period from dawn to sunrise). Nets are set at 5–15 m depth in the coastal area, up to 1 km from the shoreline. For FC analysis, the standardized catch per unit effort (CPUE) for abundance and biomass was calculated and standardized for 75 m length of gillnet per 24 h. CPUE serves as an indirect measure to estimate relative abundance and biomass for a population in a given time and/or place, therefore, is widely used for stock assessment [41].

For calculation of total CPUE and below-described fish community-based indices, all caught fish species were included in the analysis, while only nine most common and important fish species were used to assess species-level upwelling impact.

2.4. Fish Community-Based Indices for Marine Environment Status Assessment

To understand if upwelling can influence the assessment of the ecological status of coastal waters we analysed fish community diversity (H), Trophic (TI), and Piscivorous fish indices [42]. The biodiversity of the fish community was quantified using the Diversity index based on the Shannon index:

$$H = -\Sigma_{i=1}^{S} p_i \ln p_i \quad (1)$$

where: s—number of species; p_i—ratio between the number of a specific species (n) and the total number of fishes in the sample (N).

H combines species richness and evenness of abundance distribution into a single value. The higher values are observed, the better and richer diversity there is, and a lesser number shows that there are a few species or there is a dominance of a specific species [43].

The fish community Trophic index reflects the general trophic structure at the community level and is based on estimates of the proportion of fish at different trophic levels:

$$TI = \Sigma_i (TL_i) * (p_i) \quad (2)$$

where: TL_i—trophic level of a specific species, taken from [44]; p_i—ratio between the number of a specific species (n) and the total number of fishes in the sample (N).

Very low TI values may indicate overfishing and/or domination of species favoured by eutrophic conditions, while high levels of the index may reflect a decreased abundance of some naturally dominating non-piscivore species [45].

Piscivorous fish index is based on predatory fish (trophic level 4 or higher) in the samples and is expressed as the relative abundance of piscivorous in numbers for one standardized fishing effort (CPUE). As commercial fisheries often target piscivorous fish, low or decreasing abundances of piscivorous fish may indicate high fishing pressure [46].

These indices are used not only to assess the structure of fish communities but also to assess good environmental status (GES), according to MSFD. Evaluation of GES consists of setting GES limits and calculating values for the study period. To calculate the limits, the baseline data set should typically cover ten or more years of fishery [47]. The sampled values are then compared with the limits of GES and are determined, whether the indicator shows good environmental status or bad. Although, due to a lack of historical datasets, our tentative reference period was partly overlapping with the assessment period. To avoid the misinterpretations of index boundaries and, accordingly, assessment of good environmental status, we did not calculate the limits of GES, but analysed the general variability of fish community-based ecological indices during an upwelling event.

2.5. Data Analysis

Considering that coastal fish monitoring is performed independently from occurring upwelling events, only those fish sampling dates that coincided with upwelling either before or during, or both, were selected. The time period chosen as "before" the upwelling event was up to 10 days and was considered as a control fish assemblage to compare with the upwelling-affected assemblage. Two datasets were used in the analyses: (1) all available fish sampling data from different locations (Figure 1) that coincided with upwelling events either before (n = 80) or during (n = 101) were used as independent samples for general control versus upwelling-impacted assemblages assessment; (2) 36 concurrent pairs of fish samplings that have been performed before and during the same upwelling event were analysed as dependent samples.

Basic descriptive statistics (frequency of occurrence, minimum, maximum, mean and median values, percentage distribution of fish) were used to estimate fish community parameters before and during upwelling events. Before the statistical analysis described below, FC data were tested for normality and square-root transformations were applied for the number of fish (CPUE) and fish biomass (CPUE) datasets to meet the normality conditions. Statistical comparison between the control (before upwelling) and upwelling groups of the first dataset was performed by applying the Welch *t*-test, which is used to estimate the statistical significance of differences between two groups of samples with possibly unequal variances [48]. In addition, to test for the site (Klaipeda, Karkle, Sventoji) and season (spring and summer) effect on fish response to upwelling, three-way ANOVA was applied (before/during upwelling $\times$ site $\times$ season). Spring season included April and May months and the summer season was from June to the end of September. Correlation (Pearson) analysis was applied to test for pairwise relation between the main species in the assemblage and with the total CPUE and diversity, while for potentially more complex inter-relations between a set of species in the assemblage, the multivariate principal component analysis (PCA) was applied to the fish assemblage characteristics (diversity index and square-root transformed total CPUE and separate species CPUE) from the first data set of all available fish assemblages sampled under upwelling conditions (n = 101). The number of principal components to interpret was selected by the 'elbow' rule, plotting the eigenvalues and looking for an 'elbow' in the scree plot [49]. Multivariate redundancy analysis (RDA) was used to relate changes in the main parameters of fish assemblages (diversity, abundance, and biomass CPUE of sampled assemblage) to the upwelling patterns and other environmental variables (n = 36) which may have an effect on fishing efficiency. The changes in CPUE abundance, biomass, and diversity (ΔCPUE, ΔBiomass and ΔDiversity) were used as response variables, showing the difference between parameter values before and during the upwelling (calculated as the relative difference in percentage, with positive values meaning increase, negative values decrease and 0 as no change). The change in SST (ΔSST) and salinity (ΔSalinity) before and during upwelling was calculated as an arithmetic difference. Upwelling index (UI) representing a measure of the volume of water that upwells at the coast was used as a measure of upwelling intensity, more details can be found at [18]. Additional environmental parameters, which can influence fish activity and fishing efficiency, therefore the size and structure of the determined fish assemblage, were air temperature, and moon phase during the sampling under upwelling. Besides, the moon phase (half to fool moon vs. descending to the young moon), season (spring and summer), and coastal section (Klaipeda, Karkle, or Sventoji) were added to the analysis as the nominal variables. For the second dataset paired-samples Student *t*-test was used to check if there were statistically significant changes in general and in species parameters (abundance and biomass CPUE, diversity of assemblage) after the upwelling effect. All analyses were performed using R 3.5.1 and Brodgar (Highland Statistics Ltd.) version 2.7.5 software. The multivariate analyses were performed using the "vegan" package in R [50]. Significance level for all tests was $p < 0.05$.

3. Results

3.1. Fish Catches

In analysed fish assemblages, in total 38 fish species were recorded, with 33 different fish species recorded in Klaipeda, 29 in Sventoji, and 23 in Karkle. It was also noted, that marine fish species were relatively more often observed during upwelling (18 species during and 16 before upwelling), while before upwelling freshwater species were recorded more frequently (12 species before and 10 during upwelling). In addition, six diadromic migrants were also observed before and seven during upwelling.

The most abundant species recorded in the whole dataset both, before and during upwelling was flounder. It was observed during all fish samplings in Sventoji and was also the most frequently observed fish during samplings in Klaipeda and Karkle. In addition, perch (*Perca fluviatilis*), vimba (*Vimba vimba*), and Baltic herring were relatively abundant in all sampling locations. The comparison of the frequency of occurrence of different fish species before and during upwelling (Figure 2) showed that, for example, the occurrence of perch decreased by 8 to 12% during upwelling. The frequency of vimba occurrence was observed to decrease in Klaipeda and Karkle by 12–14%. Twaite shad (*Alosa fallax*) appeared to be less commonly observed, especially in Klaipeda, where the frequency of its occurrence dropped by 35%. The frequency of freshwater fish species occurrences, such as bream (*Abramis brama*) and roach (*Rutilus rutilus*), decreased up to two times in Klaipeda, while there were no considerable changes in other sites. On the other hand, turbot was more commonly observed during upwelling than before with an increase of frequency by 11% in Klaipeda and by 24% in Karkle. It is also interesting to note that not-so-common fish species in the SE Baltic Sea, i.e., two individuals of fourhorn sculpin (*Triglopsis quadricornis*), three individuals of sole (*Solea solea*) were only observed during upwelling.

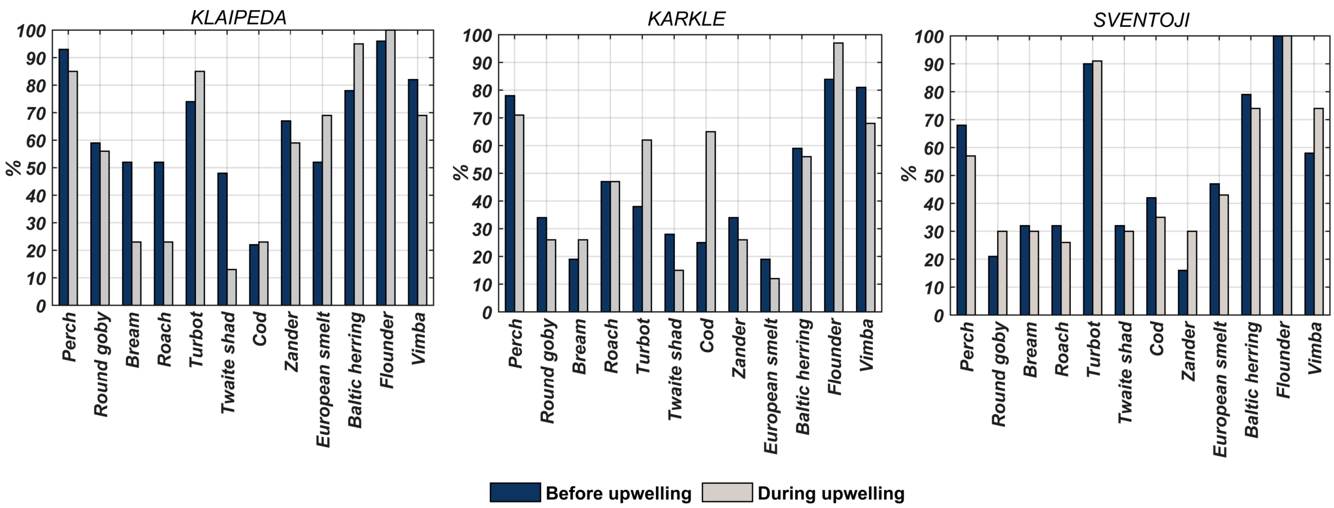

Figure 2. The frequency of occurrence (%) of different fish species before and during upwelling events.

In addition, Figure 3 was compiled from independent samples of assemblages before and during three different locations, to analyse changes in fish assemblage structure under the upwelling. It shows the percentage distribution of the most common coastal species expressed as an average relative CPUE abundance in the assemblage.

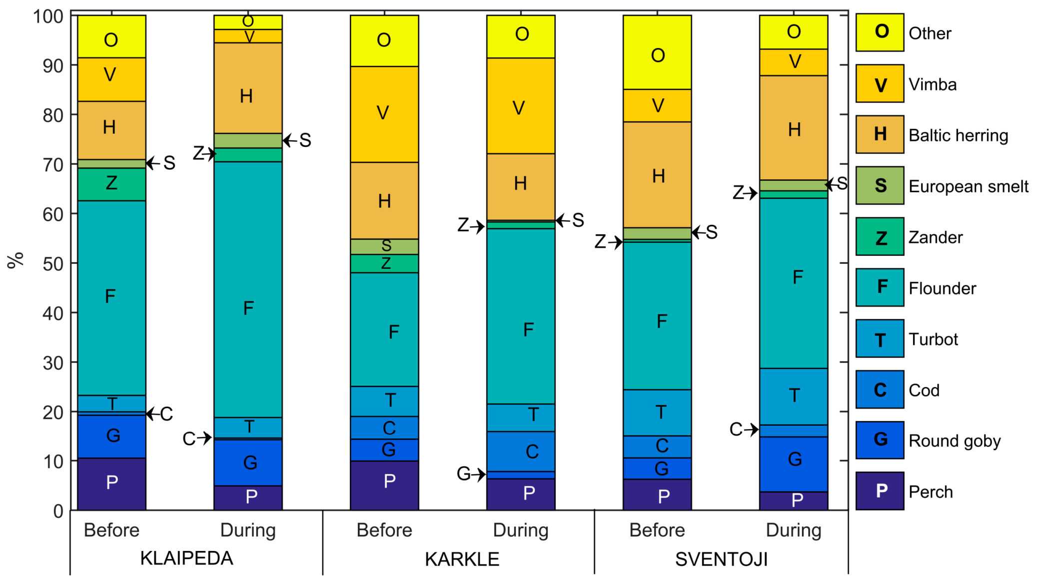

Figure 3. Fish assemblage structure before and during upwelling in three sampling locations.

During upwelling decreased not only the frequency of occurrence but also the share in the assemblage for perch and vimba in all three locations with the biggest drop of ~6% of both fish species observed in Klaipeda (Figure 3). On the contrary, the relative increase in the assemblage of flounder by 12–13% in Klaipeda and Karkle was observed while in Sventoji the increase was slightly smaller, by ~5%. The increase of Baltic herring by 7% was observed in Klaipeda, while in Sventoji round goby (*Neogobius melanostomus*) increased by 7% than compared to observations before upwelling. In addition, this also demonstrates that the number of other fish species was lower during upwelling than before, suggesting, that the fish community is less diverse due to the presence of upwelling. The highest abundance in fish community constituting flounder increases its relative share in the community even more during upwelling, with statistically significantly higher average square-root transformed CPUE abundance and biomass in upwelling-affected versus control assemblages (Welch *t*-test, $p = 0.049$ and $p = 0.036$, respectively). However, all other separate analysed species and total CPUE and biomass were not statistically significantly different analysing parameters before and during upwelling as independent samples (Welch *t*-test, $p > 0.05$ in all cases).

Testing for the site (Figure 1) and season (spring and summer) effect on separate important species and total CPUE abundance and biomass, three-way ANOVA reveals high importance of a location (Holm-Sidak test, corrected for Bonferroni-type FWER and adjusted to $\alpha = 0.008$) for total and all species, except cod (*Gadus morhua callarias*) CPUE abundance, reaching highest values in Klaipeda sampling location $p < 0.001$. Season also has a statistically significant effect on some species: smelt (*Osmerus eperlanus*) and Baltic herring reach higher CPUE in spring, perch, zander (*Sander lucioperca*) and vimba—in summer ($p < 0.05$), while turbot, round goby, cod, and total CPUE abundance did not differ in two seasons ($p > 0.05$). There were only weak or no interactions of factors, i.e., upwelling × season, upwelling × site, season × location, and upwelling × season × location, therefore more precise paired-samples Student *t*-test was applied to pooled 36 concurrent pairs of fish assemblages, sampled in different locations and seasons consistently before and during upwelling. Significant increases in CPUE numbers and biomass were found for flounder and turbot (paired-samples Student *t*-test, $p = 0.031$, 0.045, 0.037, and 0.049, respectively) during upwelling, while for most other species (cod, perch, Baltic herring, European smelt, vimba, zander) and total CPUE abundance and biomass, no statistically significant changes were found ($p > 0.05$). These separate species were related to the total abundance and diversity index of fish assemblages under upwelling conditions using principal component analysis (Figure 4).

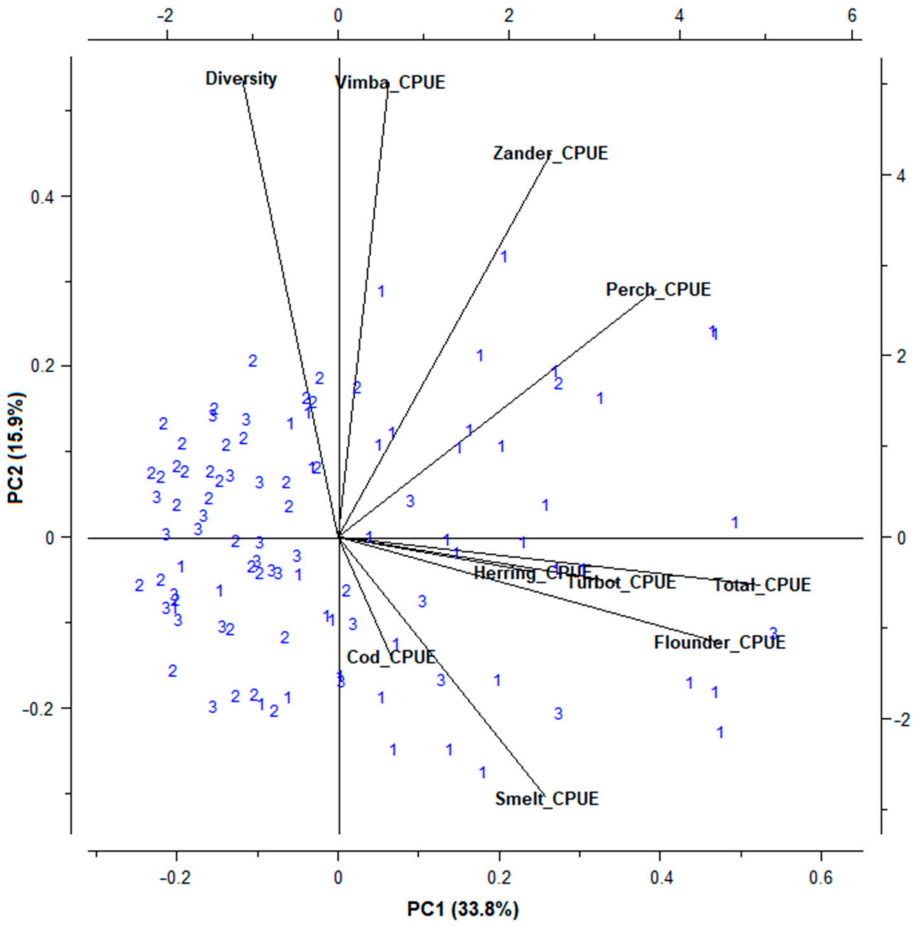

Figure 4. PCA correlation biplot for the diversity and square-root transformed total and main species CPUE of coastal fish assemblages under upwelling conditions. Blue number of samples refers to the fish assemblages from different sampling locations: 1—Klaipeda, 2—Karkle, 3—Sventoji.

The first two axes explained 50% of the data variability (34% and 16% respectively). First axis approximated variation in total CPUE under upwelling, which highly correlated with CPUE of typical SE Baltic coastal marine species such as turbot, flounder, and herring. The second PC axis approximated variation in diversity and CPUE of vimba and zander, related also to other cyprinids and percids originating from the freshwater lagoon and contributing to a higher diversity index. On the other side, the CPUE of cod and smelt tend to be negatively related to diversity. That could be explained by the fact that these species are more common and abundant at the coast earlier in the season, when freshwater fish from the lagoon is not yet at the coast. Taking the pairwise Pearson correlation analysis results, diversity statistically significantly but weakly correlated only with flounder (r = −0.39, p = 0.0001) and vimba (r = −0.23, p = 0.021) and total abundance of fish assemblage (r = −0.311, p = 0.0016). Total CPUE strongly positively correlates only with flounder (r = 0.84, $p < 0.0001$), meanwhile other species, except cod and vimba ($p > 0.05$) have highly statistically significant ($p < 0.001$) but weak to moderate positive correlation. For the second set of consistent data (n = 36), the multivariate redundancy analysis was applied to relate various upwelling characteristics and other environmental parameters which may have an impact on the fish community during upwelling (Figure 5).

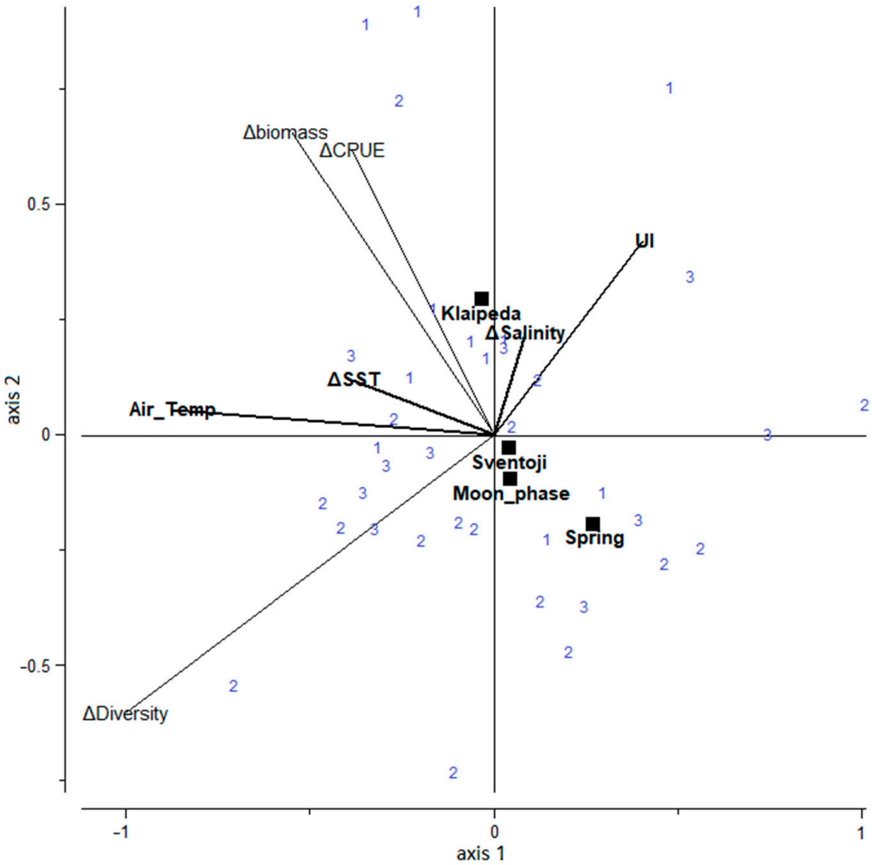

Figure 5. RDA triplot for coastal fish assemblage characteristics (changes in total CPUE abundance (ΔCPUE), biomass and diversity index) with upwelling (UI, ΔSST, ΔSalinity) and other environmental parameters such as air temperature, and the moon phase, sampling location (Klaipeda, Karkle, and Sventoji) and sampling period (spring and summer) used as nominal explanatory variables. The numbers refer to the fish assemblages from different locations: 1—Klaipeda, 2—Karkle, 3—Sventoji.

The redundancy (RDA) analysis showed that changes in sea surface temperature and salinity, upwelling index and air temperature during the upwelling event, and also full or half-moon phase, location, and season as nominal variables explained only 17% of the variation in upwelling-impacted fish community response to upwelling through changes in CPUE abundance and biomass and diversity, while 86% of this were represented by the first two axes (53% and 43% first and second axis, respectively). The forward selection and permutation test results indicated that none of the analysed explanatory variables were statistically significant ($p > 0.05$). However, there is a clear trend in the decrease of the Diversity index by increasing the upwelling index (UI), which represents the intensity of the oceanographic event. The decrease in CPUE abundance and biomass is most prominent in the Klaipeda location during springtime upwelling.

3.2. Upwelling Influence on Fish Community-Based Ecological Indices

To evaluate the upwelling-related changes in fish community-based ecological indices, fish biomass (CPUE) and the number of fish (CPUE) index values before and during upwelling were compared (Figure 6). Analysis of 36 cases, that had concurrent measurements before and during the same upwelling event also hinted at changes in the fish community, i.e., the median value of the fish biomass (CPUE) and the number of fish (CPUE) were higher during upwelling with an increase of the later during upwelling observed in 64% and 67% of the cases, accordingly.

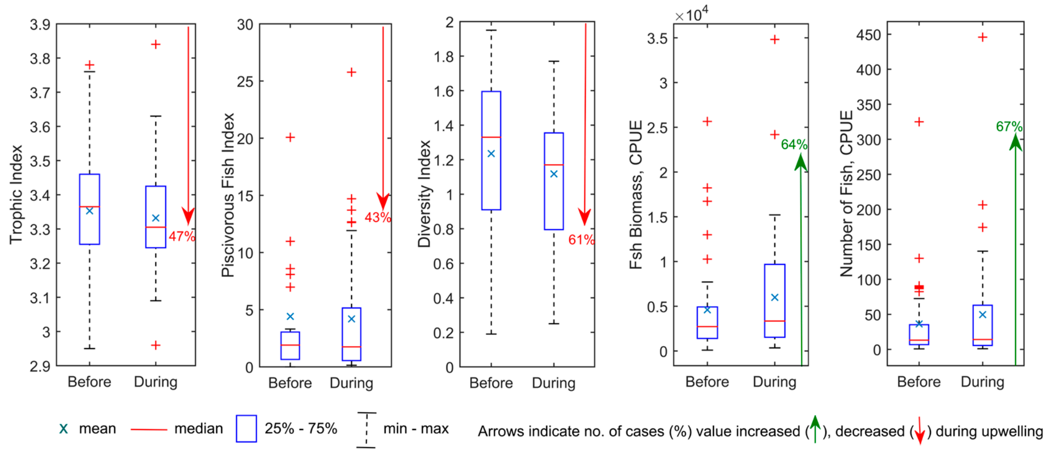

Figure 6. The minimum, maximum, mean, and median values of fish community-based ecological indices, fish biomass, and number of fish before and during an upwelling event. Boxplots indicate 25–75% percentiles.

Even though there were no statistically significant differences in the index values when analysing concurrent pairs before and during upwelling (paired-samples Student *t*-test, $p > 0.05$), the analysis showed that estimated values of the Trophic, Piscivorous fish, and Diversity indices are lower during upwelling in around 50–60% of the analysed cases. On the other hand, when statistical comparison was conducted using the entire dataset, a statistically significant difference in the Diversity index before and during upwelling was observed (Welch *t*-test, $p = 0.014$). After performing a more detailed analysis of the upwelling influence on the Diversity index (Figure 7) it is determined that the average and median values of the index are lower during upwelling events in all three study sites with slightly larger differences observed in Klaipeda.

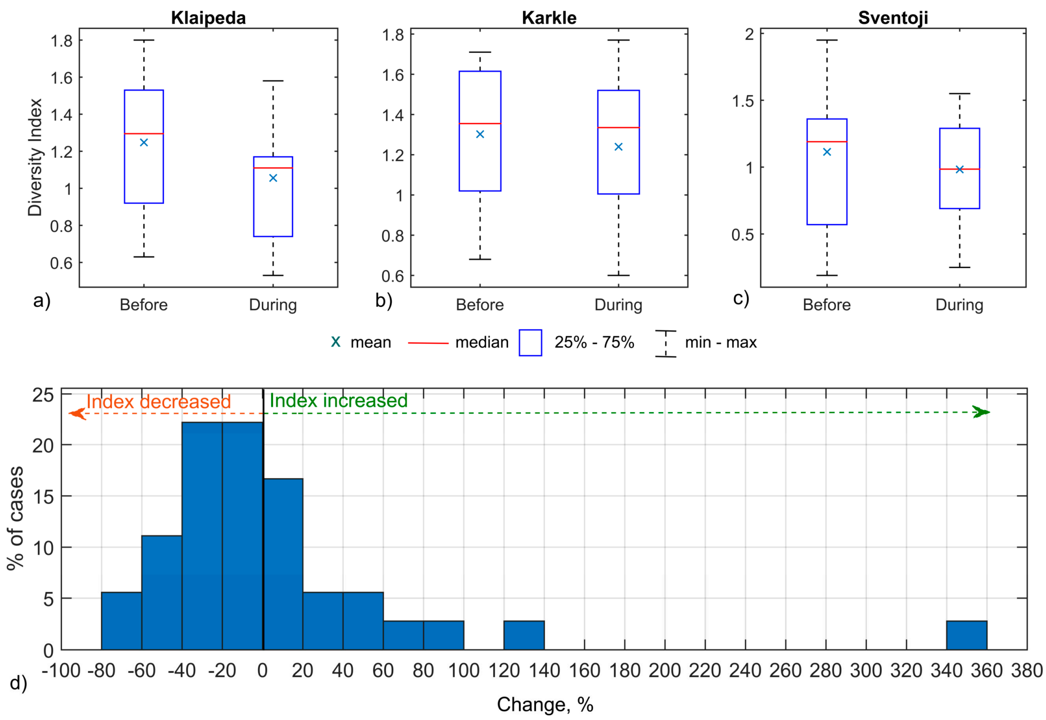

Figure 7. The minimum, maximum, mean, and median values of the Diversity index in all three study sites. Boxplots indicate 25–75% percentiles (**a**–**c**). Percentage change of Diversity index during upwelling event (**d**).

A further comparison of Diversity index changes showed, that in the majority (61%) of the cases the index values decreased during upwelling when compared to the values before the same upwelling event. Typically, the decrease was up to 40%, although in ~17% of the cases the index decreased by 40–80% from the values observed before the same upwelling event. On the other hand, cases when the index increased drastically were also observed, although they were not so frequent.

4. Discussion

4.1. Fish Community Response to Short-Term Upwellings

It is documented that coastal upwelling in the Baltic Sea is responsible for a rapid but short (on average 2–6 days) drop of SST, changes in water transparency, salinity, and nutrient availability [18,23,51,52] that might strongly influence coastal ecosystems through the direct effects of temperature on species performance, and indirectly through species interactions [53]. In turn, many studies analysed upwelling impact on nutrients, Chl-a concentration, or phytoplankton community in the Baltic Sea (e.g., [21,22,54]) and it was found that upwelling might affect not only single phytoplankton species but could also result in changes to the entire phytoplankton community [21,22]. However, little effort has been directed toward characterising upwelling impacts on higher trophic levels in the region. Only a few studies have addressed the relative impacts of drivers on the structural change of coastal communities and the knowledge of the relative importance of variables acting on different geographical scales is still lacking [55]. There is a general perception among fisheries biologists, that the fish community structure in the Baltic Sea is significantly affected by water temperature fluctuation, not only seasonal but also by wind-driven upwelling effect [56,57]. To the best of our knowledge, this is the first empirical data-based study in the Baltic Sea investigating the influence of coastal upwelling on fish assemblages and the reliability of fish community indices-based environmental monitoring.

The analysis revealed that with the presence of coastal upwelling, the frequency of occurrence of several fish species is changing. For example, perch and twaite shad are less commonly observed during upwelling, also the numbers of perch and vimba are prone to decrease. Such variations might be related to the upwelling-induced changes in abiotic parameters, when an upwelling-induced drop in water temperature and increase in salinity [18] might encourage certain fish species to migrate to the locations, not/less affected by upwelling, specifically in the Klaipeda study site case—to the freshwater Curonian Lagoon. This was evident with freshwater species such as roach and bream which are considered as warm water [57] and their main habitats are in the lagoon. Experimental behavioral studies with juvenile perch [58] showed that young-of-the-year fish avoided cooler water (12 °C versus 18 °C) in two salinity conditions (0 and 6), therefore, likely the temperature rather than the salinity are a more important driver of short-term changes in fish distribution between coastal brackish waters and the Curonian Lagoon.

The systematic study by [59] showed that water temperature in the Baltic Sea coastal area is one of the most important factor shaping seasonal variation of perch and cyprinids abundance, while the avoidance behavioral studies such as the one of [58] on short-term fish reaction to dropping temperatures are still scarce. During some events, upwelling-induced SST values might be very low and atypical for the given months. For example, SST in the SE Baltic can drop down to as low as 3–4 °C in May due to upwelling while normally, average May water temperatures are around 10–12 °C [18]. Besides the possibility for certain fish species to migrate to other, more favorable locations, the reason they may be less frequently observed during upwelling is that the stronger drop in temperature simply reduces the activity and mobility of fish for some time [28]. On the contrary, the numbers of marine species, such as Baltic herring or flounder in the coastal waters in larger numbers are related to colder water [60], and, accordingly, we found the numbers of the latter to increase during upwelling.

It was also observed that fish biomass (CPUE) and the number of fish (CPUE) have a tendency to increase during upwelling, as it was found that in the majority of the cases, the fish biomass (64% of the cases) and the number of fish (67% of the cases) increased during upwelling when compared to the values before upwelling. This might be related to an enrichment of the euphotic layer with nutrients during upwelling and higher plankton biomass accumulation in the frontal zones created by upwellings [61,62].

We would also like to note, that in this study we only analysed and demonstrated changes in fish communities, nevertheless, upwelling-induced changes in abiotic environment might have some other consequences that have not been addressed yet. In turn, upwelling impacts might vary widely depending on different species and their optimal temperature [63] and salinity [64] range. For example, salinity has a significant effect on the fertilisation and hatching success of turbot with minimum salinity of 5.5–6 required for fertilisation and egg development, although higher fertilization rates are reached at higher ($\geq$7) salinities [64]. Thus, an increase in salinity during upwelling might have a positive effect, also considering the displacement of the more diluted water in the Curonian Lagoon plume-zone. Even though surface salinity increase during upwelling events in the Baltic Sea usually does not exceed 0.5, upwelling can still result in salinities favouring fertilization success. For example, during the SE Baltic Sea upwelling case in July 2006 the surface salinity increased from around 6.75 to 7.41, as in situ coastal measurements have shown [18]. On the other hand, the same study indicates that the optimum conditions for turbot egg development are at ~12–18 °C with a considerably lower viable hatch at 9 and 21 °C; the highest viable hatch of turbot is recorded at 12–15 °C [64]. Therefore, a significant drop in temperature during upwelling might have a rather stronger negative effect on spawning success resulting in increased mortality of fish eggs during distinct upwelling situations. On the other side, as optimal spawning and egg incubation temperatures are of critical importance, physiological or behavioural adaptations for these short-term local oceanographic conditions potentially exist. Significant drops in temperature may be more critical for early ontogenetic stages of some non-indigenous less adapted warmer water species, which appearance and the possibilities for reproduction in various parts of the Baltic Sea are more likely with changing climate and oceanographic local conditions [60]. One such example is garfish (*Belone belone*), which appear and spawn at the coasts of Lithuanian Baltic waters in May-June more and more often in the last two decades. The optimal egg incubation temperature is above 15 °C, while temperatures below 12 °C cause low egg survival and incubation success [65]. Period of garfish spawning and egg incubation at the Lithuanian coast closely coincides with most expected upwellings in June, with temperatures below 12 °C [18], so even short-term cool-water upwelling may have a significant impact on incubation success and, in turn, recruitment of non-indigenous stocks in newly acquired territories.

Upwelling can also have an impact on the chances of later fish survival, as the first growing season is the most critical period in fish life [66]. For example, positive effects of summer (especially, June-July) temperatures on the recruitment and growth of perch and zander were found in several studies, noting, that fast growth and large size after the first summer improve their chances of survival through the critical first winter [67–69]. Taking into account that upwelling in the SE Baltic is occurring about four times per season with a clear peak in July and that it might cover up to 30% of the warm period duration [18], we can speculate that upwelling might have negative effects on survival rates of certain fish species juveniles. However, a complete study on upwelling impacts would require a broad set of biophysical observations and/or experiments, which was beyond the scope of this study.

4.2. Upwelling Influence on Fish Community-Based Ecological Indices

Indicators of ecological health based on biological communities are widely used to assess and report the condition and status of aquatic ecosystems [70]. Changes in the structure of the ecosystem can affect the functioning of the system and can result in the loss of economic and ecological values [55], therefore, it becomes very important to consider the impacts of environmental variability. HELCOM [40] has proposed various indices describing the status of fish communities: fish community Diversity index, fish community Trophic index, Piscivorous fish index, Large fish abundance index, Key species abundance index, etc., which were adopted for assessment of the environmental status of coastal marine waters under MSFD, by assigning sampled fish assemblage to GES or not. Therefore, it is important, that the assessment of fish communities, and, at the same time, environmental status, would be performed as accurately as possible, so that ecosystem changes were predicted and actions were taken in time. However, upwelling was found to cause "random noise" to time series, making monitoring programs with temporally limited sampling challenging [71]. Considering this, we analysed if upwelling might influence the fish community-based ecological indices, as well. Nevertheless, we would like to emphasize here, that our aim was not to assess the environmental status of Lithuanian coastal waters, but to identify, whether upwelling would influence the assessment itself.

The comparison of fish community indices (Trophic, Piscivorous fish, and Diversity) gave some valuable insights on upwelling impact. For example, we observed that median values of the aforementioned indices are lower during upwelling than before and in the majority of the cases, the index values decreased during upwelling. It is interesting to note, that the lesser numbers of diversity index confirm the dominance of a specific species [43], since higher numbers of flounder and Baltic herring were observed during upwelling. The most apparent differences in fish Diversity index were observed in Klaipeda—the location in the closest vicinity to the freshwater Curonian Lagoon. This might be related to the fact that freshwater species (such as bream or roach) are more prone to persist in the lagoon during upwelling events and, therefore, the diversity of fish in the coastal waters is declining, compared to 'normal' conditions. As well, even though the differences were not statistically significant (except the Diversity index), this implies, that a sudden change in environmental conditions due to upwelling may lead to the detection of unusual values of fish community indicators that are not typical for that season of the year. Therefore, the assessment of GES may be misleading when calculating the indicators based on the upwelling-affected fish assemblage. This suggests that the timing of monitoring is important as fish community structure during upwelling events might be considerably different from the typical community and may lead to misinterpretations.

5. Conclusions

In this study, the first results of the coastal upwelling influence on fish communities and fish community-based ecological indices in the SE Baltic Sea are presented. The analysis showed that before upwelling the fish community was more diverse with a higher number of different fish species observed. During upwelling, the frequency of occurrence, fish species composition, and abundance was changing with the numbers of marine species, such as Baltic herring or flounder, increasing while the numbers of freshwater species such as perch, roach, bream decreased during upwelling, indicating that upwelling events can potentially influence fishery during certain upwelling periods.

In addition, through the changes in fish abundance and species composition, upwelling was also responsible for the changes in fish community indices. The average and median values of the fish community Diversity index were observed to be lower during upwelling events, again indicating lower diversity of species and high dominance of 1–2 main species. A decrease in Trophic, Piscivorous fish, and Diversity indices was observed in the majority of the cases. This implies that the identified fish indicators carried out during upwelling may have unusual values, which may affect the assessment of the marine environment status.

The results produced in this study contribute to the understanding of the changes in fish communities in the Baltic Sea due to the predominant oceanographic factors, such as coastal upwelling, and provide more details on upwelling influence on GES assessment in the Baltic Sea. Upwelling can affect both the quantitative and qualitative characteristics of coastal fish communities. Therefore, it is important to take this into account when dealing with coastal monitoring of low temporal and spatial coverage and calculating various indices of coastal communities, as unusual coastal fish samples or outliers in time series could be observed due to upwelling. In addition, knowledge of short-term upwelling impact on reproduction, recruitment, and growth of distinct fish species could benefit fisheries scientists and decision-makers in stock assessment, and in shaping exploitation strategies for conservation and restoration of fish stocks, therefore further empirical investigation is required.

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Data Availability Statement: Level-2 MODIS Terra/Aqua SST data freely available in NASA OceanColor website (http://oceancolor.gsfc.nasa.gov/). Further inquiries can be directed to the corresponding author.

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