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The rise of novelty in marine ecosystems: The Baltic Sea case

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Abstract

Global environmental changes have accelerated at an unprecedented rate in recent decades due to human activities. As a consequence, the incidence of novel abiotic conditions and biotic communities, which have been continuously emerging in the Earth system, has rapidly risen. Despite growing attention to the incidence and challenges posed by novelty in terrestrial ecosystems, novelty has not yet been quantified in marine ecosystems. Here, we measured for the rate of novelty (RoN) in abiotic conditions and community structure for three trophic levels, i.e., phytoplankton, zooplankton, and fish, in a large marine system - the Baltic Sea. We measured RoN as the degree of dissimilarity relative to a specific spatial and temporal baseline, and contrasted this with the rate of change as a measure of within-basin change over time. We found that over the past 35 years abiotic and biotic RoN showed complex dynamics varying in time and space, depending on the baseline conditions. RoN in abiotic conditions was smaller in the open Central Baltic Sea than in the Kattegat and the more enclosed Gulf of Bothnia, Gulf of Riga, and Gulf of Finland in the north. We found a similar spatial pattern for biotic assemblages, which resulted from changes in composition and stock size. We identified sea-surface temperature and salinity as key drivers of RoN in biotic communities. Hence, future environmental changes that are expected to affect the biogeochemistry of the Baltic Sea, may favor the rise of biotic novelty. Our results highlighted the need for a deeper understanding of novelty development in marine ecosystems, including interactions between species and trophic levels, ecosystem functioning under novel abiotic conditions, and considering novelty in future management interventions.

KEYWORDS
rate of novelty, rate of change, marine ecosystem, Baltic Sea, abiotic conditions, trophic levels, drivers of novelty

1 | INTRODUCTION

Global environmental change has accelerated at an unprecedented rate in recent decades (Chin et al., 2017; Waters et al., 2016). Humans have been a significant force driving the Earth system dynamics in this epoch, which sometimes has been referred to as the Anthropocene (Jouffray et al., 2020; Steffen et al., 2007, 2011, 2015; Williams et al., 2015). The rapid growth of the human population, accelerated technological development, and increased consumption of resources have contributed to major

local, regional and global changes in climate, biogeochemical cycles and biodiversity, challenging the ability of ecosystems to cope with the increased pace of events and disruptions (Jackson et al., 2001; Nyström et al., 2019; Paine et al., 1998; Waters et al., 2016). These combinations of changes towards new novel environmental conditions have led to novel biotic communities and both have rapidly emerged globally (e.g. Ordonez et al., 2016; Six et al., 2014; Williams et al., 2019). Such novelty is generated when a system, in a specific temporal and spatial context, is pushed beyond its historical range of variation (Mora et al., 2013). Novelty is not a new phenomenon but has been continuously emerging at different rates throughout Earth's history (Jackson, 2013; Pandolfi et al., 2020). However, the extent of its emergence may have accelerated due to human activities (Finsinger et al., 2017; Radeloff et al., 2015).

It is important to distinguish between change and novelty because places that change the most are not necessarily the most novel (Dornelas & Madin, 2020; Radeloff et al., 2015). For example, a system can experience a fast rate of change but can at the same time also experience a large seasonal and interannual variability, where the magnitude of change is small compared to its regional variability. In the case of the Arctic, the rate of temperature change is high but its thermal novelty may be low at the global scale (Williams et al., 2007). In contrast, the increase in temperature in other places like the tropics might be much smaller, but may shift the tropics towards a state for which there is no recent observation at a global scale, making climates there historically novel (Mora et al., 2013; Ordonez et al., 2016; Radeloff et al., 2015; Williams et al., 2007). This illustrates the difference between change and novelty and it is important to note that a lack of novelty does not imply that the ecological effects are neglectable or less serious.

The question here is why is it important to measure and monitor novelty? A long-term study of Cenozoic marine plankton communities has shown that the emergence of novel communities is associated with the increase of local extinction, origination and emigration (Pandolfi et al., 2020). The understanding of this emergence of novelty processes is important for conservation purposes as management needs to focus on preventing the transition to additional previously unseen ecosystem states (Pandolfi et al., 2020). In the 21st century, the emergence of novel species composition is expected to be driven by the rapid pace of climate change, the emergence of novel climate states, and other growing human pressures (Burke et al., 2019; Radeloff et al., 2015). Hence, management needs to consider the rate at which novelty and global change emerge and to understand the processes, and examine the drivers causing the increasing rate (Dornelas & Madin, 2020; Leclère et al., 2020; Pandolfi et al., 2020). Therefore, there is an urgent need to measure novelty, its rate of emergence in ecosystems and the contributing drivers. Here the past can be a good guideline as the understanding of when and where novelty has emerged in the past could help to estimate where, and under which conditions, novelty is most likely to increase in the coming decades (Burke et al., 2019).

In recent years, novelty in ecological communities and ecosystems has been mainly approached in two ways: (i) in conservation biology, novel ecosystems were used as a concept for biodiversity conservation created by individuals and societal values (Backstrom et al., 2018). They were defined as ecological systems that, under human influence, have crossed an irreversible threshold and differ from their historical state, that is, prior human influence state (Hobbs et al., 2013). (ii) In palaeoecology, biogeography and climatology, novelty has been considered as a continuous process of ecosystem dynamics applied to a large range of terrestrial systems, using different geological epochs and temporal scales as baseline conditions (Burke et al., 2019; Finsinger et al., 2017; Fitzpatrick et al., 2018; Mahony et al., 2017; Ordonez et al., 2016; Williams et al., 2007, 2019). In this case, human agency was not considered as the only driver for novelty. The latter approach measured novelty as a degree of dissimilarity of a specific system relative to a specific temporal and spatial baseline (Radeloff et al., 2015; Williams et al., 2007).

The crossing of a threshold after which a system cannot reverse to its previous state requires the identification of a shift towards a different regime, usually characterized as a large, abrupt, persistent change in the structure and function of the system (Andersen et al., 2009; Folke et al., 2004; Scheffer et al., 2001). This is difficult as it involves identifying a transition to a different state in different functions, characteristics and dynamics of the ecosystem. Additionally, categorizing novel and non-novel ecosystems has been heavily criticized because it can send the wrong message for conservation as no action will be taken when assuming that a system cannot be restored (Aronson et al., 2014; Murcia et al., 2014; Simberloff et al., 2015). Therefore, in our paper, we follow the second approach and avoid categorizing novelty. We apply the continuous approach to a marine ecosystem and quantify the rate of novelty (RoN) relative to a specific spatial and temporal baseline.

Despite the significant exploitation of global oceans, the race for ocean food, material and space known as 'blue acceleration' (Jouffray et al., 2020), and the unprecedented range shifts of marine species (Murawski, 1993; Perry et al., 2005; Pinsky et al., 2020; Richardson & Poloczanska, 2008), the concept of novelty has rarely been developed, applied and quantified in marine ecosystems (but see Graham et al., 2014; Harborne & Mumby, 2011; Perring & Ellis, 2013; Reygondeau et al., 2020; Schläppy & Hobbs, 2019). In this study, we explore the development of novelty in one of the most studied marine systems in the world, the Baltic Sea, using long-term monitoring data of abiotic and biotic components, spanning more than three decades.

The Baltic Sea represents a particularly stressed system due to its enclosed bathymetry, combined with the effects of multiple anthropogenic drivers such as climate change, overexploitation of fish resources, hazardous substances and eutrophication (Elmgren et al., 2015). This ecosystem is one of the marine areas with the highest recorded sea surface temperature increase during the past century (Belkin, 2009; Rutgersson et al., 2014; The BACC II Author Team, 2015). It has recently been suggested as a time machine for understanding climate-induced changes in global coastal oceans (Reusch et al., 2018).

Here we quantify the rate at which change and novelty have emerged in a marine ecosystem. We include, for the first time to the authors´ knowledge, three major trophic levels, that is, phytoplankton, zooplankton and fish, as well as nutrient concentrations and hydrographical conditions of the Baltic Sea across 10 basins over 35 years. We aim to identify abiotic drivers of biotic novelty, by exploring whether single or multiple abiotic variables can explain the emergence of biotic novelty. As such this study will contribute to filling the research gap of empirically quantifying novelty in a marine ecosystem across trophic levels and to identify important abiotic drivers.

2 | MATERIALS AND METHODS

2.1 | Data

The Baltic Sea is one of the largest estuaries in the world and has a strong salinity and temperature gradient, decreasing from southwest to northeast (Figure 2; Elmgren et al., 2015; The BACC II Author Team, 2015; and references therein). For the analyses, abiotic and biotic monitoring data were used for the period 1980–2015, obtained from different data providers (see Table S1) for 10 Baltic Sea basins, illustrated in Figure 1 (HELCOM, 2013).

We included abiotic variables that are of high biological relevance (e.g. HELCOM, 2018; The BACC II Author Team, 2015), that is, seasonally averaged sea surface temperature (SST; in spring, summer and autumn), annually averaged sea surface and bottom salinity, bottom oxygen concentrations and averaged winter (December–February) sea surface nutrient (dissolved inorganic nitrogen, DIN and dissolved inorganic phosphorus, DIP) concentrations (Table S1; Figure 2; Figures S1–S3).

The data on biotic components include phytoplankton biovolume, zooplankton biomass and fish species catch per unit of effort (CPUE; Table S1), which were used as a proxy for stock size. To account for changing taxonomic identification over the 35 years, we homogenized the taxonomies of the phytoplankton data to the class level (19 classes) and used genus-level identification for the zooplankton data (46 genera). For the fish data, the species-level taxonomy (61 species, all occurring at least three times in the time-series) was kept as provided from the data source (Baltic International Trawl Surveys; BITS, ICES, 2014).

2.2 | Data aggregation

To account for different spatial and temporal resolution in the sampling across the abiotic and biotic components (Table S1), we calculated basin-specific annual averages, except for the seasonal SSTs. To reduce further the influence of interannual variability, we calculated the average for 5-year periods, which we refer to as 'bins' (e.g. the 1980 bin represents the average of the annual averages from 1980 to 1984, and so forth). Basins for which we lacked complete time-series were excluded from the biotic analyses (see Table S1). For instance, the Kattegat, Arkona Basin and Western Gotland Basin were excluded from the phytoplankton analyses and the Kattegat, Arkona Basin and Bornholm Basin from the zooplankton analyses. Moreover, the analyses based on the fish survey data did not include the northern basins (Gulfs of Bothnia, Finland and Riga, and Northern Baltic Proper). Additionally, the available time-series for the fish component are shorter (1991–2015).

2.3 | Rate of change (RoC) and rate of novelty (RoN)

We distinguished between the rate of change (RoC; change within-basin) and the rate of novelty (RoN; change across-basins) as two separate measures (Figure 3) because basins that changed the most

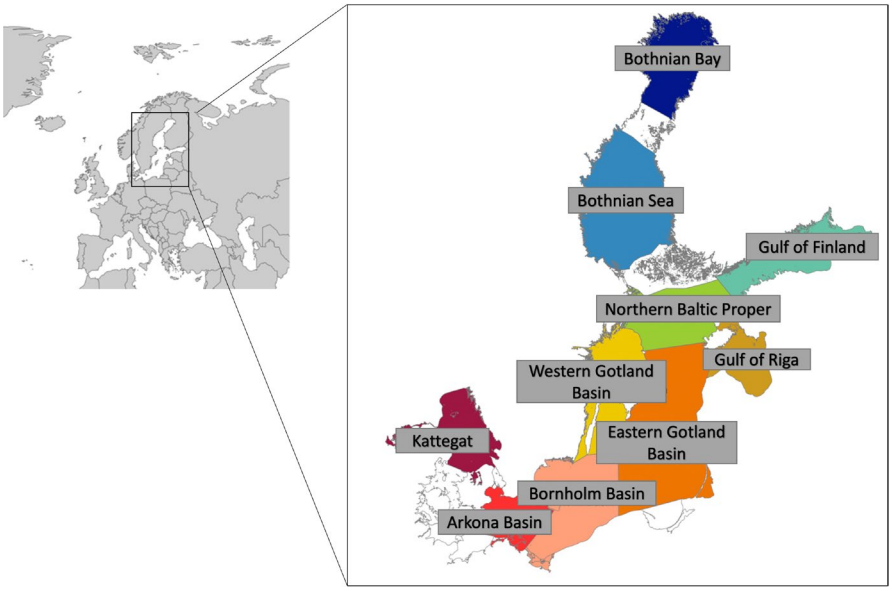

FIGURE 1 Map of the Baltic Sea divided according to HELCOM sub-basins

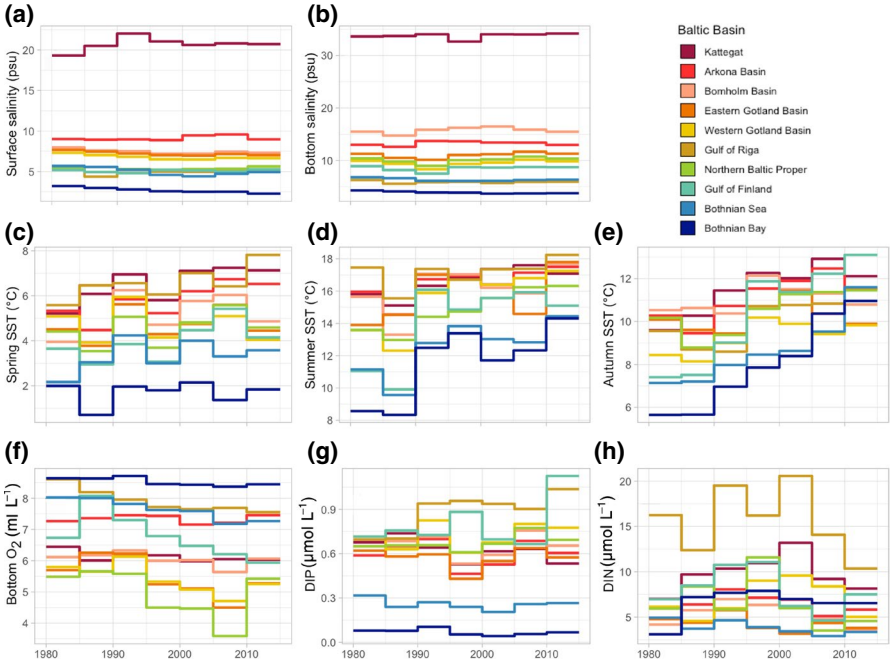

FIGURE 2 Abiotic variables in the Baltic Sea basins (5-year averages referred to as bins): (a) annual surface salinity, (b) annual bottom salinity, (c) spring sea surface temperature (SST), (d) summer SST, (e) autumn SST, (f) annual bottom oxygen concentration, (g) dissolved inorganic nitrogen (DIN) and, (h) dissolved inorganic phosphorus (DIP). The color scale indicates the different Baltic Sea basins. Detailed basin specific changes and trends of abiotic variables are found in the appendix Figures S1–S3

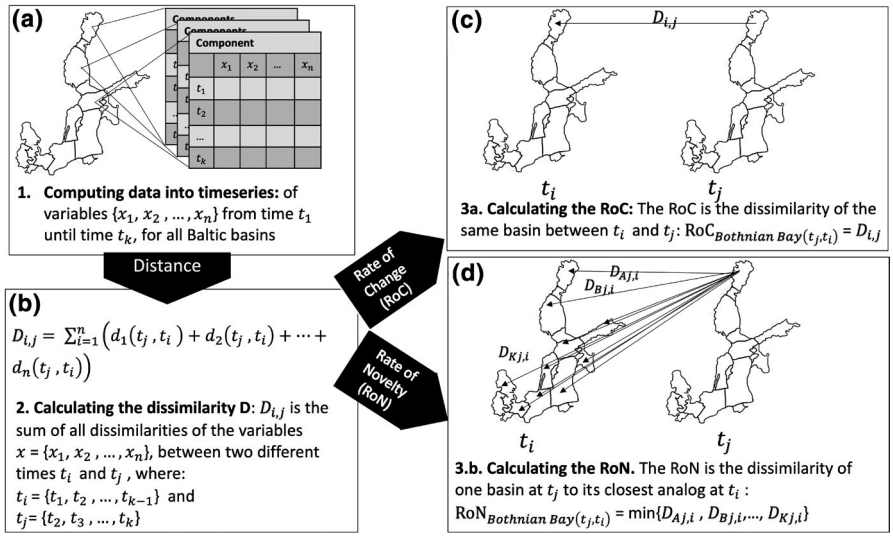

FIGURE 3 Conceptual figure presenting the steps to quantify the rate of change (RoC) (c) and the rate of novelty (RoN) (d). The steps are described as following: (a) Computing the time-series for each component, according to time and basin; (b) calculating the dissimilarity *Di,j* between two bins (i and j). For RoC (c), *Di,j* is measured for each basin between two different bins. For RoN (d), *Di,j* is the minimum dissimilarity of a basin at a certain bin for all basins in relation to a bin in the past, resulting in the dissimilarity to the closest basin

are not necessarily the most novel (Radeloff et al., 2015). We expect that climatic changes and anthropogenic pressures have changed the system and may have led to a certain rate of novelty in the Baltic Sea ecosystem. Thus, we quantified for each of the basins the amount of change over time, that is, RoC, of a component (i.e. abiotic conditions, phytoplankton, zooplankton and fish) within individual basins (Figure 3c), between the 1980 reference and later inference periods (and between two consecutive time intervals in the supplementary information Figure S5). By contrast, to determine the RoN we first calculated for each basin the dissimilarities at a certain moment in time (the period of inference) relative to all basins from a specified baseline (Figure 3d), and selected the minimum dissimilarity value as the dissimilarity between the target bin and its closest counterpart in the reference baseline. For example, the abiotic RoN at 2010 with respect to 1980 is based on comparing abiotic conditions from 1980 with those from 2010, thus assessing the effects of changes over a 30 year period upon the emergence of novelty across the basins. A RoN equal to zero indicates that the basin at a certain time had an exact analogue in the past, that is, no novel conditions. If the minimum dissimilarity of a basin is the basin itself, the RoC and RoN are equal. Hence, the RoN can never be greater than the RoC (Finsinger et al., 2017).

The RoC and RoN were computed for each ecosystem component (the ensemble of eight abiotic variables, phytoplankton, zooplankton and fish assemblages) separately. A direct comparison between the biotic assemblages is not possible, because the biotic components have different spatial and temporal data resolutions due to sampling. An analysis of abiotic novelty using the same spatial and temporal distribution of each of the biotic assemblages is found in the supplementary information (Figure S7). This analysis was based on the R code from Finsinger et al., (2017), but adapted to our approach and the quality of our data.

2.4 | Dissimilarity indices

The dissimilarities were calculated at 5-year bin intervals (e.g. between 1980 [1980–1984] and 1985 [1985–1989], and so forth) using the following indices for the RoC and RoN analyses:

2.4.1 | Dissimilarity indices for abiotic conditions

For the abiotic RoC and RoN, the Standard Euclidean Distance (SED; Prentice, 1980) was used, which is an appropriate distance measure for environmental data and has been used to quantify novelty previously in many studies (e.g. Fitzpatrick et al., 2018; Radeloff et al., 2015; Williams et al., 2007). This dissimilarity preserves the signal of individual variables (Williams et al., 2019) while standardizing variables that have different units to the same unit. SED was calculated as follows:

$$\mathrm{SED}_{ij} = \sqrt{\sum_{k=1}^{n} \frac{\left(b_{kj} - a_{ki}\right)^2}{s_{kt}^2}},$$

where k refers to one of the n variables (n = 8 abiotic variables: SST in spring, summer and autumn and surface, and bottom salinity, DIN, DIP and bottom oxygen concentration, see Figure 2); $b_{kj} - a_{ki}$ is the difference between the values of the abiotic variable k in a basin at a time bin t_j and a basin at a previous time bin t_i; s_{kt}^2 is the standard deviation of k over all basins during the whole studied period.

2.4.2 | Dissimilarity indices for biotic assemblages

The interactions between species sustain the structure, function and resilience of food webs rather than individual species identity and diversity (McCann, 2007; Pinsky et al., 2020). The emergence of novel interactions that increase species homogenization could jeopardize the resilience of ecosystems (Fricke & Svenning, 2020). Thus, we focus on changes in composition or the turnover (presence–absence and compositional differences in terms of species proportion) of the whole assemblages to assess the rate of emergence of novel compositions which could suggest the establishment of novel interactions. Aside from that, changes in species biomass or abundance (here stock size) can be much larger than changes in species composition and distribution (Harborne & Mumby, 2011; Simpson et al., 2011). Therefore, we account for and quantify both composition and stock size changes.

The changes in composition, that is, temporal turnover, was assessed using the Hellinger distance (HD), which is a measure recommended for clustering or ordinating abundance data (Birks & Lotter, 2012; Prentice, 1980; Rao, 1995) and considers the turnover rate associated to both presence–absence and compositional differences in the dataset. HD uses square-root transformed values to reduce the importance of the most dominant taxa and increase the influence of less abundant taxa (Prentice, 1980). HD was calculated as follows:

$$\mathrm{Hellinger}_{ij} = \sqrt{\sum_{k=1}^{n} \left(\sqrt{\frac{b_{kj}}{b_j}} - \sqrt{\frac{a_{ki}}{a_i}} \right)^2},$$

where k refers to one of the n taxa of the biotic component (with n = 19 for phytoplankton, n = 46 for zooplankton and n = 61 for fish, Table S1), and $\frac{b_{kj}}{b_j}$ and $\frac{a_{ki}}{a_i}$ are the relative abundances of the kth taxon for a basin at a time bin and a basin at a previous time bin respectively.

To calculate the dissimilarity in stock size, the Euclidean distance was used and normalized (weighted) by the maximal dissimilarity in the whole dataset for each biotic assemblage. This Normalized Euclidean Distance (NED) allowed us to calculate a dissimilarity that ranges within the interval [0,1] (which is not the case for SED), thus a dissimilarity that is comparable and summable with the HD. Prior to the dissimilarity computation, the data were log-transformed to reduce the asymmetry of the species distributions within the dataset. This metric was calculated as follows:

$$\mathrm{NED}_{ij} = \sqrt{\frac{1}{W} \sum_{k=1}^{n} \left(b_{kj} - a_{ki}\right)^2},$$

where k refers to one of the taxa [1, n] from the biotic components (with n = 19 for phytoplankton class, n = 46 for zooplankton genera and n = 61 for fish species, Table S1); b_{kj} and a_{ki} are the value of the kth taxon for a basin at a time bin t_j and a basin at a previous time bin t_i, respectively; W is the maximal dissimilarity of the whole dataset of the biotic component.

Both HD and NED were scaled to the range [0, √2], and averaged to obtain one dissimilarity measure, that allowed the description of RoC and RoN of biotic assemblages in both composition and stock size.

2.5 | Generalized Additive Models (GAM)

Generalized Additive Models (GAM) were used to test the hypothesis of whether change in single or multiple abiotic variables could explain the amount of novelty accumulated through time from the baseline period (1980; 1995 for fish) to 2010 for the three biotic components: phytoplankton, zooplankton and fish. A GAM model allows the smoothing of non-parametric functions, for a flexible specification of the dependence response (Wood, 2017). The RoN of biotic assemblages relative to the 1980 baseline was the dependent variable. As explanatory variables, we used: (1) the distance of abiotic variables at the target bin to their value at the baseline closest analogue, and (2) the values of abiotic variables at the target bin. The *gam* function in mgcv R package (Wood, 2017) was applied with a smoothing parameter setting of $k < 4$ and the thin plate regression

spline as a smoothing basis. A correlation was considered significant when $p < 0.05$. Only the significant correlations were shown in the result section.

All our analyses were performed using the R environment (version 3.6.3; R Core Team, 2020) and the additional packages 'analogue' (0.17-4; Simpson, 2007; Simpson & Oksanen, 2020), 'vegan' (2.5-6; Oksanen et al., 2019) and 'mgcv' (1.8-31; Wood, 2011).

3 | RESULTS

3.1 | Rate of change

The median RoC relative to the 1980 baseline is highest in 1995 and 2005 for all studied ecosystem components (except for fish where the time-series is shorter; Figure 4), and 2010 for abiotic conditions. The median change of abiotic conditions shows an increasing long-term trend, where abiotic conditions gradually changed away from the baseline conditions (Figure 4a). Phytoplankton assemblages show a higher median change (>0.5) than other biotic components, but no continuous increase or decrease in RoC is detected over time (Figure 4b). RoC of the zooplankton assemblages increased over time until the 1995 period (RoC = 0.75) and then was levelled off (Figure 4c). The RoC of the fish assemblage (Figure 4d), shows a marked increase in 2005 to a high level of >0.7 (relative to the 1995 baseline), which remained high towards 2010.

3.2 | Rate of novelty

3.2.1 | Abiotic novelty

The RoN of abiotic conditions relative to the 1980 baseline (Figure 5a,b) shows similar trends as the RoC, but with a lower magnitude. In some target bins, the closest analogues (closest abiotic conditions to those in the target bin) are found in a baseline basin that is different from the target basin (Figure 5a, see closest analogs in Figure S5). For example, the abiotic conditions of the Bothnian Bay in the 2010 target bin are closer to the 1980 baseline conditions of the Bothnian Sea than to the baseline conditions of the Bothnian Bay itself (Figure S5). When exploring all potential target-baseline combinations (Figure 5a, *y*-axis), the highest magnitudes of RoN are identified, in all targets relative to the 1985 baseline. A smaller and directional change in magnitude takes place after the 1990 baseline. Overall, the RoN increased and decreased over time repeatedly depending on the baseline conditions.

The range of RoN relative to the 1980 baseline (shown as vertical whiskers in Figure 5b) is largest in the 2010 target bin. The basins with the highest RoN in 2010 relative to the 1980s baseline are the confined Gulfs, that is, the Gulf of Bothnia (Bay and Sea), Gulf of Riga and Gulf of Finland and Kattegat (Figure 5d). The RoN is also highest in the Gulfs and Kattegat across all target bins in relation to the 1980 baseline (Figure 5c). In contrast, lower RoNs are found in the Central Baltic Sea. These findings indicate that abiotic conditions

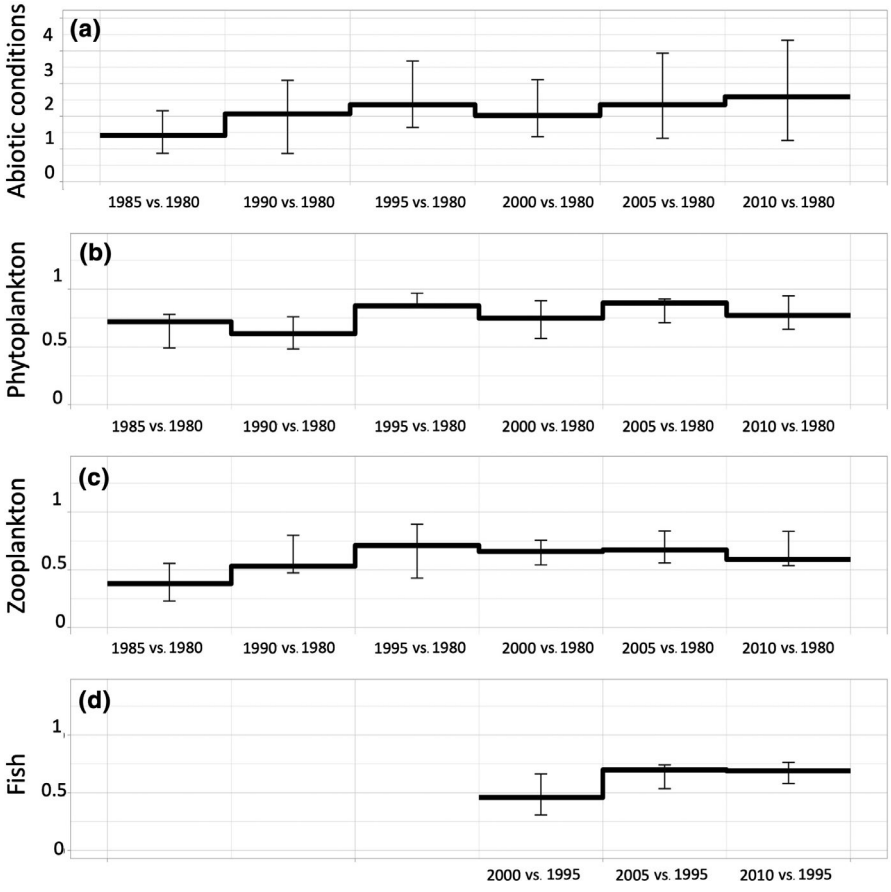

FIGURE 4 Median accumulated within-basin change for the Baltic Sea in relation to the 1980 baseline for (a) abiotic conditions, (b) phytoplankton, (c) zooplankton, and (d) fish assemblages. The vertical whiskers represent the minimum and maximum change values

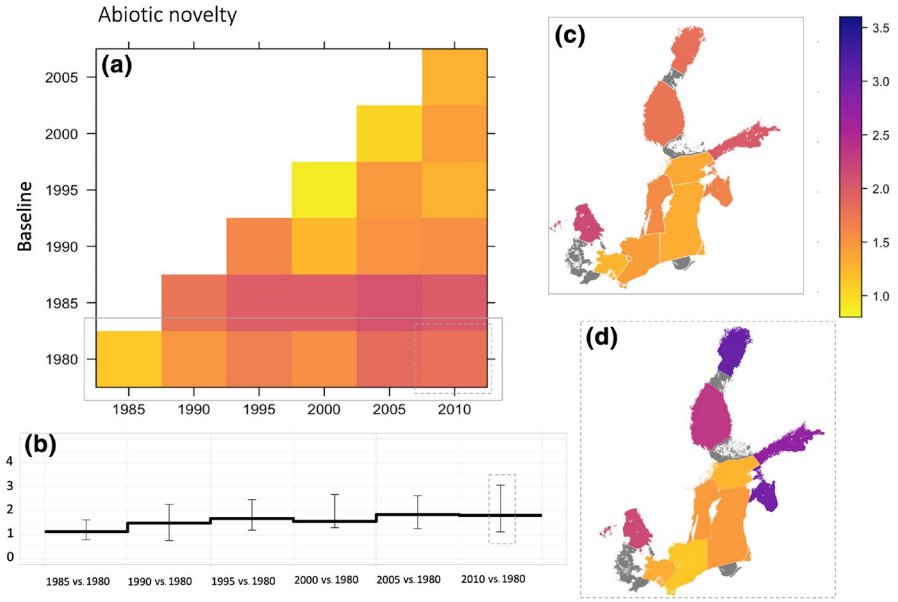

FIGURE 5 Spatial and temporal changes in the rate of novelty (RoN) of abiotic conditions: (a) Temporal median RoN in all baseline-target combinations, (b) Temporal changes in the median RoN across the whole Baltic Sea relative to the 1980 baseline, vertical whiskers show the range of RoN values among the Baltic Sea basins; (c) Median RoN across all target bins relative to the 1980 baseline; (d) Accumulated novelty between 1980 and 2010. The intensity of change in RoN is indicated by the colors

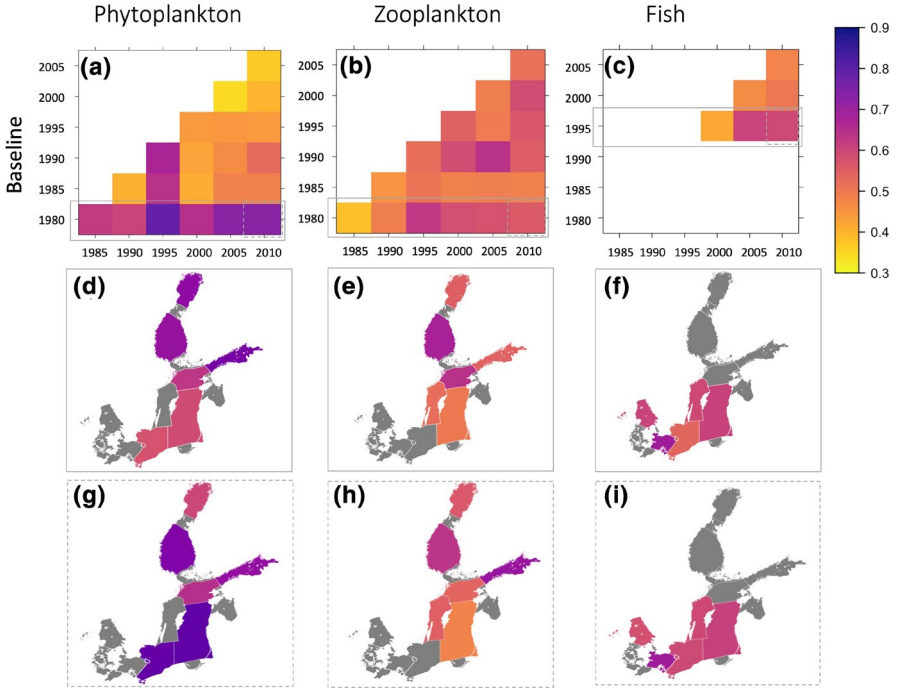

FIGURE 6 Spatial and temporal changes in the rate of novelty (RoN) of phytoplankton (a, d, g), zooplankton (b, e, h), and fish (c, f, i). (a–c) Temporal median RoN in the Baltic Sea in all baseline-target combinations; (d–f) Median RoN across all target bins in relation to the 1980 baseline; (g–i) RoN in 2010 target bin relative to the 1980 baseline. The intensity of change in RoN is indicated by the colors. The scale is within the range [0, √2]

in the confined Gulfs and Kattegat changed over time from the 1980 baseline more than in the Central Baltic Sea basins, and that abiotic novelty emerged faster in the Gulfs and Kattegat than in the Central Baltic Sea.

3.2.2 | Biotic novelty

As identified for the median RoC (Figure 4b,c), the median RoN is highest for 1995 (in relation to the 1980 baseline) for phytoplankton and zooplankton assemblages (Figure 6a,b). Nonetheless, different temporal patterns emerge in these two assemblages. For instance, the 1980 baseline (all targets) shows a high median RoN (>0.7), indicating a median RoN of more than 50% in the composition and stock size of the phytoplankton assemblage after the 1980–1984 period. Likewise, the 1995 target (relative to its previous baselines) shows a high median RoN (>0.7), indicating a high change in phytoplankton assemblage in the 1995 bin relative to the previous baselines. However, a smaller range of variation over time between bins and lower magnitudes of median RoN in the zooplankton assemblages are displayed over the entire study period (Figure 6d; see closest analogs in Figure S5). Median RoN of fish assemblages shows similar trends than median RoC relative to the 1995 baseline and a similar magnitude in the following baselines (Figure 6c), which indicates a fast change in composition and stock size in the southern Baltic Sea.

Large spatial variation in the magnitude of RoN over time is identified in the phytoplankton and zooplankton assemblages. The spatial visualization of median RoN across the target bins in relation to the 1980 baseline (Figure 6d,e) shows higher magnitudes of RoN in the northern basins, that is, in the Gulf of Finland and the Gulf of Bothnia for phytoplankton, and in the Bothnian Sea and Northern Baltic Proper for zooplankton. However, the RoN in the 2010 target bin relative to the 1980 baseline (Figure 6g,h) indicates high novelty in all basins for the phytoplankton assemblages, and higher novelty in the Gulf of Finland for zooplankton assemblages.

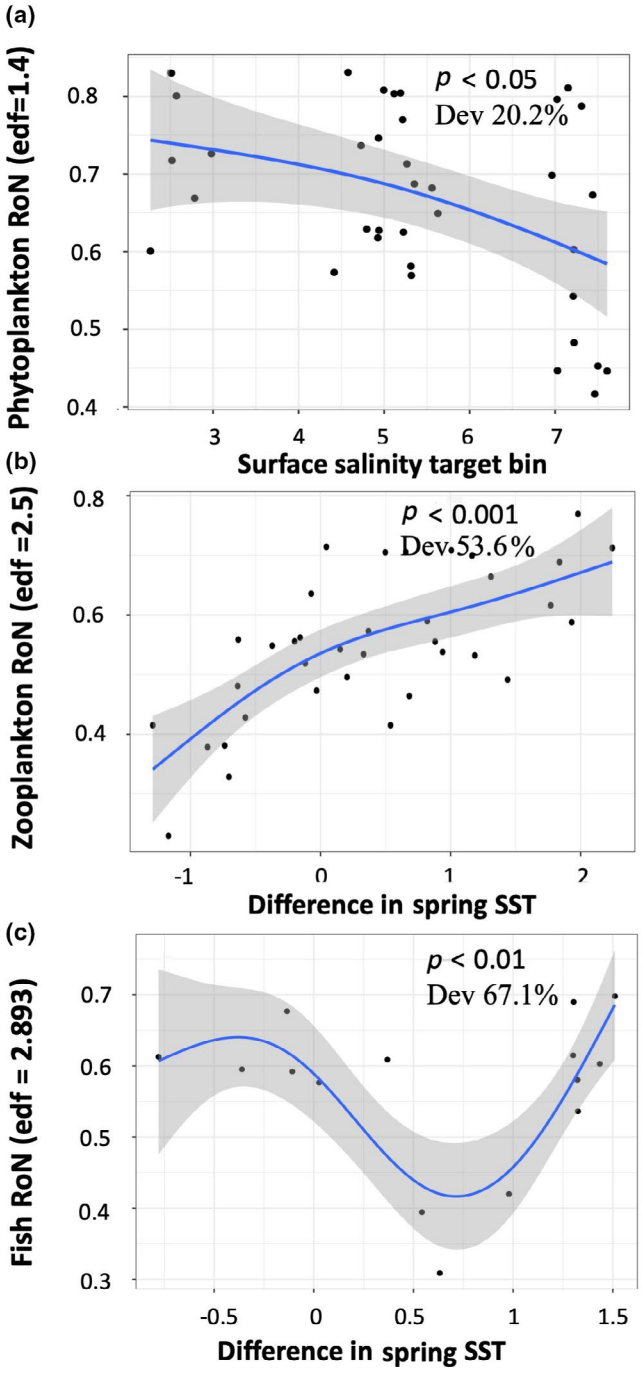

FIGURE 7 Significant ($p < 0.05$) relationships between changes in abiotic conditions and accumulated novelty in biotic assemblages. (a) Rate of Novelty (RoN) of phytoplankton in response to annual sea surface salinity at the target basin and time, (b) RoN of zooplankton in response to spring sea surface temperature (SST) change from the 1980 baseline to 2010, (c) RoN of fish communities in response to the difference in spring SST from the 1995 baseline to 2010. The blue lines indicate the smoothed ($k < 4$) splines of the generalized additive model (GAM). The grey areas indicate the lower and upper 95% confidence intervals

3.3 | Drivers of biotic novelty (GAM)

To explore how biotic novelty is related to changes in abiotic conditions, we analysed the relationships between abiotic variables and the RoN of the three biotic assemblages as explained in the method section, and only show the significant relationships in Figure 7. The RoN of phytoplankton is negatively affected by annual sea surface salinity at the target basin ($R^2 = 0.167$; $p < 0.05$; Figure 7a), suggesting that the phytoplankton assemblages in the basins with lower salinity manifest higher RoN than basins with higher salinity. This means that changes in basins where salinity is already low have a greater influence. The RoN of zooplankton is positively correlated with an increase in spring SST, which is indicated by the difference in spring SST between target basins and their 1980 baseline closest analogues ($R^2 = 0.5$; $p < 0.001$; Figure 7b; see closest analogue Figure S5 and spring temperature trends Figures S1–S3). A similar positive relationship is found for the RoN of fish, even though the time-series is much shorter ($R^2 = 0.586$; $p < 0.01$; Figure 7c).

4 | DISCUSSION

This paper is an attempt to quantify both the rate of change (RoC) and the rate of novelty (RoN) of abiotic and biotic components in a large marine ecosystem. Our findings highlighted the difference between within basin RoC and across basins RoN, at the scale of the Baltic Sea, a marine region impacted by multiple stressors. Abiotic and biotic novelty varied in time and space, depending on the baseline conditions. Although the dynamics of novelty in this system seemed to be rather complex, our analyses showed that the rate of abiotic novelty is higher in the confined northern Gulfs and Kattegat than in the Central Baltic Sea. A similar general pattern was detected in the case of biotic assemblages. Furthermore, our findings suggest that salinity and temperature play a key role in the emergence of ecological novelty.

4.1 | Abiotic and biotic novelty in the Baltic Sea

At the Baltic Sea scale, abiotic RoC and RoN were directional, and the abiotic conditions were found to have changed continuously away from the 1980 baseline conditions (Figures 4 and 5). The increase in temperature (increase in SST between 1 and 3°C in spring, 1 and 4°C in summer and 0.5 and 5°C in autumn across all

the Baltic Sea basins) and changes in salinity (e.g. surface salinity has decreased by 1 PSU in the Bothnian Sea and increased by 3 PSU in Kattegat) in recent decades (Figure 2; Figures S1–S3) have caused an increase in abiotic RoN. Indeed, SST has increased over time, and since 1990, annual mean SST has increased by up to 1°C per decade in the Baltic Sea (The BACC II Author Team, 2015). This annual mean SST rise has been stronger in the north, that is, in the Gulf of Bothnia, the Gulf of Finland, Northern Baltic Proper and the Gulf of Riga (The BACC II Author Team, 2015; Figure 2; Figures S1–S3). Besides, changes in the precipitation patterns and the increase of freshwater inflow in the Baltic Sea have affected the surface salinity (Elken et al., 2015; Lehmann et al., 2011; Meier, Hordoir, et al., 2012; Meier & Kauker, 2003), which has decreased in most basins, except Kattegat, Arkona Basin and Northern Baltic Proper where it has increased (Figures S1–S3). These combinations of directional changes in temperature and salinity, particularly those in the Gulf of Bothnia and Kattegat, which were not encountered in the early 1980s, were important driving factors of abiotic novelty locally and in the Baltic Sea as a whole. In addition, eutrophication-related factors (i.e. DIN and DIP), particularly in the Gulf of Riga and Gulf of Finland (Figures S1 and S2), combined with the increased temperature and decreased salinity, have also contributed to the increasing abiotic novelty in these Gulfs. Conditions resulting from changes in abiotic conditions in the central Baltic Sea were more similar to those in the early 1980s than the resulting changes in the Gulfs. Therefore, RoN in the central Baltic Sea was lower than in the Gulfs. Hence, the combination of climate-related changes and eutrophication-related drivers in specific basins for which no precedent existed in the early 1980s, contributed to the higher abiotic RoN, especially in the confined Gulfs and Kattegat.

The temporal and spatial emergence of biotic novelty was more complex. Despite the constraints of different spatial and temporal resolutions due to sampling preventing a direct comparison of RoC and RoN across trophic levels (Figure 6), common general trends were identified. For phytoplankton and zooplankton, we found the largest RoC and RoN in the 1995 target bin relative to the 1980 baseline. These patterns were identified in the Gulfs of Bothnia and Finland and Northern Baltic Proper for phytoplankton, and in numerous basins for zooplankton (Figure S5). This finding is consistent with previous studies that identified a shift around 1995 in the north of the Baltic Sea for phytoplankton assemblages (Jaanus et al., 2011; Suikkanen et al., 2013), and in most basins for the zooplankton assemblages (Gorokhova et al., 2016; Suikkanen et al., 2013).

In terrestrial systems, the abiotic novelty has been designated as the strongest predictor of accumulated biotic novelty (Burke et al., 2019; Jackson & Overpeck, 2000; Williams & Jackson, 2007). In our marine case, we found similar trends in spatial and temporal patterns of novelty for abiotic and biotic components (Figure 6; Figure S7). The RoN was higher mainly in northern enclosed basins in both abiotic and biotic components. This indicates that abiotic novelty could be a strong predictor of biotic novelty in the Baltic Sea. However, it seems that the emergence of novelty over the 1980 baseline is more similar between abiotic and phytoplankton (Figure 6d; Figure S7d) than between abiotic and other biotic assemblages (Figure 6e,f; Figure S7e,f). This suggests that in addition to abiotic novelty, other processes such as interactions between species and trophic levels could be drivers of biotic novelty at higher trophic levels in marine ecosystems.

In the Baltic Sea, it is known that the North-South gradients of salinity and temperature shape species distributions (Möllmann et al., 2000; Pecuchet et al., 2016; Viitasalo et al., 2015; Vuorinen et al., 1998), and thereby determine the biotic community structure. Our results revealed that salinity and temperature are also important drivers of biotic novelty in the Baltic Sea (Figure 7). For example, surface salinity was identified as a driver of summer phytoplankton novelty, and phytoplankton assemblages in basins with lower salinity manifested higher RoN than basins with higher salinity. The gradually decreasing salinity in the northern basins, which already have low salinity (decrease in Bothnian Bay from 3.3 to 2 PSU), may have favoured the presence of phytoplankton assemblages that were not detected in the 1980s. The RoN of zooplankton and fish assemblages was linked to changes in spring temperature (between 3 and 6°C of change; Figure 7). The increase in spring SST that occurred in the Baltic Sea over time (Figures S1–S3) may have increased novelty in the Baltic Sea zooplankton and fish assemblages by means of different processes. For instance, warmer spring temperatures could have extended the season of summer zooplankton, since it has been proven that spring zooplankton has a shorter window of occurrence when spring temperatures are higher (Aberle et al., 2012). Changes in seasonality can also affect the structure of the fish community, for example, by altering reproductive and migration seasons, limiting prey availability at critical life stages and causing physiological and behavioural stress (Casini et al., 2016; MacKenzie et al., 2007). Hence, salinity and temperature which were identified as main contributors to high abiotic RoN, are also important drivers of biotic RoN in the Baltic Sea. In general, climate-induced changes such as salinity and temperature are globally changing, and may be important drivers of biotic novelty in marine ecosystems.

The RoN may further rise in the Baltic Sea ecosystem in the future, due to climate change and other anthropogenic drivers. Indeed, anthropogenic climate change is not a disturbance after which conditions will return to their previous state but is a combination of directional changes from baseline conditions and changes in frequency and intensity of extreme events (Fisichelli et al., 2016). Various studies projected substantial changes in climate-related factors in the Baltic Sea (e.g. Breitburg et al., 2018; Meier, Müller-Karulis, et al., 2012; Ryabchenko et al., 2016). For instance, temperature is projected to increase by 2°C in southern basins and 4°C in the northern Baltic Sea, and will be greater in the Gulf of Bothnia in summer and in the Gulf of Finland in spring by the end of the 21st century (Meier, 2015). Moreover, although salinity projections differ considerably due to the uncertainties in the precipitation and therefore in the projected river runoff, most models projected lower salinity by the end of the 21st century (Meier et al., 2018, 2019; Saraiva et al., 2019). These projections suggest that biotic communities in

the northern Baltic basins which are more subject to change due to abiotic changes, may be more vulnerable to further rise of biotic novelty in the Baltic Sea.

4.2 | Rate of novelty versus rate of change

The understanding of the impacts of climate change in combination with natural and anthropogenic changes suggest that species and ecosystems will adapt and change, but are unlikely to revert to previous species assemblages as the underlying conditions will no longer exist (Fisichelli et al., 2016). For instance, in the Baltic Sea, many species have previously adapted to the north–south gradient of temperature and salinity. This may suggest that in the case of further changes in the gradient, changes in the composition, structure and function of the system will occur to adapt. Thus, studying novelty provides a possibility to assess multidimensional changes across multiple abiotic and biotic components and their magnitude. It also provides a new framework to understand the consequences of ecosystem changes on ecological communities (Williams et al., 2019). In this context, the RoN analysis provides an assessment of how much and how fast an entire system (e.g. the Baltic Sea) shifted or at least changed from its historically known range of variation, which is not provided by an RoC analysis only focused on basin-specific changes.

The perception of baseline can be linked to human perception of the shift of the system (Heger et al., 2019; Papworth et al., 2009; Pauly, 1995; Rodrigues et al., 2019). The baseline also depends on the context of the study, the time scale and the characteristics of the system considered. For instance, Rodrigues et al. (2019) suggest that the baseline should be tailored to each population, and assigned a conceptual baseline in the absence of human actions while making the best use of the information available. The term historical baseline could therefore be used as a past reference state that could be needed as a guideline in specific contexts. In the context of this study, data were not available from the period before 1930, often seen as the pristine state of the Baltic Sea system. In fact, in most marine ecosystems, intensive observational monitoring only began during the 1950s. Although knowledge of the onset of eutrophication in the 1940s–50s, hypoxia and other climate-related changes in the recent past (Gustafsson et al., 2012; The BACC II Author Team, 2015; Zillén et al., 2008), the available Baltic Sea wide monitoring data covering the variables we included in this analysis started in the mid to late 1970 s. Thus, we used monitoring data for the last 35 years, and the earliest baseline available, that is, the 1980 baseline (1995 for fish assemblages), to capture the RoN on the longest period available. Hence, the baseline here provides a reference point to compare the rate of the emergence of novelty, rather than a comparison to the pristine conditions of the Baltic Sea.

The spatial and temporal baselines determine the level of novelty related to the multidimensional change over time (Figures 5 and 6) because novelty is only meaningful in relation to a specific temporal and spatial baseline (Radeloff et al., 2015). Previous studies have quantified the accumulated RoN over long periods of time throughout the past (e.g. 15,000 years in Burke et al., 2019; and in Finsinger et al., 2017; more than 100 years in Radeloff et al., 2015; and in Williams et al., 2019). The analysis of such long-term datasets increases the likelihood of identifying truly novel conditions (i.e. conditions that deviate considerably from the baseline) and allows estimating climate-induced emergence of novelty (as human pressure on ecosystems was likely negligible several millennia ago). Factors such as generation times and study periods are also important to consider in the comparative analysis of frequency or drivers of novelty in communities (Pandolfi et al., 2020). We, therefore, focused on the RoN rather than novelty as in such a time scale, that is, 35 years, it is difficult to identify truly novel communities. Exploration of longer term palaeoceanographic datasets of marine biotic communities (e.g. de Vernal et al., 2005; Pandolfi et al., 2020) may help to fill this knowledge gap.

We focused on the rate at which novelty and change emerge and compared the RoN to the RoC. Temporal changes in novelty of both abiotic and biotic components followed the within-basin trends, but the RoN was slower than the RoC (Figures 4–6). This means that some basins of the Baltic Sea have become similar to other basins in the 1980 baseline, instead of displaying relatively novel conditions at the scale chosen. This is expected and has been explained in the methodology used where the RoN can never be greater than the RoC. We considered novelty to occur when a system is pushed beyond its historical range of variation (Mora et al., 2013), which here was the 1980 baseline (1980–1984 of all Baltic basins) range of variation. But we also applied different baseline-target combinations and found that abiotic and biotic RoN increased and decreased repeatedly over time and space, which has been referred to as backward cycling (Finsinger et al., 2017; Jackson, 2013). This underlines the difficulty of assigning a threshold beyond which conditions cannot revert to their previous state. These patterns reflect the complex dynamics of ecosystems, linked to interactions between species, and species with their environment, where novelty is not a linear function of time (Figures 5 and 6) and follows baseline-specific trajectories (Radeloff et al., 2015).

There is always a degree of turnover in biotic communities, even in relatively stable states (Dornelas & Madin, 2020; Pandolfi et al., 2020). All biotic assemblages in our analysis showed different trajectories of change in composition and stock size over time (Figure S4). Together, these different dynamics contributed to the rise of biotic RoN. We acknowledge that we did not consider some aspects of ecological communities, for example, species diversity and richness that influence how ecosystems evolve (Gotelli et al., 2017), as well as functions, interactions and feedbacks. These aspects could be included in future studies and provide more insights on the emergence of novelty in biotic communities. Nonetheless, we consider our study as a first robust quantitative attempt to explore the temporal and spatial biotic RoN in a marine ecosystem.

The choice of the variables determines the results of novelty for each component. For instance, the phytoplankton novelty, which

was assessed at the class taxonomic level and showed high values in general throughout the Baltic Sea (Figure 6a,d,g) does not provide an indication of the rise of novelty at the species level. Such limitations were also encountered when assessing long-term novelty trends based on palaeoecological records (e.g. Burke et al., 2019; Finsinger et al., 2017). However, when comparing the emergence of novelty between trophic levels, using datasets with the same spatial, temporal and taxonomic resolutions may be important to detect the influence of trophic cascades on novelty trends. This would be greatly needed especially in the case of the enclosed Gulfs, which seemed to be more vulnerable to the fast emergence of novelty in abiotic conditions, phytoplankton and zooplankton, but could not be tested as we lacked data on the fish assemblages for these basins. Likewise, the highest and fastest RoC as well as RoN occurred in the late 1980s and early 1990s compared to the 1980 baseline. In this period, a regime shift was documented in the fish community in the Central Baltic Sea, has changed fish species dominance from the piscivore cod (*Gadus morhua*) to a small pelagic clupeid fish sprat (*Sprattus sprattus*), and cascaded down to lower trophic levels (Möllmann et al., 2008, 2009). Data limitations of this period in the fish component, have prevented us to understand if and how the high RoN in the same period was related to this regime shift and the effects on all trophic levels. Furthermore, accounting for the effects of fishing, and of other anthropogenic factors in the Baltic Sea [e.g. plastic pollution, heavy metals and other hazardous substances], may improve our understanding of the driving factors of biotic novelty. For instance, fishing has been suggested to contribute, besides climate, to the regime shift of the Central Baltic Sea (Lade et al., 2015; Möllmann et al., 2008, 2009), which could as well contribute to change the food web dynamics and push species to reshuffle into novel combinations. Overall, there is a need for more research on the emergence of novelty and its drivers, to assess the importance of considering novelty in future management interventions in the Baltic Sea as well as in other marine ecosystems.

Choosing appropriate baselines allows novelty metrics to flexibly target the problem, the management context, and the system of interest (Heger et al., 2019; Williams et al., 2019). In our study, the spatial scale was chosen to meet the unit of management of the Baltic Sea. Nonetheless, studying the emergence of novelty at different scales provides learning at which scales different types of novelty (e.g. compositional, functional) may arise which will help to inform how to manage at the appropriate scales. For instance, in the case of Kattegat, the RoN was equal to RoC for both abiotic conditions and fish assemblages (Figures 5 and 6; Figure S5). This basin with the highest salinities in the Baltic Sea (annual surface salinity is 20 PSU) close to marine water systems, and the greatest fish species diversity (46 species in our dataset) compared to the entire Baltic Sea (Pecuchet et al., 2016), is different from the rest of the Baltic Sea. Estimates of abiotic and biotic novelty in this basin may have been lower if the scale of our analysis included, for example, the North Sea. Thus, there is a need to advance research on multidimensional changes and the potential rise of novelty in marine ecosystems, across local, regional and global scales.

5 | CONCLUSION

The potential impacts of exploration and understanding of novelty provides different benefits, for example, policy development, understanding how resilience is generated, measuring social-ecological resilience and developing more targeted planning and management methods (Allen & Holling, 2010; Chaffin et al., 2016; Collier, 2015; Dudney et al., 2018). Exploring novelty on a regional scale provides a richer contextualization and a deeper interpretation of the patterns of change and novelty (Williams et al., 2019). By focusing on the Baltic as a case study, we found high novelty in abiotic conditions and biotic assemblages mainly in the confined northern Gulfs and Kattegat. We addressed two aspects to study novelty in biotic assemblages, that id, changes in composition and stock size. Other aspects, for example, species traits, could be addressed in the future. We identified salinity and temperature as the main drivers of biotic novelty. These climate-induced factors, which are projected to change further in the future, may together with other anthropogenic drivers increase the biotic novelty in the Baltic Sea. In general, certain marine areas are more susceptible to the rise of novelty than others. Therefore, more research is needed on the processes that lead to novelty in marine ecosystems, including interactions between species and trophic levels, and the functions of ecosystems under high abiotic novelty. In fact, great uncertainty is associated with the future functioning of ecosystems in highly novel abiotic conditions (Fitzpatrick et al., 2018), which may increase the uncertainties associated with projecting future changes in, for example, species distributions or biomass, important for environmental policy and management decisions (Barnosky et al., 2017; Blois et al., 2013; Silliman et al., 2018). Accordingly, understanding of how novelty is generated locally, regionally and globally, its processes in different ecosystem components, and the effects on different trophic levels, may reduce the risk of missing opportunities for biodiversity conservation, and of unintended management outcomes. Advancing the research about novelty and the rate of its emergence is crucial, not only for biodiversity conservation, but also for securing ecosystem services for human well-being and long-term sustainability.

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DATA AVAILABILITY STATEMENT

The data that support the findings could be obtained from: the Baltic Nest Institute at http://nest.su.se/bed/ACKNOWLE.shtml; the International Council for the Exploration of the Sea (ICES) at https://ocean.ices.dk/Helcom/Helcom.aspx?Mode=1, www.dome.ices.dk/views/Phytoplankton.aspx, and the Baltic International Trawl Surveys (BITS: http://doi.org/10.17895/ice.pub/7580); the Finish Environmental Institute (SYKE) at www.st.nmfs.noaa.gov/COPEPOD/data/fi-05101/html_src/data.html.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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