Study title

Forecasting bryozoan assemblage dynamics under simulated climate change

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Abstract

The shallow Antarctic continental shelf experiences strong physical disturbances in the form of ice-scour which play a key role in maintaining biodiversity. Due to climate change, both the extent and duration of sea ice cover is expected to rapidly decline, leading to complex shifts in disturbance regimes with unknown impacts on successional dynamics and biodiversity in benthic communities. We introduce an individual-based model to study the assemblage dynamics of Bryozoa, sessile, suspension feeding animals which are key pioneers in the shallows. The model captures colonisation events, colony growth as well as intra- and interspecific overgrowth competition for space between colonies. Mortality due to predation is modelled as the removal of zooids within small areas of the model world. Using the model, we simulate various disturbance regimes, e.g. by varying the timing of ice-scour events, the length of the growing season and the spatial distribution of predation events. We find that the timing of ice-scour events throughout the growing season has only minor short-term effects on successional dynamics in bryozoan assemblages, while an extended growing season substantially accelerates succession in the long term. We furthermore find that relatively rare but large predation events lead to a slower recovery, whereas relatively frequent but small events result in a faster succession with higher overall abundances. These results highlight that in order to understand how benthic biodiversity will be impacted by climate change, it is necessary to consider the interplay between biotic interactions and complex changes in physical disturbance regimes.

Keywords

agent-based modelling, Intermediate Disturbance Hypothesis, competitive exclusion, competition- colonisation trade-off, Antarctica, overgrowth competition, multiple disturbances

1 Introduction

The shallow Antarctic shelf is a disturbance-driven ecosystem heavily impacted by climate change [1, 2, 3, 4]. Every year, varying amounts of the sea surface freeze in autumn or winter and thaw in spring. This freezing locks icebergs into a stationary position, but as they start to melt icebergs can drift and may collide with the seabed, a process termed ice-scouring. Ice-scours can plough several meters deep and thereby kill most organisms directly hit on the way [5]. Rising air and sea temperatures are impacting the duration and extent of sea ice in Antarctica [6], with ice thawing earlier and faster, resulting in substantially altered disturbance regimes [2, 7]. In the short term (decades), climate-forced shortening of sea ice duration, glacier retreat and ice shelf collapse is expected to increase ice-scour. If the expected warming trend continues, ultimately all ice-scours will cease to happen as glaciers retreat past their grounding lines onto land, ice shelves break out to land, and rising temperatures eliminate most sea ice [8].

Despite frequent disturbances by ice-scours in the shallows, the Antarctic continental shelf is very species-rich [2]. In fact, frequent disturbances enable the coexistence of pioneer and climax species, as they repeatedly reset successional dynamics, and thus play a key role in maintaining biodiversity in these systems [9, 10, 11]. The expected changes in disturbance regime will therefore have potentially strong negative impacts in this ecosystem, especially as many polar benthic species are considered to be highly vulnerable and sensitive to change [12, 13]. However, predicting community responses to changing disturbance regimes is difficult, as the physical impacts are heterogeneous in time and space and because they may also affect the biotic interactions within ecosystems.

Bryozoan assemblages are an ideal study system for analysing how community dynamics are determined by an interplay of physical disturbances and biotic interactions. Bryozoans are sessile, suspension-feeding organisms that grow in colonies on the seabed. They are a very common and species-rich taxon, which is particularly well represented on the Antarctic shelf [2]. Additionally, bryozoan colonies compete for space by overgrowing each other, offering the unique possibility to directly observe and quantify competitive interactions [14]. In general, bryozoan assemblages are characterised by a strong trade-off between colonisation rate and competition strength: strong competitors typically grow very slowly and establish new colonies at a low rate, but are able to overgrow and hence eventually exclude weaker competitors [2]. Those weaker competitors, on the other hand, are able to compensate for competition losses by relatively fast growth and the ability to easily and rapidly colonise newly available space (disturbed areas) [15]. Changing disturbance regimes thus threatens bryozoan biodiversity, as pioneer species depend on the availability of open space.

Previous research provides some insights into the effects of changing ice-scour frequency on bryozoan assemblages [2, 11, 16]. Deeper areas of the shelf generally experience less ice-scours than shallower areas [17], and it has been shown that this coincides with gradients in species richness. In concordance with the intermediate disturbance hypothesis, the highest species richness was found in association with intermediate ice-scour frequencies [16, 18]. Furthermore, it has been shown that increased ice-scour frequency leads to a change in the competitive structure of bryozoan assemblages, with more disturbed assemblages being dominated by pioneer species as opposed to forming complex networks with many competitive interactions [2]. If ice-scours become more frequent in the near future, we might expect that bryozoan assemblages from slightly deeper areas start to resemble those from shallow depths today, while those from the shallows are likely to become species-poor deserts dominated by rapidly colonising pioneers with little role for spatial competition [2, 16].

However, the specific impacts of climate change on physical disturbance regimes are heterogeneous at both temporal and spatial scales. In the case of bryozoan assemblages, we can expect that rising temperatures will not only lead to a change in the frequency of destructive ice-scours but also affect the timing of those ice-scours within the growing season as well as the length of the growing season itself [2, 7]. Bryozoans show a clear seasonality in their dynamics, as they are active during Austral summer and mainly inactive during winter, when little light penetrates the cover of sea ice, due to trophic dependency on limited primary production [16, 18]. Furthermore, weaker competitors become active relatively early during the growing season, while strong competitors often recruit later [19]. Finally, there might be further indirect effects on assemblage dynamics due to changes in predation as rising temperatures and sea ice loss also affect other trophic levels [20, 21, 22], potentially leading to changes in the frequency, type and spatial distribution of predators.

Here, we use an individual-based model to investigate the effects of different climate change impacts on successional dynamics and coexistence in bryozoan assemblages. The model is initialised with an empty surface, representing the seabed directly after an ice-scour, and captures the most characteristic properties of real-world assemblages. Individuals represent zooids of different species, which form colonies on the seabed and, on meeting each other, compete for space. Species with high competitive strength are able to overgrow weaker species, but this competitive advantage comes at the cost of having relatively low colonisation rates, slow colony growth and a later onset of activity during the growing season. Mortality due to predation is modelled as the removal of zooids within small areas of the model world.

We use this model to explore how shifts in the timing and spatial distribution of disturbance events, as a result of climate change, will influence bryozoan assemblage dynamics. How bryozoan assemblages respond to climate change is likely determined by an interplay of all these factors, but studying their combined effects in field experiments is extremely difficult (Ashton et al. took many years to explore just the effect of temperature [4]). Therefore, we run simulation experiments in which we vary the length of the growing season, the timing of ice-scour events as well as the spatial distribution of predation events to test how the combination of these factors shape successional dynamics and coexistence. We hypothesise that an earlier timing of ice-scour during the growing season will disadvantage strong competitors during the early stages of assemblage development, as weaker competitors can benefit from their temporal advantage of having an earlier onset of activity (H1). We furthermore hypothesise that a longer growing season will change assembly composition by accelerating succession and hence shortening the period with high diversity, as strong competitors have more time to exclude weaker species (H2). Finally, we hypothesise that the spatial distribution of predation events further modulates assemblage dynamics. Predation events that are clustered in space instead of widely distributed could hit strong competitors disproportionately hard, as they have fewer colonies to regrow from and lower chances to recolonise disturbed areas (H3).

2 Methods

This study was conducted using an individual-based simulation model implemented in Netlogo (v6.4.0, [23]). All analyses were performed using R Statistical Software (v4.3.3) [24]. The code for reproducing the results is available as online supplementary material. In the following, we first provide a complete model description, following the Overview, Design concepts, Details (ODD) protocol for describing individual- and agent-based models [25, 26], before explaining how the model was analysed.

2.1 ODD Protocol

2.1.1 Purpose

The model simulates the development of polar bryozoan assemblages shaped by seasonal growth, external disturbances and competition for space. Sexually produced larvae can disperse through the water column, settle and metamorphose on rocky substrates. After successful recruitment, the initial zooid, termed an ancestrula, can colonise space by growing new zooids clonally. Colonies compete for space by attempting to overgrow each other (see Fig. 1 b). A competition-colonisation and a competition-growth trade-off is assumed, meaning that strong competitors (climax species) are able to overgrow weaker competitors (pioneers) at the cost of having lower colonisation and growth rates. Furthermore, the model incorporates seasonal species-specific growth, where strong competitors become active later in the growing season compared to good colonisers.

The model can be used to investigate how different disturbance regimes affect assemblage dynamics. Specifically, we look at a set of disturbance scenarios by varying three factors in the model: the timing of ice-scour events, the duration of the growing season as well as the spatial distribution of predation events. Insights from this model can be used to predict future biodiversity dynamics of benthic bryozoan assemblages under climate change.

2.1.2 Entities, State Variables, Scales

The model world consists of a grid of 201x201 patches, wrapped in both dimensions. Each patch corresponds to approximately 0.5 x 0.5 mm of the surface of a submerged rock on the polar seabed. This leads to a modelled area of 10x10 cm^2, which is the same size as the reference test areas in climate response studies [4]. Each grid cell can be occupied by a single living zooid, and each zooid has two state variables, namely *species ID* and *colony*

ID. The former determines the species-specific competitive strength, colonisation rate and colony growth rate, as explained further below in the context of model initialisation. The latter is used to count abundances and to identify zooids on the edge of colonies, which is necessary to model colony competition. Each model time step represents the time a zooid needs to clone itself, which is roughly a week in polar environments.

2.1.3 Process Overview and Scheduling

In total, the model includes five processes, which are executed at each time step and in the order indicated below. Note that the processes ***growth*** and ***colonisation*** can be executed in two different versions to capture a relatively short growing season, as observed in the past, versus an extended growing season, as expected due to climate warming [7].

- The ***update-time*** procedure keeps track of the weeks, months and years that have passed since simulation start.
- The ***growth*** procedure describes how colonies grow in space. Zooids on the edges of colonies have the chance of spawning a clone on a neighbouring patch to increase the colony size. If the neighbouring patch is already occupied, the attacking zooid attempts to overgrow. All growth stops during Austral winter and restarts at species-specific time points in spring or summer.
- The ***colonisation*** procedure describes how new colonies are established on randomly selected patches. The colonising species is chosen based on its colonisation rate. Again, if the randomly chosen patch for colonisation is already occupied, the colonising zooid attempts to overgrow. Colonisation stops during winter and restarts at species-specific time points in spring or summer.
- The ***predation*** procedure simulates zooid mortality due to predation, in addition to mortality due to ice-scour. The frequency and severity of these predation events can be varied.
- The (optional) ***visualisation*** procedure is used to update the model world to facilitate interpretation of the results.

2.1.4 Design Concepts

The **basic principles** used in the model are (1) interference competition for a limiting resource, in this case space, (2) the concept of competition-colonisation and competition-growth trade-offs and (3) competitive exclusion. Community structure, the abundances and spatial distribution of pioneer and climax species **emerges** from species **interactions**, in this case overgrowth competition between bryozoan colonies. Many processes have **stochastic elements**. For example, the location of colonisation and disturbance events are chosen randomly, as well as the neighbouring patch that is chosen during colony growth. Stochasticity also plays a role in the outcome of overgrowth competition. Note that colonies can be seen as an intermediate level of organisation, given that they consist of many zooids with the same *colony ID*, meaning that in principle they can be seen as **collectives**. However, all processes are implemented at the zooid level, so there is no colony-specific behaviour. Colony IDs are only relevant for **observation**, as they are needed to record abundances.

The design concepts **Adaptation**, **Objectives**, **Learning**, **Prediction** and **Sensing** do not play a role in this model.

2.1.5 Initialisation

Each simulation run starts with an empty model world, which represents the state of the seabed right after an ice-scour. We do not simulate the ice-scour itself, which represents a mass mortality event in which all the colonies are scraped off the substrate. Thus, the state variables of all zooids (namely *species-ID* and *colony-ID*) are initialised with the default value zero. The temporal variables *week* and *month* are initialised based on the chosen starting month, which corresponds to the timing of ice-scour. We define October as the start of the year. Selecting October as the starting month, which corresponds to an ice-scour in the last week of September, results in the variables *week* and *month* both being initialised to 0. The last possible starting month is May, which corresponds to an ice-scour in the last week of April, and to the variable *week* being initialised as 28 and *month* being set to 7. Table 1 gives an overview over all model variables and their values at initialisation.

The model parameter *number-of-species* controls the size of the species pool. Each species in the species pool is assigned a competitive strength $c_i \in [0,1)$. The model parameter *competition-list* contains a list of all competitive strengths (see Table 2 for a list of all model parameters). For the study presented here, we chose a fixed pool of 5 species with the following fixed competitive strengths: 0.1 (species 1), 0.2 (species 2), 0.5 (species

3), 0.8 (species 4) and 0.9 (species 5). We chose those values because we wanted to cover the whole range of potential competitive strengths, and simulate assemblages with a clear distinction between pioneers (species 1 and 2) and climax species (species 4 and 5). The species-specific colonisation rate x_i and growth rate r_i are then calculated via $x_i = 1 - c_i$ and $r_i = 0.75 - 0.5c_i$, respectively. This reflects the fact that we expect stronger differences in colonisation rates than in growth rates. High competitive strengths thus translate into low colonisation and growth rates, and vice versa.

Patch-specific model variables		
Name	Description	Value at initialisation
species-ID	determines which species the zooid belongs to, used to determine competitive strengths	0 (indicating an empty cell)
colony-ID	determines which colony the zooid belongs to, used to detect colony edges and abundances	0 (indicating an empty cell)
Global variables		
Name	Description	Value at initialisation
year	counts the number of years since the last ice-scour	0
week	determines current week within the year (0 = beginning of October; 47 = end of September)	0,1,2...28 (depending on chosen starting month)
month	determines current month within the year (0 = October, 11 = September)	0,1,2...7 (depending on chosen starting month)

Table 1: A summary of all patch-specific and global variables used in the individual-based model

2.1.6 Input Data

There is no input data.

2.1.7 Submodels

Update-time

During this procedure, temporal variables are updated to keep track of how the number of model time steps translates into weeks, months and years. One model time step corresponds to one week, so that at each time step, the variable *week* is incremented by one. The variable *month* is incremented after every fourth week. After 12 months or 48 weeks, a new year starts. The variable *year* is then increased by one and the variables *month* and *year* are reset to 0. Note, that we start counting weeks and months at the beginning of the growing season, so that week 0 corresponds to the first week of October.

Growth

This submodel describes how colonies grow in space through cloning of individual zooids located on the edge of the colony. Zooids can only clone themselves when they have enough resources, which is not the case during polar winter. Additionally, we assume that a species' onset of activity in spring is related to their competitive strength, with stronger competitors requiring more resources and thus becoming active later. At each time step, all zooids that can potentially produce a clone are identified. These zooids must (1) belong to a species that is active in a given week (see Fig. 1 a for an overview of when species become active) and (2) be located on the edge of their colony.

Zooids located on the edge of a colony differ from at least one of their direct neighbours in the value of the state variable *colony ID*. For each of the edge zooids, we then select one of these neighbours at random. With a probability that is given via the species-specific growth rate r_i, we assume that the edge zooid attempts to establish a clone on the selected neighbouring patch. Two cases can occur: First, if the target patch is empty, then we assume that the attempt is automatically successful, meaning that the state variables *colony ID* and *species ID* of the target patch are updated with the values of the corresponding state variables of the edge zooid. Second, if the target patch is already occupied by another zooid, we assume that the selected zooid attempts to overgrow.

The success of an overgrowth attempt is determined based on the ratio of both species' competition strengths, c_i/c_j, which is larger than 1 if the attacking zooid (i) is a stronger competitor compared to the defender (j), and smaller than 1 in the opposite case. We consider the overgrowth attempt successful, if the following condition is fulfilled:

$$\frac{c_i}{c_j} + h > 1 + overgrowth\text{-}threshold \tag{1}$$

As occasionally, a weaker zooid can also overgrow a strong one, we add some stochasticity to this decision by adding a random number h between 0 and 0.2 (set via the parameter *overgrowth-stochasticity*). However, on average, the attacker needs a clear competitive advantage to be successful because we assume that the model parameter *overgrowth-threshold* is larger than zero. If the overgrowth attempt is successful, then the state variables *colony ID* and *species ID* of the target patch are updated with the values of the corresponding state variables of the attacking zooid.

Colonisation

This procedure describes how new colonies are established. As with growth, species only have enough resources to produce larvae and hence establish new colonies during their species-specific growing season [11, 19]. To model the establishment of new colonies, we first randomly select *max-colonisation-events* patches in the model world. For each of these patches, one of the species that is currently active (see Fig. 1 a) is chosen with a probability that reflects that species' colonisation rate. Species with a high colonisation rate get chosen more often and are hence quicker at establishing new colonies. The chosen species then attempts to colonise the empty patch. Three cases occur: First, if the target patch is empty, colonisation is always successful. Second, if it is already occupied by a different colony of the same species, colonisation fails. Third, if it is occupied by a colony from a different species, the colonising zooid attempts to overgrow the existing zooid, exactly as explained above in the context of the growth procedure. After a successful colonisation or overgrowth attempt, a new colony is established and both state variables of the target patch are updated accordingly.

Predation

This procedure mimics zooid mortality due to predation, e.g. by sea urchins. The frequency of predation events is controlled by the model parameter *predation-number*, while their intensity in terms of affected area is controlled by the parameter *predation-radius*. We first randomly select *predation-number* patches and then remove all zooids inhabiting patches in a distance smaller than *predation-radius* to that target patch by setting their state variables *species-ID* and *colony-ID* to zero.

Visualisation

Each species is assigned a specific colour to visualise the development of the assemblage, as shown in Figure 1 c. Empty patches with state variables *species-ID* and *colony-ID* equalling zero are coloured white. Overgrown patches have a slightly darker shade of the overgrowing species' colour. More details on the visualisation procedure can be found in the simulation code provided as online supplementary material.

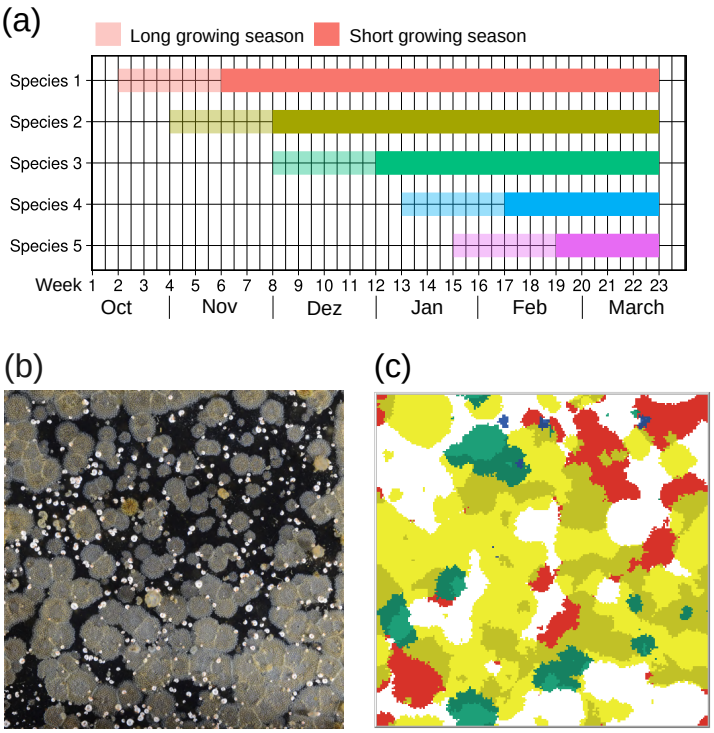

Figure 1: **An individual-based model of bryozoan assemblage dynamics** (a): Species-specific onset of activity in short and long growing season scenarios. We assume that species with higher competition strengths generally become active later during the growing season. For example, species 1 with competitive strength $c_1 = 0.1$ is able to start colonising and growing after week 6 (mid November) in the short growing season scenario and after week 2 (mid October) in the long growing season scenario. By contrast, species 2 with competitive strength $c_2 = 0.2$ is able to start after week 8 or 4, respectively. (b) Image of a real bryozoan assemblage (photo by: British Antarctic Survey, Cambridge, UK) (c) Screenshot of the model world depicting bryozoan colonies competing for space in a simulation with long growing season after 70 time steps. The simulation started in October, and the predation regime with few large disturbances was chosen. All other model parameters were chosen as in Tab. 2. Species 1=red, 2=yellow, 3=green, 4=blue and 5=purple (not yet established). Overgrown zooids have a slightly darker shade of the overgrowing species' colour.

2.2 Disturbance scenarios and analysis

We used the individual-based model described above to simulate a range of disturbance scenarios in which we varied (1) the length of the growing season, (2) the timing of ice-scour events and (3) the spatial distribution of predation events. All other parameters were chosen as in Tab. 2.

In particular, we first contrasted simulations with a short growing season (November-April) and those with an extended growing season (October-May). The timing of ice-scour was then varied by changing the starting-month of the model run. In the case of a short growing season, we considered 6 possible starting months (namely November, December, January, February, March or April). By contrast, in the extended growing season, we additionally considered October and May as possible starting months. Due to the species-specific onset of activity the starting month affects which species are able to start colonising at the start of the simulation run. We furthermore considered two different predation regimes. In a first scenario, we simulated few large disturbance events with only one predation event per week that cleared a relatively large space (*predation-number* = 1 and *predation-radius* = 15, as in Fig. 1). In the second scenario, we included many small predation events (*predation-number* = 9, *predation-radius* = 5). In both scenarios, the total area cleared per time step was comparable (based on the area of a circle: $1 \cdot \pi \cdot 15^2 = 9 \cdot \pi \cdot 5^2 \approx 707$), even though the realised number of patches was occasionally slightly lower if areas of impact overlapped.

Combining all three factors resulted in a total number of $14 + 14 = 28$ disturbance scenarios. Every scenario was replicated 10 times, resulting in a total number of 280 simulations. During each simulation, the number of zooids per species and the number of colonies per species were tracked over time. All simulations ran for 500 weeks, which is roughly ten years in the model world.

Parameter name	Description	Standard values for this study
number-of-species	size of the species pool	5
competition-list	contains competitive strength of each species in the species pool, chosen by us	[0.1, 0.2, 0.5, 0.8, 0.9]
colonisation-list	contains colonisation rate of each species in the species pool, calculated based on competitive strengths	[0.9, 0.8, 0.5, 0.2, 0.1]
growth-list	contains growth rate of each species in the species pool, calculated based on competitive strengths	[0.7 0.65 0.5 0.35 0.9]
overgrowth-threshold	difference in competitive strengths that leads to overgrowth (instead of a tie)	0.1
overgrowth-stochasticity	boundary of the distribution used to add stochasticity to competitive outcomes	0.2
max-colonisation-events	Number of colonisation attempts per time step	5
predation-number	number of circular areas cleared by predation	1 or 9
predation-radius	radius of each circular area cleared by predation	15 or 5

Table 2: A summary of all parameters used in the individual-based model and the values used for our simulation experiments

3 Results

3.1 General pattern of succession

Regardless of the specific scenario (considering starting month, season length and predation regime, see section 2.2), assemblage development in our model was always characterised by the same step-wise pattern of succession, as shown in Fig. 2. Note that only two possible starting months are shown, to visualise the most important differences between scenarios that started at the beginning of the growing season (November) versus scenarios that started in the middle of the growing season (January). Scenarios that started late in the season are not discussed here, as they showed very similar patterns compared to scenarios starting early, due to the effective loss of the first growing period and the absence of activity during winter. Corresponding figures showing the number of colonies instead of the number of zooids can be found in Supplementary Figure 1.

The first species that settled on the empty seabed at the beginning of the simulation is a pioneer species (species 1 in red, with lowest competition strength but highest colonisation and growth rates). Initially, the abundance of this species grew quickly due to the high availability of uninhabited space and hence the lack of competition. However, its abundance also declined quickly soon after reaching a maximum value, as the amount of available space decreased and competition intensified. Following this, species 2 (in yellow) was the most abundant one, then species 3 (in green), followed by species 4 (in blue) and finally species 5 (in purple). The described dynamics are superimposed by recurrent drops in abundances, which occurred during the winter months when all bryozoan activities stopped but predation continued.

The replacement of dominant species was relatively fast at the beginning of the simulation but slowed down during simulation runtime. This is due to the assumed competition-colonisation and competition-growth trade-offs: each species was replaced by the next best competitor because of that species' competitive advantage, which comes at the cost of having slower colonisation and colony growth rates, so that the whole dynamics decelerated over time. The replacement could eventually become so slow, that the dominance of species 4 and 5 was not observed within a simulation runtime of 500 weeks. We nevertheless decided against even longer simulation runtimes because empirical data suggests that it is unlikely for a seabed area to remain undisturbed by an ice-scour for more than five years [3, 7].

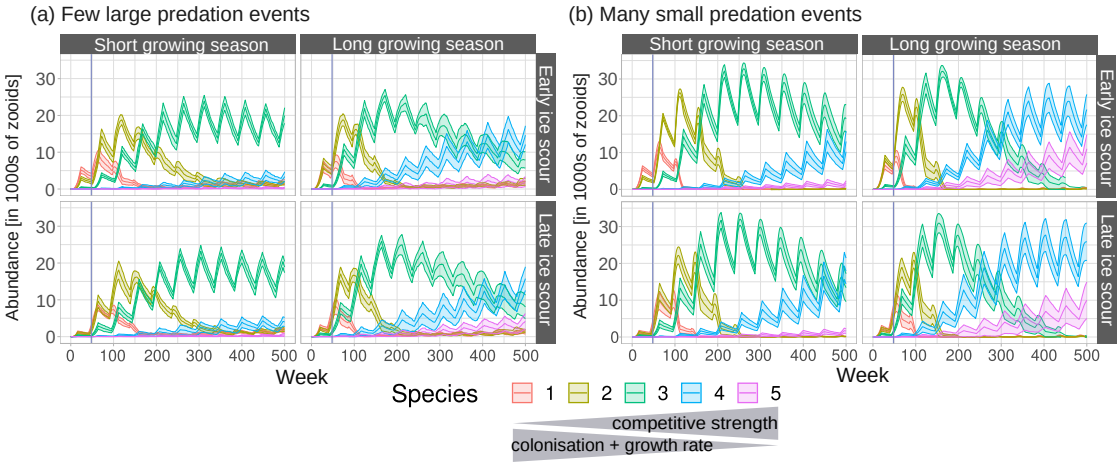

Figure 2: **Successional dynamics in bryozoan assemblages under varying disturbance regimes.** We simulated impacts of changes in disturbance regime by varying (1) the length of the growing season, (2) the timing of ice-scour events within the growing season and (3) the spatial distribution of predation events. Short growing season (left panels) refers to a current growing season from Nov-April, while long season (right panels) refers to an extended growing season due to climate warming (Oct-May). Upper panels show dynamics after an ice-scour hit early in the growing season (Starting Month: November) while lower panels show dynamics after an ice-scour hit in the middle of the growing season (Starting Month: January). Finally, we considered two scenarios of predation, one with few, large events (a) and a second one with many smaller predation events (b). All other parameters were chosen as in Tab. 2. Data shown is the mean of 10 replicates, shaded areas correspond to standard deviation. The vertical lines indicate abundances after exactly one year (48 weeks) as shown in Fig. 4

3.2 Speed of succession depends on season length and predation regime

We found that longer growing seasons lead to an accelerated succession (compare left and right panels in Fig. 2 a and b, respectively). This result was expected, given that longer growing seasons directly translate into more active weeks per year, that is more time for colonisation, colony growth and competition between colonies. A short season length implies that the number of weeks in which all species are active is low, so that pioneer species have relatively many weeks in which they hardly experience spatial competition. The longer the season length, the more biomass loss due to competition is expected because those species that act as strong competitors have more time to colonise and exclude others.

An accelerated succession also occurred with smaller but more frequent predation events (compare panels a and b in Fig. 2), which was coupled with overall higher abundances. This effect of the predation scenarios was at first sight surprising, given that the number of patches that have been cleared per week is almost identical (see section 2.2). The observed effect must therefore arise from the spatial distribution of predation events. Larger areas take longer to be refilled by colony growth from the side, meaning there is more time for recolonisation, which mostly benefits pioneer species. They can easily establish new colonies on the cleared ground without experiencing much competition. Small and widely distributed areas, on the other hand, are not only quickly filled by colony growth from the side, but they are also less likely to kill whole colonies, which mostly benefits climax species.

We furthermore found that the effects of season length and predation regime superimposed, meaning that the fastest succession was observed with many small predation events in combination with a long growing season (right panels in Fig. 2 b). The slowest succession, on the other hand, occurred with few but large predation events in combination with a short growing season (left panels in Fig. 2 a). By contrast, the exact timing of an ice-scour and hence the starting month of the simulation had only a minor impact on the speed of succession (compare top and bottom panels in Fig. 2 a and b, respectively).

Note that, as a result of these impacts on successional speed, pioneer and climax species benefitted from different scenarios. Pioneer species 1 and 2 survived longest in scenarios with a short season length in combination with few but large predation events (Fig. 3 a and b). Climax species 4 and 5, on the other hand, benefitted in scenarios with a long season length in combination with many small predation events (Fig. 3 c and d).

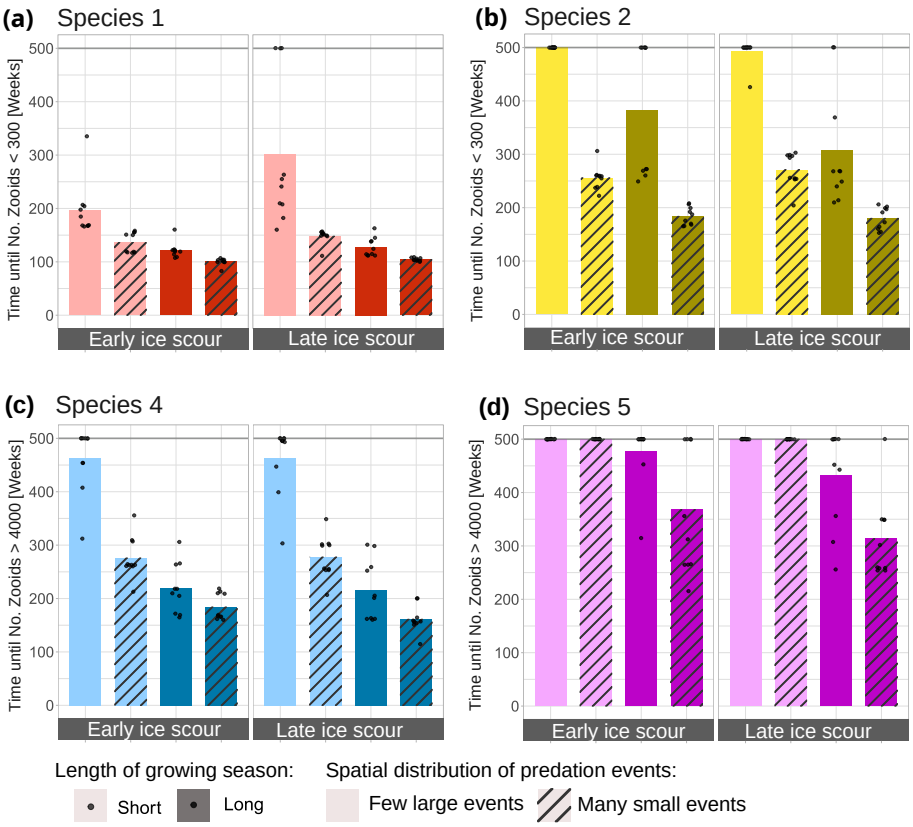

Figure 3: **Key time points in the dynamics of pioneer and climax species under varying disturbance regimes**. For pioneer species 1 (a) and 2 (b) we compared the number of time steps until they were almost excluded by stronger competitors. Due to ongoing (re-)colonisation, we never actually observed extinction. Instead, we considered a threshold of 300 zooids as the time point where a species becomes irrelevant for overall assemblage dynamics. For climax species 4 and 5, we considered the time points at which they first surpass the threshold of 4000 zooids. Predation scenarios are as in Fig. 2. For both cases, if the threshold was not reached within the simulation runtime of 500 weeks, the plot shows 500 as the key time point. Data points represent individual simulation runs, bar plots represent the mean values.

3.3 Timing of ice-scour events affects early assemblage development

Although the overall pattern and speed of succession was almost unaffected by the timing of the ice-scour, it did affect short-term dynamics at the beginning of the simulation. This becomes apparent when looking at the mean abundances of all species after one year, as shown in Fig. 4. In general, earlier starting months showed lower abundances, as these correspond to assemblages that just went through winter when many zooids were lost due to predation. Total abundances thus increase with later starting months, and this increase is stronger in the longer growing season (right panels).

In short season simulations, we additionally found that when ice-scours hit in the middle of the growing season, this had a small negative effect on the abundance of the pioneer species 1. This was because weaker competitors lose their temporal advantage of having an earlier onset of activity when icebergs hit in the middle of the season. Overall, we thus saw a U-shaped relation between abundance and starting month in simulations with a short growing season. The negative effect of starting in the middle of the growing season became less strong when season length is increased and when many small predation events are considered.

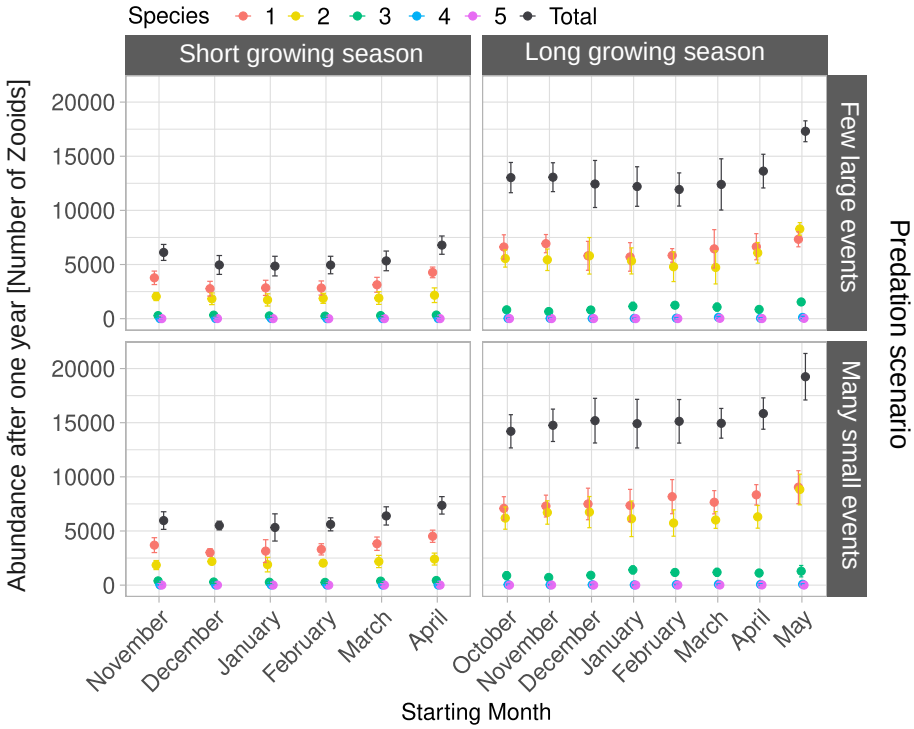

Figure 4: **Timing of ice-scour events affects abundances in the early stages of assemblage developments.** Abundances are shown for 1 year after the simulation start and thus the ice-scour event. The effect of timing of ice-scouring is compared in simulations with a short season length (left panels) and an extended season length due to climate change (right panels), as well as for our two different predation regimes (upper vs. lower panels).

4 Discussion

The goal of this study was to investigate how successional dynamics in bryozoan assemblages are affected by complex changes in disturbance regimes due to climate-driven sea ice loss. Using an individual-based model, we ran simulation experiments in which we varied the timing of ice-scouring, the length of the growing season and the spatial pattern of predation. Our simulation results suggest that the composition of a given bryozoan assemblage is not only tightly linked to its age since last disturbance by ice-scour, as expected [11, 16], but also to the length of the growing season and to the spatial distribution of predation events.

We expected earlier ice-scouring to benefit pioneers during early successional stages (H1) and could confirm this in simulations with a short growing season, but not in those with a longer growing season. However, our results confirmed H2 and H3. Fast succession occurs in scenarios with many small predation events in combinations with a long growing season, while slow succession can be observed in scenarios with few large predation events and a short growing season. It is likely that we did not see pioneers benefitting from earlier ice-scours in scenarios with a longer growing season because the potential advantage from earlier onset of activity was not strong enough to compensate the negative effect of a longer growing season. In general, the effects of the timing of ice-scours were small and only appeared in very early stages of assemblage development.

Our simulations allow us to derive predictions about the effect of changing ice-scour frequencies, even though we did not explicitly vary this factor in our scenarios. In our model, frequent ice-scouring translates into short simulation runtimes and hence dominance of pioneer species. Rare ice-scouring, on the other hand, translates into long simulation runtimes that allow for competitive exclusion and hence dominance of climax species. Thus, we can expect that bryozoan richness (and diversity) on the shallows of the Antarctic shelf is highest in areas that have a moderate rate of ice-scouring, which is in line with previous empirical work [10, 11, 27, 18, 16] and the intermediate disturbance hypothesis [28, 29, 30, 31, 32, 33].

In order to keep the model structure and computing requirements manageable, despite the multi-level complexity of the empirical system, we had to make several simplifying assumptions. This is particularly true for constant colonisation rates, which reflect the assumption that recruitment happens from sites that are relatively far away and hence not affected by changing conditions, or at least not simultaneously. A more realistic model version would be based on a much larger model world, resembling trophic metacommunities [34], in which colonies are able to produce larvae that can travel from one

assemblage to another. Ice-scour disturbances would then affect only part of the model world, leading to a high heterogeneity of successional stages, as observed in the real world [9]. However, building and analysing such an extended model version would go far beyond the scope of this study.

Due to its simplicity, and because parameters have not been calibrated based on empirical data, our model is not well suited to make quantitative predictions of future bryozoan assemblage dynamics. This is mostly due to a lack of empirical data for the observed competition-colonisation and competition-growth trade-off functions. Collection of such data in polar nearshore environments is expensive and logistically challenging, partly because it requires SCUBA to recover substrata with competing assemblages on. Very few polar research stations have SCUBA facilities and of those that do, only two also monitor ice-scouring (Carlini and Rothera, [3]). However, we have no reason to expect that the general patterns observed in our study (i.e. how the factors we varied affected the speed of succession by favouring either pioneer or climax species) depend on exact parameter values.

Despite the discussed simplifications, we can derive qualitative predictions for future changes in observed large-scale biodiversity patterns based on our simulation results. Short-term climate-change scenarios involve an increased frequency of ice-scours [2, 7], so on average, bryozoan assemblages would be younger. In the shallows, this means that very diverse systems might turn into deserts dominated by very few pioneers [2, 5]. Such a rapid loss of diversity would also imply a loss of hierarchy in the system, which could further threaten those systems, given that competitive hierarchies in bryozoan assemblages have been shown to mitigate network instability by keeping destabilising feedback loops relatively weak [35, 36]. Our simulation results suggest that this trend could be counteracted by an extended growing season, which benefits climax species and leads to overall increased abundances. Along similar lines, intermediate or long-term climate-change scenarios involve low frequencies or even the absence of ice-scours [8], which would again benefit climax species. Here, an extended growing season could have an additive or even amplifying effect. Taken together, this means that extended growing seasons might first mask the effect of more frequent ice-scours and then accelerate the effect of less frequent ones, so that observed changes in assemblage composition over time might occur more rapidly than previously expected.

Potential changes in predation patterns are another factor that can modulate successional dynamics in bryozoan assemblages. Our results suggest that, depending on the spatial distribution of predation events, either pioneer or climax species can be favoured by such changes. It is well-known that sea ice plays a critical role in structuring antarctic

ecosystem dynamics [22] and that a loss of sea ice cover due to global warming has impact on all levels of the food web [20]. These effects are usually studied with a focus on understanding the consequences for upper trophic levels (e.g. the effect of phytoplankton blooms on krill and penguin populations [21, 22]) while our understanding of impacts on lower trophic levels, including benthic communities, remains very limited. In this study, we chose two very general predation scenarios in which we compared the spatial distribution of predation events, which could for example reflect a change in the dominant predator species. Our results indicate an effect of the predation scenario on successional speeds, suggesting that it is worthwhile to study changes in predation regimes in more detail, for example by extending the individual-based model to include other potential predator impacts.

Our study constitutes an important step towards understanding how benthic biodiversity will be impacted by climate change. Our simulations revealed that not only the frequency of ice-scours is important for the maintenance of benthic biodiversity but also other factors that modulate the biotic interactions in this disturbance-driven ecosystem, like the length of the growing season or the spatial distribution of predation events. This interplay between complex changes in physical disturbance regimes on the one hand and biotic interactions on the other is likely to also play a role in many other disturbed ecosystems. To understand combinations of different climate change impacts on higher levels of biological organisation like communities and ecosystems, such biotic interactions necessarily need to be considered [37], which highlights the need for an ecological network approach to multiple stressors research [38]. Our study demonstrates that using individual-based models that allow us to assess the impact of different types of climate change effects, both individually and in combination, can be valuable tools in this context.

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