The Role of Disturbances for the Antarctic Benthos

- A Simulation Study -

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I remember my friend Johnny von Neumann used to say, “with four parameters I can fit an elephant and with five I can make him wiggle his trunk.”

Enrico Fermi, quoted by Freeman Dyson in “A Meeting with Enrico Fermi” (Nature 427 p297.)

Zusammenfassung

Aufgrund ihrer Unzugänglichkeit sind marine Systeme, insbesondere die benthischen Gemeinschaften des antarktischen Schelfs, schwer zu untersuchen. Simulationsmodelle sind ein alternatives Werkzeug, um Hypothesen und Ideen über relevante Prozesse und Mechanismen dieser Systeme zu untersuchen und zu testen. Mit unterschiedlichen Simulationsmodellen wurden die Bedeutung und der Einfluss verschiedener Faktoren, wie Ausbreitungsmuster und Lebensspanne einzelner Arten und Störungen durch Eisbergstrandungen für antarktische Schelfgemeinschaften untersucht.

Mit einem Simulationsmodell wurde die Bedeutung eines fleckenartigen Larvenausbreitungs- und Rekrutierungsmusters untersucht. Solche Muster sind in marinen Lebensräumen häufig anzutreffen. Mit dem Modell konnte gezeigt werden, dass diese Muster eine hinreichende Bedingung für Artenkoexistenz darstellen und somit förderlich für die Diversität sind.

Generell wird für viele antarktische Arten ein eingeschränktes Ausbreitungspotential angenommen. Als Grund hierfür wird die starke Saisonalität der Primärproduktion in hohen Breiten gesehen. Anhand eines Simulationsmodells konnte gezeigt werden, dass in einem dynamischen System, in dem neue Lebensräume durch Störungen entstehen, aufgrund der Langlebigkeit der Individuen eine weit reichende Ausbreitung für das lokale Überleben einer Pionierpopulation nicht notwendig ist. Generell hat die Langlebigkeit für die Ausbreitungsdistanz eine große Bedeutung. Die minimale Ausbreitungsdistanz, die zum Überleben einer Pionierpopulation notwendig ist, hat eine nicht-lineare, hyperbolische Abhängigkeit zur Lebensdauer. Daher profitieren besonders kurzlebige Arten von einer möglichen Verlängerung ihrer Lebensspanne. Eine Art könnte mit der halben Ausbreitungsdistanz auskommen, wenn sie ihr Überleben um das drei bis vierfache verlängern könnte.

Basierend auf Daten über den Störungsumfang und die Lebensdauer von Pionierorganismen aus dem Weddell-Meer könnte ein sechsjähriger Primärbesiedler von Eisbergkratzerspuren mit einer Ausbreitungsdistanz von weniger als 1000 m auskommen. Daher kann das eingeschränkte Ausbreitungspotential vieler antarktischer Arten eine Anpassung an den hoch dynamischen Lebensraum darstellen.

In weiteren Simulationen wurde der Einfuß verschiedener physikalischer Eigenschaften einer Störung, wie Störungsgröße und Frequenz, auf die Sukzession untersucht. Die Simulation zeigte, dass es einen Unterschied zwischen kleinen, zahlreichen und wenigen, aber großen Störungen bei gleicher Gesamtgröße des Störungsareals gibt. Dabei bestimmt das Ausbreitungspotential der vorhandenen Arten die Reaktion und Zusammensetzung der entstehenden Artengemeinschaft. Weiterhin zeigte sich ein großer Einfluss von Überlebenden einer Störung auf die Elastizität der Gemeinschaft. Schon eine Überlebenswahrscheinlichkeit von 1% kann die Regenerationsdauer um bis zu 25% verkürzen. Dieser Effekt ist auf einen so genannten „räumlichen Speicher-Effekt“ zurückzuführen. Ähnlich wie z.B. Bäume, die nach einem Waldbrand wieder ausschlagen und fruchten, wird besonders bei Arten mit geringem Ausbreitungsvermögen die Zeit zur Besiedlung gestörter Gebiete stark reduziert.

Schätzungen für die direkte Mortalität durch Eisbergstrandungen für das Benthos liegen nahe bei 99%. Allerdings könnten durch unregelmäßige Kielform von Eisbergen Bereiche zwischen gestörten Flächen unberührt bleiben. Dadurch entsteht ein Mosaik aus verschieden stark gestörten Flächen, die sich ähnlich positiv auf die Elastizität antarktischer Gemeinschaften auswirken.

Summary

Due to their remoteness marine systems in general and the Antarctic benthic shelf assemblages in special are difficult to investigate. Computer simulation models provide an alternative tool to test hypotheses and ideas on the process that structure and influence these systems. Several computer simulation models were used to explore the importance of different factors like dispersal pattern and longevity of single species and disturbance due to iceberg scouring for benthic Antarctic shelf assemblages.

In a simulation the outcome of a clumped or patchy larvae dispersal and settlement pattern was analysed. Such patterns are commonly found in marine systems. In the simulation they were found to be a sufficient condition for species coexistence and thus enhanced diversity.

It is often assumed that Antarctic species have a limited dispersal potential. The reason thereof is seen in the high seasonality of primary production at high latitudes. A simulation model revealed that in a dynamic environment, where suitable habitat is the result of disturbances, the species longevity can make long range dispersal unnecessary for the local persistence of a pioneer population. The longevity plays a central role for the minimal dispersal distance. This minimal dispersal distance has a non-linear dependency on species longevity. Thus especially short living species can profit much from a prolonged lifespan. A species can cope with a halved dispersal distance if it could extend its lifespan three to four times.

Based on disturbance and pioneer lifetime data from the Weddell Sea a minimum dispersal distance of less than 1000 m might be sufficient for a primary coloniser of iceberg scours with a lifespan of about 6 years. Thus the limited dispersal potential of Antarctic species can be an adoption the highly dynamic environment.

In a further simulation the role of physical disturbance properties such as disturbance size and frequency was explored. The simulation showed a difference between numerous, small and rare large disturbances with the same total perturbed area. The dispersal limitation of the involved species influenced the community structure and response to different disturbance regimes. Additionally single surviving individuals had great influence on the resilience of the assemblages. Even a 1% survival probability reduced the recovery time up to 25%. This effect can be attributed to a spatial storage effect. Similar to trees that survived a burning and re-sprout, the time

to invade recently disturbed habitats can be dramatically reduced, especially for species with a high dispersal limitation.

Estimates on the severity of iceberg scouring to the Antarctic benthos are close to 99%. However, irregular keel forms may lead to undisturbed areas between scour marks. By this a mosaic of areas in different states emerges, that has a similar positive effect for the resilience of Antarctic assemblages.

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1. The Antarctic

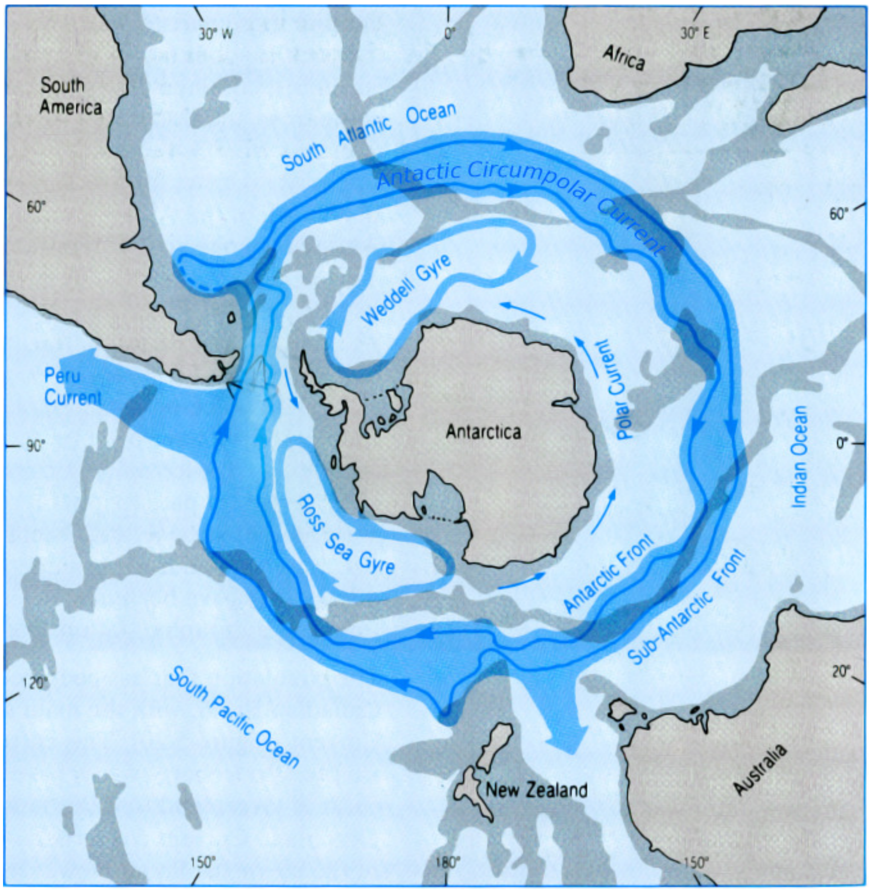

Figure 1, Distribution of the Sub-Antarctic and Polar Fronts and associated currents in the Antarctic. The approximate positions of the Weddell Gyre and the Ross Sea Gyre are also shown. The Antarctic Divergence is between the Polar Current and the Antarctic Circumpolar Current. Blue-grey shadings indicate water depth less than 3000 m (modified after Brown et al. 1990).

1.1 The Antarctic, origin and current conditions

The Antarctic (Figure 1) includes the ice covered continental landmass encompassing the South Pole and the surrounding southern ocean. The landmass originates from the super-continent *Gondwana, which* started to break up around the late Jurassic (170 mya). At this time the isolation of the Antarctic started. During Eozaen, 55 mya ago, the separation and north drift of Australia occurred. About 26 mya before present, the opening of the Drake Passage cut off the last remaining land bridge to South America (Walter 2005). Since the final establishing of the deep sea trench forming the Drake Passage, the Antarctic continent has no direct connection to other landmasses. This facilitated the formation of a ring ocean around Antarctica. Several wind systems drive the current system of this ocean. The main components are two counterwise rotating currents. The outer, most northward one is the Westwind drift with a speed of about 0.5 km h^{-1}. Due to the lack of a land barrier, it floats clockwise around the entire continent and is termed Antarctic Circumpolar Current (ACC). The ACC affects the water body down to the bottom of the sea (Walter 2005). It consists of several water fronts. Its northern most border is the Sub-Antarctic Front. The Polar Front (referred to as the Antarctic Convergence in older literature) is located around 50 degree south, but its exact location changes with the seasons (Figure 1). The Polar Front separates the cold Antarctic waters from warmer oceans. With a temperature gradient, the water temperature falls from about 10°-8°C to a temperature just below 2°C, it is a strong physiological barrier limiting the faunal exchange with other biota.

The Antarctic divergence is located around the 65th degree south. South of this zone strong eastward winds cause an anti-clockwise rotating current system. Due to the Corilois force, originating from the earth rotation, this current receives a southward impulse and is pushed against the continent. Over the shelf region this results in a strong, westward running current parallel to the cost, termed Antarctic costal current, Polar current or simply Eastwind Drift. This steady and homogeneous current affects the environmental conditions over the Antarctic shelf region. The Antarctic shelf is generally deeper than other continental shelfs. Due to the ice shields on the continental landmass that pushes down the continental plate it can reach up to 800 m in depth.

1.2 The Antarctic environment

The Antarctic marine environment is characterised by several abiotic factors (see Arntz et al. 1994). The constant low water temperature shows only a small annual amplitude and the fluctuations in seawater salinity are also low. Contrarily the sea ice cover exhibits strong seasonal fluctuations. During the austral winter it covers up to two-thirds of the southern ocean (~$20*10^6$ km²) and strongly restricts the light irradiation depth in the water body. In this period only icealgae within a lacuna-system in the sea ice and, to some extend, in the ice-water contact zone may be photosynthetic active. Primary production in the open water is restricted to the short period of the austral summer when the sea ice has retreated to about $4*10^6$ km².
When sea ice bakes up in spring, the release of ice algae from their confined habitats and leads to a first spring bloom (Bathmann 1995). A second algae bloom follows this spring bloom later in summer (Bathmann 1995, Lochte and Smetacek 1995). Consequently, organic matter supply to the sea floor is mainly restricted to the summer period. At some locations this seasonal food rain accumulates to several centimetre thick layers on the sea floor (**Figure 2**). Such a situation may be comparable to the North Atlantic, where thick algae mats, originating from under-ice algae, rapidly sink to the abyssal sea floor and present strong local food pulses in spring (Schewe and Soltwedel 2003).

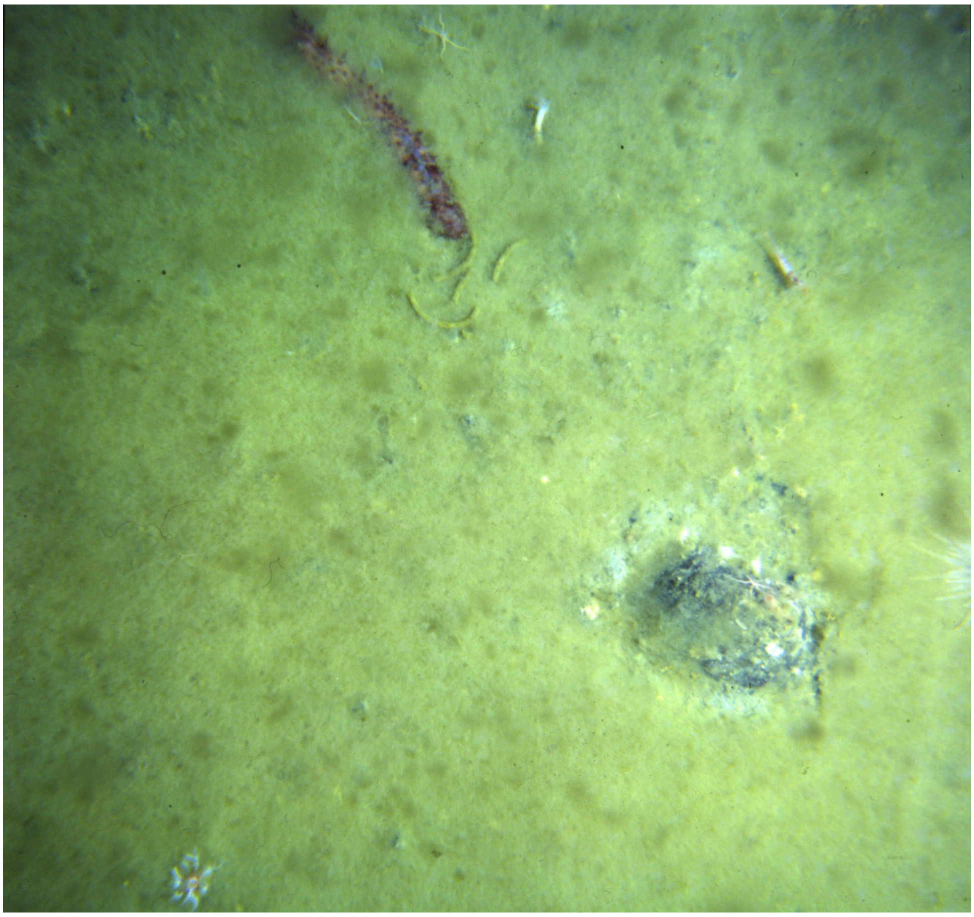

Figure 2: An approximately 3 cm thick phytodetritus layer on the sea floor of the Antarctic shelf (Lazarev Sea). In the upper left part a holothurian is visible, with its body almost completely immersed in the phytodetritus. According to Mincks et al. (2005) such detritus layers can persist for years and serve as benthic food banks. We postulate that iceberg scouring may be a major source of resuspension that makes the phytodetritus available to benthic filter feeders, especially in winter. (Photo © J.Gutt / AWI)

From a coarser ecological view the environmental conditions over the Antarctic shelf resemble a relatively homogeneous ring around the continent, mostly with a width of less than 100 km. At some locations huge parts additionally are below a permanent shelf ice cover. The rich marine life and these steady conditions led Dayton et al. (1994) to realise “Perhaps the most interesting question of polar marine biology relates to the fact that Antarctic has a much higher species richness (…) yet lacks the ecological diversity of the Arctic”.

1.3 Antarctic Benthic Marine Life

The diversity of the shelf fauna, especially of the sedentary species, is high. Gutt et al. (2004) estimated a total of around 17.000 species. Many sedentary species belong to the epifauna, living on the sediments of the shelf or colonise biogenic structures (e.g. sponges). Compared to other soft sediment systems (e.g. the North Sea or Deep Sea), relatively few infauna elements exist. The comparable high degree of endemism (in some groups, e.g. amphipods 80%, pycnogonids 90% see Clarke and Johnston 2003) as well as the dominance of some groups, e.g. hexactinellid sponges (Barthel 1992) is conspicuous, as is the deficit in other groups like higher decapods or chondrichtheys. This fauna inventory is a direct consequence of the evolutional and thus geo- and glacial history of Antarctica (Thatje et al. 2005). One important factor for the recent fauna composition is the isolation of the continent, restricting the faunal exchange with other biota and fostering the radiation of successful colonisers.

1.4 Reproduction and dispersal traits of Antarctic species

The Antarctic life is considered to be strongly influenced by the conditions of the Antarctic, representing a permanent cold but highly seasonal environment. The proposed effects include slow, seasonal growth, prolonged lifespan, low mortality and large adult size (Arntz et al. 1994). Regarding the reproductive traits, Arntz et al. (1994) listed a prolonged gametogenesis and a delayed maturation. They further proposed a general low fecundity, slow embryonic development and a seasonal reproduction pattern to be typical for Antarctic species. In general Antarctic species seem to produce either large yolky eggs with a non-pelagic development or show brood protection by brooding or viviparity (Arntz et al. 1994). Besides the slowing down of biological processes due to the cold, one reasons for such life history traits are seen in the strong seasonality (Clarke 1990, Brockington and Clarke 2001).

A general lack of meroplanktic development was proposed for the Antarctic since the first early expeditions (see Pearse et al. 1991, Arntz et al. 1994). The apparent decline in planktonic larvae from low to high latitudes led to the formulation of “Thorson’s rule” (Mileikovsky 1971). This theory was originally based on Thorson’s analysis of prosobranch gastropod larvae (see Gallardo and Penchaszadeh 2001). After Thorson’s concept the amount of species with planktotrophic larvae and an indirect development should decrease from the equator towards the poles whereas the number of species with lecitotrophic larvae and direct development rises. The main reason for such a shift is seen in the increasing seasonality of the primary production towards high latitudes. Low or nearly absent numbers of meroplanktic larvae in plankton samples seem to be in line with this hypothesis as well as the high amount of species with brooding or budding behaviour in Antarctic assemblages.

However, the number of papers dealing with meroplanktic larvae in south polar waters continuously rose in the past years (see Shreeve and Peck 1995, Bhaud et al. 1999, Stanwell-Smith et al. 1999, Absher et al. 2003, Freire et al. 2006 and Sewell 2005) and Thorson's rule is controversially discussed. Nevertheless, the general larval density within the water body as well as the known number of larval morphotypes seems to be rather low when compared to other regions (Thatje et al. 2005).

Thatje et al. (2005) proposed that the glacial history of the Antarctic might be a reason for a disadvantage of meroplanktic development in the southern ocean. The current disturbance regime may also explain a part of the riddle.

Recently David Bowden published the results of a comprehensive three-year study on recruitment and settling of sedentary species on artificial settling plates at Ryder Bay, Antarctic Peninsula (Bowden 2005b, 2005a, Bowden et al. 2006). This work resumes the currently available data on settling experiments in Antarctic waters. The experiments were conducted in shallow, near shore waters, but the general findings may be representative and confirm some of the hypothesis of Arntz et al. (1994):

- Colonisation and growth speed is low
- Recruitment generally can occur throughout the year. However, recruitment of single taxa seems to be strongly seasonal with an overall peak in later winter
- Growth of most species seems to be highly seasonal and coincident with the period of primary production
- Some species recruit throughout the year (e.g. spirorbids polycheates) or show exceptional fast growth (e.g. *Ascidia sp.*, see also Rauschert (1991) and its discussion by Bowden).
- Assemblage composition seems to be controlled by post-settlement mortality (predation and disturbance by ice)

1.5 The influence of ice

After the formation of the Antarctic Circumpolar Current a period of cooling down followed, resulting in the present climate situation (see Clarke 1990, Thatje et al. 2005). According to recent data (Holbourn et al. 2005), the final cool down and the formation of the Antarctic ice shields happened within a relatively short time span about 14 mya bp. Most probably a cyclic expansion and reduction of the Antarctic ice in terms of longer time periods has occurred since then. During glacial maxima, the shelf ice eventually covered the complete shelf (Anderson et al. 2002). Based on deep scour marks on the shelf, it is evident that the ice grounded at least at many locations (see Thatje et al. 2005). For the Weddell Sea it must be assumed that the ice grounding line was along the current 500 m depth line 13.000-27.000 years ago (Anderson et al. 2002). Therefore, these areas were not available for colonisation to any species.

There is evidence of a geographical different glacial history for the east and west Antarctic (see Thatje et al. 2005). It is possible, that the fauna moved lateral along the continental shelf to escape the advancing ice. It is also possible that some refuge areas persisted, e.g. deep trenches or pockets under the ice sheet that enabled some species to survive. An other common hypothesis assumes that a majority of the fauna migrated to the continental slopes and recolonised the shelf after the retreat of the ice. The general eurybathy, the wide depth range of many Antarctic species, is often explained this way (Brey et al. 1996). Recently Thatje et al. (2005) supposed that the migration to the slopes would have exposed any species to severe disturbance due to a high amount of suspended sediments and turbidity flows caused by the advancing glaciers. Thus, the slopes must be considered as an unsuitable habitat to survive a glacial period.

Additionally, a much higher sea ice cover must be expected during a glacial, resulting in a severe reduction of the primary production (Bonn et al. 1998) with according consequences for all trophic levels. Thus, the glacial history of the Antarctic is a sequence of unstable, changing environmental conditions. However, the changes occurred probably not rapidly but over relative long time scales (hundreds or even some thousand years). Species can cope with such gradual climate changes when some refuge possibilities, e.g. alternative habitats, exist or when they are pre-adopted.

1.6 Icebergs

Regarding shorter time scales, it is known that icebergs are the major source for disturbance to the shelf fauna (Gutt et al. 1996, Gutt 2001). In the Antarctic a typical iceberg calves form the shelf ice. This results in a shape with strait edges and a flat top (see Figure 3). Therefore, Antarctic icebergs are often characterised as tabular icebergs. Due to their regular shape the draught is roughly 7 times the height above the sea surface (which can be up to 100 m according to Wüthrich and Thannheiser). However, as icebergs become older and disintegrate, they might loose their regular shape. The thickness of a tabular iceberg is determined by the thickness of the shelf ice it originates from. The shelf ice thickness, and thus iceberg thickness, varies between 150 m and 550 m with a mean around 250 m (Gladstone et al. 2001, see Figure 4).

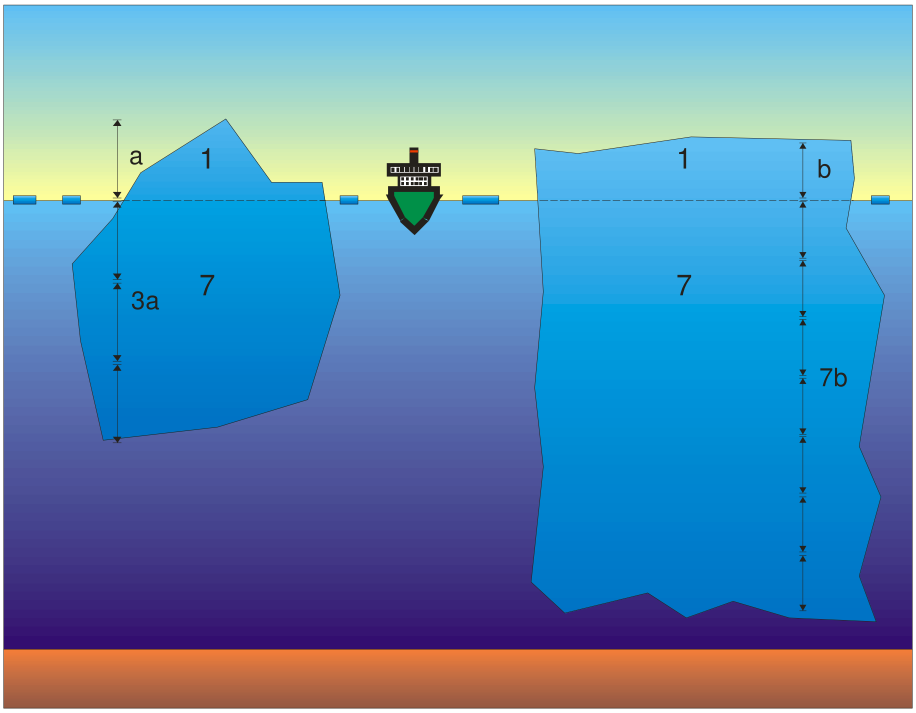

Figure 3, Comparison and characteristics for Arctic (left) and Antarctic (right) icebergs. Roughly 1/8th of the volume is visible as the “tip of an iceberg”. Due to their origin from glaciers Arctic icebergs tend to have an irregular shape and extending sideways under the ocean surface. This makes them dangerous for shipping. The draught can be estimated to be 3 times the visible height (a). Antarctic icebergs normally have a more regular shape with a flat top and do not extend much sideways. Due to their regular shape, the draught is approximately 7 times the height above the water line (b). (Changed and redrawn according to Wüthrich and Thannheiser).

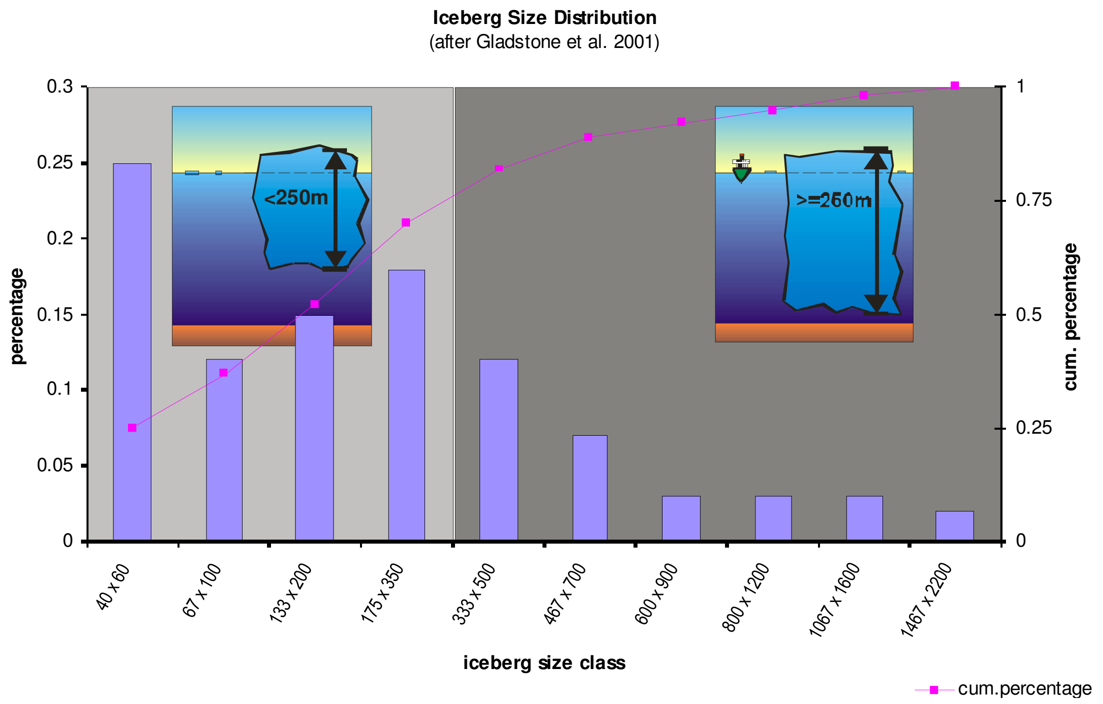

Figure 4, Size class distribution of calving icebergs according to Gladstone et al. (2001). Size classes (x-y dimensions) smaller than 175x350 m are assumed to have a draught <250 m (left panel). These make up to ~75% of all icebergs. Bigger icebergs with a draught >= 250 m (right panel) are rare (~25%).

1.7 Iceberg population

Icebergs are possible shipping dangers. Therefore, data on shipboard iceberg sightings and size classes have been recorded since many years (Hamley and Budo 1986). Estimates for the population of icebergs south of the Antarctic convergence are in the order of $2*10^5$-$3*10^5$ (Orheim 1987, 1988). However, this data may be biased (Gladstone and Bigg 2002) and satellite remote sensing has become a more accurate tool for tracking of iceberg population and drift today (Young et al. 1998, Gladstone and Bigg 2002, Silva and Bigg 2005). Satellite observations, however, only cover a limited area. A true census of the Antarctic iceberg population using satellite images has not been carried out yet.

1.8 Iceberg drift

Several forces influence the drift of an iceberg. Main components are the water and air drag forces. Thus icebergs move within a water body. The east wind drift takes the icebergs on a track along the coast. Strong katabatic winds may further accelerate an iceberg and cause a drift speed higher than the surrounding water (Gladstone et al. 2001). Therefore the average drift speed for the Weddell Sea is estimated to be 7.5 km d^{-1} near the coast and only 3.5-4.5 km d^{-1} for the open ocean (Gladstone and Bigg 2002). Older data (Tchernia and Jeannin 1984) reported a slightly higher speed (10.4 km d^{-1}), with strong variation (1.8-55 km d^{-1}). The same authors point out that iceberg drift occurs the whole year round; hence icebergs are not stopped by the winter sea ice. Contrarily, Lichey and Hellmer (2001) estimate that sea-ice strongly influences the drift and a sea-ice cover over 90 % may lock icebergs. Thus, the observation of Tchernia and Jeannin (1984) must be explained by the fact that they used radio satellite beacons and no visual observation methods. When their tagged icebergs got locked within the sea ice, they simply drifted together with it. Nevertheless, this points out that iceberg drift can impact the ecosystem throughout the whole year.

Figure 5, Iceberg drift pattern according to the model of Gladstone et al. (2001). Solid arrows indicate dominant drift directions; dashed line shows the northern border of the iceberg concentration near the coastline. Colours represent the depth scale (redrawn and modified from fig.3 in Gladstone et al. 2001).

If an iceberg enters the circum polar current, it may travel around the whole Antarctic within a few years. However, most icebergs stay close to the coast over the shelf area (Figure 5, see Gladstone et al. 2001, Gladstone and Bigg 2002, Silva and Bigg 2005). Gladstone and Bigg (2002) reported a 20-35 times higher iceberg concentration near the coast than further north during a satellite based study of iceberg drift in a 400 km by 100 km zone stretching away from the Antarctic coast at 18°W off Riiser–Larsen Ice Shelf (Weddell Sea). They estimated a yearly passage of more than 950 icebergs for this area. The same work reported that the iceberg concentrations in a 300 km by 100 km strip east of the Antarctic Peninsula near to the Larsen Ice Shelf was lower than that for the Weddell Sea (yearly passage of ~150 icebergs). However, the near coast concentration of icebergs was 2 times higher than for the open ocean. A similar picture is drawn by Young et al. (1998) for the east Antarctic. They reported the width of the strip where icebergs concentrate to be 140-160 km and only sometimes up to 550 km off the coastline.

The higher near shore concentrations are caused by the Coriolis-force that results in a southward directed impulse, pushing icebergs towards the coast (Gladstone et al. 2001). Notably, the magnitude of this force is proportional to the size of the iceberg. Thus smaller icebergs can easier leave the shelf zone, whereas bigger icebergs are trapped within the east wind drift.

On their way along the coast, icebergs do influence the ecosystem in a number of ways. Only giant icebergs may influence the pelagic ecosystem directly. However, the degree of disturbance is then very high. Examples are fragments of the giant B-15 iceberg (~10,000 km^2), which calved on March 2000 off the Ross Ice Shelf, which hindered the normal sea ice drift in the southwestern Ross Sea. This resulted in a much higher sea ice cover than normal and reduced the local primary production up to 40% (Arrigo et al. 2002). Similar, the C-19 iceberg, calved 26 months later in the same region, reduced the primary production as much as 90% (Arrigo and van Dijken 2003). This has severe consequences for all trophic levels (see cited literature).

However, such giant icebergs are rare events. The influence of smaller icebergs on the pelagic ecosystem is assumed to be low (Schodlok et al. 2005). The main phenomena may arise from freshwater influx by meltwater, affecting the oceanographic parameters in the vicinity of the iceberg.

Principle mechanisms of iceberg-seafloor interaction in the Antarctic

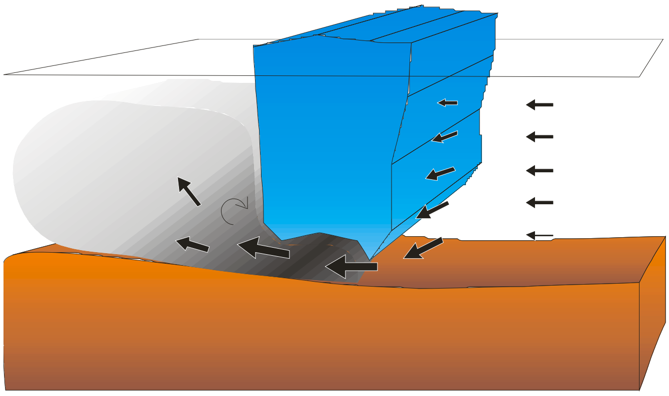

Figure 6, Icebergs alter the flow pattern around them. Thus they have an indirect impact on the sea floor even if no physical impact occurs, e.g. accelerated flows causing resuspension of sediments.

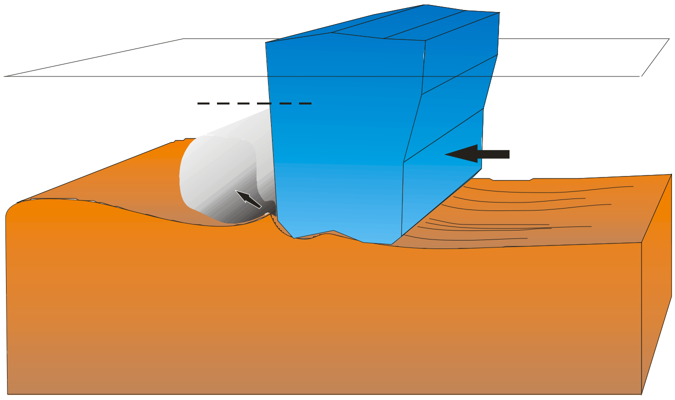

Figure 7, Direct impact on the sea floor. Icebergs touch the seafloor and slip over it. This causes severe damage to all organisms, leaving devasted areas with characteristically plough marks. In front of the moving block, a rampart of sediment is heaped up. The sediment is turned over and partially resuspended.

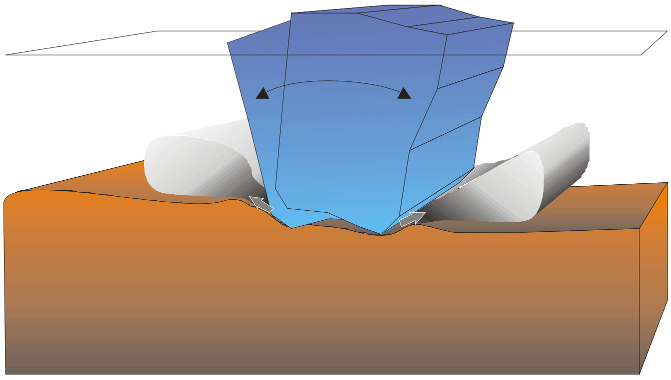

Figure 8, If an iceberg has scoured and moved into too shallow water it gets trapped. Changing currents, e.g. tidal movements, may cause the iceberg to seesaw, causing a pump-mechanism at the grounding zone. This may cause substantial resuspension and creates local debris slides on the sides (redrawn from Lien et al. 1989).

1.9 Influence of icebergs on the Antarctic sea floor

The influence of icebergs on the sea floor and benthic communities can be manifold. Most impressive is the physical impact on the sea floor (see Figure 6,Figure 7 and Figure 8). The high mass and impulse of an iceberg lead to easily observable scour or plough marks at the impact zone. In general, iceberg plough marks resemble a flattened U with some small ridges on the sides. Like a bulldozer, the icebergs push the sediment in front of it into a berm. Numerical modelling indicates that this movement affects the sediment up to tree times the scour depth (Yang and Poorooshasb 1997). While moving, this front berm is turned over and the sediment is partially resuspended. Parts of the sediment are bulldozed to the sides and piled up into ridges along the iceberg track. The height of these berm ridges varies from few centimetres up to several metres. Rearic et al. (1990) estimated that in the shallow Harrison Bay (Alaska), coarse-grained material (>63 µm) is moved as far as 7 m in the direction of the ice movement. Finer sediments (<63 µm) can be transported even more than 500 m due to bottom currents.

When a iceberg is nearly of finally stranded it may seesaw due to changing currents, e.g. tidal movement. This results in strong currents around the contact zones (Lien et al. 1989). These currents can be the source of massive resuspension of sediments. Together with the normal plough marks that can be several kilometres long and hundreds of meters wide (Lien et al. 1989), this “iceberg pump” mechanism could be a major source of sediment resuspension.

Based on the analysis of underwater video transects by Gutt and Starmans (2001) Potthoff et al. (2006) estimated 25 - 125 grounding events per year for a 300 km² region of the Weddell Sea, depending on water depth and topography. This leads to a rough estimate of about 1 - 5 grounding events per 10 km² for the whole shelf (0-500 m water depth). Assuming a disturbance interval of roughly 250 - 350 years for each m² of the sea floor (numbers based on Gutt 2001), approximately 0.004-0.003 % of the whole shelf (<500 m depth) is disturbed each year. Assuming the total shelf area (<500 m) to be between 1.2-2.2*10^6 km² (Barnes (1986), Gutt (2001); in comparison Clarke and Johnston (2003) list 2.97*10^6 km² <1000 m not under a permanent ice shelve) this results in a yearly perturbation area between 3.1-9.2*10^3 km².

2. Ecological Modelling

“The human intellect is impossible to think in other ways than in models. Also we experience nature always in a reduced way. No one has access to all aspects of an object in total and is able to store this information. To get essential information, we are forced to select and to abstract. Already when thinking what is essential, the formulation of a theory begins.”[1] (Freely adapted from Wissel 1989)

Ecological modelling is, like statistics, a very valuable tool for ecologists. In general, a model is the simplified representation of a phenomenon from a certain point of view. The reason to model or simulate natural phenomena is either to get a better understanding of the involved processes, to make predictions about the system response or simply to conduct experiments that cannot carried out in reality. To achieve such goals, several kinds of modelling approaches exist. The following passage references mainly to Wissel (1989), who coarsely classified three different model types used in the field of ecology:

- Conceptional models
- Descriptive models
- Simulation models

2.1 Conceptional Models

Conceptional models are used to create a better theoretical understanding of processes and phenomena (Wissel 1989). They are closest to classic mathematical models. This class of models often implies strong abstraction and reduction. An example for this model type is the well-known Lotka-Volterra model of two interacting species. The absolute focus of this model is the interaction of two species. External sources of mortality other than inter- and intraspecific competition of the two species are ignored.

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[1] “Der menschliche Geist ist unfähig, anders als in Modellen zu denken. Wir machen uns auch von der Natur immer vereinfachte Bilder. Kein Mensch kann alle Eigenschaften eines Objektes erfassen und alle erreichbaren Informationen darüber abspeichern. Er ist also gezwungen auszusondern, zu abstrahieren, um wesentliche Informationen zu erhalten. Breits beim Nachdenken darüber, was wesentlich ist, beginnt eine Theorie.” (Wissel 1989)

No one will ever assume that any natural population can be represented by such a simplified set of parameters. However, the Lotka-Volterra model has become one of the most influential models in theoretical and practical ecology even due to its simplicity.

It is worth to mention that the empirical background of some conceptional models is sometimes vague. For example, the well-known lynx-hare data cited in most text books (e.g. Begon et al. 1998). This data set has widely been used to explain models of the Lotka-Volterra type. However, only few acknowledge the fact that the data for the hare population comes from Eastern Canada, while the lynx data from Western Canada (see discussion in Hall 1988). Thus it is unlikely that both populations did directly interact with each other. Therefore, theoretical ecology and the search for general and universal ecological laws have often been criticized (Hall 1988, O'Hara 2005).

2.2 Descriptive Models

In contrast to conceptional models, descriptive models are used to classify and characterise systems. The goal of such models is to summarise and condense all available information of a system. Therefore, such characterisations may be used to extrapolate the system behaviour in the first hand and not to gain a mechanistic understanding. A very basic descriptive model is thus a simple linear regression. Even an ecological index like Shannon's *H* may be seen as simple descriptive model of the diversity of a community.

2.3 Simulation Models

The last class, simulation models, are in between both other types. Simulations are often created to obtain knowledge on the system behaviour and involved processes. Predicting the future state of a system, e.g. the population size of some commercial exploited stocks under different harvesting regimes, is also a common modelling task.

Simulation models are typically applied when the system is rather complex and a simple, mathematical solution is impossible. But also even quite simple systems may require simulation models to understand their behaviour. For example, cellular automats, like Conway's Game of Live or the Travelling Ant, have quite simple rules but the final spatial patterns they create are not predictable and highly complex (see box “The Travelling Ant Example”).

In general, a perfect model should be realistic, precise and universal. According to the principle of Occam’s razor[2] the model should further not contain unnecessary information and processes. Creating simulation models is thus the art of finding the necessary level of abstraction and complexity. Incorporating more and more details into a model, the covered processes become more and more realistic. On the other hand the uncertainty about the parameterisation rises. Thus, an optimal level for complexity exists (Wissel 1989).

However, models can just represent factors and mechanisms that were feed into the model *a-priori*. In principle this holds true even for models using evolutional algorithms. Therefore, results are valid only under the assumptions and restrictions defined also *a-priori*. It is important to be aware of this. Models are just a tool helping to extend our intellect. Caswell (1988) states that models are to theoretical problems what experiments are to empirical problems. They can be used for checking if hypotheses can work, to find logical cues of concepts and to stimulate a further discussion on the ideas. But they must never be used without critically evaluating their results.

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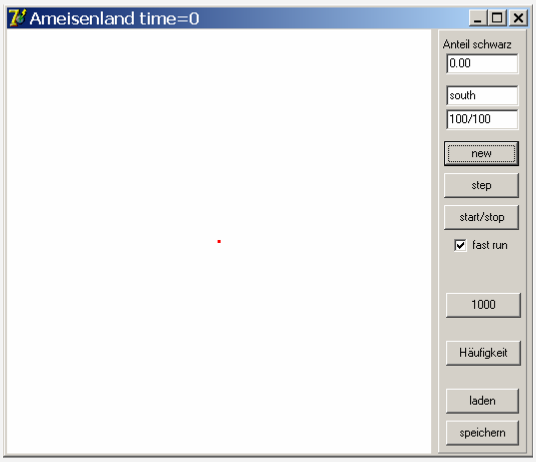
[2] “*Entia non sunt multiplicanda praeter necessitatem*” (Entities should not be multiplied beyond necessity), attributed to William Ockham (1295–1349)

“Occam's razor states that the explanation of any phenomenon should make as few assumptions as possible, neliminating, or "shaving off," those that make no difference in the observable predictions of the explanatory hypothesis or theory. In short, when given two equally valid explanations for a phenomenon, one should embrace the less complicated formulation.

Furthermore, when multiple competing theories have equal predictive powers, the principle recommends selecting those that introduce the fewest assumptions and postulate the fewest hypothetical entities. It is in this sense that Occam's razor is usually understood” (Occam's razor. (2006, September 28). In *Wikipedia, The Free Encyclopedia*. Retrieved 14:33, September 29, 2006, from “http://en.wikipedia.org/w/index.php?title= Occam%27s_razor&oldid=78232637)”

The Travelling Ant Example

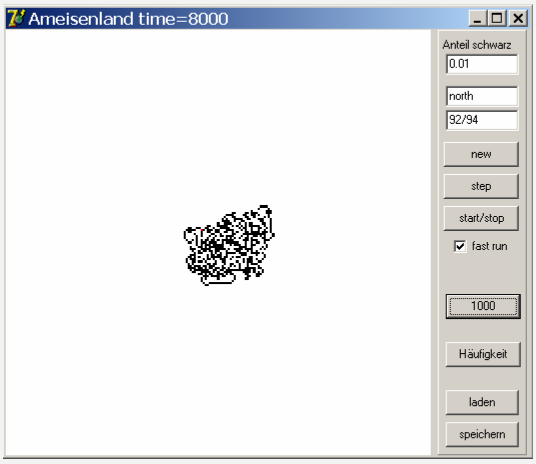
The Travelling Ant is a cellular automat like Conway's Game of life. The ant lives in a gridded, infinite plane. Each grid element can be black or white. If the ant is on a white grid cell, it makes the cell to become black, turns left and moves one step forward. On a black cell, it changes the colour to white, turns right and then moves forward. These two simple rules can create astonishing complex patterns. On a complete, initially white plane, the ant starts its journey and by time a very regular, ladder alike pattern emerges. However, if the plane is randomly initialised with black and white cells, it is impossible to predict when and where this characteristic ladder shows up. Although the behaviour of the ant is completely determined and the starting conditions are fully known, you have to run through the complete simulation to answer this question.



Ameisenland time=0

Anteil schwarz
0.00
south
100/100
☑ fast run

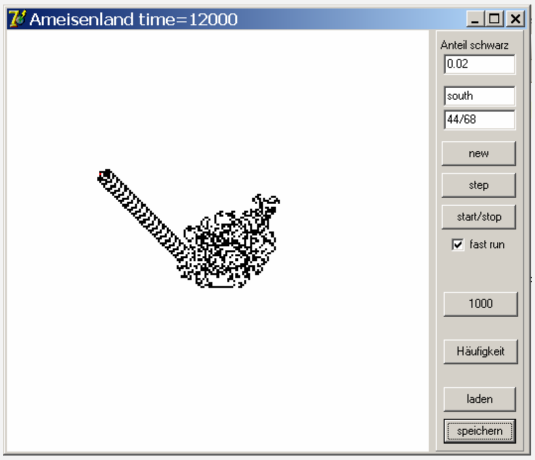
The ant starts in the middle of the picture



Ameisenland time=8000

Anteil schwarz
0.01
north
92/94
☑ fast run

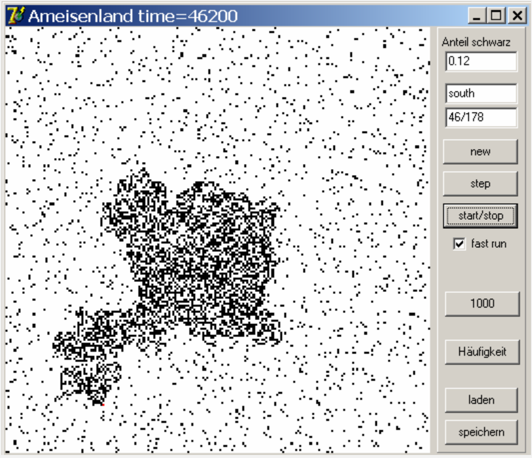
After 8000 steps a complex, however unordered movement pattern can be observed.



Ameisenland time=12000

Anteil schwarz
0.02
south
44/68
☑ fast run

After about 10000 steps the ant starts to build the characteristic ladder like ant street.



Ameisenland time=46200

Anteil schwarz
0.12
south
46/178
☑ fast run

On a randomly scattered plane it is impossible to predict when and where the ant street will be build

2.3.1 Spatial explicit models

Many models do not explicitly contain spatial information. Many conceptional models e.g. assume that every entity can interact freely with each other, the so called mean-field assumption. Also for models targeting at population sizes, spatial information is possibly unnecessary and should be left out (Occam's razor cut's here). However, as Murrell et al. (2001) pointed out, the spatial arrangement has a great influence on a system and every natural system is subject to spatial phenomena.

Spatial explicit models contain properties describing the spatial relation of their entities, e.g. their position in space or distance to each other. The addition of a further dimension "space" to a model can produce completely different results. Coexistence in classical ("un-spatial") models for example is only possible under some restrict assumptions. Including special aspects, coexistence can simply emerge due to the (spatial) separation of the species.

2.3.2 Individual Based Models

Individual based models (IBM) or agent based models (ABM) are a special class of simulation models. Basic elements of such simulations are one or several entities, typically representing a single individual and rules or directives that describe their behaviour. The meaning of individual may even cover a group of identical individuals e.g. a fish swarm. In this case modellers often refer to superindividuals. Despite a simple set of parameters and behaviour rules describing each entity the emerging complexity of individual based models, the final interplay of entities among themselves and their environment, can be very high.

IBMs offer a simple and easy way to describe complex, spatial systems. A further advantage is the fact of an easy and intuitive access of non-modellers to the underlying ideas. However, the exact formal description of IBMs can be difficult (Grimm et al. 2006).

2.3.3 Simulation Models and Biodiversity

Biodiversity, or biological diversity, has been defined as:

> "Biological diversity" means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems. (DIVERSITY 1992)

This implies that diversity comprises the abundance of species and their spatial layout. Spatial explicit IBMs include both the abundance and spatial arrangement of individuals. Therefore, spatially explicit IBMs are especially suited to study biodiversity in a simulated habitat and the factors influencing it.

2.4 The Modelling Cycle

Modelling or creating computer simulations involves several steps:

1) Formulation of the aim or question to be solved
2) Identification of the key processes and mechanisms
3) Formulation of a conceptional model
4) Creating an appropriated model representation (i.e. a computer programme)
5) Verification if the model performs according to the conceptional model
6) Validation if the model reproduces reasonable results
7) Conducting the actual experiments
8) Interpretation of the results

Especially verification and validation are very important steps. If the model does not satisfy these points, the interpretation of the results will be, at best, questionable. If the verification fails (the model produced no suitable results, i.e. in a marine ecosystem the filter feeders prey on the whales), the model representation may be wrong. If the validation fails (i.e. the filter feeders prey on plankton but they never starve if they fail to catch something) there are strong hints that the model does not include all necessary process. Therefore, the above listed steps may be repeatedly carried out in different orders during the modelling process.

3. The Aim of this study

Due to their remoteness, marine systems in general and the Antarctic shelf in special are difficult to investigate and data on species traits like dispersal properties or life spans are spare. It is also unclear, how specific species traits and the environment influence the coexistence and diversity in these systems. The aim of this study is therefore to investigate the influence of disturbances and selected species traits on the diversity of marine systems and possible effects of the special Antarctic environment using computer simulation models.

The Antarctic shelf harbours a wide range of highly adopted species and is subject to intense disturbance events caused by grounding icebergs. Such grounding events cause catastrophic disturbance on the sea floor and are lethal to most affected individuals. After a disturbance a succession occurs, from diverse, unpredictable pioneer assemblages to a more defined climax state (Gutt and Piepenburg 2003, Teixido et al. 2004). This succession is influenced by the dispersal potential of the colonisers. In general, many marine sedentary species disperse via larvae. The larvae release often happens very seasonal, i.e. occurs over a short time period. If the larvae respond similar to their environment, they stay together and become dispersed as a group or swarm. This will result in clumped dispersal and settlement pattern. What is the outcome of such dispersal pattern? How do the dispersal traits of Antarctic species interact with such pattern? In general the dispersal potential of most Antarctic species is considered to be low. Theoretical work based on terrestrial systems has shown that short dispersal can foster competitive displacement (Bolker and Pacala 1999). In the first manuscript I focus in on the following questions:

- How does clumped dispersal influence the coexistence and diversity?
- How does it interact with the proposed short dispersal of most Antarctic species?
- Are there differences in the performance of terrestrial and aquatic systems?

The second manuscript targets the general coexistence of two species competing for space. Coexistence in this case refers to the long-term local persistence of both species. It is known that such coexistence can be mediated by a competition-dispersal trade-off (Tilman 1994). This means that the inferior species, typically a pioneer, has to explore new habitats before the superior species arrives and displaces the pioneer. If new habitats are created by disturbances (like the scour marks on the Antarctic shelf) the disturbance regime (disturbance size and frequency) plays an important role. It is reasonable to assume that dispersal implies cost for a species. Therefore dispersal should be effectively and cost efficient. The second manuscript studies the following questions:

- Is there a dispersal distance threshold, a minimum dispersal distance that allows the species to persist under the aspect of cost efficiency?
- How does this threshold depend on the disturbance regime?
- How does the proposed prolonged longevity of Antarctic species affect the dispersal distance?

Besides biological factors the succession after a disturbance is controlled by several abiotic factors. The disturbance regime, namely the average size of a single disturbance event, the frequency of such events and their severity interact with the species traits and influence the succession process. The last manuscript analyses the role of these disturbance properties for the succession process. It uses a simulation of a multispecies community on the Antarctic shelf, which is subject to intense disturbance. With this simulation model the questions are explored:

- In the same time interval numerous small disturbances can perturb the same total area as rare large disturbances can. Is only the total area important or lead numerous small disturbances to other results as infrequent but larger disturbances?
- Which role has the average size of a single disturbance?
- How important is the disturbance frequency?
- How do possible survivors influence the recovery process?

The following sections contain summaries of the publications and manuscripts describing the scientific work carried out during this thesis. The first two manuscripts have been already published; the third is ready to be submitted. After the summary of the manuscripts a brief discussion of the results follows. Detailed model descriptions, results and discussions can be found in the text of the manuscripts in the chapters 7-9.

As a last section a detailed manual for SIMBAA (Simulation Model of Benthic Antarctic Assemblages) follows. The development of SIMBAA was a main task during this thesis. The source code of SIMBAA spans about 35 single files with together more than 16.000 lines of code and was completely written from the scratch, using Borland Delphi 7.0 Professional. A portable pseudo-random-generator was taken form the Numerical Recipes Series (Press et al. 1991). Additionally, a freeware colour space conversion routine written by Grahame Marsh and some code lines to display the compile date of the executable programme were taken from the Internet (see SIMBAA manual for details). This foreign code is not essential for the model, but primary reduced the development time. In case of the pseudo-random-generator the selection of a fully accessible and proven code simplifies the validation, quality and reusability of the whole model.

4. Publications and Manuscripts

4.1 “Clumped Dispersal and Species Coexistence”

The idea, model programming, evaluation of the result and the first draft of the manuscript was done by myself. The co-authors contributed to the writing and discussion of the final manuscript.

4.1.1 Bibliographic record

Title: **Clumped Dispersal and Species Coexistence**
Authors: Michael Potthoff, Karin Johst, Julian Gutt, Christian Wissel
Status: published, Ecological Modelling Volume 198 (1-2), Pages 247-254
doi:10.1016/j.ecolmodel.2006.04.003

4.1.2 Short summary of ideas, problems, solutions and results:

Many sedentary marine species disperse their propagules passively. Compared to air, the high water density allows species to easily adopt the buoyancy of their larvae to be negative, positive or neutral. Thus dispersal using oceanic currents can involve comparable few metabolic costs. However, the risks of becoming dispersed to unsuitable habitats or falling prey during the dispersal phase raises as longer the dispersal lasts. Often planktonic larvae exhibit sophisticated vertical migration patterns, triggered by intrinsic and/or external factors, to avoid these risks.

Larvae are often released only over a short period, e.g. within a few days during the mass spawning observed at some coral reefs. It must be assumed that factors triggering larvae migration pattern are species specific. Thus larvae of one species respond similar to their environment. This may lead to a separation and concentration of species specific larvae in specific water masses. Consequently the arrival of such larvae swarms and the settlement co-varies. On a local scale this will resemble a wave or pulse like larvae and settlement pattern. On a coarser spatial resolution a patchy pattern will emerge.

To investigate the role of such clumped and patchy dispersal and settlement of larvae for coexistence and diversity we implemented a spatial explicit IBM. The species in the model differed only in their dispersal traits, all other traits where equal. The key idea was to introduce a two-phase dispersal mechanism: in the first phase the average dispersal distance of the larvae swarm is determined. The swarm virtually centres around the resulting point. Swarm members are then distributed around this point. This dispersal mechanism is very flexible. Depending on the chosen values for the dispersal distances either patchy and clumped or an isotropic, source centred larvae pattern can be generated.

We analysed the role of clumped dispersal for diversity (in sense of species richness) and its competitive performance with isotropic dispersal with this model. In all tested cases clumped dispersal allowed multi-species coexistence over long time periods, whereas isotropic dispersal fostered competitive displacement and quickly lead to the extinction of most species when only one dispersal strategy (clumped/isotropic) was available. When both dispersal strategies competed, coexistence was possible when clumped dispersal had the superior dispersal distance (depending on the environment).

4.2 “How to survive as a pioneer species in the Antarctic benthos: minimum dispersal distance as a function of lifetime and disturbance”

The idea, model programming, evaluation of the result and the first draft of the manuscript was done by myself. The co-authors contributed to the writing and discussion of the final manuscript.

4.2.1 Bibliographic record

Title: **How to survive as a pioneer species in the Antarctic benthos: minimum dispersal distance as a function of lifetime and disturbance**
Authors: Michael Potthoff, Karin Johst, Julian Gutt
Status: published, Polar Biology 2006, 29 543-551
doi: 10.107/s00300-005-0086-1

4.2.2 Short summary of ideas, problems, solution and results:

Under the assumption that dispersal induces costs for a population, species should disperse cost efficient, i.e. only as far as the colonisation rate of new habitats allows the persistence of the population. However, if individuals live for more than one season, they have several chances for successful dispersal. Thus the dispersal distance should be a function of habitat distance and lifespan. In a dynamic environment, where new habitat is created by disturbances, the disturbance regime plays also an important role.

The aim of this study was to find out if a threshold in the dispersal distance exists that allows a species to persist in a dynamic environment and how this threshold depends on species longevity and the disturbance regime. We implemented a spatial explicit IBM with two species living in a dynamic environment. This environment is characterised by catastrophic disturbance events. Effected regions are completely disturbed and become free of any inhabitants. One of the modelled species depends on the colonisation of such free areas as it can only recruit in the absence of the other species. Thus it is the inferior coloniser and represents a classic pioneer species. The second, superior species is able to competitively displace the pioneer and quickly colonise all space not utilised by it.

It is well known that coexistence of both species is possible under a dispersal-colonisation trade-off (Tilman 1994). This means that the inferior species must have a dispersal distance that allows it to colonise new habitats before the superior species arrives. However, the exact threshold and the dependency of the dispersal distance on the disturbance regime and lifespan of the pioneer are unclear.

The key idea of our implementation was to use circular disturbance events and circular dispersal shadows. This allowed us to easily compute distances between different patches using a simple Euclidian distance. Experimental manipulation of the disturbance regime, dispersal distance and life span allowed us to determine a dispersal distance threshold for the persistence of the inferior species.

The results show that the dispersal distance must be at least slightly higher than the average distance to the next free habitat. Thus, with raising disturbance intensity, more disturbances create more free space in the vicinity of a pioneer population. Consequently, the dispersal distance sufficient to allow the pioneer to persist can be reduced. However, under a very high disturbance regime the dispersal distance must raise again as the probability for a catastrophic disturbance rises. Thus the threshold shows a U-shaped relationship to the disturbance intensity.

Long living species can cope with low dispersal distances as they have more chances for successful dispersal. Virtually a doubled lifetime doubles the chances, e.g. it creates a lower average new habitat distance. On the other hand the probability of a catastrophe rises. The interplay of both processes brings about a non-linear, hyperbolic relationship of dispersal distance and lifespan.

Our model indicates that a species could persist with half the dispersal distance if it could raise its lifespan three to four times. Thus, in a dangerous world with high dispersal costs, becoming older is a good strategy. Caused by the hyperbolic relationship, especially short living species can profit much if they can extend their lifespan.

4.3 "How the disturbance severity drives the benthic diversity on the Antarctic shelf"

The idea, model programming, evaluation of the result and the first draft of the manuscript was done by myself. The co-authors contributed to the writing and discussion of the final manuscript.

4.3.1 Bibliographic record

Title:	**How the disturbance severity drives the benthic diversity on the Antarctic shelf**
Authors:	Michael Potthoff, Karin Johst, Julian Gutt
Status:	unpublished

4.3.2 Short summary of ideas, problems, solution and results:

Generally disturbance is defined as a relatively distinct event in space and time that disrupts the ecosystem, community or population structure and changes resources, substrate availability or the physical environment (White and Jentsch 2001). On the Antarctic shelf physical disturbance by grounding icebergs is the major disturbance agent for the benthos, disrupting local communities and populations and influencing the local physical environment and substrate characteristics. The aim of this manuscript was to characterise the importance of such disturbances for the succession and diversity. In particular we were interested in how the disturbance size and frequency influenced the succession and recovery speed. Changes in flow and sediment conditions and their influence on the communities were not considered.

We created a spatially explicit IBM with multiple species organised in different guilds. In the model we used intra-guild neutrality. This concept combines the idea of neutral and traditional succession models. Intra-guild neutrality means that species of one guild shared the same species traits whereas among the guilds great differences existed.

We used 4 guilds, a pioneer guild, an early and a late coloniser and a climax guild, characterised by appropriate species traits. The general lack of reliable data on species traits, like lifespan, fecundity and dispersal properties for most Antarctic species made the parameterisation of the model extremely difficult. Therefore, we parameterised a nullmodel with literature and theoretical data and used this as reference. The model response to different disturbance parameters was then evaluated in relation to this nullmodel.

The model showed that disturbance severity has a great influence on the climax recovery speed (approximated by the average age of the climax state). Surviving individuals represent a spatial storage effect (Chesson 2000a). The lower the disturbance severity is the faster is the succession. The results demonstrate that the relation of recovery speed and disturbance severity is non-linear. When the disturbance size was fixed, even a disturbance severity of 99% (analogue to a survival probability of 1%) can reduce the climax recovery time up to 10% on average. In extreme cases it might even fasten the recovery up to 25%. A disturbance severity of 90% shortens the recovery speed about 50% on average.

When the size of a single disturbance is fixed, the model shows further that recovery speed is linear related to the rotation period (statistically the time to disturb the whole landscape once). When the rotation period is fixed, the disturbance size determines the relative guild abundances. The abundance of a guild seems then to be linear related to the disturbance size. However, the different guilds show different behaviour, mostly caused by their dispersal limitation. Thus the climax guild, with the strongest dispersal limitation, showed the highest and the pioneer, with almost no dispersal limitation, the weakest relation.

5. Summary and Discussion

The first manuscript concerns a general phenomenon of larvae dispersal and settlement pattern in marine systems. The dispersal of larvae swarms released simultaneously leads to a pulsed or wave like settlement pattern on local scale. On broader spatial scales this will result in a patchy or clumped pattern. Such pulsed or clumped dispersal and settlement pattern can often be found in marine systems. We were interested in how such pattern generally can affect diversity and coexistence. We found that a clumped dispersal can foster diversity and coexistence by greatly slowing down competitive displacement without the need for further mechanisms or trade-offs.

Clumped dispersal leads to a spatial accumulation of intraspecific competitors. This raises the intraspecific relative to the interspecific interactions. On a broader spatial scale this has a stabilising effect for the coexistence of different species (Chesson 2000b). If species disperse in an isotropic way, thus without a favoured direction, the larvae are placed around the parental stock with the centre of the larvae density being equal to this stock. This high larvae density hinders other species to invade the parental area. By time a concentric front may grow and displace other species. This effect is known as phalanx growth mechanism (Bolker and Pacala 1999). If species disperse in a patchy or clumped way, the larvae density centre is not located at the parental stock origin. The centre of the clumping is decupled from the parental source each time. Thus competitive displacement by a phalanx growth mechanism is hindered.

Patches of simultaneously established individuals are similar to a positive growth-density covariance Chesson and colleagues proposed for intraspecific aggregation due to local dispersal under the presence of favourable habitats for particular species (Chesson and Neuhauser 2002, Snyder and Chesson 2003). Such covariance measures the degree to which competing species can accumulate in favourable locations (Snyder and Chesson 2004). It occurs when limited dispersal allows rare species to build up densities in some areas, resulting in an increase of their overall *per capita* growth (Amarasaekare 2003). The key process for a positive growth-density covariance is a dispersal strategy that permits the establishment of a group of new individuals in suitable environments. This can be the result of local aggregation of larvae around the parental stock due to isotropic dispersal in environments with species specific favourable habitats (Amarasaekare 2003, Snyder and Chesson 2003). However, this can also be the result of a dispersal strategy where the aggregation of larvae causes temporarily suitable habitats due to the absence of competitors.

These results suggest that the coexistence in many marine assemblages, like corrals reefs or the benthic communities in the Antarctic, is greatly influenced by the reproduction timing, population synchrony and larvae behaviour. Important is a pulsed larvae release. The marine environment then makes an isotropic dispersal virtually impossible. Oceanic currents and the behaviour of the dispersal stages will generally lead to a clumped dispersal and settlement pattern. At local scale the resulting grouping of conspecific recruits may entail a lower α-diversity. However, on regional scale the general species diversity is raised. Thus clumped dispersal has a positive effect on β- and γ-diversity (note that the quality of local and regional scale depends on the swarm size and dispersal distance).

The second manuscript concerns questions about an ecological meaningful dispersal distance to persist in a dynamic environment. In particular we wanted to know, if there is a minimal dispersal distance necessary to persist in habitats like the Antarctic shelf, that is subject to intense iceberg scouring (Gutt et al. 1996, Gutt and Starmans 2001, Gutt and Piepenburg 2003). The results of the second paper demonstrate that in such a dynamic environment the minimal dispersal distance for a pioneer population to persist locally is a function of habitat spacing and species longevity. If the availability of new habitats, respectively the habitat density, is the result of disturbances, the minimal dispersal distance and the disturbance intensity show a U-shaped relationship. Until an intermediate level raising disturbance intensity leads to a falling minimal disturbance distance for a species to persist locally. Further raising disturbance intensity leads to a raising dispersal distance, since the probability of a catastrophic, lethal disturbance raises.

Long living species can cope with lower dispersal distances since a longer lifespan leads to more chances of successful dispersal. At the same time the probability of a lethal disturbance rises. This results in a hyperbolic relation of lifespan and minimal dispersal distance. According to the simulation results a species can cope with half the dispersal distance if it can extend its lifespan three to four times. Especially short living species profit much from this hyperbolic relationship.

True annual pioneer species of the Antarctic shelf benthos have not yet been described. Based on measurable growth marks of an early coloniser of iceberg scours Gutt and Starmans (2001) timed the first successful macrobenthic recolonisation state to last about 10 - 15 years. This implies that such pioneer species in the Antarctic could cope with very low dispersal distances. Based on a rough estimate deducted from actual disturbance data, the minimum dispersal distance could approximately be less than 1000 m for pioneers with a lifespan of about 6 years. Therefore, long lasting dispersal stages are not necessary for a pioneer population on the Antarctic shelf to persist locally. This could add a further explanation of the rarity of long lasting meroplanktic larvae dispersal in polar waters.

The last manuscript focuses on the influence of physical disturbance on the diversity of Antarctic shelf assemblages. These assemblages are subject to severe disturbance due to iceberg scouring. Once disturbed, local assemblages return to a climax state, or at least to a state indistinguishable from the undisturbed surrounding community (Gutt and Starmans 2001, Gutt and Piepenburg 2003, Teixido et al. 2004). The length of the trajectory of this succession is often referred as resilience of the system (Begon et al. 1998). It depends on the type of disturbance, its frequency and intensity (Connell 1978, Huston 1979), but also on the nature of the community (Schratzberger and Warwick 1999).

The last manuscript covers the influence different physical properties of iceberg scouring for the succession process. In particular we questioned, if only the total per timer interval perturbed area is important or which role the average disturbance size and disturbance frequency play. Further we were interested in the consequences of individuals surviving a disturbance event. The simulation showed that such survivors are a very important factor for the resilience of the Antarctic benthos. In general, the influence of individuals surviving a disturbance on the climax recovery speed is non-linear. In the simulations even a 1% survival probability, a value that might fit for the Antarctic shelf, shortened the recovery process up to 25%. A 10% survival probability can reduce the recovery time to 50% on average. This positive effect on the resilience of an assemblage can be ascribed to a spatial storage effect (Chesson 1994) induced by single surviving individuals. Similar to seed banks in terrestrial systems, such single surviving individuals store a population's potential to high growth over unfavourable times. Especially species with a high dispersal limitation may profit much, as the time to invade the disturbed areas can be greatly reduced.

The model also demonstrates that the rotation period, the time to statistically disturb the whole landscape, is very important parameter for the resilience and diversity. It is a non-linear function of the disturbance size and frequency. If the average size of a single disturbance event does not change, the recovery time depends linear on the rotation period. Since the rotation period is a non-linear function of the disturbance size and its frequency, this is equal to a non-linear response to changing disturbance frequencies. If the disturbance frequency is small, small changes can cause a high change in the recovery speed. Small changes at higher disturbance frequencies to not cause the same effect.

If the rotation period is fixed, which means that only the total perturbed area per time interval is important, the recovery time depends linear on the disturbance size. In other words, there is a difference between small numerous and rare large disturbances of equal total size. In the simulation the relative species composition of the resulting assemblages and proportions of the different recolonisation states are determined by the dispersal limitation of the different species. This is comparable to the response of a meiofauna community to a disturbance by organic matter enrichment. The same amount of organic matter administered in many small doses has a milder effect on community structure than when administered in fewer but larger doses (Schratzberger and Warwick 1998).

These results can be interpreted on the background of a possible change of the disturbance regime due to the global climate change. If the climate change influences the iceberg calving rate the influence on the diversity depends on the new iceberg dimensions. One probable scenario currently discussed is a global warming. The disintegration of several large ice shelfs observed within the last years demonstrates that giant icebergs may become a more common phenomena in future. However, the direct influence of such giants is out of the focus of this work. Nevertheless, such giants will break up and finally raise the numbers of smaller icebergs. It can be assumed that a global warming will in general lead to a higher calving rate. Thus I expect the number of icebergs to be positively correlated with a global increase in temperature. This will lead to a reduced rotation period, as more icebergs will faster disturb a certain area. According to the simulation results, a faster recovery process can then be expected. As the dispersal limitation interferes with this process, the relative community structure and proportions of the succession states will change.

Thus a community shift can arise. Species with a strong dispersal limitation will decline in numbers whereas broadcasting species will rise in numbers.

6. Literature

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7. Clumped Dispersal and Species Coexistence

Clumped Dispersal and Species Coexistence

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7.1 Abstract

Anisotropic clumped (patchy) dispersal of species is a widespread phenomenon in nature, however its relevance for structuring communities and maintaining biodiversity is still a matter of debate. We used a spatially explicit simulation model to assess the effects of spatial aggregation through this dispersal strategy compared to isotropic clumped (local) dispersal on the diversity of a model community of sessile species. The species differed only in terms of their dispersal distance and no a priori trade-offs between dispersal and local competitive strength were assumed. We investigated spatially homogeneous and heterogeneous environments without and with temporally fluctuating reproduction success. In all cases patchy dispersal allowed the long-term coexistence of a variety of species – in contrast to local dispersal. In particular, patchy dispersal was found to decouple the mechanism of spatial aggregation from the dispersal distance. This supports species coexistence even in environments where local dispersal was a superior or inferior dispersal strategy. Thus, the specific way of spatial aggregation can be decisive for coexistence. Spatial aggregation independent of the dispersal distance is an attribute of dispersal offering new possibilities for trade-offs with life-history traits and with the dispersal distance itself.

7.2 Introduction

Much theoretical research has been done to reveal and understand the mechanisms that lead to the coexistence or to the exclusion of species and subsequent succession. Dispersal is one of the major factors shaping communities and mediating coexistence. Field observations show that dispersal patterns can be highly complex. Most marine species for example disperse through pelagic larvae stages (Roughgarden et al., 1988; Muko and Iwasa, 2000). Since they are exposed to the same environmental influences and originate simultaneously from a specific location, they often behave as a swarm and disperse as a group (Hofmann et al., 1998; Flierl et al., 1999; Lockwood et al., 2002). This will result in an anisotropic and clumped (patchy) dispersal pattern. Such patchy dispersal seems to be a widespread phenomenon in nature, not restricted to marine environments (David et al., 1997; Heard and Remer, 1997; Smith and Witman, 1999; Nathan and Muller-Landau, 2000; Wenny, 2001). It can be generated by various abiotic or biotic dispersal agents (wind and water currents, animals) or a combination thereof (Nathan and Muller-Landau, 2000; Stoyan and Wagner, 2001; Wenny, 2001; Wang and Smith, 2002; Wagner et al., 2004). Using abiotic dispersal agents, landscape elements can act as an attractor or interceptor for dispersal stages (Reed et al., 2000) like any kind of obstacle, e.g. a scrub in an open landscape or a rock in the sea. Using biotic dispersal agents, patchy dispersal can emerge due to the behaviour of the agent (Heard and Remer, 1997; Wenny and Levey, 1998; Fragoso and Huffman, 2000; Hartley and Shorrocks, 2002; Wehncke et al., 2003). Secondary dispersal processes such as scatter hoarding may also be an important source of patchy dispersal (Nathan and Muller-Landau, 2000; Wang and Smith, 2002; Roth and Vander Wall, 2005). Notably, fertilization success of sedentary organisms like wind-pollinated plants or sessile marine animals is greatly influenced by anisotropic gamete dispersal as well (Claereboudt, 1999).

Theoretical approaches modelling dispersal, however, often assumed isotropic global dispersal (mean-field assumption) where all units can freely interact over all scales. This is appropriate as long as suitable habitat is abundant (King and With, 2002). However, as Durrett and Levin (1998) point out, it neglects spatial aspects and thus can have important consequences for diversity (Murrell et al., 2001). More realistic approaches distribute dispersal stages according to particular dispersal kernels over certain distances but assume the adult at the centre and dispersal of individual propagules or offspring being possible in all directions (Clark et al., 1999; Hovestadt et al., 2000; Levin and Muller-Landau, 2000; Nathan and Muller-Landau, 2000; Johst et al., 2002). This isotropic (around the source) and local dispersal may lead to local clustering and has a positive effect on diversity when there is a competitive difference among the species with respect to favourable habitats (Chesson, 1994; Chesson and Neuhauser, 2002; Snyder and Chesson, 2003).

Modelling a realistic seed abscission process for anemochorous plants Schippers and Jongejans (2005) demonstrated that an anisotropic seed shadow can emerge, that strongly influences the long distance dispersal which in turn is essential for maintaining diversity (Higgins et al., 2003). A theory linking such anisotropic dispersal and diversity is the aggregation model of coexistence (Shorrocks et al., 1979; Hartley and Shorrocks, 2002). This theory has been used to explain the high diversity of insect communities utilising ephemeral resources. It states that individuals of a species may be clumped together in a way limiting their own population growth such that resources that are left free can be utilised by inferior competitors (Hartley and Shorrocks, 2002). Thus, the basic mechanisms are the well known coexistence criteria “intraspecific competition higher than interspecific competition” (see e.g. Begon et al. 1998; Murrell et al.2001) and dispersal limitation of a superior competitor (Hurtt and Pacala, 1995). These mechanisms also play a role in the so-called competition-colonisation trade-off mechanism (Tilman, 1994 but see Higgins and Cain, 2002). It assumes that in a spatially structured population the locally superior competitor is the inferior disperser, e.g. has the shorter dispersal distance.

All these mechanism relate diversity to dispersal and have been found to work in theory as well as having been demonstrated in nature. However, they are based on species difference and spatial heterogeneity to work and cannot explain the coexistence of apparently similar species in homogeneous environments. For example, it is unclear whether coral reefs or rain forests provide enough niches to explain the high diversity in these habitats. The unified neutral theory (Hubbell, 2001) tries to fill this gap. One major assumption of this theory is that niches are absent and extinction, immigration and speciation are the essential processes structuring the communities on evolutionary time scales (Hubbell, 2001; Volkov et al., 2003). Dispersal influences the long-term structure of a neutral community via its influence on the extent of species mixing. Although neutral models are able to reproduce species-area relationships surprisingly well (Hubbell, 2001; Chave, 2004; McKane et al., 2004) even slight violations of the neutrality can lead to a quick breakdown (Fuentes, 2004). Therefore, the neutral theory has been controversially discussed (Nee and Stone, 2003; Adler, 2004; Alonso and McKane, 2004).

In general four forms of dispersal may be distinguished: a) global dispersal (isotropic non-clumped), b) local dispersal (isotropic clumped), c) directed dispersal (anisotropic, e.g. along a vector) and d) patchy dispersal (anisotropic clumped). Dispersal kernels of the type a) and b) have been extensively studied as the isotropic approach has the advantage of simple analytical tractability.

Directed dispersal (type c) has been found to affect the diversity and genetic flow of populations (Wenny, 2001) and spatial heterogeneity in sedentary organisms (Reed et al., 2000). Wagner et al. (2004) modelled anisotropic seed dispersal using a cluster point process and proposed a positive effect for long distance disperser (e.g. pioneer species) when suitable habitat is rare.

More complicated dispersal kernels (e.g. type d) and the consideration of spatially and temporally variable environments (which can influence the competitive advantage of a dispersal strategy) complicate analytical tractability. Simulation models provide an alternative way to investigate such complex situations. Some attempts have been made using correlated random walk or Lagrangian models (Yamazaki and Haury, 1993; Yamazaki and Okubo, 1995). However, these explicit methods are time consuming and not well suited for high individual numbers. Therefore, simplified approaches are needed when analysing the influence of complex dispersal pattern on diversity.

In the following we will focus on patchy (anisotropic clumped) dispersal. To our knowledge and compared to type b) dispersal, its relevance for species coexistence has not yet been investigated. What are the characteristically properties of such a type d) dispersal mechanism? Although patchy dispersal results in a high number of propagules at some sites, thus creating spatial aggregation similar to local dispersal, the peak propagule density is not at the original site. Therefore, patchy dispersal bears aspects of both local and global dispersal and it is not obvious which aspects dominate in different environments and competitive scenarios. For that reason we investigate the effects of patchy dispersal on diversity (in the sense of species richness) with a simulation model for neutral (with respect to demographic parameters) and hierarchical communities in different environments. We demonstrate that patchy dispersal can promote coexistence in heterogeneous as well as in homogeneous environments and between competitively equal and competitively different species. Thus we show that patchy dispersal is able to mediate coexistence even in situations in which local dispersal is unable for it. Although we use the terms ‘adult’ and ‘larva’, these terms can be replaced by others such as tree and seed, as our model is general and can describe many sessile and sedentary organisms in many kinds of habitats.

7.3 The model

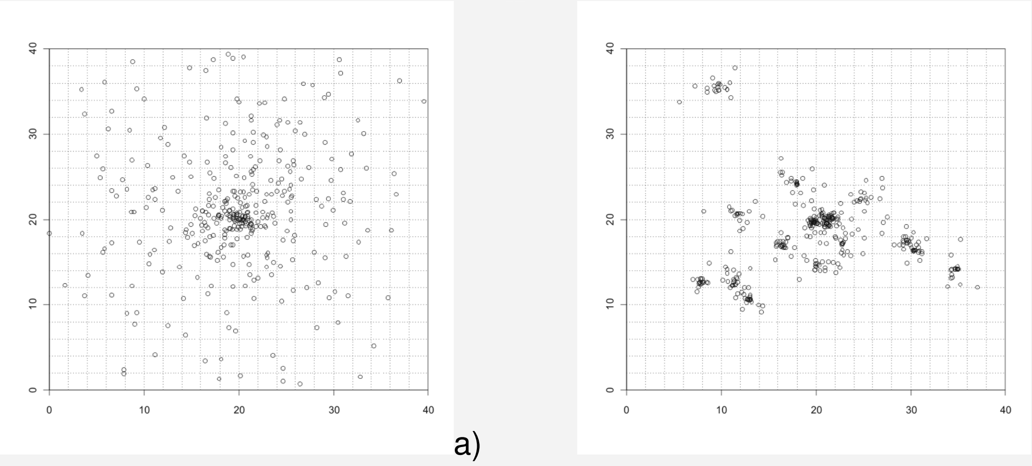
The model space is represented by a rectangular, two-dimensional grid of 50×50 cells. To avoid boundary effects we use periodic boundary conditions, i.e. simulation is performed on a torus around which all the borders of the grid are warped. Each cell is equivalent to a site which can support a total number of individuals corresponding to the local carrying capacity K_C of the site.

7.3.1 Homogeneous versus heterogeneous environments

If all the sites have the same local carrying capacity, we refer to a homogenous environment. If the local carrying capacity changes from site to site we refer to a heterogeneous environment. For simplicity, we distinguish only two different site types: “high capacity sites” where $K_C = K_H$ and “low capacity sites” where $K_C = K_L$. In such a heterogeneous environment the carrying capacity of each site is randomly chosen with the probability p of being K_H and $1-p$ of being K_L and remains constant during a simulation.

7.3.2 Species definition

To focus on the effects of the dispersal pattern on diversity, all the species in our model have the same competitive strength and mean reproductive rate (number of larvae, see constant vs. fluctuating environment below) . We do not assume any trade-offs or disturbance events. Differences in the species traits consist in the mean dispersal distance D_S before settlement (see below). As we consider sessile species, we assume larvae to be the only dispersal stages. Further on, we distinguish between two dispersal modes: local (“isotropic clumped dispersal”) and patchy (“anisotropic clumped dispersal”). The modes are described below in more detail.



a) b)

Figure 9, Examples of the spatial dispersal pattern generated by the different dispersal strategies. a) local (isotropic clumped) dispersal, b) patchy (anisotropic clumped) dispersal. Each picture shows the final larvae pattern after the dispersal of 20 × 20 larvae originating from the centre.

7.3.3 Local dispersal

Commonly used dispersal kernels are exponential or Gaussian distributions (Nathan and Muller-Landau, 2000). In our model the direction α of dispersal was randomly chosen (0°-359°) and the actual distance d was determined according to d=D_S*-ln(p) with p being a random number evenly distributed in the interval [0..1]. The Larva settles at the position given by the relative polar coordinate P(d, α). An example of a resulting larvae distribution pattern emerging from this dispersal mode is shown in Figure 9a.

7.3.4 Patchy dispersal

Here all the larvae of a species at a particular site are considered as a group. For this group the centre of dispersal is chosen using the same dispersal kernel as above. Then, all the larvae of this group are distributed around this centre according to a kernel with a perimeter of 2 cells. This results in a patchy aggregation of larvae. The resulting dispersal pattern can be seen in Figure 9b.

7.3.5 Local dynamics

In each time step an adult individual of any species produces *L* larvae (see below). After reproduction larvae dispersed, resulting in a local larvae pool of different species for each cell (see dispersal). Adult individuals die with a fixed probability $p_d = 0.2$ resulting in free positions in a cell. All larvae in a local larvae pool compete for empty positions described by lottery competition. For each empty position a larva is randomly taken from the local pool, which reduces the number within the pool. This is repeated until either the number of established individuals reaches K_C or there are no larvae left. Larvae that are unable to establish are discarded.

7.3.6 Constant versus fluctuating environments

The carrying capacities of the grid cells remained fixed in all cases. Environmental fluctuations are assumed to affect the reproduction success of established individuals. Therefore *L* was set to L=1 and not modified in constant environments. In fluctuating environments *L* was randomly chosen to be L=0, L=1 or L=2 for each cell and in each time step.

7.3.7 Initial conditions

The first quarter of the grid was initially filled with a random community consisting of all available species. For each cell in this area, one of the species was randomly assigned and occupied all the available space in this cell. All simulations were allowed to run either until a certain final time or were stopped when either all species had gone extinct or just one had survived. In both cases it was assumed that the species composition would not change again until the final time step was reached.

7.4 Computer simulation experiments

In the first experiment we implemented a neutral model to see if there is a general difference between local and patchy dispersal. We assumed 15 species with identical traits all using firstly local dispersal and secondly patchy dispersal. The species had an intermediate dispersal distance (D_S=5). In this experiment we assumed both homogenous (K_H=5, K_L=5) and heterogeneous (K_H=7, K_L=3 and p=0.5) space. The experiment ran until time step 1.5*10^5 with 200 replicate runs.

In a second experiment we again assumed 15 species but now with different dispersal distances ranging from 1 to 15 cells in steps of 1. As shown by Hovestadt et al. (2000) this reflects different competitive abilities of the species. In this experiment we used the same environmental scenarios like in the first experiment. Additionally, we tested both temporally constant and fluctuating environments. Maximal runtime was 2*10^5 time steps and we computed 200 replicates

The first two experiments concentrated on the impact of patchy and local dispersal on community structure separately, that is all species used either local or patchy dispersal. In the third experiment we studied the competition between these two dispersal modes. First the local dispersal was rather short-ranged (D_S=2) and the patchy dispersal was long-ranged (D_S=10), then the dispersal distances were exchanged. To account for the influence of spatial heterogeneity we used a gradient from homogeneous to heterogeneous space by setting K_H=i and K_L=10-K_H with i running from 5 to 10 and p=0.5 such that the total amount of habitat was equal for all simulations. Again we tested temporally constant and fluctuating environments. Due to the low species number maximal runtime was set to 0.75*10^5 time steps and 100 replicate runs.

7.5 Results

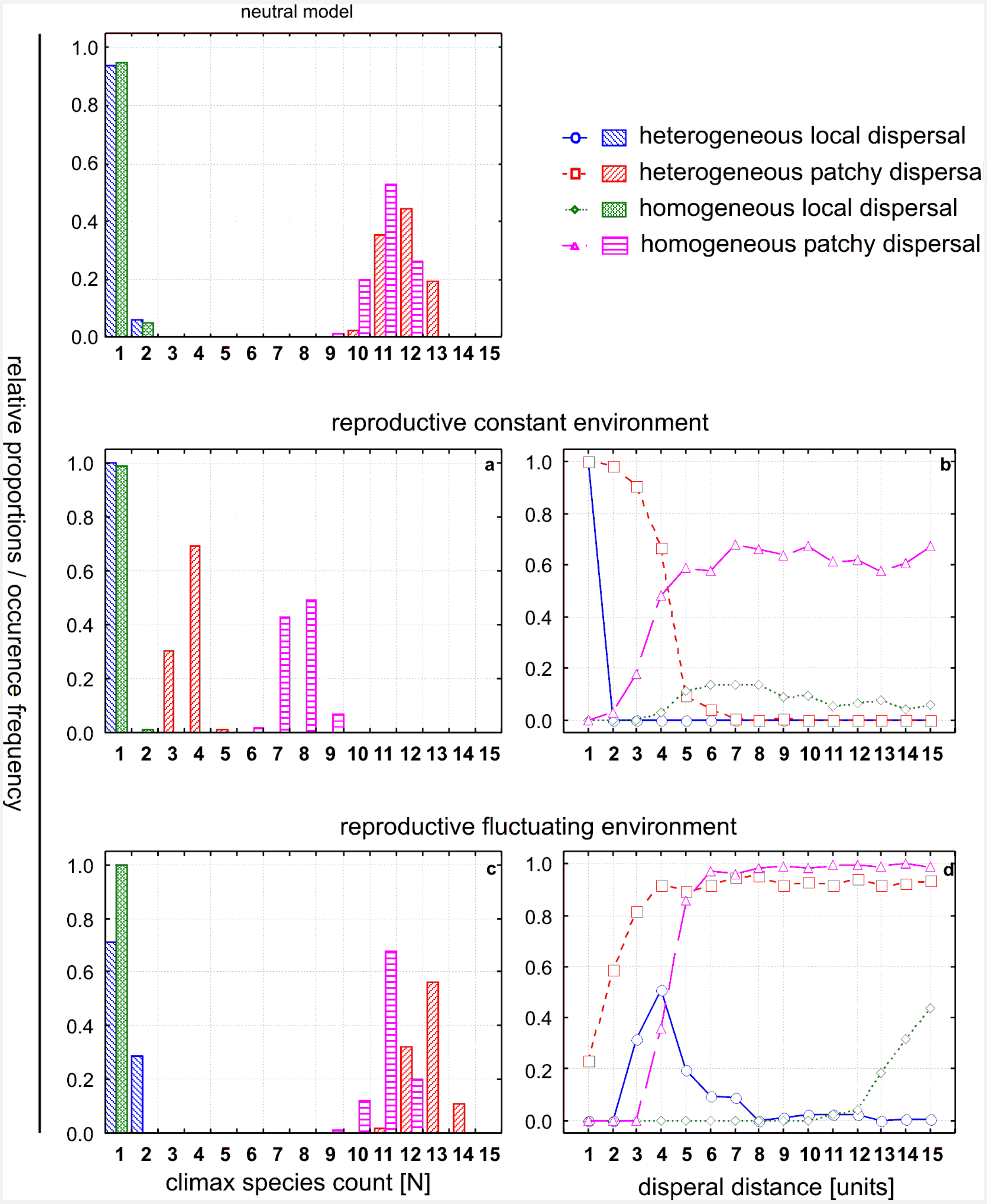


Figure 10, Species count and survival of single species, depending on different environments and species traits. Left: probability (y-axis) of n species (x-axis) survival after 100 replicate runs ($T_{max}=2*10^5$). Right: probability of survival until the climax is reached (y-axis) for species i (i=1-15).

7.5.1 Experiment 1 (neutral model)

Figure 10 shows the proportions of species in the climax stage. Nearly all runs with local dispersal ended in single species communities (Figure 10). Mean convergence time ΔT_C into a single species system was $\Delta T_C(D_S=5,\text{hom}) \sim 0.67*10^5$ (±0.28) and $\Delta T_C(D_S=5,\text{het}) \sim 0.66*10^5$ (±0.28) time steps. Simulations with local dispersal and different dispersal distances showed that ΔT_C could be described by a power law: $\Delta T_C(\text{hom}) \sim 0.89*10^5 * D_S^{-0.084}$ ($r^2=0.41$) and $\Delta T_C(\text{het}) \sim 0.86*10^5 * D_S^{-0.269}$ ($r^2=0.81$). See also Figure 11 for a comparison of the species extinction speed. Assuming patchy dispersal, 10–13 species were able to coexist at least for $1.5 * 10^5$ time steps.

7.5.2 Experiment 2 (different mean dispersal distances, single dispersal mode)

Figure 10a shows that neither of the local dispersal strategies led to a notable coexistence of several species. In contrast, the patchy dispersal strategies led to the coexistence of several species in all cases: In a constant environment this dispersal strategy allowed 7–9 species (homogeneous environment) or 3–4 species (heterogeneous environment) to coexist. In a fluctuating environment even more species coexisted: about 10-12 in the homogeneous and 12-14 in the heterogeneous environment (Figure 10c). In the homogeneous environment the surviving species were intermediate to long-range dispersers (Figure 10b). In the heterogeneous environment short-range dispersers (Figure 10d). The clear ranking of abundance according to dispersal distance in the heterogeneous environment was not found in the homogeneous environment albeit the general failure of short range dispersers.

7.5.3 Experiment 3 (different mean dispersal distances and two dispersal modes)

Depending on the environmental conditions local or global dispersal could coexist with patchy dispersal. Table 1 lists the relative abundances of both dispersal strategies in different environments and different degrees of spatial heterogeneity. In constant environments coexistence between global long- and patchy short-range dispersal was possible when space was sufficiently heterogeneous. In reproductively fluctuating environments coexistence between these dispersal modes was possible under strong spatial heterogeneity. Coexistence between local short- and patchy long-range dispersal was possible when space was homogeneous.

environment	competing dispersal strategies local / patchy		mean relative abundance after $0.75*10^5$ time steps [N=100]											
constant	long	short	1.00		1.00		1.00		0.88	0.12	0.79	0.21	0.71	0.29
	short	long	1.00		1.00		1.00		1.00		1.00		1.00	
fluctuating	long	short	1.00		1.00		1.00		1.00		1.00		0.93	0.07
	short	long	0.72	0.28	0.79	0.21	0.97	0.03	1.00		1.00		1.00	
heterogeneity (high:low capacity)			5:5		6:4		7:3		8:2		9:1		10:0	

Table 1, Relative abundances of competing dispersal strategies after $0.75*10^5$ time steps [N=100]. Depending on spatial heterogeneity and favourable dispersal distance, coexistence between isotropic and anisotropic dispersal is possible. Scenarios where coexistence occurred are shaded in grey.

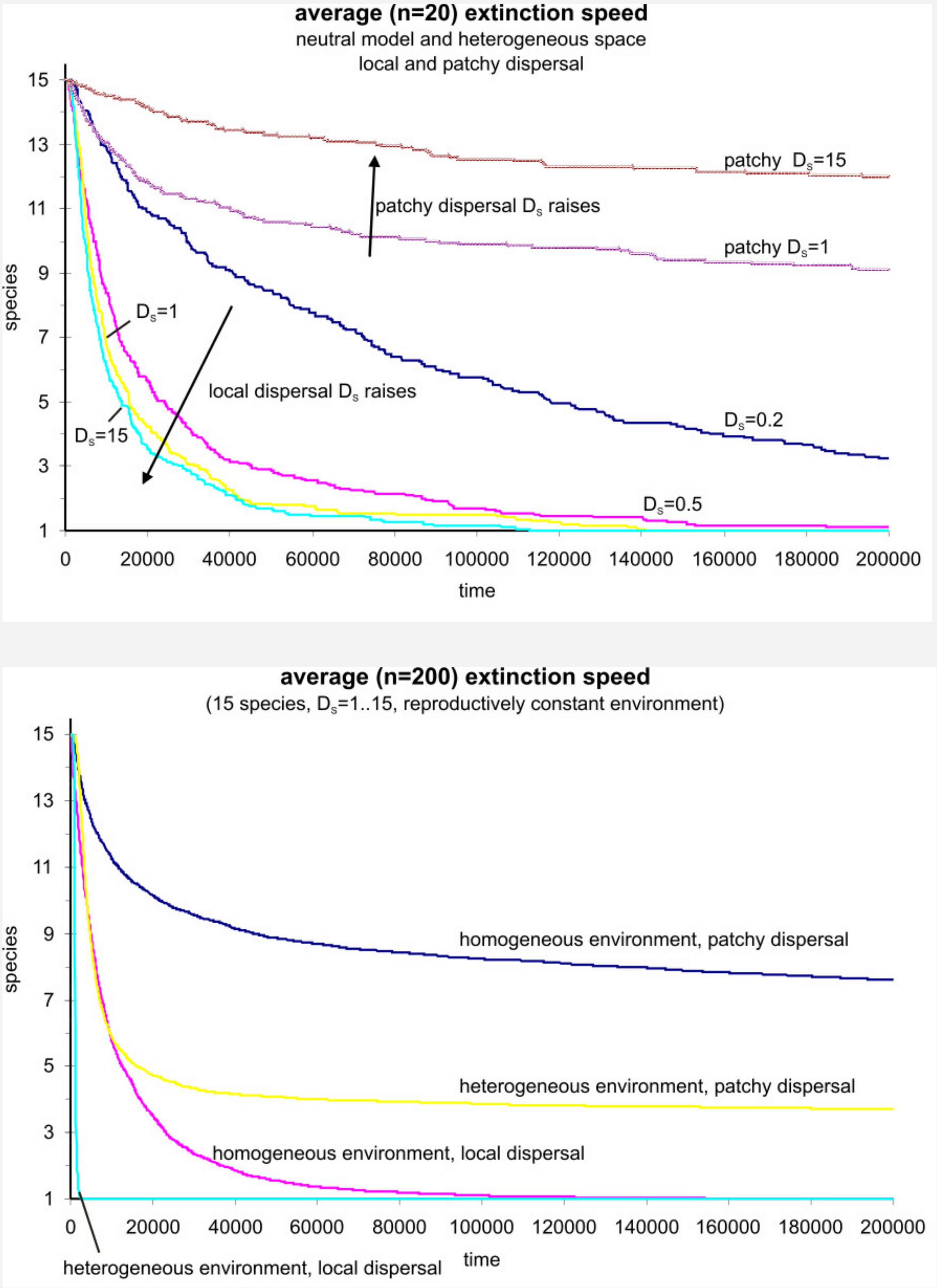


Figure 11, Comparison of the extinction speed of isotropic versus anisotropic dispersal. a) for Experiment 1 in a heterogeneous environment (compare Figure 10a). Note that higher dispersal distances accelerate the extinction speed for isotropic modes, whereas anisotropic clumped dispersal the extinction decelerates the speed (see arrows). b) for Experiment 2 in a constant environment (compare Figure 10a)

7.6 Discussion

Although patchy dispersal is known from field observations (e.g. dispersal as a group of larvae), previous modelling approaches considered mainly local dispersal as source of clustering in the context of species coexistence (e.g. Warren and Topping 2004). As both dispersal modes cause spatial aggregation, the comparison between patchy and local dispersal in terms of their potential to mediate coexistence is especially interesting and helpful for understanding coexistence mechanisms.

In our simulation experiments, patchy dispersal resulted in species-rich communities even under conditions that resulted in single species systems when local dispersal was assumed. This was true both within the neutral model assumption (experiment 1; for this assumption see also Chave, 2004) and the successional model assumption (experiment 2; for this assumption see also Hovestadt et al. 2000).

In contrast to local dispersal, patchy dispersal enabled the long-term coexistence of 1/4 or up to 3/4 of all competing species (Figure 10 a,c). Note that the exclusion of species is due to stochastic events in the neutral model, but due to competitive inferiority (based on the different dispersal distances) in the successional model. These competitive differences also explain the different likelihoods to occur in the climax community for the different dispersal distances respectively species (Figure 10b and c). The associated dispersal distances of coexisting species tally with theoretical studies on the evolution of dispersal. In this context spatial heterogeneity discourages dispersal, i.e. species with patchy short-range dispersal coexisted in spatially heterogeneous environments (Figure 10b), whereas spatial homogeneity or fluctuating reproduction encourages dispersal (Hamilton and May, 1977; Hovestadt et al., 2000), i.e. species with patchy long-range dispersal coexisted in these environments (Figure 10d). The advantage of particular dispersal distances reflects the fact that patchy dispersal can partially utilize the competitive advantages of the appropriate dispersal distance in the corresponding environment but that there are additional mechanisms preventing the collapse into a single-species system.

In general*, neutral* models can be expected to show random extinction of all but one species (Tilman, 1994; Hubbell, 2001). If a species by chance becomes rarer, it will have fewer opportunities to win in the next time step and so forth as all species are assumed to be equal. Hence its abundance is spiralling down to extinction and coexistence is non-stable *sensu* Chesson (2000 a). Figure 11a exemplifies the extinction speed of a neutral community of 15 species with identical traits in a heterogeneous environment for different dispersal modes and distances. With isotropic dispersal higher dispersal distances lead to higher species mixing, thus stronger interspecific competition and consequently a faster extinction. Interestingly with patchy dispersal increasing dispersal distances decelerate the extinction process. In order to enable similar coexistence times, local dispersal would need to be extremely local (e.g. "clumped", D_S<0.1, i.e. virtually no dispersal). The effects of patchy dispersal are able to slow down the random exclusion of species in a neutral community to such an extent that it virtually allows coexistence up to evolutionary timescales (approximated e.g. for the homogeneous environment about $3.7 \cdot 10^{12}$ time steps, Figure 11).

The main difference between local and patchy dispersal is that patchy dispersal decouples the area where the larvae compete from the adult individual whereas local dispersal ensures that this area is always centred around the adult. Thus patchy dispersal decouples the larvae aggregation from the source. This has several important consequences.

First, similar to the aggregation model of coexistence (Shorrocks et al., 1979) the concentration of larvae leaves some sites free which can be utilized by other competitors. This concentration of conspecific competitors represents a strong dispersal limitation and has a stabilizing effect as it increases intraspecific relative to interspecific interactions (Chesson, 2000 a).

Furthermore, local aggregation can cause competitive displacement due to a 'phalanx growth' mechanism as demonstrated by Bolker and Pacala (1999). This mechanism is based on the exclusion of heterospecifics due to high self-recruitment, allowing a single species to seize habitats and displace competitors. In order to work, this process demands either a high number of larvae continuously placed around an adult (e.g. by local dispersal) or competetive differences. As patchy dispersal decouples the site where larvae compete from their origin, there is no continuous rain of larvae at the same place and consequently no high rate of self-recruitment. Therefore patchy dispersal hinders a phalanx-growth mechanism and weakens the displacement of species.

This effect is similar to the effect of positive growth-density covariance Chesson and colleagues found for intraspecific aggregation due to local dispersal under the presence of favourable habitats for particular species (Chesson, 2000 b; Chesson and Neuhauser, 2002; Snyder and Chesson, 2003). Such a covariance occurs when limited dispersal allows rare species to build up densities in favourable areas, resulting in an increase of their overall per capita growth (Amarasaekare, 2003). It measures the degree to which competing species can accumulate in favourable locations (Snyder and Chesson, 2004). The key process for a positive growth-density covariance is a dispersal strategy which permits the establishment of a group of new individuals in suitable environments. This can be the result of local aggregation of larvae around an adult due to local isotropic dispersal in environments with species specific favourable habitats (Chesson, 2000 b; Amarasaekare, 2003; Snyder and Chesson, 2003). However, this can also be the result of a dispersal strategy where the aggregation of larvae causes temporarily suitable habitats due to the absence of competitors. Thus it depends in principle neither on local dispersal nor on species specific favourable habitat but solely on the aggregation of larvae at a certain suitable place.

These mechanisms also work in the *successional* model, where species have competitive differences and hierarchies caused by different dispersal distances (Hovestadt et al., 2000). With isotropic dispersal, only one species could survive (e.g. the local disperser in spatially heterogeneous constant environments or the global disperser in homogenous fluctuating environments (Figure 10c and e), which tallies with other theoretical studies (Hamilton and May, 1977; Hovestadt et al., 2000). With patchy dispersal, coexistence of several species was possible. An interesting result is that more species could coexist in the homogeneous than in the heterogeneous environment irrespective of the temporal fluctuations (Figure 10 b,d). As in the homogeneous environment all patches are equal, short dispersal distances are not favoured and the competitive exclusion is weaker. Consequently more species are able to coexist. The same is true with respect to long dispersal distances in environments with fluctuating reproduction success.

Coexistence between local and patchy dispersal in competition was only possible when patchy dispersal had the superior dispersal distance in the corresponding environment, similar to the classic colonisation-competition trade-off (Chave et al., 2002; Amarasaekare, 2003; Kneitel and Chase, 2004). The reason is that isotropic dispersal is a better strategy to search an area for favourable habitats. Such dispersers spread their larvae broadly such that sites which are free of competitors (e.g. due to patchy dispersal) can be quickly colonized.

Given these advantages of isotropic dispersal, why should anisotropic (patchy) dispersal exists in nature? Introducing additional dispersal traits such as the batch size and the dispersal patch radius, patchy dispersal allows a variety of further trade-offs both within the dispersal traits themselves and with respect to other life-history traits. For example, it may be much more effective to protect a group of larvae or seeds in one dispersing unit like a capsule or cone than to protect a single seed with the same effect.

Frequency-dependent predation may also discourage isotropic dispersal, as it leads to a more frequent predator-prey encounter probability (Gendron, 1987). Schooling is a common strategy to minimize an individual's risk of falling prey, and similar effects can be assumed for patchily distributed larvae.

Finally, it should be questioned whether ideal isotropic dispersal is possible in nature as most habitats are subject to some kind of directional phenomena (Levine, 2003). The potential of patchy dispersal to foster species coexistence demonstrates that dispersal strategies and the subsequent spatial pattern can greatly influence species richness in communities. Our results suggest that besides the dispersal distance, the variety of other dispersal traits offers far more possibilities for spatial aggregation and thus for species coexistence than presently considered and investigated.

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8. How to survive as a pioneer species in the Antarctic benthos

How to survive as a pioneer species in the Antarctic benthos: Minimum dispersal distance as a function of lifetime and disturbance

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8.1 Abstract

Very few details exist concerning the dispersal traits of Antarctic species and dispersal distances in particular are mostly unknown. Especially the general low number of mesoplanktonic larvae has caught attention, leading to the formulation of Thorson's rule. From this concept, originally concerning only trophic aspects, sometimes a reduced dispersal distance is deduced. Using a generic simulation model we show that in a benthic habitat exposed to iceberg scouring even short dispersal phases of few hours are sufficient for a pioneer species to persist. This is very surprising for a pioneer species that should be able to disperse widely and colonise distant disturbed areas that are free of superior competitors. Our model revealed that the reason for this is the non-linear dependence of the dispersal distance on the disturbance regime and on species longevity. Thus, it is the combined effect of life history and disturbance traits which is important here: a sufficiently high disturbance frequency due to iceberg scouring and a long individual lifetime due to the low temperature decrease minimum dispersal distances required for persistence and thus coexistence and present an additional explanation for the relative rarity of planktonic larvae.

8.2 Introduction

The Weddell Sea benthos is relatively diverse (Clarke and Johnston 2003; Gutt et al. 2004), shaped by disturbance events due to scouring icebergs, which form one characteristic of the system (Arntz et al. 1994; Brown et al. 2004; Gutt and Piepenburg 2003; Gutt et al. 1996). Recent field work on the succession after iceberg scouring revealed unpredictable primary succession stages ending in a local climax-like community in a site (Ragua-Gil et al. 2004; Teixido et al. 2004). Succession is slow, possibly over hundreds of years (Gutt and Starmans 2001). Several life history traits determine such a succession of which dispersal is one of the most important (Bolker and Pacala 1999). In terrestrial systems dispersal or dispersal shadows can be measured by direct observation, tagging, traps and molecular markers. In aquatic systems the methods theoretically work in the same way. However, the reduced accessibility of these systems (due to visibility, depth and remoteness) make the application difficult when a relatively high spatial and temporal resolution is required. This is especially the case when tiny mesoplanktonic larvae, as the predominant dispersal form among marine species (Muko and Iwasa 2000; Roughgarden et al. 1988), have to be considered. Generally, larvae may stay in the water column for less than one minute or have an extended pelagic phase of up to several months (Largier 2003; Shanks et al. 2003). Although the dispersal distance seems to be correlated with the length of the pelagic phase (Shanks et al. 2003), recent work showed that larvae often settle close to their parents, regardless of a long pelagic phase (Fisher 2005; Jones et al. 2005; Todd 1998). Nevertheless, almost nothing is known about the actual dispersal distances of most marine species (Grantham et al. 2003). Summarising the current literature on pelagic larvae in Antarctic waters (see Bhaud et al. 1999; Stanwell-Smith et al. 1999; Shreeve and Peck 1995; Absher et al. 2003 and Sewell 2005), larval density in the austral summer is seemingly low. A decline in pelagic dispersal stages with indirect development and increase in lecithotrophic larvae and direct development with higher latitudes is known as “Thorson’s rule” (Mileikovsky 1971). This is often supposed to reduce the potential dispersal distance simply by an assumed shorter dispersal time for lecithotrophic larvae and direct development. The ecological constraints leading to such shifts are not well understood, but recently Thatje et al. (2005) attempted to link these to the glacial history of Antarctica. However it is not entirely clear, how disturbance regime and environmental conditions may have influenced the life history traits of Antarctic species.

Especially the combined effects of the disturbance regime and lifespan on the dispersal traits are uncertain. The interplay of these two factors is of great interest as they influence the coexistence of species and communities. In the Antarctic the constant low temperatures are considered to slow down life in the majority of species (Arntz et al. 1994), but there are also some normal or comparably fast growing forms (Barnes 1995; Brey et al. 1998; Kowalke et al. 2001). As longevity fosters the local competitive ability of sessile organisms, it can cause the dispersal distance to decline. This is the usually assumed trade-off between colonisation and competitive ability to ensure the regional coexistence of species (Tilman 1994). But qualitative and quantitative knowledge about the functional form of this trade-off and about the dependence on the disturbance regime are lacking.

The main aim of this study is to investigate the combined effects of the dispersion of larvae and the longevity of adults on the persistence of a population of pioneers under the influence of disturbances. How far must a pioneer species disperse under a given disturbance regime to persist in the competition with a superior competitor? How do both the lifetime of the organisms and the disturbance rate influence this minimum necessary dispersal distance for persistence? Experimental field work to answer these questions is nearly impossible to carry out. Computer simulation models provide an alternative way. We use a spatially explicit simulation model to study these questions and apply the results to the benthic assemblages of the Weddell Sea. In particular, we want to find out whether the general trend of dispersal distances supports or contradicts Thorson's rule.

8.3 Methods

The dispersal distance being sufficient to reach at least the closest suitable habitat should be a function of the process that generates such habitats, in other words of the disturbance regime. Therefore we first analysed the spacing of disturbed areas in dependency on the disturbance regime. In a simulation model we determined the mean distance between the borders (D_{BD}) of two nearest neighbouring disturbed areas. Assuming circular disturbances allowed us to calculate D_{BD} using the distance from centre to centre (D_C) and the radius r of the disturbances. Therefore first D_C had to be calculated in dependency on the disturbance frequency.

In a second simulation we determined the minimum dispersal distance (d_{min}) for a pioneer species to persist and coexist with a superior competitor. This was done again for different disturbance regimes and in respect to the lifespan of the pioneer. This enabled us to relate d_{min} and D_{BD} (respectively the disturbance regime).

In a third step we then applied our theoretical results to Antarctic pioneer assemblages. We estimated a minimum dispersal distances a pioneer species needs to persist locally on the continental shelf under current disturbance conditions. For this we used knowledge about disturbance regimes and species life history traits of benthic assemblages composed of sedentary animals derived from the literature.

8.4 Computer simulations

8.4.1 Habitat spacing

To compute the distance from border to border (D_{BD}) first the distance from centre to centre (D_C) of two nearest neighbouring disturbances must be determined. To do this a number N [per time step] of circular disturbances of a given radius r were placed randomly within a square area (1 unit length) and D_C was measured. This was done for different N (N = 2, 3, 4, 6, 8, 10, 14, 18, 24, 30, 36, 44, 50, 60, 80, 100) and with each 1,000 replicates. D_C only depends on the disturbance frequency N and a curve fitting allowed us to compute D_C for any given N. The mean distance from border to border (D_{BD}) depends on D_C and the disturbance radius r and can be computed as

$$D_{BD}(N;r) = D_C(N) - 2*r \qquad [1]$$

Note that both D_{BD} and D_C are relative to the box scale. As $D_C(N)$ is constant for a fixed N, $D_{BD}(N;r)$ is a strait falling line with a slope of –2.

8.5 Minimum dispersal distance of a pioneer species (d_{min})

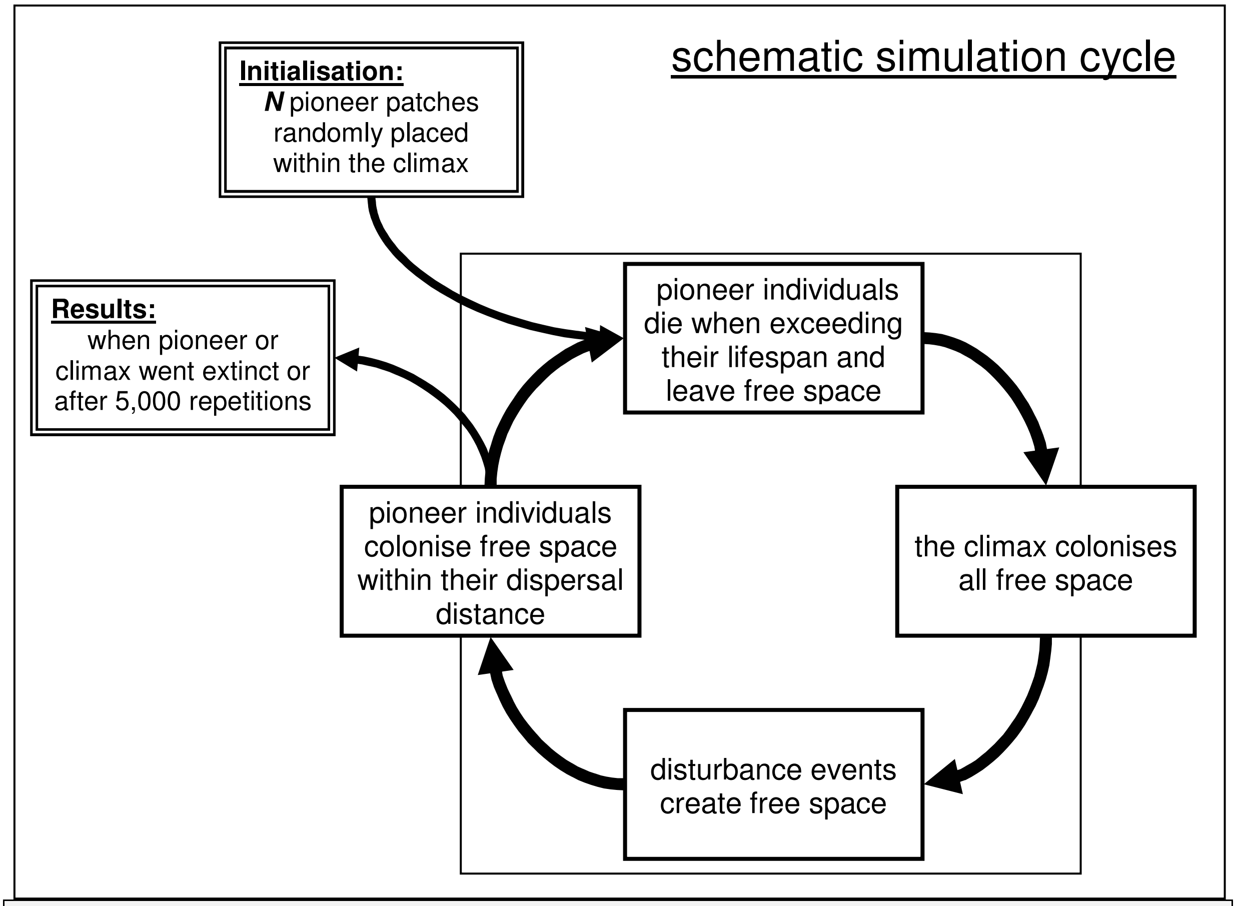

Figure 12, Model simulation cycle. After the initialisation the simulation is performed for 5,000 time steps or until a break condition.

To determine the minimum dispersal distance for a pioneer species to persist and coexist with a superior competitor a grid-based model with periodic boundary conditions was used. This means that any object leaving the grid on one side re-enters the grid on the opposite side. This avoids disadvantages for individuals at the borders. The spatial dimension of the grid was 100x100 grid cells. A cell could be inhabited by either a pioneer species, defined by its dispersal distance (measured in grid cells) and lifespan (in time steps), or the climax assemblage, characterised by its competitive superiority (once the climax assemblage has taken over a position it will remain there unless the space is opened by disturbance). Figure 12 shows a flowchart of the simulation cycle. Within one simulation the grid was initially filled with

N randomly placed circular patches with the radius *r*, colonised by the pioneer species. The remaining cells were assigned to the climax. In each of the simulated time steps the age of any pioneer individual increased. Once it reached its maximum age it died and the grid cell became empty. Subsequently, all empty cells (empty due either to the death of the pioneers or to not having been colonised) were overgrown by the climax because of its superiority. Then disturbance was simulated by a given number *N* of circular disturbances with the radius *r*, randomly placed over the entire grid. Affected cells were cleared of any inhabitants. This free space was potentially colonised by the recruits (of age 0) of any pioneer individual when within its dispersal range. For simplicity reason we assumed dispersal to be equal in all directions and that the amount of larvae was not limited. Thus any available habitat within a circle according to the dispersal distance could be colonised by the pioneer.

These steps were repeated either until the pioneer or the climax assemblage had gone extinct or 5,000 steps had been executed and both pioneer and climax still coexisted. Simulations typically reached equilibrium within fewer than 100 time steps. The minimum dispersal distance for the persistence of the pioneer was determined by simulations with dispersal distances ranging from 1 (local) to 50 cells (quasi global dispersal) in two cell steps. These procedures were repeated with 100 replicates each. These calculations were repeated for varying disturbance regimes (function of radius and frequency) and lifespans (1, 2, 4, 8, 16, 32, 64) of the pioneer.

8.6 Results

8.6.1 Habitat spacing

Figure 13, Distance D_C from centre to centre of the nearest disturbance for different disturbance counts per time step. The distance decreases hyperbolically with increasing N.

Figure 13 shows the mean and standard deviation for the empirical determined values of D_C for different N. $D_c(N)$ has the form of a hyperbola. Curve fitting resulted in the following formula:

$$D_c(N) = (0.681 * N^{-0.557}) \quad [r^2>0.99,\ N\text{=disturbance frequency}] \qquad [2]$$

8.6.2 Minimum dispersal distance

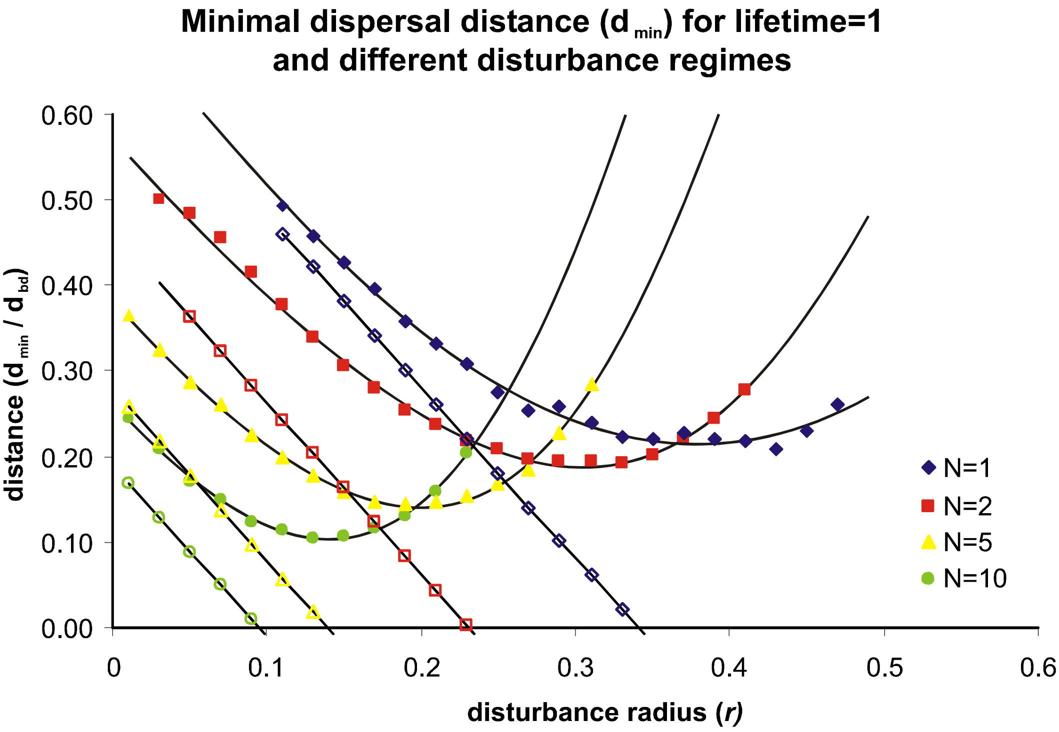

Figure 14, Influence of the disturbance regime on the dispersal distance d_{min} for a fixed lifespan. Different symbols and shades represent different disturbance frequencies (N=1, 2, 5 and 10), filled symbols are model results whereas open symbols show the according D_{BD}. Also regressions are shown where the straight lines show the distance D_{BD} for a regime and the curves the corresponding minimal necessary dispersal distance d_{min}. (D_{BD} calculated according to formula [1] and [2] for lifetime=1).

The closed symbols in Figure 13 show the minimum dispersal distance (d_{min}) of the pioneer needed for the coexistence with a superior climax as a function of the disturbance radius (x-axis) and for different disturbance frequencies (different symbols). The open symbols represent the according distance D_{BD} derived from formula 1 and 2. Figure 13 shows only the data for lifetime=1 but other lifetimes result in similar pictures although with shorter distances (see below) and the general features are the same. For better readability the symbols are connected by fitted lines (see appendix for detailed values).

d_{min} is always higher than the according D_{BD} (Figure 13). The curves of d_{min} are u-shaped and opened upwards. For small disturbance radii d_{min} first progresses nearly parallel with D_{BD} and decreases with increasing disturbance radius. With further decreasing D_{BD} the deviation between D_{BD} and d_{min} increases. When D_{BD} approaches zero (disturbed areas start to overlap), d_{min} raises until a value around d_{min}~0.35. Above these value no coexistence occurred in the model because both the pioneer and the climax went extinct. For regression, coefficients and goodness of fit for all parameter sets see Table 2 in the appendix.

8.6.3 Dependency of the minimum dispersal distance on longevity

Figure 15 shows the influence of lifetime (*lt*) and disturbance on the minimal dispersal distance (d_{min}) allowing the pioneer to coexist with the climax. Exemplarily Figure 15a represents a low disturbance frequency (N=1), whereas Figure 15b shows a high disturbance frequency (N=10). Analysis of the results showed that the dependency of d_{min} on lifetime can be described by:

$$d_{min}(lt) = d_{min\,1} * lt^{b} \qquad [d_{min\,1}=d_{min} \text{ for lifetime 1; } lt\text{=lifetime}] \qquad [3]$$

Note that, although the functional form is generally valid, d_{min1} depends on the particular disturbance regime as shown above. The exponent b determines the form of the curve. For light to moderate disturbance regimes, formula 3 is in a good agreement with the simulation results (r^2>0.95, see Table 3 appendix) and for these cases *b* is in a range between 0.5 and 0.7. The narrow range means that d_{min} is approximately halved when lifetime is prolonged by three to four times. The predictability (r^2 values) was better with longer lifetimes than with very short ones as well as for small disturbance diameters. For details see Table 3 in the appendix.

Figure 15, Influence of lifetime on dispersal distance d_{min} under different disturbance regimes (frequency and radius): a) low disturbance frequency, b) high disturbance frequency. Generally the dispersal distance decreases with increasing lifetime. Under a severe regime this might not hold, only long dispersal will allow survival (e.g. 4b, r=0.16). Also shown are the according regressions $d_{min}=d_{min1}*lt^{-b}$; see Table 3 for details.

8.7 Application of the results to the benthic assemblages of the Weddell Sea

The Antarctic shelf is subject to disturbance events by grounding icebergs (Gutt et al. 1996). Based on the analysis of underwater video transects, Gutt and Starmans (2001) determined the disturbance regime for different locations in Antarctica. One region ('large iceberg bank') has an area of 300 km² of which approximately 37.3 % had been disturbed at last once in the last 15 years. An other region ('level plateau') contained less recently disturbed areas (7.3% see Gutt and Starmans 2001 for details). Assuming a typical iceberg scour mark to be 500 m long and 120 m wide (see data in Hohmann 2002) this is equivalent to a total of 1,865 grounding events in this period or on average 124 events per year! Applying the same approach to the 'level plateau' region leads to only 24 events per year. These frequencies result in a mean distance between the centres of disturbed areas of about 782 m for the large bank and 1,972 m for the plateau (based on a box width of √300 km²~17 km and $D_c(124) = 0.046$ and $D_c(24) = 0.116$ respectively; see Eq. 2).

We want to apply our theoretical results to the benthic assemblages of the Antarctic. How far must a pioneer species disperse under the disturbance regime of the 'large iceberg bank' or the 'level plateau' to persist regionally? Teixido et al. (2004) analysed the biological succession after iceberg scouring and compiled a list of key species for different recolonisation stages. Among the very first sedentary pioneer organism are various polychaetes, bryozoans, gorgonians, sponges and some ascidians. For most species no detailed data on life-history traits exist. Comparatively well known is the solitary ascidia *Molgula pendunculata* Herdmann (1881). We have chosen this species, respectively its life-history traits, as characteristic for a pioneer of the Antarctic shelf. *M. pendunculata* show an fast growth and may reach an age of 3-12 years (Kowalke et al. 2001; Kühne 1997). It is a simultaneous hermaphrodite

(Sahade et al. 1998) and is assumed to reproduce viviparously with short dispersal (Kühne 1997; Sahade et al. 1998; Svane and Young 1989).

An estimated average age of 6 years for *M. penduncutata* leads to a minimum dispersal less than $d_{min}(124)$= 266 m for the large iceberg bank and $d_{min}(24)$= 670 m for the plateau. Assuming an average current velocity of 0.05 ms^{-1} (see values for the shelf regions reported in Fahrbach et al. 1992), a dispersal phase of 90 min for the iceberg bank, respectively 225 min for the plateau, would be sufficient to cover these distances.

The later successional stages are dominated by long-living species with budding or brooding behaviour (Teixido et al. 2004, Teixido *in press*). Such a species with an assumed age of 200 years needs a minimum dispersal of less than $d_{min}(124)$= 31 m on the bank and $d_{min}(24)$= 79 m on the plateau if dependend on recruitment in recently disturbed areas. These distances can easily be covered by budding or brooding species (Grantham et al. 2003) with a dispersal phase of a few minutes to less than half an hour.

8.8 Discussion

8.8.1 The Simulation Model

Using a simulation model we studied first the mean spacing of disturbed areas in a landscape as a function of a disturbance regime (frequency and size/radius). In a second step we showed that the minimum dispersal distance d_{min} needed for the persistence and the coexistence of a pioneer species with a superior climax assemblage, is strongly related to the mean spacing of disturbed areas and thus to the disturbance regime.

At low disturbance rates the dispersal distance d_{min} needed for persistence is slightly higher than the mean distance between the borders of nearest disturbed areas D_{BD} (Figure 14). The parallel progression of d_{min} and D_{BD} for small disturbance radii is conspicuous. With increasing size (or frequency) of the disturbances, d_{min} falls quasi parallel to D_{BD} as the disturbed areas become closer to each other and dispersal from disturbance to disturbance is possible with a smaller dispersal distance. d_{min} reaches its minimum when D_{BD} approaches zero, in other words, when the disturbances are so frequent that the disturbed areas start to overlap statistically. A further increasing disturbance regime, however, stops the decrease in d_{min} and leads to an increase again. This is due to the resulting landscape dynamics and the high mortality risk that demand higher dispersal distances for persistence of any species (Johst et al. 2002). At a certain disturbance intensity, the whole area is completely disturbed each time step and neither species can persist.

The resulting u-shaped form of d_{min} brings together theoretical knowledge of species interactions and species persistence in dynamic landscapes. With weak disturbances, competition among species demands a high dispersal potential or other trade-offs for pioneers to be able to coexist with a superior species (Durrett and Levin 1998; Snyder and Chesson 2003).

Besides the disturbance regime, the second determinant of d_{min} is the species lifetime. As expected, with increasing lifetime d_{min} decreases (Figure 15). However, two things are important. First, the trade-off is nonlinear and has a hyperbolic form. This hyperbolic relationship means that a species can survive with halved dispersal distance if it has a lifespan that is three to four times longer. Furthermore, the greatest relative differences in dispersal distance exist between short-lived species. The older species become, the smaller the differences in required dispersal distances can be and, consequently, the less important the potential for far dispersal becomes (Figure 15a). Secondly, the dependence of dispersal distance on the lifetime is strong when the disturbance regime is light to moderate (Figure 15a) but breaks down when the regime is too severe (Figure 15b). Under a strong disturbance regime d_{min} is generally low and may not decrease with lifetime – instead it is constant or even increases (Figure 15b, e.g. r=0.16).

The absolute competitive superiority of the climax assemblage, especially its ability to acquire all the space not colonised by the pioneer, regardless of how far it is from any climax cell is a very rigorous assumptions. If the competitive strength of the climax species is weaker, a smaller dispersal distance than our predicted d_{min} would allow persistence. Furthermore, iceberg scours are rectangular rather than circular. However a circle has the smallest diameter to area relationship of all geometric figures. Disturbances of the same area but of a different shape would be closer together, thus requiring less dispersal.

For the 'large iceberg bank' region with frequent scouring the order of magnitude calculated for the spacing of the disturbed areas correlates well with a map of scour marks of this region in Hohmann (2002). For the 'level plateau' region with infrequent scouring unfortunately no data are available, but we believe our approach is able to present the properties correctly. Therefore, our results serve as a worst-case scenario i.e. our d_{min} is an upper limit for the ecologically necessary dispersal distance. Dispersal distances higher than d_{min} are not primarily designed to ensure regional survival with minimised dispersal cost but to conform to other ecological needs.

8.8.2 Relevance for the Antarctic communities

Applying the model results to the benthic assemblages of the Weddell Sea lead to the conclusions that a dispersal phase of 1.5-4 hours is enough for a pioneer species like *M. pendunculata* to persist regionally due to the high disturbance regime and current speed. As stated above, these distances are an estimate for the upper limit distances needed for regional persistence. The actual dispersal distances could be smaller when some pioneer individuals are scattered within the climax and could serve as a stepping stone for the colonisation of distant habits. With high tidal current speeds up to 0.7 ms^{-1} (Fahrbach et al. 1992) dispersal distances up to as much as 5-10 km are possible. This might even be sufficient to explain a circumpolar distribution after the last glacial period (compare values for distance in Gutt 2000).

The pelagic larvae observed in the Antarctic waters (see introduction) belong mainly to potential pioneer phyla listed by Teixido et al. (2004). Recently Bowden (2005) published data on settlement experiments at Ryder Bay, (Antarctic Peninsula) and reviewed the currently available literature on similar experiments in Antarctic waters. However this data contains only information about the arrival of species and were conducted in shallow areas. Dispersal distances are still unknown for most species, especially for those from the continental shelf. Genetic markers may provide insights in the dispersal processes in the future but to day only theoretical approaches exists. It is commonly assumed that true pioneer species should depend on a long-range dispersal. However, due to the disturbance regime and their comparably long lifetime, the Antarctic species seem to be able to cope with rather short dispersal distances when compared with species from temperate or tropical regions. Our model does not explain why broadcasters like *Sterechinus neumayeri* have a pelagic phase of up to 120 days (Bosch et al. 1987). Even some of the key species of the later successional stages are assumed to be mid- to long-range dispersers (see Teixido et al. 2004). One reason might be simply slower development and thus longer pelagic phases in cold waters (Bosch et al. 1987). The capacity for long-range dispersal however pays off when the habitat is fragmented and strongly dynamic or strong competition occurs. Coral reefs provide a good example, as many long-living corals disperse through true mesoplanktonic larvae (Connell et al. 2004) and suitable shallow, temperate habitats are patchily distributed and limited in terms of space (Muko et al. 2001) when compared to the more or less homogeneous Antarctic shelf.

However, in the last glacial periods the Antarctic shelf was nearly completely covered with ice and suitable habitats were rare. One assumption is that species moved to the upper parts of the continental slope (for further literature see Gutt 2000). Recently Thatje et al. (2005) supposed that survival was even not possible on the slopes (due to sediment and turbidity flows) and species had to migrate down into the deep sea. However, some areas under the ice may have provided some sheltered refuges or isolated island habitats. It must be expected that such a spatial separation fostered allopatric speciation in Antarctica during glacial periods. In such fragmented but at least temporally constant environments short dispersal is advantageous (Bolker and Pacala 1999) as it allows large local stocks to be built up. But species relying only on short dispersal have to face a high risk of extinction when the environment changes (Johst et al. 2002). A bimodal means of dispersal (short- as well as long-range dispersal) would be more beneficial, as this would enable the benefits of local dispersal as well as allowing distant habitats to be explored. Species could dominate confined areas and would be still able to jump from one sheltered island to another. At the beginning of an interglacial period recolonisation of the shelf would also be fostered by an establishment in a former inaccessible habitat enabled by long distance dispersal, followed by a quick domination due to mass recruitment mediated by short dispersal. This can lead to a strong founder effect with consequences for evolution, e.g. the separation of sibling or cryptic species.

Clonal organisms like sponges have such a second dispersal mode as they are able to disperse by fragments (Jackson 1986, Teixido *in press*), e.g. lifted up by anchor ice or rafting on the fragments eroded from iceberg keels (Dayton et al. 1969; Gutt 2001). The achieved dispersal distances typically exceed the normal dispersal distances by considerable magnitudes (Jackson 1986). The importance of such an unusual mode of dispersal for biodiversity is known (Higgins et al. 2003; Jackson 1986).

The suitability of long-distance dispersal (or its absence) might explain some features the observed community structure e.g. the dominant role of clonal organisms, especially sponges (Gatti 2002), and the extinction of other groups in Antarctica. Thorson's rule, a decline in planktotrophic larvae towards the poles may be explained, at least partially, by strong seasonal primary production and a resulting food limitation in these regions or by special habitat features (Gallardo and Penchaszadeh 2001). However our results suggest that long-distance dispersal, and thus a long pelagic larval phase, is not needed for regional coexistence under current environmental conditions. In the Antarctic the disturbance regime with a moderate reoccurrence frequency leads to a mosaic of different habitats. Regular reoccurrence superposes local competition and the relative proximity of habitats possibly eliminates the need for long-distance dispersal. Thus our results may present an additional explanation for the relative rarity of planktonic larvae in the Weddell Sea.

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8.9 Appendix

Table 2, Dependency of d_{min} on disturbance regime; lifetime=1

$d_{min} = ax^3 + bx^2 + cx + d$; x= disturbance radius;

Lifetime=1

	a	b	c	d	r^2
$d_{min}(1)$	1.8720	2.1734	-2.4757	0.7390	>0.99
$d_{min}(2)$	8.3652	-0.8773	-1.7530	0.5668	>0.99
$d_{min}(5)$	15.0880	0.1764	-1.8356	0.3806	>0.99
$d_{min}(10)$	14.2940	4.4379	-2.0458	0.2638	>0.99
$d_{min}(20)$	18.203	7.9288	-2.0113	0.1807	>0.99

(note $d_{min}(20)$ not shown in the graph; values supplied for convenience)

Table 3, Dependency of d_{min} on lifetime

$d_{min} = d_{min1} * \text{lifetime}^{-b}$

Low disturbance frequency N=1			
radius	d_{min1}	b	r^2
0.01	0.7931	0.5125	0.9884
0.04	0.7628	0.6160	0.9795
0.07	0.7008	0.6776	0.9829
0.10	0.5615	0.6628	0.9858
0.16	0.3797	0.5638	0.9475

High disturbance frequency N=10			
radius	d_{min1}	b	r^2
0.01	0.2539	0.5964	0.9952
0.04	0.1723	0.5594	0.9657
0.07	0.1150	0.3886	0.8475
0.10	0.0888	0.2350	0.7669
0.16	0.1000	0.0689	0.6000

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9. How the disturbance severity drives the benthic diversity on the Antarctic shelf

How the disturbance severity drives the benthic diversity on the Antarctic shelf

-Preliminary-

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9.1 Abstract

With a computer simulation we analysed the role of physical disturbance for the succession of the benthic communities at the Antarctic shelf. In particular we were interested in how the physical disturbance properties influenced the succession. We found that the disturbance severity, the mortality a disturbance causes, has great influence on the recovery time of the mature stage. Even a 1% survival probability could reduce the recovery time up to 25%. In general the severity influenced the recovery time in an exponential manner. The reasons for the speed-up were surviving individuals of long living species with a low dispersal potential. These survivors shortcut the succession process in acting as spatial storage, similar to seed banks in terrestrial plant communities. We further found the recovery time to be linearly increasing with the rotation period and disturbance size.

9.2 Introduction

The misbelieve of the Antarctic benthic shelf environment to be a very constant and sparsely disturbed habitat must be considerate outdated (Arntz & Gili 2001). It is now accepted that disturbance by ice, in deeper water mainly due to iceberg scouring but in shallow areas also anchor- and sea-ice, is the major disturbance agent for benthic as well as for pelagic ecosystems in Antarctica (Dayton et al. 1969, Barnes & Lein 1988, Gutt et al. 1996, Barnes 1999, Gutt 2000, Brenner et al. 2001, Gutt & Starmans 2001, Arrigo et al. 2002, Gerdes et al. 2003, Gutt & Piepenburg 2003).

It has been postulated that disturbance by iceberg scouring in the Antarctic is among the severest disturbance events an ecosystem on earth can meet (Gutt & Starmans 2001). Assuming a disturbance interval of roughly 250-350 a for each m² of the sea floor, approximately 0.004-0.003 % of the whole shelf (<500 m depth) is affected each year (numbers based on Gutt 2001). Assuming the total shelf area (<500 m) to be between 1.2-2.2*10^6 km² (Barnes 1986, Gutt 2001) thus between 3.1-9.2*10^3 km² (about the size of the Mediterranean island Corsica) is disturbed each year. Due to their bathymetry some places are even subject to much higher disturbance frequency. For the Hilltop-region (Auståsen) it has been estimated that up to 37% of the area is disturbed within 15 years (Gutt & Starmans 2001). This is equivalent to a theoretical rotation period, the time needed to statistical disturb the complete area, of only 40 years and communities in these areas do possibly not reach a climax state at all.

Generally the intermediate disturbance hypothesis (IDH, Dayton & Hessler 1972, Connell 1978) or the patch-dynamics concept can be used to relate the high species diversity to the disturbance intensity, depending on whether you focus on species or succession stage as both theories are closely linked (Wilson 1994). However, it is unclear how the physical disturbances properties influence the succession and how it interacts with species traits to promote and maintain coexistence.

Obviously, some species traits have a great influence on this process. For example dispersal is known to influence succession and coexistence (Hovestadt et al. 2000, Poethke et al. 2003, Cadotte 2006). It is commonly believed that dispersal distances of marine species with meroplanktic larvae are of quite different orders than that of terrestrial species. However, the dispersal distances of the most marine species are still speculative as of today (Todd 1998, Armsworth 2002, Lockwood et al. 2002) and the knowledge about actual dispersal of sedentary species in the Antarctic is, optimistically, sparse. For temperate and tropical regions it has been demonstrated that sedentary or hemi-sessile organisms, even when having a prolonged pelagic larval phase, possibly do not disperse as wide as formerly believed (Todd 1998, Mora et al. 2003, Jones et al. 2005). However, with the exception of very few organisms (e.g. *Sterechinus neumayeri,* see Bosch *et al.* 1987*)* even the duration of the larval phase of most Antarctic organism is still unknown as are the covered dispersal distances. Interestingly, the former postulated general lack of meroplanktic larvae in south polar waters is nowadays refuted. The number of papers dealing with planktonic larvae in the southern ocean rises continuously (e.g. Bhaud et al. 1999, Stanwell-Smith et al. 1999, Arntz & Gili 2001, Absher et al. 2003, Sewell 2005).

In a theoretical approach we have recently postulated that due to their longevity some Antarctic species do not need long distance dispersal at all to persist locally on the Antarctic shelf (Potthoff et al. 2006a). Further we have shown that in general the dispersal mechanism can have great influence on the diversity and coexistence (Potthoff et al. 2006b). This earlier work focuses on species traits and species-specific dispersal mechanisms. To characterise the benthic Antarctic shelf ecosystems we now investigate the role of the physical disturbance events. In particular we want to explore the role of the physical properties of a disturbance event. In particular we want to know how the community recovery is influenced by:

- The disturbance frequency, respectively the rotation period
- The disturbance size
- The disturbance severity

9.3 Material and Methods

9.3.1 General description of the model:

We used a spatially explicit and individual based simulation model to address our questions. In the model time proceeded in discrete intervals, approximately analogue to complete seasons. Thus every individual could pass through a complete life cycle in each interval or time step. This means it grows, reproduces, disperses larvae and adults may die. The landscape consists of a regular grid of 100x100 cells with periodic boundary conditions; this means that any object leaving the grid on one side re-enters immediately on the opposite border again. This prevents disadvantages for individuals at the grid boundaries.

Each cell represents a certain area of the sea floor and several individuals can be present in such a cell. The maximum number of individuals a cell supports is denoted its carrying capacity (*Cap)*. Differences in carrying capacities among cells can be seen to represent ecological relevant environmental conditions, e.g. food supply or sediment conditions. In order to create a spatially correlated distribution of carrying capacities, a fractal-generated map was used (see Figure 16). The carrying capacities varied between $Cap = 1$ and $Cap = 10$ with an average of about $Cap = 5$ resulting in approximately $5*10^4$ individuals in the entire simulation grid at any time. However, due to the calculative constrains and the limited spatial resolution individuals in the simulation must be seen rather as superindividual, representing e.g. a colony or a small group rather than a single individual in reality.

9.3.2 Simulation of Iceberg Scouring, Disturbance Regime

According to White & Jentsch (2001) a disturbance is characterised by its spatial distribution (dimensions, orientation) and frequency. In the model simulated iceberg scouring events are always rectangular, defined by their mean width and height in cells and the possible range of deviation around these values. We use a length width ratio of 4:1 based on data of iceberg scours reported by Hohmann (2002). The normal disturbance size is 50±25 by 13±7 cells with random orientation. The rate of mortality a disturbance causes in the affected area is denoted disturbance severity. Thus a severity of 95% means a mortality of 95% in a disturbed area.

The disturbance regime is further characterised by its rotation period. This is the time needed to statistically disturb an area equivalent to the entire simulation grid once. Thus it is a function of the disturbance size and frequency (see the appendix).

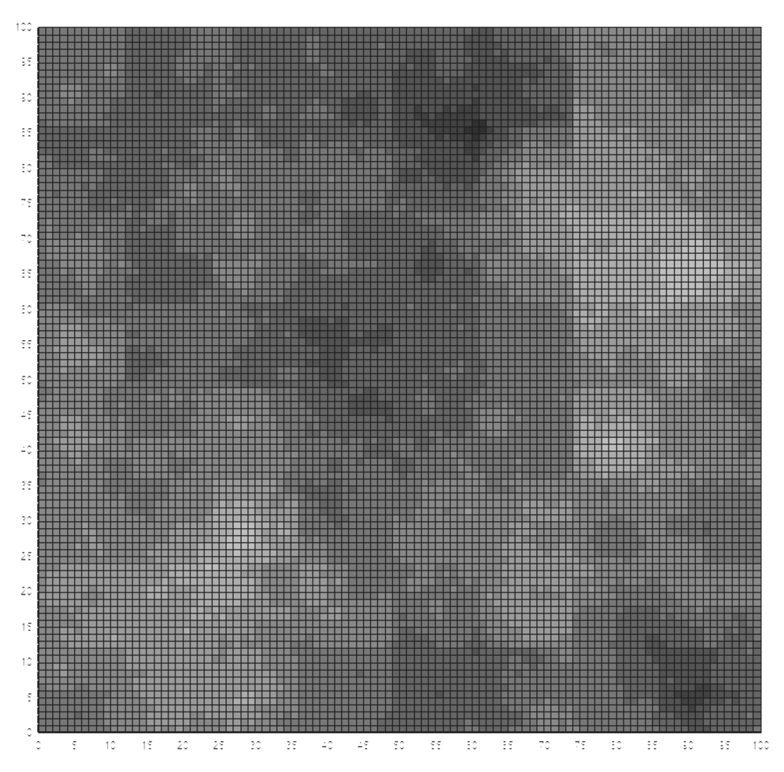

Figure 16, Distribution map of cell capacities used for the simulation. The brighter the colour, the higher the actual capacity. Lowest capacity is *CAP*=1, highest *CAP*=10. Average cell capacity is about *CAP*=5. Thus around $5*10^4$ individuals are present in the grid.

9.3.3 Species Traits

Individuals in the model can be attributed to different species, defined by their specific traits. The species are organised in different guilds: the pioneer guild (R0), early colonisation (R1), late colonisation (R2) and climax guild (UD). This scheme follows earlier classifications (Teixido et al. 2002, Gutt & Piepenburg 2003, Teixido et al. 2004). We assumed intra-guild neutrality; this means that species of the same guild share the same species traits. However, between the guilds great differences in species traits exist. In particular we used 5 members in each of the four guilds. Thus all simulations were done with 20 species in total.

Basically, the R0 guild represents short living, fast growing species with a high dispersal and recruitment potential. R0 members disperse over long distances via planktonic larvae. This guild is capable to immigrate from outside and may recolonise the simulation area even when they got extinct. There is no way to immigrate from an outside pool for any other guild. The R1 guild members live longer and have a lower dispersal distance than those of the R0 guild. The species of the R2 guild live slightly longer than the R1. Main difference to the latter guild is the low dispersal potential. R2 members are considered to disperse via budding or brooding. The longest living UD guild is also considered to be capably of short distance dispersal only. It produces the lowest number of recruits and needs the longest time to reach maternity.

9.3.4 The Nullmodel

In total we defined 6 species traits: fecundity, age of maternity, larval dispersal (actual two variables, see below), immigration potential form outside, instaneous mortality (based mean life span, see appendix) and maximal life span. The currently available information on comparable species traits of Antarctic species is, optimistically expressed, sparse. In order to parameterise the traits with real data extensive studies would be necessary, which is out of scope of this work.

Therefore the traits in the model where parameterised based on estimates derived from literature (e.g. Dayton 1979, Winston 1983, Arntz et al. 1992, Barnes 1995, Gutt & Koltun 1995, Stanwell-Smith & Barnes 1997, Brey et al. 1998, Leys & Lauzon 1998, Brey et al. 1999, Gutt & Starmans 2001, Kowalke et al. 2001, Gatti 2002, Teixido et al. 2004) and ecological theory. In an initial process the trait values were adjusted to allow the model to run in a relatively stable scenario where most species persist. This scenario S_0 represents the nullmodel for our simulation. See Table 4 for the parameters of this S_0-scenario. As mentioned, data for the model validation is not available. Therefore the parameters of our nullmodel represent the initial situation. To test the model response of a specific parameter (e.g. disturbance size), the according parameter was changed and the model response was evaluated in relation the nullmodel.

9.3.5 Larval dispersal

As we focus on sedentary species only larval or propagule dispersal was considered. All larvae originating from a species in a cell disperse simultaneously as a group. This group travels a certain distance DD_1 [measured as grid cells], according to an exponential dispersal kernel ($DD_1 = \textit{dispersal distance} * -\ln(p_1)$) and in a random direction. After dispersal all larvae settle within a circular area defined by a second exponential kernel ($DD_2 = patch\ size * -ln(p_2)$; p_1, p_2 being uniform random numbers in the interval [0..1]) around the resulting point. The characteristic distances *dispersal distance* and *patch size* are species-specific dispersal traits. In Figure 17 a sketch of the dispersal process is depicted. Note that sedentary species are known to produce often vast numbers of larvae. However, most produced larvae fail to recruit and establish due to various reasons (mortality, predation, insufficient habitat). Our simulation does not cover any mortality related processes during the larval period. Thus fecundity in the model must be seen as a proxy for the number of larvae that become competent and compete for suitable space after the dispersal phase.

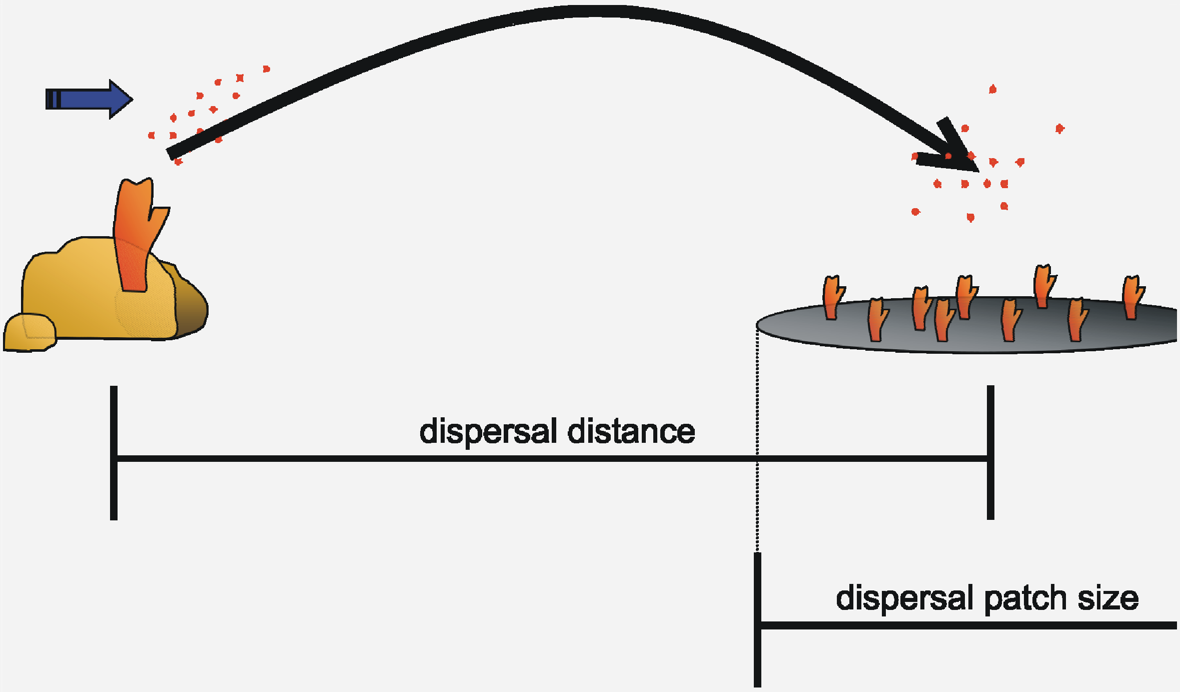

Figure 17, Sketch of the dispersal process used in the simulation. In a first step all larvae travel as a swarm for a certain distance DD_1. In a second step, the larvae individually settle within an area with a radius of DD_2. Exponential kernels parameterised by the species traits „dispersal distance“ and „patch size“ determine both distances.

9.3.6 Competition

Due to the lack of information regarding the competition between most Antarctic species we decided to use a lottery competition. This is a common approach in marine models, e.g. for the recruitment of corals or reef fish (e.g. Connell 1978, Danilowicz & Sale 1999, Connell et al. 2004, Munday 2004). In a lottery a pool of potential recruits, mostly but not necessary out of different species, exist. All members of such a pool compete with each other. Thus if the pool has *n* members, each (regardless of its species) has a *1/n* chance. As we explicitly model larval dispersal, each grid cell has its individual pool of competitors (that are the larvae that have been dispersed to this particular cell in the actual time step). If there is free space (that is, the cell hold less individuals than its carrying capacity), randomly one of the competing larvae is selected and allowed to establish. This larvae is removed form the pool and the process is repeated until the carrying capacity is reached or the pool becomes empty. Larvae that did not establish are removed from the simulation at the end of each time step.

9.3.7 Succession pattern / succession state definition.

Theoretically, only a pioneer assemblage (mainly species from the R0-guild) should colonise an area shortly after a disturbance. Then an early R1 and a later R2 community develop. Finally members of the climax guild (UD) dominate. Certain succession states can now be defined on some abundance thresholds for each guild. E.g. as long as the community shows a dominance of more than *x*% of the R0 guild, the assemblage is defined to be in the R0 state. Analogue, the R1 state could be defined on the condition that the R1 guild must have more than *m*% and the R2 guild has less than *n*%. R2 und UD state definitions follow the same scheme.

The succession state definitions (listed in Table 5) were derived from the S_0 nullmodel, and used for every simulation run. The states were identified from early to later states and the first match was accepted. This was done to resolve some ambiguous situations, e.g. if a cell had the relative abundances R0 = 0.35, R1 = 0.05, R2 = 0.09 and UD = 0.51 it was assigned to be in the R0 state rather than the UD state.

9.3.8 Succession speed

After a simulation run the succession states for all grid cells were computed. The results of all runs with the same parameters from the same experiment were pooled and the mean age for all cells in a certain succession state was determined. Of particular interest was the climax UD state as this state is the final one. Thus its mean age, respectively the time needed to reach this state can be used as proxy for the overall succession speed. The means were checked for correlation with the simulation parameters.

9.3.9 Starting and stop conditions/ runtime

For every simulation a random mixture of all available species initially populated the grid. All individuals had a random life history within the possible range of their species, e.g. random age and time since last reproduction. To ensure comparability, all simulations were allowed to run at least 5000 time steps. To ensure that all simulations ended in a comparable situation, the next occurrence of a disturbance event was then awaited and the simulation was stopped 10 time steps later.

9.4 Experiments:

In a first experiment we wanted to know how the disturbance regime influences the succession speed. Therefore we varied the rotation period from 200 to 700 time steps. The disturbance size was fixed at 50±25 x 13±7 cells. Thus the variation of the rotation period is equivalent to a changed disturbance frequency (Table 6 lists the rotation period with the equivalent disturbance frequency). Please note that a low rotation period means a short time to disturb the simulation grid once and thus defines a high disturbance intensity scenario whereas a high rotation period means a low disturbance intensity. Further we looked at three different levels of disturbance severity (90%, 95% and 100%). To account for stochastic process within the simulation we repeated each simulation n (6) times.

In a second experiment we focused on the impact of the disturbance dimension on the succession. Therefore we used a fix rotation period (350 time steps) and changed the disturbance size while keeping the rotation period constant. This was done by reducing the area of a single disturbance for a certain proportion while trying to keep the length-width ratio (~1:4) constant. The deviation range for both the length and width was set to 50% of the according value. All simulations were repeated 10 times and the average of the response variables computed. We run the simulations with the three different severity levels (90%, 95% and 100%). Table 7 lists the disturbance definitions used.

9.5 Results

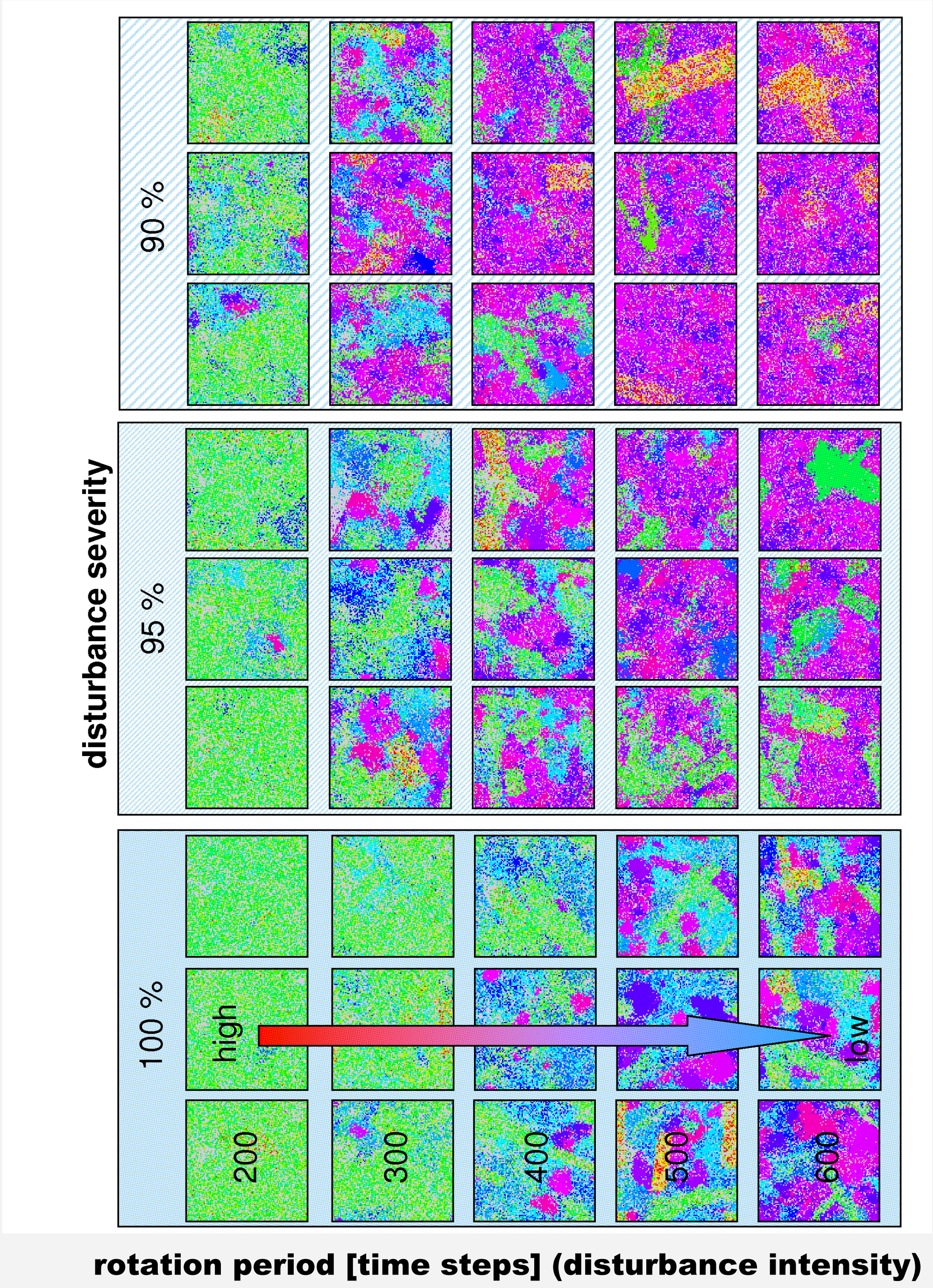

Figure 18, Exemplary dominance maps of simulations with different disturbance severity levels. For each severity three runs are shown. The distribution of the most abundant species in a grid cell of a final simulation state is mapped. Colours represent different species respectively guilds (orange and red =R0, greenish=R1, bluish=R2 and violet=UD; grey=undefined dominance). Disturbance intensity (coloured arrow) decreases from the left (rotation period=200) to the right (rotation period=600).

9.5.1 Experiment 1

In Figure 18 exemplary results of the simulation results are shown. For each severity level and some selected rotation periods dominance maps of two random selected runs are shown. In the dominance map the colour of a grid cell simply show the most abundant species within the cell. Colours follow a rainbow scheme, from the red-orange R0 guild over greenish R1, blue R2 and violet UD guild. Grey colour indicates that no dominance could be determined. Visually it is evident hat the succession as faster as lower the severity level is.

Table 8 gives the complete data for the mean cell age of a succession state together with the correlation coefficient **r²** of rotation time and mean age. Figure 19 shows a plot of the mean climax age (UD-state) as proxy for the recovery speed at different disturbance severity levels. It shows older mean cell ages under lower disturbance intensity (higher rotation periods). In general recovery time seems to be linear liked to the rotation period when disturbance size is fixed.

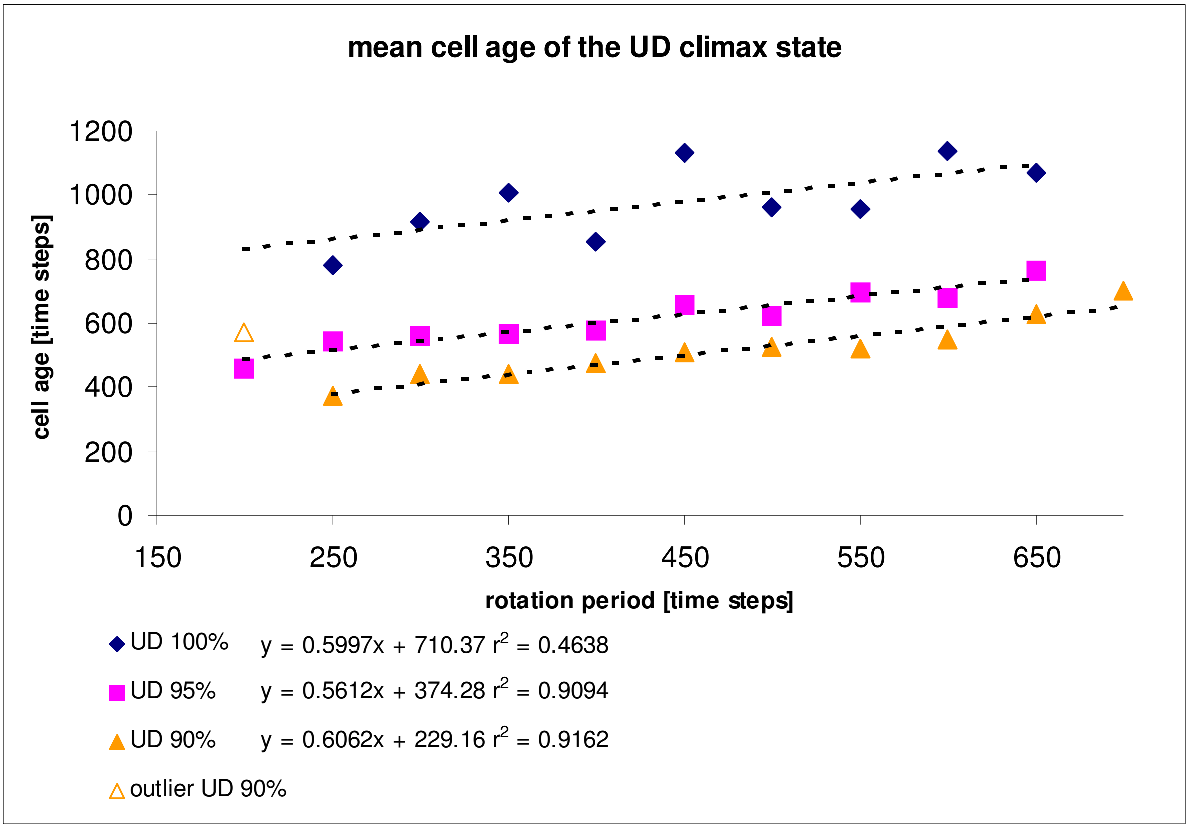

Figure 19, mean cell age of the climax state UD as proxy for the succession speed at different disturbance severity levels. Scattered lines represent linear regressions. Note that the data point rt=200 for the 90% severity level was considered to be an outlier and not included in the regression.

9.5.2 Experiment 2

Table 9 lists the mean cell age for the different succession states and severity levels for different disturbance size (rotation period const. rt = 350). Figure 20 exemplarily shows a graphical representation for the 100% level with some inscribed linear regression lines. The other severity levels behave similar. In general the slope of the linear regressions for the R0 show slopes near zero whereas R2 and UD have individual differing, positive ones. R1 also has a positive, however not so pronounced slope.

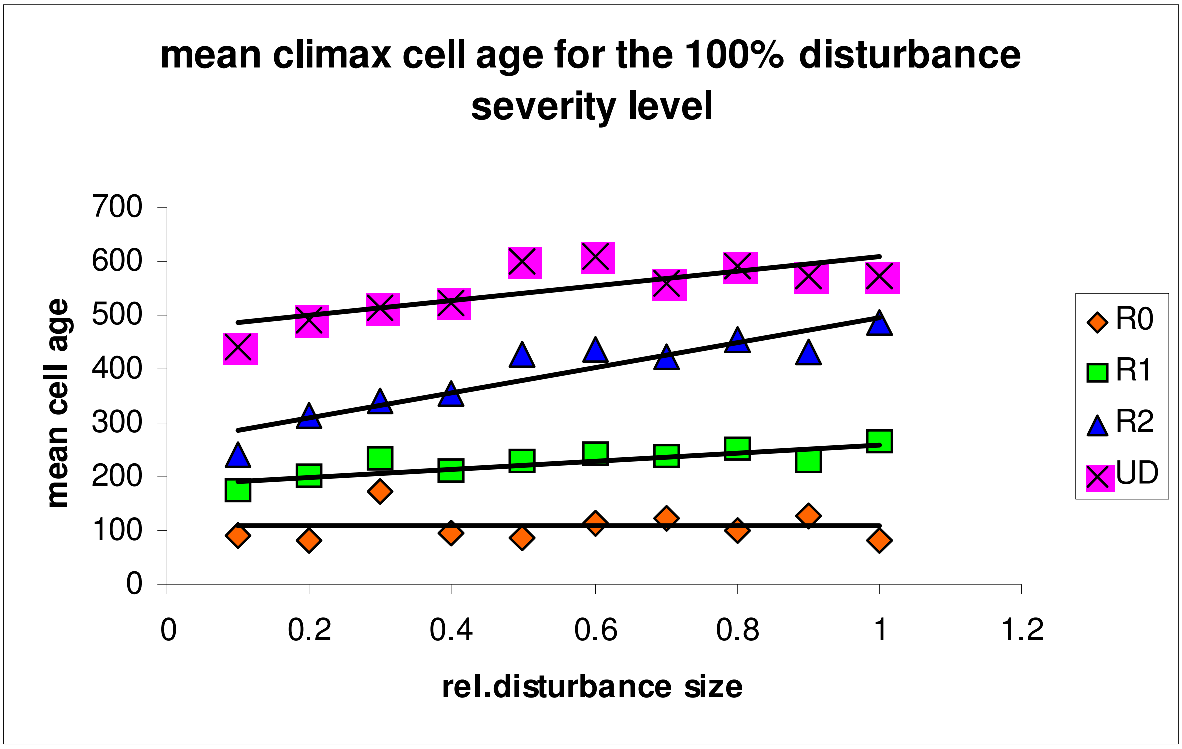

Figure 20, mean cell age for the succession states for different relative disturbance size at the 100% disturbance severity level with additionally inscribed linear regressions. Regression parameters can be found in Table 9.

9.6 Discussion

The benthos communities on the Antarctic shelf are subject to intense disturbance due to iceberg scouring. After a disturbance a succession can be observed (Teixido et al. 2004). To get more insights into the disturbance mechanism and its importance for the succession we implemented a spatially explicit simulation model. Our main interest was to explore the role of the physical disturbance parameters for the succession. Our simulation model makes several simplifying assumptions. For most traits of Antarctic species no comprehensive data exist that could be used for the parameterisation of the model. Therefore the values for the species traits are based on the limited literature data and common assumptions deduced from other, even terrestrial systems. E.g. it was assumed that pioneer species have a comparably short lifetime but high dispersal potential and climax species become comparably old but show less dispersal potential, which is the realisation of the well-known dispersal-competition trade off. To combine the power of neutral and common simulation models we introduced the concept of intra-guild neutrality. This has, to our knowledge, not been done before. The results demonstrate that the physical disturbance parameter can have a significant impact on the system behaviour.

The mean age of cells in the climax state UD can be used as a proxy for the overall succession speed and thus resilience of the system as this state marks the point when community recovery is completed. Figure 19 shows a plot of the mean age of cells in the UD state for all disturbance severity levels used in the first experiment. Regarding the succession speed this figure reveals that in our model speed depends linearly on the rotation period when disturbance size is fixed. The slopes of the regression lines are remarkable consistent around the value ~0.59 between the different severity levels. This suggests a common dependency of mean UD state cell age and rotation period. Further, succession is faster for lower severity levels.

To analyse this phenomena we repeated the first experiment with additional severity levels (93%, 94%, 96%, 97%, 98% and 99%). We only inspected the mean cell ages of the UD state in these additional experiments. Figure 21 shows the average (in respect to all used rotation periods) climax age as proxy for recovery speed for the different disturbance severity levels expressed relative to the values of the 100% disturbance severity level. In general the climax recovery process is much faster with a lower severity. Even a slight reduction in severity to 99% can shorten the recovery time up to 25%. At a 90% severity level the climax recovery needs on average only half the time.

Figure 21, Influence of disturbance severity on the mean climax cell age. Shown are the mean age of all climax cells of all rotation periods at a specific rotation period and the min-max rage (vertical bar) relative to the 100% disturbance severity level. The figure reveals a non-linear, falling dependency of cell age and disturbance severity, i.e. with a lower disturbance severity the mean cell age is much lower. Even a 99% disturbance severity level can lead to a 75% reduction in cell age. At the 90% disturbance severity level the mean cell age is only about half the age compared to the 100% level.

With the first experiment we have shown that succession or recovery speed depends linearly on rotation period and in a non-linear way on the disturbance severity level when disturbance size is fixed. In the second experiment we investigated the role of the disturbance size. The results of this experiment suggest a linear relationship of succession speed and disturbance size, at least for the later R2 and UD state (Figure 20).

It is also worth noting that the different succession states behave different. Deducted from a regression slope near zero, the primary pioneer state R0 seem not to be influenced much (compare slopes in Table 8 and Table 9). This can be explained by the fact that this state has the lowest dispersal limitation in the model. It can even immigrate from an “outside”-pool. Thus its long distance dispersal and immigration potential makes it less dependent on local disturbance phenomena. The other states show different behaviour, indicated by a non-zero slope of the linear regression (see Figure 20 and Table 9). Each state seems to have its own response, indicated by individual slopes. Thus transition times between the successional stages, respectively their relative numerical proportions, are influenced by the physical disturbance parameters. These transition times are main factors shaping the diversity–disturbance curve and the position of the diversity maximum within the ‘intermediate disturbance hypothesis’ (Johst et al. in press, Johst & Huth 2005). Wide maximum plateaus or even bimodal diversity–disturbance curves may occur at certain successional patterns e.g. when early and late succession stages were separated by a long-lived (compared to the early stages) intermediate successional stage (see Johst & Huth 2005). This may be the case in Antarctic communities, as the temporal distance between the R1 and R2 stages are highest with high disturbance severity (see Figure 20). Our results suggest flexible/variable instead fixed transition times or rates in the corresponding succession models (e.g. as a function of neighbourhood effects in spatially explicit models; (Johst et al. in press, Johst & Huth 2005) or directly as a function of the disturbance regime in non-spatial models) when considering a large range of disturbance size, frequency or severity. One should also note that large infrequent disturbances can lead to uncertain and variable successional trajectories with alternative outcomes (Turner et al. 1998).

The question is how severe the physical disturbance by iceberg scouring is in the Antarctic. The general physical processes of iceberg-seafloor interaction have been descript by Woodworth-Lynas et al. (1991). However, these observations were made in the shallow Artic. For the deep Antarctic shelf no comparable data exists but may be deduced from underwater video and photos. Based on our experience fresh scour marks look usually complete devastated and bare of any species other than mobile forms (Figure 25). However, photo or video transect usually cover only very small proportions of the sea floor, typically 1 m² or a 100 cm wide strip in case of consecutive video images. To our knowledge, no scour mark has been fully mapped and censed. Thus it is difficult to estimate how severe iceberg scouring really is.

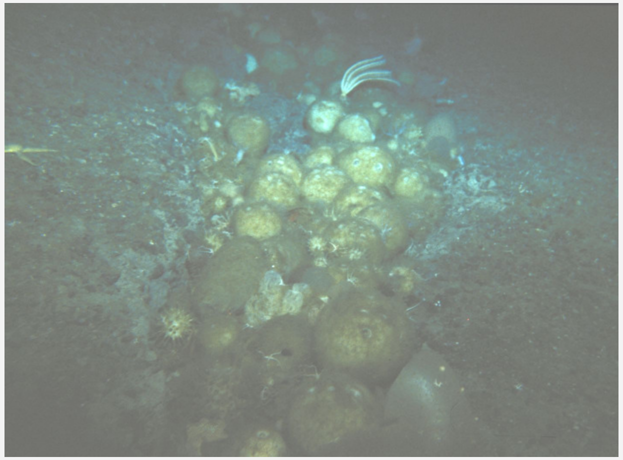

Figure 22, Rare situation where a grove or pit seem to have sheltered some benthos, mainly the sponge from an catastrophic iceberg sour around them.

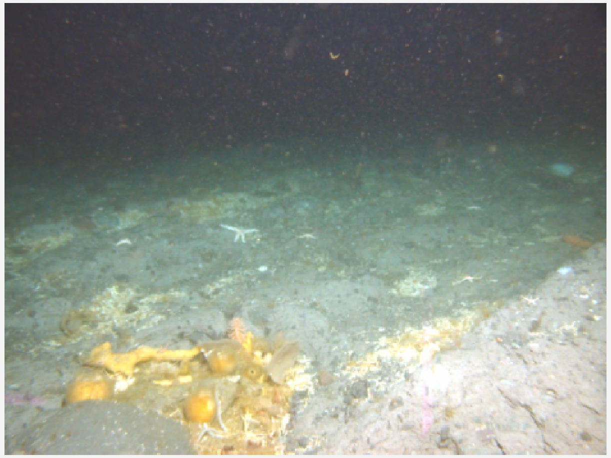

Figure 23, Fragments of the old community sometimes survive an iceberg scouring. These survivors may greatly accelerate the succession, especially when dispersal limited species are involved.

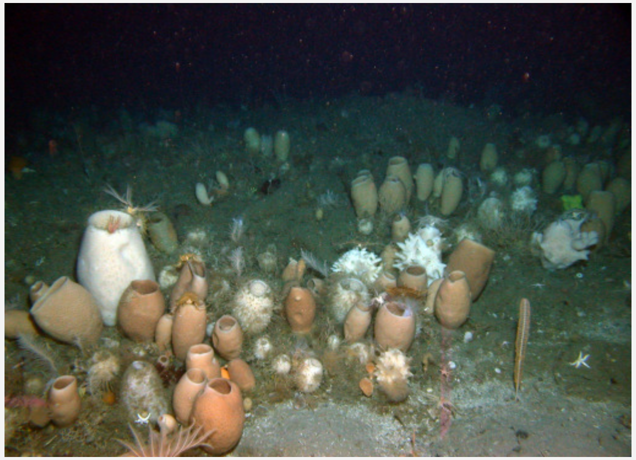

Figure 24, Example of a patchy sponge dominated benthic community of the Weddell Sea.

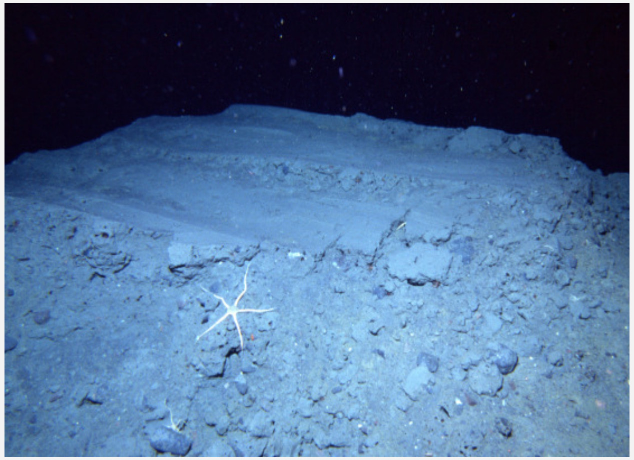

Figure 25, Bare sediment after an iceberg sour. Only mobile organism have already recolonised the sediment.

(Photos © J.Gutt / AWI)

In our photo library (*http://www.pangea.de*) some rare pictures show individuals to be sheltered at groves or other seabed features (Figure 22, Figure 23). A look at a previously published data set on the abundance of Weddell Sea benthos by Gutt & Piepenburg (2003) reveals that the proportion of slow growing hexactinellid sponges (intermediate to large in size) in R0 areas is around 0.4-0.8 % relative to the abundance in UD areas (see table 1 in Gutt & Piepenburg 2003). The occurrence of such large individuals can be explained by two mechanisms: apart from being survivors of a catastrophic iceberg scour hexactinellid sponge, at least juveniles, may grow very fast.

The assumed slow growth of hexactinellids is based on observations of large, not growing specimen by Dayton (1979). Also the determination of the growth speed by Gatti (2002) was based on larger individuals. Possibly, growth in hexactinellid sponge is age dependent as in many other animals. In comparison, Arctic hexactinellid species are known to grow several cm a^{-1} (Leys & Lauzon 1998).

We cannot prefer one of either hypothesis explaining the occurrence of large hexactinellid sponges in recently scoured areas. In general we estimate that the iceberg disturbance severity on the Antarctic shelf is close the 99%. However, even this small survival probability can considerably shorten the recovery time on average around 10%, in single experiments even up to 25% (see Figure 21).

Much more prominent than single survived individuals within an iceberg scour are the sharp borders of distinct, neighbouring areas in different succession states. Photo sledge images often do not give the appropriate overview but on consecutive video images one can often see very sharp transitions between areas with different succession states. Clear sediment breams may separate the areas but often no physical parting line can be detected. Sometimes, these distinct areas are very small in size, most probably created by multi-keel icebergs as indicated by small, parallel scour marks between them. Small undisturbed patches within a mosaic of recently disturbed areas seem to be a common feature on the Antarctic shelf (Figure 23). We think that iceberg scouring creates a mosaic of areas in different succession states on the sea floor. Sometimes even some individuals or patches of slow growing species with a high dispersal limitation may survive a scouring event. These patches or remnants are comparable to survivors of ecological catastrophes in other systems, e.g. unburned patches or single, unburned trees after a forest fire or aquatic species surviving a drought in a deep pool. Similar to seed banks they store a populations potential to high growth over unfavourable times and thus form a “spatial storage” effect *sensu* Chesson (1994).

The following succession process may therefore be much faster or even cut short as the time to invade into a recently disturbed area can be reduced. The effect is long known to terrestrial ecologist (Chesson & Warner 1981, Chesson 1994, 2000, Groeneveld et al. 2002). Some species, e.g. fire-sprouters have even successfully adapted to such environmental factors.

Several traits of sedentary Antarctic species may be the result of such an adaptation too (see also Potthoff et al. 2006a, Potthoff et al. 2006b). For example, during the cruise ANT XXI of the RV Polarstern in 2003/2004 we found a young sponge specimen, identified as *Rossela racovizae*, in the funnel of a net (Figure 26). The opening of the net was about 0.5 m above the sea floor and it was lifted vertically. Thus we conclude that the specimen was transported by water currents into the net as Dayton (1979) reports that young individuals of these species can be easily moved by currents resulting from a divers hand moving 20-25 cm away.

Therefore, some sponge species, at least young *Rossela racovizae,* seem to be able of secondary dispersal. Other species show intense brooding behaviour, releasing competent juveniles (Teixido et al. 2006). Despite the possibility to raft on iceberg fragments, it must be assumed that such dispersal units have a limited dispersal range. The dispersal of young, competent individuals into recently disturbed, competition free areas represents an ecological advantage. It reduces the time to establish a vital, reproductive population as the juveniles can spend the time of their first growth in relative safe, suitable areas (as proofed by occurrence of their parents).

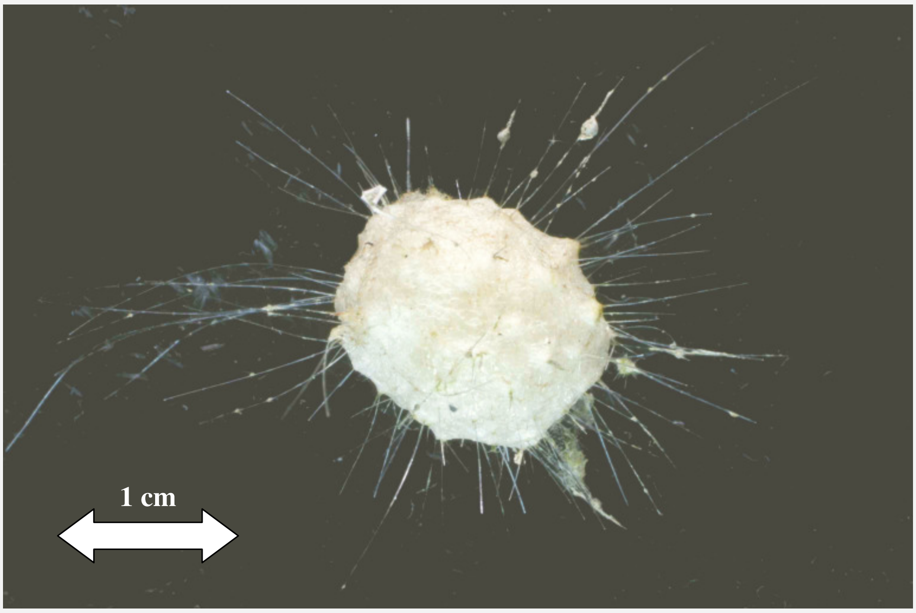

Figure 26, A young sponge individuals, possibly *Rossella racovitzae*. The body diameter is about 1 cm. This specimen was found in the funnel of a net, positioned 0.5 m above the seafloor in a depth of about 250 m. The picture was kindly taken by Dr. Martin Rauschert during the ANT XXI/2 cruise of the RV Polarstern in 2003/2004. Note the long spiculae to enhance the shape resistance, which makes the individuals more susceptible to water currents (see Dayton 1979)

But what does this mean for the stability of the Antarctic benthic ecosystems? Turner et al. (1993) proposed a framework to describe the dynamics of disturbed landscapes. Most interesting is their conclusion that most systems are stable (in the sense of stable relations of the relative abundances of different succession states) unless the disturbance interval is much shorter than the recovery time and a large proportion of the landscape is affected (Turner et al. 1993). When the disturbance interval is comparable to the recovery time and a large proportion of the landscape is affected, the system is stable but exhibits large variance.

With an estimated recovery time between 250-500 years and the relative high disturbance intensity, the Antarctic shelf seems to be a stable system with large variance. At frequently disturbed areas like shallow iceberg rest places the system may be even unstable. Then the proposed high variation equals to general raised between habitat diversity (β diversity) but a low point diversity (α diversity), especially for unstable sites. This confirms expectations from earlier work (Gutt & Piepenburg 2003).

9.7 APPENDIX

9.7.1 Calculation of instantaneous mortality on mean life time

Instantaneous mortality (IM) was calculated according to the following formula:

$$IM = \frac{\ln(0.5^{-1})}{mean\ life\ span}$$

This means that a population exponentially declines to half of its size in the given time. Explicitly the abundance *N* at time *t* is $N_t = N_0 * e^{-IM*t}$.

9.7.2 Calculation of the rotation period

The rotation period can be calculated as: $rt = \left(\frac{total\ area}{frequency * disturbance\ size} \right)$

Thus it is a power-function of the relative disturbed area and the disturbance frequency.

9.7.3 The concept of intra-guild neutrality

The intra-guild neutrality is based on Root's original guild definition ("A guild is defined as a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to taxonomic position, that overlap significantly in their nice requirements." (Root 1967) and the general lack of knowledge on species traits of most Antarctic groups. There are differences in species traits among different species within a guild. However, since they share the same niches their basic requirements must be comparable. Thus we assume that differences become equalized due to the small sub-set of species traits realised in the model. Indeed, although we do not present data in this manuscript, different species within a single guild exhibit remarkable different spatio-temporal distribution patterns. We think that this neutral guild concept may stimulate more complex models in future.

TABLES

species trait	guilds (á 5 members)			
	R0	R1	R2	UD
Fecundity (see below)	20	6	5	3
age of maternity [time steps]	1	3	10	35
dispersal distance [grid cells]	70	10	0	0
dispersal patch size [grid cells]	2	1	2	1
immigration	yes	no	no	No
mean life span [time steps]	5	30	50	200
(instantaneous mortality	*0.139*	*0.023*	*0.014*	*0.003)*
maximal life span [time steps]	5	200	500	2000
Disturbance size	50±25 x 13±7 cells			
rotation period	350 time steps (p=0.044)			
severity	95%			

Table 4, Guild and disturbance definitions of the S_0-scenario

Succession state	R0	R1	R2	UD
Relative guild composition	R0 > 0.30	R0 < 0.25 R1 > 0.20	R2 > 0.40 UD < 0.50	UD > 0.50

Table 5, Definition of the relative guild composition for each succession state

Rotation period	200	250	300	350	400	450	500	550	600	650	700
Frequency	0.077	0.062	0.051	0.044	0.038	0.034	0.031	0.028	0.026	0.024	0.022

Table 6, Rotation periods and respective disturbance frequencies for experiment 1

rel. Size	Length	width	Frequency
0.10	16±8	4±2	0.4464
0.20	22±11	6±3	0.2165
0.30	27±14	7±4	0.1512
0.40	32±16	8±4	0.1116
0.50	35±18	9±5	0.0907
0.60	39±20	10±5	0.0733
0.70	42±21	11±6	0.0618
0.80	45±23	12±6	0.0529
0.90	47±24	12±6	0.0507
1.00	50±25	13±7	0.0440

Table 7, disturbance definitions used in experiment 2

rt	Disturbance severity											
	100%				95%				90%			
	R0	R1	R2	UD	R0	R1	R2	UD	R0	R1	R2	UD
200	106	195	349		74	193	416	458	68	167	331	572
250	111	205	553	783	70	231	400	546	98	171	265	375
300	86	227	458	919	79	220	373	559	40	167	265	439
350	94	318	618	1010	47	195	319	568	51	162	219	439
400	127	315	537	852	68	217	383	575	63	206	320	478
450	143	376	617	1133	110	209	313	659	106	192	302	508
500	88	322	519	964	71	230	236	623	17	164	193	526
550	102	291	533	956	48	223	286	695	51	189		522
600	130	310	578	1136	80	211	312	680	86	170	363	550
650	70	375	555	1069	86	259	275	765	63	191	286	631
700	68	353	508	1055	74	252	237	774	50	177		703
intercept	122	162	450	742	67.5	185	469	372	74.3	165	268	340
slope	-0.04	0.3	0.18	0.52	0.01	0.08	-0.33	0.57	-0.03	0.03	0.04	0.4
r^2	0.09	0.62	0.15	0.46	0.02	0.43	0.74	0.93	0.03	0.1	0.01	0.53

Table 8, mean cell age for the succession states and rotation periods (rt) for all different severity levels. Intercept and slope of linear regression of rotation period and mean cell age show the response of the different states. The last line shows the correlation coefficient r² for the correlation between rotation period and cell age. Grey cells indicate that the appropriate state could not be found due to a extinct guild.

		Disturbance severity											
		100%				95%				90%			
		R0	R1	R2	UD	R0	R1	R2	UD	R0	R1	R2	UD
relative disturbance size	0.1	91	171	240	443	65	152	188	363	49	133	161	325
	0.2	83	200	313	489	68	165	235	412	63	141	179	349
	0.3	171	232	343	512	74	175	245	430	65	142	195	359
	0.4	95	208	353	522	69	185	269	444	40	163	209	386
	0.5	85	229	428	600	154	194	296	458	41	151	236	364
	0.6	114	240	437	609	133	196	313	462	60	144	228	380
	0.7	125	238	421	561	110	207	335	475	54	159	235	402
	0.8	102	249	456	590	82	205	338	467	44	142	246	382
	0.9	126	226	430	574	90	172	313	457	72	174	275	417
	1	81	262	485	575	45	182	313	468	46	155	214	373
intercept		107.8	185.9	263.9	470.9	85.1	165.4	206.1	392.2	53.7	136.7	168.7	337.5
slope		-0.909	71.939	230.424	139.333	7.030	32.545	142.485	93.455	-0.485	24.848	89.333	65.879
r		-0.010	0.828	0.921	0.781	0.063	0.556	0.882	0.827	-0.013	0.607	0.806	0.758
r^2		0.000	0.685	0.849	0.610	0.004	0.309	0.777	0.684	0.000	0.368	0.649	0.575

Table 9, mean cell age for the different succession states and severity levels for a fix rotation period (rt=350) but different disturbance size. Also the regression parameter for a linear regression of age and disturbance size is shown. Regression lines for the 100% severity level are displayed in Figure 20.

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10. SIMBAA MANUAL

SIMBAA

SImulation Model of Benthic Antarctic Assemblages

Short

SIMBAA MANUAL

-Version 2-

(This manual covers SIMBAA GUI 1.6b and SIMBAA core 1.20.G or higher)

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10.1 Introduction

SIMBAA is a spatial explicit, individual based simulation model. Its main purpose is the analysis of disturbance events on an assemblage of marine sedentary organisms. It was programmed at the Alfred-Wegener-Institute for Polar and Marine Research by Michael Potthoff during his PhD thesis 2003-2006 on the influence of iceberg scouring on the benthos of the Weddell Sea. Therefore some special terminology on marine and polar science may be used throughout this manual, however the mechanisms and features implemented in SIMBAA are quite general and can be applied to other fields of interest as well.

As every other model or simulation SIMBAA makes some assumptions and generalisations. The purpose of this chapter is to introduce these basic mechanisms and generalisations.

10.1.1 Time in the model

Time in SIMBAA proceeds in discrete steps. One time step is equivalent to one simulation cycle, e.g. every individual in the simulation can (according to its state) reproduce, disperse, die (so it can complete its own life cycle ones), disturbance events may happen and free space may be colonised by recruits. The best equivalent of one simulation time step is one season in real life. Internally all information is handled in a way that the update, e.g. the change of the states of all individuals, occurs synchronously.

10.1.2 The environment (a-biotic parameters)

10.1.3 The space

As SIMBAA is a spatial explicit simulation, every individual occupies a certain position in space. Dispersal and competition is dependent on the particular properties of that position in space. However, SIMBAA does not use continuous space. Instead SIMBAA is based on a regular grid of small discrete areas, thus it is a grid-based simulation. The illustration shows the principle orientation of the grid. The grid origin is the lower left corner. Directions are analogue to common maps, 0° (north) is to the top, 90° (east) to the right, 180° (south) towards the bottom and 270° (west) to the left. The smallest spatial resolution is one single grid cell. The equivalent space in nature depends on other model properties and can be a single square meter, 10^{th} of square meters or even more. It is mandatory to have in mind that one grid cell is the basic spatial unit as all other spatial information (e.g. dispersal distances) are measured in units of grid cells!

The user can determine the grid dimensions, how many individuals (max 100) may life inside of one grid cell and if every cell of the simulation grid can hold the same amount of individuals or not. All Individuals of a cell are placed within a 10 x 10 sub-grid. This information is only used when displaying the individuals and has no other meaning. However, this limits the amount of individuals per cell to 100 individuals.

Each cell has 8 boolean properties S_1-S_8 (“Yes-No” or “enabled-disabled”), representing environmental e.g. sediment conditions. These can influence individuals living in this cell. Individuals in the cell may alter the properties as well as disturbance events do. By default S_1 is enabled. See species traits for more details.

By default the world represented in SIMBAA is a torus- or doughnut-scenario. This means that any object leaving the grid on one side re-enters the simulation on the opposite border. Thus border effects are avoided e.g. no larvae can be lost by “falling” off the grid. When periodic boundary conditions are enabled SIMBAA is a closed system. However, the periodic boundary conditions can be switched off. In this case SIMBAA is an open system and the simulation borders absorb any object leaving the simulation area. Figure 27 illustrates the spatial grid properties.

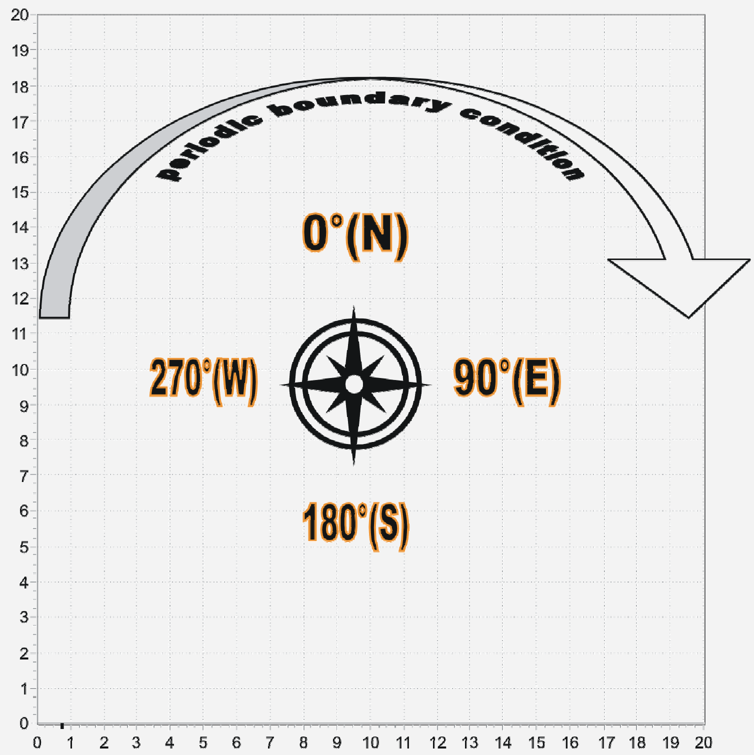

Figure 27, Orientation of the simulation grid in SIMBAA

10.1.4 Disturbance events

In a SIMBAA-simulation disturbance events can be defined. Each disturbance event is characterised by its spatial information, intensity and occurrence probability. Disturbance events may be restricted to start in a certain proportion of the simulation grid. This region is always rectangular and orthogonal to the grid axis. Disturbances may be clipped by this area, what means that they do not affect any space outside the defined region (see Figure 2).

Disturbances are always rectangular with a defined length and width and aligned in a certain direction. All these spatial information may deviate within a given, normally distributed region around the average values (see illustration below).

Disturbance probability is independent on prior realisations and can be given as probability. However, it is mainly expressed in terms of the **rotation period**. This is the time in which the whole simulation grid is (statistically) disturbed once. The rotation period can be computed by Formula 1:

$$rotation\ period\left[time\ steps\right]=\frac{simulation\ grid\ size\left[x*y\right]}{disturbance\ size\left[x*y\right]*disturbance\,probability\left[\frac{1}{time\ steps}\right]}$$

Formula 1, computation of the rotation period

SIMBAA allows a disturbance event to consist of several sub-events. Then several disturbance events of the same size and intensity happen at the same time. Thus a disturbance with 2 sub-events means that these two disturbances occur always together, although their start points are independently chosen. However, as they are sub-events, the disturbance probability and rotation period are based on their co-occurrence. This gives the possibility to create temporal and spatial correlated disturbance.

Disturbance area definition and clipping

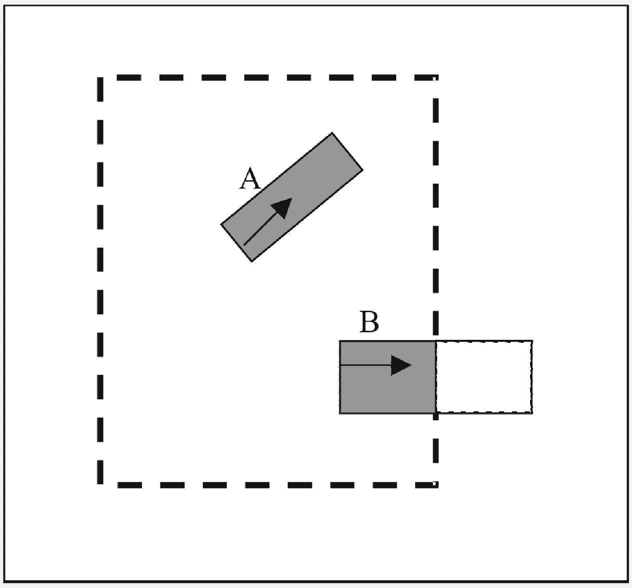

Figure 28, This is an example for disturbance definitions. The white area represents the complete simulation area. Disturbance A is completely in the disturbance area, defined by the dashed line. Disturbance B starts in this area (indicated by the arrow). However, it extends partially outside the disturbance area. If clipping is enabled, the shaded part would be omitted and B would be restricted to the defined area.

10.1.5 Disturbance severity

If an event occurs, the proportion of individuals removed from the disturbed area is analogue to the disturbance severity, e.g. 100% means all individuals are removed whereas 50% means, that any individual has a 50% chance to be removed.

10.1.6 The flow

As SIMBAA is used to model marine systems it contains a hydrographical sub-model of the flow to model larval dispersion. However the hydrographical sub-model is very simplified. The user can define how many flow cells lie on top of the entire simulation. If there is only one cell, its flow properties define the flow of the entire simulation grid. If there are more flow cells, each simulation grid cell is projected to the flow cell on top of it. If you use the same number of flow and grid cells you can define the flow properties for each grid cell individually. It is not advisable to use more flow cell than grid cells on the simulation. The flow property of a cell is based on the flow speed and flow direction (heading and deviation). The hydrographical sub-model is static in time. Therefore this information must be defined before a simulation run and cannot be changed while the simulation is running. However, each time step the flow is sampled a deviation of the given order around its average heading is computed. Thus the flow is normally distributed around the given average heading and standard deviation. Figure 29 illustrates the general properties:

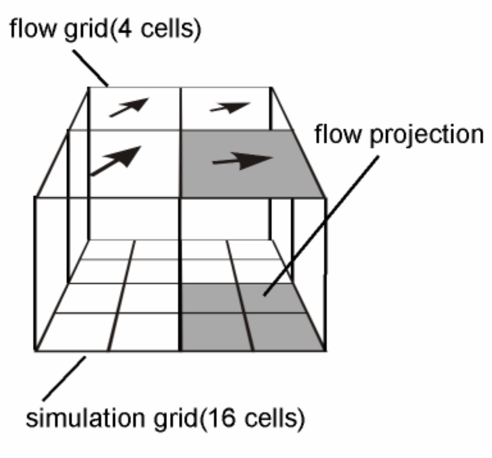

Figure 29, Schema of the hydrographical sub-model of SIMBAA. Arrows represent the direction and strength of flow. In this example the flow grid consists of 4 cells (top), the simulation grid of 16 cells (bottom). Thus each flow cell is projected to a cluster 4 simulation grid cells (e.g. shaded in the grey).

10.2 The biology model of SIMBAA (biotic parameter)

SIMBAA is an individual based simulation. This means that the smallest biological information is one individual. However, the user can see an individual as super-individual, representing more than one individual organism in reality (e.g. a colony). Each individual in the simulation belongs to one of several species. Currently up to 50 different species can be defined. All individuals of a particular species share the same species traits. In particular SIMBAA contains the following life-history traits:

10.2.1 List of species traits available in SIMBAA:

General	
Species name	Name listed in the graphs and data files
Guild	Guild of the species
POV output	number of species macro used by POV
Colour	Colour used for screen drawing
Reproductive traits	
Fecundity	number of potential recruits (see below!)
First reproduction	age of maternity [simulation time steps]
Reproduction interval	[simulation time steps]
Reproduction synchrony	
Dispersal traits	
Dispersal distance	[grid units]
Dispersal patch size	[grid units]
External drift	(migration possibility)
Lifetime traits	
Normal lifespan →mortality	[simulation time steps]
Maximal lifespan	[simulation time steps]
Other	
Growth on/ changes substrate	
Growth mode	

The following sections describe these traits in some more details:

10.2.2 General information

1.1.1.1 Species Name

The species name is used to identify the species to which an individual belongs

1.1.1.2 Guild

A species can belong to one of four guilds. The possible guilds are: R0, R1, R2 and UD. These guild names are arbitrary. This association is not necessary and can be undefined (guild “*”). The guild information can be used to define succession states and to assign a succession state to a grid cell.

1.1.1.3 POV-Output

This is used when a snapshot of the simulation is saved as POV[3]-file for 3D output.

1.1.1.4 Colour

This is the colour used for graphical representation of an individual. Although it is not necessary, SIMBAA tries to assign each species a unique colour based on its position in the species list.

10.2.3 Reproductive Traits

SIMBAA does not include detailed information about an individual’s sex. It is assumed that all individuals are capable of reproduction. Thus species in SIMBAA reproduce either vegetative or by parthenogenesis. In case of modelling a species with different sex, individuals represented by SIMBAA must be seen as the reproductive active sex (most commonly female) and that fertilisation is not limited.

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[3] POV (Persistence Of View) is a freeware raytracer. Raytracer can render photo realistic pictures of scenes. SIMBAA is capable to write a simulation snapshot in the POV scene description language (SDL). These scene files can be used to render a realistic 3D view of the simulation. However, the scene files may require extensive manual refinement, so the user needs good knowledge of the POV SDL and experience in this field.

1.1.1.5 Fecundity

This is a fractional number, roughly representing the per capita number of possible recruits rather than the real fecundity. SIMBAA does not model real larvae trajectories nor does it include larval mortality. Thus this species trait represents the number of possible recruits taking part in the competition for space after they have completed their dispersal phase and have become competent for recruitment.

In nature the number of produced larvae may be enormous, but only a fraction of these become competent and only an even smaller fraction of these will really recruit. This last phase, the recruitment, modelled in SIMBAA and in some more detail explained when the lottery competition is explained.

1.1.1.6 First reproduction

This is the time period in simulation time steps an individual needs to become maternal after recruitment.

1.1.1.7 Reproduction interval

This is the time period in simulation time steps between two consecutive larvae releases of an individual. This is normally based on the age of an individual. SIMBAA can be initialised in a special way thus that all individuals of a particular species are in the same reproduction phase. Thus it is possible to create a reproductive separation in time for different species. It is also possible to force a synchronisation on model time. Then the reproduction interval is triggered when the simulation time is dividable by the reproduction interval.

1.1.1.8 Reproduction synchrony (experimental feature)

This trait is only of interest when the species has a reproduction interval different from 1. In this case all individuals do not reproduce in each time step. Normally, the reproduction of a single individual is determined by its life cycle, i.e. the time since its last reproduction. When species are reproductively synchronised, many (or most) individuals reproduce at the same time. The reproduction synchrony gives quality of the synchronisation as probability of an individual’s reproduction cycle to be in phase with the whole population. 100% means that an individual will only reproduce when the reproduction interval is valid, whereas 90% means that any individual has a 10% chance to reproduce even when it is not in the reproduction cycle.

10.3 **Dispersal traits**

1.1.1.9 Dispersal Distance

This is the distance [in grid cells] all larvae of a specie originating from a specific grid cell travel together as a swarm. If one does not want the larvae to be distributed as a swarm, set this number to zero. This distance is modified (multiplied) by the flow speed of the originating cell.

1.1.1.10 Dispersal patch size

This is the diameter [in grid cells] of the area where the larvae of a swarm “reach” then simulation grid after dispersal and compete for space.

1.1.1.11 External drift

This is a switch that defines if a species has the potential to migrate from outside the grid. If enabled, you can globally define the probability of such a migration event and the maximal number of larvae migrating.

10.4 The dispersal in SIMBAA

SIMBAA does not follow each released larvae and does not simulate larval mortality. Instead it uses a simplified approach. It is assumed that all larvae of a species released in a specific grid cell become dispersed together as a swarm. As a time step in SIMBAA roughly represents a whole season and real larval dispersal may be completed within a shorter time, just the characteristic distance of this first dispersal phase is given as dispersal distance. Please note that SIMBAA only models simplified larval trajectories. Dispersal occurs always along a strait vector or line. The length and orientation of this vector is depended on the flow properties of the birth cell and the selected dispersal kernel (see below).

After the first dispersal phase it is assumed that the whole swarm becomes competent and sinks to the sea floor. The centre of this patch where the larvae land is defined by the dispersal distance. The diameter of the area is defined by the dispersal patch size. Figure 30 illustrates the principle dispersal mechanism and Formula 2 shows a pseudo-code for the algorithm in SIMBAA.

Dispersal mechanism used in SIMBAA

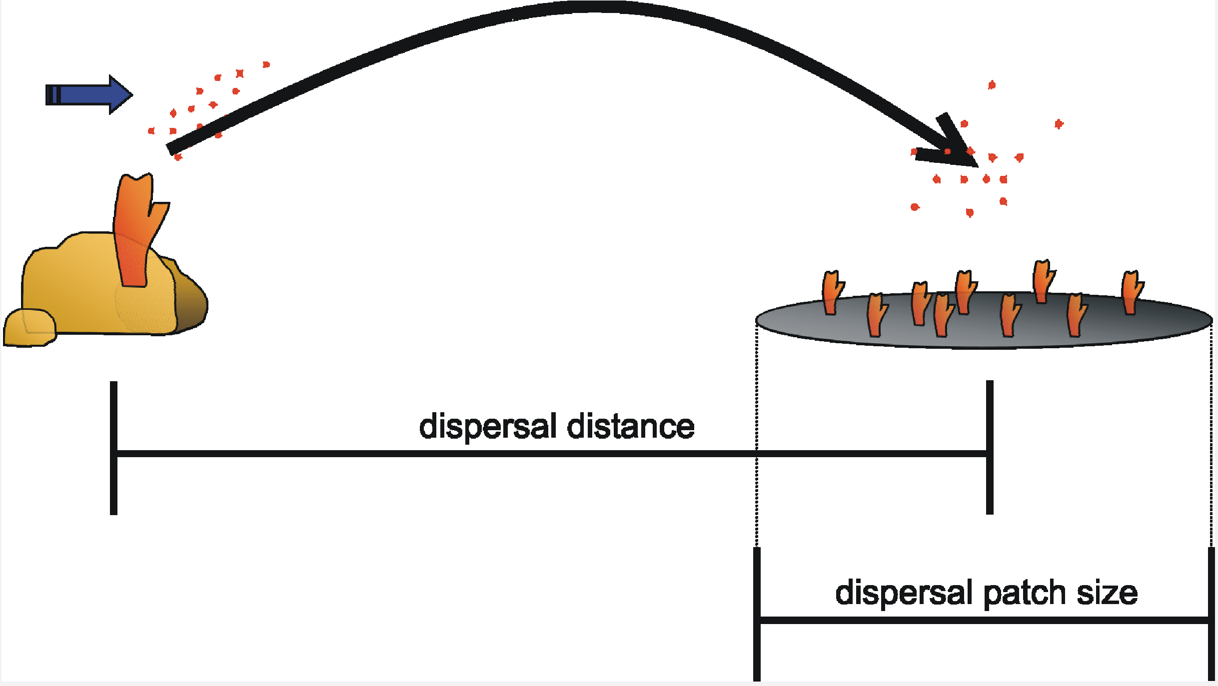
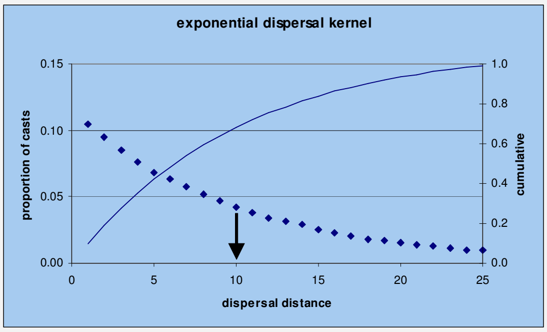
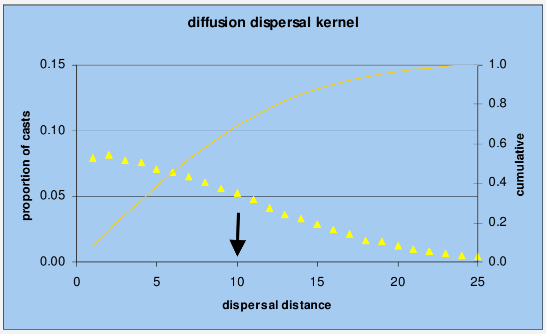
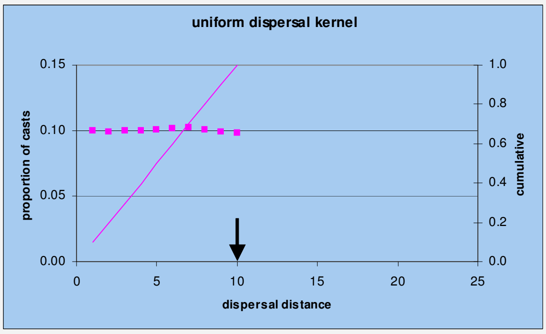


Figure 30, sketch of the dispersal mechanism used in SIMBAA. The mature individual on the left releases the larvae. A current (blue arrow) disperses the swarm over the “dispersal distance” to a new habitat on the right. Then the larvae swarm settles within a “dispersal patch size” area. Both dispersal distance and patch size are species-specific traits.

To compute the realised dispersal distance and the distribution within the dispersal patch, SIMBAA offers three different dispersal kernels: **exponential**, **diffusion** and **uniform**. These are descript in detail below. It is possible to select the kernels for the dispersal distance independently from the kernel for the patch size. However, these selections are global and it is (currently) not possible to select the kernels for each species independently.

The dispersal results in a local larvae pool for each single simulation grid cell. All larvae reaching a cell are colleted in this pool and compete for free space. Some recruit successful, however larvae that do not recruit die at the end of a time step. Thus no larvae live longer than one time step. For a detailed description of the recruitment process see the section lottery competition below.

10.4.1 Overview of dispersal kernels available in SIMBAA:

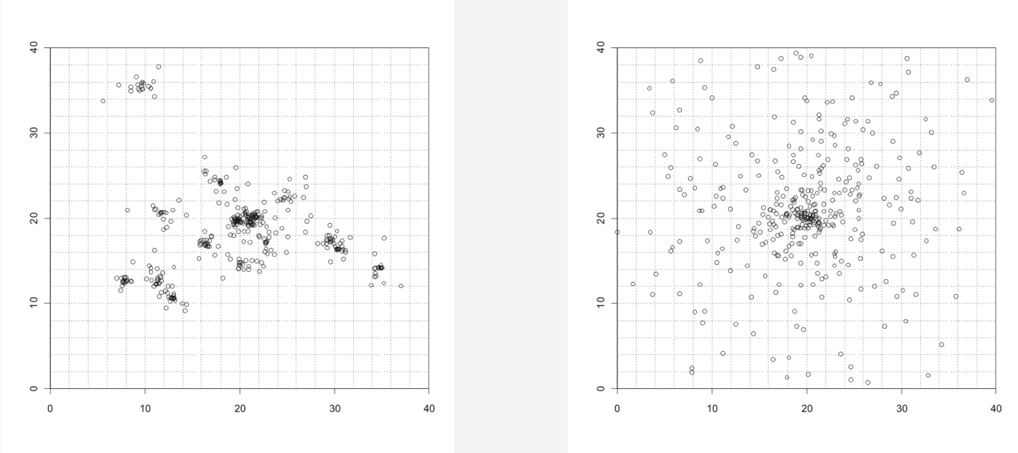
Dispersal Kernel	Description
	**Exponential dispersal kernel** Formula: `−ln(rnd) * d` Roughly ~70% of all casts are below d. Some extreme distances may occur, but rarely.
	**Diffusion kernel** Formula: `norm_rnd * d` Similar, ~70% of all casts have shorter distances and extreme values are possible but less likely than with an exponential kernel.
	**Uniform kernel** Formula: `rnd * d` All distances are uniform distributed between 0 and d. No values higher than d can occur.
The examples assume a dispersal distance=10. Dots represent the realized dispersal distance, lines the cumulative distribution. (10000 cast each).	d= dispersal distance rnd= uniform random number between 0 and 1 norm_rnd = normal distributed random number (μ=0, φ=1)

Dispersal Algorithm of SIMBAA

```
• count larvae of a species released from a position (X)
• determine flow speed and flow direction (s, $\alpha$ ) of X
• compute centre of dispersal patch (CODP) according to
  the dispersal distance (d), dispersal kernel ($f_{kernel}$),
  flow speed and flow direction

  → $(CODP = X + f_{kernel}(s*d,\alpha))$

• distribute each larvae around CODP according to the
  patch kernel ($f_{patch}$) and patch size (ps)

  → $(larva\ position=COPD + f_{patch}(s*ps,\alpha))$
```

Formula 2, Pseudo-code for the dispersal mechanism of SIMBAA

Example of a dispersal pattern generated by SIMBAA



Clumped dispersal

Isotropic dispersal

Figure 31, Both pictures show the final larvae pattern resulting from repetitively (10x) distributing same number of larvae (10) from the centre of the pictures. An exponential kernel was used both for dispersal distance and patch size. The flow speed was 1 and no specific flow direction was given (e.g. direction = any angle, deviation ±360°). The difference between both pictures was that in the right picture the dispersal distance was set to zero, so no larvae where distributed as swarm. Patch size was set to 10. Instead in the left picture patch size was set to 1 and dispersal distance to 10. This resulted in the patch distributed larvae clusters whereas in the first case no clusters apart from the origin can be observed.

1.1.1.12 Migration, external drift

SIMBAA offers the possibility of an external larvae pool independent on the actual simulation situation. From this outside pool a migration or external drift of larvae can occur. As the external pool is independent on the simulation it may contain larvae of species that have actually become extinct in the simulation.

The probability of such a migration event is globally defined. Each time step and for each cell it is individually checked, if such an event occurs. If so, the number of larvae is determined (draw from a uniform random distribution between 1 and a user defined max) and the according number of larvae is added to local larvae pool of that cell. The species of these larvae are randomly chosen out of the species that are capable of external drift.

1.1.1.13 Lottery competition

In SIMBAA competition and interaction between individuals occurs only in the settlement phase. Once established, individuals do not interact with each other. SIMBAA does not include a detailed competition module. It uses the simplest competition model available: lottery competition. This means that all larvae in a local larvae pool of each cell compete for available space in that cell. If there is space, either by the death of established individuals or due to a disturbance event, one larva out of the local pool is randomly selected and allowed to recruit. All larvae in the pool have the same chance to win. The established larva is removed from the pool. If there is still free place this procedure is repeated until either no free space is left or the local larvae pool is depleted. At the end of a time step, all local larvae pools are cleared. Thus no larvae are carried over into the next time step.

10.4.2 Lifespan / mortality

SIMBAA uses a special approach to determine the mortality of an individual. The user can define a “normal life span”. From recruitment at age 0 until this time an individual has a fixed mortality. The exact mortality can be given an absolute number. However, SIMBAA offers the possibility to simply define what proportion of a population (survival rate) shall reach this age and then computes the **instaneous mortality** according to Formula 3:

$$instaneous\ mortality = \frac{-\ln(survival\ rate)}{normal\ life\ span}$$

Formula 3, computation of instaneous mortality

If an individual becomes older than the defined “normal life span”, is mortality rises linear until it reaches “1” with the age “maximal life span”. Figure 32 illustrates the mortality of an individual during its life:

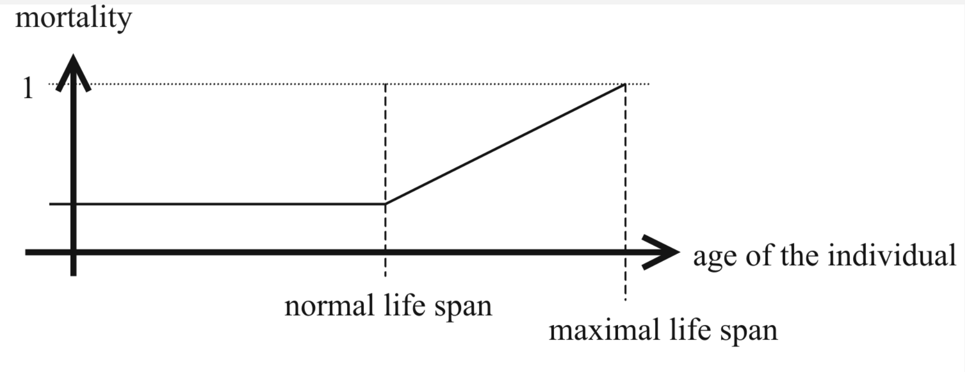
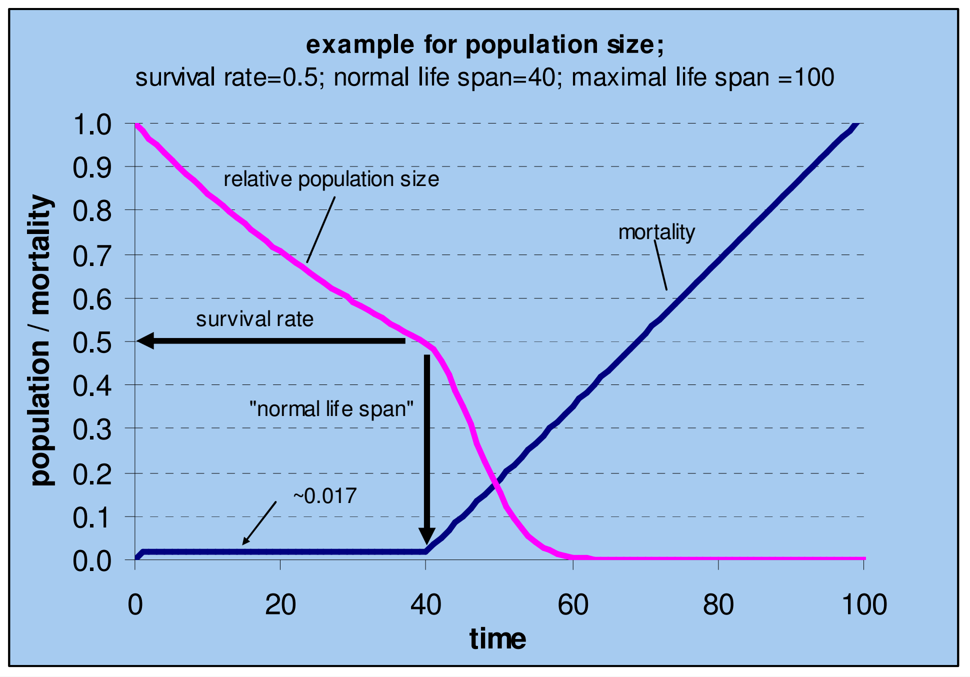


Figure 32, mortality computation in SIMBAA

NOTE:

When *selecting survival rate = 0.5* the “normal life span” is equal to the average life span!

Example calculation of population size & mortality:



Survival rate = 0.5

Normal life span = 40

Maximal life span = 100

Mortality = -ln(0.5) / 40

~ 0.0173

While an individual is younger than 40 time steps its mortality is constant (~0.0173). Between an age of 40 to 100 time steps, the mortality raises linear with a rate of (1-0.0173)/(100-40)~ 0.0164 per time step. However, rarely any individual becomes older than 60 time steps.

10.4.3 Other species traits

1.1.1.14 Growth on/ changes substrate

This mechanism offers a possibility to mimic substrate specific features. These features are implemented as simple binary (“enabled-disabled”) switches. In total 8 different substrate switches S_1-S_8 are available. Each species can have special demands on the substrate conditions (“growth on”-conditions). When an individual of a species becomes older than its “normal life span”, it alters the substrate state according to a defined rule (“changes to”-rules).

! **NOTE:** !

The “changes to” rule is technically implemented as a XOR-operation! The following examples assume that □=disabled and ■=enabled.

Rule	Sediment condition	“Changes to”	→Resulting state
A	□	□	□
B	□	■	■
C	■	□	■
D	■	■	□

A disturbance resets all substrate switches to the first switch (S_1=enabled). By default, all species can life on S_1. If more than one species lives inside a cell, all possible interactions are summed up and work together:

“changes to”	S_8	S_7	S_6	S_5	S_4	S_3	S_2	S_1
Species A	□	□	□	□	□	□	□	■
Species B	□	□	□	□	□	□	□	■
Species C	□	□	□	□	□	■	■	□
Result	□	□	□	□	□	■	■	■

Some examples:

Example 1

	S_8	S_7	S_6	S_5	S_4	S_3	S_2	S_1
growth on	☐	☐	☐	☐	☐	☐	☐	■
changes to	☐	☐	☐	☐	☐	☐	☐	☐

This is the default. A species with this schema will grow on a substrate S_1 and does not change it. As (by default) all cells have substrate state S_1 enabled and disturbances reset the state to S1 this is equivalent to a situation where no sediment properties are relevant.

Example 2

	S_8	S_7	S_6	S_5	S_4	S_3	S_2	S_1
growth on	☐	☐	☐	☐	☐	☐	☐	■
changes to	☐	☐	☐	☐	☐	☐	■	■

In this example the species will also grow on S1. However, if it becomes older than its “normal life span” it will alter the switches S_1 and S_2. As S_1 is enabled (probability, as it is necessary for the recruitment of the species), it will turn off the S_1-state (rule D). When S_2 was disabled it will also turn on S_2 (rule B). In this example the species is likely to prepare the sediment conditions for S_2 and, when older than its normal life span, hinders its own species to recruit at this particular place.

10.4.4 Growth mode

The growth mode determines how the age is translated into an individual's size. This information is only used for visualisation purpose and does not influence the simulation. The user can select two different growth modes:

1.1.1.15 Linear growth: (default)

This is the default growth mode. The size is linear to the age, respectively to the "normal life span" when it becomes "max size". If an individual becomes older than "normal life span" the size does not grow further.

1.1.1.16 Exponential growth:

The size growth is exponential with age. When selecting this growth mode, the user must give a growth factor and a maximal growth. Formula 4 is used to compute the size:

$$size = \max size * (1 - \exp\left[\frac{-\,growth\ factor}{\left(\dfrac{100 * age}{\max life\,span}\right)}\right])$$

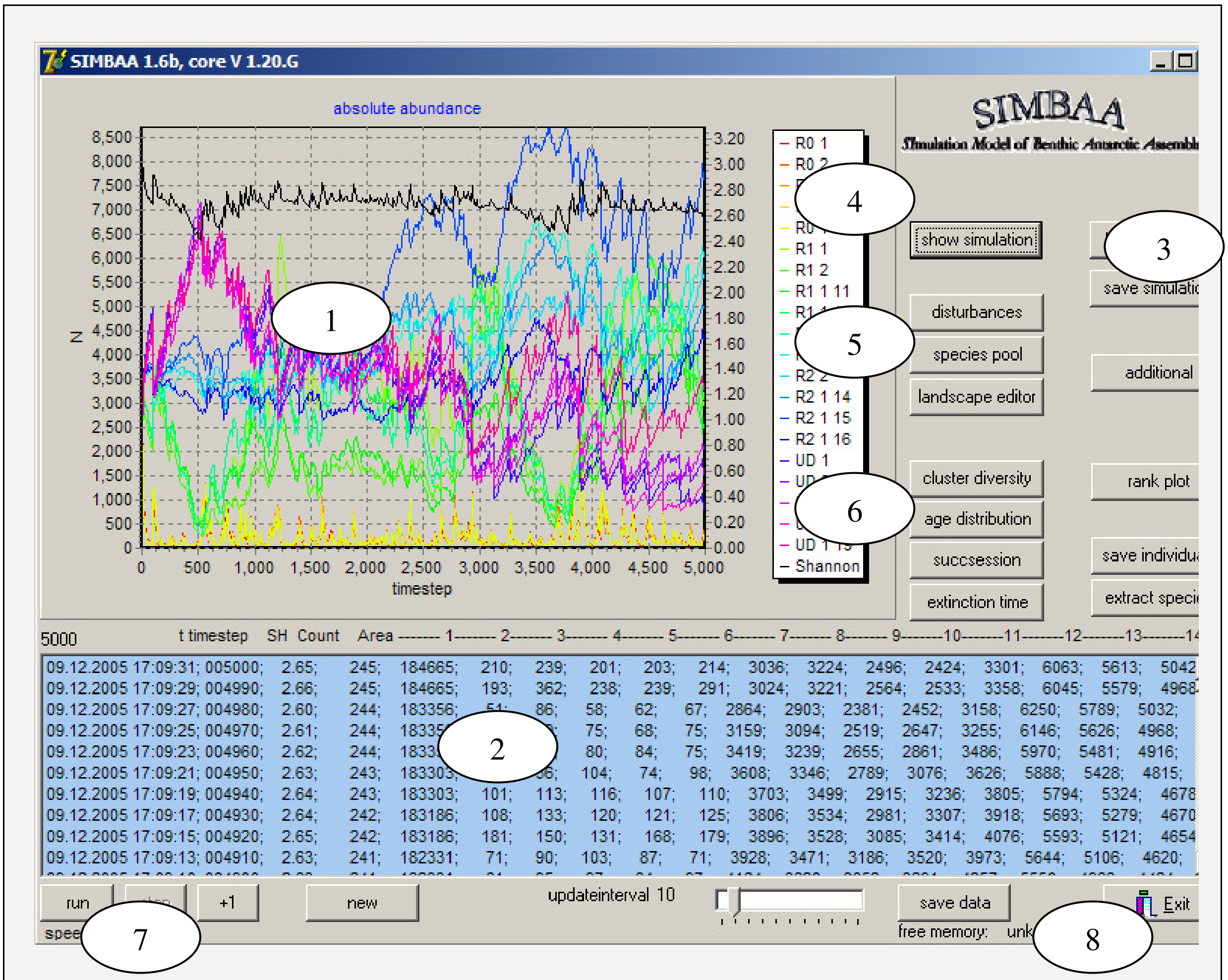
Formula 4, exponential growth function

10.5 The SIMBAA Graphical User Interface (SIMBAA-GUI)

The SIMBAA GUI is the main user interface for the simulation program. Simulations can be created, executed and evaluated on the Windows-desktop using this interface. When the program is started, first an info-screen is shown and then the main window (Figure 27) is loaded.

The following sections will show a screen-shot of the several windows used to interact with SIMBAA. A short explanation will be given. Circles with inscribed numbers make interface elements that are further descript in the text.

10.5.1 The main window

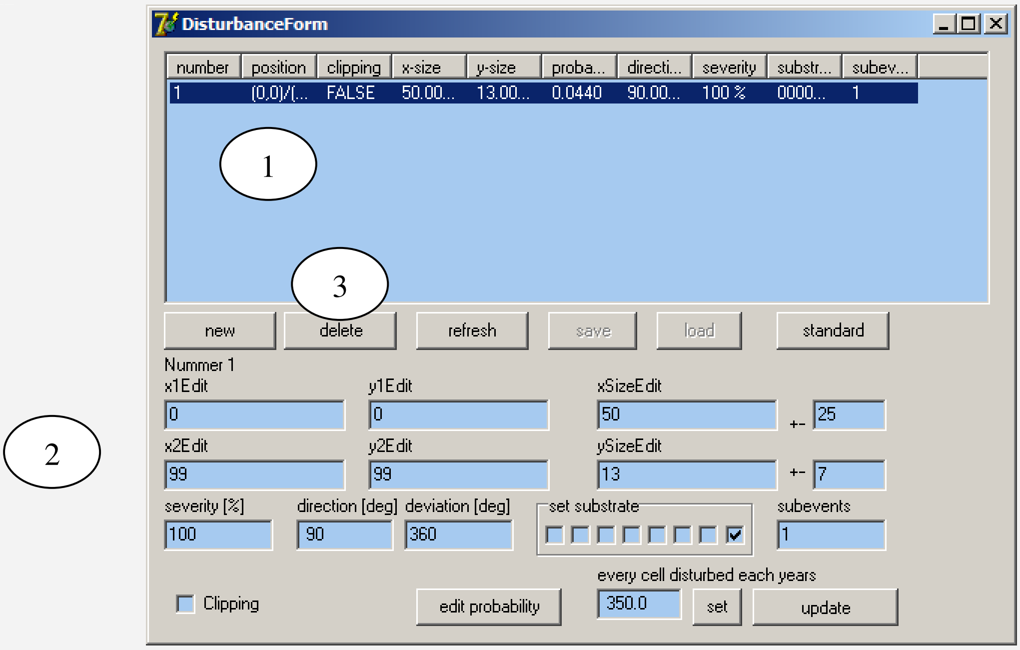


```
5000            t timestep   SH  Count   Area ------- 1------- 2------- 3------- 4------- 5------- 6------- 7------- 8------- 9-------10-------11-------12-------13-------14
09.12.2005 17:09:31; 005000;  2.65;    245;  184665;  210;  239;  201;  203;  214;  3036;  3224;  2496;  2424;  3301;  6063;  5613;  5042
09.12.2005 17:09:29; 004990;  2.66;    245;  184665;  193;  362;  238;  239;  291;  3024;  3221;  2564;  2533;  3358;  6045;  5579;  4968
09.12.2005 17:09:27; 004980;  2.60;    244;  183356;   51;   86;   58;   62;   67;  2864;  2903;  2381;  2452;  3158;  6250;  5789;  5032;
09.12.2005 17:09:25; 004970;  2.61;    244;  18335                75;   68;   75;  3159;  3094;  2519;  2647;  3255;  6146;  5626;  4968;
09.12.2005 17:09:23; 004960;  2.62;    244;  1833                 80;   84;   75;  3419;  3239;  2655;  2861;  3486;  5970;  5481;  4916;
09.12.2005 17:09:21; 004950;  2.63;    243;  183303;        56;  104;   74;   98;  3608;  3346;  2789;  3076;  3626;  5888;  5428;  4815;
09.12.2005 17:09:19; 004940;  2.64;    243;  183303;  101;  113;  116;  107;  110;  3703;  3499;  2915;  3236;  3805;  5794;  5324;  4678
09.12.2005 17:09:17; 004930;  2.64;    242;  183186;  108;  133;  120;  121;  125;  3806;  3534;  2981;  3307;  3918;  5693;  5279;  4670
09.12.2005 17:09:15; 004920;  2.65;    242;  183186;  181;  150;  131;  168;  179;  3896;  3528;  3085;  3414;  4076;  5593;  5121;  4654
09.12.2005 17:09:13; 004910;  2.63;    241;  182331;   71;   90;  103;   87;   71;  3928;  3471;  3186;  3520;  3973;  5644;  5106;  4620;
```

Figure 33, Main SIMBAA window elements:

1. Visualisation of the development of the population structure over time
2. List of population structure and other simulation parameter
3. Buttons to load/save the current simulation
4. Open the spatial visualisation tool window
5. Edit simulation parameter, e.g. disturbances, species pool, landscape
6. Different analyse functions
7. Start/stop the current simulation
8. Exit the programme

10.5.2 The disturbance editor



number	position	clipping	x-size	y-size	proba...	directi...	severity	substr...	subev...
1	(0,0)/(...	FALSE	50.00...	13.00...	0.0440	90.00...	100 %	0000...	1

Nummer 1

x1Edit: 0

y1Edit: 0

xSizeEdit: 50 +- 25

x2Edit: 99

y2Edit: 99

ySizeEdit: 13 +- 7

severity [%]: 100

direction [deg]: 90

deviation [deg]: 360

set substrate: ☐ ☐ ☐ ☐ ☐ ☐ ☐ ☑

subevents: 1

☐ Clipping

every cell disturbed each years: 350.0

Figure 34, The disturbance editor window

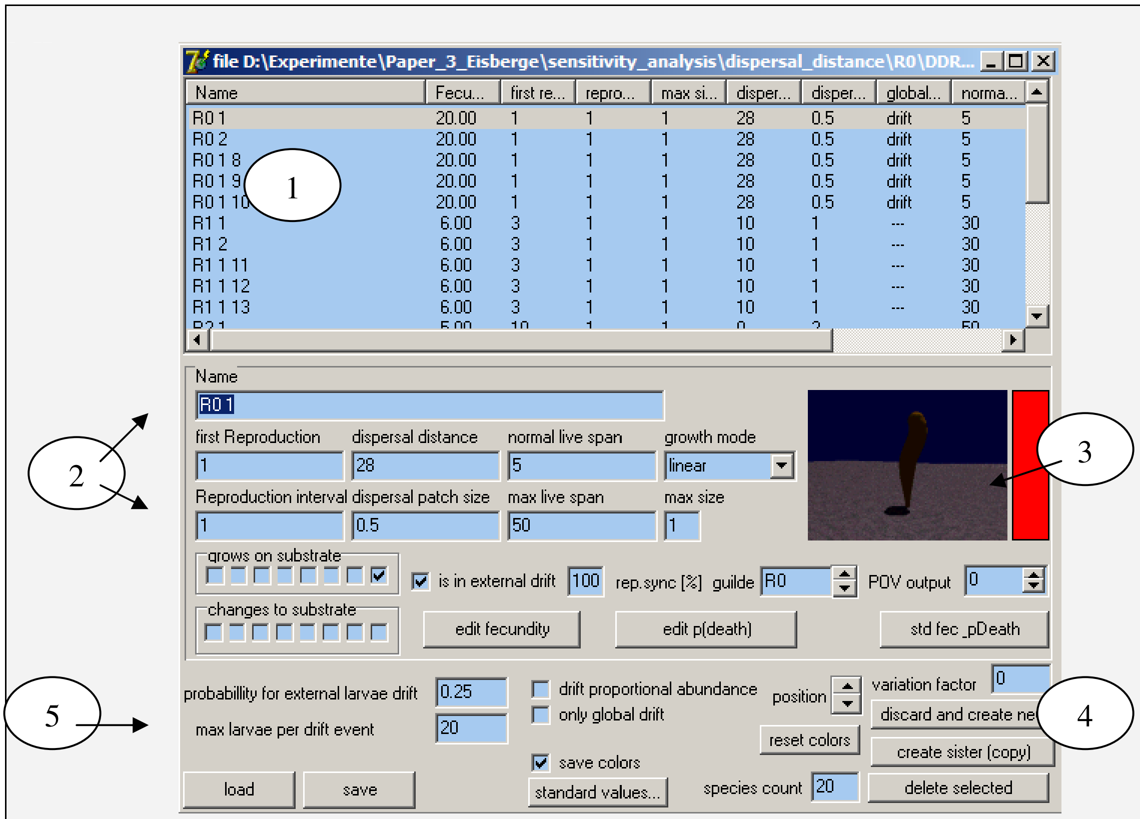
When selecting the button "**disturbance**" in the main window (Figure 33) the disturbance editor is opened (Figure 34). This editor is used to create, change and delete disturbance events. In the upper part (1) all defined disturbance events are listed. The user can select one disturbance out of the list by a double-click. Then the information (2) is updated. On the left side, the area where the disturbance may start [(x1/y1) - (x2/y2)] and clipping can be defined. The disturbance size can be edited on the right part of the panel. In the lower row disturbance severity, directional information, resulting substrate state and number of sub-events can be entered.

The rotation period can be directly entered. Please use "set" to calculate the according probability. However, it is also possible to enter the disturbance probability directly by the "edit probability"-button. Then a new input window is opened.

Please use the "update"-button, especially when it is coloured in red, to update the disturbance definition.

(3) gives you the possibility to create a new disturbance with the information of the edit-panel ("new") or delete existing disturbances form the list.

10.5.3 The species editor


file D:\Experimente\Paper_3_Eisberge\sensitivity_analysis\dispersal_distance\R0\DDR...

Name	Fecu...	first re...	repro...	max si...	disper...	disper...	global...	norma...
R0 1	20.00	1	1	1	28	0.5	drift	5
R0 2	20.00	1	1	1	28	0.5	drift	5
R0 1 8	20.00	1	1	1	28	0.5	drift	5
R0 1 9	20.00	1	1	1	28	0.5	drift	5
R0 1 10	20.00	1	1	1	28	0.5	drift	5
R1 1	6.00	3	1	1	10	1	---	30
R1 2	6.00	3	1	1	10	1	---	30
R1 1 11	6.00	3	1	1	10	1	---	30
R1 1 12	6.00	3	1	1	10	1	---	30
R1 1 13	6.00	3	1	1	10	1	---	30

Name: R0 1

first Reproduction: 1
dispersal distance: 28
normal live span: 5
growth mode: linear
Reproduction interval: 1
dispersal patch size: 0.5
max live span: 50
max size: 1

grows on substrate: ☐ ☐ ☐ ☐ ☐ ☐ ☐ ☑
changes to substrate: ☐ ☐ ☐ ☐ ☐ ☐ ☐ ☐

☑ is in external drift
100 rep.sync [%]
guilde: R0
POV output: 0

probabillity for external larvae drift: 0.25
max larvae per drift event: 20
☐ drift proportional abundance
☐ only global drift
☑ save colors
variation factor: 0
species count: 20

Figure 35, The species editor window

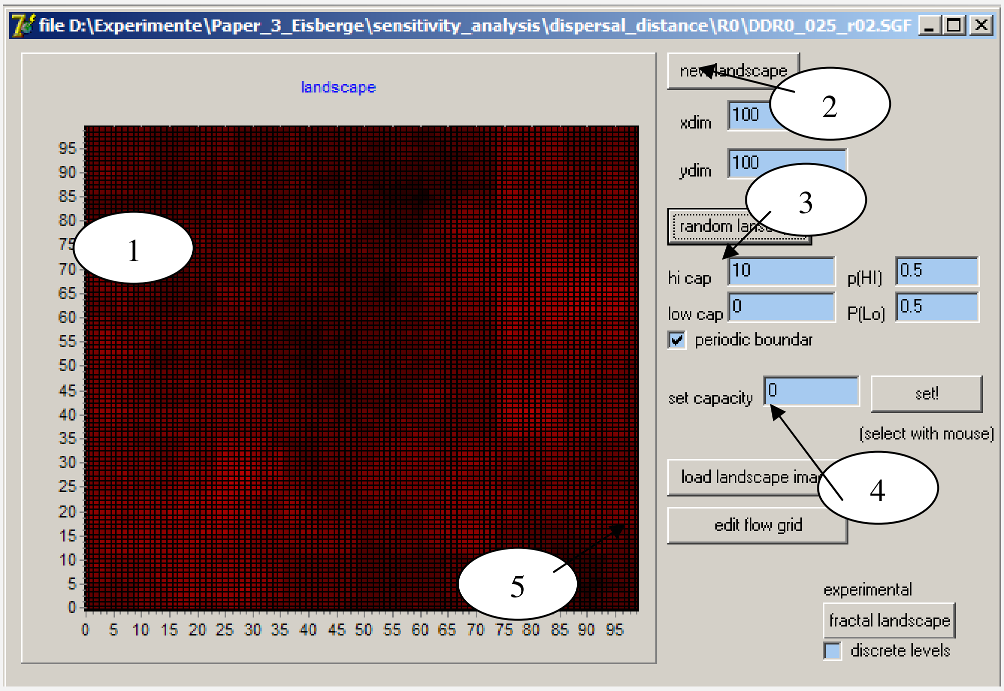
When selecting “species pool” in the main window (Figure 33), the species pool editor is opened (Figure 35). Using the species editor all species traits can be controlled. For a detailed description of all species traits see preceding chapter.

The upper panel (1) lists all defined species with their traits. By a click in this list a species can be selected. The traits of the selected species can be edited in the middle panel (2). The buttons “edit fecundity” and “edit p(death)” open new input windows to edit fecundity, respectively mortality. On the right side, a graphical representation is shown and colour information is shown (The picture shows a early version of the POV output). By default, SIMBAA tries to assign each species a unique colour in the spectrum, determined by the position in the species list. A click on the colour bar opens a standard colour dialog, where the user can select the colour. The lower right part of the panel (4) contains elements to control and manipulate the pool. With the position-buttons, the currently selected species can be moved up and down in the list. “reset colours” re-calculates the colour scheme according to the current species order. If “save colors” is not selected, the colour information is not saved in the simulation file and recalculated on loading each time.

“Discard and create new” removes the current species pool and creates a new one with “species count” species. “create sister” and “deleted selected” create a copy of the current selected species, respectively removes the selected species from the pool.

On the bottom left the global drift (migration) properties can be modified. Please see the dispersal chapter for more details. You can define the probability for a migration event and the maximal number of larvae added to the local larvae pool in case of such an event. If “drift proportional abundance” is selected, the probability for a species to occur in the global drift is proportional to its (global) abundance. When “only global drift” is selected, no explicit larval dispersal is computed (**thus SIMBAA’s dispersal model is turned off**) and only global drift is used.

10.5.4 The landscape editor



file D:\Experimente\Paper_3_Eisberge\sensitivity_analysis\dispersal_distance\R0\DDR0_025_r02.SGF

xdim 100

ydim 100

hi cap 10

p(HI) 0.5

low cap 0

P(Lo) 0.5

☑ periodic boundar

set capacity 0

☐ discrete levels

Figure 36, The landscape editor

The landscape editor (Figure 36), where the simulation grid is defined is opened by the button “landscape editor” in the main window (Figure 33). On the left panel (1), the complete simulation grid is shown. Different shades of red indicate the cell capacity. As lighter the colour, as higher the cell capacity (number of individuals, the cell can support). A white colour represents matrix cells with a zero capacity. These cells do not support any individual and will remain empty. On the right panel, the simulation grid size can be defined (2). If you create a new landscape, all cells will start with a zero capacity!

! **NOTE:** **!**

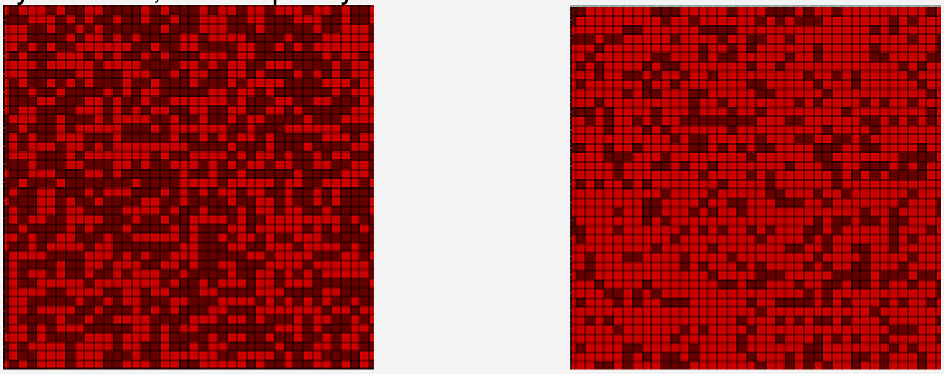
Changing the simulation grid clears all disturbance event definitions!

You can now create a random distribution of the cell capacity (3). SIMBAA supports “high capacity” sites and “low capacity” sites. These are distributed according to the given probabilities. Note: if you change a probability, the other is automatically updated! You can also define the capacity of a rectangular area by hand (4). Enter the desired capacity and click on “set” Then select the area be pressing the left mouse and dragging while keeping the mouse button pressed. Use the “edit flow grid” button (5) to invoke the flow grid editor (see below).

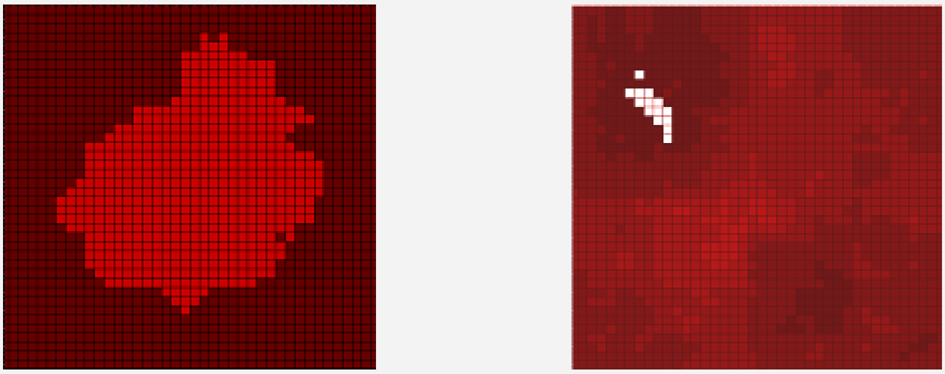
As experimental feature you can use a midpoint displacement algorithm (commonly known as “fractal” landscape generation algorithm) to create spatial correlated distribution of the cell capacities. When “discrete levels” is enabled, only “high capacity” and “low capacity” cells are created. When disabled, all integer values between “low” and “high” are used.

You can also load a bitmap with the capacity information encoded as grey scales. The picture is internally converted into grey scale (if coloured) and scaled to fit the simulation grid. The cell capacity is set between “low cap” and “high cap” according to the grey value. As darker the grey value, as higher the resulting cell capacity. A white colour in the image will result in a matrix cell with zero capacity. See the example below.

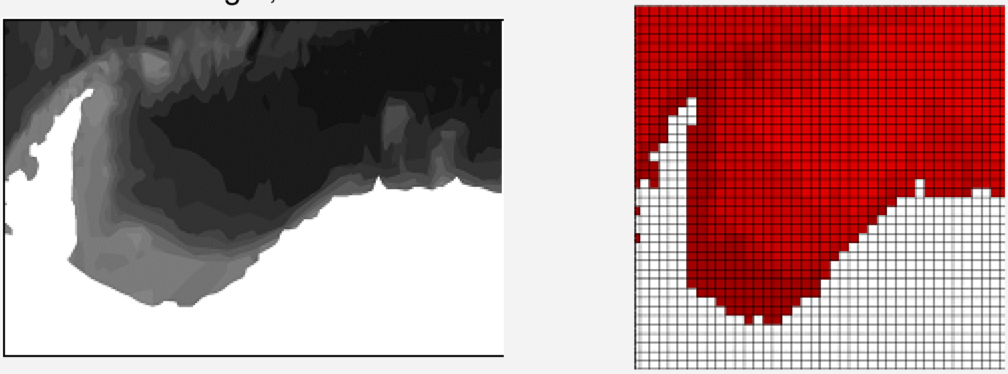
Examples of capacity distribution maps created by different approaches. “Hi capacity” was 10, “low capacity”= 5 in all cases.



Random capacity maps with different probabilities. On the left, both cell types have the same probability (0.5 each). On the right, the high capacity sites (light red) have a probability of 0.75 and the low capacity sites accordingly 1-0.75 = 0.25.

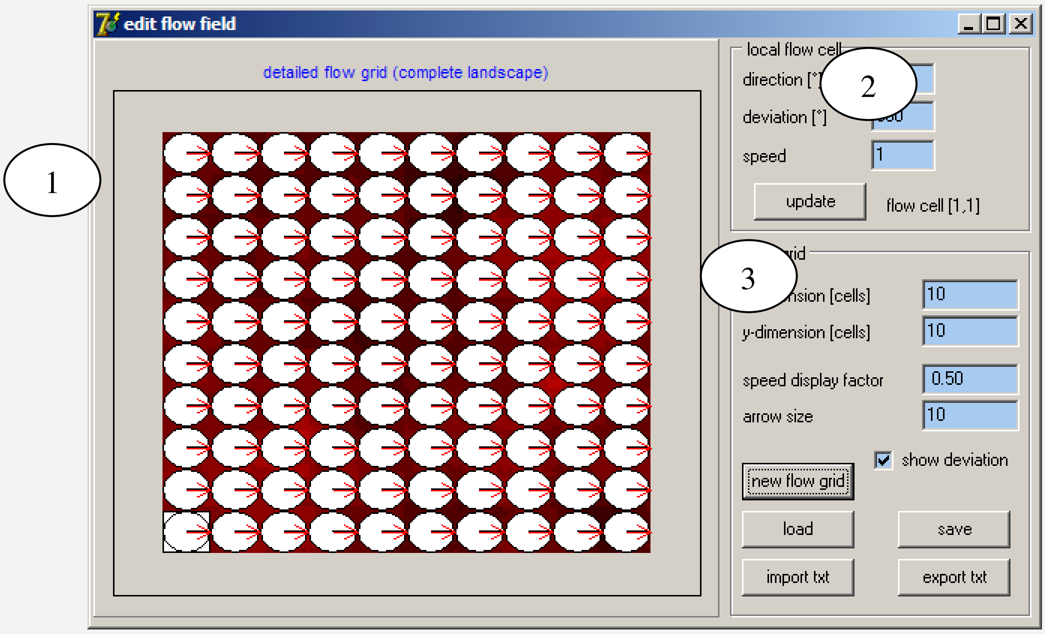


Example of “fractal” capacity maps. On the left “discrete level” was used, whereas on the right, all levels are used.



This is an example for a grey scale image loaded as information source for the capacity of the landscape. The image is a depth map of the Weddell Sea, thus the depth information will be encoded as capacity. Note the stretching as the image is rectangular but the simulation grid is quadratic. The white area of the image (shelf ice and land region) is translated in matrix cells with zero capacity, the darker grey colours in higher capacities.

10.5.5 The flow editor



direction [°]

deviation [°]

speed 1

flow cell [1,1]

nsion [cells] 10

y-dimension [cells] 10

speed display factor 0.50

arrow size 10

☑ show deviation

Figure 37, The flow grid editor

This editor window (Figure 37) is displayed when the “**edit flow grid**”-button of the landscape editor (Figure 36) is pressed. The left panel (1) shows a picture of the simulation grid (cell capacities as shades of red) and the flow direction, represented by an arrow. The length and orientation of this arrow are proportional to the flow speed and direction of the flow in that cell. If the “show deviation” checkbox is checked, the deviation is displayed as sector (see above).

To select a flow cell, click on the corresponding arrow. A white frame highlights the selected flow cell and in the upper right panel (2) the flow properties of the selected cell is shown and accessible.

In the lower right panel (3) you can define the size of the flow grid. You can also load and save the flow grid and export/ import as text file. If you create a new flow field, all flow cells will contain the flow properties defined in the upper panel.

The “speed display factor” and “arrow size” are just used to display the flow field. If you have different flow speeds, you can use the first to scale the length of the arrow, the second parameter determines the size of the arrows point.

10.5.6 The visualise tool window

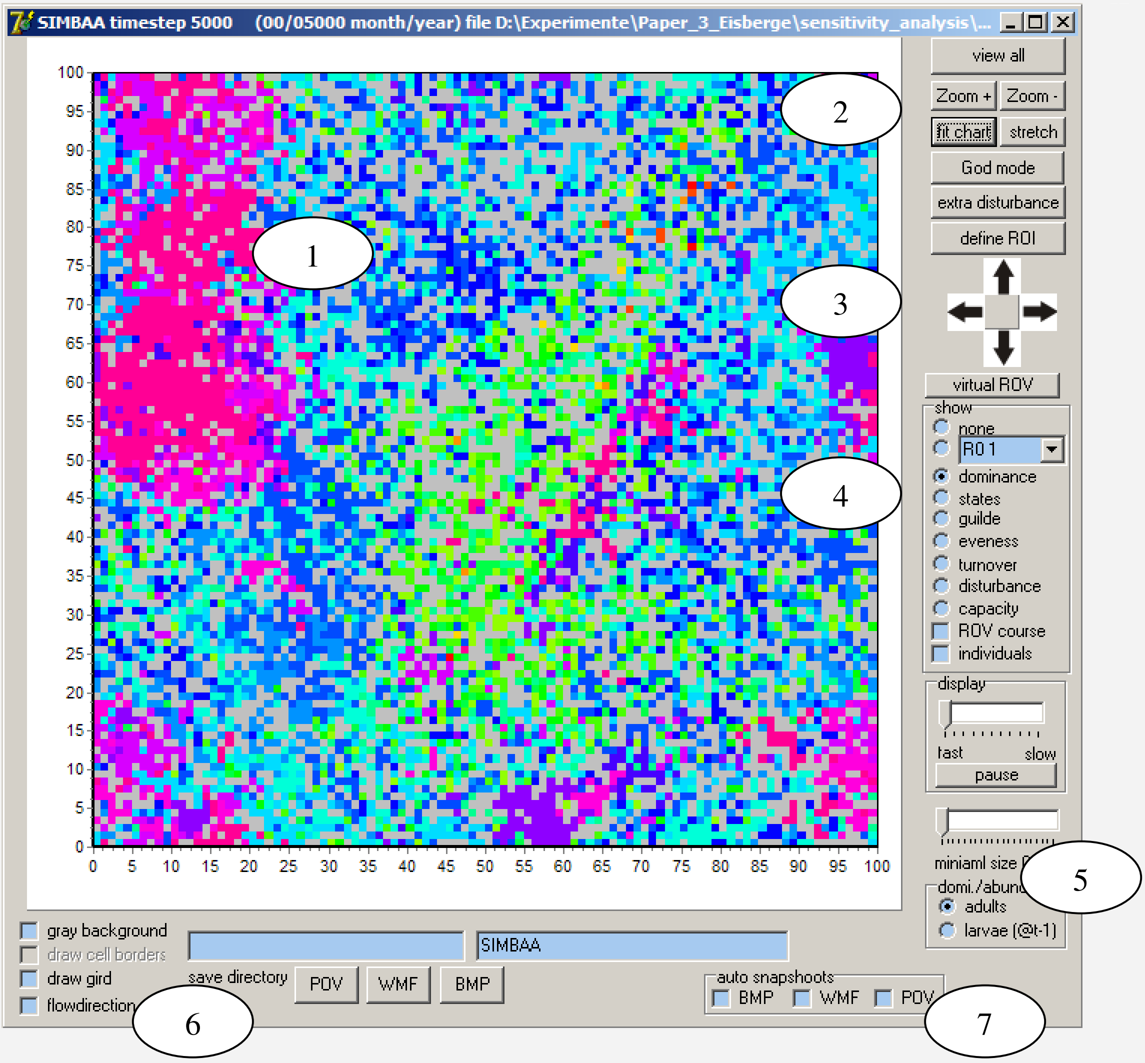


Figure 38, The visualisation tool window

This is the main visual inspection tool. You can check the simulation grid and display various aspects of a simulation run. The main panel (1) shows a graphical representation of the grid. It is possible to zoom (left-button) and pan (right-button) the image by the mouse or the cursor buttons. With the buttons in the upper right (2) the user can reset the viewport to the whole simulation. The button “fit chart” tries to rescale the left panel to archive an aspect ration of 1:1 whereas “stretch” rescales the panel to use all available window space. You can also move the visual part by the cursor buttons (3). The view is updated on a regular interval (see main panel). However, if the simulation is not running or the update interval is too sparse, the middle button of (3) redraws the current view. If the simulation is too fast, the middle panel “display” can be used to slow down the redraw or even pause the simulation.

You can display various aspects using the middle right panel (4).

Display options:

None:	No cell information is displayed, only (when enabled) virtual ROV transect and individuals
Species:	Select a species of the drop-down list to display its spatial distribution. The intensity of the colour is proportional to the number of individuals of the species in a cell.
States:	Succession states according to the current state definition. **R0** is red, **R1** yellow, **R2** green and **UD** blue.
Guild:	Displays the dominant guild of a cell. Same colour-schema as above: R0 is red, R1 yellow, R2 green and UD blue.
Evenness:	Displays Pielou’s evenness *J’* based on the species composition of the cell. Colour scheme: like a spectrum with low evenness (few species) represented by cold (blue) and a high evenness (many species) as hot (red) colours.
Turnover:	Different shades of blue show the overall disturbance history of a cell. As darker as fewer disturbances events occurred at a cell.
Disturbances:	Show a detailed map of the disturbance history within a certain time period. As brighter the red colour as younger the disturbance is. Cells with have not been disturbed since a defined time (not the changing slider “minimal size” respectively “max age”!) are shaded grey.
Capacity:	Shows the cell capacity in different shades of red like in the landscape editor. Bright shades represent higher capacities.

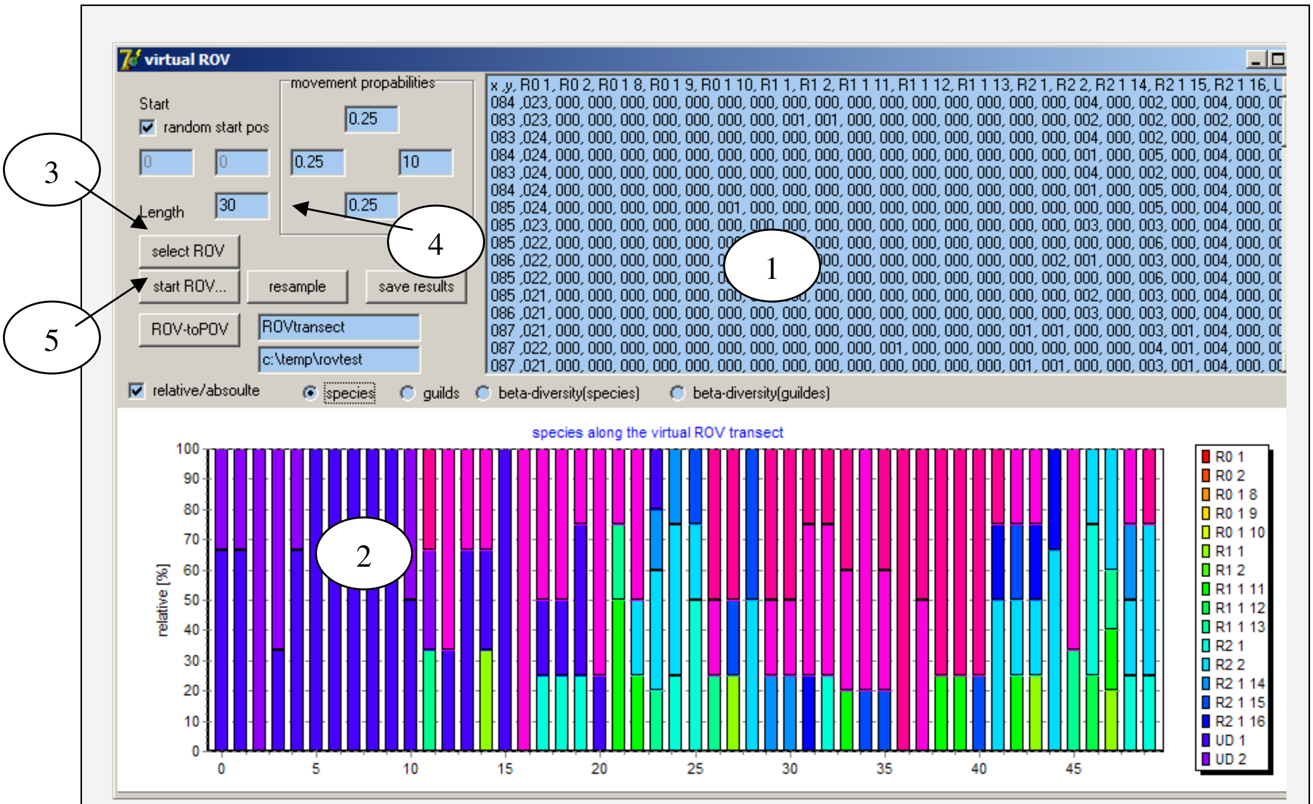
Switch “**ROV course**”: displays the current virtual ROV track as light blue line on top of the map

Switch “**Individuals**”: draw each individual as a circle. The colour of the circle represents the species and the diameter is proportional to the size of the individual (see growth-function). NOTE: drawing individuals can be quit time consuming and slows down the whole simulation!

It is possible to use either the abundance of established individuals over a certain size (slider “min size for visual”) or the larvae distribution **of the previous time step** (“larvae @t-1”) when displaying dominance and species pattern. **NOTE: the value “minimal size for visual” determines the size of any individual to be considered by several functions of the model and is used throughout the simulation. E.g. all individuals below this size are not considered for diversity measurements and not displayed as individuals and so!**

The lower panel (6) allows toggling various display options (e.g. cell border etc.). It is also possible to generate snapshots in various formats on demand or automatically, each time the map is redrawn. These are stored in the directory given by the first entry field “save directory” and with a filename consisting of the given name appended by the time step. Example: “save directory= “c:\simulation\snapshot\“, “name=TEST” and “BMP” will generate “test00000.bmp”, test00001.bmp” in the directory “c:\simulation\snapshot” and so forth. **Note the last slash in the save director!**

10.5.7 The virtual ROV



☑ random start pos
0 0
Length 30
0.25
0.25 10
0.25
ROVtransect
c:\temp\rovtest
☑ relative/absoulte ● species ○ guilds ○ beta-diversity(species) ○ beta-diversity(guildes)

```
x ,y, R0 1, R0 2, R0 1 8, R0 1 9, R0 1 10, R1 1, R1 2, R1 1 11, R1 1 12, R1 1 13, R2 1, R2 2, R2 1 14, R2 1 15, R2 1 16,
084 ,023, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 004, 000, 002, 000, 004, 000,
083 ,023, 000, 000, 000, 000, 000, 000, 000, 001, 001, 000, 000, 000, 000, 000, 000, 000, 000, 002, 000, 002, 000, 002, 000,
083 ,024, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 004, 000, 002, 000, 004, 000,
084 ,024, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 001, 000, 005, 000, 004, 000,
083 ,024, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 004, 000, 002, 000, 004, 000,
084 ,024, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 001, 000, 005, 000, 004, 000,
085 ,024, 000, 000, 000, 000, 000, 001, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 005, 000, 004, 000,
085 ,023, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 003, 000, 003, 000, 004, 000,
085 ,022, 000, 000, 000, 000, 000, [illegible], [illegible], [illegible], [illegible], 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 006, 000, 004, 000,
086 ,022, 000, 000, 000, 000, 000, [illegible], [illegible], [illegible], [illegible], 000, 000, 000, 000, 000, 000, 002, 001, 000, 003, 000, 004, 000,
085 ,022, 000, 000, 000, 000, 000, [illegible], [illegible], [illegible], [illegible], 000, 000, 000, 000, 000, 000, 000, 000, 000, 006, 000, 004, 000,
085 ,021, 000, 000, 000, 000, 000, 000, [illegible], [illegible], [illegible], 000, 000, 000, 000, 000, 000, 000, 002, 000, 003, 000, 004, 000,
086 ,021, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 003, 000, 003, 000, 004, 000,
087 ,021, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 001, 001, 000, 000, 003, 001, 004, 000,
087 ,022, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 001, 000, 000, 000, 000, 000, 000, 000, 004, 001, 004, 000,
087 ,021, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 000, 001, 001, 000, 000, 003, 001, 004, 000,
```

Figure 39, The virtual ROV

Figure 39 shows the virtual ROV[4] window. With the virtual ROV you can sample the simulation grid similar to a real ROV. The virtual ROV moves along a transect and samples each grid cell on its way and lists its species composition (1). From this a graphical representation is drawn, either on an absolute scale or relative to all cell individuals (2). It is also possible to show the β-diversity based on species respectively guild composition. In this case the first sampled cell is the reference.

The transect can be selected manually (3) or a correlated random walk is performed. When manual selection is desired, the user must select start and endpoint of the transect in the visualiser window by clicking the middle mouse button. Note that the transect is not drawn until selection is complete. When performing a correlated random walk either a random or a defined start position can be used and the length in cells along the transect must be given. Note that a random correlated walk can lead to respectively sample the same cell(s). The probabilities for directional changes

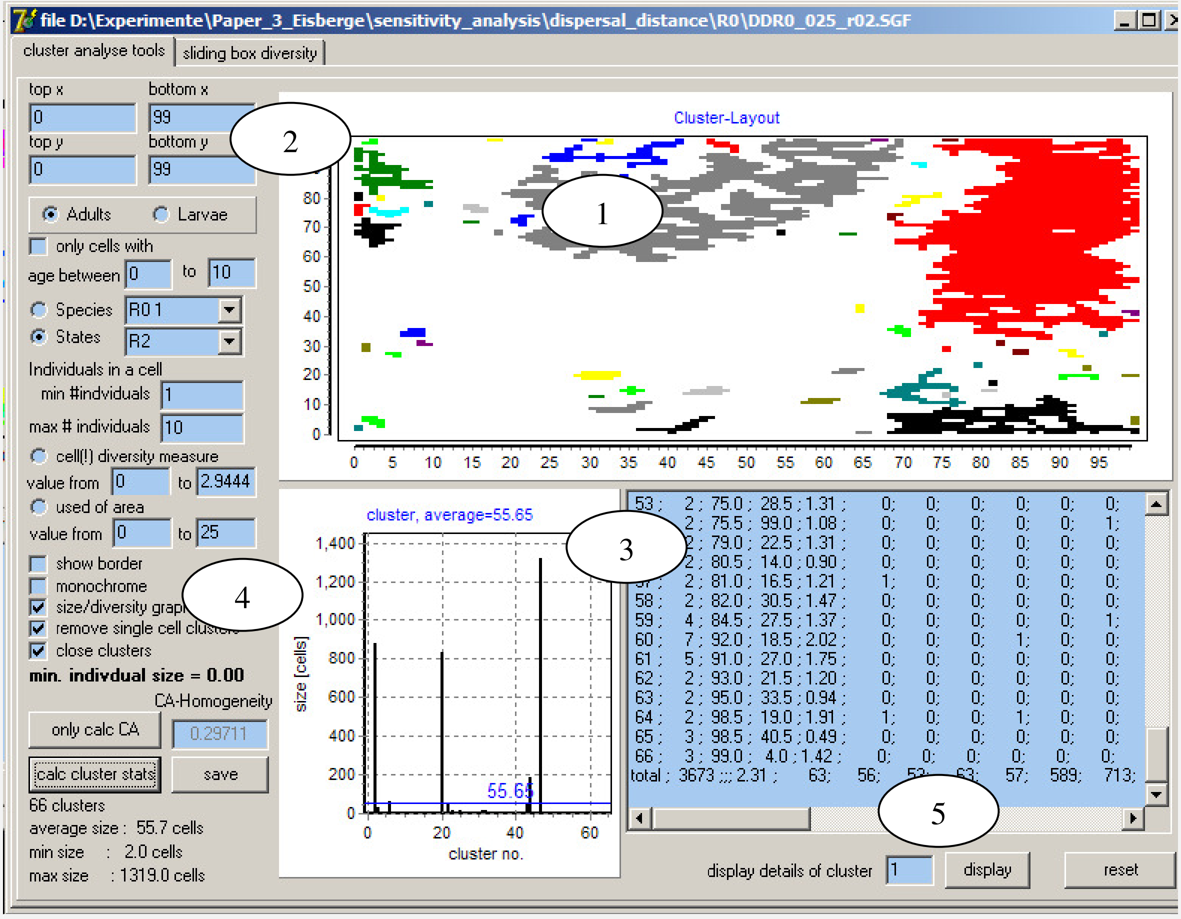
---

[4] ROV = remote operated vehicle, normally equiped with a camera. Used to sample tansects of the sea floor.

are normalised according to the given numbers (4). In the example the probability to move east is [10/(10+0.25+0.25+0.25)]~0.93 and ~0.02 for each other direction.

Once a transect has been created by starting the virtual ROV (5), it is stored in memory and can be re-sampled. This is very useful when following a temporal development. The results can be saved and an experimental feature allows to create a POV-scene file according to the transect data.

10.5.8 Cluster analysis tool



top x: 0
bottom x: 99
top y: 0
bottom y: 99

● Adults ○ Larvae

☐ only cells with age between 0 to 10

○ Species R0 1

● States R2

Individuals in a cell
min #indviduals 1
max # individuals 10

○ cell(!) diversity measure value from 0 to 2.9444

○ used of area value from 0 to 25

☐ show border
☐ monochrome
☑ size/diversity grap
☑ remove single cell cluste
☑ close clusters

min. indivdual size = 0.00

CA-Homogeneity 0.29711

66 clusters
average size : 55.7 cells
min size : 2.0 cells
max size : 1319.0 cells

```
53 ;   2 ; 75.0 ; 28.5 ; 1.31 ;     0;    0;    0;    0;    0;    0;
       2 ; 75.5 ; 99.0 ; 1.08 ;     0;    0;    0;    0;    0;    1;
       2 ; 79.0 ; 22.5 ; 1.31 ;     0;    0;    0;    0;    0;    0;
       2 ; 80.5 ; 14.0 ; 0.90 ;     0;    0;    0;    0;    0;    0;
       2 ; 81.0 ; 16.5 ; 1.21 ;     1;    0;    0;    0;    0;    0;
58 ;   2 ; 82.0 ; 30.5 ; 1.47 ;     0;    0;    0;    0;    0;    0;
59 ;   4 ; 84.5 ; 27.5 ; 1.37 ;     0;    0;    0;    0;    0;    1;
60 ;   7 ; 92.0 ; 18.5 ; 2.02 ;     0;    0;    0;    1;    0;    0;
61 ;   5 ; 91.0 ; 27.0 ; 1.75 ;     0;    0;    0;    0;    0;    0;
62 ;   2 ; 93.0 ; 21.5 ; 1.20 ;     0;    0;    0;    0;    0;    0;
63 ;   2 ; 95.0 ; 33.5 ; 0.94 ;     0;    0;    0;    0;    0;    0;
64 ;   2 ; 98.5 ; 19.0 ; 1.91 ;     1;    0;    0;    1;    0;    0;
65 ;   3 ; 98.5 ; 40.5 ; 0.49 ;     0;    0;    0;    0;    0;    0;
66 ;   3 ; 99.0 ;  4.0 ; 1.42 ;    0;    0;    0;    0;    0;    0;
total ; 3673 ;;; 2.31 ;    63;    56;                 57;   589;   713;
```

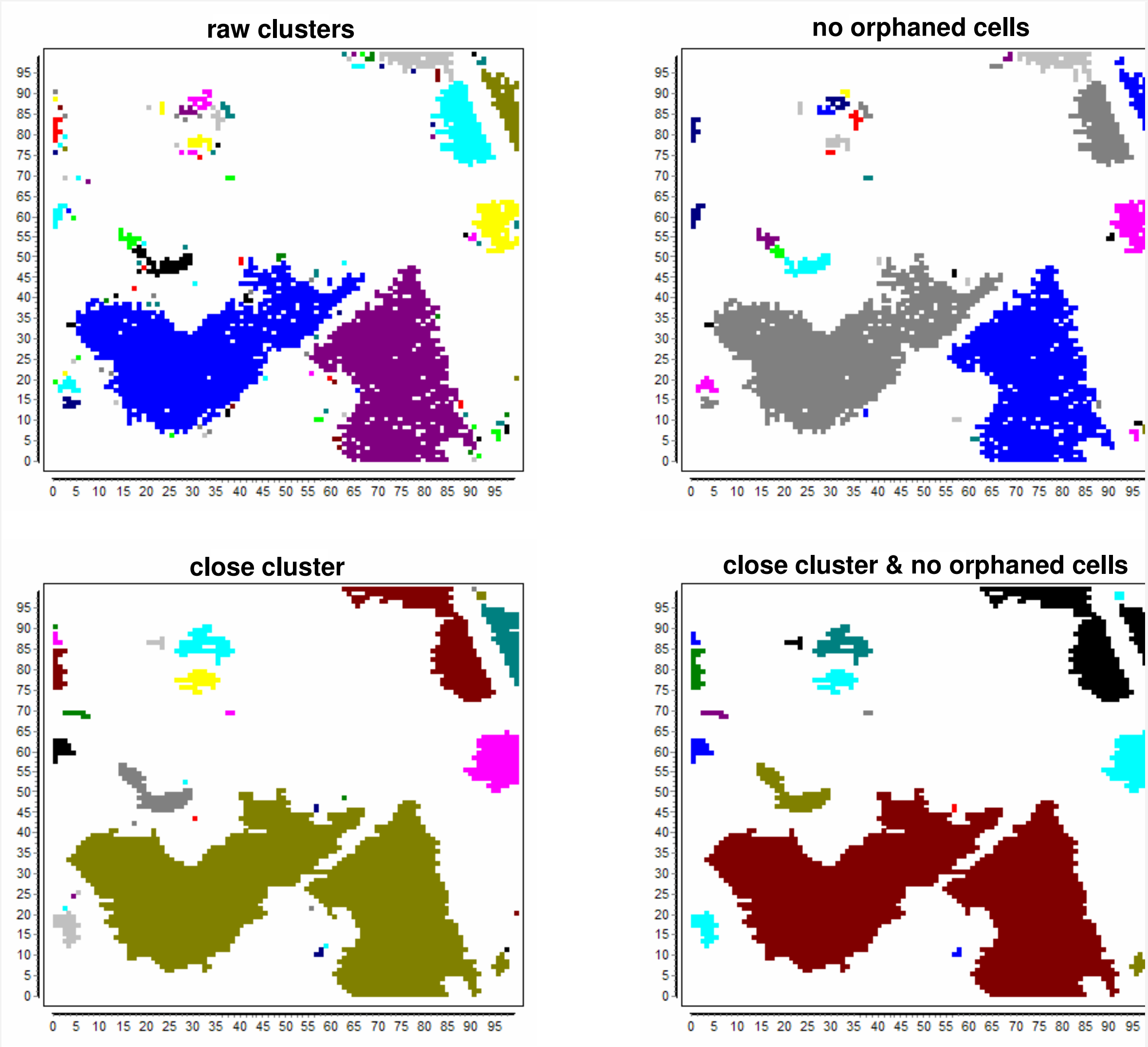
display details of cluster 1

Figure 40, The cluster analysis tool window

This tool allows to estimate and quantify the spatial clustering within a defined area the simulation grid. Based on some criteria (i.e. species, age etc), internally an attribute map of the simulation grid is created. Then clusters of connected regions in this map are identified using a *Hoshen-Kopelmann* (*HK*-) algorithm. As this algorithm internally uses a *von Neumann*-neighbourhood (each cell has four direct neighbours), a cluster may be split into several distinct clusters. This is a well-known phenomena of the algorithm and not avoidable. The tool lists all identified clusters and their properties that can be saved for further analysis. It is possible to apply several manipulations to the feature map to simplify the analysis. The switch "close clusters" applies a "dilate and erode" procedure to the feature map before the cluster identification. This is a common image manipulation filter and results into a "closed" map. The idea is to overcome the constrains of the *HK*-Algorithm and force bigger, cohesive clusters. The second switch "remove single cell cluster" has a similar the effect and removes clusters of a single cell, thus with no direct neighbours, before analysis. (An example can be found below)

The upper panel (1) shows a display of the feature map with the clusters. Identified clusters a randomly coloured when not forced to be monochrome. On the left, the sample area and feature list can be selected (2). Using "calc cluster stats" calculates the clusters and updates the information display (3). On the left part of the summary, a histogram of the size (or diversity) over all identified clusters is shown and on the right side a detailed list of the clusters and their properties. Detailed information on a certain cluster is shown using the number of a cluster and the "display" button on the bottom (5).
Additionally, the so called "*cellular automata (CA) measures for homogeneity*" (*CA*-Homogeneity, {Hütt, 2001 #662}) is computed for the selected feature. This gives the average number of cells with the same nearest neighbourhood configuration.

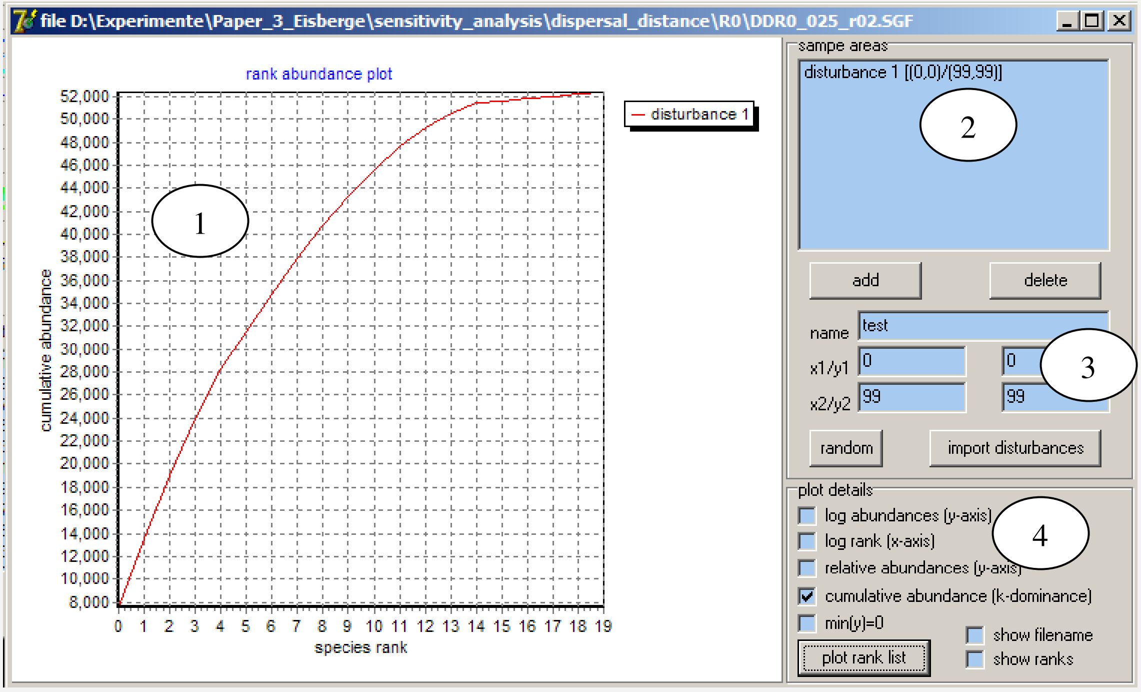
The following Figure 41 shows the consequences of the operations „no orphaned cells“ and „close clusters“ on a sample data set. Identified cluster are marked with different colours. However, due to technical reasons only 20 different colours were available. Thus adjacent clusters may have the same colour and appear as single cluster.



	identified cluster	average size	standard deviation
raw cluster	125	20.6	124.7
no orphaned cells	41	60.7	213.9
close cluster	32	94.6	402.1
close cluster & no orphaned cells	18	167	531

Figure 41, Example of the cluster identification and resulting cluster properties

10.5.9 Rank analysis tool



file D:\Experimente\Paper_3_Eisberge\sensitivity_analysis\dispersal_distance\R0\DDR0_025_r02.SGF

sampe areas

disturbance 1 [(0,0)/(99,99)]

name: test
x1/y1: 0 0
x2/y2: 99 99

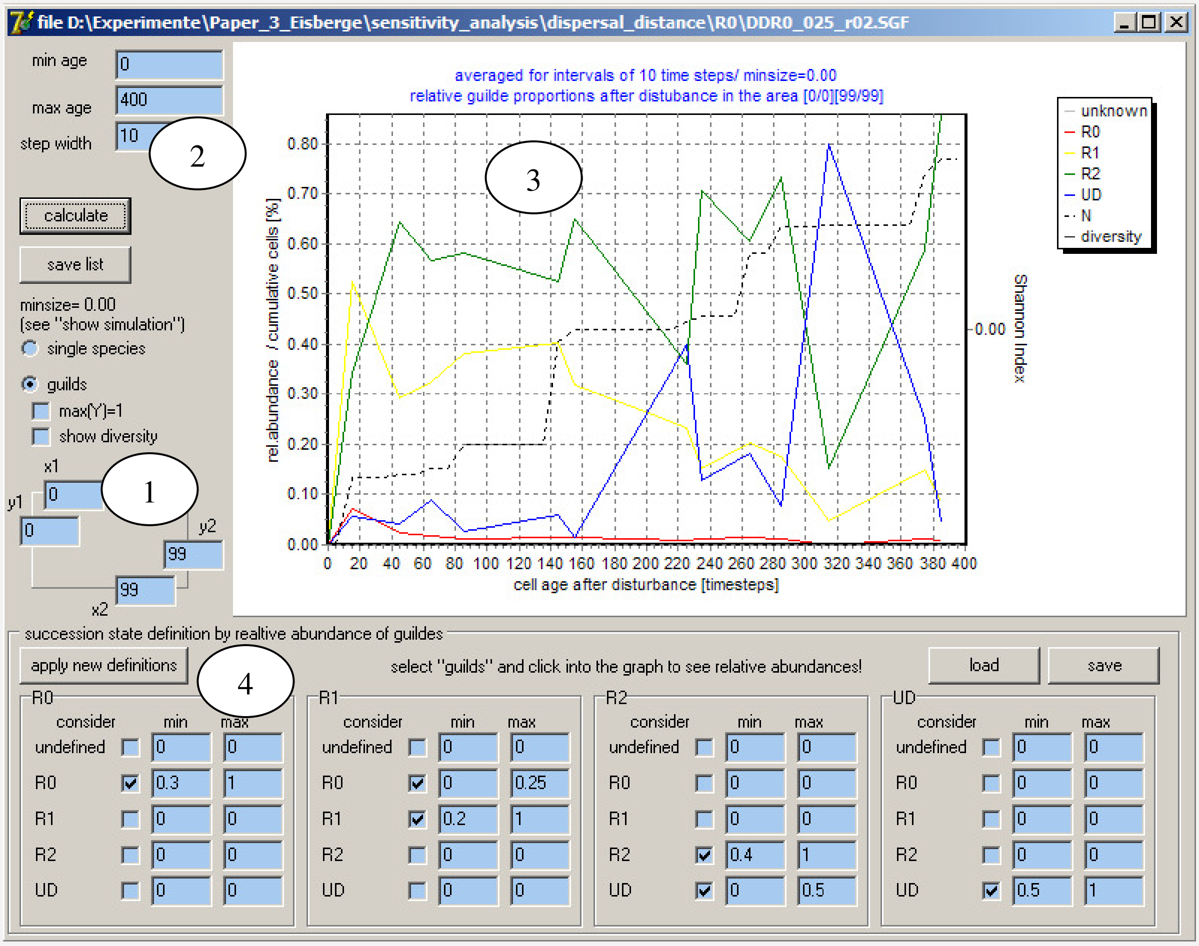
plot details

☐ log abundances (y-axis)
☐ log rank (x-axis)
☐ relative abundances (y-axis)
☑ cumulative abundance (k-dominance)
☐ min(y)=0
☐ show filename
☐ show ranks

Figure 42, The rank analysis window

This window (Figure 42) allows to sample a defined rectangular area and compute various species-rank plots. The left panel (1) shows the rank plots. On the upper right panel (2) all sampled areas are listed. By default the list is empty. Using “import disturbances” all defined disturbance areas can be imported. The user can define own sample areas or create random sample areas as well (3). On the lower right panel (4) various plot options can be configured. If the switch “show filename” is enabled, the current filename is displayed in the plot caption. “show ranks” adds the species names in order of their rank to the plot.

10.5.10 Succession analysis tool, succession state definition



min age: 0

max age: 400

step width: 10

minsize= 0.00
(see "show simulation")

○ single species

● guilds

☐ max(Y)=1

☐ show diversity

x1: 0

y1: 0

y2: 99

x2: 99

succession state definition by realtive abundance of guildes

select "guilds" and click into the graph to see relative abundances!

R0

	consider	min	max
undefined	☐	0	0
R0	☑	0.3	1
R1	☐	0	0
R2	☐	0	0
UD	☐	0	0

R1

	consider	min	max
undefined	☐	0	0
R0	☑	0	0.25
R1	☑	0.2	1
R2	☐	0	0
UD	☐	0	0

R2

	consider	min	max
undefined	☐	0	0
R0	☐	0	0
R1	☐	0	0
R2	☑	0.4	1
UD	☑	0	0.5

UD

	consider	min	max
undefined	☐	0	0
R0	☐	0	0
R1	☐	0	0
R2	☐	0	0
UD	☑	0.5	1

Figure 43, The succession analysis window

This window (Figure 43) allows to examine the succession of a defined area of the simulation grid (1). By default, the whole grid is sampled. All cells of a given age range (time since last disturbance) are considered and grouped in bins of a given width (2). All individuals in a bin are considered and the average species and guild composition of the bin is computed and displayed (3). Additionally the diversity of a bin can be shown.

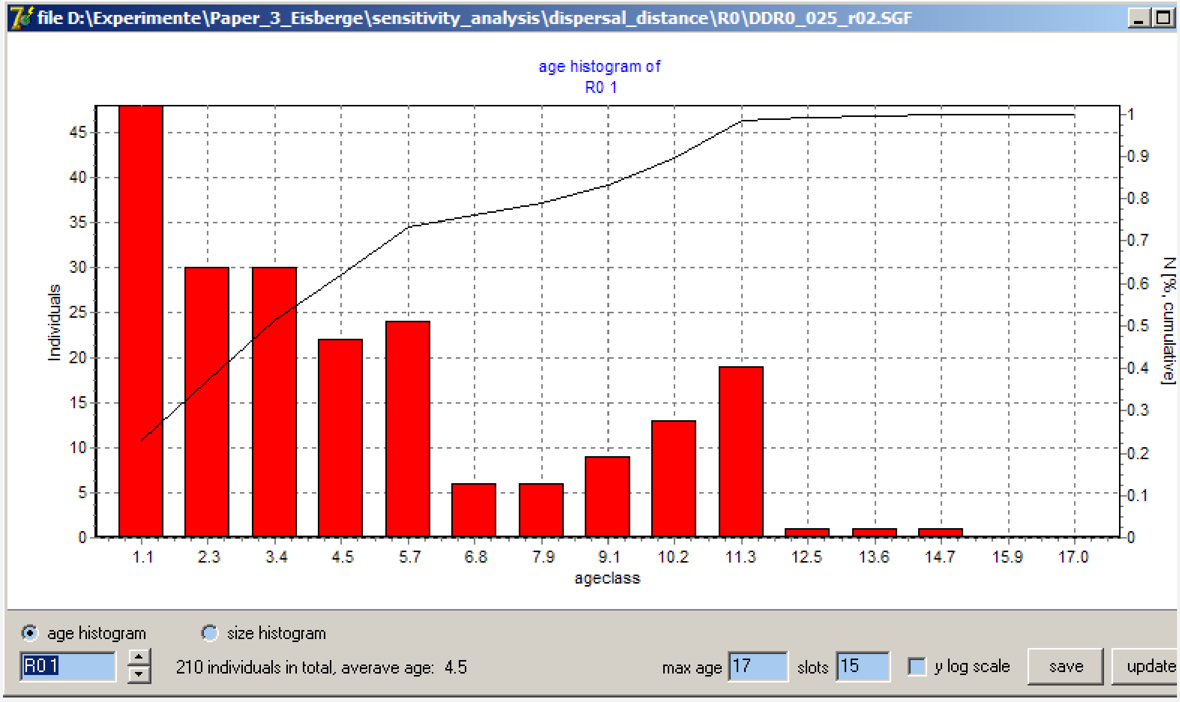
In the above example all cells of the area (0/0) - (99/99) that have been disturbed in the last 400 time steps (age between 0 and 400) are considered. These are binned in steps of 10 time steps. Thus the first bin contains all cells with an age of 0-9 time steps, the second all with an age of 10-19 time steps and so on. The average species (or guild) composition is drawn with the average cell age of a bin as x-axis coordinate. If the relative guild composition is displayed, on can click on a data point and the relative guild composition of this point is shown in a popup window.

In the lower panel (4), the guild composition of the succession states R0, R1, R2 and UD can be defined. This information is used to classify a cell to be in a certain succession state according to its species composition, respectively guild composition. For each succession state the (relative) guild composition can be defined. An enabled checkbox of a guild means that this guild is considered and a minimal and maximal range (relative proportion of the guild) must be given. If two ore more guilds are used, all conditions must match to identify a state. The state definition is saved within a simulation. However, you can save and load to separate files as well.

In the above example, the **state R0** is defined solely by a relative proportions of guild R0 to be between 0.3 and 1. This means that any cell in which more than 30% of all individuals are members of the R0-guild is classified the be in the **R0 state**. For a cell to be classified in the **R1 state**, the relative proportion of individuals belonging to the R0 guild must be smaller than 25% and more than 20% must belong to the R1-guild. Analogue, the **R2 state** is defined by more than 40% individuals of the R2 guild and less than 50% UD guild members. Finally, the **UD-state** is characterised by more than 50% of all individuals belonging to the UD - guild.

Attention:
Do not confuse guild and state definition! An assemblage of several guilds often defines a state. If you want to say "less than *x*%" follow the above example and use "min = 0, max = *x*". Analogue for defining "more than *z*%" use "min = *z*, max = 1".
Avoid ambiguous state definitions. The states are checked in ascending the order (R0, R1, R2, UD) and the first match is used to identify a state. If no match is found, the state is set to be "undefined".

10.5.11 Age structure analysis tool



file D:\Experimente\Paper_3_Eisberge\sensitivity_analysis\dispersal_distance\R0\DDR0_025_r02.SGF

● age histogram ○ size histogram

R0 1

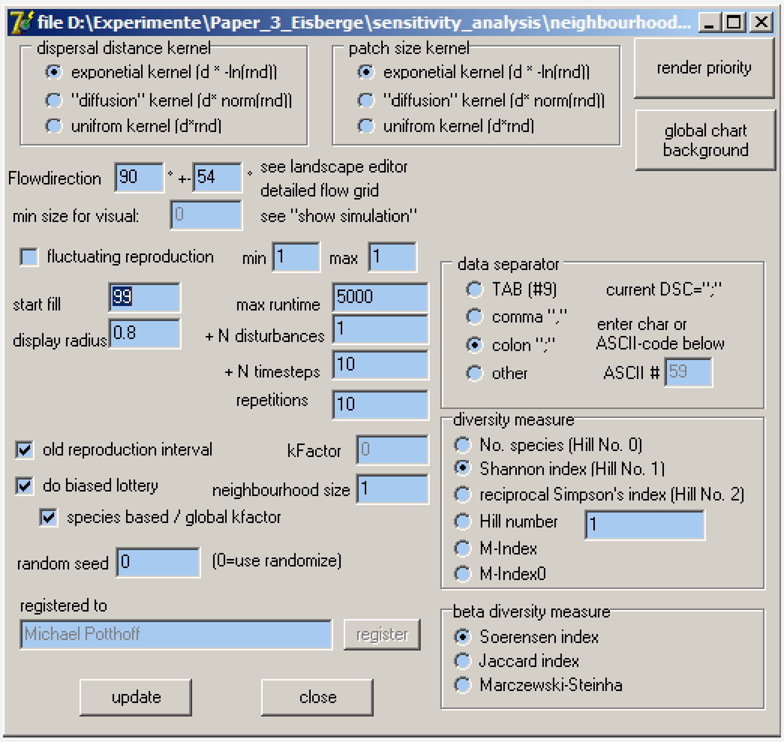
210 individuals in total, averave age: 4.5

max age 17 slots 15 ☐ y log scale

Figure 44, The age analysis tool

Figure 44 show the age analysis tool. This tool can be used to create an age or size histogram of a species. Always the whole simulation grid is sampled. You can select the species of interest and define how many bins the histogram should have and the maximal age considered. By default, the maximal age is computed to potentially contain more than 90% of a population according to the mortality. The graph shows the histogram and the cumulative distribution. Additionally, the average age is given as well as how many individuals are counted and, if any, are outside the specified range.

10.6 Additional simulation parameter dialog



file D:\Experimente\Paper_3_Eisberge\sensitivity_analysis\neighbourhood...

dispersal distance kernel
● exponetial kernel (d * -ln(rnd))
○ "diffusion" kernel (d* norm(rnd))
○ unifrom kernel (d*rnd)

patch size kernel
● exponetial kernel (d * -ln(rnd))
○ "diffusion" kernel (d* norm(rnd))
○ unifrom kernel (d*rnd)

Flowdirection 90 ° +- 54 ° see landscape editor detailed flow grid
min size for visual: 0 see "show simulation"

☐ fluctuating reproduction min 1 max 1

start fill 99
display radius 0.8
max runtime 5000
+ N disturbances 1
+ N timesteps 10
repetitions 10

☑ old reproduction interval kFactor 0
☑ do biased lottery neighbourhood size 1
☑ species based / global kfactor

random seed 0 (0=use randomize)

registered to
Michael Potthoff

data separator
○ TAB (#9)
○ comma ","
● colon ";"
○ other
current DSC=";"
enter char or ASCII-code below
ASCII # 59

diversity measure
○ No. species (Hill No. 0)
● Shannon index (Hill No. 1)
○ reciprocal Simpson's index (Hill No. 2)
○ Hill number 1
○ M-Index
○ M-Index0

beta diversity measure
● Soerensen index
○ Jaccard index
○ Marczewski-Steinha

Figure 45, Additional simulation parameter window

The additional simulation parameters (Figure 45) can be invoked by the "additional" button of the main window (Figure 33). This dialog can be used to select features of the SIMBAA core and other model related options.

In the upper panel the **kernels** for "dispersal distance" and "dispersal patch size" can be selected. Note that this selection is global and applies to all species. See chapter "dispersal" for more details.

1.1.1.17 Render priority

The button "**render priority**" on the upper right opens a dialog to change the priority of the SIMBAA GUI. Note that this option influences the multitasking of the host system. If you want to run a simulation while doing other computing tasks, you may select "below normal" or "normal". However, this will result in fewer computation time (CPU time), thus slows down the simulation. To speed up the simulation you may select "above normal" or even "high" but this will degrade the performance of other programs (e.g. word processing) running simultaneous on the same machine.

1.1.1.18 Data separator

The panel "**data separator**" on the middle right allows to select the character used to separate data values when saving any data into text files, thus also the run log. This selection is stored in the SIMBAA grid file. To import SIMBAA data into a spreadsheet or statistical software, you commonly select to import text or "CSV" ("comma/colon separated values")/TAB data.

The both lower right panels are used to select the global used a- and b diversity measure. See chapter "Diversity Measurements available in SIMBAA" for more details and formulas.

The fields "**flow direction**" are remains of an older version and have no meaning (will be removed in a later version)

1.1.1.19 "Fluctuating reproduction"

If this switch is enabled, the number of larvae of a species is multiplied by a random value between "min" and "max".

A little example (a single dispersal event): number of individuals of a species in a cell: 4, fecundity: 2 → disperse 4 * 2 = 8 larvae of this species. Fluctuating reproduction enabled, min = 0.5 max = 2 → draw a random fluctuating factor between 0.5 and 2, let's say 1.4 This will result in 8 * 1.4 = 11.2, rounded 11 larvae to be dispersed. In an other cell, the factor may be 0.65 resulting in 8*0.65=5.2 rounded 5 larvae.

1.1.1.20 "start fill"

Every time you create a new simulation (by "new" in the main window), the whole simulation grid is cleared first. As initial population a random species assemblage is then created. This assemblage fills a strip of the grid from the left side (0/0) to the x-position "startfill" (startfill/ y-dimension). The initial population consists of individuals of random selected species (out off all available species) with their life history traits (e.g. age, last reproduction) randomly spread over their possible range. The cell capacity, e.g. all available space, is completely used.

1.1.1.21 “old reproduction interval”

This switch determines if a possible synchronisation of a species is based on simulation time step (old reproduction interval = **disabled**) or on the individuals age and time of last reproduction (default, old reproduction interval = **enabled**).

1.1.1.22 “Random seed”

This determines the initialisation of the random generator. Without additional hardware it is impossible to generate “real” random numbers with a computer. Thus any random number generated in SIMBAA is generated using a pseudorandom process[5]. Such a process starts with a “seed”. Any value other than zero will result in a fix sequence of random numbers, making a simulation repeatable, e.g. the same simulation parameter will finally give the same results. A value of zero will start the random generator with a seed computed of the current time and data each time, thus the same parameter will give different results each run. For detailed information on the topic of random numbers and computers see the Internet (key words: pseudo random numbers”)

1.1.1.23 “display radius”

This value is used to scale the size of an individual when displayed in the visualisation window.

10.6.1 Simulation stop conditions:

1.1.1.24 “max runtime”

This determines the runtime of the simulation. Any other value than zero will stop the simulation after “max runtime” time steps have been computed

---

[5] “A pseudorandom process is a process that appears random but is not. Pseudorandom sequences typically exhibit statistical randomness while being generated by an entirely deterministic computational process.” (source: Wikipedia)

1.1.1.25 “+ N disturbances”

This determines how many disturbances must occur **after** the maximal runtime has occurred

1.1.1.26 “+ N time steps”

This is an opportunity to make the simulation run for some final time steps after the above criteria have been fulfilled.

In the shown example, the simulation will run for 5000 time steps, then proceed until (at least) one further disturbance event occurs and finally stop 10 steps after the time step when this happened.

Trick: to run the simulation until ***n*** disturbance events have occurred:

set **“max runtime = 1”** and **“+ N disturbances = *n*”**

1.1.1.27 “repetitions”

This value is only used by the SIMBAA tools “Rechenknecht.exe” and “GUIKnecht.exe”. It defines how many times the simulation is repeated. (Note: only meaningful when “random seed = 0”)

1.1.1.28 “do biased lottery”/”neighbourhood size” and “k-factor”

These switches influence the lottery competition. Normally (do biased lottery=disabled), the lottery is strictly neutral and every larva in the pool has the same chance to win. If “do biased lottery” is enabled, the chance of a larva is influenced by the neighbourhood of the cell (see Formula 5).

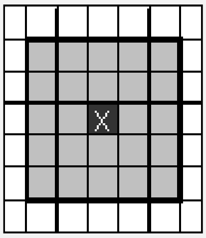
$$biased_S = pool_s * (1 + kfactor * w_{N,S})$$

$$p_s(win) = \frac{biased_S}{\sum biased}$$

Formula 5, Biased lottery description

The chance to win a lottery is determined by the relative proportion of a species in the biased pool. This is computed by the unbiased proportion (*pool*$_S$) weighted by $W_{N,S}$, the relative proportion of the species in the neighbourhood of the size *N*. The weight is modified by the *kfactor*.

Example of a biased lottery with 4 species



Neighbourhood size: 2 (grey shaded)
kfactor 2

Species	Unbiased *pool*$_S$ $p_S(win)$		Neighbourhood ($W_{N,S}$)	*biased*$_S$ pool
A	0.20	0.20	0.280	0.199
B	0.34	0.00	0.340	0.241
C	0.16	0.54	0.333	0.236
D	0.30	0.26	0.456	0.324
Σ	1.00	1.00	1.409	1.000

Figure 46 shows the influence of a kfactor between -2 and +2 on the winning chance of the species from the above example:

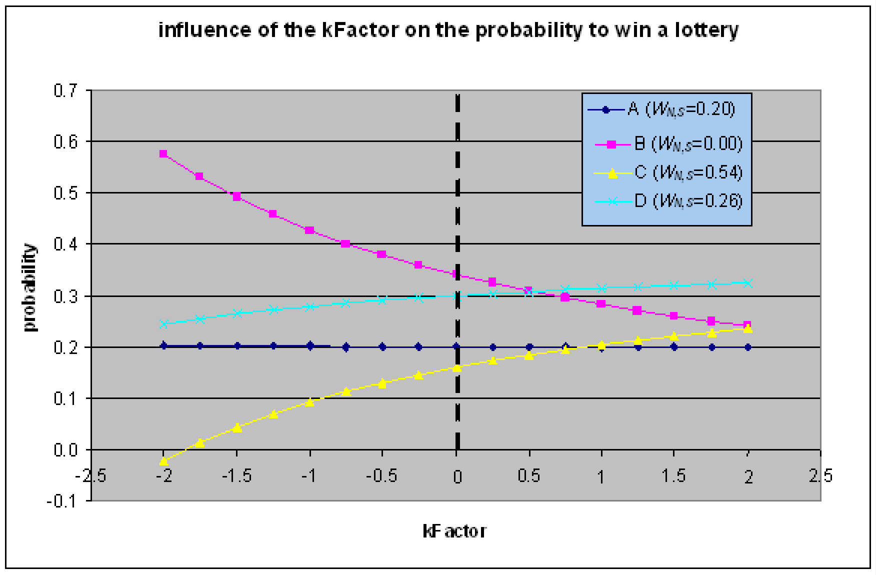


Figure 46, Influence of the kfactor on the lottery

10.7 Diversity Measurements available in SIMBAA

10.7.1 α-Diversity

These indices measure α- or point diversity. In SIMBAA the computation is based on a list of individuals. Typically this list is the inventory of a single sample, e.g. a simulation grid cell or a cluster of cells.

In SIMBAA the following α-diversity are available:

1.1.1.29 Shannon Index (Shannon Entropy)

$$H' = -\sum p_i * \log(p_i)$$

1.1.1.30 Simpson's Index (reciprocal)

$$D = \sum p_i^2 \qquad or \quad \frac{1}{D}$$

1.1.1.31 Hill Numbers

The Hill Numbers form a group of diversity measurements. They are based on the *Rényi* entropy where α is the order, S is the sample size i.e. species count, p_i the relative proportion of the ith species:

Rényi entropy $$H_\alpha = \frac{1}{1-\alpha} \log \sum_{i=1}^{S} p_i^{\alpha}$$

Mark Hill proposed using $N_a = \exp(H_a)$. Thus N_a is the "Hill number". Although *a* (respectively α) can be any number (and SIMBAA allows to compute it), some have a common interpretation:

N_0 = number of species
N_1= exponential Shannon Index
N_2= inverse Simpson Index

1.1.1.32 M-Index

The M-Index is a special measurement and was designed during this thesis. It does not compute traditional diversity but allows to order an assemblage according to the dominance of its members, e.g. “pioneer dominated” or “climax dominated”. It is descript in an own chapter.

10.7.2 β-Diversity

The concept of β-diversity is sometimes not well defined. In SIMBAA β-diversity measures the similarity (respectively complementarily) of two assemblages. Following β-diversity functions are available:

(In the following examples let *a* be the total number of species in both samples, *b* number of species in the first sample and *c* the number of species in the second sample)

1.1.1.33 Sørensen Index

$$C_S = \frac{2a}{2a+b+c}$$

1.1.1.34 Jaccard Index

$$C_J = \frac{a}{a+b+c}$$

1.1.1.35 Marczewski-Steinhaus Distance

$$C_{MS} = 1 - \frac{a}{a+b+c}$$

10.8 The M-Index

The M-Index is a simple, dimension-less index for analysing the configuration of hierarchical species communities. If no hierarchy is detected, the M-Index is equal to 0. Other extreme values (M-Index = -1 or M-Index = 1) occur when the composition consists only of members of the respective end of the hierarchy. For other configurations the M-Index takes values between -1 and +1 that reflect the skewness of the community, e.g. it gives an indication to which end of the hierarchy the community is more developed.

For each possible species within the community a hierarchy value *OR* (Objective Rank) must be defined first. This value *OR* characterises the position or relevance of a species in the hierarchy. It can be simply defined by the rank order relation of the species as:

$$OR_i = -1 + \left[(2 * \frac{(r_i - 1)}{(R - 1)} \right]$$

where OR_i is the hierarchy-value of the i^{th} species and r_i its rank among the *R* possible hierarchy ranks. Using the about formula the species hierarchy-value OR_i is ranked from -1 to +1 with equal distances from rank to rank. However, OR_i -values may be also assigned „by hand“, enabling a defined hierarchy if desired. In general, a value of $OR_I = 0$ means that the (i^{th}) species is not relevant for the hierarchy whereas $OR_I = -1$ and $OR_i = +1$ represent the lower, respectively upper end of the hierarchy.

Species abundances A_i may be log+1 transformed and normalised by the sum of the log+1 transformed abundances. This log+1 transformation is used to down-weight high abundances. Of course, any other transformation may be used or the transformation can be omitted completely, using only the relative species proportions. In this case (using untransformed relative species abundances) the final index should be called “M-Index$_0$”). This gives the relative species quotient q_i for each species.

$$qi = \frac{\log(1 + A_i)}{\sum \log(1 + A_i)}$$

or simply $$qi = \frac{A_i}{\sum A_i}$$

The M-Index can be computed as the sum of q_i weighted by OR_i:

$$M - Index = \sum OR_i * q_i$$

10.8.1 M-Index, an example:

Assume a collection of 8 species. This 8 species can be grouped into 5 bins, e.g. based on their occurrence in a succession after disturbance events where the rank 1 attributes a pioneer species and 5 a climax member:

species	A	B	C	D	E	F	G	H
rank	1	1	1	2	2	3	3	4
OR_i	-1.00	-1.00	-1.00	-0.33	-0.33	0.33	0.33	1.00

Now these communities are sampled at 5 stations:

sample	absolute abundance							
sample 1	100	25	0	0	0	0	0	0
sample 2	0	0	0	0	0	0	0	100
sample 3	100	100	100	100	100	100	100	100
sample 4	50	10	100	0	12	137	10	5
sample 5	5	50	0	10	10	100	137	12

Applying the above transformations [2] this results in the following q_i-values

sample	q_i							
sample 1	0.586	0.414	0.000	0.000	0.000	0.000	0.000	0.000
sample 2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
sample 3	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125
sample 4	0.174	0.106	0.204	0.000	0.113	0.218	0.106	0.079
sample 5	0.079	0.174	0.000	0.106	0.106	0.204	0.218	0.113

The relative abundances ([2a]) are

sampe	q_i							
sample 1	0.80	0.20	0.00	0.00	0.00	0.00	0.00	0.00
sample 2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
sample 3	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13
sample 4	0.15	0.03	0.31	0.00	0.04	0.42	0.03	0.02
sample 5	0.02	0.15	0.00	0.03	0.03	0.31	0.42	0.04

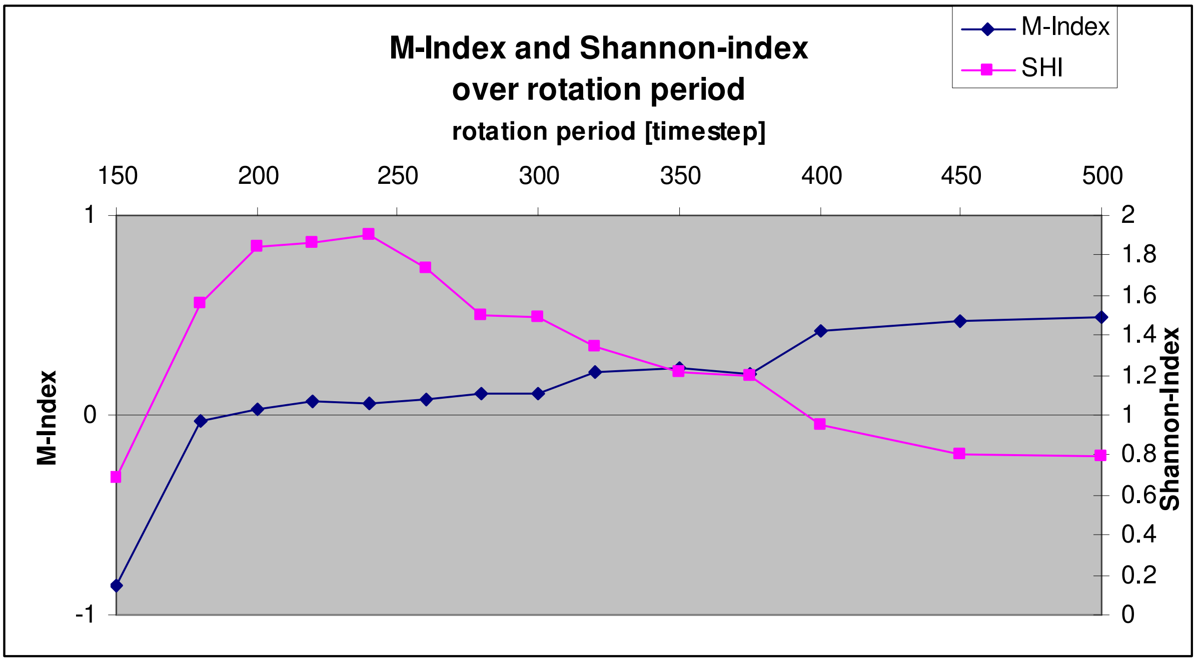
Calculating the M-Index finally gives:

sample	M-Index	M-Index$_0$	Shannon
sample 1	**-1.00**	-1.00	0.50
sample 2	**1.00**	1.00	0.00
sample 3	**-0.25**	-0.25	2.08
sample 4	**-0.33**	-0.34	1.42
sample 5	**-0.07**	0.09	1.42

As expected, the sample 1 and 2, consisting only of pioneer –respectively climax-species are just mapped on their corresponding ends of the given hierarchy. Together with the Shannon-Index a more complete picture of the community state can be drawn: e.g. the Shannon-index of sample 1 (SHI = 0.50) indicates that sample 1 consists of several species whereas sample 2 (SHI = 0) has only one counting species. Although the Shannon-index of sample 3 represents the maximal expectable Shannon-index (all species have the same relative proportions), thus indicating the highest diversity, the M-Index clearly indicates a skewed community, in this case (because pioneer species or early successional stages, have been assigned the negative end of the rank), towards early succession. However, a value of M-Index = -0.25 represents an advanced succession state rather than the very first beginning. Sample 4 and sample 5 share the same Shannon-index of SHI = 1.42 but their M-Index clearly separates them into an early (sample 4: M-Index = -0.33) and a rather balanced (sample 5: M-Index = -0.07) stage.

An other example from a simulation study about the influence of disturbance events on the community of a model system. The species where again grouped according to their succession potential, ranging from -1 for pioneer species (species group R0) to +1 for climax species (species group UD). Aim of this study was to qualify the influence of different disturbance regimes towards the final community stage. The disturbance regime can be characterised by the rotation period RT, which is the time needed to statistically disturb the whole simulation area once. It is depending on disturbance area and disturbance frequency. As disturbance area was kept constant, the ascending RT represents a descending disturbance frequency. Simulations started with a random community and ran for 10000 time steps. The following table summarises the simulation results. Given are species abundance and both Shannon- and M-Index.

RT	**Abundance**								**SHI**	M-Index
	R01	**R02**	**R11**	**R12**	**R21**	**R22**	**UD1**	**UD2**		
150	76238	74253	0	0	0	14	0	0	0.69	-0.86
180	23246	23972	1853	1995	51852	42243	2908	2436	1.56	-0.03
200	5779	7195	10775	14215	41934	41242	11158	18207	1.84	0.03
220	2842	2852	15074	17571	25262	29033	19672	38199	1.86	0.06
240	3358	6030	16174	17116	23362	15010	33814	35637	1.90	0.05
260	2159	3456	9629	17067	15206	13788	41282	47759	1.74	0.08
280	1108	1749	9223	6375	11861	9162	58580	52358	1.50	0.10
300	1188	1195	6776	9073	9104	11913	54354	56709	1.49	0.11
320	2072	0	6339	8774	6173	5531	58177	63411	1.34	0.22
350	947	0	6979	7803	6680	781	62078	65072	1.22	0.23
375	5588	0	3530	4810	2641	3436	68092	62378	1.20	0.21
400	0	0	6406	4583	0	0	68365	70917	0.95	0.42
450	0	0	2249	1232	0	0	75074	71561	0.80	0.47
500	0	0	2682	413	0	0	70614	76526	0.79	0.49



These pictures represent the final model state after 10000 time steps. Drawn is the succession stage (red = pioneer / R0-group, yellow = early settler / R1-group, green= late settler/R2-group, blue = climax / UD-group) based on the dominant succession potential at a particular location.

You can easily see that with RT = 150 only the R0 (=pioneer) species survive whereas with longer RT the R0-group (red) and, interestingly, the R2-group (late settlers, green) vanish. The visual impression that the model shows between RT = 200 and RT = 260 the most diverse (mixed) cases are confirmed by both a high Shannon-index and a: M-Index near zero. In general, the: M-Index ascends with ascending rotation period, indicating a shift towards dominance by later succession stages, supporting the visual results. The: M-Index can be interpreted as 4 different situations, separated by distinct levels in the curve. The first consists only of RT = 150 and has a: M-Index of: M-Index = -0.86, showing a high dominance of pioneer species. The abundance data reveal that only very few other individuals (14 individuals of R22) prevent the: M-Index from becoming its extreme value. The next level near zero indicates a well mixed or better not clearly dominated community. However, with ascending rotation period there is a slight shift towards more climax-dominated communities. The next level (RT= 320-375) with a: M-Index around +0.2 is clearly climax dominated. The main reason for this is the loss of a complete R0-species ($R0_2$), which seems to coincide with higher abundance in the UD-group (see abundance table). The last level (RT > 375, M-Index around +0.45) is caused by the loss of the complete R0- as well as the R2-group. The: `M`-Index value is underlined by the visual impression of the dominant UD-group.

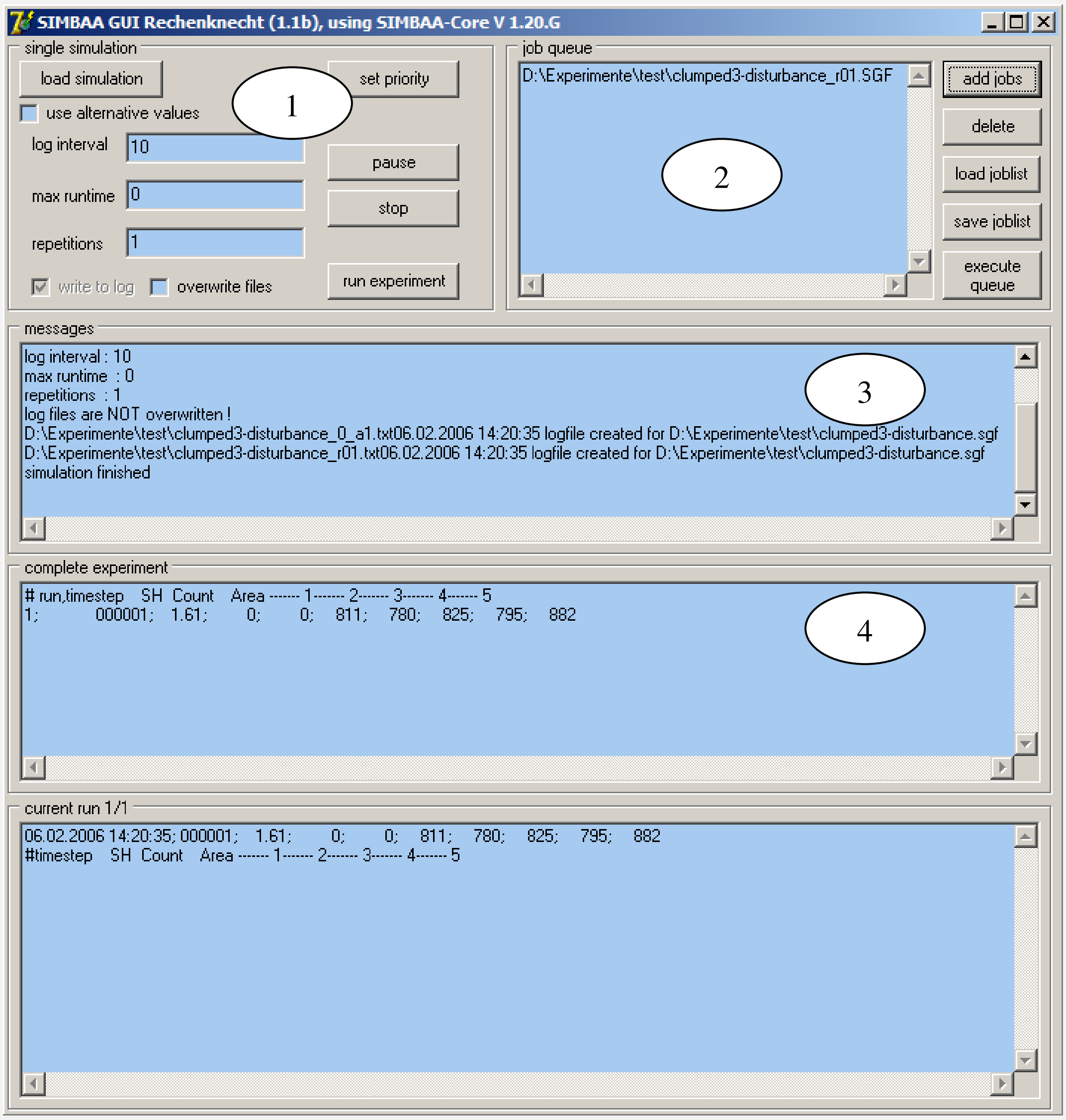
10.9 General SIMBAA tips

All graphs are capable to be saved or copied to the clipboard. A simple double click on the graph will open a save dialog. Graphics are saved by default as enhanced windows meta file (*.emf/ *.wmf). By holding down the left SHIFT-Key, the graphic is copied into the clipboard.

SIMBAA Tools

SIMBAA has some additional tools. Most useful are „Rechenknecht.exe" and "GuiKnecht.exe". Both programs can load pre-configured simulations and just compute them.

7



☐ use alternative values
log interval 10
max runtime 0
repetitions 1
☑ write to log ☐ overwrite files

job queue: D:\Experimente\test\clumped3-disturbance_r01.SGF

```
log interval : 10
max runtime  : 0
repetitions  : 1
log files are NOT overwritten !
D:\Experimente\test\clumped3-disturbance_0_a1.txt06.02.2006 14:20:35 logfile created for D:\Experimente\test\clumped3-disturbance.sgf
D:\Experimente\test\clumped3-disturbance_r01.txt06.02.2006 14:20:35 logfile created for D:\Experimente\test\clumped3-disturbance.sgf
simulation finished
```

```
# run,timestep    SH  Count    Area ------- 1------- 2------- 3------- 4------- 5
1;          000001;   1.61;       0;       0;    811;    780;    825;    795;    882
```

```
06.02.2006 14:20:35; 000001;   1.61;       0;       0;    811;    780;    825;    795;    882
#timestep    SH  Count    Area ------- 1------- 2------- 3------- 4------- 5
```

Figure 47, The SIMBAA tool "GuiKnecht.exe"

Figure 47 shows the window of the "GuiKnecht". You can either load a single simulation of a list of simulations (2) or process this list in a batch mode. All options are normally read from the simulation but it is possible to override some options by changing the values in (1). “execute queue” tries to load and execute every entry in the job list. In the upper panel (3) status information are listed, the middle panel (2) lists the final simulation result or the final results of an each repetition. The bottom panel (3) list the status of the current running simulation.

Rechenknecht.exe is a command line tool that can be used to run a simulation from a command line. This is mainly useful when simulation is done on a remote machine.

An other very useful tool is “Replaceproject.exe”. This is also a command line utility for manipulating various aspects of a simulation. The following screen appears when started with no parameters:

```
Microsoft Windows XP [Version 5.1.2600]
(C) Copyright 1985-2001 Microsoft Corp.

C:\>replaceproject
SIMBAA ReplaceParameter, using SIMBAA-Core V 1.20
no parameter!!!

ReplaceProject [datafile] KEYWORD [newValues]


accepted keywords are:

    FLOWDIR : set flow direction to specified angle [deg]
    FLOWDEV : set flow deviation to specified range [deg]
    RESETEX : reset species extinction times
   REPETITION : set repetition count to N
    RUNTIME : set max runtime to N
  SPECIESPOOL : replace species pool with pool from file
    STATEDEF : replace sucession state definition with definition from file
    MINSIZE : replace the "min-size-for-visual" with new value
   FLOWSPEED : set flow speed to specified range
    RANDSEED : pseudo random generator seed (0=use randomize)
```

A very useful batch file to call program with a set of parameters where the first parameter is always a filename out of a list of all files matching a given filemask is:

“forall.bat”

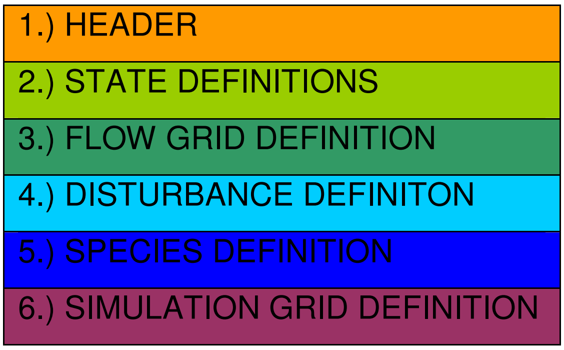
```
@Echo OFF
ECHO rekursiv durch alle directorys
IF "%1"=="" goto using
IF "%2"=="" goto using
FOR /R %%d in (%1) do %2 "%%d" "%3" "%4" "%5" "%6" "%7" "%8"
GOTO ende
:using
ECHO USAGE:
ECHO.
ECHO %0 FILEMASK PROGRAM
ECHO.
:ende
ECHO goodbye
```

An example to use this batchfile would be “c:\>forall *.sgf ReplaceProject runtime 1000”. This would result replacing the “runtime” of all SIMBAA grid files (*.sgf) in the current (and deeper directory(s) to be replaced with the value “1000”.

10.9.1 Appendix

1.1.1.36 File Format of the SIMBAA GRID FILE *.SGF

This is the file format for a simulation. It contains all information. The SGF is a binary file format. It is organised in different sections.



1.) HEADER
2.) STATE DEFINITIONS
3.) FLOW GRID DEFINITION
4.) DISTURBANCE DEFINITON
5.) SPECIES DEFINITION
6.) SIMULATION GRID DEFINITION

The first section in the file is a header with relevant information. All sections are descript below in detail. For easier access outside the SIMBAA environment, both type and size of the data field is listed along with its offset in bytes from the beginning of the structure. Sometimes the data fields are aligned by the compiler in a way that there are spare bytes. This is indicated by the real size of this field in brackets. Thus e.g. a size of 1(4) means that the data field just uses the first byte but covers 4 bytes in total. The reason for this and the order of the fields is the growth and change of the structures during development of SIMBAA. Also the Delphi-style type definition is given.

10.9.2 SGF-Header

This header contains most information on the simulation.

Name	type	size [byte]	offset	explanation
ID	char	16	0	This field must contains `'SIMBAA GRID FILE'` and is used to identify a valid SGF file
Version	char	6	16	The version string (e.g. `'V 1.20'`)
DEXB1	byte	2	22	Reserved 2 byte
Species count	integer	4	24	Number of defined species
Xdim	integer	4	28	Grid dimension on x-axis
YDim	integer	4	32	Grid dimension on y axis
Disturbances	integer	4	36	Number of defined disturbances
DisturbedArea	integer	4	40	Cummulative amount of disturbed area
Timestep	integer	4	44	Current time step
DisturbanceCount	integer	4	48	Cummulative number of occurred disturbances
ExternalDriftCount	integer	4	52	Max Number of larvae for a external drift event
ExternalDriftEvent	double	8	56	probability for an external drift event
HiC	integer	4	64	capacity of a high capacity cell
LoC	integer	4	68	capacity of a low capacity cell
pHiC	double	8	72	probability for a high capacity cell
Flow dir	double	8	80	flow direction (unused)
Flow dev	double	8	88	flow deviation (unused)
Dietime	51 integers	204	96	List of the extinction time of all species (0=not extinct jet)
lasttAb	51 integers	204	300	abundance of all species in the last time step
Maxtime	integer	4	504	maximal runtime of simulation (0=unlimited)
Repetitions	integer	4	508	repeat simulation N times
Periodic	boolean	1	512	periodic boundary condition state
OnlyDrift	boolean	1	513	disable SIMBAA's explicit dispersal model
ProportionalDrift	boolean	1	514	dirft is proportional to speces abundance
DSCChar	char	1	515	data separating charachter, ASCII char used to separate data values
SeedSyncAgeClasses	boolean	1	516	synchronise the age of all individuals of a species based on reproduction interval

DEXB2	byte	3	517	reserved 3 byte
Vminsize	double	8	520	minimal size for visual
SubVersionChar	char	1	528	subversion identifier (e.g. `’D’`)
DispersalKernelF	byte	1	529	Bit-based dispersal kernel flag, upper nibble for "patch size kernel", lower nibble for "dispersal distance" $01=exponentioal kernel, $02=diffusion kernel, $04=uniform kernel, $08 reserved
DoBiasedLottery	byte	1	530	flag for biased lottery
kFactor	shortint	1	531	unused
SizeNeighbourhood	byte	1	532	neighbourhood size for biased lottery
DEXB3	byte	3	533	reserved 3 byte
kFaktor2	double	8	536	koppel faktor for biased lottery
RepFluc	boolean	1	544	flag for fluctuating reproduction
RepFlucMin	integer	4	545	flucutating reproduction minimal
RepFlucMax	integer	4	549	flucutating reproduction maximal
RandSeedValue	integer	4	553	random number seed
Reserved	byte	51	557	reserved

Delphi-type definition:

```
TSimFileHeader = packed RECORD
          ID : Array[1..16] of Char;
          version : Array [1..6] of Char;
          DEXB1 : ARRAY[0..1] of byte; // dummy extra bytes 1
          SpeciesCount, Xdim, Ydim, Disturbances,DisturbedArea,
          Timestep, DisturbanceCount,
          externalDriftcount : integer;
          externalDriftEvent : double;
          HiC,LoC : integer;
          pHiC : double;
          flowDir, FlowDev : double;
          dietime,lasttAb : TSpeciesList;
          maxtime, repetitions : longint;
          periodic : boolean;
          onlyGDrift,
          proporionalDrift : boolean;
          DSCChar : char;
          SeedSyncAgeClasses : boolean;
          DEXB2: ARRAY[0..2]of byte; // dumme extra bytes 2
          VminSize : double;
          SubVersionChar : char;
          DispersalKernelF : byte; // 0000-0000 patch & distance kernel
          DoBiasedLottery : byte;
          KFaktor : shortInt;
          SizeNeighbourHood : byte;
          DEXB3 : ARRAY[0..2] of byte; // dummy extra bytes 3
          kFaktor2 : double;
```

```
  RepFluc : boolean;
  RepFlucMin, RepFlucMax : integer;
  RandSeedValue : integer;
  RESERVED : ARRAY[0..100-sumofChange] of byte;
END;
```

10.9.3 State definitions

The state definitions is a four element list holding the definitions for each of the states R0,R1,R2 and UD. Each definition itself is a 5 element list. Each element of this list holds the information on a particular guild (if used, min, max proportions)

TTransStateDef

Name	type	size [byte]	offset	explanation
R0	TStateDef	120	0	state definition
R1	TStateDef	120	120	
R2	TStateDef	120	240	
UD	TStateDef	120	360	
total size		**480**		

TStateDef

Name	type	size [byte]	offset	explanation
undefined	TStateGuildeDef	24	0	definition of the min/max and if used
R0	TStateGuildeDef	24	24	
R1	TStateGuildeDef	24	48	
R2	TStateGuildeDef	24	72	
UD	TStateGuildeDef	24	96	
total size		**120**		

TStateGuildeDef

Name	type	size [byte]	offset	explanation
useThisGuilde	boolean	1(8)	0	if this guild is essential for the state
relativeMin	double	8	8	min. rel. proportion of individuals
relativeMax	double	8	16	max rel. proportion of individuals
total size		**24**		

Delphi-type definition:

```
TTransState = (undefined,R0,R1,R2,UD);

TStateGuildeDef = RECORD
           UseThisGuilde : boolean;
           relativeMin,relativeMax : double;
         END;
TStateDef = ARRAY[0..nGuilds] of TStateGuildeDef;
TTransStateDef = ARRAY [R0..UD] of TStateDef;
```

10.9.4 Flow Grid definition

The flow grid contains all information about the flow grid.

Name	type	size [byte]	offset	explanation
FlowGridXDim	integer	4	0	flow cells on x-axis
FlowGridYDim	integer	4	4	flow cells on y-axis

FlowData	array of TlocalFlowDef	X*Y*24	8	map of local flow definition savin scheme:
				`(0/0),(0/1),(0/2)....`
				`(1/0),(1/1),(1/2)....`
				`....`
				`(x/0),(x/1).....(x/y)`

total size		**various**		

TLocalFlowDef

Name	type	size [byte]	offset	explanation
lFlowDirection	double	8	0	flow direction
lFlowDeviation	double	8	8	flow deviation
lFlowSpeed	double	8	16	flow speed
total size		**24**		

```
// definition of flow grid
TLocalFlowDev = RECORD
         lFlowDirection,
         lFlowDeviation,
         lFlowSpeed : float;
        END;
TFlowGrid = RECORD
       FlowGridXDim,FlowGridYDim : integer;
       FlowData : ARRAY of ARRAY of TLocalFlowDev;
      END;
```

10.9.5 Disturbance definitions

Name	type	size [byte]	offset	explanation
Disturbances	TDisturbaceDef	N*112		a list of all disturbance definitions
total size		**various**		

TDisturbanceDef

Name	type	size [byte]	offset	explanation
xleft	integer	4	0	Disturbance area definition
ytop	integer	4	4	
xright	integer	4	8	
ybottom	integer	4	12	
xmean	double	8	16	Disturbance size definition
xstd	double	8	24	
ymean	double	8	32	
ystd	double	8	40	
clipping	**boolean**	1(8)	48	Clipping enabled
probabiltiy	double	8	56	probability per time step
lasttime	integer	4	64	Last occurence
serverity	double	8	68	0-100 %
changeSubstrate	**byte**	1(8)	**80**	Binary switch S_1-S_8
DisturbanceDirection	double	8	88	Direction
disturbanceDirDeviation	double	8	96	Deviation
subDisturbanceEvents	integer	4(8)	104	Number of sub events
total size		**112**		

Delphi type definition

```
TDisturbance = Record
         xleft, ytop,        // area def
         xright, ybottom : integer;

         xmean, xstd,     // mean size and standard deviation
         ymean, ystd : float;

         clipping : boolean; // clip at area border
         probability : TSubTimeValues;
         Lasttime : integer;

         // changed in v1.2
         severity : float;        // 0 - 1.0 ==0-100%
         ChangeSubstrate : bytE;     // reset subtrate to
         DisturbanceDirection,      // direction 0..2Pi
         DisturbanceDirDeviation : float; // deviation 0..2Pi
```

```
     SubDisturbanceEvents : integer; // do x sunbevents...

    End;
```

10.9.6 Species definitions

A linear list of all defined species

Name	type	size [byte]	offset	explanation
species	TSpeciesDef	N*496		a list of all species
total size		**various**		

TSpeciesDef

Name	type	size [byte]	offset	explanation
Name	string[20]	20	0	Name
dispersalDistance	double	8	24	Dispersal distance
dispersalPatchSize	double	8	32	Dispersal patch size
MaxSize	double	8	40	Max size
deathProbability	double	8	48	Mortality per time step
Fecundity	double	8	56	Fecundity per reproduction
maxLifeSpan	integer	4	64	Maximal life span
meanLifeSpan	integer	4	68	„normal" life span
firstReproduction	integer	4	72	Age of marternity
ReproductionInterval	integer	4	76	Reproduction interval
HasGlobalDrift	boolean	1	80	Is capable of migration
belongsToState	byte	1(4)	81	Belongs to guild
GrowsOnSubstrate	**integer**	4	**84**	Binary substrate S_1-S_8
ChangesToSubstrate	integer	4(8)	88	Binary substrate S_1-S_8
degTimeSync	double	8	**96**	Proability to be in reproduction syncronisation
DisplayColor	integer	4	104	Display color, RGB-value
GrowthModel	integer	4	108	0=linear 1=exponential
growthK	double	8	112	Exponential growth constant
RESERVED	byte	373(376)	120	
total size		**496**		

```
  TSpeciesDef = RECORD
           name : string[20];
           dispersalDistance,
           dispersalPatchSize,
           maxSize      : float;
           deathprobability,
           fecundity     : TSubTimeValues;
           maxLifeSpan,
           meanLifeSpan,
           firstReproduction,
           ReproductionInterval : integer;
           HasGlobalDrift : boolean;
           belongsToState : TState;
           GrowsOnSubstrate,
           ChangesToSubstrate : integer;
           degTimeSync : float;
           DisplayColor : integer; // 4 byte = TColor;
           GrowthModel : integer;
           growthK : float;
           RESERVED    :    ARRAY[0..4*99-(2*sizeOf(float)+2*sizeOf(integer))]    of    byte;
//integer=4Byte!
         END;
```

10.9.7 Simulation grid definition

This is a map of all simulation grid cells. The cells are stored consecutive in the following order:

```
(0/0),(0/1),(0/2)....
(1/0),(1/1),(1/2)....
....
(x/0),(x/1).....(x/y)
```

Each cell has a cell is stored with a header, containing the cell info and a list of all individuals in this cell. The data types are listed below:

Name	type	size [byte]	offset	explanation
Cell Header	TCellHeader	20	0	cell definition
Individuals	TIndividual	N*32	20	list of all individuals in the cell
total size		**various**		

TCellHeader

Name	type	size [byte]	offset	explanation
capacity	integer	4	0	cell capacity
totalDist	integer	4	4	total number of disturbances
lastDisturbance	integer	4	8	time since last disturbance
SubstrateType	integer	4	12	substrate S1-S8
Individuals	integer	4	16	number of individuals in the cell
total size		**20**		

TIndividual

Name	type	size [byte]	offset	explanation
isSpecies	integer	4	0	is of species Nr.
age	integer	4	4	age of the individual
size	double	8	8	current size
lastReproduction	integer	4	16	time steps since last reproduction
xPos	integer	4	20	sub-grid x-position
yPos	integer	4(8)	24	sub-grid y-position
total size		**32**		

Delphi-style defintions:

```
TFileCellHeader = RECORD
        capacity,
        totalDist,
        lastDisturbance,
        SubstrateType,
        Individuals : integer;
       END;

 TIndividual = RECORD
          isSpecies    : integer;
          age       : integer;
          size       : float;
          lastreproduction : integer;
          xPos,yPos    : integer; // pos in subgrid;
        END;
```

10.10 Acknowledgement, external code

SIMBAA was completely written from the scratch using Borland Delphi 7 Professional. It makes extensive use of some packages supplied by Borland. However, some code was taken and modified from other sources:

The pseudo random generator procedures in the unit MyRandom.pas were taken form "Numerical Recipes in Pascal: The Art of Scientific Computing" (Press, Teukolsky, Vetterling and Flannery, Cambridge University Press, ISBN 0-521-37516-9). This was done in order to use a defined portable pseudo random generator.

The colour routines are based on source of *Grahame Marsh*, released as freeware:

```
//-----------------------------------------------------------------------------
//
// HSL - RGB colour model conversions
//
// These four functions can be used to convert between the RGB and HSL colour
// models. RGB values are represented using the 0-255 Windows convention and
// always encapsulated in a TColor 32 bit value. HSL values are available as
// either 0 to 1 floating point (double) values or as a 0 to a defined integer
// value. The colour common dialog box uses 0 to 240 by example.
//
// The code is based on that found (in C) on:
//
//  http:/www.r2m.com/win-developer-faq/graphics/8.html
//
// Grahame Marsh 12 October 1997
//
// Freeware - you get it for free, I take nothing, I make no promises!
//
// Please feel free to contact me: grahame.s.marsh@corp.courtaulds.co.uk
//
// Revison History:
//  Version 1.00 - initial release 12-10-1997
//
//-----------------------------------------------------------------------------
```

(copyright notice of the HSL-RGB source code in unit HSLUtils.pas)

The function to read the compile time of the executable (About-Dialog) was taken from:
http://www.delphipraxis.net/topic13233_datum+und+uhrzeit+der+kompilierung+compile+date+time.html
SIMBAA may contain other code parts inspired by information found at various places of the internet. In particular these parts address one specific problems and solutions for these, such as the above mentioned colour conversion and portable random generator. However, these are not essential for the simulation itself but made the work much easier (Man muss das Rad nicht mehrfach erfinden!).

Erklärung gemäß §10 Absatz 2b und §10 Absatz 2c der Prüfungsordnung vom 11.12.2003 der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg.

Hiermit erkläre ich, das ich die vorliegende Arbeit selbstständig verfasst und nur die angegebenen Hilfsmittel benutzt habe. Teile des vorliegenden Werkes sind zum gegenwärtigen Zeitpunkt bereits veröffentlicht. Die entsprechenden Passagen sind als solche gekennzeichnet und die bibliografischen Daten sind angeführt.

Die vorliegende Dissertation liegt bzw. lag weder in Gänze noch in Teilen einer anderen Hochschule in einem Promotionsverfahren vor.

____

Bremerhaven, den ___.____.___________

Lebenslauf gemäß §16 Absatz 3 der Prüfungsordnung vom 11.12.2003 der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg.

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