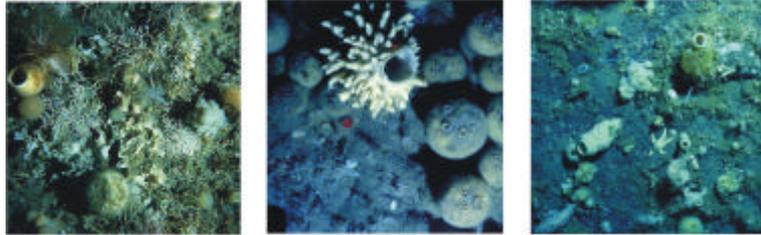


**Stiftung Alfred-Wegener-Institut
für Polar- und Meeresforschung, Bremerhaven**



**Analysing benthic communities
in the Weddell Sea (Antarctica):
a landscape approach**

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Als meus pares Joana i Víctor, i

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Abstract

Antarctic benthos exhibits highly complex communities with a wide array of spatial patterns at several scales which have been poorly quantified. In this study, I introduce the use of methods borrowed from landscape ecology to analyse quantitatively spatial patterns in Antarctic mega-epibenthic communities. This discipline focuses on the notion that communities can be observed as a patch mosaic at any scale. From this perspective I investigated spatial patterns based on landscape indices in an undisturbed benthic assemblage across different stations; and through successional stages after iceberg disturbance. The present study i) characterizes coverage and abundance of sessile benthic fauna, ii) describes faunal heterogeneity using ordination techniques and identifies “structural species” from each successional stage, iii) analyses changes of growth-form patterns through succession, and iv) relates the life-history traits of “structural species” to differences in distribution during the course of Antarctic succession.

For this purpose, underwater photographs (1m² each) corresponding to 6 stations from the southeastern Weddell Sea shelf were investigated. Overall, the different stations within the undisturbed assemblage showed large differences in patch characteristics (mean size and its coefficient of variation, and shape indices), diversity, and interspersions. Canonical Correspondence Analysis (CCA) revealed a gradual separation from early to older stages of succession after iceberg disturbance. Conceptually, the results describe a gradient from samples belonging to early stages of recovery with low cover area, low complexity of patch shape, small patch size, low diversity, and patches poorly interspersed to samples from later stages with higher values of these indices. Cover area was the best predictor of community recovery.

There were changes in the occupation of space of benthic organisms along the successional stages. Uncovered sediment characterized the early stages. The later stages showed high and intermediate values of benthic coverage, where demosponges, bryozoans, and ascidians exhibited high abundance. Several “structural species” were identified among the stages, and information on their coverage, abundance, and size is provided. Early stages were characterized by the presence of pioneer taxa, which were locally highly abundant. Soft bush-like bryozoans, sheet-like sabellid polychaetes, and tree-like sponges, gorgonians, bryozoans, and ascidians represented the first colonizers. Mound-like sponges and ascidians and also tree-like organisms defined the late stages. I conclude by comparing the selected “structural species” and relating their life history traits to differences in distribution during the course of Antarctic succession.

The pace of reproduction and growth of Antarctic marine invertebrates is considered generally very slow. These characteristics may have a strong effect on all aspects of the species' life history and should determine the time needed for a species or a community to respond to disturbance. Changes in the magnitude, frequency, and duration of disturbance regimes and alterations of ecosystem resilience pose major challenges for conservation of Antarctic benthos.

ZUSAMMENFASSUNG

Im antarktischen Benthos haben sich sehr komplexe Gemeinschaften mit einer Vielzahl struktureller Merkmale auf unterschiedlichen Ebenen entwickelt, die bislang kaum quantifiziert worden sind. In dieser Arbeit führe ich eine Methode zur Beschreibung der Struktur der epibenthischen Megafaunagemeinschaft mit Hilfe von Indizes aus der Landschaftsökologie ein. Diese Disziplin basiert auf der Annahme, daß Gemeinschaften als räumliche Mosaik von allen Betrachtungsebenen aus beobachtet werden können. Auf dieser Basis wurden strukturelle Merkmale an verschiedenen Stationen innerhalb einer ungestörten Benthosgemeinschaft und unterschiedliche Sukzessionsstadien nach der Störung durch Eisberge untersucht. Die vorliegende Studie charakterisiert den Bedeckungsgrad und die Abundanz sessiler benthischer Fauna, beschreibt die Heterogenität der Fauna unter Berücksichtigung von Ordinationstechniken und identifiziert dabei die Schlüsselarten aller Sukzessionsstadien. Schließlich analysiert sie Veränderungen in den dominanten Wachstumsmustern während der Sukzession und setzt die Anpassungen in der Lebensweise von Schlüsselarten in Bezug zu Verteilungsunterschieden während der Sukzession.

Zu diesem Zweck wurden Unterwasserfotografien (je 1m² Fläche) von 6 Stationen des südwestlichen Weddellmeerschelfs untersucht. Insgesamt zeigten die verschiedenen Stationen der ungestörten Gemeinschaft deutliche Unterschiede in ihrer Struktur (mittlere Größe und deren Variationskoeffizient, Formindex, Diversität und Verteilung der Besiedlungsflecken). Die "Canonical Correspondence"-Analyse (CCA) zeigte eine graduelle Trennung der Sukzessionsstadien nach einer Eisbergstörung. Generell beschreiben die Ergebnisse einen Gradienten vom ersten Wiederbesiedlungsstadium mit geringem Bedeckungsgrad, geringer Komplexität an Strukturen, geringer Strukturgröße, niedriger Diversität und niedrigem Streuungsgrad der Flächen zu späteren Stadien, deren Indizes allesamt höher ausfallen. Der Bedeckungsgrad (*cover area*) macht die beste Vorhersage für den Erholungsgrad der Gemeinschaft.

Im Verlauf der Sukzessionsstadien wurden Veränderungen in der Flächendeckung durch benthische Organismen beobachtet. Unbedeckte Sedimente charakterisieren frühe Stadien. Spätere Stadien zeigten mittlere und hohe Werte benthischer Bedeckung, wobei Demospongien, Bryozoen und Ascidien hohe Abundanzen aufzeigten. Mehrere Schlüsselarten wurden innerhalb der Sukzessionsstadien unterschieden. Informationen zu ihrem Bedeckungsgrad, ihrer Abundanz und Größe sind dargestellt. Frühe Stadien wurden durch die Anwesenheit von Pionierarten charakterisiert, die lokal sehr häufig auftraten. Weiche und buschartige Bryozoen, flächige (*sheet*) sabellide Polychaeten,

baumförmige (*tree*) Schwämme, Gorgonarien, Bryozoen und Ascidien stellen die Erstbesiedler. Sowohl hügelartige (*mound*) Schwämme und Ascidien als auch baumförmige Organismen charakterisieren späte Stadien. Im direkten Vergleich wird die Verteilung der Schlüsselarten während der Sukzession auf Unterschiede in ihrer Lebensweise zurückgeführt.

Reproduktion und Wachstum antarktischer Evertebraten gelten generell als sehr verlangsamt. Diese Grundcharakteristika werden als wichtige Faktoren angenommen, die auf alle Lebensbereiche einer Art einwirken. Sie bestimmen insbesondere die Zeitskala auf der eine Art oder Gemeinschaft auf Störungsprozesse reagiert. Veränderungen in Ausmaß, Häufigkeit und Dauer von Störungsprozessen und Änderungen in der Resilienz des Ökosystems stellen große Herausforderungen für das antarktische Benthos dar.

RESUMEN

El bentos antártico muestra comunidades muy complejas con un amplio arreglo de patrones espaciales que han sido pobremente cuantificados. En este estudio, se introdujeron métodos utilizados en la Ecología del Paisaje (*Landscape Ecology*) para analizar cuantitativamente patrones espaciales de las comunidades megaepibénticas antárticas. Esta disciplina se funda en la idea que las comunidades pueden observarse a cualquier escala como un mosaico compuesto por varios parches (*patches*). Desde esta perspectiva, se aplicaron índices de paisaje para el estudio de patrones espaciales (en una serie de estaciones) en una comunidad no perturbada y a lo largo de estadios de sucesión después de perturbaciones por el paso de *icebergs*. En este estudio i) se caracteriza la cobertura y abundancia de fauna béntica sésil, ii) se describe la heterogeneidad faunística usando técnicas de ordenación y se identifican “especies estructurales” para cada estadio de sucesión, iii) se analizan cambios en los patrones de las formas de crecimiento a lo largo de la sucesión y iv) se relaciona rasgos de la historia de vida de las “especies estructurales” con diferencias en la distribución en el curso de la sucesión.

Con este propósito se investigaron fotografías submarinas (cada una representa 1m²) de 6 estaciones de la plataforma continental sudeste del Mar de Weddell. En general, las estaciones correspondientes a la comunidad no perturbada mostraron grandes diferencias en las características de los *patches* (tamaño promedio y su coeficiente de variación e índices de forma), diversidad e interspersión. El Análisis de Correspondencia Canónica (CCA) mostró una separación gradual en la sucesión después de la perturbación por *icebergs* desde los estadios tempranos hasta los más tardíos. Conceptualmente, estos resultados describen un gradiente de muestras correspondientes a los primeros estadios de sucesión – caracterizados por *patches* con poca cobertura, baja complejidad de forma, tamaño pequeño, baja diversidad y poca interspersión -, a muestras de estadios tardíos con valores altos de los índices mencionados. En este contexto, la cobertura de área fue el índice que mejor predijo la recuperación de la comunidad.

También se detectaron cambios en la ocupación del espacio por organismos bénticos a lo largo de los estadios de sucesión. El sedimento sin cubrir caracterizó los primeros estadios. En cambio, los estadios tardíos tuvieron valores intermedios y altos de cobertura bentónica donde las demosponjas, briozoos y las ascidias mostraron abundancias altas. Varias “especies estructurales” fueron identificadas en todos los estadios y la información sobre su cobertura, abundancia y tamaño también se presenta

en este estudio. Los estadios tempranos se caracterizaron por la presencia de taxones pioneros los cuales fueron localmente muy abundantes. Estos primeros colonizadores estuvieron representados por: Briozoos de consistencia suave, poliquetos sabelidos con forma tipo “hoja” y esponjas, gorgonias, briozoos y ascidias con forma tipo “árbol”. Las esponjas y las ascidias con forma tipo “montículo” y organismos con forma tipo “árbol” definieron los estadios tardíos. Se concluye comparando las “especies estructurales” seleccionadas y relacionando los rasgos de su historia de vida con las diferencias en distribución a lo largo de la sucesión antártica.

El ritmo de reproducción y crecimiento de los invertebrados marinos antárticos se considera muy lento en general. Estas características pueden tener un efecto importante en todos los aspectos de la historia de vida de las especies y deben determinar el tiempo que las especies o las comunidades necesitan para responder a una perturbación. Los cambios en la magnitud, frecuencia y duración de los regímenes de la perturbación y las alteraciones de la resiliencia del ecosistema suponen grandes retos para la conservación del bentos antártico.

RESUM

El bentos antàrtic presenta comunitats molt complexes amb una àmplia col·lecció de patrons espacials, a diferents escales, les quals fins a l'actualitat han estat poc quantificades. En aquest estudi, s'utilitzen els mètodes desenvolupats en l'ecologia de paisatge (*Landscape Ecology*) per analitzar quantitativament els patrons espacials de les comunitats megaepibèntriques antàrtiques. Bàsicament, aquesta disciplina es fonamenta en l'observació i l'anàlisi, a qualsevol escala, de les comunitats com un mosaic de taques (*patches*). Amb aquest punt de vista, s'ha aplicat els índexs de paisatge a l'estudi dels patrons espacials (en una sèrie d'estacions) d'una comunitat no perturbada i al llarg d'estadis de la successió després del pas dels *icebergs*. En el treball i) es caracteritza la cobertura i l'abundància de fauna bentònica sèssil; ii) es descriu l'heterogeneïtat faunística utilitzant tècniques d'ordenació i s'identifiquen les "espècies estructurals" en cada estadi de la successió; iii) s'analitza els canvis en els patrons de forma de creixement durant la successió i finalment, iv) es relacionen els trets de la història de vida de les "espècies estructurals" amb les diferències de distribució durant el transcurs de la successió.

Per assolir els objectius s'han investigat fotografies subaquàtiques (d'1m² cada una) corresponents a 6 estacions situades en la plataforma continental sud-est del Mar de Weddell. En general s'ha detectat que a les estacions on la comunitat no està perturbada hi han clares diferències en les característiques de les taques (mitjana de la mida, coeficient de variació i dels índexs de forma), en la diversitat i en la interspersió. Així mateix, l'Anàlisi Canònic de Correspondències (CCA) ha mostrat una separació gradual dels estadis inicials de la successió cap als estadis més madurs; posteriorment a les perturbacions produïdes pels *icebergs*. Conceptualment, els resultats descriuen un gradient de mostres corresponents als estadis inicials de recuperació, - caracteritzades per taques de mida petita, amb baixa àrea de cobertura, baixa complexitat de formes, baixa diversitat i poca interspersió -, cap a mostres que pertanyen als estadis més madurs; caracteritzades per valors més alts d'aquestes mesures. En aquest context, l'àrea de cobertura ha estat el millor predictor de la recuperació de la comunitat.

També s'han detectat canvis en l'ocupació de l'espai per part dels organismes bentònics al llarg dels estadis de successió; trobant-se que els estadis inicials es caracteritzaren per la no cobertura del sediment. En canvi, els estadis finals mostraren valors intermedis i alts de cobertura bentònica, amb una alta abundància de demosponges, briozous i ascidies. Així mateix, s'han identificat diverses "espècies estructurals" entre els estadis, i se n'ha

quantificat la seva cobertura, l'abundància i la mida. Els estadis inicials es caracteritzaren per la presència de taxons pioners, trobant-se que localment eren molt abundants. Aquests primers colonitzadors varen presentar formes flexibles i suaus de briozous, formes de tipus "fulla" (poliquets sabèlids) i formes de tipus "arbre" (esponges, gorgonies, briozous i ascidies); mentre que les formes "turó" (esponges i ascidies) i els organismes tipus "arbre" varen definir els darrers estadis. L'estudi finalitza comparant les "espècies estructurals" i relacionant els seus trets de la història de vida amb les diferències de distribució durant el transcurs de la successió antàrtica.

El ritme de reproducció i creixement dels invertebrats marins antàrtics es considera molt lent en general. Aquestes característiques poden tenir un efecte molt marcat en tots els aspectes de les històries de vida de les espècies i pot condicionar el temps necessari en el que una espècie o una comunitat respon a una pertorbació. Qualsevol canvi en la magnitud, la freqüència i la duració dels règims de pertorbació suposa una alteració de la resiliència de l'ecosistema i, per tant, un gran repte per a la conservació del bentos antàrtic.

1. Introduction

A main purpose of ecological research is to *understand* ecological processes and the resultant patterns of distribution, abundance, diversity, and interactions of species (McIntosh 1985, Underwood et al. 2000). Furthermore, Margalef (1984, 1997) pointed out the importance of understanding the relationships among processes at different scales of organization, and the emergence of macroscopic pattern from microscopic phenomena.

Recent studies have emphasized that the variability in abundance and interactions of species at different spatial and temporal scales plays an important role in ecosystem dynamics following disturbance (Connell et al. 1997, Peterson et al. 1998, Chapin et al. 2000). In many biological communities these distribution and abundance patterns bear the reminiscences of historical events (Dudgeon & Petraitis 2001).

Antarctic benthos is influenced by different combination and intensity of biotic (predation, competition, recruitment) and abiotic factors (substratum, depth, sedimentation, currents-food supply, ice scouring) (Dayton et al. 1974, Dayton 1989, Arntz et al. 1994, Slattery & Bockus 1997, Stanwell-Smith & Barnes 1997, Gutt 2000). In addition, historical processes such as tectonic and climatic events, dispersal and migration, extinction and speciation during the past have influenced the evolution of the present Antarctic fauna (Lipps & Hickman 1982, Clarke & Crame 1992, Clarke 1997).

Remote imaging techniques have provided valuable information on Antarctic benthic communities mainly on the shelves of the Ross and Weddell Seas. These studies focused on identifying assemblages, describing distributional patterns, and quantifying diversity at large and intermediate scales (e.g., Bullivant 1967, Dearborn 1977, Gutt & Piepenburg 1991, Barthel & Gutt 1992, Gutt & Koltun 1995, Gutt & Starmans 1998, Starmans et al. 1999, Orejas et al. 2002). Moreover, they revealed the impact of iceberg scouring on benthic communities and provided sound evidences of the “driving force” behind this disturbance in structuring Antarctic benthos (Gutt et al. 1996, Gutt & Starmans 2001, Gutt & Piepenburg 2003). Nevertheless, there still is a paucity of analytical methods to obtain ecologically relevant data from images (Teixidó et al. 2002). As a consequence, landscape indices were applied to analyse Antarctic benthic community images in order to improve our understanding of spatial patterns in these communities.

1.1. Landscape ecology

The term *landscape ecology* was introduced by the German biogeographer Carl Troll in 1939 relating forest vegetation with aerial photography. *Landscape* has been defined in various ways, but all emphasize two important aspects: landscapes are composed of multiple elements (or patches) and the variety of these elements creates heterogeneity within an area (Wiens 2002). Landscapes are characterized by their structure (the spatial arrangement of landscape elements - patches-), their ecological function (the interactions among patches within that structure), and the dynamics of change (the alteration in the structure and function of the landscape over time). For a recent general information about landscape ecology see Turner et al. 2001, Gergel & Turner 2002, Gutzwiller 2002, Ingegnoli 2002.

Landscape ecology has developed rapidly over the last decades (Forman & Gordon 1986, Turner 2001). This recent emergence resulted from three main factors: 1) broad-scale environmental issues and ecological problems (e.g., global climatic change, deforestation); 2) the development of new strategies based on a spatial-temporal scale at which the phenomenon of interest occurs; and 3) technological advances, including availability of remotely sensed data such as satellite images, and development of powerful computer software packages called geographic information systems (GIS) for storing, manipulating, and displaying spatial data.

The ability to quantify landscape structure is a prerequisite to study landscape function and change (Turner et al. 2001). Within this context, much emphasis has been placed on the development of a large collection of indices to describe dynamics and patterns of landscapes (e.g., O'Niell et al. 1988; Turner 1989, Kineast 1993, Wiens et al. 1993, Riitters et al. 1995). These indices have been applied successfully at many spatial-temporal scales, ranging from broad scale (kilometres) (e.g., O'Niell et al. 1988, Turner & Ruscher 1988, Kineast 1993, Hulshoff 1995, McGarrigal & McComb 1995, Ritters et al. 1995, Drapeau et al. 2000) to finer scale (metres and centimetres) (Teixidó et al. 2002, Garrabou et al. 1998, Saunders et al. 1998). However, it remains challenging to determine the influence of spatial patterns on ecological processes (Levin 1992, Gustafson 1998).

Within this frame, it is assumed that Antarctic benthic communities (as landscape) can be observed as patch mosaics, where patches are assigned to different categories (e.g., species, cluster of species). From this perspective, community spatial patterns and dynamics can be analysed by focusing on the characteristics of the patch mosaic.

1.2. The benthic community on the southeastern Weddell Sea shelf

The unusually deep continental shelf of the Weddell Sea exhibits locally a complex three-dimensional community with a large biomass, intermediate to high diversity, and patchy distribution of organisms (Gutt & Starman 1998, Gili et al. 2001, Teixidó et al. 2002, Gerdes et al. 2003). The Kapp Norvegia region belongs to the Eastern Shelf Community described by Voß (1988) as the richest high Antarctic community. The fauna in this area is dominated by a large proportion of benthic suspension feeders such as sponges, gorgonians, bryozoans, and ascidians, which locally cover the sediment completely (Gutt & Starman 1998, Starman et al. 1999, Teixidó et al. 2002). In many areas off Kapp Norvegia the benthos is dominated by sponges, e.g., the hexactinellids *Rossella racovitzae*, *R. antarctica*, *R. nuda*, and the demosponge *Cinachyra barbata*.

The benthic community inhabiting areas affected by iceberg scouring exhibits a wide range of complexity: from areas almost devoid of any fauna through stages with few abundant species to highly complex communities characterized by a high species richness and extremely high biomass (Gutt et al. 1996, Gerdes et al. 2003). The successional stages differ in faunistic composition and abundance (Gutt et al. 1996, Gutt & Starman 2001). Early successional stages are considered precursors toward the final slow-growing hexactinellid sponge stage (Dayton 1979, Gatti 2002), assuming that many decades or even centuries may be necessary to return to such a mature community after disturbance.

1.3. Objectives of this study

The major aim of this thesis is to quantify organisational patterns in an Antarctic benthic community on the shelf of the Weddell Sea by applying landscape analysis to underwater photography. Within this context, the different objectives of this thesis are:

- i)** to quantify organisational patterns in an undisturbed assemblage on the shelf of the Weddell Sea by applying landscape analysis to underwater photography
- ii)** to study community succession after iceberg disturbance by applying measures of landscape pattern to detect spatial changes, and to better understand how Antarctic benthic communities are structured and organised through successional stages
- iii)** to describe changes in benthic composition and growth-form patterns in the occupation of open space along succession
- iv)** to identify “structural species” and relate their life history traits to differences in distribution in the course of Antarctic succession

1.4. Structure of this thesis

This thesis is structured in four sections. The first section includes a general introduction, material and methods, study area, and discussion. The second section consists of the publications related to this study sent to international journals (Fig. 1). Each one provides sufficient information to be considered independent. The second publication is the core of this thesis. The reference section lists all the literature cited along this thesis. Finally, the appendix section contains concrete information about photographic stations, their bathymetry, list of species analysed, and equations of landscape indices.

	objectives	method	data analysis	stage
Publication I	quantification of spatial patterns	landscape pattern indices (LPI)	multivariate (CVA and PCA) and univariate (ANOVA) analyses	UD
Publication II	quantification of spatial patterns through succession	landscape pattern indices (LPI)	multivariate (CCA) and univariate (Kruskal-Wallis) analyses	R0, R1, R2, UD
Publication III	changes in benthic composition and growth-forms identification of "structural species" and their life history traits	coverage and abundance	multivariate (MDS) and univariate (Kruskal-Wallis) analyses	R0, R1, R2, UD

Fig. 1. Diagrammatic summary of the present study. For abbreviations see Appendix 8.1.

2. Study area

2.1. General description of the study area

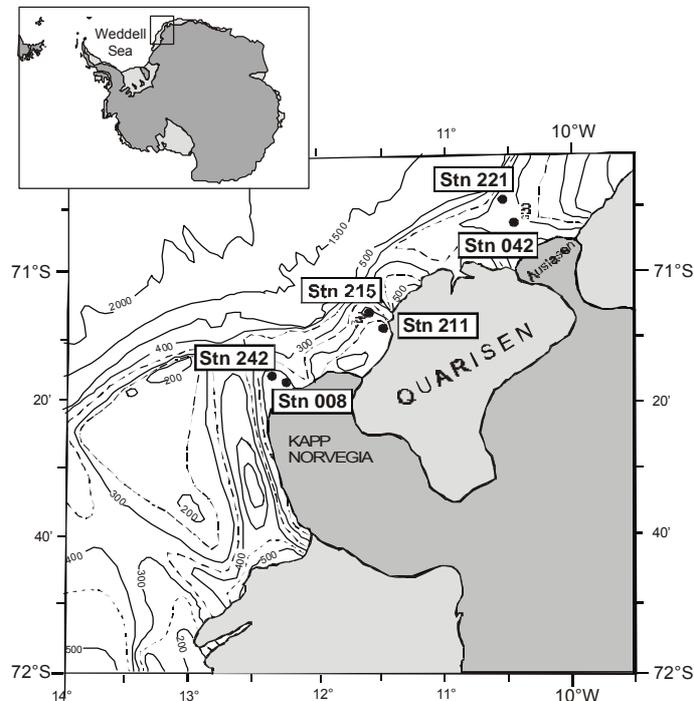


Fig. 2. Study area in the southeastern Weddell Sea (Antarctica) showing the location of photographic stations and their depths: Stn 008 (171 m), Stn 042 (251m), Stn 211 (117 m), Stn 215 m (160 m), Stn 221 (265 m), and Stn 242 (159 m). (Subsection of chart AWI BCWS 553).

Kapp Norvegia is located in the southeastern Weddell Sea (Fig. 2), where the continental shelf is relatively narrow (less than 90 km) and reaches depths of 300-500 m (Carmack & Foster 1977, Elverhøi & Roaldset 1983). Seasonal sea ice covers the continental shelf and extends beyond the continental break, (Tréguer & Jacques 1992) but coastal polynyas of varying size may occur (Hempel 1985). Water temperature close to the seafloor is low and very constant throughout the year, ranging from $-1.3\text{ }^{\circ}\text{C}$ to $-2.0\text{ }^{\circ}\text{C}$ (Fahrbach et al. 1992). There is a marked summertime peak in primary production (Nelson et al. 1989, Gleitz et al. 1994, Park et al.

1999), reflected by the organic matter flux from surface waters to the seabed (Bathmann et al. 1991, Gleitz et al. 1994). Hydrodynamics affect food availability (e.g., by resuspension and lateral transport) and determine sediment characteristics such as grain size and composition, which are of ecological relevance for benthic communities (Dunbar et al. 1985, Gutt 2000).

2.2. Iceberg scouring disturbance on benthic communities

Ice disturbance is regarded as a common event in the evolutionary history of Antarctic and Arctic benthos (Clarke & Crame 1989, Clarke 1990, Anderson 1991, Dunton 1992, Grobe & Mackensen 1992, Zachos 2001) and among the more important factors structuring these communities (Dayton et al. 1970, Arntz et al. 1994, Conlan et al. 1998, Peck et al. 1999, Gutt 2000). The major disturbance acting on the benthos of the deep continental shelves is the grounding and scouring of icebergs (Gutt et al. 1996, Lee et al. 2001, Gutt & Starmans 2001, Knust et al. *in press*). They severely damage large areas of the seafloor, affecting the physical and biological environment by removing both hard and soft substrates and eradicating benthic life (Gutt et al. 1996, Gutt 2000). Their impact initiates recolonization processes and provides the opportunity to study successional patterns.

The keels of icebergs can create gouges up to 1375 m wide, 10.5 m deep, and several km in length (Lewis & Blasco 1990). On deep seafloors, large gouges may take millennia to disappear (Josenhans & Woodworth-Lynas 1988). The pumping effect of icebergs may be important for sediment transport and winnowing on a local scale and depends on iceberg size, shape, stability, and sediment characteristics (Lien et al. 1989). Large tabular icebergs originate as a result of rifts that cut through the ice shelf (Lazzara et al. 1999). Antarctic ice shelves have produced 70,000 icebergs (> 10 m wide) between 1981 and 1985 (Lien et al. 1989) (Fig. 3), which scoured the seabed up to 500 m water depth (Barnes & Lien 1988, Lien et al. 1989, Gutt et al. 1996) and created drastic rifts in the bottom relief. Gutt & Starmans (2001), considering areas with different bottom topography and concentration of grounded icebergs, calculated a proportion between 20 % and 60 % of undisturbed seafloor in the eastern Weddell Sea.

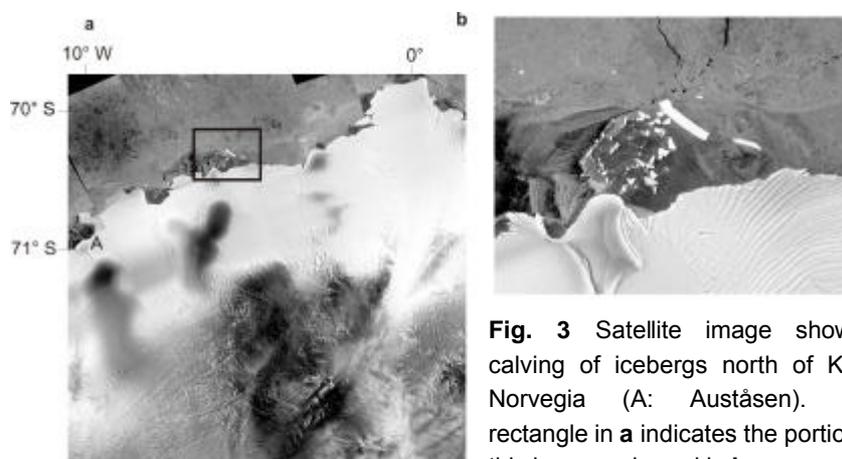


Fig. 3 Satellite image showing calving of icebergs north of Kapp Norvegia (A: Auståsen). The rectangle in **a** indicates the portion of this image enlarged in **b**.

2.3. Description of the successional stages

As earlier mentioned the benthic community inhabiting areas affected by iceberg scouring exhibits a wide range of complexity. The successional stages differ in faunistic composition and abundance and features of the seabed relief (Gutt et al. 1996, Gutt & Starmans 2001). Table 1 shows the main characteristics for each stage analysed. Based on this information, the four stages were identified within the photographic stations (Fig.4).

Table 1. Description of the successional stages identified in the southeastern Weddell Sea. They include 3 stages of recolonisation (from younger to older: R0, R1, R2) and an undisturbed assemblage (UD).

Stage	Description
R0	Sediment surface shows recent mechanical disturbance or is barely covered by organisms. It consists of a high proportion of gravel and detritus. Presence of motile fauna such as fish or echinoderms. First pioneers of sessile species appear with relatively low number and abundance.
R1	Increase of abundance of pioneer sessile species. Occasionally some occur in higher densities e.g., sponges (<i>Stylocordila borealis</i> and <i>Homaxinella</i> sp.), bryozoans (<i>Cellaria</i> sp., <i>Camptoplites</i> sp.), gorgonians (<i>Primnoisis antarctica</i>), ascidians (<i>Synoicum adareanum</i>), and sabellid and terebellid polychaetes (<i>Pista</i> sp.). Sediment surface partially covered by fauna.
R2	Composed of a mixture of sessile suspension feeders, which mostly cover the sediment. Higher no. of species and abundance than R1 and R0. There are no large hexactinellid sponges (≥ 20 cm tall).
UD	Large specimens of hexactinellids, which are known to grow very slowly (Dayton 1979, Gatti 2002) and consequently provide an estimate of the relative age of the assemblage. Composed of a mixture of sessile suspension feeders, which partially cover the sediment. It can be strongly dominated by single sponges (e.g. <i>Rossella racovitzae</i> , <i>R. antarctica</i> , <i>R.nuda</i> , and <i>Cinachyra barbata</i>).

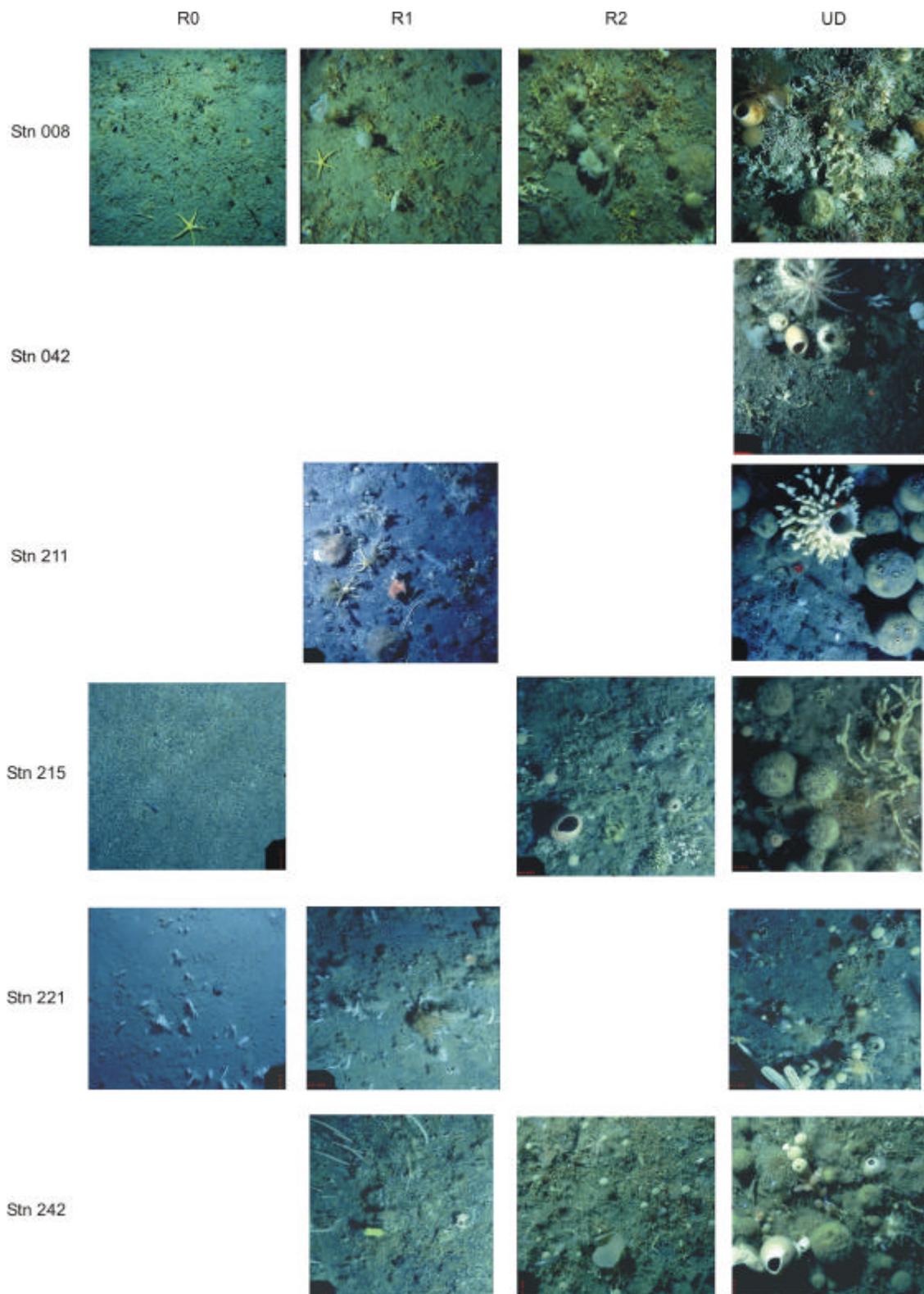


Fig. 4. Overview of the successional stages analysed.

3. Material and Methods

The first part of this chapter gives a brief summary of how the underwater photographs were sampled and processed using a geographical information system (GIS). The second part reports the classification of benthic growth-forms and the use of landscape pattern indices (LPI). Finally, this chapter ends with a general overview of the data analysis used in this study.

3.1. Photosampling

Photographic records of the seafloor were obtained during the expeditions ANT XIII/3 and ANT XV/3 on board R/V 'Polarstern' during the austral summers of 1996 and 1998 (Arntz & Gutt 1997, 1999), within the Ecology of the Antarctic Sea Ice Zone programme (EASIZ) of the Scientific Committee on Antarctic Research (SCAR). A 70-mm underwater camera (Photosea 70) with two oblique strobe lights (Photosea 3000 SX) (Fig. 5) was used at 6 stations (depth range: 117- 265 m) (Fig. 2). At each station sequences of 80 perpendicular colour slides (Kodak Ektachrome 64), each covering approximately 1m² of the seabed, were taken at evenly spaced time intervals along a transect. The optical resolution was around 0.3 mm. At each stage, 7 photographs were studied and processed. In total, an area representing of 42 m² (publication I) and 112 m² (publication II and III) of the seafloor was analysed.



Fig. 5. The underwater camera used in this study.

Table 2. List of the 6 photographic stations in the southeastern Weddell Sea. 7 photographs were analysed along the 3 stages of recolonisation (from younger to older: R0, R1, R2) and the undisturbed assemblage (UD), wherever these occurred.

Stations	Depth (m)	Identified assemblages			
		R0	R1	R2	UD
008	171-173	7	7	7	7
042	260-243	-	-	-	7
211	77-117	-	7	-	7
215	167-154	7	-	7	7
221	261-270	7	7	-	7
242	159-158	-	7	7	7
N° photos		21	28	21	42

3.2. Image analysis

Each photograph was projected on an inverse slide projector and all distinguishable patch outlines were traced onto an acetate sheet at a map scale of 1:5. The drawings were scanned at 100 dpi resolution. The resulting raster images (TIFF format) were imported into a public domain image application NIH Image (National Institutes of Health), where they were subjected to different technical procedures (converted into black and white and the lines were thinned to unit width). Then, the images were imported into Arc/View 3.2 (© ESRI) geographical information system (GIS) where they were spatially referenced. Arc/View routine procedures were used to label all the patches. Each individual patch was assigned to different categories (e.g., species, cluster of species) being solitary or colonial, irrespectively and its information was measured for each photograph. Areas of uncovered substrate were also reported. The images were then converted to vector polygon format for further calculations using the Arc/Info 8.1 program (© ESRI) (Fig. 6).

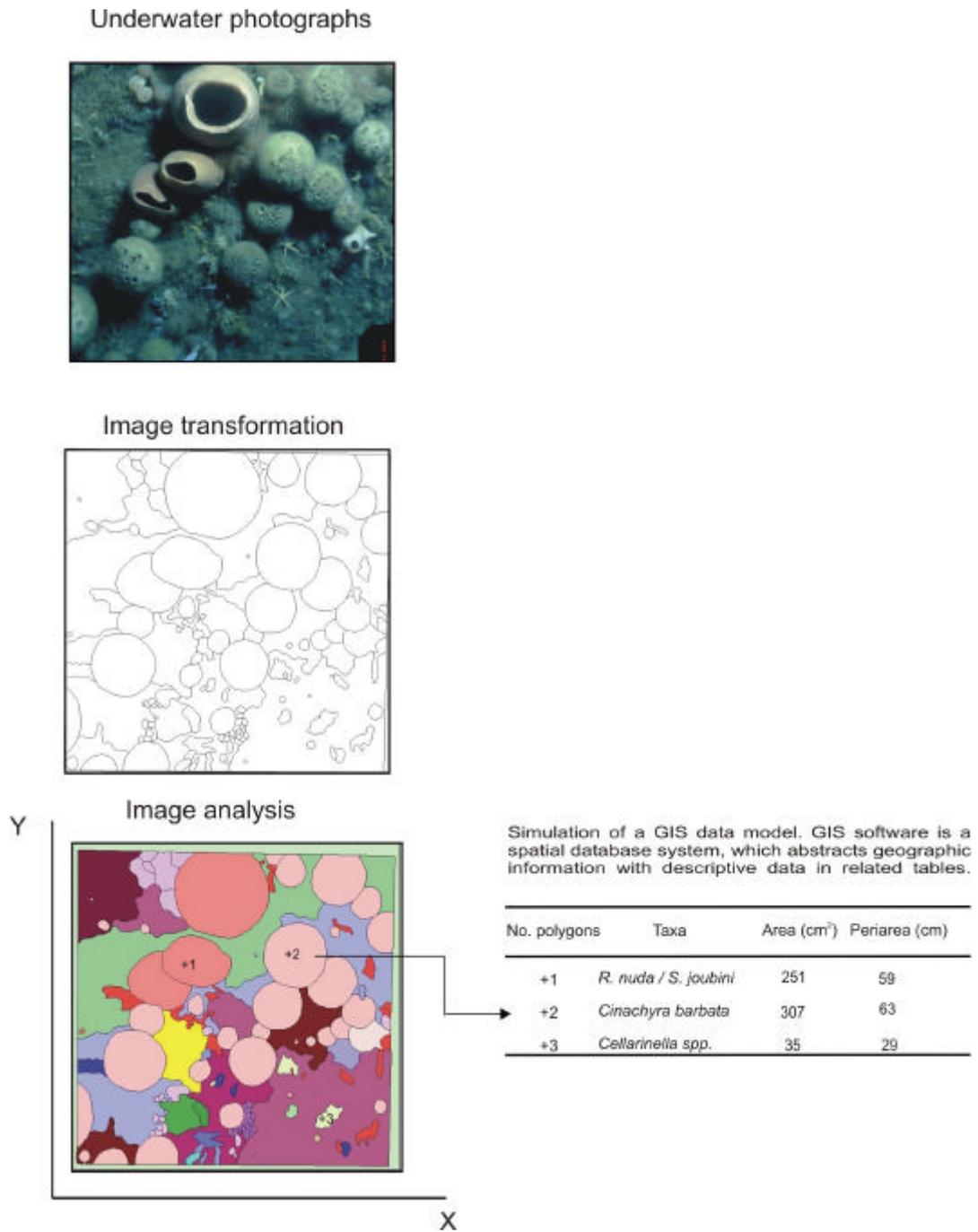


Fig. 6. From underwater photographs to vector computer images. Image transformation: the drawings were scanned and submitted to different technical processes (converted into black and white and the lines were thinned to unit width). Image analysis: the images were imported into Arc/View 3.2 (© ESRI) where they were georeferenced and labeled. Finally, the images were transformed to vector coverage data to calculate LPI using the program Fragstats v3.0 for Arc/Info (© ESRI).

3.3. Identification

Mega-epibenthic sessile organisms, approx. > 0.5 cm in body size diameter, were identified to the lowest possible taxonomic level by photo interpreting following Thompson and Murray 1880-1889, Discovery Committee Colonial Office 1929-1980, Monniot & Monniot 1983, Hayward 1995, Sieg & Wägele 1990, and by the assistance of taxonomic experts (see Acknowledgements).

A total of 118 sessile and sediment cover categories (see Appendix 8.4) was recognized. These included species/genus (106), class/phylum (5), “complex” (7), and substratum (5). Within the species/genus category some unidentified sponges (e.g., “Yellow Branches”) were named according to Barthel and Gutt (1992). Irregular masses composed of bryozoan matrices together with demosponges and gorgonians of small size and similar filamentous morphology defined the seven “complex” cover classes.

3.4. Growth-form patterns

The 118 sessile benthic cover categories were grouped into four growth forms in order to facilitate the analysis and the interpretation of cover area, mean patch size, and number of patch changes through the succession process. The growth forms considered were bushes, sheets, mounds, and trees (see Table 2 for a description of each growth form). This classification was based on previous studies on clonal organisms in coral reefs (e.g., review by Jackson 1979, Connell & Keough 1985). This categorization takes into account relevant ecological strategies followed by benthic species to occupy space on rocky benthic habitats.

Table 3. Description of growth forms used in this study.

Growth form	Description
Bush	Upright forms branching from the base, mainly flexible hydrozoans and bryozoans; with a restricted area of attachment to the substratum
Sheet	Encrusting species of sponges, bryozoans, sabellids, and ascidians growing as two dimensional-sheets; more or less completely attached to the substratum
Mound	Massive species of sponges, anemones, ascidians, and pterobranchs with extensive vertical and lateral growth; attached to the substratum along basal area
Tree	Erect species of sponges, gorgonians, bryozoans, and ascidians, more or less branched; with a restricted area of attachment to the substratum

3.5. Landscape pattern indices (LPI)

Landscape pattern indices (LPI) were calculated for each image by using the spatial pattern program Fragstats v3.0 for Arc/Info (© ESRI). Fragstats calculates landscape indices separately for i) patch (basic elements of the mosaic), ii) class (each particular patch type), and iii) landscape (mosaic of patches as a complete unit) levels. A total set of 17 indices concerning distinct aspects of spatial patterns were calculated at landscape level (Table 1 in Publication I). For more information about these indices (descriptions and equations) see Appendix 8.6 and McGarrigal & Marks (1995).

3.6. Data analysis

Fig. 7 shows a summary of the data analysis used along the different publications. For a detailed description of each analysis see the respective publications.

First, multivariate ordination techniques were used i) to identify spatial pattern relationships within a benthic assemblage across different stations (Canonical variate analysis - CVA, Publication I) and through the successional stages (Canonical Correspondence Analysis - CCA, Publication II), and ii) to determine the combinations of indices that were most strongly associated to the different stages (Publication II). There was relatively strong redundancy among some of the LPI and therefore these indices were not included in the ordination analyses (SIDI, MSIDI, and SIEI in Publication I and PSCV, NP, TE, AWMSI, SIDI, MSIDI, SIEI, and PR in Publication II).

Second, forward stepwise selection was used to choose a subset of LPI. This procedure has the ability to reduce a large set of variables to a smaller set that suffices to explain the variation among the whole data set.

After these analyses, univariate statistics (ANOVA and nonparametric Kruskal-Wallis) were used to test for differences in the subset of LPI among stations (Publication I) and among successional stages (Publication II). Post hoc comparisons i) of means were performed using Tukey's tests (Sokal & Rohlf 1981) (Publication I) and ii) of ranks using the Nemenyi test (Sachs 1984) (Publication II).

Non-metric multidimensional scaling (MDS, Kruskal and Wish 1978) was applied to the similarity composition matrix to describe the faunal heterogeneity through the successional stages. Species representatives for each stage were determined with the

similarity percentage (SIMPER) procedure (Clarke & Warwick 1994), indicating their specific coverage, abundance, and size (Publication III).

Finally, Kruskal-Wallis analysis was used to test for differences in growth-form patterns (CA, NP, and mean patch size- MPS) among the successional stages (Publication III).

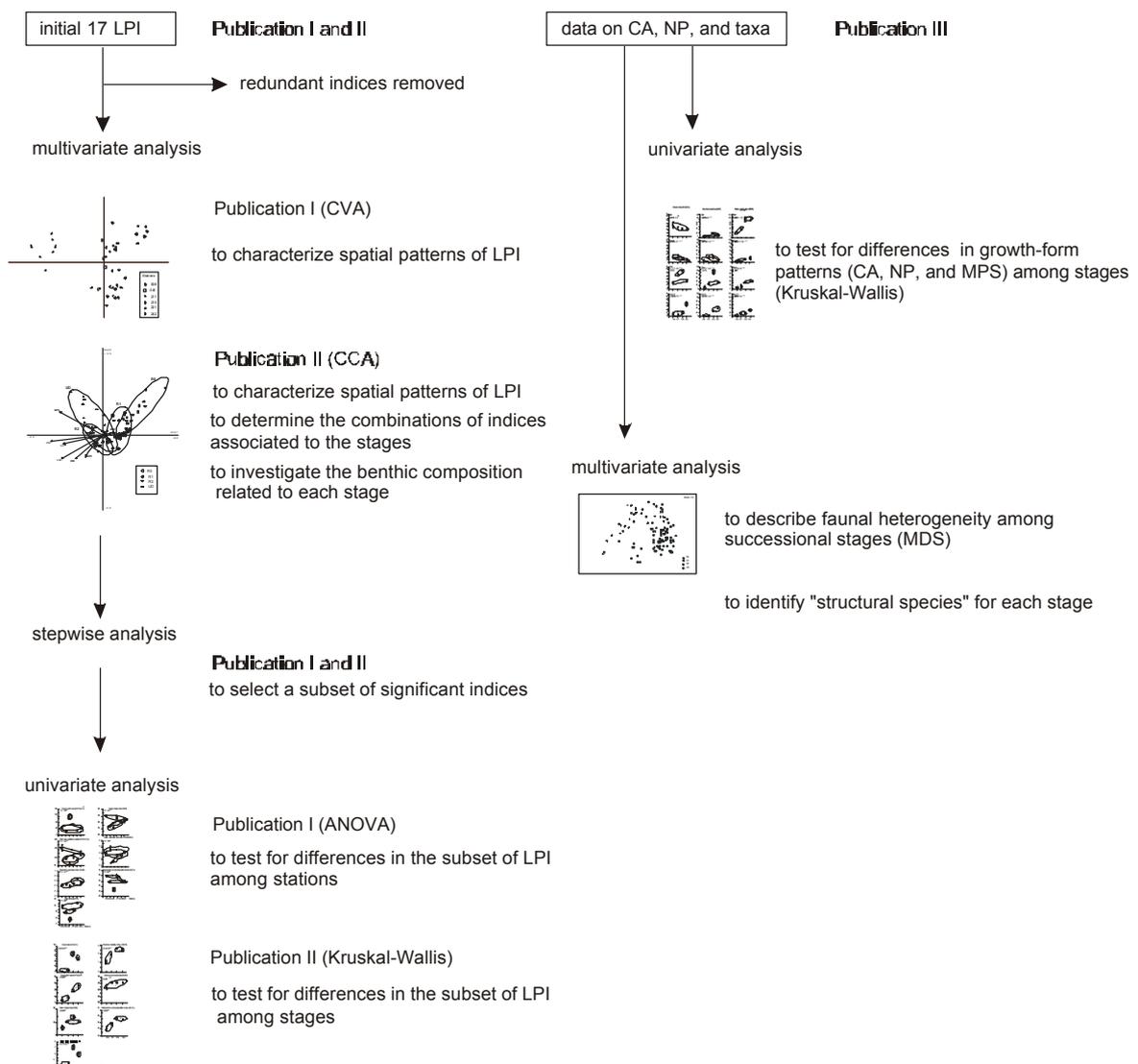


Fig. 7. General overview of the data analysis used in this study.

4. Results and Discussion

In the present chapter I summarize and discuss the most important results of this thesis. For a more detailed discussion see the attached publications. The first two parts of this chapter focus on the quantification of organizational patterns in an undisturbed assemblage and through successional stages by applying measures of landscape analysis to underwater photography. The third part concentrates on recovery, changes in benthic organisms and their structural patterns through succession. In the final part, I suggest further studies on Antarctic benthic communities. In addition, I propose a comparison of different marine benthic communities using the landscape approach.

4.1. Spatial pattern quantification of Antarctic benthic communities using landscape indices

The application of LPI in this study was successful to characterize spatial organization of an undisturbed Antarctic benthic assemblage across different stations (Publication I) and through successional stages after iceberg disturbance (Publication II). LPI provided comprehensive measurements over different aspects of spatial patterns (patch size and form, diversity, and interspersion) within the undisturbed assemblage (Fig. 8) and along the different successional stages, from earlier to late: R0, R1, and R2, and an undisturbed assemblage: UD (Figs. 9 and 10).

4.1.1 Spatial patterns in an Antarctic undisturbed benthic assemblage

The 14 metrics of LPI analysed through the combination of Canonical Variate Analysis (CVA, Fig. 8) and the interpretation of the ANOVA analysis (Fig. 5 in Publication I) revealed a trend of dispersion and significant differences among the stations. Overall, stations differed in size and diversity of patches and in heterogeneity patterns (size variability, shape, and interspersion of patches). These photographic records only referred to the undisturbed assemblage (characterised by a mixture of sessile suspension feeders) (Gutt & Starman 2001) for which minor differences in spatial patterns would be expected. Nevertheless, LPI showed a great discriminatory power detecting significant differences among stations within this assemblage and among successional stages after iceberg disturbance (Publication II, and see below).

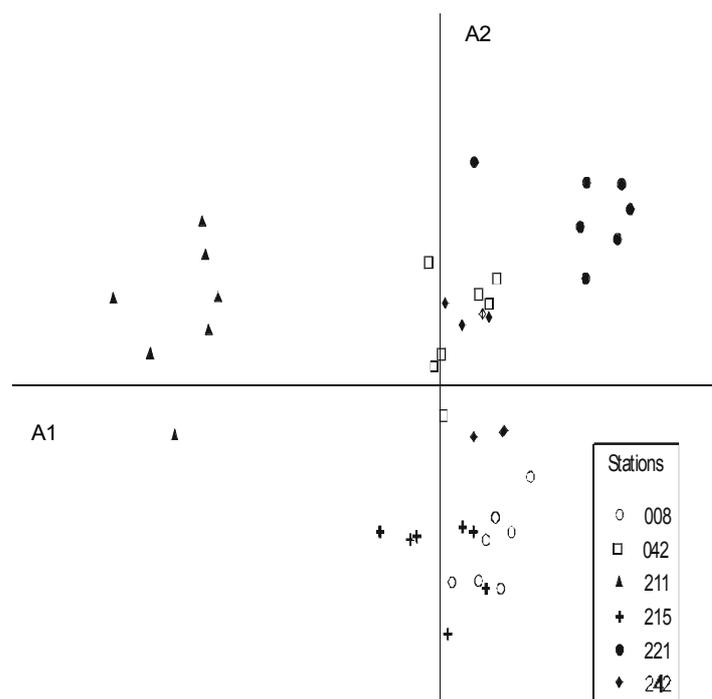


Fig. 8. Canonical variate analysis (CVA) defined by the two first axes (81 % of the total variability) based on LPI for the 6 stations. Each point corresponds to one photograph analysed. Indices included in the analysis: CA, MPS, PSSD, PSCV, NP, TE, MSI, AWMSI, LSI, PERIAREA, SHDI, SHEI, PR, and IJI.

Spatial complexity and diversity patterns of the undisturbed benthic assemblage increased from station 211 to the rest of stations. Station 211 was mostly dominated by volcano-shape hexactinellid sponges and the spherical-shape demosponge *C.barbata*. As a consequence large patches of similar size partially covered and monopolised the substrate. The patches showed less complex shapes, were less diverse, and less interspersed. Station 008 showed the most complex and relatively diverse pattern, with intermediate and variable patch size. The patches exhibited complex shapes, were highly different in composition, relatively equally distributed, and well interspersed. Heterogeneity patterns (variable patch sizes, patches with complex shapes, and interspersed) decreased from station 215 through 242 to 042. These three stations and station 008 were composed of different well-mixed groups of benthic sessile organisms (e.g., sponges, gorgonians, bryozoans, and ascidians), which covered the major part of the bottom sediment. The most diverse pattern occurred at station 221 characterised by demosponges, gorgonians, and bryozoans, which partially covered the seafloor. However, this station did not show high heterogeneity patterns such as stations 008, 215, and 242.

Based on LPI values of this study, spatial patterns and diversity did not converge towards a particular scenario. On the contrary, LPI results suggest a separation between rich and diverse stations, which partially covered the seafloor and those with high values of pattern heterogeneity (highest patchiness, form complexity, and interspersion). These differences within the undisturbed assemblage show the importance of quantification of different aspects of spatial patterns (diversity alone did not discern among all stations). In addition, the observed result in the MDS plot based on benthic composition among photographic samples from different successional stages (Fig. 11) did not determine differences within the undisturbed assemblage (with the exception of station 211, which was grouped apart).

Conclusions:

- The successful description of Antarctic benthos through landscape pattern indices provides a useful tool for the characterisation and comparison of spatial patterns in marine benthic habitats.
- LPI proved to be valuable in determining spatial differences among stations within an Antarctic undisturbed benthic assemblage.
- Overall, stations differed in size and diversity of patches and in heterogeneity patterns (size variability, shape, and interspersion of patches).

4.1.2. Spatial patterns of different successional stages after iceberg disturbance

The best predictor of recovery after iceberg disturbance was CA, reflecting great differences along the successional stages (Figs. 9 and 10). This result agrees with the main conclusions derived from studies on succession in other subtidal marine areas (Grigg & Maragos 1974, Pearson & Rosenberg 1978, Arntz & Rumohr 1982, Dayton et al. 1992, Connell et al. 1997). Overall, the results showed that spatial complexity and diversity increased as succession proceeded. The early stages were mainly characterized by poor coverage of small patches, which showed low complex shapes, were less diverse, and less interspersed. Pioneer sessile taxa composed these stages (see below). A later stage of succession (R2) exhibited the most complex and diverse pattern. The patches exhibited intermediate size and complex shapes, were highly different in composition, relatively equally distributed, and well interspersed. Different well-mixed groups of benthic sessile organisms (e.g. sponges, gorgonians, bryozoans, and ascidians) covered most of the sediment in this stage. The UD assemblage was also composed of different well-mixed groups of benthic taxa, which partially covered the sediment. Interspersion and diversity patterns tenuously decreased at this stage. Larger patches did not show high complexity shape patterns as in R2. The findings using LPI can be compared with abundance and diversity derived from previous studies on iceberg disturbance on polar

shelves (Gutt et al. 1996, Conlan et al. 1998), which also reported an increase of abundance and diversity from disturbed to undisturbed areas.

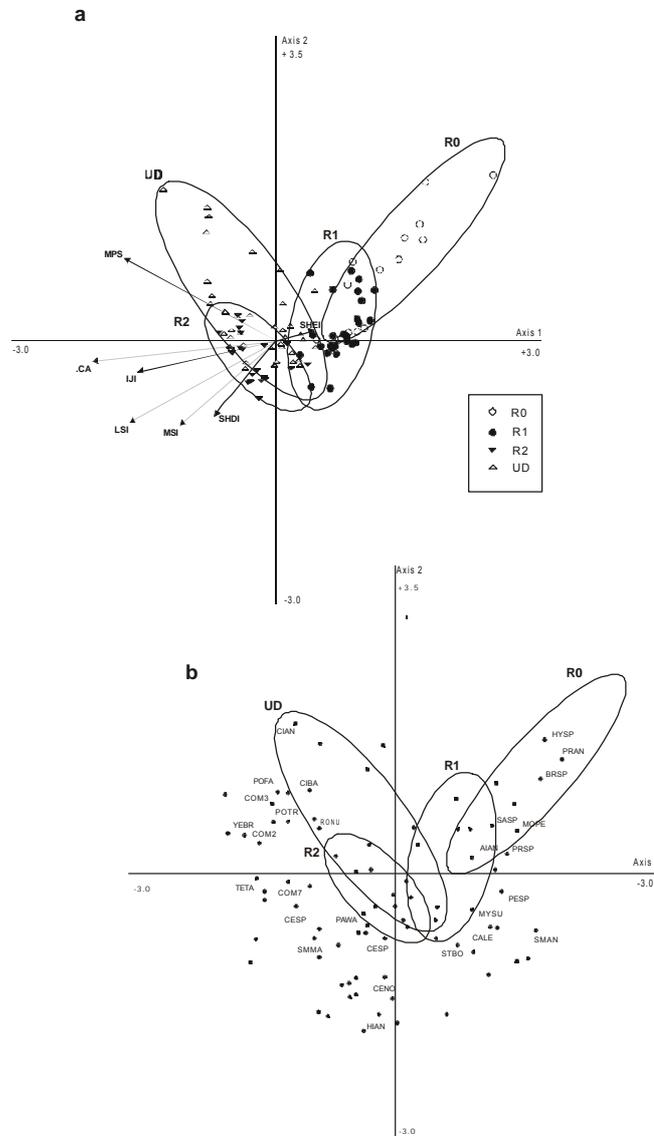


Fig. 9. Ordination of **a)** the samples (each point corresponds to one photograph analysed) and the landscape index variables; and **b)** Antarctic benthic fauna obtained from a Canonical Correspondence Analysis (CCA). Fauna plotted with codes include those taxa whose variance explained exceeded 20% from the first two axes. Codes are as follows: AIAN, *Ainigmaptilon antarcticum*; BRNI, Bryozoa non identified; CALE, *Camptoplites lewaldi*; CESP, *Cellaria* spp.; CESP, *Cellarinella* spp.; CIAN, *Cinachyra antarctica*; CIBA, *Cinachyra barbata*; COM2, *Cellarinella* sp. complex 2; COM3, Demosponge complex 3; COM7, bryozoan and “Yellow branches” complex 7; HIAN, *Himantozoum antarcticum*; HYNI, Hydrozoa non identified; MOPE, *Molgula pedunculata*; MYSU, *Myxicola* cf. *sulcata*; PMAA, *Paracellaria wandeli*; PESP, *Perkinsiana* spp.; POFA, *Polyclinidae* fam. 1; POTR, *Polysyncraton trivolutum*; PRAN, *Primnoisis antarctica*; PRSP, *Primnoella* sp., RONU, *Rossella nuda*/ *Scolymastra joubini*; SANI, Sabellidae non identified; SMAN, *Smittina antarctica*; SMMA, *Smittoidea malleata*; STBO, *Stylocordyla borealis*; TETA, *Tedania tantula*; YEBR, “Yellow branches”.

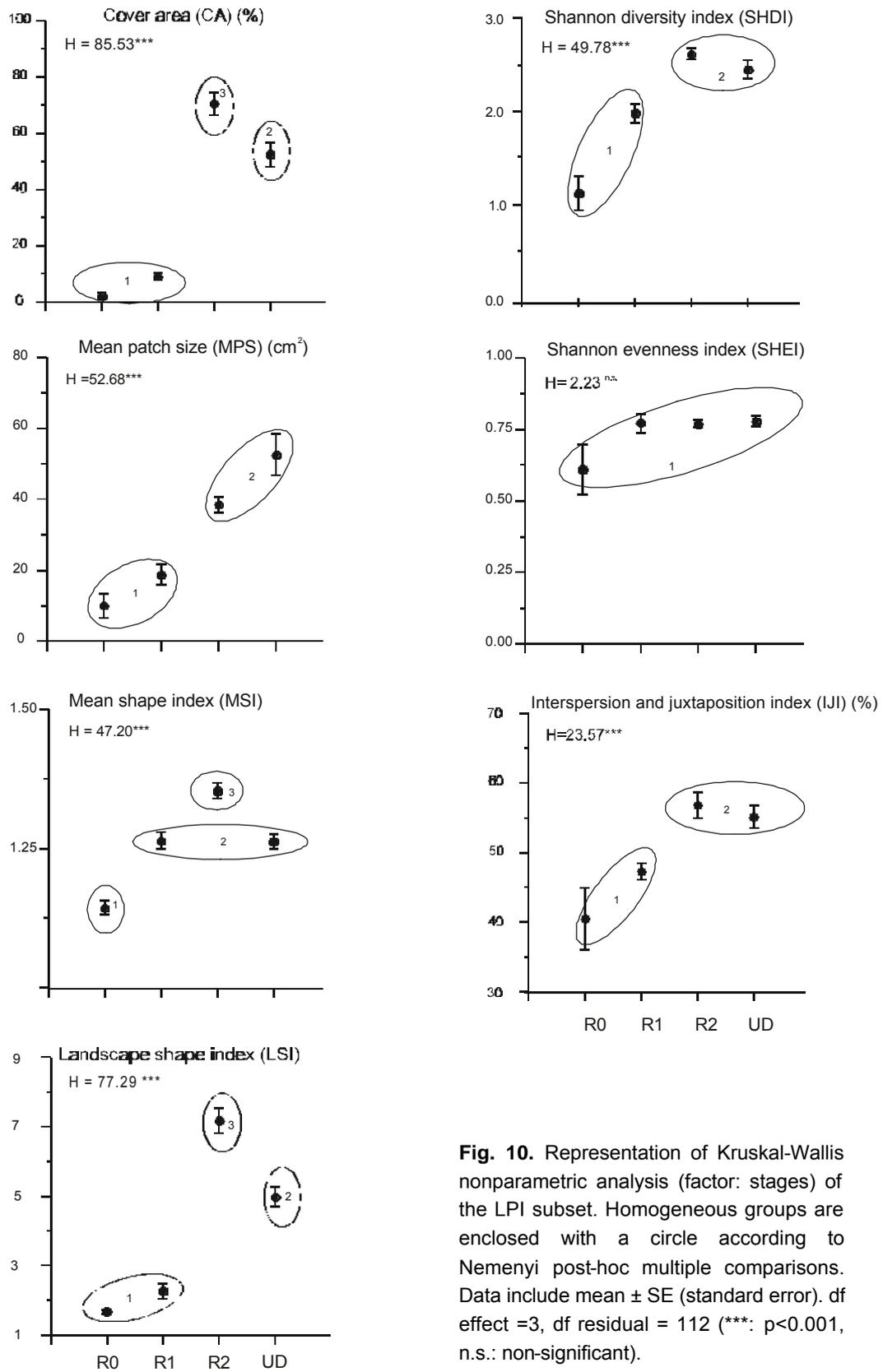


Fig. 10. Representation of Kruskal-Wallis nonparametric analysis (factor: stages) of the LPI subset. Homogeneous groups are enclosed with a circle according to Nemenyi post-hoc multiple comparisons. Data include mean \pm SE (standard error). df of effect =3, df residual = 112 (***: $p < 0.001$, n.s.: non-significant).

Overall, CA and MPS increased during the succession (Fig. 10). The ecological implication of these findings can be related to the “facilitation mode” between earlier and subsequent colonizing species proposed by Connell & Slatyer (1977). From these results it can be suggested that the net effect of earlier on later species favours the recruitment and growth of the latter. Space can be an important limiting resource for sessile marine organisms (Branch 1984, Buss 1986). It seems that space competition pressures explain the decrease in CA and shape complexity indices (MSI and LSI) in the undisturbed assemblage (UD). This does not exclude that sessile organisms compete for space in the advanced successional stage (R2). As described earlier, different well-mixed groups of benthic organisms were present in the later stage (R2), with high coverage of branching species of bryozoans and demosponges with irregular forms. In contrast, these branching species were not often found in the undisturbed assemblage where massive organisms with simple forms, such as hexactinellids, round demosponges, and ascidians prevailed. I hypothesize that the replacement of complex forms by more simple forms in the undisturbed assemblage may be interpreted as a response to competition for space. These simple-form species grow very slowly (Dayton 1979) and may be superior competitors over other benthic organisms with more complex forms. It may be that differences of growth rates, chemical mechanisms, and biological interactions (competition, predation, and epibiotic relationships) best explain the observed cover and form patterns along Antarctic succession. Furthermore, it remains poorly understood how the “continuum” of interactions within the successional sequence affects the mechanisms of Antarctic succession.

Frequency of disturbance by ice and glacial sedimentation in shallow Antarctic benthic communities is related to exposure and depth (Dayton et al. 1970, Dayton 1990, Arntz et al. 1994, Klöser et al. 1994, Barnes 1995, Sahade et al. 1998). Sahade et al. (1998) found a depth gradient in soft bottom communities in Potter Cove, where ascidians, due to local conditions, appeared as the most abundant group below 20 m. Dayton et al. (1970) also identified a depth gradient in hard-bottom communities in McMurdo Sound, from the shallowest zone (above 15 m) devoid of sessile organisms, poorly structured, and controlled by physical factors (due mainly to ice scour and anchor-ice formation), to the deepest zone (below 33m) inhabited by slow-growing sponge species, with high diversity and structural complexity and controlled by biological factors. Garrabou et al. (2002) using LPI found a benthic organization pattern with depth in Mediterranean hard bottom communities. In the “deep” communities (below 11 m), dominated by species with low growth rates, the greatest spatial pattern complexity was observed. The authors argued that a decrease in dynamics with depth might enhance high diversity and thus complex

spatial patterns. Margalef (1963) noted that the lower the degree of community “maturity”, the greater the influence of abiotic factors to resident population dynamics.

On large time and spatial scales Antarctic benthos appeared to be very constant and ancient, features that have been related to the “stability-time hypothesis” (Sanders 1968, 1969). This hypothesis states that the older, more constant, and predictable the environment is the more diverse it will be. Comparisons of deep sublittoral communities, coral reefs in the tropics, and the deep Antarctic shelf (both old systems but with different age), with very young systems such as the Baltic Sea and the northern North Sea supported this hypothesis (Arntz et al. 1999). However, while the old age component seems to hold, the assumed “constancy” of conditions was never valid for Antarctic benthos (Arntz & Gili 2001), which is impacted by extreme seasonality of food input from plankton blooms and the disturbance of ice affecting both shallow and shelf benthos habitats (Dayton et al. 1970, Gutt 2000). However, iceberg scouring contributes to enhance diversity at regional scales by producing habitats, which are a complex mosaic of disturbed and undisturbed assemblages co-existing in different stages of succession (Gutt & Piepenburg 2003).

Conclusions:

- Landscape indices were successful to describe spatial patterns of Antarctic successional stages, which provide new and valuable insights into the structural organization along the succession process.
- The best predictor of recovery after iceberg disturbance was the cover area (CA), reflecting great differences among the successional stages.
- Overall, the results showed that spatial complexity and diversity increased as succession proceeded.
- Differences of growth rates, chemical mechanisms, and biological interactions could explain the observed cover and form patterns along Antarctic succession.

4.1. Recolonisation processes after iceberg disturbance

4.1.1. Benthic pioneer taxa

Disturbance creates new pathways of species composition and interactions, which will define the successional process (Connell & Slatyer 1977, Pickett & White 1985, McCook 1994). As mentioned before, several pioneer taxa appeared during the first stages of recolonization, which locally showed high abundance and patchy distribution (Table 3 in Publication III). For example, the fleshy *Alcyonidium "latifolium"* and rigid bryozoans of the genus *Cellarinella*, the sabellid polychaete *Myxicola cf sulcata*, and the "bottle brush" gorgonian *Primnoisis antarctica* exhibited a maximum of 153, 51, 31, and 30 patches m⁻², respectively (Table 3 in Publication III). Previous studies using Remotely Operated Vehicles (ROV) have also identified some of these benthic taxa as pioneer organisms (Table 5) (Gutt et al. 1996, Gutt & Piepenburg 2003). I attribute the differences of observed pioneer taxa among distinct studies to i) their patchy distribution, ii) the higher resolution of the underwater photographs compared to ROV-acquired images, and iii) the larger total area sampled using ROV images. The patchy distribution may explain the high heterogeneity of species composition during the first stages (Fig. 11). Gutt (2000) found that there is no specific pattern of species replacement along succession in Antarctic benthic communities. Nevertheless, species composition along the early stages (R0-R1) shared common pattern characteristics (low coverage, small patches with low complex shapes, and less diverse and interspersed patches) (Figs. 9 and 10). In addition, Sutherland (1974) and Gray (1977) suggested that the dominance by several species in subtidal hard-substrate communities represented alternative "multiple stable points". Whether one community or another exists may depend on the order in which different species arrive, on their initial densities, or on the existence of "facilitators" or competitors (Sutherland 1990, Law & Morton 1993).

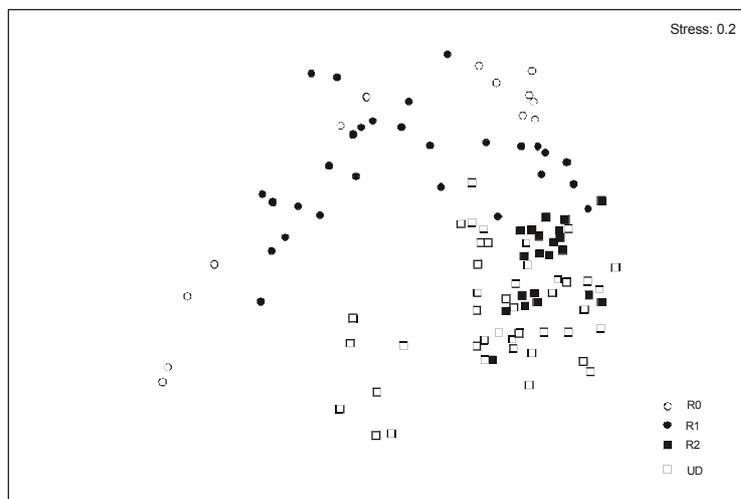


Fig. 11. MDS diagram of photographic sample similarity according to benthic taxa composition through the successional stages.

Taxa	Group	Reference
Homaxinella spp.	DEM	1
Stylocordyla borealis	DEM	1,2, 3, this study
Latrunculia apicalis	DEM	2
Corymorpha sp.1	HYD	1
Corymorpha sp.1	HYD	1
<i>Hydrozoa sp. 3</i>	HYD	this study
Oswaldella antarctica	HYD	1
<i>Ainigmaptilon antarcticum</i>	GOR	1, this study
Arntzia sp.	GOR	1
Primnoella antarctica	GOR	1
Primnoella sp.	GOR	this study
<i>Primnoisis antarctica</i>	GOR	1, this study
Thouarella/ Dasystemella	GOR	1
Alcyonidium "latifolium"	BRY	this study
Camptoplites lewaldi	BRY	this study
Camptoplites cf. tricornis	BRY	1
Cellaria incula	BRY	4
Cellaria spp.	BRY	2
Cellarinella nodulata	BRY	this study
Cellarinella spp.	BRY	this study
Melicerita obliqua	BRY	1, 4
Smittina antarctica	BRY	this study
Systemopora contracta	BRY	this study
Myxicola cf. sulcata	POL	1, this study
Perkinsiana spp.	POL	1, this study
Pista sp.	POL	1,2
Molgula pedunculata	ASC	this study
Synicum adareanum	ASC	2
Sycozoa sp.1	ASC	1

Table 5 Summary of benthic sessile pioneer taxa identified on the Weddell Sea shelf. DEM: Demospongiae, HYD: Hydrozoa, GOR: Gorgonaria, BRY: Bryozoa, POL: Polychaeta, ASC: Ascidiacea. 1:Gutt & Piepenburg 2003; 2: Gutt et al. 1996; 3: Gatti et al. *submitted*; 4: Brey et al. 1999; 5: Brey et al. 1998.

In the present study I did not analyse mobile organisms such as fish and some echinoderms but they also appeared as first immigrants (see Appendix 8.5). Some species of the Antarctic fish genus *Trematomus* (Brenner et al. 2001) as well as crinoids, ophiuroids, and echinoids (Gutt et al 1996, Gutt & Piepenburg 2003) have been reported to be dominant in disturbed areas in the Weddell Sea.

In this study, benthic composition converged in the later stages (Fig. 11). However, it is important to note the separation of the undisturbed assemblage characterized by the long-lived volcano-shaped hexactinellid species and the round demosponge *Cinachyra barbata* (Fig. 11). The separation within this assemblage (UD) shows that local dominance of sponges reduces diversity and shape complexity patterns at small scale (Fig. 8).

Conclusions:

- Several pioneer taxa appeared during the first stages of recolonization, which locally showed high abundance and patchy distribution.
- These pioneer taxa shared common pattern characteristics such as low coverage, small patches with low complex shapes, and less diverse and interspersed patches.

4.1.2. Patterns of benthic coverage and abundance

Iceberg scouring on Antarctic benthos disturbs large distances (several km) creating a mosaic of habitat heterogeneity with sharp differences within few metres. The present study reported a pattern of change in coverage, abundance, and size of species at small scale (1m²) (Fig. 12 and Table 3 in Publication III). However, studies at all scales of time and space are necessary and the appropriate scale of observation will depend on the question addressed (Levin 1992, Connell et al. 1997). Both small- (this study) and large-scale spatial and temporal studies can greatly contribute to a better assessment of the response of Antarctic benthic communities to iceberg disturbance.

Overall, this study provides evidence of recovery of the benthic community with an increase of coverage, abundance, and size through the successional stages (Fig. 12 and Table 3 in Publication III). This general tendency agrees with predicted effects of disturbance, which appears to be an important process in driving the dynamics of benthic communities (Dayton & Hessler 1972, Huston 1985, Thistle 1981, Gutt 2000). The first stages were characterized by a low percentage of benthos coverage (Figs. 10 and 12, Table 3 in Publication III). Few and small patches of demosponges, gorgonians, bryozoans, polychaetes, and ascidians barely covered the sediment. Gerdes et al. (2003) studying the impact of iceberg scouring on macrobenthic biomass in the Weddell Sea found low values (9.2 g wet weigh m²) in disturbed areas, where polychaetes represented approx. 40%. This result agrees with the occurrence of sabellid polychaetes, which accounted for 27% of the benthic coverage in R0.

The advanced stage (R2) exhibited the highest coverage and abundance (Figs. 10 and 12). Bryozoans were important in both coverage and abundance (mean value of 24.7 % and 75.6 patches m²), whereas demosponges and ascidians exhibited a relatively high abundance. It is important to note that most of the sediment was covered by few and large matrices of thin bryozoans, demosponges, and gorgonians, which could not be distinguished. These “complex categories” composed the basal substrata of the benthos with a coverage of 36% for R2 and 16.7 % for the undisturbed stage (UD).

The UD stage was characterised by an intermediate coverage of demosponges, bryozoans, ascidians, hexactinellids, and gorgonians (Fig. 12), where the three former taxonomic groups exhibited intermediate abundance of 27, 31, 30 patches m² (Table 3 in Publication III). In addition, Gerdes et al. (2003) determined high variability in sponge biomass, between 1.9 and >100 kg wet weight m², indicating also their patchy occurrence

in undisturbed stations. Big specimens of hexactinellids and the demosponge *Cinachyra barbata* were found in UD, where *Rossella nuda*/ *Scolymastra joubini* exhibited a maximum size of 666 cm² (approx. 30 cm in diameter) and locally high abundance (maximum of 11 patches m⁻²) (Table 3 in Publication III). The size of these hexactinellid sponges agrees with previous results from the Weddell Sea, where intermediate values were reported (Gutt 2000) compared to giant sizes described below 50 m in the Ross Sea (1.8 m tall, with a diameter of 1.3 m, and an estimated biomass of 400 kg wet weight, Dayton 1979). It remains unclear whether the hexactinellids of the Weddell Sea reach the size of their counterparts in the Ross Sea. Gutt (2000) suggested that the local protection from large iceberg scouring in McMurdo Sound favours larger sizes due to longer time intervals between disturbances.

Conclusions:

- Both small- (this study) and large-scale spatial and temporal studies can greatly contribute to better assessment of the response of Antarctic benthic communities to iceberg disturbance.
- Few and small patches of demosponges, gorgonians, bryozoans, polychaetes, and ascidians characterized the first stages of succession.
- The advanced stage (R2) exhibited the highest coverage and abundance, whereas bryozoans were the most representative group.
- Demosponges, bryozoans, ascidians, hexactinellids, and gorgonians represented the undisturbed stage (UD) with intermediate coverage and abundance.

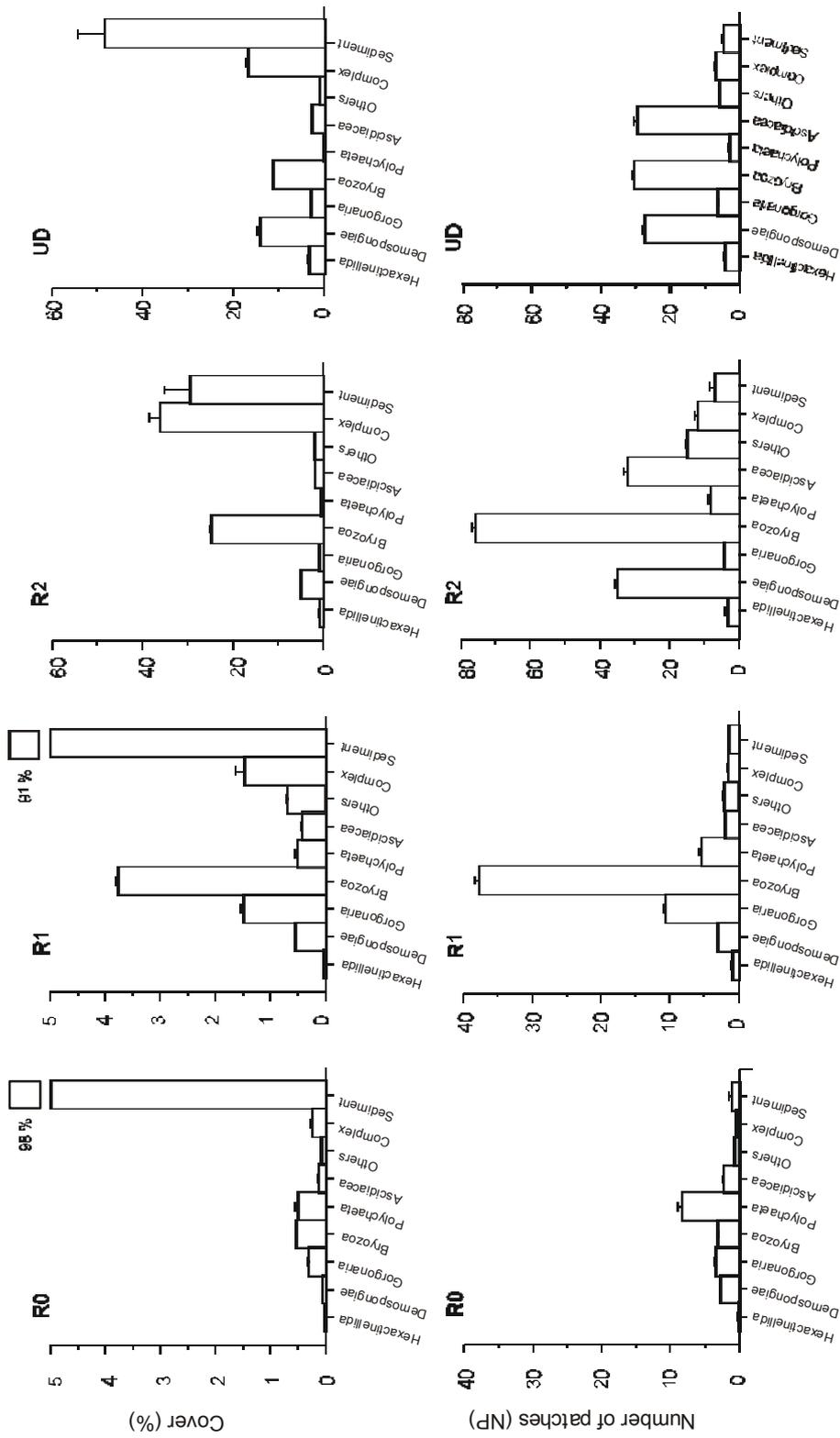


Fig. 12. Cover percentage and number of patches (mean \pm SE) of different categories through successional stages. * Others: in R0 and R1: Hydrozoa (0.07 and 0.6 %); in R2: Hydrozoa, Actinaria, Holothuroidea, and Pterobranchia (0.8 %); in UD: Hydrozoa, Actinaria, Holothuroidea, and Pterobranchia (0.8 %).

4.2.3. Patterns of cover by different growth-forms

When cover area of benthic organisms is compared among stages, a growth pattern emerges: taxa with bush growth form dominated at R0 and those with a tree growth form were more abundant in the R1 and R2 stages. In addition, taxa with a massive growth form represented the UD. Differences in growth forms for CA, NP and MPS are explained in detail and discussed in Publication III.

Despite the inferior competitive capacity of bush morphology (Connell & Keough 1985), this category occupied the space constantly along succession, although with a major proportion during the early stages (Fig. 13). This presence may be related to epibiotic relationships (Dayton et al. 1970, Gutt & Schickan 1998), whose development reduces competition for poor competitors such as bush-like organisms. They take advantage growing on the surface of larger organisms and colonies (Jackson 1979). The space between large organisms may be rapidly occupied by these ephemeral organisms, with a refuge-oriented strategy (Buss 1979). Sheet and mound forms are predicted to be generally superior in competition to bushes (Jackson 1979), and therefore are expected to dominate the later stages. The results were in partial agreement with this prediction. The coverage of mound forms increased in the undisturbed assemblage, however the sheet-growth forms decreased along the later stages (R2 and UD). The presence of tree-like forms was relatively high through the successional stages, whereas a dominance of mound-like forms was evident in UD (Fig. 13). These successful strategies might be due to temporarily high sedimentation rates and lateral transport of organic matter and sediment close to the sea bottom in the Weddell Sea (Elverhøi & Roaldset 1983, Fahrback et al. 1992, Gleitz et al. 1994, Park et al. 1999). Such conditions favour these growth forms (trees and mounds), which efficiently exploit the particles in the water column and escape from burial by settling sediment (Jackson 1979, Gutt 2000). The arborescent sponge growth form is known as a morphological strategy to reduce the effect of i) competition by growing on relatively narrow bases on the substratum; thus being more competitive than prostrate forms and ii) predation due to a reduced area to face predators (Dayton et al. 1974).

Conclusions:

- Despite inferior competitive capacity of bush forms, this morphology occupied the space constantly along succession.
- Temporarily high sedimentation rates and lateral transport of organic matter in the Weddell Sea favours tree and mound growth forms because they efficiently exploit the particles in the water column and escape from burial by settling sediment.

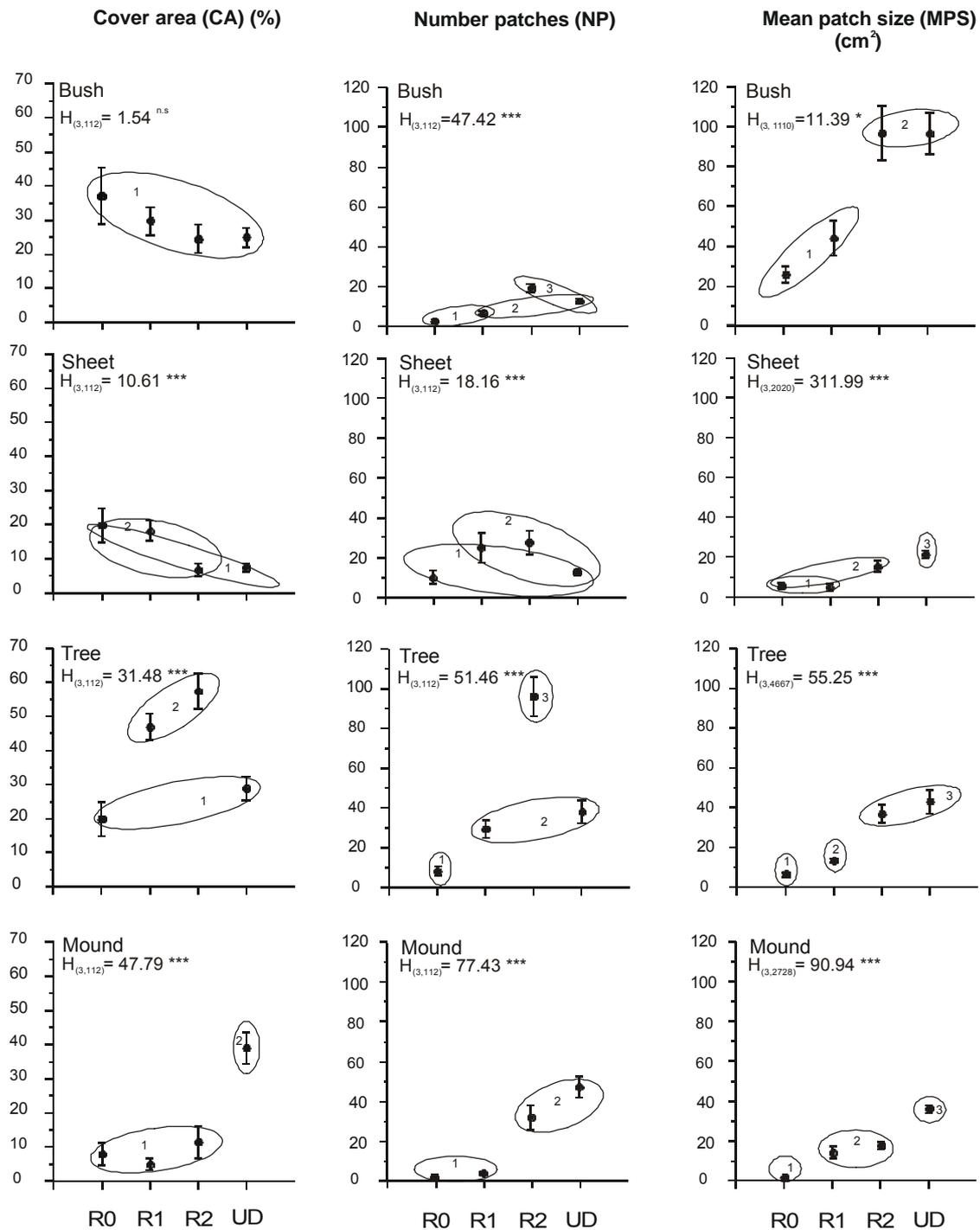


Fig. 13. Cover area (CA), number of patches (NP), and mean patch size (MPS) of growth form categories through succession. Homogeneous groups are enclosed with a circle according to Nemenyi post-hoc multiple comparisons. Data include mean \pm SE (standard error). See Table 3 (Material and Methods) for growth form descriptions. Note: The sum of different growth form categories exhibits ~ 85 % of cover area in R0 due to the absence of sessile benthic fauna in some photographs.

4.2.4. Recovery and life-history traits

It should be considered that the pace of reproduction and growth of Antarctic marine invertebrates is generally very slow (Clarke 1983, Pearse et al. 1991, Arntz et al. 1994), which may have a strong effect on all aspects of the species' life history and should determine the time needed for a species or a community to respond to disturbance.

The existence of propagules is a fundamental determinant of successional patterns both in marine and terrestrial habitats (Clements 1916, Connell & Keough 1985, Pickett et al. 1987) and might be especially sensitive to the combination of both disturbance intensity and its spatial extent (Turner et al. 1998). Sessile organisms may invade open patches by i) vegetative regrowth of existing colonies at the edge of the disturbed area, ii) settlement of propagules produced vegetatively (as detached buds or fragments broken off survivors), or iii) sexually (as gametes or larvae) outside the affected area (see Sousa 2001). Iceberg scouring removes completely the benthic fauna over large areas. In these areas recolonisation by larvae may be more important than vegetative regrowth and/or asexual propagule settlement (Connell & Keough 1985). For example, two studies of settlement supposedly by demersal larvae revealed very high levels of recruitment at McMurdo Sound and Maxwell Bay (King George Island) (Dayton 1989, Rauschert 1991). These episodic events were associated with the heavy 1982-84 El Niño-Southern Oscillation.

Brooding of larvae has been identified as the reproductive mechanism of some pioneer species of this study (Cancino et al. 2002, Orejas 2001, Sarà et al. 2002) and to be the dominant modus of deep-dwelling polar invertebrates (Dell 1972, Picken 1980, Arntz et al. 1994, Pearse et al. 1991), with very slow embryonic and larval development and low dispersal capabilities (Clarke 1982, Hain 1990, Pearse et al. 1991). This short-distance dispersal (philopatry) of larvae may be an explanation of the patchy distribution of these species along the early stages of recovery, in particular, and of the Weddell Sea benthos in general (Barthel & Gutt, 1992, Gutt & Piepenburg 1991, Starmans et al. 1999). However, the ascidian *Molgula pedunculata* and the sabellid polychaete *Perkinsiana cf. littoralis* exhibit higher dispersal capabilities due to gametes freely spawned without parental care (Svane & Young 1989, Gambi et al. 2000). Based on mathematical models, habitat instability such as that caused by iceberg scouring should favour recolonization of species with long distance dispersal (Lytle 2001, McPeck & Holt 1992).

The pioneer taxa found during the early stages exhibited mainly a tree-growth form and showed relatively fast growth. For example, *M. pedunculata* is a stalked, cartilaginous, and solitary ascidian and is reported to grow very fast (Table 4 in Publication III). Based on growth models, Gatti (2002) calculated an estimated age of 10.4 y for a body area of 4.4 cm² for the lollypop-like *Stylocordyla borealis*. Smaller individuals of *S. borealis* were found in R0 with a mean size of 1.2 cm², indicating a younger age. Flexible, bushy and erect, rigid bryozoans occurred through the different successional stages with moderate growth rates (Table 4 in Publication III). Overall, relatively fast growth rates and different dispersal strategies within pioneer taxa may determine their success in recolonizing recently disturbed areas. This study showed that massive mound-form hexactinellids and demosponges grow big, are abundant in areas of low disturbance, and have a patchy distribution (Table 3 in Publication III). These sponges exhibited the lowest growth rates, the longest life-span, the biggest size, and short-distance dispersal (philopatry) because of asexual reproduction (budding) (Table 4 in Publication III). However, Maldonado & Uriz (1999) showed that fragments of Mediterranean sponges transported larvae, thus enhancing their dispersal ability and genetic variability among populations. This strategy could also be a reasonable mechanism for the Antarctic recolonization process of disturbed areas.

Conclusions:

- Due to the low pace of reproduction and growth of most Antarctic marine invertebrates, Antarctic benthos recovery is predicted to be much slower than most other marine habitats.
- The dispersal abilities of propagules (produced vegetatively or sexually) are supposed to have a substantial influence on the composition of Antarctic benthos after iceberg disturbance.
- Apparently, taxa with tree-like forms, high growth rates, and short-intermediate offspring dispersal were among the first colonizers of recently disturbed areas.
- Big mound-like hexactinellids and demosponges were abundant in the later successional stages. They showed the lowest growth rates and short-distance dispersal of the offspring.

4.2.5. Community resilience

Understanding the effects of large disturbances causes concern for conservation and Antarctic benthic diversity considering potential implications of global climate change. Although the co-existence of many different successional stages within the impacted areas favours diversity at a larger spatial scale (Gutt & Piepenburg 2003), it is important to emphasize that adaptation of Antarctic benthos to iceberg disturbance developed over a long evolutionary period (Clarke & Crame 1992). Gutt (2000) estimated a rate of one disturbance per square metre of the seafloor every 320 years along the depth range of the shelf (<500m). These low disturbance frequencies were based on known growth rates of pioneer organisms (Brey et al. 1999) and estimated community development times (Gutt 2000). However, in view of a possible increase of iceberg-calving frequency (Lazzara et al. 1999, Rignot & Thomas 2002), and the slow growth of many species in the Antarctic benthic ecosystem, the question arises of how resilient these communities are. If global warming continues, Antarctic benthic communities might be exposed to more frequent iceberg disturbance over a short period of time to which they are not adapted. With this increase of frequency and/or intensity, the Antarctic benthos might not recover to its prior state and nor return to the long-lived mature community found in the undisturbed stage.

Conclusion:

- Changes in the magnitude, frequency, and duration of disturbance regimes caused by global climatic change might lead to alterations of ecosystem resilience, posing major challenges to the existing diverse Antarctic benthos communities.

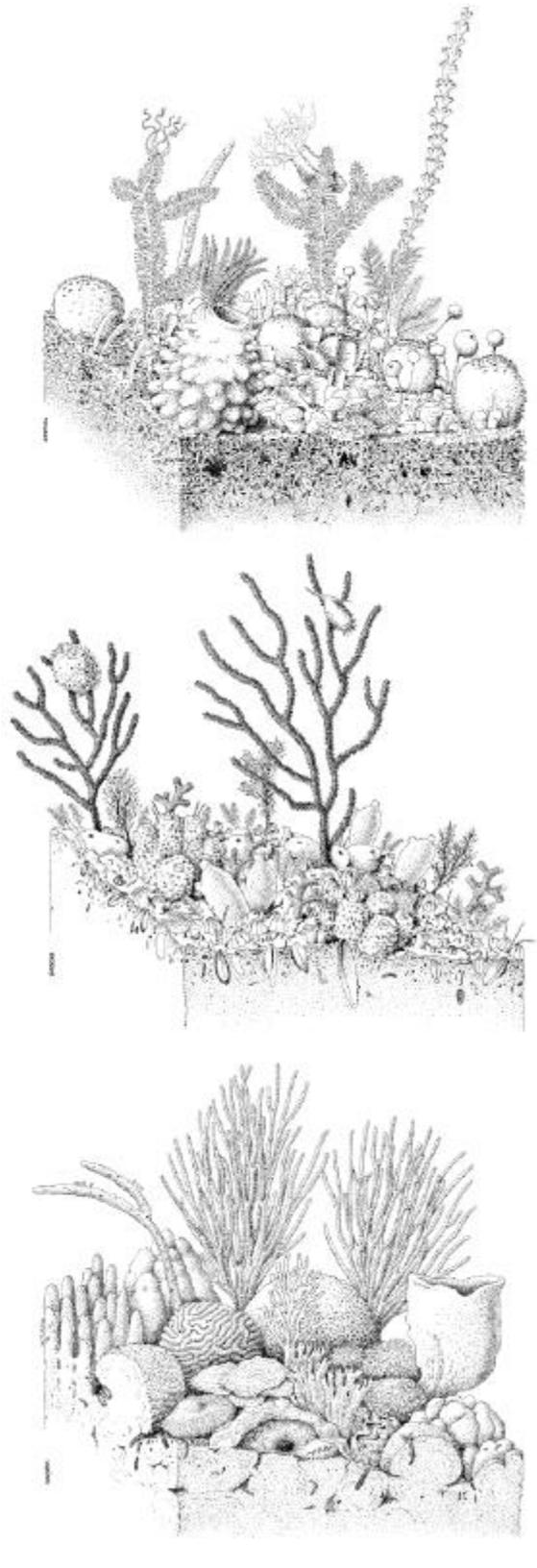
4.3. General conclusions

I have reported the suitability of landscape indices to describe spatial patterns of Antarctic benthic communities, which provide new and valuable insights into the structural organization within an undisturbed assemblage and through successional stages after iceberg disturbance. Moreover, I characterized coverage and abundance of sessile benthic fauna and their changes of growth-form pattern during the occupation of open space along succession. Available information on Antarctic benthic species was compiled to better understand the variation of life history patterns through the successional process. Along this study, I have pointed out the importance of near bottom currents, sedimentation, propagules and their dispersal abilities, recruitment, growth rates, chemical defense, competition, and ecosystem age in determining Antarctic benthic successional patterns.

4.4. Further studies

During the development of this study some ideas emerged and new questions arose. To answer them and further study spatial patterns in Antarctic benthos, I would like to suggest the following research topics:

- In Antarctica many ecological processes take place slowly (Clarke 1996) and long-term studies are needed. However, recolonization episodes over short time have revealed valuable information on benthic dynamics (Dayton 1989, Rauschert 1991). For example, during the “Polarstern” expedition (ANT XVII/3, 2000) high sponge abundance (*Rossella nuda/ Scolymastra joubini*) with spectacular outgrowths (buds) on their surface was observed. Studies at various scales of time and space are necessary to understand the mechanisms that determine the dynamics of Antarctic benthos.
- The dispersal abilities of benthic fauna should have a substantial influence on colonization during the early phase following iceberg disturbance. Studies on reproduction, propagule dispersability, and near-bottom current patterns are needed to better relate the contribution of non-disturbed benthic areas to the recolonisation process of recently disturbed areas.
- It remains challenging to identify the factors that control dynamics and spatial patterns of Antarctic succession. Therefore, studies on recruitment, growth, age estimation, chemical defences, and species interactions (epibiosis, competition, predation) are still required.
- In view of a possible increase of iceberg-calving frequency due to recent climate change and the slow growth of many species in the benthic ecosystem, long-term monitoring programmes with underwater cameras in the deep Weddell Sea continental shelf and in littoral habitats will provide valuable insights into the sequence and duration of successional processes in Antarctic benthic habitats.
- The observed three-dimensional structure created by benthic suspension feeders on Antarctic soft bottoms is similar to that usually found on rocky bottoms in temperate and tropical seas (e.g. coral reefs) (Fig. 16). The application of landscape analysis to benthic communities at different latitudes may be useful to compare spatial patterns of these marine habitats. This comparison will provide new insights on how environmental conditions and biological interactions affect the structural patterns of these communities. Hence, further application of this landscape approach will improve our understanding on structural and ecological processes in these complex habitats.



a) Sponges: massive *Rossella racovitzae*, round *Cinachyra barbata*, and lollypop-like *Stylocordyla borealis*; gorgonians: the bottle brush *Thouarella* sp. and unbranched colonies of *Ainigmaptilon antarcticum* and *Primnoella* sp.; the rigid bryozoans *Melicerita obliqua* and *Reteporella* sp.; the holothurian *Ekmocucumis turqueti*; and the compound ascidian *Synoicum adareanum*.

b) The sponges *Chondrosia reniformis* and *Dysidea fragilis*; the soft hydrozoans *Eudendrium racemosum* and *Plumarella* sp.; the gorgonian *Paramuricea clavata*; the rigid bryozoan *Myriapora truncata*, the solitary ascidian *Halocynthia papillosa*, and the bivalve *Lithophaga lithophaga*.

c) Sponges: tube-shaped *Aplysina lacunosa*, erect *Iotrochota birotulata*, and vase-shaped *Spinosella plicifera*; gorgonians: *Pseudoplexaura porosa* and *Plexaura flexuosa*; the anemone *Condylactis gigantea*; corals: hemisphere *Siderastrea radians*, flower *Eusimilia fastigiata*, boulder *Montastrea annularis*, crenelated fire *Millepora alcicornis*, lettuce-leaf *Agaricia agaricites*, and brain *Colpophyllia natans*.

Fig. 16. Idealized diagram of a) Antarctic benthic shelf community, b) Mediterranean "coralligenous" benthic community, and c) coral reef benthic community. Representative species are indicated. Drawn by J. Corbera (Gili et al. 1998 and Gili et al. 2001).

5. Publications

The articles of this thesis are listed below and my contribution is explained.

Publication I:

Teixidó N, Garrabou J, Arntz WE (2002)

Spatial pattern quantification of Antarctic benthic communities using landscape indices
Mar Ecol Prog Ser **242**: 1-15*

I developed the methodological and conceptual approach to apply landscape analysis to Antarctic underwater photographs in close cooperation with the second author. I wrote the first version of the manuscript, which was discussed and improved with the co-authors.

Publication II

Teixidó N, Garrabou J, Gutt J, Arntz WE

Impact of iceberg scouring on Antarctic benthic communities: new insights from the study of spatial patterns
Ecology (*submitted*)

I applied the methodological approach to underwater photographs, which encompassed different successional stages after iceberg disturbance. The photograph selection was conducted in close cooperation with the third author. After writing the first draft of the manuscript, I discussed and revised it with the co-authors.

Publication III

Teixidó N, Garrabou J, Gutt J, Arntz WE

Succession in Antarctic benthos after disturbance: species composition, abundance, and life-history traits
Mar Ecol Prog Ser (*submitted*)

The initial idea for this publication was developed by the first two authors. I conducted the photograph and data analyses and wrote the first version of the manuscript, which was revised and discussed in cooperation with the co-authors.

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Publication I

**Spatial pattern quantification
of Antarctic benthic communities
using landscape indices**

N. Teixidó, J. Garrabou, W. E. Arntz

Spatial pattern quantification of Antarctic benthic communities using landscape indices

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ABSTRACT: Antarctic benthos exhibits highly complex communities showing a wide array of spatial patterns at several scales which are poorly quantified. In this study, we introduce the use of methods borrowed from landscape ecology to study quantitatively spatial patterns in the Antarctic megaepibenthic communities. This discipline focuses on the notion that communities can be observed as a patch mosaic at any scale. From this perspective we investigated spatial patterns in an Antarctic benthic assemblage across different stations based on landscape indices, and we chose the optimal subset for describing Antarctic benthic patterns. For this purpose, 42 photographs (1 m² each) corresponding to 6 stations from the Weddell Sea shelf were investigated. Canonical variate analysis (CVA) showed the arrangement of photographic records along a patch size and diversity gradient on the first axis and a heterogeneity pattern gradient (cover area, interspersion and juxtaposition, landscape shape indices) on the second axis. Based on a forward stepwise selection, mean patch size (MPS), patch size coefficient of deviation (PSCV), patch richness (PR), interspersion and juxtaposition index (IJI), mean shape index (MSI), Shannon's evenness (SHEI), and periarea index (PERIAREA) were chosen as the adequate subset of indices to describe the Antarctic benthos. Principal Component Analysis (PCA) was used to identify relationships among them. The resulting 3 factors were interpreted as (1) a heterogeneity pattern (related to patch size, form, diversity, and interspersion indices), (2) an equitability pattern (represented by the evenness index), and (3) a perimeter-area pattern (characterised by the periarea index). Analysis of variance (ANOVA) was carried out to detect differences among the stations based on the subset of indices. Overall, the results showed large differences in patch characteristics (mean and its coefficient of variation, and shape indices), diversity, and interspersion. The successful description of Antarctic benthic communities through landscape pattern indices provides a useful tool for the characterisation and comparison of spatial patterns in these diverse marine benthic habitats, which gives insights in their organisation.

KEY WORDS: Antarctic · Benthic communities · Landscape indices · Multivariate ordination · Underwater photographs · GIS

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INTRODUCTION

During the last decades considerable research has been carried out on Antarctic benthic communities, mainly related to aspects of systematics, zoogeography, reproduction, and foraging biology (Dayton 1990, Arntz et al. 1994, Gutt 2000). Studies on patterns and

processes in benthic Antarctic communities are of general interest to understand their development, to describe their structure and to characterise their function (Hedgpeth 1971, Dell 1972, White 1984, Arntz et al. 1994, Clarke 1996).

Communities generally exhibit heterogeneity and patchiness on a broad range of scales. Understanding patterns in terms of scale is of fundamental interest in terrestrial and marine ecology (Levin 1992). Large-scale biogeographic patterns of the Antarctic macro-

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benthos have been extensively described using traditional sampling techniques (e.g. dredges, grabs, and trawls) (Knox 1960, Bullivant 1967, Hedgpeth 1969, Dell 1972, Arnaud 1977, Sarà et al. 1992). Recently, observations by remote underwater photographs, ROV (remotely operated vehicle) supported video records, and SCUBA diving have been supplemented to studies at intermediate and finer scale. These studies focused mainly on the distribution, structure, and vertical zonation of Antarctic benthos (Gruzov et al. 1968, Hedgpeth 1969, Dayton et al. 1970, Arnaud 1974, Kirkwood & Burton 1988, Gambi et al. 1994, Barnes 1995, Gutt & Starmans 1998, Starmans et al. 1999).

The use of modern imaging techniques provides a view of non-destroyed benthic community structure with high resolution over large areas. Nevertheless, there still is a paucity of analytical methods to obtain ecologically relevant data from images. As a consequence, the general aim of this study is to introduce landscape pattern indices as a new tool to analyse Antarctic benthic community images and to improve our understanding of spatial patterns in these communities, in particular, and of marine habitats in general (Garrabou et al. 1998, Garrabou et al. in press).

Landscape ecology has developed rapidly over the last 10 yr (Forman & Gordon 1986, Turner 1989). The driving force lies in the need to tackle ecological problems (e.g. global climatic change, deforestation) on a broad range of spatial-temporal scales (Turner 1989). In recent years landscape ecologists have concentrated their efforts on the development of a large collection of indices to describe dynamics and patterns of landscapes (e.g. O'Niell et al. 1988; Turner 1989, Kineast 1993, Wiens et al. 1993, Riitters et al. 1995). These indices have been applied successfully at many spatial-temporal scales, ranging from a broad scale (km) (e.g. O'Niell et al. 1988, Turner & Ruscher 1988, Kineast 1993, Hulshoff 1995, McGarrigal & McComb 1995, Riitters et al. 1995, Drapeau et al. 2000) to a finer scale (m and cm) (Garrabou et al. 1998, Saunders et al. 1998).

However, the large number of landscape metrics used to quantify landscape patterns and structure provides redundant information (O'Niell et al. 1988, Riitters et al. 1995, Hargis & Bissonette 1998). Different procedures of multivariate analysis have been applied to reduce the large amount of information to a smaller set of indices (Riitters et al. 1995, Cain et al. 1997). There is, however, not an ideal standard subset of indices to describe terrestrial patterns, nor is there one to describe benthic marine habitats.

In this study, we investigated the Antarctic benthos spatial patterns at a fine scale (1 m) through the application of landscape pattern indices (LPI). We considered 1 m² as the appropriate scale of observation for both image resolution and sampling area obtained.

The indices quantify spatial patterns assuming that benthic communities can be observed as patch mosaics, where patches are associated to different categories (e.g. species). From this perspective, community spatial patterns and dynamics can be analysed by focusing on the characteristics of the patch mosaics.

The objectives of this study were: (1) to apply landscape pattern indices to characterise quantitatively, at a finer scale, spatial patterns in an Antarctic benthic assemblage across different stations, and (2) to choose a subset of landscape pattern indices which is the best suited for describing benthic patterns.

MATERIALS AND METHODS

Study area and benthic communities. The Antarctic continent is largely covered with ice, which at some places extends from the continent into the sea forming the ice shelves (Knox 1994). The continental shelf in the southeastern Weddell Sea is relatively narrow (less than 90 km) and ranges to a depth of 500 m (Carmack & Foster 1977, Hempel 1985). Kapp Norvegia is located in the eastern Weddell Sea (Fig. 1), where the shelf undergoes seasonal pack-ice coverage (Tréguer & Jacques 1992) and where, especially during summer, coastal polynyas of varying size occur (Hempel 1985). Water temperature close to the sea bottom is low and relatively constant, ranging from -1.3 to -2.0°C (Fahrbach et al. 1992). There is a marked seasonal variation in primary production, mostly confined to summertime under the sea ice and in open water (Nelson et al. 1989, Gleitz et al. 1994, Park et al. 1999). The organic matter flux from surface waters to the seabed through the water column shows temporal variation, e.g. with high values after a sinking bloom of diatoms in summer (Bathmann et al. 1991, Gleitz et al. 1994). Hydrodynamics do not only affect the food availability from the water column but also determine the sediment characteristics (e.g. grain size and composition), which are of ecological relevance for benthic communities (Dunbar et al. 1985, Gutt 2000). Iceberg scouring dramatically disturbs benthic communities at certain depths on the continental shelf, mainly between 150 and 300 m (Gutt et al. 1996, Peck et al. 1999).

Antarctic benthic communities have been described as 'multistoried assemblages', meaning the epibiotic relationship between species, which serve as a substratum for other species (Knox & Lowry 1977, Gutt & Schickan 1998 and citations therein). The benthos of the Antarctic continental shelf and slope in the eastern Weddell Sea is generally known as an ecosystem with intermediate to high species richness (Starmans & Gutt 2002), locally extreme high epifaunal biomass with up to 1.67 kg m⁻² wet weight (Gerdes et al. 1992), and

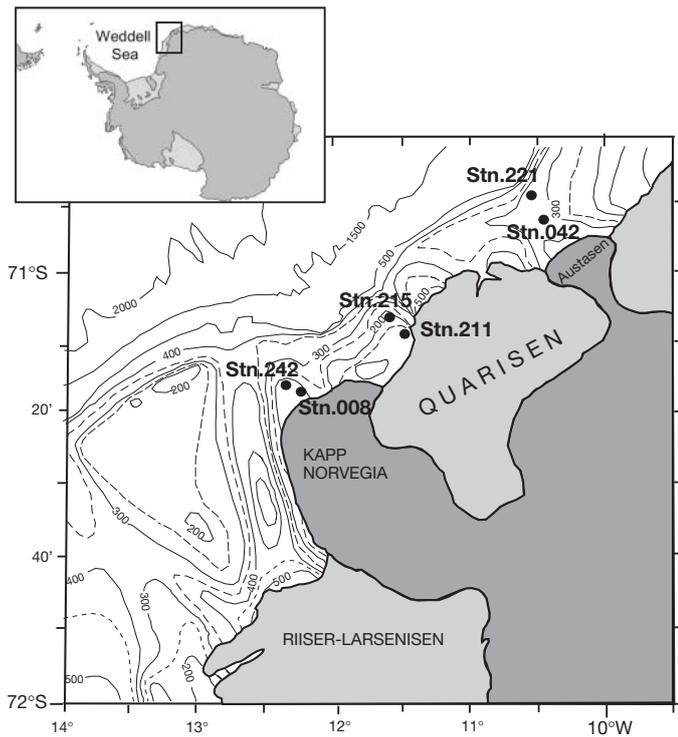


Fig. 1. Study area in the southeastern Weddell Sea (Antarctica) showing the location of photographic stations and their depths: Stn 008 (171 m), Stn 042 (251 m), Stn 211 (117 m), Stn 215 (160 m), Stn 221 (265 m), and Stn 242 (159 m). (Sub-section of chart AWI BCWS 553)

patchy distribution (Starmans et al. 1999). The Kapp Norvegia region belongs to the Eastern Shelf Community described by Voß (1988) as the richest high Antarctic community. The fauna in this area is dominated by sessile suspension feeders, e.g. sponges, gorgonians, bryozoans, and ascidians, which locally cover the sediment completely (Gutt & Starmans 1998, Starmans et al. 1999). In some areas off Kapp Norvegia the benthos can be dominated by sponges, e.g. the hexactinellids *Rosella racovitzae*, *R. antarctica*, *R. nuda*, and the demosponge *Chinachyra barbata*.

Photosampling. Photographic records of the seafloor were obtained from expeditions ANT XIII/3 and ANT XV/3 on board RV 'Polarstern' during the austral summers of 1996 and 1998 (Arntz & Gutt 1997, 1999). This research was performed within the EASIZ (Ecology of the Antarctic Sea Ice Zone) frame as a part of a SCAR (Scientific Committee on Antarctic Research) programme. A 70 mm underwater camera (Photosea 70) with 2 oblique strobe lights (Photosea 3000 SX) was triggered at a fixed distance (1.4 m) from the seafloor by a bottom contact switch while the ship drifted (Gutt & Starmans 1998). This device can obtain perpendicular photographs of the sea bottom at a constant height above it. The optical resolution is around 0.3 mm. At

each station a series of 80 pictures (Kodak Ektachrome 64) were taken at evenly spaced time intervals along a transect. Each one covered approximately 1 m². Six stations were chosen (depth range: 165 to 265 m) on the continental shelf off Kapp Norvegia (Fig. 1). At each station 7 photographs, which encompassed different scenarios of the 'undisturbed assemblage' previously defined by Gutt & Starmans (2001), were studied and processed. They represent different benthic views according to species composition variability. A total of 42 seafloor photographs was analysed representing an area of 42 m².

Image analysis. Each photograph was projected on an inverse slide projector and all distinguishable patch outlines were traced onto an acetate sheet (Garrabou et al. 1998). The drawings were scanned at 100 dpi resolution. The resulting raster images (TIFF format) were imported into a public domain image application NIH Image (U.S. National Institutes of Health, Version 1.61; <http://rsb.info.nih.gov/nih-image>), where they were subjected to different technical procedures (converted into black and white and the lines were thinned to unit width). Then, the images were imported into Arc/View 3.2 (ESRI) geographical information system (GIS) where they were spatially referenced. Arc/View routine procedures were used to label all the patches (e.g. cover categories). After these processes the images were converted to Arc/Info vector data format for further calculations using the Arc/Info 8.1 program (ESRI) (Fig. 2).

Photo identification. Megaepibenthic sessile organisms (approx. >0.5 cm body size diameter that live on the seabed) visible in photographs were identified to the lowest possible taxonomic level by referring to the literature (Thompson & Murray 1880 to 1889, Discovery Committee Colonial Office 1929 to 1980, Monniot & Monniot 1983, Sieg & Wägele 1990, Hayward 1995) and by the assistance of taxonomic experts (see 'Acknowledgements').

We recognized a total of 138 sessile cover categories. These included species/genus (123), phylum (3), 'complex' (7), and substratum (5). Within the species/genus category, some unidentified sponges (e.g. 'yellow branches') were named according to Barthel & Gutt (1992). Irregular masses composed by matrices of bryozoans together with demosponges and gorgonians of small size and similar filamentous morphology were assigned to one of the 7 'complex' cover classes.

The benthos in the Weddell Sea locally presents different stratum levels of organisms. The images analysed may underestimate the contribution of the basal stratum to the epibenthic assemblage. However, we decided to use 2D seabed images to quantify spatial patterns in Antarctic benthic communities because they retain most of the spatial pattern characteristics.

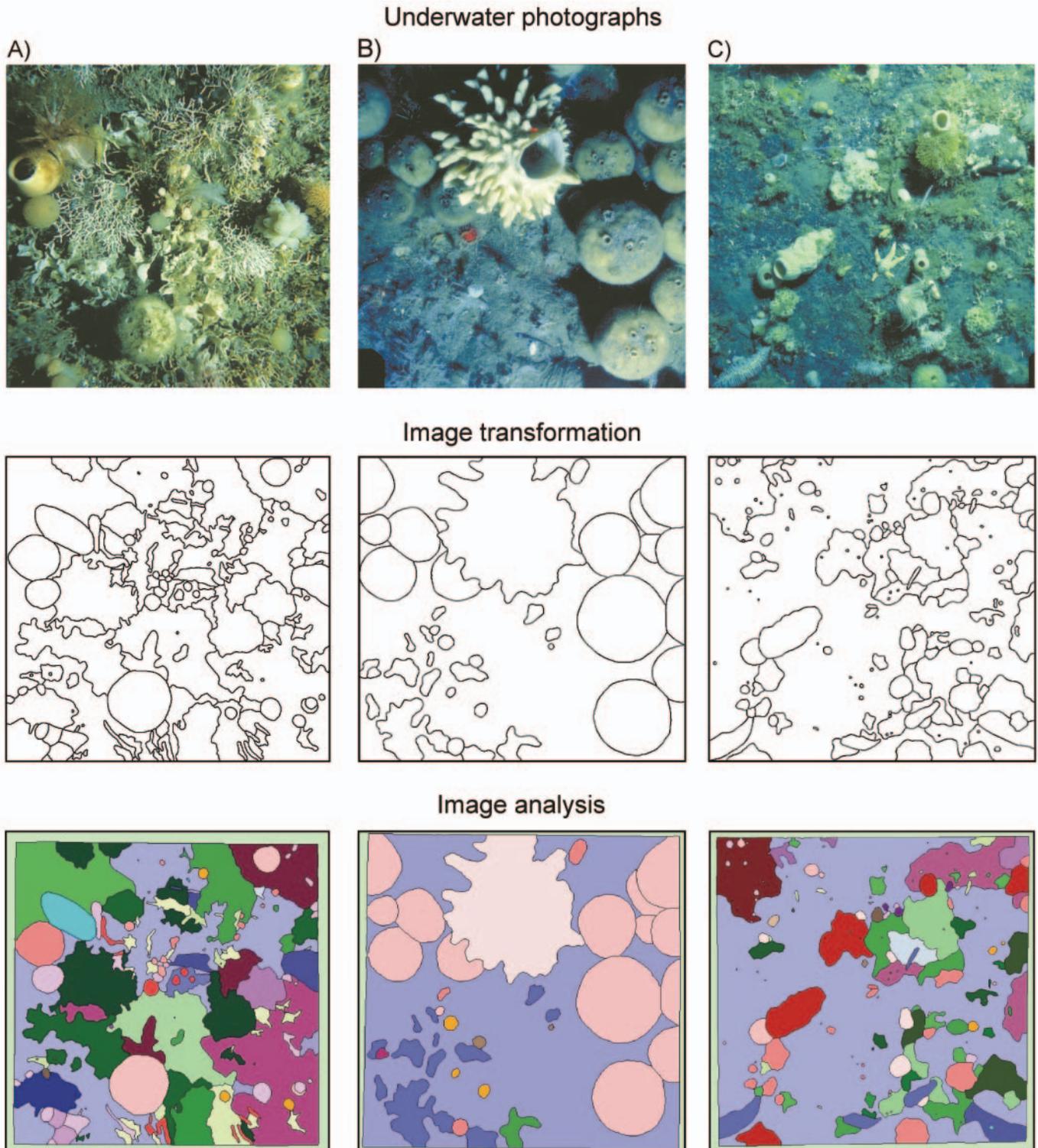


Fig. 2. Underwater photographs: undisturbed Antarctic benthic assemblage: (A) dominated by different groups of benthic suspension feeders (e.g. sponges, gorgonians, bryozoans, and compound ascidians; Stn 008), (B) composed mainly of sponges (*Rossella* sp., *Cinachyra barbata*; Stn 211), and (C) characterised by demosponges, gorgonians, and bryozoans, which partially cover the seafloor; Stn 221). Image transformation: the drawings were scanned and submitted to different technical processes (see text). Image analysis: the images were imported into Arc/View 3.2 where they were georeferenced and labeled. Finally, the images were transformed to vector coverage data to calculate landscape pattern indices (LPI) using the program Fragstats v3.0 for Arc/Info. Underwater photographs: J. Gutt, D. Piepenburg

Landscape pattern indices (LPI). LPI were calculated for each image by using the spatial pattern program Fragstats v3.0 for Arc/Info (Pacific Meridian Resources). Fragstats calculates landscape indices separately for (1) patch (basic elements of the mosaic), (2) class (each particular patch type), and (3) landscape (mosaic of patches as a complete unit) levels. A total set of 17 indices concerning distinct aspects of spatial patterns were calculated at landscape level (Table 1). For more information about these indices (descriptions, mathematical equations, and examples) see McGarrigal & Marks (1995).

Statistical analysis. As an initial step, multivariate ordination techniques were used to identify spatial pattern relationships within a benthic assemblage across different stations from the southeastern Weddell

Sea. Such methods arrange multidimensional data (e.g. stations, species) along axes (or dimensions) on the basis of variables (e.g. landscape indices, environmental variables). Canonical variate analysis (CVA) was conducted on the LPI data matrix to provide a representation of the photographic stations on the ordination diagram. Data for CVA typically consist of measurements (n) on variables (m). Each of the measurements is associated with an object belonging to one of predefined groups (g). The standardized coefficients of the canonical axes indicate the relative contributions of the original variables to each axis (Legendre & Legendre 1998). CVA was considered an adequate multivariate technique for this study because the photographic records were organised in different groups (= stations).

Table 1. Landscape pattern indices used to quantify spatial patterns of photographs (1 m²) of an undisturbed Antarctic benthic assemblage (southeastern Weddell Sea). The entire set of indices was calculated by Fragstats v3.0 for Arc/Info at landscape level except PERIAREA index, which was calculated from patch data level. Acronyms correspond to those used in Fragstats; see McGarrigal & Marks (1995) for a complete description and definition of each index

Abbreviation	Index name (units)	Description
CA	Cover Area (%)	Patch coverage
Patch size and variability indices		Landscape configuration
MPS	Mean patch size (cm ²)	Mean size of patch. MPS > 0
PSSD	Patch size standard deviation (cm ²)	Absolute measure of patch size variability. PSSD ≥ 0
PSCV	Patch size coefficient of variation (%)	Relative measure of patch size variability. PSCV ≥ 0
NP	Number of patches	Number of patches. NP ≥ 1
TE	Total edge (cm)	Total length of edge involving all landscape patches. TE ≥ 0
Patch shape indices		Landscape configuration in terms of complexity
MSI	Mean shape index	Mean patch shape complexity; equals 1 when all patches are circular and increases as patches become noncircular. MSI ≥ 1
AWMSI	Area weighted mean shape index	Similar to MSI, but weighted by patch area. AWMSI ≥ 1
LSI	Landscape shape index	Perimeter-to-area-ratio for the landscape as a whole, equals 1 when the landscape consists of a single circular patch and increases as landscape shape becomes noncircular and the amount of internal edge increases. LSI ≥ 1
PERIAREA	Mean perimeter to area ratio	Perimeter-to-area-ratio for all landscape patches. PERIARE > 0
Diversity indices		Landscape composition
SHDI	Shannon's diversity index	Function between number of different patches and their abundance. SHDI ≥ 0
SIDI	Simpson's diversity index	Calculates the proportion of patches in the different patch types. 0 ≤ SIDI ≤ 1
MISDI	Modified Simpson's diversity index	Same as Simpson's diversity Index with logarithmic transformation. MISDI ≥ 0
SHEI	Shannon's evenness index	Function between the proportional abundance of each patch type and the number of patch types. 0 ≤ SHEI ≤ 1
SIEI	Simpson's evenness index	Same as SHEI but calculated using Simpson's diversity index. 0 ≤ SIEI ≤ 1
PR	Patch richness	Measures the number of patch types. PR ≥ 1
Interspersion indices		Landscape configuration
IJI	Interspersion and juxtaposition index (%)	Measures the extension to which each patch type is interspersed with all other landscape patch types. 0 ≤ IJI ≤ 100

There was relatively strong redundancy among some of the LPI (see Table 1 for abbreviations used from this point): notably, SHDI and SIDI (correlation = 0.94), SHDI and MSIDI (0.97), and SHEI and SIEI (0.77). Therefore, SIDI, MSIDI, and SIEI were not used in the CVA.

Secondly, forward stepwise selection was used to choose a subset of LPI (Legendre & Legendre 1998). This procedure has the ability to select a reduced group of the explanatory variables, which has the power to discriminate among the whole data set. At each step, the analysis reviews all the variables and includes those, which contribute most to the discrimination. Monte Carlo permutation test (ter Baak 1995) using 199 random permutations was performed to test the significance of the LPI.

Thirdly, principal component analysis (PCA) was carried out to represent relationships among the subset of indices selected.

After these analyses, univariate statistics (ANOVA) were used to test for differences in the subset of LPI among stations to elucidate trends in spatial pattern characteristics. Post hoc comparisons of means were performed using Tukey's tests (Sokal & Rohlf 1981).

Prior to statistical analyses the data were standardized to ensure that (1) all the indices have equal weight, and (2) they followed a normal distribution in the multivariate analyses. The standardized indices were calculated separately by each raw score (each index per photo) minus the group (= station) mean and divided by the standard deviation of the group (= station). The various ordination techniques and tests were carried out using the programs STATISTICA (Version 5.5, StatSoft) and CANOCO (Version 4, ter Braak & Smilauer 1998).

RESULTS

Table 2 shows the values of the 17 LPI calculated for 42 images from 6 stations. It includes means and standard deviations at landscape level.

Ordination and selection analyses

CVA illustrates the ordination trend of benthic spatial patterns based on LPI among stations. The analysis arranges the photographic samples on the first (A1) and second (A2) axes, respectively (Fig. 3). The first 2 axes accounted for 81% of the total variation of the data set. The most distinct groups occurred between Stn 211 and the rest of stations, which were ordered along A2. A discontinuity along this axis separated Stn 221 from Stns 008, 042, 215, and 242. Each axis is interpreted ecologically from the correlation between the axes and each of the LPI variables (Table 3). Patch richness ($r = 0.61$) was the predominant variable in A1. Shannon's diversity index (0.43), mean patch size (-0.38), and the interspersed and juxtaposition index (0.35) were also important. Conceptually, these variables describe a gradient from stations with higher patch diversity and interspersed values and lower mean patch size on one extreme, to stations with opposite values, on the other. Four variables characterised A2: percent cover area (-0.52), interspersed and juxtaposition index (-0.45), landscape shape index (-0.45), and total edge (-0.44). The separation of the stations on this axis followed a gradient from higher values of cover area, patch interspersed and juxtaposition, shape complexity, and total edge at one extreme, to lower values of these indices at the other.

Table 2. Means \pm standard deviations of landscape pattern indices from 42 images ($n = 7$ per station). See Table 1 for abbreviations

Landscape indices	Stn 008	Stn 042	Stn 211	Stn 215	Stn 221	Stn 242
CA (%)	83.5 \pm 8.5	21.2 \pm 7.8	44.3 \pm 24.5	76.3 \pm 8.7	29.9 \pm 8.1	59.5 \pm 27.5
MPS (cm ²)	43.6 \pm 8.9	22.7 \pm 12.9	115.2 \pm 45.7	65.8 \pm 14.3	26.2 \pm 5.37	41.8 \pm 13.4
PSSD (cm ²)	209.4 \pm 108.2	51.4 \pm 33.2	128.1 \pm 60.2	174.6 \pm 67.5	51.2 \pm 17.6	151.2 \pm 113.8
PSCV (%)	468.9 \pm 176.9	228.6 \pm 93.1	115.6 \pm 45.3	258.5 \pm 54.5	192.2 \pm 41.8	338.5 \pm 172.8
NP	187.7 \pm 49.8	94.5 \pm 29.7	32.4 \pm 6.2	110.5 \pm 21.1	106.1 \pm 20.6	132.7 \pm 60.3
TE (cm)	2520.1 \pm 375.1	1188.2 \pm 185.2	974.9 \pm 150.3	1919.5 \pm 164.3	1575.1 \pm 267.3	1923.2 \pm 649.3
MSI	1.35 \pm 0.02	1.20 \pm 0.03	1.17 \pm 0.07	1.32 \pm 0.06	1.25 \pm 0.02	1.29 \pm 0.10
AWMSI	3.26 \pm 1.18	1.47 \pm 0.50	1.15 \pm 0.12	1.95 \pm 0.46	1.61 \pm 0.18	2.44 \pm 1.38
LSI	7.47 \pm 1.09	3.54 \pm 0.54	2.88 \pm 0.44	5.63 \pm 0.48	4.63 \pm 0.80	5.69 \pm 1.88
PERIAREA	2.07 \pm 0.23	2.78 \pm 1.00	0.81 \pm 0.29	1.77 \pm 0.14	1.61 \pm 0.14	2.23 \pm 0.64
SHDI	2.51 \pm 0.26	2.29 \pm 0.24	1.48 \pm 0.63	2.55 \pm 0.18	3.22 \pm 0.11	2.72 \pm 0.31
SIDI	0.85 \pm 0.04	0.82 \pm 0.05	0.61 \pm 0.21	0.88 \pm 0.03	0.94 \pm 0.01	0.87 \pm 0.06
MISDI	1.95 \pm 0.33	1.78 \pm 0.32	1.11 \pm 0.69	2.19 \pm 0.25	2.95 \pm 0.15	2.15 \pm 0.5
SHEI	0.74 \pm 0.06	0.76 \pm 0.07	0.64 \pm 0.18	0.80 \pm 0.05	0.90 \pm 0.01	0.79 \pm 0.09
SIEI	0.88 \pm 0.04	0.86 \pm 0.06	0.66 \pm 0.25	0.92 \pm 0.03	0.95 \pm 0.01	0.90 \pm 0.05
PR	29.8 \pm 4.5	20.7 \pm 3.3	9.4 \pm 4.4	23.1 \pm 1.6	35.0 \pm 3.8	30.3 \pm 3.7
IJI (%)	65.3 \pm 4.4	53.3 \pm 4.1	38.0 \pm 8.7	63.8 \pm 4.8	55.7 \pm 4.1	54.4 \pm 5.2

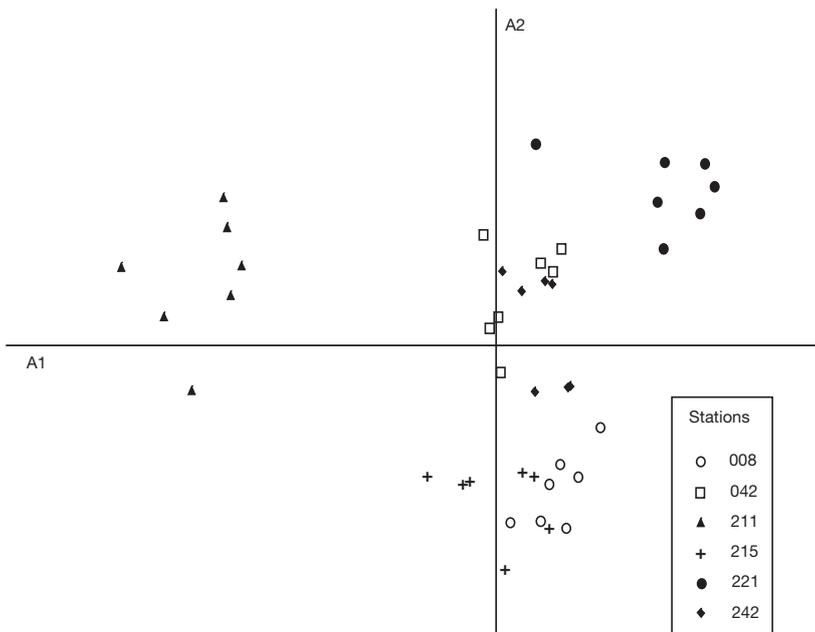


Fig. 3. Canonical variate analysis (CVA) defined by the 2 first axes (81% of the total variability) based on LPI for the 6 stations. Each point corresponds to one photograph analysed

Table 3. (a) Result of canonical variate analysis CVA performed for the photographs on the 14 landscape pattern indices (LPI) observed. (b) Correlation coefficients between LPI and the canonical axes. See Table 1 for abbreviations; *** $p < 0.001$

Information	A1	A2
(a)		
Eigenvalue	14.18	6.46
χ^2 test	229.4***	146.7***
Degrees of freedom	65	48
Cumulative percentage of variance	56	81
(b)		
Variables:		
CA	0.01	-0.52
MPS	-0.38	-0.08
PSSD	-0.04	-0.29
PSCV	0.14	-0.28
NP	0.26	-0.30
TE	0.23	-0.44
MSI	0.18	-0.33
AWMSI	0.11	-0.24
LSI	0.24	-0.45
PERIAREA	0.21	-0.08
SHDI	0.43	0.06
SHEI	0.20	0.15
PR	0.61	-0.01
IJI	0.35	-0.45

In summary, the ordination of photographs over the plane defined an arrangement of an undisturbed benthic assemblage along A1 according to a size and diversity gradient, and A2 according to a cover area, adjacency, and shape complexity gradient.

Forward stepwise procedure was carried out to choose a subset of indices, which best discriminate across stations. Table 4 provides the entry order into the model and the significance for each index. The significant indices ($p < 0.05$) were MPS, PSCV, PR, IJI, MSI, SHEI, and PERIAREA. These indices were very similar to the predominant indices already described for A1 and A2, suggesting that this subset is appropriate for data interpreting. Then, this subset of indices was considered as the optimal for the description of spatial patterns of Antarctic benthos. CVA was repeated using the selected subset of indices. The resulting 2 first axes explained 80% of the variance and the ordination diagram (not shown) revealed the same general pattern of station distributions as in Fig. 3.

PCA was performed to explore relationships between the subset of indices (Fig. 4). Each index had a correlation < 0.75 with any other indices selected, indicating no redundancy among them. The first 3 factors

Table 4. Summary of forward stepwise selection from landscape patterns indices (LPI). Monte Carlo permutation test was used to choose a subset of significant indices, which are ordered by decreasing contribution. See Table 1 for abbreviations

Variables	Step	F to enter/remove
MPS	1	6.22**
PSCV	2	3.58**
PR	3	3.79**
IJI	4	2.97**
MSI	5	2.64**
SHEI	6	2.05**
PERIAREA	7	1.72**
SHDI	8	1.56
PSSD	9	1.51
TE	10	1.49
AWMSI	11	1.48
LSI	12	1.22
NP	13	1.32
CA	14	0.72

** $p < 0.01$, all other values non-significant

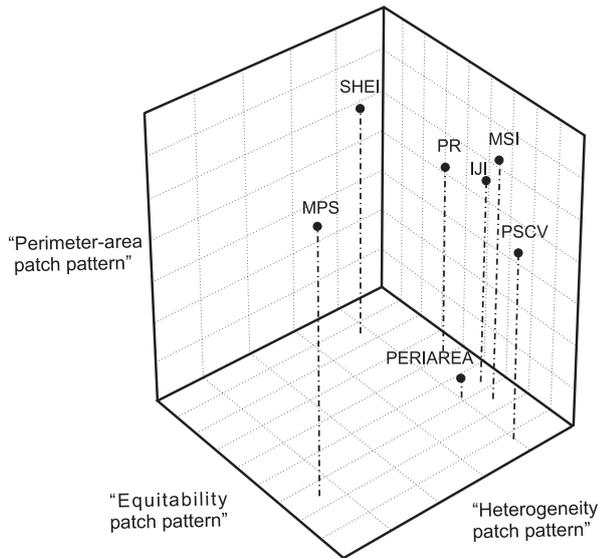


Fig. 4. 3D principal component analysis (PCA) of the subset of indices selected. The 3 first axes account for 84 % of the variance. Mean patch size (MPS), patch size coefficient of variation (PSCV), mean shape index (MSI), periaera index (PERIAREA), Shannon's evenness (SHEI), patch richness (PR), and interspersion and juxtaposition index (JJI)

explained 84 % of the variance. The first factor accounted for 52 % of the variation and discriminated between size (mean patch size) and heterogeneity patterns (patch coefficient of deviation, mean shape index, interspersion and juxtaposition index, and patch richness). It was termed 'heterogeneity patch pattern'. The second factor (17 % of the variation) was related to equitability (evenness index) and named 'equitability patch pattern'. The last factor (15 % of the variation) was associated with perimeter-area measures (PERIAREA) leading to the name 'perimeter-area patch pattern'.

Univariate analysis on LPI

ANOVA was carried out to detect differences among stations based on the values of the selected subset of LPI. There were large differences in LPI among stations (Fig. 5). For better interpretation of the results, diagrammatic representations of the stations and the homogenous groups of LPI means (those that were not significantly different from each other) were performed (Fig. 5). For mean and standard deviation values of LPI see Table 2.

Patch size and variability indices

MPS and its coefficient of variation (PSCV) showed significant differences in patchiness among stations.

Stn 211 differed significantly from the other stations, having the highest mean value for MPS (115.2 cm²), but the lowest mean value for the PSCV (115.6%). Large and equal size patches characterized this station (Fig. 5). Stn 215 presented intermediate values for both patch size indices. The rest of stations showed about similar low values for both MPS and PSCV except Stn 008, which had the maximum mean value for PSCV (468.9%).

Patch shape indices

MSI and PERIAREA showed significant differences among stations by contrasting patch shape complexity (Fig. 5). Both indices indicated similar trends in patch complexity except for Stn 042 (Fig. 5). This station with the largest mean value for PERIAREA (2.78) exhibited relatively low shape complexity for MSI (1.20). The reason for this difference between these shape indices may result from different meaning: PERIAREA index is negatively correlated with patch size and its high values indicate patches with small interior, whereas MSI measures complexity of patch perimeter (Hulshoff 1995). Stn 042 differed significantly from Stns 221 and 215 for PERIAREA (mean ratio values of 1.61 and 1.77, respectively). Stn 008 showed a relatively high mean value for PERIAREA (2.07) and the highest mean value for MSI (1.35), which differed from Stns 042 and 211. Stn 211 had the lowest mean values for both shape indices (1.17 and 0.81 for MSI and PERIAREA, respectively).

Diversity indices

Diversity indices differed significantly among stations. High values of SHEI result from landscapes where patches are equally distributed among patch types (McGarrigal & Marks 1995). The least diverse station was Stn 211, with the lowest mean values for PR and SHEI (9.4 and 0.64, respectively), whereas the most diverse station was Stn 221 with the greatest mean values for both diversity indices (35.0 and 0.90 for PR and SHEI) (Fig. 5). Stn 211 was monopolised by few patch categories. Although Stn 008 showed high diversity based on PR (with a mean value of 29.8), it had an intermediate distribution among patch types according to SHEI (mean value of 0.74).

Interspersion indices

Landscapes with high JJI values indicate good interspersion within the patch types (e.g. equally adjacent),

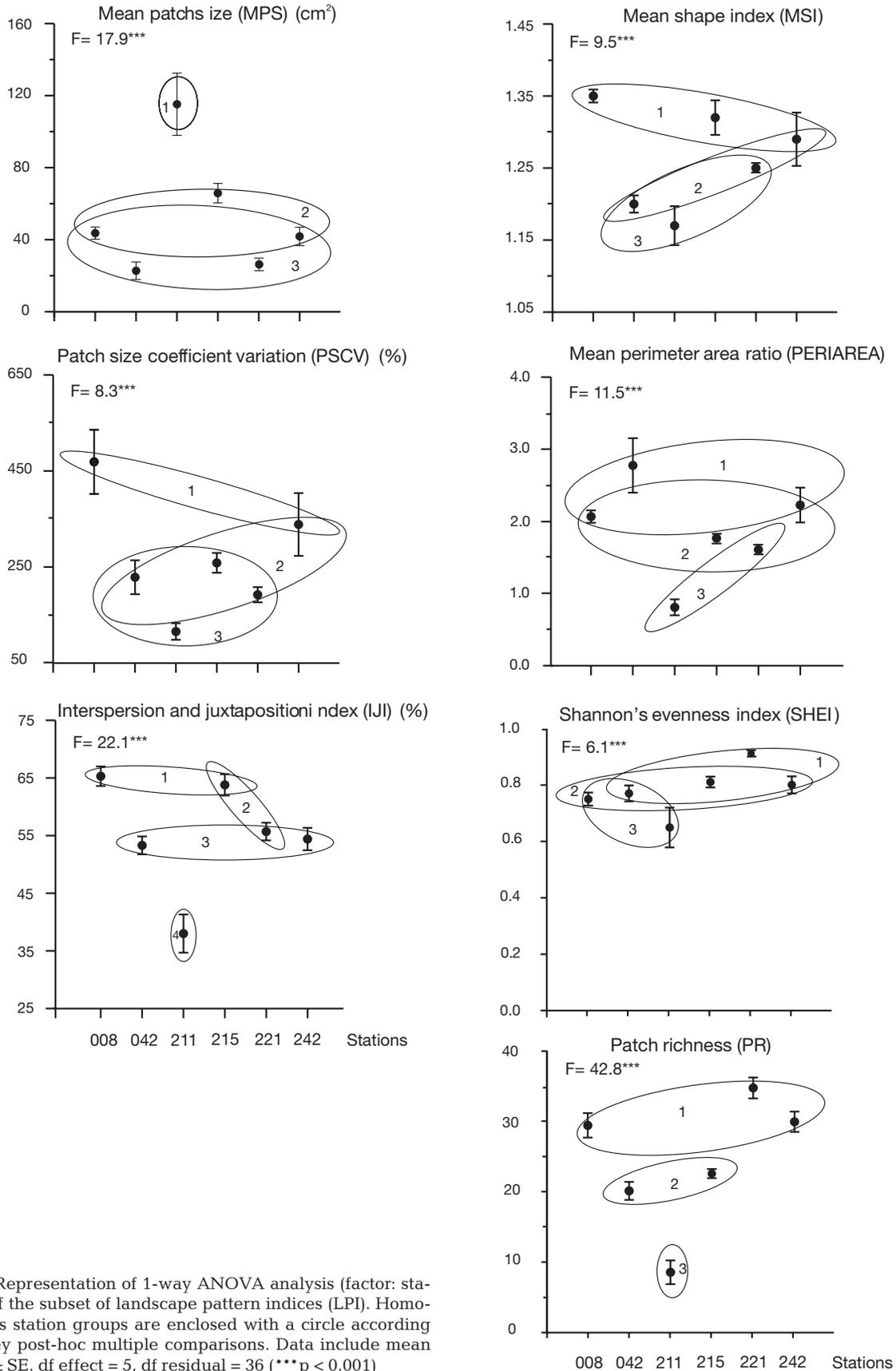


Fig. 5. Representation of 1-way ANOVA analysis (factor: stations) of the subset of landscape pattern indices (LPI). Homogeneous station groups are enclosed with a circle according to Tukey post-hoc multiple comparisons. Data include mean \pm SE. df effect = 5, df residual = 36 (**p < 0.01)

Table 5. Summary of landscape pattern indices (LPI) values selected and the major structural differences among the stations analysed. See Table 1 for abbreviations

Stations	Description of the LPI values	Spatial patterns and cover area
008 and 215	Stn 008 – Medium: MPS, PERIAREA, and SHEI – High: PSCV, MSI, PR, and IJI Stn 215 – Medium: MPS, PSCV, PERIAREA, and PR – High: MSI, SHEI, and IJI	Highest spatial complexity and intermediate diversity patterns Different well-mixed groups of benthic sessile organisms covering completely the sediment exhibited: – Intermediate but variable patch size – Complex shapes and patch types high equally adjacent – Different patch composition and relatively equally distributed
242 and 042	Stn 242 – Medium: MPS, PERIAREA and IJI – High: PSCV, MSI, SHEI, and PR Stn 042 – Low: MPS and MSI – Medium: PSCV, SHEI, PR, and IJI – High: PERIAREA	Intermediate spatial complexity and diversity patterns Different well-mixed groups of benthic sessile organisms covering the major part of the bottom sediment exhibited: – Intermediate and relatively uniform patch size – Relative/rather complex shapes and patch types equally adjacent – Different patch composition and relatively equally distributed
221	Stn 221 – Low: MPS and PSCV – Medium: MSI, PERIAREA, and IJI – High: SHEI and PR	Intermediate spatial complexity and highest diversity patterns Different highly-mixed groups of benthic sessile organisms covering partially the bottom sediment exhibited: – Relatively small and uniform patch size – Relatively intermediate complex shapes – Highly different patch composition and very equally distributed
Stn 211	Stn 211 – Low: PSCV, MSI, PERIAREA, SHEI, PR, and IJI – High: MPS	Low spatial complexity and diversity patterns Mostly sponges covering partially the bottom sediment exhibited: – Large and similar patch size – Low complex shapes – Few patch types and poorly interspersed among them

whereas low values characterise landscapes with poorly interspersed patch types (e.g. disproportionate distribution of patch type adjacencies) (McGarrigal & Marks 1995). Stn 211 showed significant differences from the rest of the stations, having the lowest interspersed patterns among patch types (mean value of 38.0%) (Fig. 5). Stns 008 and 215 presented the highest mean IJI values, 65.3 and 63.8%, respectively indicating high interspersed patterns. These stations differed significantly from Stns 042, 221, and 242 (with relatively intermediate IJI mean values of 53.3, 55.7, and 54.4%, respectively).

DISCUSSION

The application of LPI in this study was useful for characterising spatial patterns of an undisturbed Antarctic benthic assemblage and for showing differences in spatial patterns across stations. The 14 metrics of LPI analysed through the combination of CVA (Fig. 3) and the interpretation of the ANOVA analysis (Fig. 5) revealed a trend of dispersion and significant differences among the stations. Overall, stations differed in size and diversity of patches and in hetero-

geneity patterns (size variability, shape, and interspersed of patches). The photographic records analysed only referred to the undisturbed assemblage (characterised by a mixture of sessile suspension feeders) (Gutt & Starman 2001) for which minor differences in spatial pattern would be expected. Nevertheless, LPI showed a great discriminatory power detecting significant differences among stations within this assemblage (Figs. 3 & 5). Therefore, the application of LPI to quantify spatial patterns across assemblages (e.g. along depth zonation, across disturbance gradients caused by sewage or iceberg scouring) should result in an excellent discriminatory power. A previous work (Garrabou et al. 1998) was also successful in applying LPI to Mediterranean rocky benthic communities along a depth gradient. The application of this methodology to Antarctic benthos as well as to other benthic communities (from meio to macrobenthos) will increase our understanding of structural patterns and processes in these complex habitats.

Spatial patterns are expressed as several measures of mosaic structure (Table 1), which may be quantified at a particular point of time. The spatial scale of ecological data encompasses both 'grain' (resolution) and 'extent' (total area) (Turner et al. 1989). There is no

single and correct scale of analysis to investigate a system (Levin 1992). The appropriate scale of observation will depend on the questions asked, the habitat analysed, the organisms studied, and the time periods considered (Wiens 1989). In our study, an increase in the extent (1 m^2) would mean a greater sampling area but a decrease of grain (approx. 0.3 mm), thus a loss in taxonomic identification (necessary for diversity measurements). For instance, Turner & Ruscher (1988) reported distinct diversity gradients in the same set of terrestrial landscapes considering both finer and coarser spatial resolution. Therefore, preserving grain and extent is essential for comparative studies.

LPI in the Weddell Sea can only be compared in the case of diversity indices, which had been calculated before using traditional methods (absence/presence) in image techniques. Diversity index values of the present study were slightly higher than those obtained from previous calculations for the same assemblage and depths. Shannon diversity ranged from 1.48 to 3.22 versus 2.3 to 2.5 and evenness from 0.64 to 0.90 versus 0.57 to 0.6, respectively (Table 2) (Gutt & Starman 1998, Starman et al. 1999). We attribute the differences to the higher resolution of the underwater photographs compared to ROV-acquired images and their larger total area sampled.

Our analysis using stepwise selection procedure supports the argument that a subset of indices can capture significant traits of spatial pattern (O' Neill et al. 1988, Turner & Ruscher 1988, Ritters et al. 1995). We considered MPS, PSCV, PR, IJI, MSI, SHEL, and PERI-AREA as the optimal subset of LPI to discriminate across the benthic stations (Table 4). The stepwise selection analysis was an appropriate method to select these indices because it ends with a set of metrics, which has the maximal discriminatory value. Our subset of indices differs from those chosen to characterise Mediterranean benthic communities (Garrabou et al. 1998). As in terrestrial ecosystems, there is not an ideal standard subset of indices to describe benthic habitats and each case study should choose the best subset for the spatial patterns quantification.

LPI provided comprehensive measurements over different aspects of spatial patterns (patch size and form, diversity and interspersion) (Table 5, Figs. 3 & 5). Spatial complexity and diversity patterns of an undisturbed benthic assemblage increased from Stn 211 to the rest of stations. Stn 211 was mostly dominated by volcano-shape hexactinellid sponges and one spherical-shape demosponge species (*Cinachyra barbata*). Large patches of similar size partially covered and monopolised the substrate. The patches showed less complex shapes, were less diverse, and less interspersed. Stn 008 showed the most complex and relatively diverse pattern, with intermediate but variable

patch size. The patches exhibited complex shapes, were highly different in composition, relatively equally distributed, and well interspersed. Heterogeneity patterns (variable patch sizes, patches with complex shapes, and interspersion) decreased from Stn 215 through Stns 242 to 042. These 3 stations and Stn 008 were composed by different well-mixed groups of benthic sessile organisms (e.g. sponges, gorgonians, bryozoans, and ascidians), which covered the major part of the bottom sediment. The most diverse pattern occurred at Stn 221 characterised by demosponges, gorgonians, and bryozoans, which partially covered the seafloor. However, this station did not show high heterogeneity patterns such as Stns 008, 215, and 242. Based on LPI values of this study, spatial patterns and diversity did not converge toward a particular scenario. On the contrary, LPI results suggest a separation between rich and diverse stations, which partially covered the seafloor and those with high values of pattern heterogeneity (highest patchiness, form complexity, and interspersion). These differences within the undisturbed assemblage show the importance of quantification of different aspects of spatial patterns (diversity alone did not discern among all stations).

Overall, Antarctic benthos is influenced by different combination and intensity of biotic (predation, competition, recruitment) (Arntz et al. 1994, Clarke 1996) and abiotic factors (substratum, sedimentation, currents-food supply, ice scouring, depth) (Dayton et al. 1970, 1994, Gallardo 1987, Barnes et al. 1996), which might explain the different spatial pattern trends obtained through the quantification of LPI. For example, epibiotic relationships are considered as an important factor structuring Antarctic benthic communities (Dayton et al. 1970, Gutt & Schickan 1998) since these relationships contribute to the development of the diverse 'multi-storeyed assemblages'. Barthel (1992) and Kunzmann (1996) demonstrated the role of sponges as substrata for other invertebrates. Our results showed the lowest diversity values in situations where sponges were the dominant group (Stn 211) and intermediate values when sponges did not monopolise the space (Stn 042) (Figs. 3 & 5). Most of the epifauna found on the *Cinachyra barbata* (demosponge) and hexactinellid sponges with smooth surface (*Rossella nuda* and *Scolymastra joubini*) were motil organisms (not included for LPI calculations, see 'Material and methods') and there were few sessile epibenthic organisms (Stn 211). In contrast, Stn 042 exhibited some hexactinellid sponges with superficial spicules (*R. antarctica* and *R. racovitzae*) that allowed the development of a variety of sessile organisms (hydrozoans, demosponges, bryozoans, polychaetes, ascidians, and holothurians). The other stations (Stns 008, 215, 221, and 242) also showed epibiotic relationships but the sub-

strata were other sessile organisms (mainly demosponges, gorgonians, and ascidians). Kunzmann (1996) remarked the difference of the hexactinellid's surface (with and without surface spicules) for the development of epibenthic associated fauna. Our results agree with her observation and may be that biochemical composition (McClintock 1987) of *C. barbata* and hexactinellid sponges with smooth surface do not favour the settlement of sessile epibenthic organisms on their surface and in their surroundings. This phenomenon may partly be an explanation of the significant differences in diversity within the undisturbed assemblage.

Several studies in the Weddell Sea (Gutt & Piepenburg 1991, Gutt & Koltun 1995, Starman et al. 1999) described a high degree of patchiness in spatial distribution patterns of benthic communities. Sponge patchiness at a small scale, which was also observed in our study, could result from biological characteristics of single species (Gutt & Koltun 1995). Stn 211 exhibited the lowest value of IJI providing insights for strong interspecific competitive interactions (degree of species adjacencies in relation to their cover) (Turon et al. 1996) or success of species with very low dispersal of sexual and/or asexual recruits in the communities (Wulff 1991). Similar observations of aggregations of sponges were reported for *Cinachyra barbata* (Barthel & Gutt 1992) and *Rossella racovitzae* with a budding asexual reproductive mode (Dayton 1979).

The application of LPI showed relevant information to characterise the spatial organization within the undisturbed assemblage. Moreover, LPI provided some insights in the ecological factors that may be responsible for the patterns observed. These interpretations could be specifically tested by ecological data on the natural history of species and using adequate experimental designs whenever possible (Dayton & Sala 2001).

CONCLUSIONS

The successful description of Antarctic benthic communities through landscape pattern indices provides a useful tool for the characterisation and comparison of spatial patterns in marine benthic habitats. Our results also suggest that a subset of indices captures significant traits to obtain a comprehensive description of landscape spatial pattern.

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Publication II

**Impact of iceberg scouring
on Antarctic benthic communities:
new insights from the study
of spatial patterns**

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Impact of iceberg scouring on Antarctic benthic communities: new insights from the study of spatial patterns

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Abstract

This study focuses on spatial patterns of Antarctic benthic communities emphasizing the succession process after iceberg disturbance. For this purpose, underwater photographs (1m² each) corresponding to 6 stations from the southeastern Weddell Sea shelf were analysed using techniques from the field of landscape ecology. Measurements of spatial patterns (landscape indices) were used to describe changes in structural patterns along successional stages. Canonical Correspondence Analysis (CCA) showed a gradual separation from the early to older stages of succession based on sessile benthic cover area, size, shape, diversity, and interspersion and juxtaposition indices. Conceptually, the results describe a gradient from samples belonging to first stages of recovery with low cover area, low complexity of patch shape, small patch size, low diversity and patches poorly interspersed to samples from later stages with higher values of these indices. After CCA and stepwise selection analyses, we considered cover area (CA), mean patch size (MPS), Shannon diversity (SHDI), Shannon's evenness (SHEI), interspersion and juxtaposition (IJI), mean shape (MSI), and landscape shape indices (LSI) as the optimal subset of indices to describe spatial pattern across the successional stages. Cover area was the best predictor of recovery. Kruskal-Wallis nonparametric analysis showed significant differences in several spatial indices, including cover area, patch size and form, diversity, and interspersion. We conclude that a variety of factors affect the observed successional sequences of Antarctic benthic communities after iceberg disturbance, including the existence and dispersal abilities of propagules, growth rates, chemical defense, and competition between species.

Key words: Antarctic, benthic communities, disturbance, landscape ecology, multivariate ordination, succession, underwater photography, GIS

INTRODUCTION

Natural disturbance has been recognised as a common structuring force affecting both marine and terrestrial ecosystems (Southwood 1977, Pickett & White 1985, Turner & Dale 1998). Its impact promotes diversity as well as renewal processes and creates heterogeneity (Turner et al. 1994, Holling & Meffe 1996, Paine et al. 1998). Therefore, understanding the disturbance history is of fundamental interest in the study of ecosystems (Hughes 1989, White & Jentsch 2001). Adaptation of species to disturbance depends on the coupling between disturbance frequencies and lifetimes, and may be evolutionarily important (Turner et al. 1998, Lytle 2001). Natural disturbances have a broad range of influences on species composition, community structure and dynamics, and the subsequent patterns of succession (Gray et al. 1986, Petraitis et al. 1989, Berlow 1997, Connell et al. 1997, Sousa 2001).

A disturbance is defined as “a discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett & White 1985: 7). However, this definition needs to be specified according to the spatial and temporal scales relative to the system (Turner & Dale 1998). Disturbance events influence most ecological systems and include, among others, large storms in tropical rain forests (Brokaw & Walker 1991), fire across a large variety of terrestrial biomes (Attiwill 1994), hurricanes in coral reefs (Connell et al. 1997, Hughes & Connell 1999), wave exposure, battering by drift logs in rocky intertidal communities (Dayton 1971, Paine & Levin 1981, Sousa 1985), waves and currents in soft sediments (Hall 1994), and ice in polar benthos (Dayton 1990, Clarke 1996, McCook & Chapman 1997, Conlan 1998, Gutt 2001). Ice disturbance is regarded as a common event in the evolutionary history of Antarctic and Arctic benthos (Clarke & Crame 1989, Clarke 1990, Anderson 1991, Dunton 1992, Grobe & Mackensen 1992, Zachos 2001) and among the more important factors structuring these communities (Dayton et al. 1970, Arntz et al. 1994, Conlan et al. 1998, Peck et al. 1999, Gutt 2000). The major disturbance on the benthos of the deep continental shelves is the grounding and scouring of icebergs (Gutt et al. 1996, Lee et al. 2001, Gutt & Starmans 2001, Knust et al. *in press*). They severely damage large areas of the seafloor, affecting the physical and biological environment by removing both hard and soft substrates and eradicating benthic life (Gutt et al. 1996, Gutt 2000). Their impact initiates recolonization processes and provides the opportunity to study successional patterns.

The “intermediate disturbance hypothesis” (Connell 1978) summarizes the maintenance of tropical rain forest and coral reef high diversity as a result of intermediate levels of disturbance. Huston (1979, 1994) later enlarged this explanation into the “dynamic equilibrium hypothesis”, which predicts the highest diversity where disturbance and growth rates among organisms are in “optimal” balance. Within this context, Gutt & Piepenburg (2003) concluded that iceberg scouring on Antarctic benthos does not contribute significantly to the development of high diversity at local scales (1-100m) during the course of succession.

During succession in Antarctic benthos, the patterns of species abundance are assumed to depend on biological factors, such as the existence of propagules (Poulin et al. 2002), predation and competition (Dayton et al. 1974), life-history traits (Teixidó *unpublished manuscript*), and growth rates (Clarke 1996). Overall, the information available on Antarctic benthic succession agrees with empirical generalizations concerning the strength and direction of consecutive changes (Odum 1969, Margalef 1974); e.g. i) increment of complex structures in organisms, ii) increase of species number and often also diversity. These generalizations have been interpreted as the result of self-organization processes (Margalef 1997).

Succession in Antarctic benthic communities is less predictable than in some terrestrial ecosystems (Connell & Slatyer 1977) and there is no specific pattern of species replacement along succession (Gutt 2000). However, some sessile organisms have been recognised as pioneer species during the first stages of recolonization (Gutt et al. 1996). These early-successional species exhibit high fecundity, small eggs, long dispersal, high recruitment, shorter longevity, and rapid growth. Late-successional species seem to have the opposite traits. These attributes define MacArthur’s classical r- and K- selection (MacArthur & Wilson 1967). K-strategy characterises many benthic species in Antarctica (Clarke 1979) with a slow growth and long life span (Dayton 1979, Arntz et al. 1994, Brey et al 1999, Gatti 2002). Huston (1979) suggested that high densities of long-lived individuals with low growth rates should result only over relatively long periods of time under conditions of low mortality. Iceberg disturbance effects on the benthic structure are of particular interest because the communities may require very long recovery times (Gutt 2000) though there are some initial successional stages with faster growth (Dayton 1989, Rauschert 1991).

Most ice-disturbance studies have been focused on the structure of shallow-water Antarctic benthic communities (reviewed by Dayton 1990, Gambi et al. 1994, Barnes

1995, Lenihan & Oliver 1995, Peck et al. 1999), but there have been few ecological studies based on the effect of iceberg scouring on mega-epibenthic communities at greater depth (Gutt et al. 1996, Gutt & Starmans 2001). The unusually deep continental shelf of the Weddell Sea exhibits complex three-dimensional community with a great biomass, intermediate to high diversity, and patchy distribution (Gili et al. 2001, Gutt & Starmans 1998, Teixidó 2002, Gerdes et al. 2003). The fauna in this area is dominated by a large proportion of benthic suspension feeders, which locally cover the entire sediment (Gutt & Starmans 1998, Starmans et al. 1999, Teixidó et al. 2002). Studies on succession in the high-latitude Antarctic marine environment are of special ecological interest because of its unique characteristics. Furthermore, despite increasing human impact it is still much less anthropogenically disturbed than any other marine ecosystem.

A key challenge in ecological research involves determining the influence of spatial patterns on ecological processes (Levin 1992, Gustafson 1998). Iceberg scouring creates patterns across Antarctic benthic communities by producing habitats, which are a complex mosaic of disturbed and undisturbed assemblages in different stages of succession (Gutt and Piepenburg 2003). To investigate successional changes in Antarctic benthic communities of the Weddell Sea, we analysed sea floor photographs using techniques from landscape ecology. This discipline emphasizes the interaction between spatial patterns and ecological processes across a range of spatial and temporal scales (Forman & Gordon 1986, O'Neill et al. 1988, Turner 1989, Turner et al. 2001). We assumed that benthic communities can be observed as patch mosaics, where patches are assigned to different categories (*e.g.*, species, cluster of species). From this perspective, community spatial patterns and dynamics can be analysed by focusing on the characteristics of the patch mosaic. The patterns and mechanisms by which communities change during succession can be extremely variable and complex (Connell & Slatyer 1977, Paine & Levin 1981, Pickett et al. 1987, McCook 1994). However, empirical observations revealed similar and repeatable patterns of change in species abundance through time (Clements 1916, Odum 1969, Paine & Levin 1981, Sousa 1984, McCook 1994). In the Antarctic benthos, the trajectory of recovery remains poorly understood due to a lack of continuity in sampling and great difficulties in performing *in situ* experiments. Consequently, our focus is to study community succession after iceberg disturbance by applying measures of landscape pattern to detect spatial changes, and to better understand how Antarctic benthic communities are structured and organised through successional stages. This publication is part of a larger study focused on the community dynamics after iceberg disturbance (Teixidó et al. *submitted*).

STUDY AREA

Oceanographic setting

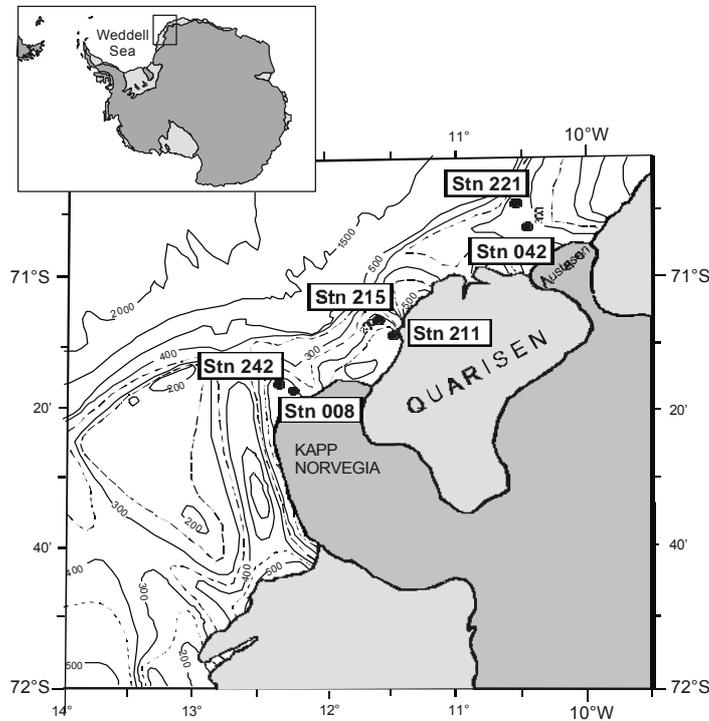


Fig. 1. Photographic stations in the southeastern Weddell Sea (Antarctica) (subsection of chart AWI BCWS 553).

Kapp Norvegia is located in the southeastern Weddell Sea (Fig. 1), where the continental shelf is relatively narrow (less than 90 km) and reaches depths of 300–500 m (Carmack & Foster 1977, Elverhøi & Roaldset 1983). Large proportions of the shelf are covered by extensions of the ice sheet (Anderson 1991). The continental shelf undergoes seasonal pack-ice coverage (Tréguer & Jacques 1992) but coastal polynyas of varying size occur especially during summer (Hempel 1985). Water temperature close to the sea bottom is low and relatively constant, ranging from $-1.3\text{ }^{\circ}\text{C}$ to $-2.0\text{ }^{\circ}\text{C}$ (Fahrbach et al. 1992)

and there is a marked summertime peak in primary production (Nelson et al. 1989, Gleitz et al. 1994, Park et al. 1999). The organic matter flux from surface waters to the seabed shows temporal variation with high values after phytoplankton blooms in summer (Bathmann et al. 1991, Gleitz et al. 1994). Hydrodynamics affect food availability and determine sediment characteristics such as grain size and composition, which are of ecological relevance for benthic communities (Dunbar et al. 1985, Gutt 2000).

Iceberg scouring disturbance on benthic communities: Grounding and scouring of drift ice disturb both shallow and deep polar seafloor habitats (Dayton et al. 1970, Conlan et al. 1998, Gutt et al. 1996, Peck et al. 1999). The keels of icebergs can create gouges up to 1375 m wide, 10.5 m deep, and several km in length (Lewis & Blasco 1990). On the deep seafloor, large gouges may take millennia to disappear (Josenhans & Woodworth-Lynas 1988). The pumping effect of icebergs may be important for sediment transport and winnowing on a local scale and its effects will depend on iceberg size, shape, stability,

and sediment characteristics (Lien et al. 1989). Large tabular icebergs originate as a result of rifts that cut through the ice shelf (Lazzara et al. 1999). Antarctic ice shelves have produced 70,000 icebergs (> 10 m wide) between 1981 and 1985 (Lien et al. 1989), which scoured the seabed up to 500 m water depth (Barnes & Lien 1988, Lien et al. 1989, Gutt et al. 1996) and created drastic rifts in the bottom relief. Gutt & Starmans (2001), considering areas with different bottom topography and concentration of grounded icebergs, calculated a proportion between 20 % and 60 % of undisturbed seafloor in the eastern Weddell Sea.

The benthic communities inhabiting areas affected by iceberg scouring exhibit a wide range of complexity: from areas almost devoid of any fauna through stages with few abundant species to highly complex communities characterized by a relatively high species richness and extremely high biomass (Gutt et al. 1996, Gerdes et al. 2003). The successional stages differ in faunistic composition and abundance (Gutt et al. 1996, Gutt & Starmans 2001). In the Weddell Sea, early successional stages are considered precursors toward the late slow-growing hexactinellid sponge stage (Dayton 1979, Gatti 2002), assuming that many decades or even centuries may be necessary to return to such a mature community after disturbance.

METHODS

Study design and photosampling: Landscape spatial patterns of Antarctic benthic communities were investigated among different stages of succession. For this purpose, 112 photographs from six stations (depth range: 165-265 m) on the continental shelf off Kapp Norvegia were investigated (Fig. 1). The photographic records of the seafloor were obtained during expeditions ANT XIII/3 and ANT XV/3 on board R/V 'Polarstern' during the austral summers of 1996 and 1998 (Arntz & Gutt 1997, 1999). This research was performed within the Ecology of the Antarctic Sea Ice Zone programme (EASIZ) of the Scientific Committee on Antarctic Research (SCAR). A 70-mm underwater camera (Photosea 70) with two oblique strobe lights (Photosea 3000 SX) was triggered at a fixed distance (1.4 m) from the seafloor by a bottom contact switch while the ship drifted (Gutt & Starmans 1998). At each station sequences of 80 perpendicular colour slides (Kodak Ektachrome 64), each covering approximately 1m² of the seabed, were taken at evenly spaced time intervals along a transect. The optical resolution was around 0.3 mm. At each station, an undisturbed assemblage (UD) and three stages of recolonisation (from

younger to older: R0, R1, R2), defined previously by Gutt & Starman (2001) (Table 1, Fig. 2), were identified. At each stage, 7 photographs were studied and processed (Table 2). In total, an area representing 112 m² of the seafloor was analysed.

Table 1. Description of the successional stages identified in the southeastern Weddell Sea. They include 3 stages of recolonisation (from younger to older: R0, R1, R2) and an undisturbed assemblage (UD).

Stage	Description
R0	Sediment surface shows recent mechanical disturbance or is barely covered by organisms. It consists of a high proportion of gravel and detritus. Presence of motile fauna such as fish or echinoderms. First pioneers of sessile species appear with relatively low number and abundance.
R1	Increase of abundance of pioneer sessile species. Occasionally some occur in higher densities e.g., sponges (<i>Stylocordila borealis</i> and <i>Homaxinella</i> sp.), bryozoans (<i>Cellaria</i> sp., <i>Camptoplites</i> sp.), gorgonians (<i>Primnoisis antarctica</i>), ascidians (<i>Synoicum adareanum</i>), and sabellid and terebellid polychaetes (<i>Pista</i> sp.). Sediment surface partially covered by fauna.
R2	Composed of a mixture of sessile suspension feeders, which mostly cover the sediment. Higher no. of species and abundance than R1 and R0. There are no large hexactinellid sponges (≥ 20 cm tall).
UD	Large specimens of hexactinellids, which are known to grow very slowly (Dayton 1979, Gatti 2002) and consequently provide an estimate of the relative age of the assemblage. Composed of a mixture of sessile suspension feeders, which partially cover the sediment. It can be strongly dominated by single sponges (e.g. <i>Rossella racovitzae</i> , <i>R. antarctica</i> , <i>R.nuda</i> , and <i>Cinachyra barbata</i>).

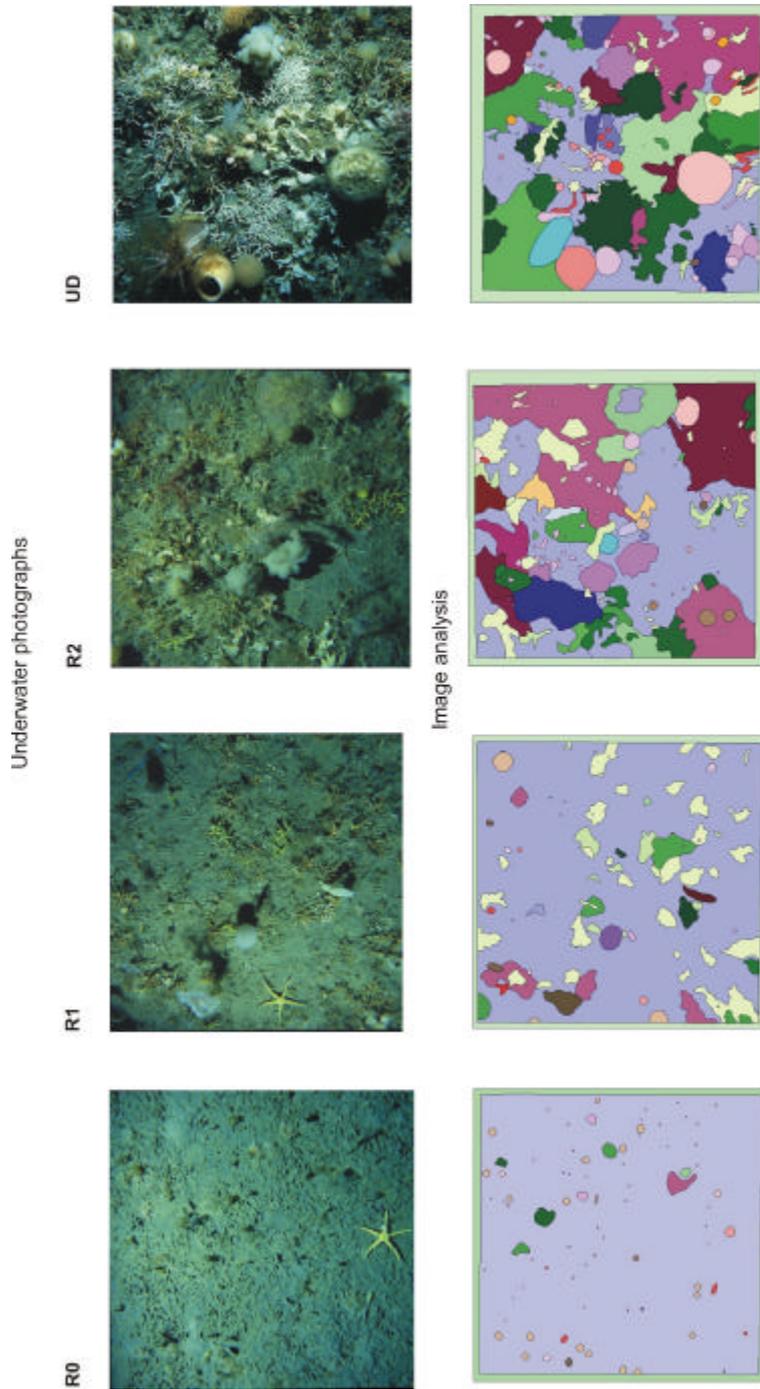


Fig. 2. Stages of recolonisation (from younger to older: R0, R1, R2) and undisturbed (UD) assemblage analysed. For each image, landscape pattern indices (LPI) were calculated using the program Fragstats v3.0 for Arc/Info. R0: Sediment surface is barely covered by sessile organisms such as lollypop like sponges (*Stylocordyla borealis*), soft bryozoans (*Camptoplites lewaldi* and Bryozoa non identified), sabellid polychaetes (*Myxicola cf. sulcata*), and solitary ascidians (*Molgula pedunculata*). Large numbers of ophiuroids are also characteristic (the yellow sponge *Iophon radiatus* covers the surface of *Ophiurolepis* spp.). R1: The yellow (*Cellarinella* spp. and *Systemopora contracta*) and white (*Hornea* sp.) rigid species of bryozoans, sabellid polychaetes (*M. cf. sulcata* and *Perkinsiana* spp.), and solitary (*M. pedunculata*) and colonial ascidians (*Distaplia cylindrica*) partially cover the seafloor. R2: Composed of a mixture of benthic organisms - round demosponges (*Cinachyra barbata*), a ramified-bushy gorgonian (*Notosis* sp.), soft (*Notoplites* spp.) and rigid bryozoans (*Cellarinella* spp. and *S. contracta*, *Reteporella* spp.), sabellid polychaetes, compound ascidians (*Aplidium* sp.3 and *Polysyncrator trivolutum*) and a pterobranchian (*Pterobranchia* sp.2) -, which may cover up to three quarters of the area. UD: A volcano-shaped hexactinellid sponge (*Rossella nuda/ Scolymastra joubini*), a round demosponge (*C. barbata*), rigid (*Smitina directa*, *Cellarinella* spp.) and cigar-like bryozoans (*Smittoidea malleata*), a salmon "bottle brush" gorgonian (*Thouarella* sp.2), a holothurian (*Ekmocucumis turqueti*), and compound ascidians (*Aplidium* sp. 3 and *Synoicum adareanum*) cover the seafloor.

Table 2. List of the 6 photographic stations in the southeastern Weddell. 7 photographs were analysed along the 3 stages of recolonisation (from younger to older: R0, R1, R2) and the undisturbed assemblage (UD), wherever these occurred

Stations	Depth (m)	Identified assemblages			
		R0	R1	R2	UD
008	171-173	7	7	7	7
042	260-243	-	-	-	7
211	77-117	-	7	-	7
215	167-154	7	-	7	7
221	261-270	7	7	-	7
242	159-158	-	7	7	7
N° photos		21	28	21	42

Image analysis: Each photograph was projected on an inverse slide projector and all distinguishable patch outlines were traced onto an acetate sheet at a map scale of 1:5. The drawings were scanned (100 dpi) and imported into the Arc/View 3.2 (© ESRI) geographical information system (GIS) where they were spatially referenced. Arc/View routine procedures were used to label all the patches. The images were then converted to vector polygon format for further calculations using the Arc/Info 8.1 program (© ESRI). For detailed description of the image analysis see Teixidó et al. (2002).

Identification: Megaepibenthic sessile organisms, approx. > 0.5 cm in body size diameter, were identified to the lowest possible taxonomic level by photo interpreting following Thompson & Murray (1880-1889), Discovery Committee Colonial Office (1929-1980), Monniot & Monniot (1983), Hayward (1995), and Sieg & Wägele (1990).

We recognized a total of 118 sessile and sediment cover categories (see Appendix 8.4). These included species/genus (106), class/phylum (5), “complex” (7), and substratum (5). Within the species/genus category some unidentified sponges (e.g., “Yellow Branches”) were named according to Barthel & Gutt (1992). Irregular masses composed of bryozoan matrices together with demosponges and gorgonians of small size and similar filamentous morphology defined the seven “complex” cover classes.

Landscape pattern indices (LPI): Spatial patterns for the Antarctic benthic successional stages were quantified with landscape pattern indices (LPI). Initially, a total set of 17 indices was calculated for each image at landscape level (mosaic of patches as a complete unit), but only 9 were used due to redundant information (Table 3, see below Data analysis). Each index measured different aspects of composition and configuration of the landscape. For more information about these indices (descriptions, mathematical equations, and examples) see Appendix 8.6 and McGarigal & Marks (1995). LPI were calculated using the program Fragstats v3.0 for Arc/Info (Pacific Meridian Resources).

Table 3 Landscape pattern indices used to quantify spatial patterns of photographs (1 m² each) from Antarctic benthic communities. The indices were calculated using Fragstats v3.0 for Arc/Info.

Abbreviation*	Index name (units)	Description
CA	Cover area (%)	Patch coverage
Patch size and variability indices		<i>Landscape configuration</i>
MPS	Mean patch size (cm ²)	Mean size of patch. MPS>0
PSSD	Patch size standard deviation (cm ²)	Absolute measure of patch size variability. PSSD□0
Patch shape indices		<i>Landscape configuration in terms of complexity</i>
MSI	Mean shape index	Mean patch shape complexity; equals 1 when all patches are circular and increases as patches become noncircular. MSI□1
LSI	Landscape shape index	Perimeter-to-area-ratio for the landscape as a whole, equals 1 when the landscape consists of a single circular patch and increases as landscape shape becomes noncircular and the amount of internal edge increases. LSI□1
PERIAREA	Mean perimeter to area ratio	Perimeter-to-area-ratio for all landscape patches. PERIARE>0
Diversity indices		<i>Landscape composition</i>
SHDI	Shannon's diversity index	Function between number of different patches and their abundance. SHDI□0
SHEI	Shannon's evenness index	Function between the proportional abundance of each patch type and the number of patch types. 0□ SHEI □1
Interspersion indices		<i>Landscape configuration</i>
IJI	Interspersion and juxtaposition index (%)	Measures the extension to which each patch type is interspersed with all other landscape patch types. 0□ IJI □100

* Acronyms correspond to those used in Fragstats (McGarigal & Marks 1995).

** See Teixidó et al. (2002) for description of the 17 indices.

Data analysis

Ordination: Canonical Correspondence Analysis (CCA, ter Braak 1986) was performed 1) to characterize spatial patterns of LPI, 2) to determine the combinations of indices that were most strongly associated to the different stages, and 3) to investigate the benthic composition related to each of the four stages along the successional gradient. CCA is a multidimensional direct gradient analysis into which regression and ordination have been integrated (ter Braak 1986, ter Braak 1987). The general aim of CCA is to turn out an ordination diagram of samples, species, and environmental variables, which optimally displays how community composition varies as a function of the environment. In this study, LPI were incorporated to CCA as environmental variables. The rules to interpret an ordination diagram are the following: samples and species are represented as points with different symbols, while environmental variables are depicted as arrows (vectors). The ordination axes are constrained to be linear combinations of the environmental variables. The length of an arrow indicates the importance of the variable; the direction points to the maximum value, where the origin of the coordinate system (0,0) represents the mean value of the variable; the angle between arrows provides an approximation of correlation between variables (0° = strongly positive, 180° = strongly negative, 90° = no correlation).

The interpretation of the points in a CCA diagram follows the same principle. Similar entities are close to each other and dissimilar entities are far apart. The occurrence of species and sample points can be ranked along the vector variables by perpendicularly projecting their position and indicates the environmental association of species and sample characteristics, respectively. CCA was considered an adequate multivariate technique for this study because it provides a simultaneous ordination of community composition, photographic samples, and index variables.

Preliminary analysis with detrended correspondence analysis (DCA) showed that the ordination axes were > 3 standard deviation units in length. Thus, the unimodal ordination CCA was more appropriate for the analysis than the linear approach (ter Braak 1987). The initial 17 landscape index variables were used in an exploratory CCA. For mean and standard error values of LPI see Appendix 1 (this publication). There was relatively strong redundancy among some of the landscape indices (variance inflation factor >10). Therefore, these 8 indices were excluded from further CCA calculations because they did not have a unique contribution and their canonical coefficient became unstable in the analysis (ter Braak 1986).

Once the second CCA with the 9 non-correlated indices was completed (Table 3), forward stepwise analysis was performed to choose a subset of LPI. This procedure has the ability to reduce a large set of variables to a smaller set that suffices to explain the variation in species composition. At each step, the analysis reviews all the variables and includes those, which contribute most to the discrimination. The Monte Carlo permutation test using 199 random permutations was used to test the significance of each index variable. For further analysis using univariate methods we considered only these significant indices. The benthic fauna abundance data were fourth root transformed prior to CCA to dampen the effects of dominant species. Only organisms occurring in 3 or more samples (=photographs) were included in the analysis (Appendix 8.4). CCA and DCA were performed using the program CANOCO (version 4.0) (ter Braak & Smilauer 1998).

Univariate methods: In order to elucidate trends in spatial pattern characteristics, Kruskal-Wallis nonparametric analysis was used to test for differences in the subset of LPI grouped by successional stages. Post hoc comparisons of ranks were performed using the Nemenyi test (Sachs 1984). We used nonparametric analysis because most of the data did not follow normality and the number of photographs was not the same per each stage. All the tests were computed using the program STATISTICA (version 5.5, StatSoft).

RESULTS

Ordination

Spatial patterns associated to successional stages

CCA provided a combined ordination of sessile benthic fauna, photographic samples, and landscape index variables (Figs. 3a and 3b). CCA of 112 photograph sites produced eigenvalues of 0.21 ($p < 0.01$) and 0.12 ($p < 0.01$) for axes 1 and 2, respectively (Table 4). Eigenvalues indicate the importance of each axis in relation to species variation (ter Braak 1986). The first two axes of CCA explained 11% of the variation in benthic-fauna data. This high level of unexplained variation is typical of ecological gradient analysis, which may show values $< 10\%$ of variation (ter Braak & Verdonschoft 1995). This is attributable to (unknown) factors not included in the analysis, as well as to the tendency for CCA to explain less variation with an increasingly large number of samples and species, and inherent feature of data with a strong presence/absence aspect (Ohmann & Spies 1998, ter Braak & Verdonschoft 1995).

The first two axes extract 52% of the variance in the landscape indices data. The analysis exhibited a strong fit between the axes and the explanatory indices (canonical correlation coefficients = 0.87 and 0.85, respectively) (Table 4). CCA indicated that the first canonical axis (axis 1) was negatively correlated with cover area (CA= -0.88), landscape shape (LSI= -0.74), mean patch size (MPS= -0.71), and interspersion and juxtaposition indices (IJI= -0.67) (Table 4). Conceptually, these variables describe a gradient from samples belonging to the first stages (R0 and R1) and part of R2 and UD with low patch cover area, low complexity of patch shape, small patch size, and patches poorly interspersed on the positive end of axis 1 (right), to samples belonging mainly to the later stages (R2 and UD) with higher values of these indices on the negative end (left) (Fig. 3a). Evenness (SHEI= 0.10) played a minor role in explaining samples that belonged to R1 and part of UD. The second axis (axis 2) was positively correlated with MPS (0.53) and negatively with mean shape (MSI= -0.52), perimeter to area (PERIAREA= -0.42), and Shannon's diversity indices (SHDI= -0.41) (Table 4). The gradient along axis 2 represents samples mainly from R2 and part of UD and R1 (on the negative side of the axis) with high values of shape complexity and diversity, to samples from R0 and part of R1, R2, and UD with lower values (on the positive side of the axis) (Fig. 3a). Higher values of MPS characterized most of the samples from UD.

Variable	Axes	
	1	2
a)		
Eigenvalues	0.21	0.12
Canonical correlation of axes	0.87	0.85
Cumulative variation (%)		
of taxa data	7.10	11.4
of taxa - landscape pattern index relation	32.8	52.4
b)		
Landscape index variables		
% CA	-0.88	-0.06
MPS	-0.71	0.53
PSSD	-0.55	-0.02
MSI	-0.47	-0.52
LSI	-0.74	-0.40
PERIAREA	0.22	-0.42
SHDI	-0.39	-0.41
SHEI	0.10	0.09
IJI	-0.67	-0.19

Table 4. Summary of Canonical Correspondence Analysis (CCA) of Antarctic benthic fauna for the first two axes (a). List of the LPI variables used in the analysis and their inter-set correlations with the axes (b). See Table 1 for abbreviations.

Forward stepwise selection procedure showed that the best indices ($p < 0.05$) related to benthic-fauna data were cover area (CA), mean patch size (MPS), Shannon's diversity (SHDI), Shannon's evenness (SHEI), interspersion and juxtaposition (IJI), mean shape (MSI), and landscape shape indices (LSI). These 7 variables accounted for 58% of the variance in the benthic fauna data. CA represents 28% of the total variance explained by the analysed landscape indices. The PSSD and PERIAREA indices were not significant in the selection procedure; thus, they were not illustrated in Fig. 3a and not considered for further discussion.

Overall succession structure and composition

The dispersion area of photographic samples over the ordination diagram indicated that variation in benthic composition was greater in the stages R0 and UD than in R1 and R2, respectively (Fig. 3a). The samples from each stage were enclosed by ellipses in Figs. 3a. R0 and UD occurred in extreme positions on the gradient indicating dissimilarity of benthic fauna composition between these stages. However, the overlap of stages showed a similarity in benthic taxa along the succession process mainly between R0-R1 and R2-UD.

The CCA benthic composition ordination diagram (Fig. 3b) shows on axis 1 a gradual trend from benthic fauna associated with disturbed areas (R0) on the right, through fauna associated with early and later successional stages (R1 and R2) in the centre to the undisturbed assemblage on the left. The benthic fauna labelled in Fig. 3b are those taxa whose variance explained by the first two axes exhibited a minimum of 20%. Disturbance by iceberg scouring creates new early-successional areas (R0-R1), which favours the presence of pioneer taxa such as the lollipop-like sponge *Stylocordyla borealis*, soft hydrozoans and bryozoans (*Hydrozoa sp. 3*, *Bryozoa non identified*, and *Camptoplites lewaldi*), bottle brush (*Primnoisis antarctica*) and unbranched colonies of gorgonians (*Primnoella sp.* and *Ainigmaptilon antarcticum*), sabellid polychaetes (*Myxicola cf. sulcata*, *Perkinsiana spp.*, and *Sabellidae non identified*), and a solitary ascidian (*Molgula pedunculata*). Taxa that characterized later stages of succession (R2) were: soft (*Cellaria spp.*) and rigid species of bryozoans (*Cellarinella spp.*, *Paracellaria wandeli*, *Himantozoum antarcticum*, and *Smittoidea malleata*), a demosponge (*Tedania tantula*) and a complex composed of soft bryozoans and "Yellow branches" demosponge. These taxa occurred in areas of higher values for cover area, interspersion and juxtaposition, complex shape, and diversity pattern. The undisturbed assemblage was represented by: volcano-shape hexactinellid sponges (*Rossella nuda/ Scolymastra joubini*), the round demosponges (*Cinachyra barbata* and *C. antarctica*), an irregularly branched

demosponge (“Yellow branches”), the compound ascidians (*Polysyncraton trivolutum* and *Polyclinidae fam. 1*), and a rigid complex of bryozoans composed of different species of *Cellarinella*. Mean patch size was the predominant index of this stage.

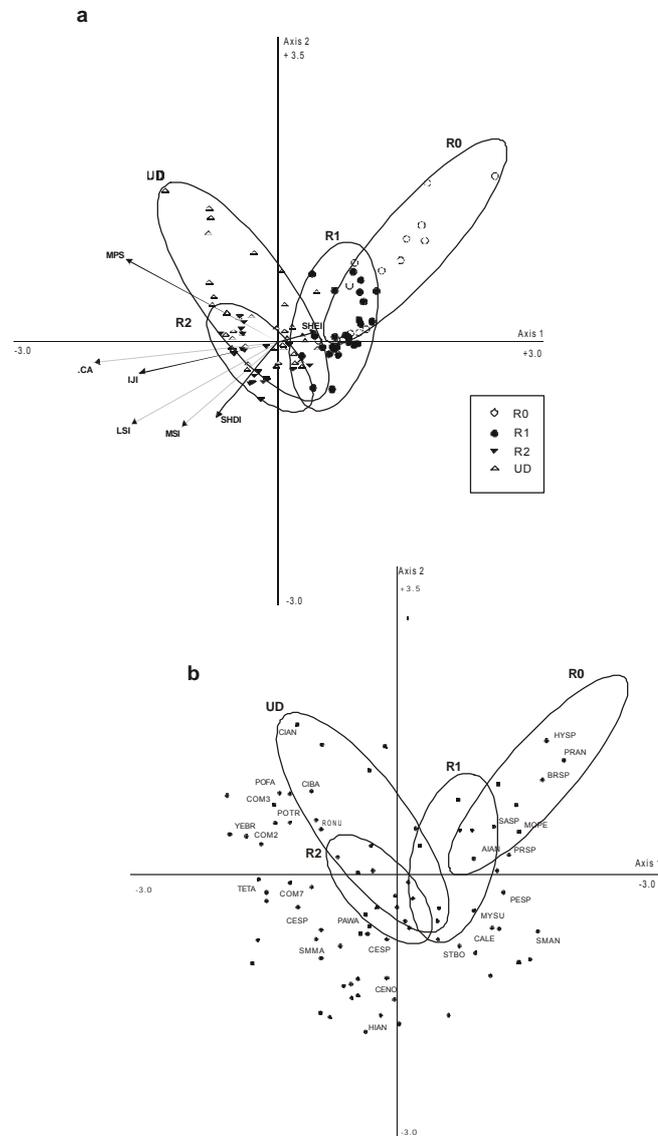


Fig. 3. Ordination of **a)** the samples (each point corresponds to one photograph analysed) and the landscape index variables; and **b)** Antarctic benthic fauna obtained from a Canonical Correspondence Analysis (CCA). Fauna plotted with codes include those taxa whose variance explained exceeded 20% from the first two axes. For each stage, circles are presented according to Fig 3a. Codes are as follows: AIAN, *Ainigmaptilon antarcticum*; BRNI, Bryozoa non identified; CALE, *Camptoplites lewaldi*; CESP, *Cellaria spp.*; CESP, *Cellarinella spp.*; CIAN, *Cinachyra antarctica*; CIBA, *Cinachyra barbata*; COM2, *Cellarinella sp. complex 2*; COM3, Demosponge complex 3; COM7, bryozoan and “Yellow branches” complex 7; HIAN, *Himantozoum antarcticum*; HYNI, Hydrozoa non identified; MOPE, *Molgula pedunculata*; MYSU, *Myxicola cf. sulcata*; PAWA, *Paracellaria wandeli*; PESP, *Perkinsiana spp.*; POFA, *Polyclinidae fam. 1*; POTR, *Polysyncraton trivolutum*; PRAN, *Primnoisis antarctica*; PRSP, *Primnoella sp.*, RONU, *Rossella nuda/ Scolymastra joubini*; SANI, Sabellidae non identified; SMAN, *Smittina antarctica*; SMMA, *Smittoidea malleata*; STBO, *Stylocordyla borealis*; TETA, *Tedania tantula*; YEBR, “Yellow branches”.

Univariate analysis on LPI

Kruskal-Wallis tests showed significant differences for most of the indices among the successional stages. For a better interpretation of the results, diagrammatic representations of the analyses were performed. The homogenous groups of LPI, those that were not significantly different from each other, are indicated (Fig. 4). For mean and standard error values of LPI see Appendix 1.

Cover area and patch size indices

There were large differences in cover area (CA) and mean patch size (MPS) in different successional stages (Fig. 4). Coverage increased abruptly between the early (R0 and R1) and the later stages (R2 and UD), with the highest mean value in R2 (70.5%). Low coverage (<10%) and small patches characterized the early stages. UD exhibited the largest MPS value (52.54 cm²), which increased gradually from early to later stages. The patches from UD partially covered the sea bottom. Stage R2 showed intermediate size patches (38.46 cm²), which covered most of the seafloor.

Patch shape indices

Mean shape (MSI) and landscape shape index (LSI) showed significant differences along the successional stages (Fig. 4). Both indices indicated similar trends in patch shape complexity, from low in the early stages (R0 and R1), to high in advanced stage (R2), through intermediate values in UD. The stage R1 did not follow this tendency for MSI, which shared an intermediate value of 1.26 with UD. The reason of this difference between MSI and LSI in the same stage may result from their different meaning. MSI calculates the average perimeter-to-area ratio for all the patches in the landscape and considering number of patches (NP) in the equation, whereas LSI measures the perimeter-to area ratio for the whole landscape as a whole, as if it were one patch. Then, the intermediate result of MSI for R1 resulted from the low NP and small size of patches, which favoured a higher value. The stage R2 showed the highest mean values for both MSI (1.35) and LSI (7.17), indicating the highest shape patch complexity.

Diversity indices

Shannon's diversity index (SHDI) differed significantly among the stages, whereas the evenness index (SHEI) did not show significant differences (Fig. 4). High values of SHEI result from landscapes where patches are equally distributed among patch types (McGarigal and Marks 1995). The least diverse stage was R0 with the lowest mean value for SHDI (1.12) and SHEI (0.60), whereas the most diverse stage was R2 with the

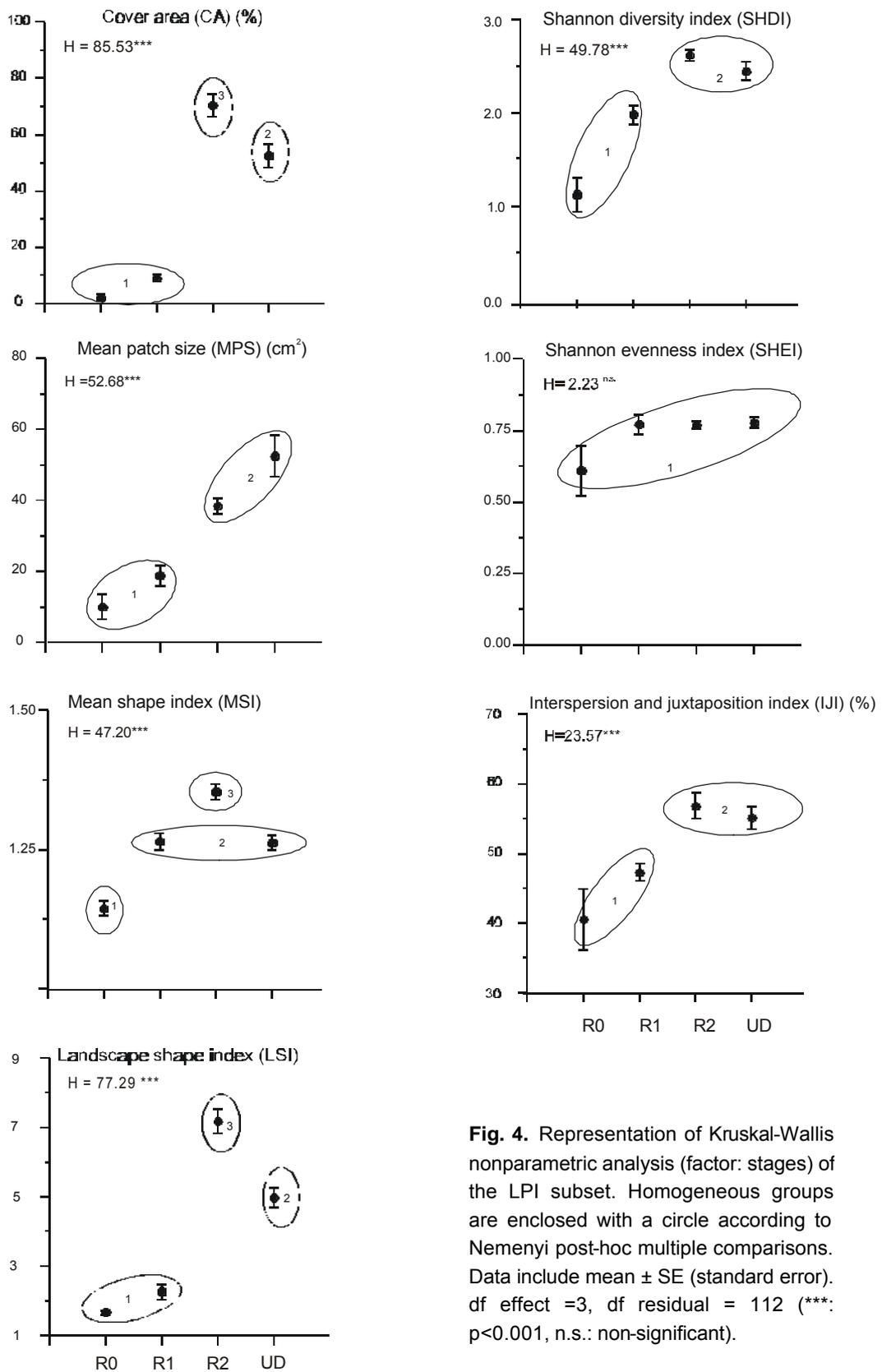


Fig. 4. Representation of Kruskal-Wallis nonparametric analysis (factor: stages) of the LPI subset. Homogeneous groups are enclosed with a circle according to Nemenyi post-hoc multiple comparisons. Data include mean \pm SE (standard error). df effect =3, df residual = 112 (***: $p < 0.001$, n.s.: non-significant).

greatest mean value of SHDI (2.61) and patch types equally distributed (SHEI= 0.60). The early stages (R0 and R1) ranged from areas that were dominated by the same patches and showing low values of SHEI to areas with very few patches but equally distributed (SHEI values of 1). This may be an explanation of the high values and variability of SHEI along these early stages. UD exhibited a high diversity based on SHDI (2.44) and relatively high mean value of SHEI (0.77).

Interspersion indices

Landscapes with high interspersion and juxtaposition index (IJI) values indicate good interspersion within the patch types (e.g., equally adjacent), whereas low values characterise landscapes with poorly interspersed patch types (e.g., disproportionate distribution of patch type adjacencies) (McGarigal & Marks 1995). The early stages (R0 and R1) showed the lowest interspersed patterns (mean value of 40.47 and 47.32 %, respectively), which were significantly different from R2 and UD (56.84 and 55.12 %, respectively) (Fig.4).

Discussion

Spatial patterns from different successional stages after iceberg disturbance

The application of LPI was successful to characterize spatial organization along succession in Antarctic benthic communities. LPI provided comprehensive measurements over different aspects of spatial patterns (patch size and form, diversity, and interspersion) along the different successional stages (from earlier to later recovery stages: R0, R1, R2, and undisturbed assemblage: UD) (cf. Figs. 3a and 4, Table 5). The best predictor of recovery after iceberg disturbance was CA, reflecting great differences along the succession stages. This result agrees with the main conclusions derived from studies on succession over other subtidal marine areas (Grigg & Maragos 1974, Pearson & Rosenberg 1978, Arntz & Rumohr 1982, Dayton et al. 1992, Connell et al. 1997). Overall, our results showed that spatial complexity and diversity increased as succession proceeded. The early stages were mainly characterized by poor coverage of small patches, which showed low complex shapes, were less diverse, and less interspersed. Pioneer sessile taxa (among them: the sponge *Stylocordyla borealis*, the gorgonians *Primnoisis antarctica*, *Primnoella* sp., and *Ainigmaptilon antarcticum*, the bryozoan *Camptoplites lewaldi*, the sabellid polychaetes *Myxicola cf sulcata* and *Perkinsiana* spp., and the ascidian *Molgula pedunculata*) composed these stages. A later stage of succession (R2) exhibited the most complex and diverse pattern. The patches exhibited intermediate size and complex shapes, were highly different in composition, relatively

equally distributed, and well interspersed. Different well-mixed groups of benthic sessile organisms (e.g. sponges, gorgonians, bryozoans, and ascidians) covered most of the sediment in this stage. The UD assemblage was also composed of different well-mixed groups of benthic taxa (represented by the sponges *Rossella nuda*/ *Scolymastra joubini*, *Cinachyra barbata*, *C. antarctica*, “Yellow branches”, complexes of bryozoans of the genus *Cellarinella*, and the ascidians *Polysyncraton trivolutum* and *Polyclinidae fam.1*), which partially covered the sediment. Interspersion and diversity patterns tenuously decreased at this stage. Larger patches did not show high complexity shape patterns as in R2. Our findings using LPI can be compared with abundance and diversity derived from previous studies on iceberg disturbance on polar shelves (Gutt et al. 1996, Conlan et al. 1998), which also reported an increase of abundance and diversity from disturbed to undisturbed areas. Concerning spatial patterns in terrestrial ecosystems, one of the most evident phenomena after disturbances is habitat fragmentation (Wu & Levin, 1994) and heterogeneity across landscape (Turner et al. 2001). For example, large fires in the Yellowstone National Park created an irregular mosaic of burned and unburned vegetation areas (Christensen et al. 1989, Turner et al. 1994), which led to significant changes in vegetation patch size, composition and persistence of species, and diversity (Romme 1982, Turner et al. 1997).

Table 5. Synthesis of LPI values and the major structural differences among the stages analysed.

Stages	Description of LPI values	Spatial patterns and cover area
		Low spatial complexity and diversity patterns
R0	Low: CA, MPS, MSI, LSI, SHDI, and IJI Intermediate: SHEI	Few groups of benthic sessile organisms covering barely the bottom sediment: - low number and small size of patches, which contributed to the low coverage - low complex shapes and patch types poorly interspersed - few patch types and relatively equally distributed
		Intermediate spatial complexity and diversity patterns
R1	Low: CA, MPS, LSI, and IJI Intermediate: MSI and SHDI High: SHEI	Different groups of benthic sessile organisms covering barely the bottom sediment: - relatively low number and small size of patches. - relatively intermediate complex shapes and patch types equally adjacent - different patch composition and equally distributed
		Highest spatial complexity and diversity patterns
R2	Intermediate: MPS, SHEI, and IJI High: CA, MSI, LSI, and SHDI	Different well-mixed groups of benthic sessile organisms covering the major part of the bottom sediment: - relatively high number and intermediate size of patches. - complex shapes and patch types equally adjacent - highly different patch composition and equally distributed
		High spatial complexity and diversity patterns
UD	Intermediate: CA, MSI, LSI, SHEI, and IJI High: MPS and SHDI	Different well-mixed groups of benthic sessile organisms covering partially the bottom sediment: - high number and large size of patches. - high complex shapes and patch types equally adjacent - highly different patch composition and equally distributed

Frequency of ice disturbance on the Antarctic shallow hard substratum benthic community is related to exposure and depth (Dayton *et al.* 1970, 1974, Dayton 1990, Arntz *et al.* 1994, Barnes 1995). Dayton *et al.* (1970) identified benthic assemblages following a depth gradient: from the shallowest zone (above 15 m) devoid of sessile organisms, poorly structured, and controlled by physical factors (due mainly to ice scouring and anchor-ice formation), to the deepest zone (below 33m) inhabited by slow-growing sponge species, with high diversity and structural complexity and controlled by biological factors. Garrabou *et al.* (2002) using LPI found a benthic organization pattern with depth in Mediterranean hard bottom communities. In the “deep” communities (below 11 m), species with low growth rates exhibited the greatest spatial pattern complexity. The authors argued that a decrease in dynamics with depth might enhance high diversity and thus complex spatial patterns. Margalef (1963) noted that the lower the degree of community “maturity”, the greater the influence of abiotic factors to resident population dynamics. Following a horizontal gradient (this study), we think that similar ecological structuring factors may be shaping the different observed successional patterns, with biological interactions such as competition for space, predation, and epibiotic relationships (Dayton *et al.* 1974, Gutt and Schickan 1998) being more important during the late stages of succession (R2 and UD).

Relating spatial patterns with recolonisation processes

The existence of propagules is a fundamental determinant of successional patterns both for marine and terrestrial habitats (Clements 1916, Connell & Keough 1985, Pickett *et al.* 1987) and might be especially sensitive to the combination of both disturbance intensity and its spatial extent (Turner *et al.* 1998). Sessile organisms may invade open patches by i) vegetative regrowth of existing colonies at the edge of the disturbed area and ii) settlement of propagules produced vegetatively (as detached buds or fragments broken off survivors) or iii) sexually (as larvae) outside of the affected area (see Sousa 2001). Iceberg scouring removes completely the benthic fauna over large areas. In these areas recolonisation by larvae may be more important than vegetative regrowth and/or asexual propagule settlement (Connell & Keough 1985). In our study, pioneer species (*S. borealis*, *P. antarctica*, *Primnoella sp.*, *A. antarcticum*, *C. lewaldi*, *M. cf. sulcata*, and *M. pedunculata*) appeared at high densities during the early stages (Fig. 3b) as described previously (Gutt *et al.* 1996). Brooding of larvae has been identified as the reproduction mechanism of these species (Cancino *et al.* 2002, Orejas 2001, Sarà *et al.* 2002) and to be the dominant modus of deep-dwelling polar invertebrates (Dell 1972, Picken 1980, Arntz *et al.* 1994, Pearse *et al.* 1991), with very slow embryonic and larval development

and low dispersal capabilities (Clarke 1982, Hain 1990, Pearse et al. 1991). This short-distance dispersal (philopatry) of larvae may be an explanation of the patchy distribution of these species along the early stages of recovery, in particular, and to the Weddell Sea benthos in general (Barthel & Gutt, 1992, Gutt & Piepenburg 1991, Starmans et al. 1999). However, the ascidian *Molgula pedunculata* and the sabellid polychaete *Perkinsiana cf. littoralis* exhibit higher dispersal capabilities due to gametes freely spawn without parental care (Svane & Young 1989, Gambi et al. 2000). Based on mathematical models, habitat instability such as that caused by iceberg scouring favours recolonization of species with long distance dispersal (Lytle 2001, McPeck & Holt 1992). Peck et al. (1999) described three major mechanisms of recolonization after iceberg impacts on shallow soft sediments at different timescales: locomotion of motile organisms, advection of meiofauna, and larval dispersal of large bivalves.

Overall, CA and MPS increased during the successional process (cf. Fig. 4). The ecological implication of these findings can be related to the “facilitation mode” between earlier and subsequent colonizing species proposed by Connell & Slatyer (1977). As already mentioned, the first colonizing species (apart from mobile invaders) are assumed to originate from sexual production when larvae settle. After this event, vegetative regrowth and asexual reproduction by fragmentation will be more significant in maintaining and increasing the area covered and the size of organisms. From our results we can suggest that the net effect of earlier on later species favours the recruitment and growth of these species. However, it remains poorly understood how the “continuum” of interactions within the successional sequence affects the mechanisms of succession (McCook 1994).

Epibiotic relationships have been described as an important factor structuring Antarctic benthic communities (Dayton et al. 1970, Gutt & Schickan 1998). These relationships would enhance a greater coverage of benthic organisms. Moreover, some branching colonies of the cellarinellid bryozoan species occurred in clumps and are reported to originate from broken colony fragments (Winston 1983). This kind of distribution and its rapid reproduction by fragmentation might contribute to the high coverage and intermediate size of colonies in the later stage (R2) (cf. Fig. 4). However, space can be an important limiting resource for sessile marine organisms (Branch 1984, Buss 1986). It seems likely that space competition pressures explain the decrease in CA and shape complexity indices (MSI and LSI) in the undisturbed assemblage (UD). This does not

exclude that sessile organisms compete for space in the advance successional stage (R2). As described earlier, different well-mixed groups of benthic organisms were present in the later stage (R2), with high coverage of branching species of bryozoans and demosponges with irregular forms. In contrast, these branching species were not often found in the undisturbed assemblage where massive organisms with simple forms, such as hexactinellids, round demosponges, and ascidians prevailed. We hypothesize that the replacement of complex forms by more simple forms in the undisturbed assemblage may be interpreted as a response to competition for space. These simple-form species grow very slowly (Dayton 1979) and may be superior competitors over other benthic organisms with more complex form patterns.

In addition, chemical strategies should be also considered as a factor in competition for space. Chemical defense mechanisms have been suggested to mediate competitive interactions among many coral reef organisms (Thacker et al. 1998) and influence patterns of succession and community structure (Atrigenio & Aliño 1996). Becerro et al. (1997) observed a habitat-related variation in toxicity within the sponge *Crambe crambe*, finding high toxicity in a space-saturated community dominated by slow-growing animal species. They explained this modulation of toxicity by differences in space competition pressures. It may be that differences of turnover, growth rates, chemical mechanisms, and competitive/ predatory interactions best explain the observed cover and form patterns along Antarctic succession.

We acknowledge that a variety of factors affect the observed successional sequences, including species-specific access to the site, hydrographic conditions, habitat suitability, chemical defenses, and species interactions (competition, predation). Studies on deep Antarctic successional trajectories has received little attention and it remains challenging to identify the factors, which control dynamics and spatial patterns at multiple scales.

“Dynamic Equilibrium Hypothesis” and spatial patterns

Despite the complexity of the entire successional process in the Antarctic benthos, we have identified some consistent and repeatable patterns of succession. Overall, with the exception of patch size, there was an increment of coverage, shape complexity, diversity, and juxtaposition patterns from early stages through undisturbed assemblages to late stages of succession (cf. Figs. 3a and 5). We propose that the benthos composition in the Weddell Sea and the exhibited spatial patterns might reflect the “dynamic equilibrium hypothesis” (Huston 1979, 1994). When disturbance is greater (or more frequent),

populations of certain slow-growing species will not recover after disturbance and fast-growing species (pioneer or r-type) will take over. Under low disturbance regimes the most competitive species with slow growth rates (K-type) will finally exclude other species. We believe that assemblages dominated by the long-lived hexactinellid species and the demosponge *C. barbata* support the idea that the absence of disturbance in Antarctic benthos can ultimately lead to a decrease in species diversity at small spatial scales (1m²). It is important to note that despite the decrease of diversity and interspersion indices, which may provide insights into interspecific competitive interactions, we did not find significant differences between the advanced stage (R2) and the undisturbed assemblage. In contrast, Teixidó et al. (2002) found greater differences of those indices when comparing the undisturbed assemblages among individual stations. We attribute the “non-difference” in the present study to the biological variability of the whole undisturbed assemblage, which partially reduces the role of these sponges. We further believe that the asexual reproductive mode “budding” reported for *R. racovitzae* and other sponges (e.g, *C. antarctica*) (Dayton 1979, Barthel et al. 1990, Barthel et al. 1997) with limited dispersability and the chemical components found in these sponges (McClintock & Baker 1997) are directly associated with competitive superiority under low-disturbance conditions, and might result in the dominance of monospecific patches of long-lived, low-growing sponges with great size, simple forms, and high degree of aggregation.

Understanding the effects of large disturbances causes concern for conservation and Antarctic benthic diversity considering potential implications of global climate change. Although the co-existence of many different successional stages within the impacted areas favours diversity at a larger spatial scale (Gutt and Piepenburg 2003), it is important to emphasize that adaptation of Antarctic benthos to iceberg disturbance developed over a long evolutionary period (Clarke and Crame 1992). Gutt (2000) estimated a rate of one disturbance per square metre of the seafloor every 320 years along the depth range of the shelf (<500m). These low disturbance frequencies were based on known growth rates of pioneer organisms (Brey et al. 1999) and estimated community development times (Gutt 2000). However, in view of a possible increase of iceberg-calving frequency (Lazzara et al. 1999, Rignot & Thomas 2002), and the slow growth of many species in the Antarctic benthic ecosystem, the question arises of how resilient these communities are. If global warming continues, Antarctic benthic communities might be exposed to more frequent iceberg disturbance over a short period of time to which they are not adapted. With this increase of frequency and/or intensity, the Antarctic benthos might not recover to its prior state and nor return to the long-lived mature community that we found in the undisturbed assemblage. We emphasize that further studies of long-term successional process

affecting the structure and dynamics of Antarctic benthic communities are urgently needed

Conclusions

Large natural disturbances have been shown as important processes affecting the structure and dynamics of both marine and terrestrial communities. Previous studies have shown the relevance of ice disturbance for the structure of Antarctic benthos (Dayton et al. 1970, Gutt et al. 1996, Peck et al. 1999, Gutt & Starmans 2001). Here we have reported the suitability of landscape indices to describe spatial patterns of Antarctic benthic communities, which provide new and valuable insights into the structural organization along the succession process. Overall, the results illustrate that as succession proceeds spatial complexity patterns increase. Moreover, we have pointed out the importance of propagules and their dispersal abilities, growth rates, chemical defense, and competition in determining Antarctic benthic successional patterns.

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Appendix I. Means \pm SE of LPI along successional stages in the Antarctic benthos.

Landscape indices	R0 (n =21)	R1 (n =28)	R2 (n =21)	UD (n =42)
CA (%)	1.8 \pm 0.5	8.9 \pm 1.2	70.5 \pm 4.1	52.5 \pm 4.2
MPS (cm ²)	8.6 \pm 3.1	18.8 \pm 2.9	38.4 \pm 2.2	52.5 \pm 5.7
PSSD (cm ²)	3.7 \pm 1.0	30.1 \pm 5.6	154.9 \pm 23.7	127.6 \pm 14.3
PSCV (%)	68.9 \pm 19.1	170.1 \pm 16.2	384.8 \pm 44.0	267.1 \pm 23.9
NP	21.3 \pm 5.2	63.5 \pm 8.8	173.2 \pm 12.2	110.2 \pm 8.9
TE (cm)	198.2 \pm 51.9	730.7 \pm 80.1	2412.7 \pm 119.8	1683.5 \pm 94.2
MSI	1.14 \pm 0.01	1.26 \pm 0.01	1.35 \pm 0.01	1.26 \pm 0.01
AWMSI	1.22 \pm 0.03	1.41 \pm 0.04	2.71 \pm 0.26	1.97 \pm 0.15
LSI	1.66 \pm 0.05	2.26 \pm 0.21	7.16 \pm 0.35	4.9 \pm 0.27
PERIAREA	2.01 \pm 0.27	2.52 \pm 0.23	2.29 \pm 0.10	1.87 \pm 0.12
SHDI	1.12 \pm 0.18	1.97 \pm 0.1	2.61 \pm 0.06	2.44 \pm 0.09
SIDI	0.51 \pm 0.07	0.75 \pm 0.03	0.86 \pm 0.01	0.82 \pm 0.02
MISDI	0.96 \pm 0.15	1.59 \pm 0.10	2.04 \pm 0.08	2.01 \pm 0.11
SHEI	0.60 \pm 0.08	0.77 \pm 0.03	0.76 \pm 0.01	0.77 \pm 0.01
SIEI	0.63 \pm 0.09	0.82 \pm 0.03	0.89 \pm 0.01	0.86 \pm 0.02
PR	5.9 \pm 1.12	14.4 \pm 1.16	30.7 \pm 1.22	24.5 \pm 1.41
IJI (%)	40.47 \pm 4.4	47.3 \pm 1.2	56.83 \pm 1.8	55.12 \pm 1.6

* Abbreviations of the indices used in the CCA and univariate analyses (see text); PSCV: Patch size coefficient variation, NP: Number of patches, TE: Total edge, AWMSI: Area weighted mean shape index, SIDI: Simpson's diversity index, MISDI: Modified Simpson's diversity index, SIEI: Simpson's evenness index, and PR: Patch richness.

Publication III

Succession in Antarctic benthos after disturbance: species composition, abundance, and life-history traits

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Succession in Antarctic benthos after disturbance: species composition, abundance, and life-history traits

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Abstract

The response of an Antarctic benthic community to disturbance was investigated using underwater photographs (1m² each) on the southeastern Weddell Sea shelf. This study i) characterizes coverage and abundance of sessile benthic fauna, ii) describes faunal heterogeneity using ordination techniques and identifies “structural species” of each successional stage, iii) analyses changes of growth-form patterns, and iv) relates the life-history traits of “structural species” to differences in distribution during succession.

We observed changes in the occupation of space of benthic organisms along the successional stages. Uncovered sediment characterized the early stages ranging from 98% to 91% of the coverage. The later stages showed high (70.5%) and intermediate (52.5%) values of benthic coverage, where demosponges, bryozoans, and ascidians exhibited high abundance. Several “structural species” were identified among the stages, and information is provided on their coverage, abundance, and size. Early stages were characterized by the presence of pioneer taxa, which only partly covered the bottom sediment but were locally abundant (e.g., the bryozoan *Cellarinella spp.* and the gorgonian *Primnosis antarctica* with a maximum coverage of 13% and 3%, and 51 and 30 patches m⁻², respectively). Soft bush-like bryozoans, sheet-like sabellid polychaetes, and tree-like sponges, gorgonians, bryozoans, and ascidians represented the first colonizers, which are characterized by faster growth and higher dispersability than later ones. Mound-like sponges and ascidians and also tree-like organisms with a long-life span and different reproductive strategies defined the late stages. We conclude by comparing the selected “structural species” and relating their life history traits to differences in distribution during the course of Antarctic succession.

Key words: Antarctic, benthic communities, disturbance, growth forms, life history traits, succession, underwater photography, GIS

Introduction

Knowledge on the abundance, spatial distribution, and diversity of species within a community is fundamental to understand ecosystems (Sousa 1980, Paine & Levin 1981, Connell et al. 1997, Newell et al. 1998). Natural disturbance is widely recognized as an important determinant of the occurrence and abundance of species (Dayton 1971, Pickett & White 1985, Huston 1994, Paine et al. 1998, Sousa 2001). Disturbance effects on species may depend on their life histories and the dispersal and recruitment patterns of their offspring (e.g., Grassle and Grassle 1973, Sousa 1980, Connell & Keough 1985, Giangrande et al. 1994, Hughes & Tanner 2000).

The unusually deep continental shelf of the Weddell Sea exhibits locally a complex three-dimensional community with intermediate to high diversity, locally extreme high epifaunal biomass, and patchy distribution of organisms (Gutt & Starmans 1998, Gili et al. 2001, Teixidó et al. 2002, Gerdes et al. 2003). The fauna in this area is dominated by a large proportion of benthic suspension feeders such as sponges, gorgonians, bryozoans, and ascidians, which locally cover the sediment (Gutt & Starmans 1998, Starmans et al. 1999, Teixidó et al. 2002). Variations in the abundance of these “structural species” (*sensu* Huston 1994) are critical to the organization of the whole community. The major disturbance affecting the benthos of this deep continental shelf is the grounding and scouring of icebergs (Gutt et al. 1996, Gutt & Starmans 2001, Knust et al. *in press*). They severely damage large areas of the seafloor, affect the physical and biological environment by removing the substrate and eradicating benthic life (Gutt et al. 1996, Gutt 2000).

Studies at all scales of time and space are necessary to understand both terrestrial and marine ecosystems (Levin 1992). The possibility to study with great detail species abundance of Antarctic benthos may allow to extrapolate and elucidate general patterns at larger scales, which are of fundamental interest to understand the response of this community to environmental changes. The impact of iceberg scouring in the southeastern Weddell Sea has been relatively well studied; from meio- (Lee et al. 2001) to macrobenthos and fish (Gutt et al. 1996, Brenner et al. 2001, Gutt & Starmans 2001, Gerdes et al. 2003, Gutt & Piepenburg *in press*, Knust et al. *in press*). However, despite the importance of “structural species” dwelling on the shelf of the Weddell Sea, which create dense aggregations (Gutt & Starmans 1998, Teixidó et al. 2002), indicating their structural importance in community organization, information is scarce about their abundance and coverage at small spatial scale (1m²). Thus, small spatial scale data will

greatly contribute to understand the process underlying the occupation of space along succession in Antarctic communities.

The abundance of morphological strategies of marine sessile clonal organisms (built up of modules-polyps or zooids) is predicted to vary in function of disturbance frequency (both biotic and abiotic), food supply, and light (see review by Jackson 1979, Connell & Keough 1985, Hughes & Jackson 1985). For example, available substrata after disturbance will be colonized in the first place by stoloniferous or runner-like morphology, which has been interpreted as a fugitive strategy, with early age of first reproduction, high fecundity, rapid clonal growth, and high mortality among modules (Jackson 1979, Coates & Jackson 1985, Sackville Hamilton et al. 1987). Other growth forms such as sheets, mounds, and trees characterize areas with low disturbance levels due to predicted higher competitive ability, lower growth rates, and lower recruitment rates compared to runner forms (Jackson 1979, Buss 1979, Karson et al. 1996).

The life history of an organism can be defined as “the schedule of events that occurs between birth and death” (Hall & Hughes 1996). Life-history theory predicts patterns of somatic and reproductive investments under different regimes of mortality (Stearns 1977, 1992), but is highly biased towards unitary (solitary) organisms. Life-history features are among the most important determinants of community structure in fluctuating environments, determining long-term patterns of abundance (Giangrande et al. 1994). Variations among life histories in both modular and solitary organisms are associated with reproduction and body size, e.g., age and/or body size at sexual maturity, sex ratios, and the compromise of number, size, protection, and survival of the offspring (Stearns 1992, Hall & Hughes 1996). Knowledge of benthic organism life-history traits thus provide insights in the understanding of succession structure and dynamics in Antarctic benthos.

In this study, we examine changes in composition of an Antarctic benthic community through successional stages after iceberg scouring. We first provide quantitative data on changes in coverage and abundance among different taxonomic benthic categories. Second, we describe faunal heterogeneity using ordination techniques and select “structural species” for each stage, indicating their specific coverage, abundance, and size. Third, we examine changes in growth-form patterns and their occupation of open space along succession. Finally, we conclude by comparing the selected “structural species” and relating their life history traits to differences in distribution during the course of succession. This publication is part of a larger study focused on successional processes after iceberg disturbance (Teixidó et al. *submitted*).

Material and Methods

Study area

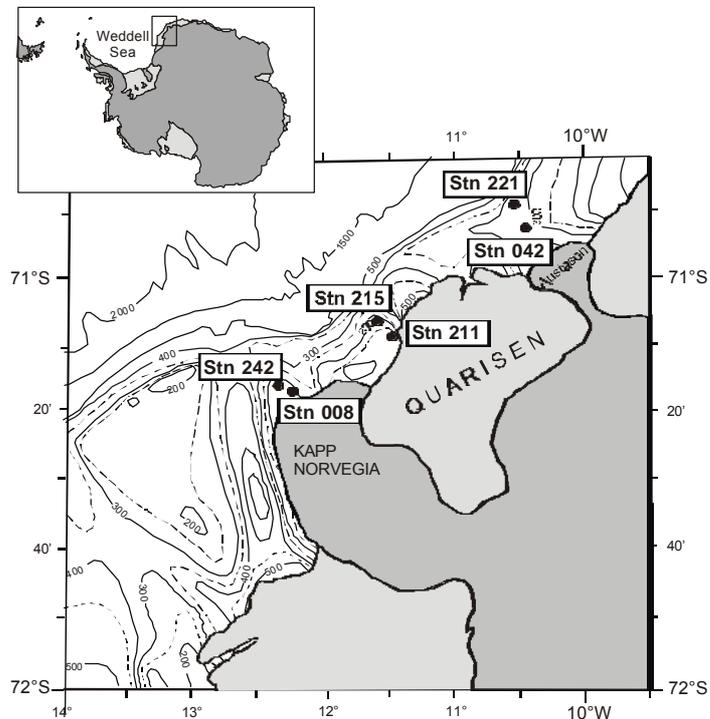


Fig. 1. Photographic stations in the southeastern Weddell Sea (Antarctica) (subsection of chart AWI BCWS 553).

Kapp Norvegia is located in the southeastern Weddell Sea (Fig. 1), where the continental shelf is relatively narrow (less than 90 km), at depths of 300-500 m (Carmack & Foster 1977, Elverhøi & Roaldset 1983). Seasonal sea ice covers the continental shelf and extends beyond the continental break (Tréguer & Jacques 1992), but coastal polynyas of varying size may occur (Hempel 1985). Water temperature close to the seafloor is low and very constant throughout the year, ranging from -1.3 °C to -2.0 °C (Fahrbach et al. 1992). There is a marked summertime peak in primary

production (Nelson et al. 1989, Gleitz et al. 1994, Park et al. 1999), reflected by the organic matter flux from surface waters to the seabed (Bathmann et al. 1991, Gleitz et al. 1994). Hydrodynamics affect food availability (e.g., resuspension, lateral transport) and determine sediment characteristics such as grain size and composition, which are of ecological relevance for benthic communities (Dunbar et al. 1985, Gutt 2000).

Benthic communities and photosampling: We identified three stages of recolonisation (from younger to older: R0, R1, R2) and an undisturbed assemblage (UD), defined previously by Gutt & Starmans (2001). The stages differ in faunistic composition and abundance and features of the seabed relief. They represent successional stages after iceberg disturbance toward the final slow-growing hexactinellid sponge stage (Dayton 1979, Gatti 2002).

Photographic records of the seafloor were obtained during the expeditions ANT XIII/3 and ANT XV/3 on board R/V 'Polarstern' during the austral summers of 1996 and 1998 (Arntz & Gutt 1997, 1999), within the Ecology of the Antarctic Sea Ice Zone programme (EASIZ) of the Scientific Committee on Antarctic Research (SCAR). A 70-mm underwater camera (Photosea 70) with two oblique strobe lights (Photosea 3000 SX) was used at 6 stations (depth range: 117- 265 m) (Fig. 1). At each station sequences of 80 vertical colour slides (Kodak Ektachrome 64), each covering approximately 1m² of the seabed, were taken at evenly spaced time intervals along a transect. The optical resolution was around 0.3 mm. At each stage (from R0 to UD), 7 photographs were studied and processed. In total, an area representing 112 m² of the seafloor was analysed (Table 1).

Table 1. List of the 6 photographic stations in the southeastern Weddell. 7 photographs were analysed along the 3 stages of recolonisation (from younger to older: R0, R1, R2) and the undisturbed assemblage (UN), wherever these occurred.

Stations	Depth (m)	Identified assemblages			
		R0	R1	R2	UD
008	171-173	7	7	7	7
042	260-243	-	-	-	7
211	77-117	-	7	-	7
215	167-154	7	-	7	7
221	261-270	7	7	-	7
242	159-158	-	7	7	7
N° photos		21	28	21	42

Image analysis: Each photograph was projected on an inverse slide projector and all distinguishable patch outlines were traced onto an acetate sheet at a map scale of 1:5. The drawings were scanned (100 dpi) and imported into the Arc/View 3.2 (© ESRI) geographical information system (GIS) where they were spatially referenced. Arc/View routine procedures were used to label all the patches. The result of a GIS process was an image related to a database table, which contained information on area, perimeter, and taxa identifier. Each individual patch was assigned to different categories (e.g., species, cluster of species) and its information was measured for each photograph. Areas of uncovered substrate were also reported.

Identification: Mega-epibenthic sessile organisms, approx. > 0.5 cm in body size diameter, were identified to the lowest possible taxonomic level by photo interpreting

following Thompson & Murray (1880-1889), Discovery Committee Colonial Office (1929-1980), Monniot & Monniot (1983), Hayward (1995), and Sieg & Wägele (1990).

We recognized a total of 118 sessile organisms and sediment cover categories (see Appendix 8.4). These included species/genus (106), phylum (5), “complex” (7), and substratum (5). Within the species/genus category some unidentified sponges (e.g., “Yellow Branches”) were named according to Barthel & Gutt (1992). Irregular masses composed by matrices of bryozoans, demosponges, and gorgonians of small size and similar filamentous morphology were assigned to one of the seven “complex” cover classes.

Data analysis

Benthic coverage and abundance: Within each stage, we calculated both sessile organism and substrate coverages and number of patches (NP). The cover of each taxonomic group was calculated by summing up the areas of each patch and dividing the total by the number of photographs. NP was counted as the sum of patches per photograph and divided by the number of photographs.

Community analysis and “structural taxa”: Taxonomic composition among photographic “samples” was compared using the Bray-Curtis similarity coefficient (Bray & Curtis 1957) of fourth-root transformed sessile benthic coverage. Benthic taxa with less than 2 % of the total coverage were excluded to minimize the bias caused by rare taxa (Field et al. 1982). Non-metric multidimensional scaling (MDS, Kruskal & Wish 1978) was applied to the similarity composition matrix to order the photographic samples in a two-dimensional plane. Low stress values (<0.20) indicate a good representation and little distortion of samples in the two-dimensional ordination plot (Clarke 1993). The analysis was also carried out with abundance data (NP) (fourth-root transformed and considering taxa present in 3 or more samples). The MDS ordination plot was essentially the same as in the former MDS for benthic coverage and for this reason is not presented in this study.

Representative species for each stage were determined with the similarity percentage procedure (SIMPER, Clarke & Warwick 1994). The analysis indicates the contribution of each species to the average similarity within a group. The more abundant a species is within a group, the more it will contribute to the intra-group similarity. As in MDS analysis, the coverage of benthic fauna was fourth-root transformed and taxa occurring in < 2% of

the samples were omitted. Moreover, complex categories (7) and taxa identified at coarse taxonomic level (5) (see Appendix 8.4) were also excluded.

Growth form: The 118 sessile benthic cover categories were grouped into four growth forms in order to search for patterns of CA, NP, and mean patch size (MPS) through succession. The growth forms considered were bush, sheet, tree, and mound (see Table 2 for a description of each growth form). This classification was based on previous studies on clonal organisms in coral reefs (e.g., review by Jackson 1979, Connell & Keough 1985). This categorization takes into account relevant ecological strategies followed by benthic species in occupying space on rocky benthic habitats. The benthos in the Weddell Sea locally presents different stratum levels of organisms. Therefore, it should be considered that the nature of the images (vertical to the seabed) could reduce the contribution of the runner-like forms to the total coverage because other organisms may cover these forms. The bryozoan *Camptoplites tricornis* exhibited a runner growth form but it was the only species of this category; for that reason it was classified into the bush form, which appear as the most similar.

Table 2. Description of growth forms used in this study.

Growth form	Description
Bush	Upright forms branching from the base, mainly flexible hydrozoans and bryozoans; with a restricted area of attachment to the substratum
Sheet	Encrusting species of sponges, bryozoans, sabellids, and ascidians growing as two dimensional-sheets; more or less completely attached to the substratum
Tree	Erect species of sponges, gorgonians, bryozoans, and ascidians, more or less branched; with a restricted area of attachment to the substratum
Mound	Massive species of sponges, anemones, ascidians, and pterobranchs with extensive vertical and lateral growth; attached to the substratum along basal area

CA, NP, and MPS were referred to the sessile benthic organisms and sediment coverage was not considered. CA and NP were calculated as previously mentioned but referring to the growth-form category. MPS was reported as the size of patches divided by the number of patches within the considered category. Kruskal-Wallis nonparametric analysis was used to test for differences in growth-form patterns among successional stages. Post-hoc comparisons of ranks were performed using the Nemenyi test (Sachs 1984). We used nonparametric analysis because most of the data did not follow normality after different transformations.

Both MDS and SIMPER analyses were performed using the PRIMER software (version 5) (Clarke & Gorley 2001). Kruskal-Wallis test was computed using the program STATISTICA (version 5.5, StatSoft).

Life-history traits: We summarized from available data in the literature the information on growth, estimated age, and reproduction modus among the “structural taxa” occurring through the successional stages.

RESULTS

Patterns of benthic coverage and abundance

Uncovered sediment characterized R0 with a mean value of 98.2 % and few benthic taxa (Fig. 2). Bryozoans, polychaetes, gorgonians, and ascidians contributed to the low benthic cover of the seafloor with a mean value of 0.5, 0.5, 0.3, and 0.1 %, respectively, whereas polychaetes showed higher NP (mean value of 8 patches m^{-2}) than bryozoans (mean value of 3 patches m^{-2}). Similarly R1 exhibited a high coverage of sediment (mean value of 91 %) (Fig. 2). Bryozoans, gorgonians, “complex category”, demosponges, polychaetes, and ascidians showed 3.8, 1.5, 1.4, 0.5, 0.5, and 0.4 % of coverage, respectively. Mean values of NP ranged from 38 (bryozoans) through 11 (gorgonians) to 2 (ascidians) patches m^{-2} . The highest mean of benthic cover area (70.5 %) and NP (173 patches m^{-2}) occurred in R2, whereas uncovered sediment declined to approx. 29.5% (Fig. 2). Mean cover percentage fluctuated from 36.1% (“complex category”), to 5% (demosponge) and 0.8 % (hexactinellids), whereas bryozoans with 24% of cover area exhibited the highest mean value of NP (76 patches m^{-2}). Demosponges (35 patches m^{-2}) and ascidians (32 patches m^{-2}) also showed a high NP. In UD, the space covered by benthic organisms was approx. 53 % (Fig. 2). “Complex category”, demosponges, and bryozoans accounted for 16.7, 14.1, and 11.1% of benthic cover area, respectively. Bryozoans, demosponges, and ascidians exhibited high NP (31, 27 and 29 patches m^{-2} , respectively). Hexactinellids showed comparatively moderate values for both mean cover area (3.1 %) and NP (4 patches m^{-2}).

Community analysis and “structural taxa”

The MDS ordination showed a gradual change in the benthic composition among samples from different successional stages (Fig. 3). Faunal dissimilarity was higher in the early stages (R0 and R1) with larger dispersion of samples than in the later stages. However, there was an overlap of samples mainly between R0-R1 and R2-UD indicating similarity in benthic taxa through successional stages. Among the samples from the UD stage 7 were grouped apart. These samples belonged to St. 211 dominated by *Cinachyra barbata* (demosponge) and hexactinellids.

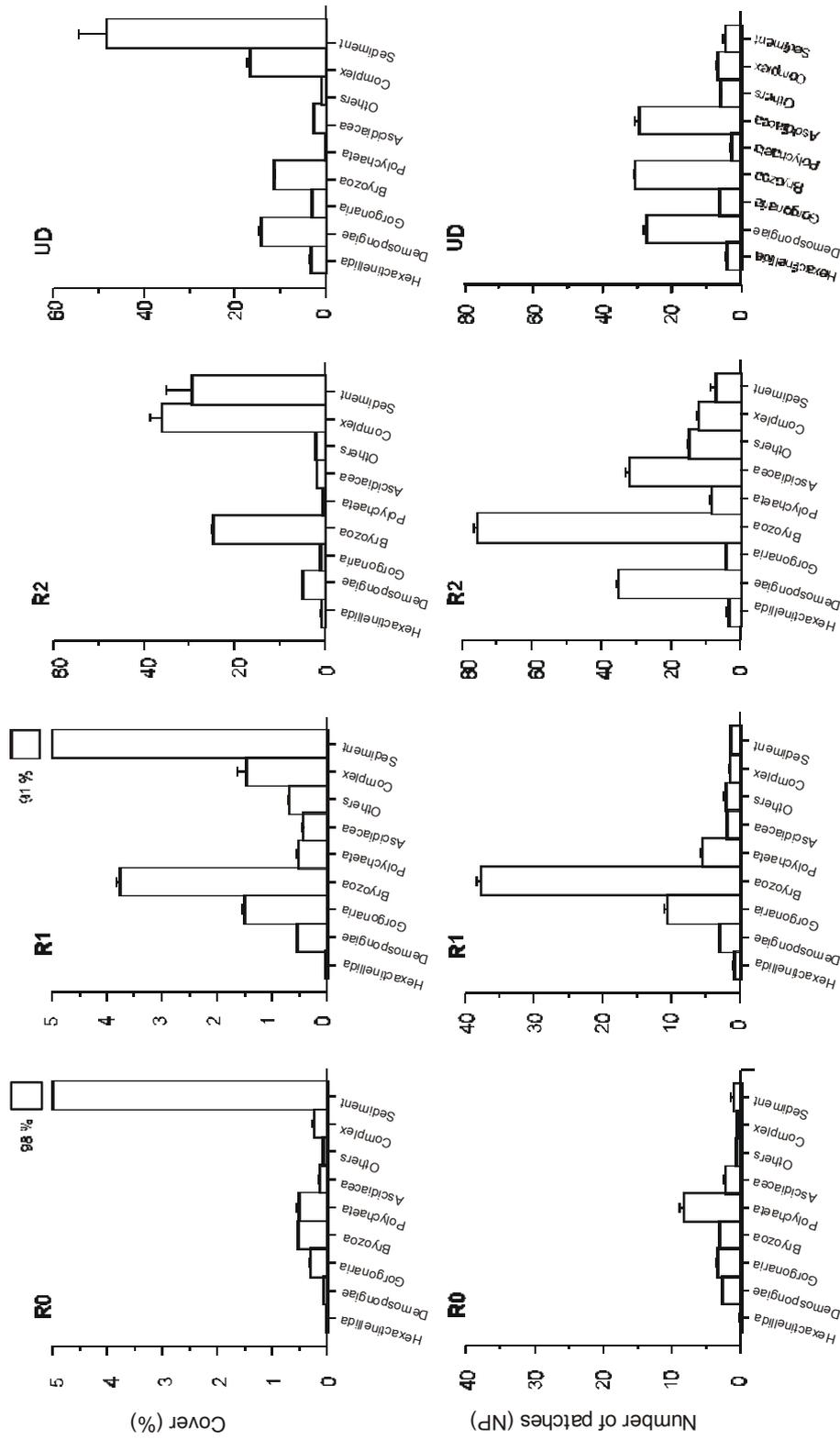


Fig. 2. Cover percentage and number of patches (mean \pm SE) of different categories through successional stages. * Others: in R0 and R1: Hydrozoa (0.07 and 0.6 %); in R2: Hydrozoa, Actinaria, Holothuroidea, and Pterobranchia (0.8 %); in UD: Hydrozoa, Actinaria, Holothuroidea, and Pterobranchia (0.8 %).

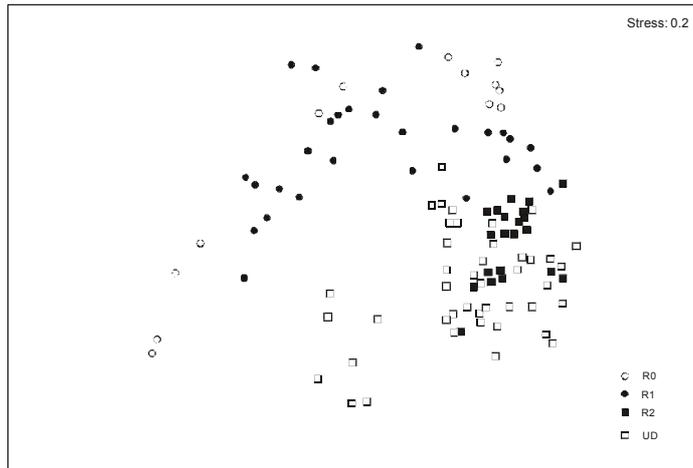


Fig. 3. MDS diagram of photographic sample similarity according to benthic taxa composition through the successional stages.

“Structural taxa” that characterized the different successional stages are shown in Table 3. The patchy distribution of most of the fauna is evident by comparing the mean value for both CA and NP and their extreme values. The most abundant taxa in R0 were the sabellid polychaetes (*Myxicola cf. sulcata* and *Perkinsiana spp.*), the solitary ascidian *Molgula pedunculata*, the lollypop-like sponge *Stylocordyla borealis*, and the soft bryozoan *Camptoplites lewaldi*. Among the pioneer sessile taxa, the sabellid polychaetes accounted for approx. 23% of the benthic coverage and close to 40% of the abundance. In general, small patches of these taxa were $<10 \text{ cm}^2$ but the bryozoan *C. lewaldi* showed a mean value of 14.9 cm^2 (Table 3). This soft species grows as an open rose-like colony and can be considerably large with a max. size of 51.8 cm^2 . Within R1, tree-like colonies of gorgonians (*Primnoisis antarctica* and *Primnoella sp.*), soft and rigid bryozoans (*C. lewaldi*, *Alcyonidium “latifolium”* and *Cellarinella spp.*, *Cellarinella nodulata*, *Smittina antarctica*, and *Systemopora contracta*), the sabellid polychaete *M. cf. sulcata*, and the sponge *S. borealis* were the most representative taxa. The tree-like bryozoan *Cellarinella spp.*, representing 16% of total benthic coverage, showed a maximum of 13% in cover area, 51 patches m^2 , and a large size of 248 cm^2 (Table 3). Benthic fauna, which characterised the later stages (R2 and UD), was more numerous and varied. Hexactinellids, demosponges, polychaetes, and compound ascidians were important in R2. Different soft and rigid taxa of bryozoans were the most representative such as *Cellarinella spp.* with a mean cover value of 12.7% and 31 patches m^2 and exhibiting a maximum cover value of 35.1% (Table 3). The same taxa were important in UD, where demosponges were distinguished reaching approx. 23% of the total benthic coverage. The massive-round demosponge *Cinachyra barbata* showed a mean coverage of 10.8% with a mean abundance of 27 patches m^2 and a patch size of 94.7 cm^2 , but locally was extremely high in coverage (45 %), abundance (48 patches m^2), and with large size (364.5 cm^2) (Table 3).

Table 3. Representative benthic organisms accounting for 75% of the average similarity within each stage. Taxa are ordered by decreasing contribution. Data include means \pm SE of cover area (CA) number of patches (NP), and mean patch size (MPS). Maximum and minimum values are shown in parentheses. Each photograph ~ 1 m². * Cover category groups are ASC: Ascidiacea, BRY: Bryozoa, COM: Complex, DEM: Demospongiae, GOR: Gorgonaria, HEX: Hexactinellida, and POL: Polychaeta. ** Growth forms are B: bush, S: sheet, T: tree, and M: mound.

Stage	Taxa	*	**	CA (%)	NP	MPS (cm ²)
R0 n= 21	<i>Myxicola</i> cf. <i>sulcata</i>	POL	S	0.34 \pm 0.16 (2.85 - 0)	4.9 \pm 2.0 (31 - 0)	6.3 \pm 0.4 (20.3 - 1.1)
	<i>Perkinsiana</i> spp.	POL	S	0.07 \pm 0.02 (0.35 - 0)	1.5 \pm 0.5 (9 - 0)	4.5 \pm 0.4 (10.5 - 1.7)
	<i>Molgula pedunculata</i>	ASC	T	0.12 \pm 0.05 (0.6 - 0)	1.5 \pm 0.6 (9 - 0)	6.7 \pm 0.4 (12.1 - 0.8)
	<i>Stylocordyla borealis</i>	DEM	T	0.03 \pm 0.01 (0.14 - 0)	1.9 \pm 0.6 (10 - 0)	1.2 \pm 0.18 (4.2 - 0.7)
	<i>Camptoplites lewaldi</i>	BRY	B	0.11 \pm 0.06 (1.2 - 0)	0.6 \pm 0.3 (6 - 0)	14.9 \pm 3.6 (19.1 - 4.9)
R1 n= 28	<i>Primnoisis antarctica</i>	GOR	T	0.46 \pm 0.15 (3.0 - 0)	3.5 \pm 1.2 (30 - 0)	7.4 \pm 0.7 (25.7 - 0.6)
	<i>Primoella</i> sp.	GOR	T	0.29 \pm 0.11 (3.0 - 0)	3.6 \pm 0.9 (19 - 0)	7.3 \pm 0.9 (22.7 - 0.5)
	<i>Cellarinella</i> spp.	BRY	T	1.48 \pm 0.62 (13.0 - 0)	9.1 \pm 2.7 (51 - 0)	14.8 \pm 1.7 (248.7 - 0.1)
	<i>Myxicola</i> cf. <i>sulcata</i>	POL	S	0.22 \pm 0.06 (1.3 - 0)	1.7 \pm 0.5 (11 - 0)	12.2 \pm 1.1 (34.4 - 0.9)
	<i>Alcyonidium</i> "latifolium"	BRY	S	0.20 \pm 0.1 (1.9 - 0)	16.9 \pm 7.6 (153 - 0)	1.1 \pm 0.04 (6.3 - 0.2)
	<i>Smittina antarctica</i>	BRY	T	0.11 \pm 0.03 (0.8 - 0)	1.3 \pm 0.3 (8 - 0)	7.8 \pm 1.4 (47.1 - 0.9)
	<i>Systemopora contracta</i>	BRY	T	0.20 \pm 0.07 (1.3 - 0)	1.3 \pm 0.3 (7 - 0)	13.3 \pm 3.3 (92.8 - 0.6)
	<i>Camptoplites lewaldi</i>	BRY	S	0.13 \pm 0.04 (0.7 - 0)	1.0 \pm 0.3 (6 - 0)	12.5 \pm 2.1 (47.9 - 1.5)
	<i>Cellarinella nodulata</i>	BRY	T	0.15 \pm 0.06 (1.5 - 0)	2.2 \pm 0.7 (20 - 0)	4.7 \pm 1.1 (53.5 - 0.1)
	<i>Stylocordyla borealis</i>	DEM	T	0.02 \pm 0.01 (0.13 - 0)	1.6 \pm 0.4 (8 - 0)	1.4 \pm 0.2 (7.4 - 0.8)
	R2 n= 21	<i>Cellarinella</i> spp.	BRY	T	12.7 \pm 2.7 (35.1 - 0)	30.8 \pm 5.8 (78 - 1)
<i>Systemopora contracta</i>		BRY	T	1.5 \pm 0.4 (8.6 - 0.02)	9.1 \pm 1.1 (19 - 1)	16.5 \pm 4.5 (184.6 - 0.2)
<i>Synocium adereanum</i>		ASC	M	0.6 \pm 0.2 (3.6 - 0.02)	7.6 \pm 1.5 (24 - 1)	8.2 \pm 1.2 (163.6 - 0.2)
<i>Cellarinella nodulata</i>		BRY	T	1.2 \pm 0.4 (7.9 - 0)	11.8 \pm 3.7 (75 - 0)	12.5 \pm 1.6 (183.2 - 0.1)
"Yellow branches"		DEM	T	0.88 \pm 0.2 (3.7 - 0)	7.2 \pm 1.5 (23 - 0)	12.5 \pm 1.2 (81.3 - 1.0)
<i>Camptoplites tricornis</i>		BRY	S	2.4 \pm 0.9 (18.8 - 0)	1.8 \pm 0.4 (6 - 0)	134 \pm 36.2 (520.1 - 0.2)
<i>Cinachyra barbata</i>		DEM	M	2.1 \pm 1.0 (22.6 - 0)	4.5 \pm 1.7 (35 - 0)	43.9 \pm 6.5 (109 - 0.9)
<i>Hornea</i> sp.		BRY	T	0.22 \pm 0.06 (1.1 - 0)	2.5 \pm 0.6 (13 - 0)	7.9 \pm 0.9 (41.8 - 0.8)
<i>Stylocordyla borealis</i>		DEM	T	0.88 \pm 0.24 (3.7 - 0)	9.8 \pm 2.8 (39 - 0)	8.1 \pm 1.1 (55.8 - 0.9)
<i>Paracellaria wandeli</i>		BRY	T	0.5 \pm 0.1 (1.6 - 0)	2.1 \pm 0.3 (5 - 0)	21.6 \pm 4.3 (119.7 - 0.5)
<i>Notosis</i> sp.		GOR	B	0.63 \pm 0.2 (4.8 - 0)	3.0 \pm 0.7 (11 - 0)	17.8 \pm 5.8 (351 - 0.1)
<i>Notoplites</i> spp.		BRY	B	0.82 \pm 0.25 (3.8 - 0)	1.4 \pm 0.4 (6 - 0)	62.8 \pm 13.3 (301 - 3.8)
<i>Rossella racovitzae</i>		HEX	M	0.2 \pm 0.06 (1.1 - 0)	2.1 \pm 0.4 (7 - 0)	21.3 \pm 13.8 (648 - 0.9)
<i>Tedania tantula</i>		DEM	T	0.2 \pm 0.06 (1.2 - 0)	8.8 \pm 3.2 (59 - 0)	2.4 \pm 0.4 (57.2 - 0.1)
<i>Myxicola</i> cf. <i>sulcata</i>		POL	S	0.25 \pm 0.09 (1.7 - 0)	4.6 \pm 1.2 (17 - 0)	4.9 \pm 0.5 (19.7 - 0.8)
<i>Polysyncrator trivolutum</i>		ASC	M	0.3 \pm 0.11 (1.9 - 0)	9.3 \pm 4.1 (82 - 0)	3.0 \pm 2.8 (20.8 - 0.5)
UD n= 42	<i>Cinachyra barbata</i>	DEM	M	10.8 \pm 2.2 (45.0 - 0)	27.4 \pm 0.4 (48 - 0)	94.7 \pm 5.1 (364.5 - 3.3)
	<i>Rossella nuda</i> / <i>S. joubini</i>	HEX	M	1.65 \pm 0.4 (12.6 - 0)	1.8 \pm 0.4 (11 - 0)	83.4 \pm 16.0 (665.9 - 5.8)
	<i>Polysyncrator trivolutum</i>	ASC	M	0.4 \pm 0.09 (3.2 - 0)	8.3 \pm 1.9 (67 - 0)	4.1 \pm 0.3 (69.1 - 0.8)
	<i>Notosis</i> sp.	GOR	B	1.65 \pm 0.5 (18.5 - 0)	2.9 \pm 0.5 (10 - 0)	29.4 \pm 4.1 (252 - 0.2)
	<i>Cellarinella</i> spp.	BRY	T	1.65 \pm 0.5 (18.5 - 0)	6.9 \pm 2.1 (63 - 0)	20.5 \pm 2.9 (580.2 - 0.1)
	<i>Synocium adereanum</i>	ASC	M	1.4 \pm 0.3 (8.23 - 0)	16.2 \pm 3.7 (38 - 0)	8.05 \pm 0.4 (66.2 - 1.3)
	"Yellow branches"	DEM	T	0.65 \pm 0.15 (3.5 - 0)	5.0 \pm 1.2 (28 - 0)	12.2 \pm 1.5 (175.3 - 1.1)
	<i>Systemopora contracta</i>	BRY	T	0.32 \pm 0.1 (2.9 - 0)	3.5 \pm 0.9 (31 - 0)	8.5 \pm 1.6 (193.5 - 0.1)
	<i>Rossella racovitzae</i>	HEX	M	1.23 \pm 0.5 (14.2 - 0)	1.4 \pm 0.3 (7 - 0)	16.9 \pm 6.5 (368 - 2.7)
	<i>Cinachyra antarctica</i>	DEM	M	0.34 \pm 0.1 (2.5 - 0)	1.2 \pm 0.3 (8 - 0)	25.1 \pm 2.8 (95.7 - 4.5)
	<i>Notoplites</i> spp.	BRY	B	1.13 \pm 0.4 (15.4 - 0)	0.7 \pm 0.1 (3 - 0)	89.2 \pm 15.4 (374 - 9.4)
	<i>Cellarinella nodulata</i>	BRY	T	0.5 \pm 0.1 (4.4 - 0)	4.5 \pm 1.4 (38 - 0)	9.4 \pm 1.2 (133.1 - 0.4)
	<i>Cellaria aurorae</i>	BRY	T	1.3 \pm 0.4 (1.6 - 0)	1.0 \pm 0.2 (6 - 0)	72.4 \pm 13.0 (284 - 1.8)
	<i>Hornea</i> sp.	BRY	T	0.08 \pm 0.01 (0.4 - 0)	1.3 \pm 0.2 (7 - 0)	5.7 \pm 0.7 (20.9 - 0.5)
	<i>Monosyringia longispina</i>	DEM	M	0.5 \pm 0.16 (4.5 - 0)	0.6 \pm 0.2 (6 - 0)	67.8 \pm 12.3 (267 - 4.31)
	<i>Cellaria</i> spp.	BRY	B	2.5 \pm 0.9 (24.1 - 0)	0.7 \pm 0.2 (4 - 0)	131.0 \pm 35.4 (957 - 2.9)
	<i>Reteporella</i> spp.	BRY	M	0.3 \pm 0.09 (2.3 - 0)	1.2 \pm 0.3 (8 - 0)	24.7 \pm 3.9 (111.5 - 0.9)

Changes in growth-form categories of CA, NP, and MPS

There were large differences in the proportion of growth forms for CA, NP, and MPS among the successional stages (Fig. 4). In R0 and R1 a similar coverage pattern was found for all the growth-form categories except for the tree-like demosponges, gorgonians, and ascidians, which showed a cover area peak at R1 (46.9%). Bush, sheet, and mound growth forms contributed approx. 60% to the coverage in these stages (R0 and R1) (Fig. 4). They showed small and few patches (e.g., mean size of 1.6 cm² and 1 patches m⁻² for the mound category in R0). NP of the tree category increased significantly (mean value of 30 patches m⁻²) and showed intermediate size values (13.1 cm²) in R1 (Fig. 4). Bush-like hydrozoans and bryozoans and sheet-like demosponges, sabellids, and ascidians showed a similar discrete coverage trend for the later stages with approx. 30% (R2 and UD), but differed slightly in size and number of patches (Fig. 4). Large (~ 96 cm² for bush) and intermediate size (~18 cm² for sheet) and moderate number of patches covered the seafloor in R2 and UD. The tree category exhibited a clear increase in coverage in R2 (up to 57.3%) with intermediate size (36.6 cm²) and high number of patches (96 patches m⁻²). Mound-like hexactinellids, demosponges, actinians, and ascidians showed significant differences in coverage between UD and the other stages, reaching approx. 40% of cover by intermediate size (35.9 cm²) and number of patches (47 patches m⁻²) in UD.

Life history traits along succession

For the representative species of each stage (Table 3), we compiled information on morphology, size (Table 3), the main reproduction modus, the dispersal abilities of the offspring, growth, and estimated age (Table 4). We summarized the available information for the 29 representative species. There are studies on reproduction and growth for 11 species; only reproduction for 17 species, and no of information for 1 species. Furthermore, information was provided of 3 species that were not selected in this study as representative, but their life-history traits were considered important for the discussion. Species were ranked from very slow to fast growth rates. The different patterns among the species provide useful ecological information to compare their life history characteristics through succession.

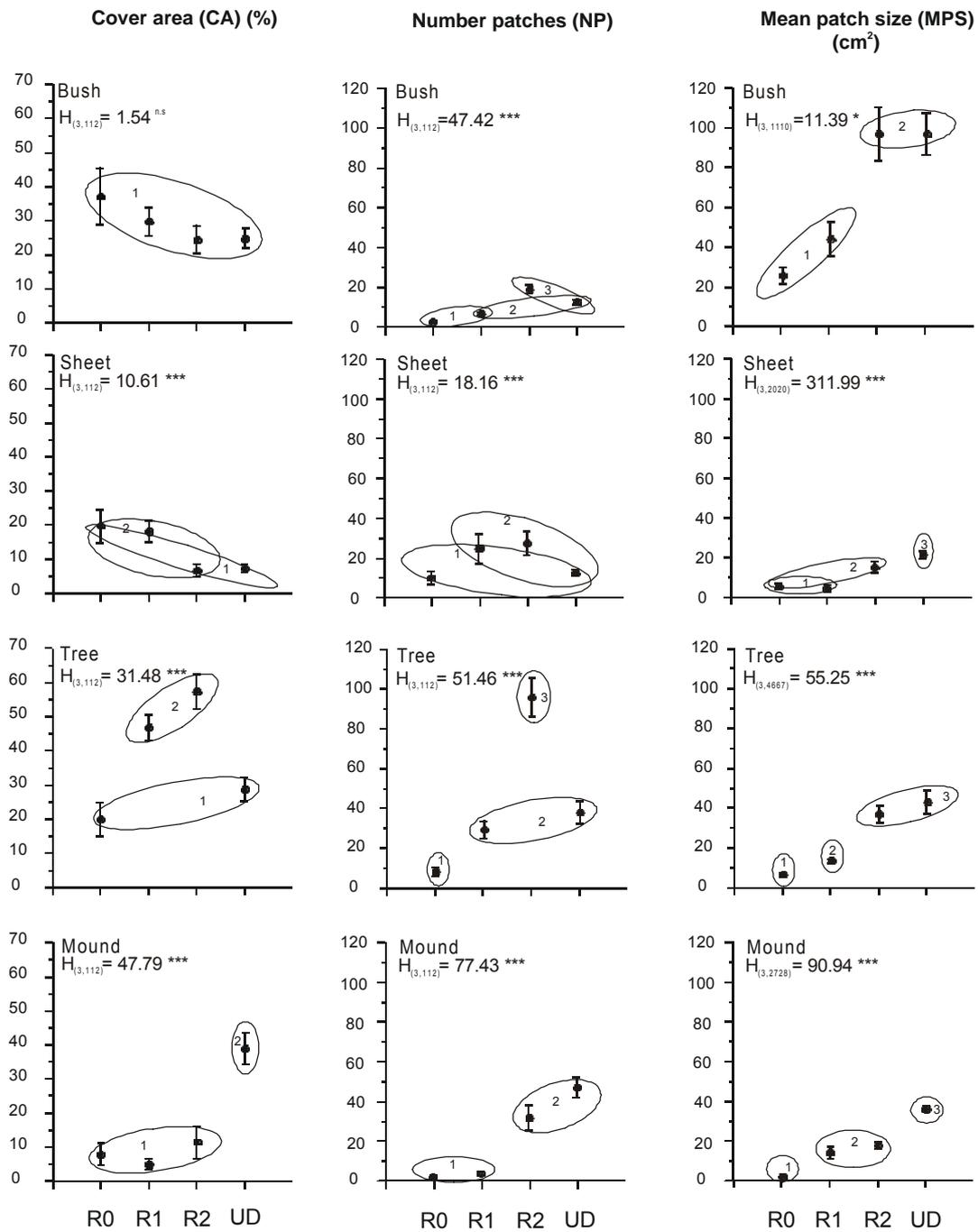


Fig. 4. Cover area (CA), number of patches (NP), and mean patch size (MPS) of growth form categories through succession. Homogeneous groups are enclosed with a circle according to Nemenyi post-hoc multiple comparisons. Data include mean \pm SE (standard error). See Table 2 for growth form descriptions. Note: The sum of different growth form categories exhibits ~ 85 % of cover area in R0 due to the absence of sessile benthic fauna in some photographs.

Molgula pedunculata and *Primnoisis antarctica* are representative species from early stages of succession (R0 and R1) and characterized by small individuals (Table 3). *M. pedunculata* exhibited a fast growth rate and high dispersal ability due to gametes freely spawned without larval stage (Table 4). Regarding morphology, *M. pedunculata* is a stalked, cartilaginous, and solitary ascidian. The “bottle brush” gorgonian *P. antarctica* seems to brood its larvae and to show moderate growth. The lollypop-like *Stylocordyla borealis* increased its size through the different stages (from R0 to R2), showed moderate growth, and short-distance dispersal of juveniles. Some bryozoan species (*Cellaria* spp., *Cellarinella nodulata*, *Cellarinella* spp., and *Systemopora contracta*) with different morphologies exhibited intermediate rates of growth and distinct dispersal strategies (lecithotrophic larvae and fragmentation) (Table 4). The latter 3 species occurred almost in all the successional stages (from R1 to UD) (Table 3). *Rossella nuda*/*Scolymastra joubini* and adults of *R. racovitzae* are known to grow very slowly and to reproduce mainly by budding. They showed the biggest size in the later stages (R2 and UD) (Table 3). They are massive and vase-shaped sponges. The other massive demosponges (*Cinachyra antarctica* and *C. barbata*) showed similar patterns as the hexactinellid sponges with slow growth rates and low dispersability of propagules (Table 4).

DISCUSSION

This section includes specific discussion on changes through successional stages (coverage, abundance, size, and growth forms) at small scale (m²) and concludes with a general review of species' life-history traits that occurred through the successional stages.

Patterns of benthic coverage and abundance

Iceberg scouring on Antarctic benthos disturbs large distances (several km) creating a mosaic of habitat heterogeneity with sharp differences within few metres. The present study reported a pattern of change in coverage, abundance, and size of species at small scale (1m²) (Fig. 2 and Table 3). However, studies at all scales of time and space are necessary and the appropriate scale of observation will depend on the question addressed (Levin 1992, Connell et al. 1997). Both small- (this study) and large-scale spatial and temporal studies can greatly contribute to a better assessment of the response of Antarctic benthic communities to iceberg disturbance.

Overall, our study provides evidence of recovery of the benthic community with an increase of coverage, abundance, and size through the successional stages (Fig. 2 and Table 3). This general tendency agrees with predicted effects of disturbance, which appears to be an important process in driving the dynamics of benthic communities (Dayton & Hessler 1972, Huston 1985, Thistle 1981, Gutt 2000). The first stages were characterized by a low percentage of benthos coverage (Fig. 2). Few and small patches of demosponges, gorgonians, bryozoans, polychaetes, and ascidians barely covered the sediment (Fig. 2 and Table 3). However, some of them occurred in high abundance such as the fleshy *Alcyonidium "latifolium"* and rigid bryozoans of the genus *Cellarinella*, the sabellid polychaete *Myxicola cf sulcata*, and the "bottle brush" gorgonian *Primnoisis antarctica* with a maximum of 153, 51, 31, and 30 patches m^2 , respectively (Table 3). Gerdes et al. (2003) studying the impact of iceberg scouring on macrobenthic biomass in the Weddell Sea found low values (9.2 g wet weigh m^2) in disturbed areas, where polychaetes represented approx. 40%. This result agrees with the occurrence of sabellid polychaetes, which accounted for 27% of the total benthic coverage in R0. In the present study we did not analyse mobile organisms but they also appeared in low abundances as first immigrants such as fish and some echinoderms. Some species of the Antarctic fish genus *Trematomus* (Brenner et al. 2001) as well as crinoids, ophiuroids, and echinoids (Gutt et al 1996) have been reported to be typical of disturbed areas in the Weddell Sea.

The advanced stage (R2) exhibited the highest coverage and abundance (Fig 2). Bryozoans were important in both coverage and abundance (mean value of 24.7 % and 76 patches m^2), whereas demosponges and ascidians exhibited a relatively high abundance. It is important to note that most of the sediment was covered by few and large matrices of thin bryozoans, demosponges, and gorgonians, which we were not able to distinguish. These "complex categories" composed the basal substrata of the benthos with a coverage of 36% for R2 and 16.7 % for the undisturbed assemblage (UD).

The UD stage was characterised by an intermediate coverage of demosponges, bryozoans, ascidians, hexactinellids, and gorgonians, where the three former taxonomic groups exhibited intermediate abundance of 27, 31, and 29 patches m^2 , respectively. In addition, Gerdes et al. (2003) determined high variability in sponge biomass, between 1.9 and >100 kg wet weight m^2 , indicating also their patchy occurrence in undisturbed stations. Big specimens of hexactinellids and the demosponge *Cinachyra barbata* were found in UD, where *Rossella nuda/ Scolymastra joubini* exhibited a maximum size of 666 cm^2 (approx. 30 cm in diameter) and locally high abundance

(maximum of 11 patches m^{-2}) (Table 3). The size of these hexactinellid sponges agrees with previous results from the Weddell Sea, where intermediate values were reported (Gutt 2000) compared to giant sizes described below 50 m in the Ross Sea (1.8 m tall, with a diameter of 1.3 m, and an estimated biomass of 400 kg wet weight, Dayton 1979). It remains unclear whether the hexactinellids of the Weddell Sea reach the size of their counterparts in the Ross Sea. Gutt (2000) suggested that local protection from large iceberg scouring in the shallow habitat of McMurdo Sound favour larger sizes due to longer time intervals between disturbances.

Benthic composition across successional stages

After disturbance, successional pathways create new species composition and interactions, which will define the successional process (Connell & Slatyer 1977, Pickett & White 1985, McCook 1994). As mentioned before, pioneer taxa appeared during the first stages of recolonization, which locally occurred with high abundance and patchy distribution (Table 3). Previous studies using Remotely Operated Vehicles (ROV) have also identified some of these benthic taxa as pioneer organisms (Gutt et al. 1996, Gutt & Piepenburg 2003). We attribute the differences of observed pioneer taxa among distinct studies to 1) their patchy distribution, 2) the higher resolution of the underwater photographs compared to ROV-acquired images, and 3) the larger total area sampled using ROV images. The patchy distribution may explain the high heterogeneity of species composition during the first stages (Fig. 3). Gutt (2000) found that there is no specific pattern of species replacement along succession in Antarctic benthic communities. Nevertheless, species composition along the early stages (R0-R1) shared common pattern characteristics. Several pioneer taxa with relatively small patch size, locally with high abundance, and barely covering the sediment represented these stages (Table 3). Experimental studies in other latitudes suggested that different successional trajectories converge towards the local resident assemblage (Berlow 1997, Chapman & Underwood 1998, Sousa 2001). In our study, benthic composition converged in the later stages (Fig. 3). However, it is important to note the separation of the undisturbed assemblage characterized by the long-lived volcano-shaped hexactinellid species and the round demosponge *Cinachyra barbata* (Fig. 3). The separation within this assemblage (UD) shows that local dominance of sponges reduces diversity and shape complexity patterns at small scale (Teixidó et al. 2002).

Patterns of cover by different growth-forms

Growth-form cover patterns changed along the successional sequence (Fig. 4). Despite the inferior competitive capacity of bush morphology (Connell & Keough 1985), this category occupied the space constantly along succession, although with a major proportion during the early stages (Fig. 4). This presence may be related to epibiotic relationships (Dayton et al. 1970, Gutt & Schickan 1998), which their development reduces competition for poor competitors such as bush-like organisms. This growth strategy takes advantage growing on the surface of larger organisms or colonies (Jackson 1979). Likely, the space between large organisms may be rapidly occupied by these ephemeral organisms, with a refuge-oriented strategy (Buss 1979). Sheet and mound forms are predicted to be generally superior in competition to bushes (Jackson 1979), and therefore are expected to dominate the later stages. Our results were in partial agreement with this prediction. The coverage of mound forms increased in the undisturbed assemblage, however the sheet-growth forms decreased along the later stages (R2 and UD). The presence of tree-like forms was relatively high through the successional stages, whereas a dominance of mound-like form was evident in UD (Fig. 4). These successful strategies might be due to temporarily high sedimentation rates and lateral transport of organic matter in the Weddell Sea (Elverhøi & Roaldset 1983, Fahrback et al. 1992, Gleitz et al. 1994, Park et al. 1999). Such conditions favour these growth forms (tree and mound), which efficiently exploit the particles in the water column and escape from burial by settling sediment (Jackson 1979). The arborescent sponge growth form is known as a morphological strategy to reduce the effect of 1) competition by growing on relatively narrow bases on the substratum; thus being more competitive than prostrate forms and 2) predation due to a reduced area to face predators (Dayton et al. 1974). Overall, our results on the cover predominance of tree and mound categories along the later stages are in accordance with a previous study on benthic zonation at Signy Island (Barnes 1995a), where the advantages of erect versus encrusting bryozoan morphologies at deeper zones were attributed to feeding, competition and substrate utilization, and resistance to water flow.

We would like to note that stoloniferous or runner-like forms are predicted to be more successful than other growth forms in disturbed environments due to faster growth and higher fecundity than late-colonizers species (Jackson 1979, Fahrig et al. 1994, Karson et al. 1996). However we found only one species (*Camptoplites tricornis*) belonging to this category. As mentioned earlier, sedimentation rates seem to be relatively high in the

Weddell Sea (Elverhøi & Roaldset 1983) and may not favour the development of this “runner” morphology in sessile organisms of the continental shelf.

Life-history traits along succession

Comprehensive studies for Antarctic benthic species are scarce, but the available information may be useful to better understand the variation of life history patterns through the successional process. It should be considered that the pace of reproduction and growth of Antarctic marine invertebrates is generally very slow (Clarke 1983, Pearse et al. 1991, Arntz et al. 1994). This characteristic may have a strong effect on all the aspects of the species' life history and should determine the time needed for a species or a community to respond to disturbance.

Table 4 suggests that tree-like *M. pedunculata* and *Homaxinella sp.* - this latter species grows very fast and is a pioneer species (Dayton 1979, Gutt & Piepenburg 2003)- showed the highest growth rates with intermediate and short distance dispersal, respectively (Table 4). In addition, *Homaxinella sp.* exhibited intense larval settlement in shallow communities of the Ross Sea (Dayton 1979). This characteristic and the fast growth seem to favour recolonization of recently defaunated substrata. The upright lollypop-like *Stylocordyla borealis* develops young complete sponges incubated in the mother body, which settle in the close vicinity showing low dispersability (Sarà et al. 2002). As previously mentioned, *S. borealis* is among the first to invade new space created by iceberg disturbance (Gutt 1996, Gutt and Piepenburg *in press*). Based on growth models, Gatti (2002) calculated an estimated age of 10.4 y for a body area of 4.4 cm². In R0 we found smaller individuals of *S. borealis* with a mean size of 1.2 cm² indicating a younger age. The upright species of gorgonians *Primnoella sp.* and *Primnoisis antarctica* appeared locally with high abundance in the R1 stage (Table 3). *Primnoisis antarctica* showed a maximum of 9 growth rings in the centre of the basal part of his calcareous axis (Table 4). However, if each growth ring represents annual cycles needs to be confirmed. The deep gorgonian *Primnoa resedaeformis* distributed throughout the North Atlantic and North Pacific Oceans (Andrews et al. 2002) belongs to a related family of *Primnoisis antarctica*. Studies on growth and radiometric analyses on *P. resedaeformis* revealed annual growth ring formation and a maximum estimated age of 112 years (Andrews et al. 2002).

Flexible, bushy and erect, rigid bryozoans occurred through the different successional stages. They showed moderate growth rates and different dispersal strategies. The erect and heavily calcified *Cellarinella wartesi* and *Melicerita obliqua* (this latter species is also

pioneer colonizer, Gutt & Piepenburg, 2003) showed annual skeletal growth check lines and are rather considered long-lived perennials with a maximum estimated age of 9 and 50 y, respectively (Barnes 1995b, Brey et al. 1998). Both species exhibit lecithotrophic larvae but cellarinellids present a high potential for fragmentation and further growth (Winston 1983, Barnes 1995b). Furthermore, the amount of embryos per colony in *M. obliqua* was reported to be about an order of magnitude higher than in the cellarinellids (Winston 1983). These different dispersal strategies within bryozoans may determine their success in recolonizing recently disturbed areas.

This study showed that massive mound-form hexactinellids and demosponges are big, abundant in areas of low disturbance, and have a patchy distribution (Table 3). These sponges exhibited the lowest growth rates, the longest life span, the biggest size, and short-distance dispersal (philopatry) because of asexual reproduction (budding) (Table 4). However, Dayton (1979) observed on *Rossella racovitzae* high reproduction activity by bud formation and rapid growth on small individuals in McMurdo Sound. The author also noted that within this species growth rates were highly variable and the bud dispersion carried by weak water currents accounted for the localized and dense patches of small *Rossella racovitzae* sponges. Concerning offspring dispersal, Maldonado & Uriz (1999) showed that fragments of Mediterranean sponges transported larvae, thus enhancing their dispersal ability and genetic variability among populations. Within this context, this strategy could be a reasonable mechanism for the Antarctic recolonization process of disturbed areas by larva release.

In summary our results using underwater photography provided new insights on the composition and abundance of sessile benthic fauna on the course of Antarctic succession. The slow growth and high longevity of Antarctic species make them vulnerable to iceberg disturbance. The long lifespan of many Antarctic species suggest that they could be an archive of the impact of recent climate change on Antarctic marine habitats. In addition, we acknowledge that further studies on reproduction, growth, larval dispersal, recruitment, and near bottom current patterns are needed to complement the recovery of Antarctic benthos after iceberg disturbance.

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Appendices**

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8. Appendix

8.1 List of abbreviations

Abbreviation	Description
CCA	Canonical correspondence analysis
cm²	Square centimetre
cm	Centimetre
CVA	Canonical variate analysis
EASIZ	Ecology of the Antarctic Sea Ice Zone
GIS	Geographical information system
m	Metre
m²	Square metre
m⁻²	Per square metre
MDS	Non-metric multidimensional scaling
PCA	Principal component analysis
R0, R1, R2	Stages of recolonisation (from younger to older)
UD	Undisturbed assemblage
Stn	Station
Indices	
AWMSI	Area weighted mean shape index
CA	Cover area (%)
IJI	Interspersion and juxtaposition index (%)
LPI	Landscape pattern indices
LSI	Landscape shape index
MISDI	Modified Simpson's diversity index
MPS	Mean patch size (cm ²)
MSI	Mean shape index
NP	Number of patches
PERIAREA	Mean perimeter to area ratio
PR	Patch richness
PSCV	Patch size coefficient of variation (%)
PSSD	Patch size standard deviation (cm ²)
SIDI	Simpson's diversity index
SIEI	Simpson's evenness index
SHDI	Shannon's diversity index
SHEI	Shannon's evenness index
TE	Total edge (cm)

8. 2 List of photographic stations analysed

Table 1. This research was performed during the EASIZ I (ANT XIII/3, January to March 1996) and EASIZ II cruises (ANT XV/3, January to March 1998) on board R/V "Polarstern".

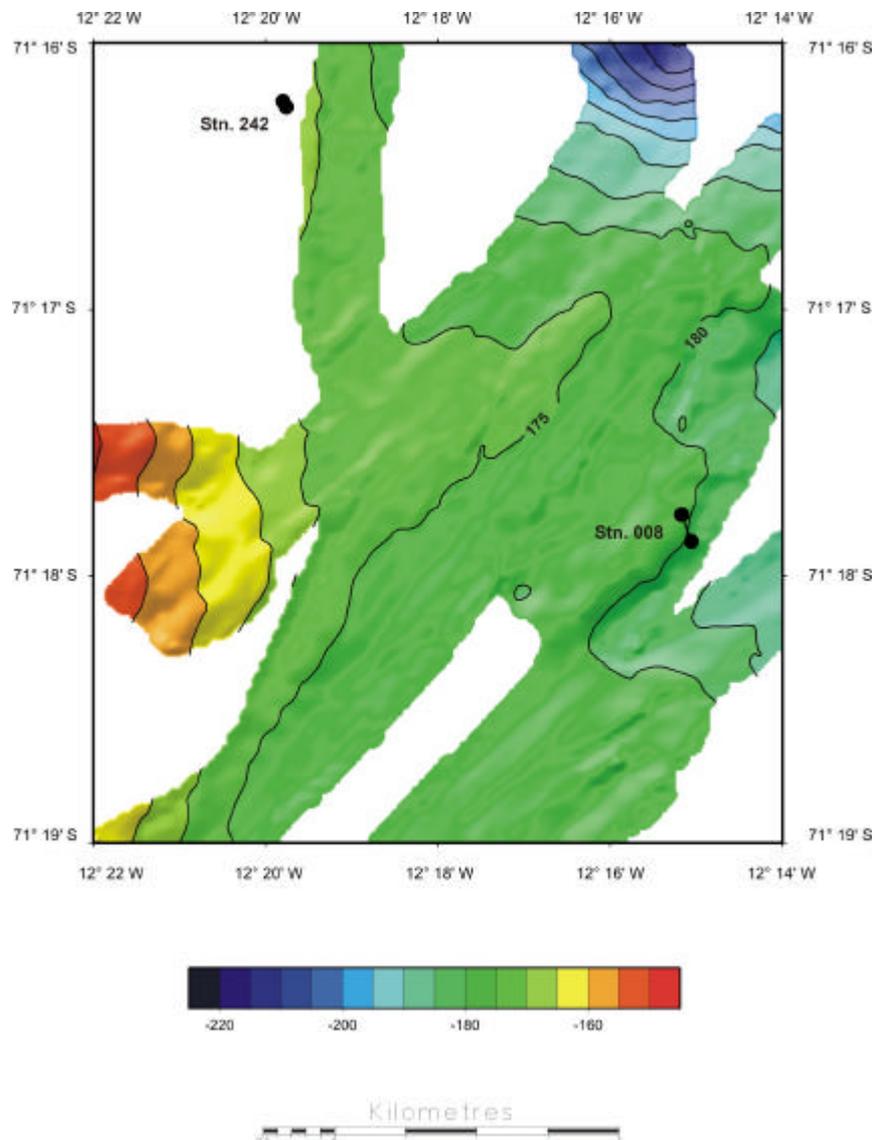
Stn	Area	Date	Time	Position (start)		Position (end)		Depth (m)	No. photos	Transect length (m)
				Lat (S)	Long (W)	Lat (S)	Long (W)			
008	KN	09.02.1996	21:00 - 21:35	71°17.87'	12°15.06'	71°17.77'	12°15.17'	171-172	77	98
042	N/KN	30.01.1998	00:05 - 00:47	70°53.98'	10°33.65'	70°54.05'	10°33.11'	260-243	70	450
211	KN	18.02.1998	14:30 - 15:38	71°07.30'	11°27.92'	71°07.54'	11°29.36'	77-117	99	1220
215	KN	18.02.1998	19:36 - 20:23	71°06.40'	11°31.87'	71°06.88'	11°31.99'	167-154	98	1093
221	N/KN	19.02.1998	12:28 - 13:25	70°50.08'	10°35.59'	70°49.70'	10°34.02'	261-270	95	947
242	KN	21.02.1998	11:05 - 11:47	71°16.24'	12°19.76'	71°16.22'	12°19.80'	159-158	97	355

Areas: KN: Kapp Norvegia, N/KN: north of Kapp Norvegia (Austå sen)

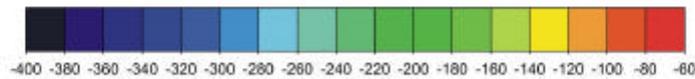
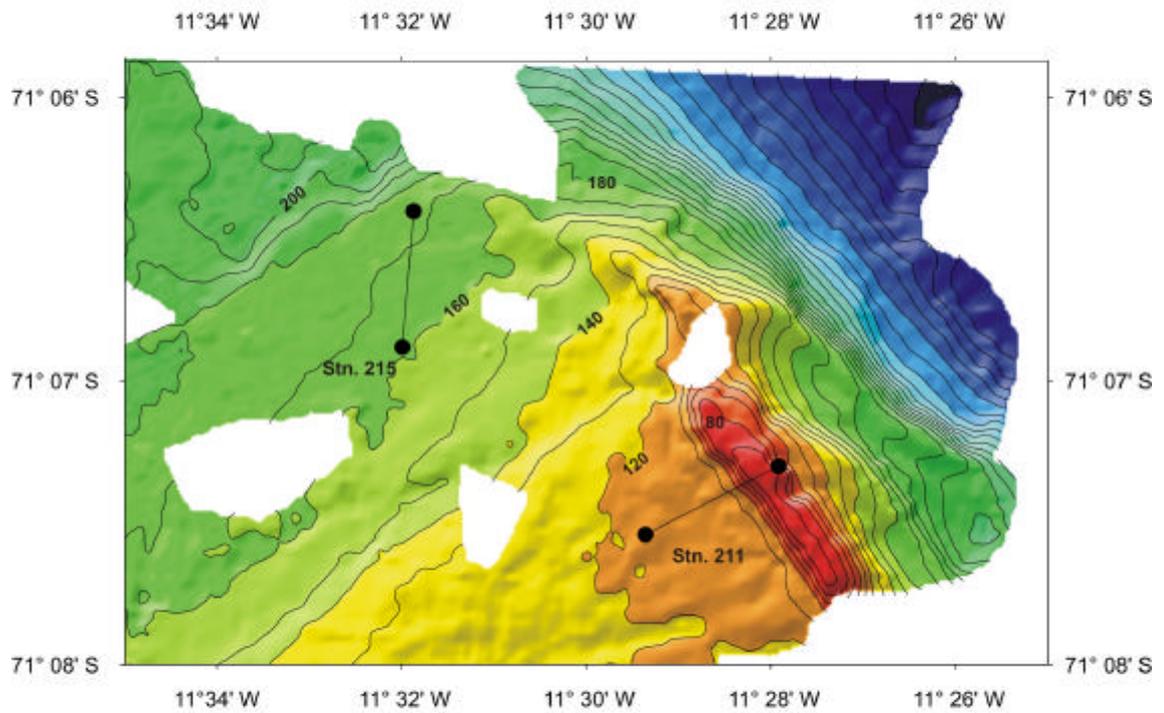
8.3. Bathymetry of photographic stations

Multibeam sonar system Hydrowsweep provides a rapid means of determining the morphology and the nature of the seafloor. Bathymetric surveys have been performed during selected cruises in the Weddell Sea on board "Polarstern". The following figures show the bathymetric profiles of the photographic stations.

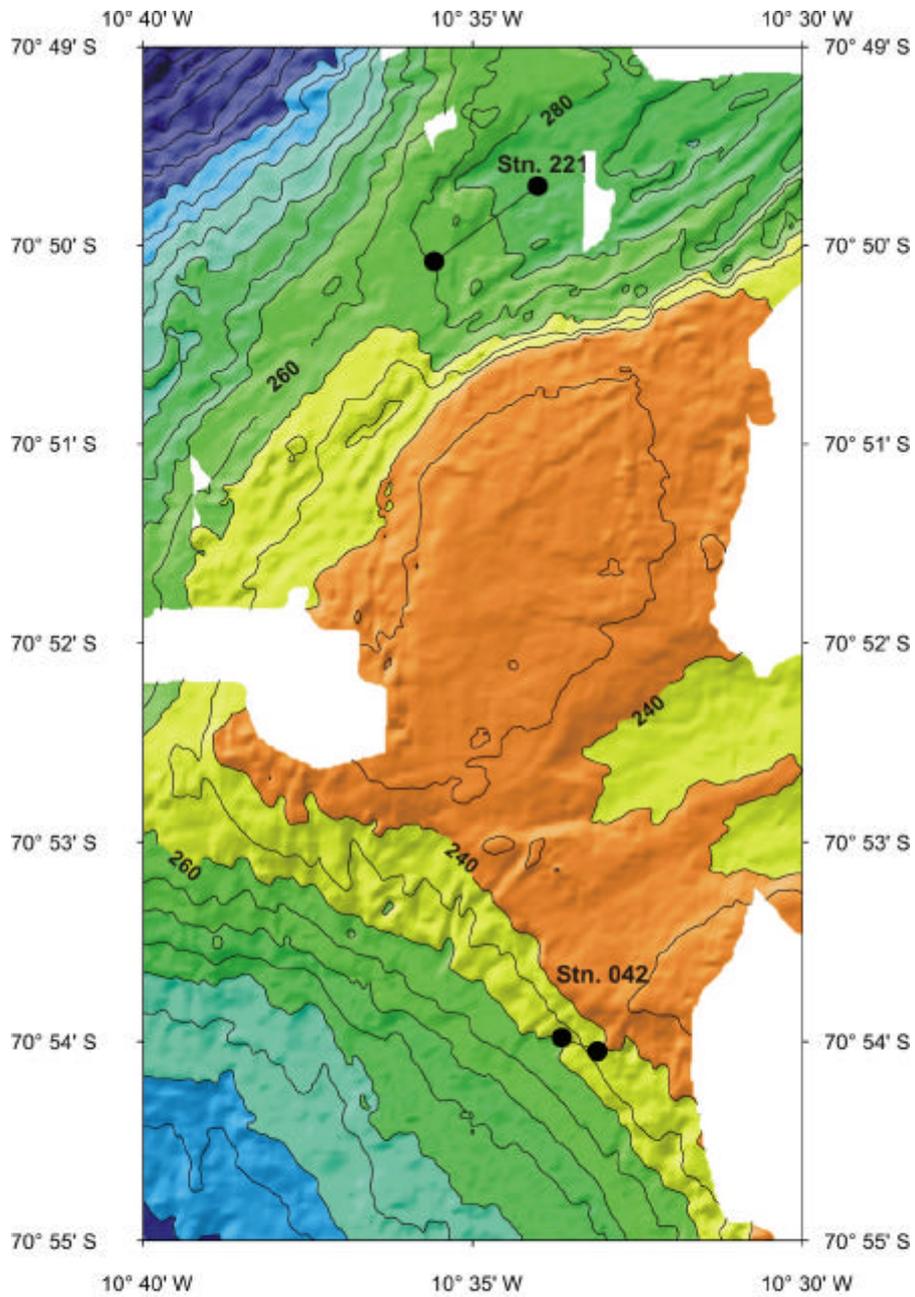
Kapp Norvegia



Kapp Norvegia



North of Kapp Norvegia (Auståsen)



8.4. List of taxa analysed

Sessile benthic organisms identified along the different stages of succession (from younger to older stages: R0, R1, and R2 and undisturbed assemblage: UD). Symbols correspond: +: presence; -: absence.

	Taxa	R0	R1	R2	UD
PORIFERA					
Cl. Hexactinellida	Rossella antarctica	-	-	-	+
	Rossella nuda/ Scolymastra joubini	-	+	+	+
	Rossella racovitzae	-	+	+	+
Cl. Demospongiae	Cinachyra antarctica	-	-	+	+
	Cinachyra barbata	-	+	+	+
	Clathria pauper	-	+	+	+
	Demosponge non identified**	+	+	+	+
	Haliclona dancoi	-	-	+	+
	Haliclonidae sp. 2*	-	-	-	+
	Haliclonidae sp. 7*	-	-	+	+
	Haliclonidae sp. 8*	-	-	-	+
	Haliclonidae sp. 9*	-	-	-	+
	Isodictya sp. 1	-	+	+	+
	Isodictya sp. 2	-	-	+	+
	Latrunculia brevia*	-	-	-	+
	Latrunculia apicalis*	-	-	+	
	Latrunculia sp.1*	-	-	+	+
	Monosyringa longispina	-	+	+	+
	Phorbis areolata	-	+	+	+
	Polymastia isidis*	-	+	+	-
	Porifera sp. 1	-	+	+	+
	Porifera sp. 27*	-	-	-	+
	Stylocordyla borealis	+	+	+	+
	Tedania cavicomuta*	-	-	-	+
	Tedania tantula	-	+	+	+
	Tedania vanhoeffeni*	-	+	-	-
"Yellow branches"	-	+	+	+	
"Yellow lobate"	-	-	+	+	
CNIDARIA					
Cl. Hydrozoa	Corymorpha parvula*	+	-	+	+
	Hydrozoa non identified**	+	+	+	+
	Hydrozoa sp. 3	-	+	+	+
	Oswaldella sp.	+	+	+	+
	Symplectoscyphus sp. 2*	-	+	-	+
	Symplectoscyphus sp. 3*	-	-	+	+
Cl. Scyphozoa	Lucernaria sp.*	-	-	-	+
Cl. Anthozoa	Ainigmaptilon antarcticum	+	+	-	+
	SubCl. Octocorallia				
	Alcyonium sp. 1*	-	+	-	-
	Alcyonium sp. 2*	-	+	-	-
	Alcyonium sp. 3*	-	+	-	-

(continued)

	Taxa	R0	R1	R2	UD
	<i>Armtzia gracilis</i> *	-	+	-	-
	<i>Dasystenella acanthina</i> *	-	+	+	+
	<i>Fannyella spinosa</i> *	-	+	-	+
	<i>Notisis</i> sp.	+	+	+	+
	<i>Primnoella</i> sp.	+	+	+	+
	<i>Primnoisis antarctica</i>	+	+	+	+
	<i>Primnoisis formosa</i> *	-	-	+	+
	<i>Rosgorgia</i> sp.	-	+	-	-
	<i>Thouarella</i> sp. 1	+	+	+	+
	<i>Thouarella</i> sp. 2	-	+	+	+
SubCl. Hexacorallia	<i>Capnea georgiana</i> *	-	+	-	+
	<i>Edwardsia</i> sp. *	+	+	+	+
	<i>Hormathia</i> sp.	-	+	+	-
	<i>Stomphia selaginella</i>	+	+	+	+
BRYOZOA					
Cl. Stenolaemata					
O. Cheilostomata	<i>Austroflustra vulgaris</i>	-	+	+	+
	<i>Bostrychopora dentata</i>	-	-	+	+
	Bryozoa non identified**	+	+	+	+
	<i>Camptoplites lewaldi</i>	+	+	+	+
	<i>Camptoplites tricornis</i>	-	+	+	+
	<i>Carbasea curva</i> *	-	-	+	+
	<i>Cellaria aurorae</i>	+	+	+	+
	<i>Cellaria</i> spp.	+	+	+	+
	<i>Cellarinella foveolata</i>	-	+	+	+
	<i>Cellarinella nodulata</i>	-	+	+	+
	<i>Cellarinella rogickae</i> *	-	-	+	-
	<i>Cellarinella</i> spp.	+	+	+	+
	<i>Chondriovelum adeliense</i>	-	+	+	+
	<i>Cornicupina polymorpha</i>	+	+	+	+
	<i>Himantozoum antarcticum</i>	-	+	+	+
	<i>Isosecuriflustra angusta</i>	-	+	+	+
	<i>Klugeflustra antarctica</i>	+	+	+	+
	<i>Klugeflustra vanhoffeni</i> *	-	-	+	+
	<i>Kymella polaris</i> *	-	-	+	+
	<i>Melicerita obliqua</i> *	-	-	+	+
	<i>Nematoflustra flagelata</i> *	-	-	-	+
	<i>Notoplites</i> spp.	+	+	+	+
	<i>Orthoporidra compacta</i> *	-	+	+	+
	<i>Paracellaria wandeli</i>	+	+	+	+
	<i>Reteporella</i> spp.	-	+	+	+
	<i>Smittina antarctica</i>	+	+	+	+
	<i>Smittina directa</i>	-	+	+	+
	<i>Smittoidea malleata</i>	-	+	+	+
	<i>Systemopora contracta</i>	+	+	+	+
O. Ctenostomata	<i>Alcyonidium "latifolium"</i>	-	+	+	+

(continued)

	Taxa	R0	R1	R2	UD
Cl. Stenolaemata	Homea sp.	+	+	+	+
O. Cyclostomata	Idmidronea cf. coerulea	-	+	+	+
	Fascicula ramosa*	-	+	+	-
ANNELIDA					
Cl. Polychaeta	Myxicola cf. sulcata	+	+	+	+
	Perkinsiana spp.	+	+	+	+
	Pista sp.	+	+	-	-
	Sabellidae sp. 2*	-	+	-	+
	Sabellidae non identified**	+	+	+	+
Echinodermata					
Cl. Holothuroidea	Dendrochirotida sp.1*	-	+	+	+
	Ekmocucumis turqueti	-	-	+	+
HEMICHORDATA					
Cl. Pterobranchia	Pterobranchia sp.2	-	-	+	+
	Pterobranchia sp.3	-	-	+	+
CHORDATA					
Cl. Ascidiacea	Aplidium meridianum*	-	-	+	-
	Aplidium sp.1*	-	-	+	+
	Aplidium sp.2	-	-	+	+
	Aplidium sp.3	-	-	+	+
	Ascidia non identified**	+	+	+	+
	Corella eumyota*	-	+	-	+
	Distaplia cylindrica	-	+	+	+
	Molgula pedunculata	+	+	-	+
	Polyclinidae fam.1	-	-	+	+
	Polysyncraton trivolutum	-	-	+	+
	Pyura bouvetensis*	+	+	-	+
	Pyura setosa*	-	-	-	+
	Sycozoa sigillinoides	-	-	+	+
	Synascidia fam.1*	-	-	-	+
	Synoicum adareanum	+	+	+	+
Complex	Thin bryozoan complex 1**	+	+	+	+
	Rigid bryozoan complex 2**	-		+	+
	Demosponge complex 3**	-	+	+	+
	Rigid bryozoan and filamentous gorgonian complex 4**	-	+	+	+
	Demosponge and filamentous gorgonian complex 5**	-	+	+	+
	Thin bryozoan, demosponge and filamentous gorgonian complex 6**	-	-	+	+
	Thin bryozoan and demosponge complex 7**	-	+	+	+

*Benthic fauna excluded from CCA (Canonical correspondence analysis) and MDS analyses (Non-metric multidimensional scaling) due to low presence (Publication II and III).

**Complex cover categories and taxa identified at coarse taxonomic level omitted in SIMPER analysis (Publication III)

8.6 List of landscape pattern index (LPI) equations

Each metric calculated in this study is described. Acronyms correspond to those used in Fragstats (McGarigal and Marks 1995). Metrics are ordered according to the aspect of landscape structure measured. Equations are for vector data.

Notation used in the algorithms:

Subscripts

$i = 1, \dots, m$ or m' patch types (classes)

$j = 1, \dots, n$ patches

$k = 1, \dots, m$ or m' patch types (classes)

Symbols

$A =$ total landscape area

$a_{ij} =$ area of patch ij

$p_{ij} =$ perimeter of patch ij

$E =$ total length of edge in landscape

$E' =$ total length of edge in landscape; includes entire landscape boundary and background edge segments regardless of whether they represent true edge

$e_{ik} =$ total length of edge in landscape between patch types (classes) i and k ; includes all landscape boundary and background edge segments involving patch type i , regardless of whether they represent true edge

$N =$ total number of patches in the landscape, excluding any background patches

$m =$ number of patch types (classes) present in the landscape

$P_i =$ proportion of each patch type (class) i to the landscape

Cover area (CA)

$$CA = A$$

Units: cm^2

Range: $CA > 0$

Description: CA equals the total area of the landscape. CA excludes the area of any background patches (uncovered sediment) within the landscape.

Patch size and variability indices

Mean patch size (MPS)

$$MPS = \frac{A}{N}$$

Units: cm²

Range: $MPS > 0$

Description: MPS equals the total landscape area divided by the total number of patches.

Patch size standard deviation

$$PSSD = \sqrt{\frac{\sum_{i=1}^m \sum_{j=1}^n \left[a_{ij} - \left(\frac{A}{N} \right) \right]^2}{N}}$$

Units: cm²

Range: $PSSD \geq 0$

$PSSD = 0$ when all patches in the landscape are the same size or when there is only 1 patch (e.g., no variability in patch size).

Description: PSSD equals the square root of the sum of the squared deviations of each patch area from the mean patch size, divided by the total number of patches.

Patch size coefficient variation

$$PSCV = \frac{PSSD}{MPS} (100)$$

Units: %

Range: $PSCV \geq 0$

$PSCV = 0$ when all patches in the landscape are the same size or when there is only 1 patch (e.g., no variability in patch size).

Description: PSCV equals the standard deviation in patch size (PSSD) divided by the mean patch size (MPS), multiplied by 100 (to convert to percent); that is, the variability in the patch size relative to the mean patch size.

Number of patches (NP)

$$NP = N$$

Units: None

Range: $NP \geq 1$

$NP = 1$ when the landscape contains only 1 patch.

Description: NP equals the number of patches in the landscape. NP does not include any background patches within the landscape.

Total edge (TE)

$$TE = E$$

Units: cm

Range: $TE \geq 0$

$TE = 0$ when there is no edge in the landscape.

Description: TE equals the sum of the lengths of all edge segments in the landscape.

Patch shape indices**Landscape shape index**

$$LSI = \frac{E'}{2\sqrt{p} * A}$$

Units: None

Range: $LSI \geq 1$

$LSI = 1$ when the landscape consist of a single circular patch; LSI increases without limit as landscape shape becomes more irregular and/or the length of edge within the landscape increases.

Description: LSI equals the sum of the landscape boundary and all edge segments within the landscape boundary, divided by the square root of the total landscape area, adjusted by a constant for a circular standard.

Mean shape index (MSI)

$$MSI = \frac{\sum_{i=1}^m \sum_{j=1}^n \left(\frac{P_{ij}}{2 * \sqrt{P * a_{ij}}} \right)}{N}$$

Units: None

Range: $MSI \geq 1$

$MSI = 1$ when all patches in the landscape are circular; MSI increases without limit as the patch shapes become more irregular.

Description: MSI equals the sum of the patch perimeter divided by the square root of a patch area for each patch in the landscape, adjusted by a constant to adjust for a circular standard, divided by the number of patches.

Area-weighted mean shape index

$$AWMSI = \sum_{i=1}^m \sum_{j=1}^n \left[\left(\frac{P_{ij}}{2 * \sqrt{P * a_{ij}}} \right) \left(\frac{a_{ij}}{A} \right) \right]$$

Units: None

Range: $AWMSI \geq 1$

$AWMSI = 1$ when all patches in the landscape are circular; AWMSI increases without limit as the patch shapes become more irregular.

Description: AWMSI equals the sum, across all patches, of each patch perimeter divided by the squared root of patch area, adjusted by a constant to adjust for a circular standard, multiplied by the patch area divided by total landscape area.

Perimeter to area ratio (PERIAREA)

$$PERIAREA = \frac{\sum_{i=1}^m \sum_{j=1}^n \left(\frac{P_{ij}}{a_{ij}} \right)}{N}$$

Units: None

Range: $PERIAREA > 0$; increases as the landscape has more patches with irregular perimeter.

Description: PERIAREA equals the sum of the patch perimeter divided by the patch area for each patch in the landscape, divided by the number of patches.

*PERIAREA is not a Fragstats index, calculated from patch data (perimeter and area)

Diversity indices**Shannon's diversity index (SHDI)**

$$SHDI = - \sum_{i=1}^m (P_i * \ln P_i)$$

Units: None

Range: $SHDI \geq 0$

$SHDI = 0$ when the landscape contains only 1 patch. SHDI increases as the number of different patch types (e.g. patch richness, PR) increases and /or the proportional distribution of area among patch types become more equitable.

Description: SHDI equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion.

Simpson's diversity index (SIDI)

$$SIDI = 1 - \sum_{i=1}^m P_i^2$$

Units: None

Range: $0 \leq SIDI < 1$

$SIDI = 0$ when the landscape contains only 1 patch. SIDI approaches 1 as the number of different patch types (e.g. patch richness, PR) increases and the proportional distribution among patch types becomes more equitable.

Description: SIDI equals 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared.

Modified Simpson's diversity index (MSIDI)

$$MSIDI = -\ln \sum_{i=1}^m P_i^2$$

Units: None

Range: $MSIDI \geq 0$

$MSIDI = 0$ when the landscape contains only 1 patch. MSDI increases as the number of different patch types (e.g. patch richness, PR) increases and the proportional distribution of area among patch types becomes more equitable.

Description: MSIDI equals minus the logarithm of the sum, across all patch types, of the proportional abundance of each patch type squared.

Shannon's evenness index (SHEI)

$$SHEI = \frac{\sum_{i=1}^m P_i * \ln P_i}{\ln m}$$

Units: None

Range: $0 \leq SHEI \leq 1$

$SHEI = 0$ when the landscape contains only 1 patch and approaches 0 as the distribution among the different patch types becomes increasingly uneven (e.g., dominated by 1 type).

$SHEI = 1$ when distribution among patch types is perfectly even (e.g. proportional abundances are the same).

Description: SHEI equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by that proportion, divided by the logarithm of the number of patch types.

Simpson's evenness index (SIEI)

$$SIEI = \frac{1 - \sum_{i=1}^m P_i^2}{1 - \left(\frac{1}{m}\right)}$$

Units: None

Range: $0 \leq SIEI \leq 1$

$SIEI = 0$ when the landscape contains only 1 patch and approaches 0 as the distribution among the different patch types becomes increasingly uneven (e.g. dominated by 1 type).

$SIEI = 1$ when distribution among patch types is perfectly even (e.g., proportional abundances are the same).

Description: SIEI equals 1 minus the sum, across all patch types, of the proportional abundance of each patch type squared, divided by 1 minus 1 divided by the number of patch types.

Patch richness (PR)

$$PR = m$$

Units: None

Range: $PR \geq 1$

Description: PR equals the number of different patch types.

Interspersion indices**Interspersion and juxtaposition index (IJI)**

$$IJI = \frac{-\sum_{i=1}^m \sum_{k=i+1}^m \left[\left(\frac{e_{ik}}{E} \right) * \ln \left(\frac{e_{ik}}{E} \right) \right]}{\ln(1/2 * [m(m-1)])} * (100)$$

Units: %

Range: $0 < IJI \leq 100$

IJI approaches 0 when the distribution of adjacencies among unique patch types becomes increasingly uneven. IJI=100 when all patch types are equally adjacent to all other patch types (e.g., maximum interspersion and juxtaposition).

Description: IJI equals minus the sum of the length of each unique edge type divided by the total landscape edge, multiplied by the logarithm of the same quantity, summed over each unique edge type; divided by the logarithm of the number of patch types times the number of patch types minus 1 divided by 2; multiplied by 100 (to convert to percentage).

