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Kelp belt ecosystem response to a changing environment in Kongsfjorden (Spitsbergen)

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ABSTRACT

The reduced sea ice extent and duration in the Arctic releases the rocky shores from one of its key physical disturbances shaping the zonation and depth extension of seaweed assemblages. In order to determine the consequences of reduced disturbance by sea ice, we studied the changes in the functioning and structure of the kelp belt at Hansneset, Kongsfjorden, between 1996-1998 and 2012–2014 using ecological network analysis (ENA). For each time period, a kelp belt flow network was constructed for 2.5 m and 5 m water depths in summer (June–July). We conducted a data-guided uncertainty analyses to evaluate the strength of the difference observed in the ENA results. At 2.5 m, the total system throughput –indicating the size of the system-significantly increased between the two periods. The number of parallel pathways (relative redundancy), the number of interactions (flow diversity) and the number of indirect interactions (Indirect/Direct) in the system were as well significantly higher at 2.5 m and 5 m in 2012–2014 compared to 1996–1998. These changes were related to the persistent colonization of the shallow sublittoral by kelps, which led to a diversification of filter feeders and an increase in omnivorous species. At 5 m, however, the kelp biomass and production decreased most likely due to the reduction of the underwater light climate between 1996-1998 and 2012–2014. In contrast, the macrozoobenthic biomass increased with a higher contribution of opportunistic and carnivorous species between these two periods. The increased values of these total system indicators suggest a more complex and mature kelp belt ecosystem in 2012–2014 compared to 1996–1998 probably due to the reduction of physical disturbances by ice. A future warming of the Arctic Ocean might enhance sea urchins grazing activity of kelp production as herbivory already increased between both periods. In a context of fast changes on ecosystem level triggered by concurrent multiple stressors, management objectives in the Arctic should be based on holistic approaches such as ENA. To do this, consistent monitoring of relevant food web components for model construction and data-guided uncertainty should be put in place.

1. Introduction

Progressing warming of the Arctic (Kattsov and Källen, 2004; Wong et al., 2014) resulted in a dramatic loss in sea ice cover extent and duration (Stroeve et al., 2007; Comiso et al., 2008). The presence of sea ice triggers the formation of unique Arctic ecosystems through physical (e.g. abrasion, light penetration) and chemical forcing (e.g. gas exchange), which influence the zonation and production of the shallow coastal habitats (Gutt, 2001; Krause-Jensen et al., 2012). Dense kelp belts, i.e. seaweed communities dominated by large, perennial species of the order Laminariales, are one of the most productive habitats worldwide (Mann, 1973), especially in Arctic coastal waters (Gómez et al., 2009). These seaweed assemblages have the potential to adapt to local environmental conditions and to maintain high primary production rate under variable temperature, irradiance, nutrient availability and disturbances (Smale et al., 2013).

In temperate coastal waters, kelp belts are known to be the most diverse and structural complex habitats on rocky shores (Steneck et al., 2002). Temperate kelp belts are characterized by high secondary production and nutrient cycling (Smale et al., 2013). They provide various resources such as substrate (Jørgensen and Christie, 2003), shelter from predation (Holbrook et al., 1990), protection against wave action and tidal currents (Eckman and Duggins, 1989) and food (Miller and Page, 2012; Leclerc et al., 2013) to their associated fauna. Kelp belts are restricted to rocky shores and their northward expansion in the Arctic is limited by temperature (Müller et al., 2009), light availability (Henley

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and Dunton, 1997) and physical disturbance such as ice scoring (Węsławski et al., 2010a). In total, the Arctic coastline (~407,680 km long) represents approximately 34% of the world's coastline (Lantuit et al., 2011) and an ice free Arctic Ocean has been predicted due to a warming climate for the end of this century (Johannessen et al., 2004). Arctic rocky shores have therefore a large potential for future seaweed colonization and kelp belt expansion (Krause-Jensen and Duarte, 2014).

In the Arctic, the seaweed species composition and distribution has been reviewed by Wiencke and Amsler (2012) with the most detailed description existing for Svalbard coastal waters. For individual fjords of the western Spitsbergen coast, the distribution of seaweed assemblages along environmental gradients (Hop et al., 2012; 2016) and their associated macrozoobenthic species composition (Lippert et al., 2001; Włodarska-Kowalczuk et al., 2009; Voronkov et al., 2013) is well studied. Along the western Spitsbergen fjords considerable changes in the seaweed assemblages were documented during a period of gradually increasing temperature of sea surface waters and decreasing sea ice extent and duration (between 1980 and 2010), with a fivefold increase in seaweed cover in Kongsfjorden (1980–1995) and eightfold increase in Smeerenburgfjord (1980–2000) (Kortsch et al., 2012). Moreover, an increase in seaweed standing stock and an upward shift in algae distribution along the coast were observed in Kongsfjorden (Bartsch et al., 2016) and Hornsund (Węsławski et al., 2010b). Therefore, understanding how these changes in seaweed assemblages and distribution might impact the total functioning and structure of Arctic coastal ecosystems would be of high value to predict potential future consequences of a warming Arctic.

Ecological network analysis (ENA) has been proven to be a useful tool to study the functioning and the structure of entire ecosystems (Baird et al. 2004, 2007, 2008). ENA consists of a set of algorithms from which several system properties can be derived (Fath et al., 2007). Results from these models provide a holistic description of food webs and significant insight into the fundamental functioning of ecosystems (Baird et al., 2004; Fath, 2015). ENA was successfully used to assess the structural complexity of flows, the magnitude and efficiency of carbon cycling and the rates of energy assimilation and dissipation of temporal coastal waters (Baird and Ulanowicz, 1989; Monaco and Ulanowicz, 1997; Heymanns et al., 2002; Baird et al., 2004, 2007; Saint-Béat et al., 2015; Schückel et al., 2015). Additionally, ENA was as well used for spatial (e.g. latitudinal) and temporal (e.g. seasons) comparison of different systems (Baird and Ulanowicz, 1993; Monaco and Ulanowicz, 1997; Scharler and Baird, 2005; de la Vega et al., 2018).

In this study, we used ENA to describe the dynamics of the Arctic kelp belt ecosystem of Hansneset, Kongsfjorden in summer. We compared the functioning of kelp belt food web models representing the summer season in two time periods: from 1996 to 1998 (1996–1998) and from 2012 to 2014 (2012–2014) to assess temporal changes in the system functioning. For each time period, we compared the kelp belt ecosystem at 2.5 m and 5 m water depths to evaluate the impact of reduced physical disturbances (e.g. ice scoring) on the holistic properties of the kelp belt ecosystem. In addition, we conducted a data-guided uncertainty analysis to evaluate the statistical significance of the differences observed in the ENA results. As perturbation by ice at shallow depth was reduced in 2012–2014 compared to 1996–1998 in Kongsfjorden (Bartsch et al., 2016), we expected the kelp belt ecosystem at shallow depth to be more developed in 2012–2014 than in 1996–1998.

2. Material and methods

2.1. Relevance of the study side

This study focuses on the kelp belt at Hansneset, the western coast of the island Blomstrandhalvøja, situated in the middle of Kongsfjorden. Kongsfjorden is located at the western coast of Spitsbergen (79°N and 12°E) in the European Arctic (Fig. 1). The fjord stretches across 21 km from southeast to northwest and is influenced by five glaciers terminating in the fjord (Zajączkowski, 2008). The Kongsfjorden's deep basin reaches depth below 300 m (Ito and Kudoh, 1997). The average tidal range is 1.8 m (Wangensteen et al., 2007). For the years 1992–1995, annual mean water temperature of the fjord was slightly above 0 °C (Ito and Kudoh, 1997) and surface water temperatures reached up to 5 °C in summer (Hanelt et al., 2001). Massive inflow of Atlantic water was reported to increase water temperatures > 0 °C during winter and > 5 °C during summer for instance in 2002 (Cottier et al., 2005). The warm Atlantic water inflow in 2006 (Cottier et al., 2007) marked this year's winter as the season with the thinnest and least sea ice recorded for the whole decade (Gerland and Renner, 2007). Since then, winters with reduced ice thickness and cover in the fjord were frequently reported (Wallace et al., 2010; Hegseth and Tverberg, 2013).

In 2007, kelp belts in Kongsfjorden roughly covered an area of 10 km^2, which represented 44% of the total subtidal area comprised from 0 m to 10 m (Ito and Kudoh, 1997; Kruse et al., 2008). Dense seaweed vegetation was found in coastal waters down to 10 m water depths (Hop et al., 2016) receiving at least 1% of the incident solar radiation (Gattuso et al., 2006). At Hansneset, the kelp belt stretching between 2 m and 10 m water depths covers an area of approximately 0.5 km^2. Because of its location, facing the mouth of the fjord, Hansneset is directly impacted by the warm Atlantic water mass entering the fjord (Cottier et al., 2005; 2007). The kelp belt at Hansneset is therefore a good case study representing kelp belts in a warming Arctic. Furthermore, the kelp belt has been already studied at this location allowing the construction of food web models representing two time periods.

Considerable changes in macrobenthic species composition and depth zonation have been observed between 1996-1998 and 2012–2014 in the kelp belt situated at Hansneset. In 1996–1998, the highest total seaweed biomass was recorded at 5 m and was dominated by the perennial kelp species *Laminaria digitata* and *Alaria esculaenta* (Bartsch et al., 2016). At 2.5 m, the total seaweed biomass was lower than at 5 m and was dominated by both the perennial kelp species *L. digitata* and the annual species *Acrosiphonia* spp. and *Spongomorpha* spp. (Hop et al., 2012). Between 1996-1998 and 2012–2014, the total biomass of kelp species (*L. digitata*, *A. esculenta*, *Saccharina latissima*) shifted from 5 m to 2.5 m water depths and the biomass of annual species such as *Acrosiphonia* spp. decreased considerably at both depths (Bartsch et al., 2016). Sessile suspension feeders were dominating the macrozoobenthic biomass at both depths in 2012–2014 (Paar et al., 2015). At 2.5 m, more than half of the macrozoobenthic biomass consisted of bivalves and barnacles. Barnacles had even higher biomass at 5 m water depths where they contribute to 47% of the macrozoobenthic biomass. The biomass maxima of the kelp associated macrofauna shifted from 5 m to 2.5 m and long-lived filter feeders (e.g. *Hiatella arctica*, *Balanus balanus*) persistently colonized the upper shallow sublittoral (Paar et al., 2015).

2.2. Model construction

Four food web models were constructed, representing the summer season in the time period 1996–1998 at 2.5 m and 5 m water depths, and the time period from 2012 to 2014 at 2.5 m and 5 m water depths. Carbon (C) was used as the currency of energy. Standing stocks are expressed in mgC.m^{-2} and all flows are given in mgC.m^{-2}.d^{-1}.

The depths were chosen based on the main differences observed in macroalgae biomass (Bartsch et al., 2016) as described in the section above. Each model consisted in 18 living compartments and 2 non-living compartments (Table 1). Due to inconsistency between the two data sets from 1996 to 1998 and 2012–2014, species of similar class or family were aggregated to allow the construction of models with the same number of compartments, a typical requirement for ENA comparison studies. The list of species or family included in each model compartment is displayed in Table 2. The dominant species in each