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Structure and robustness to species loss in Arctic and Antarctic ice-shelf meta-ecosystem webs

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ABSTRACT

While changes in the structure and dynamics of food-webs associated with sea-ice in polar regions will be among the most pronounced ecosystem-level changes on the planet that will occur with warming temperatures, little is known about how the loss of sea-ice will affect energy flow in polar food webs or whether Arctic and Antarctic sea-ice associated food-webs will respond similarly to species loss. Sea-ice ecosystems are unique from a global warming perspective as increasing temperature will result in the reduction of actual habitat substrate in addition to the air and water warming that will affect most other ecosystems. Over the next century sea-ice declines are predicted to range from 3–67% in the northern hemisphere and 8–64% in the southern hemisphere. We assembled meta-ecosystem food webs for Arctic and Antarctic sea-ice ecosystems for terrestrial and marine species that are dependent on the sea-ice to compare their topological structure and structural robustness to species loss. While the Arctic and Antarctic webs generally showed similar topology, a number of differences between the webs were identified including higher trophic species richness in the Antarctic, a right shifted trophic position distribution, and greater generality. Arctic webs had higher looping, clustering, and diet discontinuity suggesting the presence of stronger sub-webs and compartmentalization. Both the Arctic and Antarctic webs showed low robustness to the loss of low trophic position species and highly connected species, with 50% species loss occurring after the removal of ~8% of species. The Arctic web was 33% less robust to deletions when ordered from lowest to highest trophic position than the Antarctic web. Our results suggest that food webs in the Arctic webs may be more sensitive to species loss as might occur due to sea-ice declines than Antarctic food webs.

1. Introduction

It has been predicted that climate change, independent of other stressors, will result in the premature extinction of between 15 and 37% of extant species in the next 50 years (Thomas et al., 2004). Many of these extinctions will occur in the polar regions where the increase in temperature is expected to be more pronounced than in warmer regions, and where many species depend on sea-ice as a critical habitat. While changes in the structure and dynamics of food-webs associated with sea-ice in polar regions will be among the most pronounced ecosystem-level changes on the planet that will occur with warming temperatures (Smetacek and Nicol, 2005), little is known about how the loss of sea-ice will affect energy flow in polar food webs or whether Arctic and Antarctic sea-ice associated food-webs will respond similarly to species loss.

Two aspects of current climate change in polar regions suggest that warming will result in major changes to food web structure and dynamics. First, warming has been predicted to be more pronounced in polar regions than in temperate and tropical regions (Christensen et al., 2007; Turner et al., 2005). Second, warming in polar regions will result in reductions in sea-ice, an important habitat for many polar species, such as micro-algae, which are a major source of carbon (Lizotte, 2001; Meehl et al., 2007). Satellite data since 1978 has shown that annual average Arctic sea ice extent has decreased by 2.7% (*Range* = 2.1–3.3) per decade, with especially high decreases in summer of 7.4% (*Range* = 5.0–9.8) per decade (Serreze et al., 2003). In Antarctica, there is less confidence in the estimates for sea-ice decline; however Curran et al. (2003) have suggested a 20% decline in sea-ice since about 1950 in west Antarctica.

Sea-ice ecosystems are unique from a global warming perspective as warming in these ecosystems will result in the reduction of actual habitat substrate in addition to the air and water warming that will affect most other global ecosystems (Anisimov et al., 2007). Sea-ice provides critical habitat and breeding grounds for marine mammals (Wiig et al., 1999; Derocher et al., 2004) and birds (Croxall et al., 2002) and also supports sea-ice algae, one of the main basal pathways of polar food-webs (Bradstreet and Cross, 1982). The strong dependence of many polar organisms on sea-ice

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Table 1
List of previously published binary and quantitative food webs for the Arctic and Antarctic.

Region	S	Binary or quantitative	Marine or terrestrial	Reference
Arctic				
Arctic (North Norway)	65	Quantitative	Marine	Nilsen et al. (2008)
Arctic Seas	22	Binary	Marine	Dunbar (1954)
Barents Sea	41	Quantitative	Marine	Blanchard et al. (2002)
Barents Sea	30	Quantitative	Marine	Dommasnes et al. (2001)
Canadian Arctic	24	Quantitative	Terrestrial	Krebs et al. (2003)
Eastern Arctic	10	Quantitative	Marine	Tomy et al. (2004)
Eastern Bering Sea	29	Quantitative	Marine	Trites et al. (2004)
Bering Sea	41	Quantitative	Marine	Ciannelli et al. (2004)
High Arctic	65	Quantitative	Marine	Hobson et al. (2002)
Antarctic				
Falkland islands	44	Quantitative	Marine	Cheung and Pitcher (2005)
Antarctic Pack ice zone	19	Binary	Marine	Knox (1970)
Ross Sea	10	Binary	Marine	Patten and Finn (1979)
Antarctic Seas	14	Binary	Marine	Mackintosh (1945)
Antarctic Peninsula	28	Quantitative	Both	Cornejo-Donoso and Antezana (2008)
Western Antarctic Peninsula	35	Quantitative	Marine	Daniels et al. (2006)
Antarctic Shelf	490	Quantitative	Both	Jacob (2005)
Antarctic Peninsula	39	Quantitative	Both	Erfan and Pitcher (2005)
Antarctica	8	Quantitative	Marine	Mori and Butterworth (2004)

suggests that declines in the cover of sea-ice will result in major changes to the energy-flow pathways in polar webs due to changes in abundance of different trophic compartments as well as species extinctions (Tynan and DeMaster, 1997; Atkinson et al., 2004). For example, earlier melt-times for sea-ice in spring have increased the frequency of stratification in the upper water column, promoting primary production (Alexander and Niebauer, 1981). Declines in sea-ice extent and duration since 1976 have reduced the abundance of ice-algae, a critical component in the diet of krill during the winters, causing rapid declines in krill abundance from 38–75% per decade (Atkinson et al., 2004). Krill are a keystone species in the Antarctic and are a primary food resource for many fish (Takahashi and Iwami, 1997), seabirds (Barbraud et al., 2000), and marine mammals(Atkinson et al., 2004). As many species are highly dependent on krill, declines in krill abundance could have cascading effects throughout the food web (Forcada et al., 2005; Rosemond, 1993). Evidence of this has been observed during a two year study in which the krill biomass decreased four-fold, reducing the krill content of four of the main krill dependent predators diets by 88–90% (Croxall et al., 1999)

Sea-ice is also a critical habitat for marine mammals and the location of ice edges is extremely important to seabirds (Ainley and Jacobs, 1981). For example, in the Arctic the primary prey of Polar bears, the ringed seal, have declined due to reductions in sea-ice cover, which is a critical habitat for their reproduction (Derocher et al., 2004; Ferguson et al., 2005; Tynan and DeMaster, 1997). Due to the lengthening of ice-free periods on Hudson Bay, Polar bears have suffered significant population declines and reductions in body weight, which have lead to starvation (Derocher et al., 2004). The consequences of sea-ice declines have also been observed for sea-ice-dependent birds. In Antarctica, penguins (Ainley et al., 2003) and other seabirds (Croxall et al., 2002) have shown dramatic responses to changes in sea-ice extent over the past century. The sea-ice dependent Adelie (*Pygoscelis adeliae*) and Emperor Penguins (*Aptenodytes forsteri*) have nearly disappeared from their northernmost sites around Antarctica since 1970 (Barbraud and Weimerskirch, 2001).

A major impediment to developing predictive models for the effects of warming on energy-flow patterns in polar food-webs has been the lack of similarly constructed food-webs for these ecosystems (Table 1) (Jordan, 2003). In the Arctic ten food-webs have been previously compiled ranging from generalized Arctic webs, that attempt to capture major patterns of energy flow and numbers of trophic compartments (Hobson et al., 2002), to site-specific webs (e.g. Bering Sea, Blanchard et al., 2002). The number of trophic compartments in previously published Arctic food-webs ranges from 10 (Patten and Finn, 1979; Tomy et al., 2004) to 65 (Hobson et al., 2002; Nilsen et al., 2008), with none including both marine and terrestrial organisms. For the Antarctic, nine food-webs have been compiled ranging from generalized (i.e. Antarctica, Mori and Butterworth, 2004) to site-specific (e.g. Ross Shelf, Patten and Finn, 1979). The number of trophic compartments in previously published Antarctic food-webs ranges from 8 (Mori and Butterworth, 2004) to 490 (Jacob, 2005), with three including both marine and terrestrial organisms (Erfan and Pitcher, 2005; Cornejo-Donoso and Antezana, 2008; Jacob, 2005).

As a first step toward assembling highly resolved food-webs for the Arctic and Antarctic we compiled Arctic and Antarctic food-webs for ice-associated taxa that included both marine and terrestrial organisms. Our objectives were: (1) to assemble equally resolved and similarly constructed food-webs for the Arctic and Antarctic focusing on higher trophic level taxa (e.g. fish, marine mammals, birds), (2) to compare the topological structure of ice-associated food-webs for the Arctic and Antarctic and (3) to determine if the structural differences between the webs lead to differences in robustness, the number of secondary extinctions that occur, resulting from primary species loss.

2. Methods

2.1. Meta-ecosystem web assembly

We assembled cumulative meta-ecosystem food webs for each region. In a cumulative food web, feeding relationships are integrated over space and time such that the focus is on detailing energetic links among taxa that co-occur in at least part of the landscape or over some time period (Maschner et al., 2009), such as would be observed in highly seasonal systems such as the Polar regions. The webs differ from local food webs in that they are meta-ecosystem webs, defined as sets of feeding relationships connected by spatial flows of energy and organisms across ecosystem boundaries (Loreau et al., 2003). While the Arctic and Antarctic webs assembled here are composed of multiple regional and habitat specific sub-systems such as the Antarctic Peninsula, the Antarctic in particular has been previously identified as a single functional unit with transfer of energy between regional and habitat subsystems (Cornejo-Donoso and Antezana, 2008).