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Analogous aquatic and terrestrial food webs in the high Arctic: The structuring force of a harsh climate

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Abstract

Understanding food web structure and dynamics remains a central theme in ecology. Whilst differences between aquatic and terrestrial food webs have been the focus of several studies, we aim to reveal similarities where abiotic conditions are particularly extreme such as in the high Arctic. We propose that here, the combination of a short growing season, low temperature and low light, leads to the absence of predator control and the development of typically two-trophic, grazer-dominated food webs with high plant quality in terms of elemental ratios. Moreover, we advocate that this mechanism is evident in both aquatic and terrestrial high-Arctic environments, allowing the build-up of herbivore densities that consume a large fraction of plant primary production and tightly recycle nutrients. Thus, the particular abiotic conditions that characterise the high Arctic give rise to a unique environment that allows biotic factors to orchestrate food web structure and influence ecosystem function. Specially, the short growing season, low temperatures and low light levels collectively constrain the accumulation of structural autotroph tissue that, in temperate regions, effectively keeps herbivores at bay. While fundamental differences between terrestrial and aquatic ecosystems have been frequently advocated, we show here that harsh live-constraining conditions in the high Arctic have led to analogous, grazer-dominated, food web dynamics in both terrestrial and freshwater ecosystems.

Keywords: Grazer control; Light availability; Predator control; Spitsbergen; Temperature

Introduction

Since the seminal work of Summerhayes and Elton (1923) on the aquatic food web structure at Bear Island, there has been a tradition of using the high Arctic for understanding basic food web dynamics. The reason for this is not only because high-Arctic ecosystems are poor in species or taxa, but also because they offer short, simple and transparent food web structures. This view still holds true, and is commonly advocated as a reason for conducting fundamental ecological research at high latitudes. We recognise four basic features of high-Arctic ecosystems relevant in this context: (i) they are geologically young in the sense that they resemble early successional stages after glacial retreat; (ii) there is only a short seasonal window of opportunity for high biological productivity, which imposes selection for growth strategies that cope with feast and famine; (iii) prevailing low temperatures require further specialist

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adaptations in plants and animals; and (iv) the levels of incoming solar radiation are low, even during 24 h of summer daylight, because solar angles remain shallow. The combination of these extreme environmental conditions, notably the short growing season, low temperature and low light, severely constrain the diversity and productivity of terrestrial and freshwater ecosystems. According to the 'exploitation ecosystems hypothesis' only simple food webs that are characterised by limited linkage between species and two-trophic levels are predicted to emerge at low productivity (Hairston et al., 1960; Fretwell, 1987; Oksanen and Oksanen, 2000). The general absence of a functional third trophic level and hence predator control in the high Arctic follows directly from this prediction and may indeed be due to environmental severity curtailing ecosystem productivity. Here, we build on insights derived from our studies in terrestrial and freshwater ecosystems in high-Arctic Spitsbergen, where herbivores typically constitute the upper trophic level. We will focus on two types of herbivores: the crustacean *Daphnia* spp., which are key grazers in freshwater systems, and geese/reindeer that exert grazer control and influence nutrient recycling in terrestrial habitats. While several studies have explored differences between aquatic and terrestrial food webs (Cebrian and Lartigue, 2004; Shurin et al., 2006, but see Chase, 2000), our main objective is to investigate whether similarities occur that derive from the prevalence of harsh environmental conditions in the high Arctic. We postulate that the combination of a short growing season, low temperature and low light, leads to the absence of predator control and the development of grazer-dominated food webs with high plant quality in terms of elemental ratios. Moreover, we propose that such a development is evident in both aquatic and terrestrial high-Arctic environments, allowing the build-up of herbivore densities that consume a large part of the plant primary production and tightly recycle nutrients. We aim to specifically bring out parallels between aquatic and terrestrial environments through discussing: (i) grazer control of high-Arctic food webs; (ii) environmental conditions governing food quality and quantity; (iii) winter vs. summer regulation of herbivore populations; and (iv) grazer manipulation of the food resource. Finally, (v) we ask whether climatic change is likely to lessen abiotic control of high-Arctic food webs.

Grazer control of high-Arctic food webs

An ongoing debate in ecology is whether food webs are regulated by top-down predator control or by bottom-up forces through resource supply (Hairston et al., 1960; Persson et al., 1988; Sinclair, 2003). Lake systems, by their confined nature and relatively high level of nutrient mixing, are particularly suited to address this question, and some major advances have been made through limnological studies (Carpenter et al., 1985; Gulati et al., 1990 and references herein). Phytoplankton production in temperate lakes is largely controlled by inputs of phosphorus (P) to the system, and the primary grazers in these systems are pelagic herbivores like *Daphnia* spp. (frequently forming almost monocultures), which are preferred food for planktivorous fish. A reduction in abundance of planktivorous fish, resulting from either fishing or the introduction of predatory fish, typically causes increased grazer control and reduced phytoplankton biomass (Carpenter et al., 1985). The absence of planktivorous fish in many of the high-Arctic water bodies that typically freeze up in winter provides a natural analogue to this situation, and it is therefore of considerable interest to examine the outcome of this two-trophic system.

A survey of P–algae relationships in Norwegian mainland lakes and high-Arctic lakes and ponds at Spitsbergen reveal consistent differences with a very strong positive correlation between P and phytoplankton biomass (in terms of Chlorophyll *a*) in sub-Arctic and temperate mainland lakes that are populated with fish, while there is no such trend for the fish-free high-Arctic lakes (Fig. 1A). This is in support of previous studies showing low algal biomass in Arctic lakes compared with temperate water bodies (Shortreed and Stockner, 1986), which, like in Antarctic systems, could be attributed to a lack of predator control (Hansson, 1992). In these predator-free environments, the aquatic herbivore *Daphnia* exerts top-down control of autotroph biomass. Interestingly, terrestrial herbivores, notably geese, which use lakes for resting and drinking, and the surrounding catchments for grazing, enhance lake concentrations of both P and nitrogen (N) through the deposition of nutrient-rich faeces (Bazely and Jefferies, 1989; Van der Wal and Loonen, 1998). Much of the variation in P content among the high-Arctic lakes and ponds studied (Fig. 1A) could indeed be attributed to differences in goose abundance (Van Geest et al., 2007). Grazer control in the absence of predation was confirmed across the full width of this natural experimental productivity gradient, with a major fraction of P being channelled directly into grazer populations as opposed to sub-Arctic lakes with fish where a strong correlation between nutrients (P) and autotrophs was recorded (Hessen et al., 2007; Van Geest et al., 2007).

Although few data exist to evaluate grazer control of high-Arctic terrestrial food webs, a similar pattern to that found in lakes emerges, with terrestrial plants by and large failing to increase in abundance at the landscape scale when N is present in ample supply (Fig. 1B). Many factors may play a role, including direct climatic constraints on vascular plant growth (see below for extensive discussion), but vertebrate herbivores such