

Are high Arctic terrestrial food chains really that simple? – The Bear Island food web revisited

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Summerhayes and Elton's (1923) "nitrogen cycle" diagram for Bear Island (Bjørnøya), Svalbard, is widely used to illustrate the organisation of high Arctic food webs. We present a revision of the terrestrial section of this food web based on 12 years work on Spitsbergen, Svalbard. The level of complexity is much greater than Summerhayes and Elton suggested and the implications for ecological theory are discussed. In particular the low level of primary productivity does not appear to restrict the length of ectotherm food chains. This may in part be due to the open nature of the ecosystem, which receives energy/nutrient subsidies in the form of allochthonous wind-blown insects and detritus, particularly from surrounding aquatic environments. Connectivity is also significantly higher. Our data support the increasingly accepted view that many food webs presented in the literature are gross oversimplifications and that analysis of their structure can produce misleading conclusions.

The ecological literature contains many examples of unresolved, partially resolved or incomplete food webs in which major assemblages of species often are aggregated into single units and their constituent species thereby relegated into functional obscurity. Such webs are highly misleading with respect to biodiversity, food chain length, connectivity and regulation of energy flow (Martinez 1993, yet analyses of their structure has often formed the basis of food web theory (Pimm and Lawton 1980, Pimm 1982, Cohen 1990). Several recent analyses and comparisons of food webs within a range of ecosystems, from deserts and low Arctic tundra to estuaries and lakes, highlight the underlying problems associated with the study of unresolved webs (Hall and Raffaelli 1991, Martinez 1991, Polis 1991, Oksanen et al. 1996, 1997). In particular, mean chain length, apparent compartmentalisation and the links per species ratio decrease as species are aggregated. In parallel, the proportions of top and basal species tend to increase (Martinez 1993). Quantitative parameters thus vary significantly with the level of resolution employed, suggesting that reliable measurements can only be made on fully resolved webs.

A prime example of an unresolved food web, yet one considered a foundation study in trophic ecology, is Summerhayes and Elton's (1923) "nitrogen cycle" diagram for Bear Island (Bjørnøya), Svalbard, which was later reproduced as a "food cycle" in Elton's (1927) seminal book *Animal Ecology*. This basic diagram has subsequently been copied or modified in many text books up to the modern day and the underlying characteristics of the relatively simple Arctic 'food web' have been widely accepted into general ecological theory (Pimm and Lawton 1980, Pimm 1982, Colinvaux 1993, Begon et al. 1996, Morin 1999, Molles 2000, Ricklefs and Miller 2000). Despite the criticisms highlighted above, similar simplifications of Arctic terrestrial food webs, dominated by vertebrates, continue to appear (Krebs et al. 2003).

We here suggest that Elton's Arctic 'food web' diagram is a generalization, designed primarily to illustrate major pathways of nutrient/energy flux and the interdependence between the terrestrial and aquatic ecosystems, rather than to detail the intricate food web relationships. Perusal of the results of the Oxford University Expeditions, to which Elton was a major contributor, confirms that Elton was aware of a much more complex Arctic food web structure than that illustrated (Morice 1922, Jackson 1922, 1925, Stephenson 1922, Collin 1923, Waterston 1923, Elton 1925, 1929, Summerhayes and Elton 1928). These early papers indicate the presence of many invertebrate groups excluded from the food web diagram and illustrate the species richness and trophic diversity hidden within broad headings such as 'Hymenoptera' or 'Diptera'. Many subsequent faunal studies on Svalbard (summarised by Coulson and Refseth 2004) strongly reinforce these conclusions yet the myth of Arctic simplicity persists. There is often a failure to fully appreciate that Summerhayes and Elton's diagram operates at different taxonomic levels for vertebrates (species) and invertebrates (mainly Order or Class), such