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Rhythmic life of the Arctic charr: Adaptations to life at the edge

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ABSTRACT

High latitudes are characterized by strong seasonal changes in environmental conditions, including temperature and food availability. To cope with these changes, many high latitude species have developed circannual oscillators that enable them to anticipate and prepare for forthcoming environmental changes and synchronize seasonal events (e.g. reproduction) to environmental fluctuations. The Arctic charr (*Salvelinus alpinus*) is the world's northernmost freshwater fish species with a distribution largely confined within the Arctic. In the northernmost part of its distribution they have developed an anadromous life-history strategy implying annual, seaward migrations in the summer to utilize the rich feeding opportunity in the sea. Overwintering in freshwater is characterized by anorexia and energy conservation. The seaward migration in early summer is preceded by physiological and behavioral changes (smolting), by which they develop seawater tolerance (hypoosmoregulatory ability) and migratory behavior. When migrating to the sea, Arctic charr have regained a strong appetite and within 4–6 weeks in the sea they may have doubled their body weight and increased their body fat stores several-fold, in anticipation of the resources needed for reproduction in the autumn and overwintering. All these processes are regulated independently of environmental changes; captive offspring of anadromous charr kept in freshwater displays seasonal changes in seawater tolerance and strong seasonal changes in food intake and growth even when they are continuously fed in excess and held at a constant water temperature in freshwater. A correct timing of these events is crucial for their survival in the Arctic and the Arctic charr seems to possess timing mechanisms that include endogenous, circannual oscillator(s) entrainable by photoperiod. The entrainment mechanism may be linked to diel melatonin rhythms, which in this species exactly mirror overground photoperiod, even during the winter residence in lakes with thick ice and snow. Little is known, however, about how photoperiod, melatonin and putative endogenous clock(s) interact in the generation of seasonal rhythms in fish, and downstream neuroendocrine mechanisms leading to physiological changes. The anadromous Arctic charr seems ideal as a model for studying such mechanisms.

1. Introduction

The Arctic charr is the world's northernmost fresh water fish species (Johnson, 1980). Its distribution is circumpolar and largely confined to the north of the 10 °C July isotherm (Fig. 1), which is a commonly used definition of the Arctic. In other words the Arctic charr is a true Arctic species, pushed up against the cold water of the northern ice edge. Indeed, it is found as far north as it is possible to go on land, as for example at Ellesmere Island at 82°N (Klemetsen et al., 2003). As such, the Arctic charr is also a cold-water fish species; at Svalbard (78°N) this species live, eat and reproduce at temperatures that range between 0.1 °C as a minimum in wintertime and 3.6 °C as a maximum in late summer (Svenning et al., 2007).

Life at high latitudes presents challenging seasonal differences in environmental conditions. These are manifested through a long, cold and dark winter with little food and a short summer during which Arctic wildlife can replenish their depleted energy reserves. High-latitude environments also possess huge spatial differences in food availability; the marine system is in general much more productive than freshwater habitats (Gross et al., 1988).

The objective of this paper is to review the state of knowledge about how the extreme and seasonally changing environmental conditions at high latitudes, especially temperature, photoperiod and food availability, affect the life of the Arctic charr. In particular, we will discuss seasonal events including smolting (preparation for the summer feeding residence in seawater), seaward migration, appetite resumption and reproduction, and the timing of these events within the context of endogenous rhythms and environmental entrainment cues.

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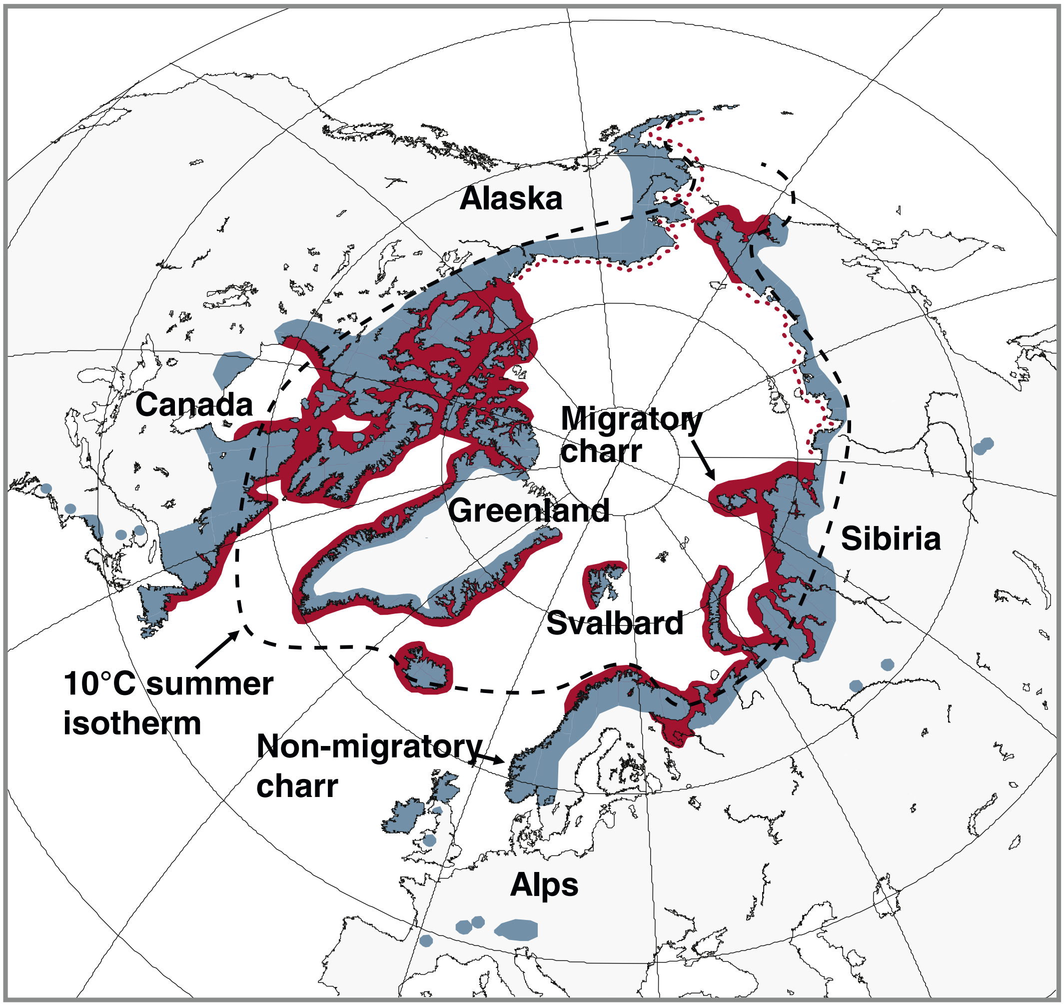

Fig. 1. Map of the Northern Hemisphere showing the circumpolar distribution (blue shading) of Arctic charr, *Salvelinus alpinus*. The red shading denotes the distribution of true anadromous (sea-migratory) Arctic charr.

2. The anadromous life-strategy of the Arctic charr

Although questioned, the contrast in productivity between freshwater habitats and the ocean may have been a driving force in the development of the anadromous life strategy of many salmonid (Salmonidae) fish species, including the Arctic charr (Gross et al., 1988). This life strategy implies that they are born in freshwater, undertake one or several migrations to the ocean to feed, and return to freshwater to spawn (Myers, 1949). In contrast to many Pacific salmon species (*Onchorhyncus* spp.), which undertake only one seaward migration during their entire life, the anadromous Arctic charr undertakes annual, short-lasting migrations during summer (Rounsefell, 1958). It has been demonstrated that some "landlocked" populations of Arctic charr and Atlantic salmon (*Salmo salar*), which have no access to the sea, possess vernal improvements in seawater (SW) tolerance similar to their anadromous counterparts (Staurnes et al., 1992; Schmitz, 1995). These findings support the concept that these populations are recently derived from anadromous populations that became landlocked due to the land-mass rising following the last glacial retreat some 6000 years ago. It has also been shown that hormone treatment (GH and cortisol) elicit a development of full SW tolerance in land-locked Arctic charr, as in anadromous charr (Ojima et al., 2009), providing further support for the notion above.

In all lakes with anadromous Arctic charr they coexist in sympatry with resident (non-migratory) charr. These morphs belong to the same gene pool since offspring segregates into both phenotypes, irrespective of parental phenotype (Nordeng, 1983), depending on conditional traits (i.e. growth rate, body size and lipid stores) in their early juvenile stage (Rikardsen and Elliott, 2000). As a consequence of the better access to food during their residence in the sea, anadromous individuals become much larger than resident individuals; resident, mature fish are seldom longer than 20 cm whereas anadromous, mature individuals may be over 70 cm long (Moore, 1975; Nordeng, 1983; Gulseth and Nilssen, 2001). Due to a markedly stronger seasonality of anadromous charr than of resident charr, the present review will be mostly limited to the life-history of anadromous charr.

Juvenile Arctic charr that adopt an anadromous life-strategy are between 12 and 20 cm long and 2–9 years old (depending on latitude) when they migrate for the first time (Randall et al., 1987; Berg and Berg, 1989; Nilssen et al., 1997; Rikardsen and Elliot, 2000). They reside in the sea for 30–60 days, depending on age and latitude (Mathisen and Berg, 1968; Finstad and Heggberget, 1993; Nilssen et al., 1997). Further, the anadromous Arctic charr undertake on an average 4 seaward runs before they reach sexual maturity in the high-Arctic (Gulseth and Nilssen, 2001), and maintain their anadromous life thereafter (Moore, 1975; Nordeng, 1983). In sub-Arctic populations, anadromous individuals normally spawn every year after they have reached sexual maturity (Nordeng, 1961), while at high latitudes, anadromous postspawners may require more than one summer to regain necessary resources for a new spawning (Dutil, 1986) and they may skip migration to the sea in some years (Radke et al., 1996).

Equipped with data storage tags, anadromous Arctic charr were followed during overwintering in freshwater. Data revealed that they