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A capital breeder in a heterogeneous environment: Lipid reserves and RNA:DNA ratio in Lake Baikal's endemic *Epischura*

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ABSTRACT

Lake Baikal (Siberia, Russia) is the oldest, the deepest and the most voluminous lake on Earth. During the last century, Baikal has experienced gradual increases in temperature but remains highly oligotrophic with increases in primary productivity limited to the warmest parts of the lake. Using whole body RNA:DNA ratio as an indicator of metabolic rate, we demonstrate that the key primary consumer in Baikal's plankton, *Epischura baikalensis* (Copepoda: Calanoida), is a capital breeder that relies on lipid storage to maintain productivity. In individuals from nature, the RNA:DNA ratio correlated with lipid content in samples from cold, low phytoplankton density locations from Baikal's North and Central basins, but not in samples from warmer South basin and Maloe More strait. Lipid reserves, both visually assessed and measured by Nile Red fluorescence, correlated positively with phytoplankton density. In laboratory experiments the RNA:DNA ratio responded to starvation and temperature in non-reproducing, low lipid storage females, but not in individuals with developed ovaries or high lipid storage. This indicates that, unlike many other zooplankton crustaceans, *E. baikalensis* uses resource storage to support current reproduction, which buffers the dependency of metabolic rate on current feeding conditions. We discuss possible effects of such buffering on *E. baikalensis* competition with non-endemic, largely income-feeding zooplankton species whose frequency is currently increasing in Baikal pelagia.

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Introduction

Allocation of resources and energy into current growth, current reproduction and storage (i.e. future growth and reproduction) is the key life-history decision organisms need to make to maximize their reproductive output (Roff, 1992; Stearns, 1992). The opposite extreme strategies of such allocation are often termed income breeding (all reproduction is supported by current feeding) and capital breeding (all reproduction is supported from storage) (Drent and Daan, 1980; Jönsson, 1997; Stephens et al., 2009, 2014). There is, of course, a continuum of intermediate strategies in between the two extremes; moreover, the same organism can be a capital or income breeder in different periods of its life cycle or both simultaneously with respect to different nutrients (see Stephens et al., 2014 for review). Which strategy is optimal depends largely on the seasonality of resource availability, organism lifespan and costs of resource storage (Sainmont et al., 2014; Stephens et al., 2014). The prevalence of capital or income breeders among

species occupying pivotal niches may, conceivably, influence ecosystem productivity and stability in cyclic or unpredictable environments, because resources stored at a given trophic level during periods of high resource availability determine the flow of energy through the trophic levels during periods of resource scarcity.

The ratio between RNA and DNA concentration in tissues and whole-body samples has been widely used as a measure of metabolic rate and secondary production in aquatic animals (Wagner et al., 1998; Gorokhova, 2003; Chicharo and Chicharo, 2008; Holmborn et al., 2009; Gusmão and McKinnon, 2011; Tang et al., 2015; Foley et al., 2016). This measure is based on the assumption that, while DNA concentration per cell is usually constant, the amount of total RNA varies and reflects the intensity of transcription (affecting mRNA concentration) and translation (affecting rRNA concentration). Thus, higher RNA:DNA ratios indicate higher rate of protein biosynthesis and, by extension, higher metabolism and biomass production, including egg production. Clearly then, RNA:DNA ratio, as a proxy for egg production, would reflect current food availability only in cases of income breeding strategy when egg production is not buffered by any stored reserves.

In fish, the joint analysis of RNA:DNA ratio and lipid content revealed that the RNA:DNA ratio reflects current feeding conditions, while lipid content is more indicative of previous, long-term history of resource availability, including the abundance of maternally-supplied resources

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(Paulsen et al., 2014; Peters et al., 2015). In zooplankton crustaceans, several studies have demonstrated positive correlations between RNA:DNA ratio and egg production and current food availability (Saiz et al., 1998; Wagner et al., 1998; Speekmann et al., 2007; Holmborn and Gorokhova, 2008; Ning et al., 2013). For several species, including cladocerans (Vrede et al., 2002) and copepods (Wagner et al., 2001), convincing calibration curves of RNA:DNA ratio to biomass production exist. Indeed, data on copepods often showing a rapid response of RNA:DNA ratio to current feeding conditions (e.g., Speekmann et al., 2007), suggest a tendency toward income breeding. Alternatively, in the case of pure capital breeding, the RNA:DNA ratio should correlate with individuals' resource storage and not with current feeding conditions.

While routine in marine zooplankton studies, the RNA:DNA ratio approach has not frequently been applied to freshwater zooplankton species (but see Bullejos et al., 2014), which exist in much more seasonally and stochastically variable environments than their marine counterparts. These environments, especially for organisms with short lifespans yet slow development due to low temperatures, are conducive for capital breeding to evolve as a successful life history strategy (Varpe et al., 2009; Sainmont et al., 2014; Stephens et al., 2014). These observations suggest that in a joint analysis of RNA:DNA ratio and stored resources, in particular in freshwater zooplankton, one might expect to observe a buffering effect of stored resources on current RNA:DNA ratio.

Here we report the application of the RNA:DNA ratio approach to test the role of resource storage in the calanoid copepod *Epischura baikalensis* Sars in Lake Baikal (Siberia, Russia). Baikal is the oldest, deepest, and largest (by volume) lake on Earth. Its benthic communities contain extremely high levels of endemic biodiversity, including amphipod, gastropod, planarian and several other endemic species flocks (Kozhov, 1963; Kozhova and Izmet'eva, 1998). Baikal zooplankton is, to the contrary, quite species poor and distinctly deprived of cladocerans, at least until recent decades (Hampton et al., 2008; Izmet'eva et al., 2016). The depauperate assemblage and its unusual bias toward copepods were first noted by Georg Ossian Sars, the discoverer of the most common Baikal zooplankton – *Epischura baikalensis* (Sars, 1900). Indeed, in most macro-zooplankton samples from open Baikal, *E. baikalensis* constitutes 96–100% of the total organism count, and it is responsible for nearly all secondary production in the open lake (Afanasyeva, 1998; Melnik et al., 1998). It is, therefore, a pivotal species for the Baikal's pelagic community (which is the component of the lake's ecosystem that is responsible for 95% of energy flow and 90% of matter turnover in the lake) and a key element of the food chain leading to endemic coregonid fishes and seals (Moore et al., 2009). Baikal *Epischura* undergoes two generations per year (Afanasyeva, 1998) with the “winter-spring” generation reaching sexual maturity in mid-summer. Summer secondary production in *Epischura* as well as its competition with non-endemic zooplankton species may therefore depend on the amount of resources accumulated during naupliar and copepodite larval studies in winter and spring and on current feeding conditions adults experience during summer months.

In the last 60 years Baikal has shown a significant increase in surface temperature, in particular in its South basin (Fietz et al., 2005; Hampton et al., 2008; Shimaraev et al., 2009; Shimaraev and Domysheva, 2013). At the same time, primary production remained low or even decreased throughout the lake, except, again, its South basin, where there has been an apparent increase in productivity (Izmet'eva et al., 2011; Izmet'eva et al., 2016). Additionally, the relatively shallow (depths below 200 m) Maloe More strait that separates Olkhon island from the mainland differs from the rest of Baikal in being warmer and more productive (Fietz et al., 2005). Possibly as the result of gradual warming and eutrophication of Baikal's very cold, very oligotrophic waters, the frequency of other zooplankton species, such as cosmopolitan cladocerans (*Daphnia* and *Bosmina*) and cyclopoid copepods (*Cyclops*), previously restricted to shallow bays, has increased in open Baikal (Melnik et al., 1998; Hampton et al., 2008; Moore et al., 2009; Izmet'eva et al.,

2016). Furthermore, the increase of cladocerans relative to the endemic *E. baikalensis* appears to be associated with the interplay between increased surface temperatures, reduced mixing, and changes in the vertical distribution of zoo- and phytoplankton (Hampton et al., 2014). RNA:DNA ratio may be instrumental in the analysis of long-term competitive interactions between fast-growing cladocerans with their rapid metabolic rate and slower-growing copepods (Bullejos et al., 2014). Because the productivity of *E. baikalensis* and the outcome of its competition with cladocerans are likely to be crucial for the composition of Baikal's pelagic community, a better understanding of this species' resource allocation strategy is of a significant interest for Baikal conservation ecology.

The goal of this study is to compare *E. baikalensis* from the warmer, less oligotrophic regions (South basin and Maloe More) with those from colder, highly oligotrophic regions (North and Central basins) with respect to the possible buffering effect of lipid reserves on productivity as measured by RNA:DNA ratio. We further test the observed relationships in starvation and temperature experiments under laboratory conditions.

Materials and methods

Sampling

Epischura baikalensis were collected in July–August 2013 by vertically towing a plankton net (mesh size = 80 μm ; diam = 39 cm) from the depth of 150 m to the surface and either immediately freezing animals in liquid nitrogen or transferring them to the laboratory for experiments. In mid-summer *E. baikalensis* population is composed of adult individuals born during winter-spring reproduction peak (Afanasyeva, 1998) with the majority of the population occurring between 250 and 50 m depths (Afanasyeva, 1998) well below the thermocline (5–25 m). Samples were collected at 12 different locations throughout the lake, representing three open lake regions or basins of Baikal (North, Central and South) and the warmer, shallower Maloe More strait (Fig. 1A). Only *Epischura* from Station 1 (South basin, 2.8 km south from the Baikal Biological Station of Irkutsk State University at Bolshie Koty) were used for laboratory experiments, which should be kept in mind as possible limitation of the observed results, given a significant variation in RNA:DNA ratio and lipids content among stations (see below).

Phytoplankton abundance at each sampling location was quantified by chlorophyll *a* readings made with vertical tows of a YSI sonde (6600 series) from 50 m (or from the bottom at depths <50 m) to the surface and by direct counts of Lugol-preserved samples obtained by a Van Dorn bottle at the depth of 75 m (highest density of *Epischura* in summer is observed between 50 and 100 m, Melnik et al., 1998). For each sample, 1 L of whole water was preserved with Lugol's solution immediately upon collection, settled for 24 h, decanted to 15 mL, and 5 mL of each concentrated sample was counted in Utermöhl chambers at 400 \times , with the following categories of algal cells recognized: small dinoflagellate (2 μm), medium dinoflagellate (5 μm), *Gymnodinium baicalense*, *Peridinium*, cyst (10 μm), *Monoraphidium*, *Koliella*, *Synedra*, *Aulacoseira baicalensis*, *Dynobryon*, *Cyclotella minuta*, *Cyclotella baicalensis*, picoplankton (1 μm), unidentified green eukaryote (3 μm), *Anabaena*.

Additionally, in order to provide a rough classification of the samples into those taken at historically warmer vs. historically colder areas, each sample was characterized by multiyear averages of temperatures at the surface, 10 and 50 m from the nearest 1–3 stations available from Limnological Institute Baikal Water Temperature database (Shimaraev et al., 2009; M.N.Shimaraev, personal communication). Stations from the South + Maloe More region are well separated from North + Central region on the plane of the two principal components (together explaining 74.2% of variance) calculated on the basis of in-situ and long term temperature data, chlorophyll concentration in 0–50 m

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