NOTE

Significance of lipid storage levels for reproductive output in the Arctic copepod *Calanus hyperboreus*

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ABSTRACT: The Arctic marine copepod *Calanus hyperboreus* reproduces at depth during winter, with egg production fuelled entirely by internal energy reserves in the form of lipids. The present study addresses the question of whether reproductive output, in the form of total egg production or hatching success, is dependent on female size (prosome length) or lipid content at the onset of spawning in this species. Egg production of individual females and the hatching of nauplii were observed under controlled temperature and light conditions in the laboratory throughout the spawning period from December to March. There was a positive relationship between female size and total egg production, and an even stronger positive relationship between initial lipid content and total egg production. No relationship was found between hatching success and either female size or lipid content. One implication of these findings is that increased water temperatures in the Arctic might have a direct negative impact on an important life history trait such as size at maturity, resulting in reduced fecundity in this species.

KEY WORDS: Zooplankton · Life history · Body size · Lipid · Fecundity · Arctic

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INTRODUCTION

Life history traits such as size and age at maturity, number of offspring, frequency of reproduction, development time and lifespan are under strong selection to maximize the number of offspring surviving to reproductive maturity in all organisms. Understanding how organisms manage to optimise reproductive output in an unpredictable environment can be a key to assessing species' adaptation potential in the context of climatic environmental changes. Due to strong seasonality and low temperatures, the marine Arctic can be regarded as an extreme environment, and many zooplankton species inhabiting this region have developed specific traits such as energy storage and diapause (state of lowered metabolism) (Hirche 1998, Hagen & Auel 2001, Lee et al. 2006). Strong seasonality in food availability has further been put forward as a factor favouring the strategy of capital breeding, i.e. reproduction fuelled by internal energy stores (and thus separated in time from the feeding period), as opposed to income breeding, where reproduction is sustained by concurrent food intake (Sainmont et al. 2014). A good example of this is the genus *Calanus*, calanoid copepods that dominate the zooplankton biomass in the marine Arctic (Thibault et al. 1999, Kosobokova & Hirche 2009). All 3 species that co-occur in the Arctic (*Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus*) build lipid reserves during the short feeding season that they use for overwintering, and to a varying degree to fuel reproduction (Niehoff et al. 2002, Madsen et al. 2008).

The 3 *Calanus* species resemble each other in the general aspects of their life cycles, but they differ in body size, and with respect to where they can be found on the income breeder–capital breeder axis.

The smallest species, *C. finmarchicus*, which has its core habitat in the North Atlantic, relies mostly on income breeding. *C. glacialis*, a slightly larger, Arctic shelf species, has a mixed strategy with an early egg production based on stored lipids, combined with the utilization of early ice algae blooms for both egg production and the developing nauplii (Tourangeau & Runge 1991, Niehoff et al. 2002, Søreide et al. 2010). However, peak egg production occurs during the main phytoplankton bloom (Hirche & Kattner 1993, Daase et al. 2013). Both species lay their eggs in surface waters, after the seasonal ascent from overwintering. The largest species, *C. hyperboreus*, has its core habitat in the Greenland Sea Gyre (Hirche 1997). It produces eggs at depth during winter (November–March), and reproduction is thus completely decoupled from primary production in time and space. Several studies have investigated egg production in *C. hyperboreus*, and the phenology of reproduction varies slightly between the areas where the species is found, possibly as a result of differences in the timing of the spring bloom (Hirche & Niehoff 1996 and references therein).

Few studies exist, however, where egg production has been measured for the entire spawning period of *C. hyperboreus* females without providing food, and where total egg production of individual females has been related to body size (Plourde et al. 2003, Hirche 2013). Size at maturity can be an important factor for the fecundity of a female (Stearns 1992), and in the case of *C. hyperboreus*, size may also have a direct effect on the amount of total lipid a female can accumulate and use for reproduction.

The objective of the present study was to investigate whether female size (prosome length) or lipid content of females at the onset of spawning have an effect on the reproductive output in terms of total egg production or hatching success in *C. hyperboreus*. This was addressed by observing egg production and hatching of nauplii in the laboratory, for individual *C. hyperboreus* females collected north of Svalbard, Norway, from December to March.

MATERIALS AND METHODS

Collection of live copepods

Specimens for the observation of copepod egg production observations were collected north of Svalbard (81° 22.19′ N, 4° 28.20′ E), Norway, during a cruise with the RV 'Helmer Hanssen' on 1 October 2012. Individuals were sampled using a 1000 μm WP-3 net with a large (20 l) non-filtering cod-end. Bottom depth at the station was 730 m, and the net was hauled from 10 m above the bottom to the surface. The station was situated in ice-covered water, and the water temperature ranged from −1.7°C at the surface, to 2–3°C in the mixed Atlantic water mass from 100 to 450 m, and −0.4°C at the bottom.

The sample was immediately diluted in a large container with ambient seawater, and placed in a dark walk-in cold room with a constant temperature of 2–4°C. Approximately 200 females were then sorted using a wide glass pipette, and transferred to 2 aerated 60 l containers (gentle air-bubbling) with pre-screened (180 μm mesh) ambient seawater. A few specimens of copepodite stage 5 (CV) were also collected in October, and kept in separate containers until they moulted into males and females in November/December. Gonad stage (GS) distribution was checked for 100 females from preserved samples from the same time and location, and they were all in GS1 (Niehoff & Runge 2003), i.e. immature. Back in the laboratory, the containers were stored in the dark in incubation chambers at a constant temperature of 2°C, corresponding to the temperature of the mixed Atlantic water mass from the sampling location in October, until the females started to ripen in early December. The containers were visually inspected at regular intervals to remove dead individuals, and to determine when the females started to show orange gonads, a sign that they were becoming ripe.

Observation and measurements of individual females

On 5 December 2012, several females with orange gonads were observed in the large containers, and 52 females in good condition were picked at random and transferred to individual 80 ml beakers filled with filtered seawater. This included 3 females that had moulted from CVs in the separate container. No false bottom was used to separate eggs from females, because the eggs are neutrally buoyant and do not sink out. This implies that an unknown proportion of the eggs produced were subject to predation by the female, evidenced by the presence of faecal pellets with eggs clearly visible inside at several occasions.

Prosome length and lipid content of females

Lipid sack area was used to estimate total lipid content (mainly wax esters, WE) of the females from

Eq. (1) in Vogedes et al. (2010): WE = $0.167A^{1.42}$, where the geometric shape for area A is the perimeter of the lipid sack. Individual females were photographed on 9 and 10 December to obtain a measure of lipid content of each of the individuals at the start of the observation period. Photographs of females lying on their side were taken with an Axio-Cam ERc5s camera mounted on a Zeiss Discovery V20 stereomicroscope. Prosome lengths were measured from the tip of the head to the tip of the last abdominal segment of the females.

Egg production and hatching success

The beakers were visually inspected daily from 5 December 2012 to 3 March 2013, and laid eggs were counted. When the observation of individual females was started on 5 December, some of the females had already laid one or several clutches in the 60 l container. All in all, for 14 females, it is reasonable to consider that all their clutches were accounted for during the observation period, and they were thus included in the calculation of total egg production. The average clutch interval for the first 5 clutches of these females was 6 d (SD = 1.7), and only females that laid their first observed clutch of eggs after 13 December (i.e. Day 8 after the start of the observations) were included. All 14 females survived the whole observation period, and their last clutch was laid 10–42 d before the end of the observation period. Oocytes were no longer visible in these 14 females on 3 March.

From each clutch, 60 eggs were picked out and incubated in 6-well plates (10 eggs in each well) filled with 5 ml filtered seawater. For the first clutches, eggs were inspected every day to assess the approximate time to hatching for a majority of the eggs. Most of the viable eggs hatched after 5 d. Hatching success was therefore measured as the fraction of hatched eggs after 10 d. Females and hatching eggs were kept in 2 separate incubation chambers at 2°C in the dark.

Data analysis

Since the response variable (i.e. total egg production) comprises count data, a general linear model with a quasi-Poisson distribution and a log link was used when comparing total egg production with female size and lipid content. Linear regressions were performed using R version 2.15.3.

RESULTS

Total egg production

Total egg production in the 14 females for which all clutches are accounted for ranged from 448 to 2541 eggs (Fig. 1).

There was a significant positive relationship between prosome length and total egg production (intercept 3.53 [SE = 1.5] and slope 0.0006 [SE = 0.0002], p < 0.01, reduction in deviance 1270.5; Fig. 2A). An even stronger positive relationship was found between lipid content of the females at the onset of spawning and total egg production (intercept 5.92 [SE = 0.20) and slope 0.79 [SE = 0.12], p < 0.001, reduction in deviance 3045.4; Fig. 2B). This relationship holds also if females for which an unknown number of clutches had been laid before the start of the observations are added (extra females denoted by open circles; dashed line shows fitted model for 24 females; intercept 5.97 [SE = 0.18] and slope 0.79 [SE = 0.12], p < 0.001; Fig. 2C).

Hatching success of eggs

There was no relationship between mean hatching success and total lipid content (or size, data not shown) of females (Fig. 3). The hatching success of the eggs was generally high, but variable (from 100 to 0%), within clutches for most females. Hatching success is presented for all females that laid eggs and stayed alive throughout the experiment. Three females laid only a few eggs that disintegrated within a few hours. These were newly moulted females, which had moulted from CV to females in October/November in the laboratory. One newly moulted female did produce viable eggs.
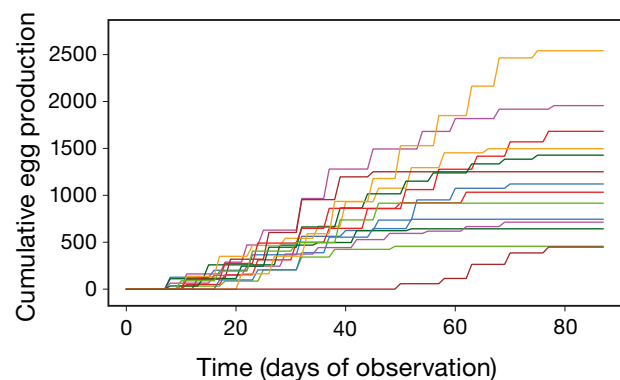

Fig. 1. Cumulative egg production of 14 female *Calanus hyperboreus* from 5 December 2012 to 3 March 2013
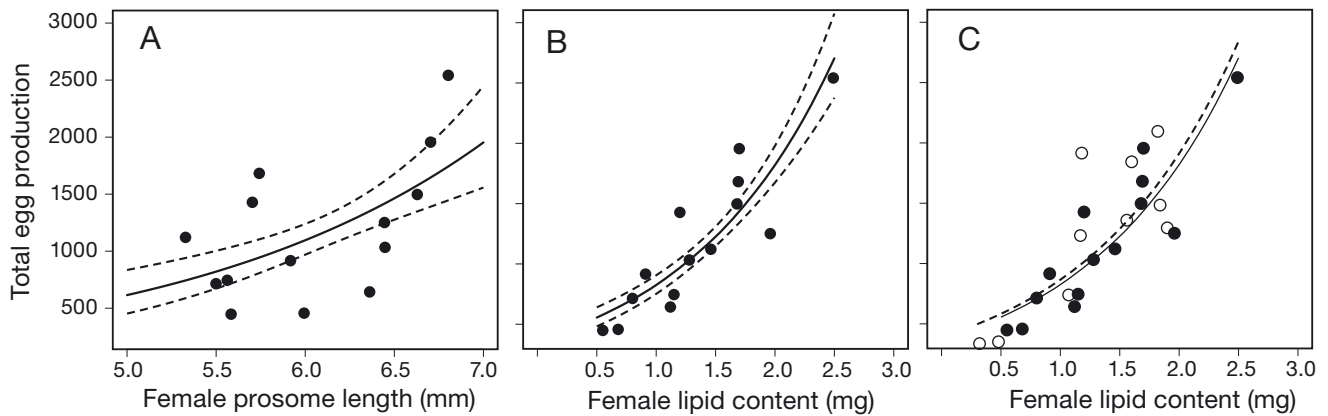
Fig. 2. (A) Total egg production of 14 female *Calanus hyperboreus* versus prosome length (mm); $\log(y) = 3.5 + 0.0006(x)$. Dashed lines denote standard error. (B) Total egg production of 14 female *C. hyperboreus* versus lipid content; $\log(y) = 5.92 + 0.79(x)$. Dashed lines denote standard error. (C) Total egg production of 14 (fitted model solid black line) and 24 (fitted model dashed line) female *C. hyperboreus* versus lipid content; $\log(y) = 5.97 + 0.79(x)$. Open circles denote females for which not all clutches were accounted for. Lines for standard error are omitted for better visualisation
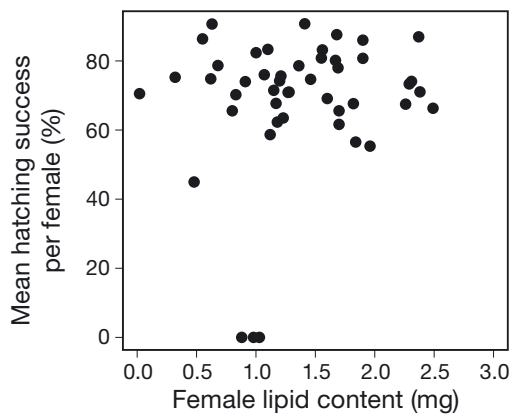

Fig. 3. Mean hatching success for *Calanus hyperboreus* nauplii (all females) versus initial lipid content of the females

DISCUSSION

The present study demonstrates that initial lipid content in *Calanus hyperboreus* females determines the reproductive success of the female in terms of total egg production. The relationship between initial lipid content and total egg production is based on a limited number of females. However, adding females that had laid an unknown number of clutches before observations started did not change the relationship (slopes identical, intercept changed from 5.92 to 5.97), indicating that the measurements are robust, and that there is a direct relationship between lipid content and remaining eggs to be produced at any time in the reproductive period in this species. Very

few studies exist where both total egg production and body size characteristics such as carbon content or prosome length have been measured for the same females. One study from the lower St Lawrence Estuary, Canada, found no positive relationship between initial carbon content of *C. hyperboreus* females and total eggs produced (Plourde et al. 2003). The authors have no explanation for this result, but state that individual reproductive potential calculated for field populations did not vary much due to relatively constant female body size at this particular site. In the present study, lipid content of the females ranged from 0.55 to 2.49 mg lipid equivalents, and there was a positive correlation between female lipid content and prosome length (linear regression, slope 0.66), affirming the effect of prosome length with regard to setting the upper limit for lipid storage. A strong relationship between initial lipid content of females and total number of eggs produced in a spawning season means that potential recruitment from a population can be estimated from measurements of the lipid sack area of freshly caught specimens, combined with abundance estimates of females. There are some constraints to the accuracy of these estimates, such as (1) mortality of females during winter, and (2) the fact that a small proportion of females does not spawn. Further, (3) if females terminate spawning and ascend to surface waters to feed on the spring bloom before lipids are completely exhausted, the number of offspring would be overestimated. Females in the present study had low lipid levels when spawning ended (visual observation), and oocytes were no longer present. Unfortunately,

the observational setup here did not allow for an evaluation of the within-population variability in timing of spawning, but studies of gonad stage distributions (E. Halvorsen pers. obs.) from January and April/May 2013 in the area indicate that a large portion of females are actively spawning or already spent in January, and all females are spent in the beginning of May. Spent females have been reported to ascend to the surface to feed on the spring bloom in April/May (Swalethorp et al. 2011, Henriksen et al. 2012), rebuild lipids and potentially re-develop gonads, which indicate that they are truly iteroparous. Assuming there is a trade-off between female survival and current reproduction, the age of the female (whether it is the first or second year of reproduction) could influence the degree of investment in egg production. A female in its first winter may be expected to save some lipid reserves to perform the vertical migration in spring and rebuild lipid reserves for a second reproductive season, whereas a female in its second winter could be expected to invest all her body reserves (not only lipids) in eggs before dying. A lipid budget can be made for each female based on the initial lipid content of the female, total number of eggs laid, and using a value of 0.55 µg lipid per egg (Henriksen et al. 2012). This gives an investment of lipids into eggs ranging from 30 to 60% in the 14 females, indicating that there is individual variability, which could be caused by the different ages of the females, but also that lipid is used for other purposes, such as metabolic expenditure and maintenance in the females during the reproductive period, as no female invested 100% of their lipids into eggs.

Since initial amount of lipid in the females determines the total number of eggs a female can produce in a spawning cycle, a lipid-rich female has the advantage of not only laying more eggs, but also of spreading her eggs over a longer time period, thereby enhancing the chances that some of the clutches are a success. There was no effect of female size or lipid content on hatching success of nauplii, indicating that the females are able to allocate a sufficient amount of essential lipid components to the eggs produced independent of total amount of lipid available (Jonasdottir et al. 2005). There was also no trend in hatching success with time for individual females. Whether total amount of lipids per egg varies between fat and lean females, and if this again influences the development of the nauplii after hatching, is still an open question. Nauplii that hatch in December may utilise the ice-algal bloom, which can start in March (Durbin & Casas 2014), or, depending on the timing of seasonal ice break-up, may

have to survive on the energy content provided with the egg for up to 6 months or more before food becomes available with the spring phytoplankton bloom. Experiments on stage development of nauplii from Disko Bay, Greenland, have shown that *C. hyperboreus* nauplii stage 3 (first feeding stage) can survive starvation for at least 30 d at 5°C (Jung-Madsen et al. 2013). Both sea temperature and lipid fatty acid composition (i.e. type and quality of the lipids provided with the egg) will probably influence the duration of starvation that nauplii can survive.

As a capital breeder, size at maturity sets an upper limit for storage of lipids in *C. hyperboreus*, thus influencing reproductive output in terms of total egg production. There is also an effect of food on body size in copepods (Vidal 1980, Klein Breteler & Gonzalez 1982), and thus food quantity and quality in the previous summers will influence the growth of different stages, and ultimately the final size of the female. *C. hyperboreus* is the most efficient of the *Calanus* species in turning phytoplankton carbon into high-energy lipids (Albers et al. 1996), with a highly specialised capacity for utilizing short but intense diatom blooms. Spawning at depth during winter ensures that eggs and naupli are present well before the ice-algal and phytoplankton bloom, a good strategy when the precise timing of the seasonal ice break-up can vary with several months between years. The exceptionally large size at maturity, long lifespan and iteroparity in this species seem to comprise a necessary strategy in the Polar Ocean, where the productive season in some years could be too short for the developing nauplii and copepodites to reach the first overwintering stage, CIII (Conover 1988). This is in contrast to Arctic shelf seas, where the smaller *C. glacialis* thrives with a more mixed strategy, with dependence of stored lipids for the early egg production phase, and then utilizing the ice-algae or phytoplankton bloom (i.e. income breeding strategy) during the peak egg production phase (Søreide et al. 2010). The climatic changes seen in the Arctic, with earlier ice break-up and a longer productive period for phytoplankton, may provide a longer period for growth and development. Higher surface temperatures in summer could increase development rates of offspring, leading to a shortening of the overall life span if later copepodite stages can be reached before the first overwintering, and increase offspring survival. The temperature–size rule, i.e. that copepods grow larger at lower temperatures (McLaren 1963, McLaren & Corkett 1981) as a result of development and growth not being equally affected by temperature (Forster et al. 2012), implies that *C. hyperboreus* growing in

Table 1. Prosome lengths (range or mean) of female *Calanus hyperboreus* from different regions

Region	Prosome length (mm)	Reference
Greenland Sea	5.9–7.4	Hirche (1997)
	6.2–6.7	Diel (1991)
	6.2–7.6	Sømme (1934)
	0.26–0.31[a]	Sømme 1934
Franz Josef-Land	6.3–7.0	Koszteyn & Kwasniewski (1992)
Yermak Plateau	5.3–7.1	Present study
Disko Bay	6.4–6.7	Swalethorp et al. (2011)
	6.0–6.5	Henriksen et al. (2012)
St. Lawrence Estuary	5.0–6.4	Plourde et al. (2003)
Georges Bank slope water	6.2	Conover (1967)
Gulf of Maine	5.4	Conover (1967)
Norwegian Sea) (Møre)	0.21–0.24[a]	Sømme (1934)
Amundsen Gulf	6.7 ± 0.80[b]	Forest et al. (2011)

[a]Carapace length; [b]median ± range

warmer water could end up with a smaller size at maturity, thus directly influencing the potential for lipid storage. A literature review (although probably not exhaustive) of female prosome lengths from various regions indicates that the largest females (>7 mm) are only found in high Arctic regions (Table 1). The overall effect of increased temperatures on *C. hyperboreus* fecundity in the Arctic will likely depend on the interplay between increased development rates and reduced size at maturity.

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