HORIZONS

Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles

ØYSTEIN VARPE*

NORWEGIAN POLAR INSTITUTE, FRAM CENTRE, N-9296 TROMSØ, NORWAY

*CORRESPONDING AUTHOR: oystein.varpe@gmail.com

Behaviour and life-history strategies of zooplankton have evolved in response to seasonal cycles in food availability, predation risk and abiotic conditions. A key challenge is to understand how different activities over the year are linked. For instance, how does a change in spring activities, such as the timing or amount of egg production, influence autumn activities, for instance energy storage or migration? Trade-offs viewed in relation to individual lifetime fitness consequences couple these events. The framework of optimal annual routines provides theory and methodology for consistent analyses of these temporal trade-offs. Here I describe the key parts of optimal annual routine models and how the models can be used to: (i) study phenology, life-history strategies, and population dynamics; (ii) predict responses to environmental change; and (iii) guide future zooplankton studies. I mainly discuss the adaptations of zooplankton species inhabiting high latitude oceans where the seasonal cycle and its effects are particularly strong. Empirical challenges include issues of seasonal resolution, state-dependent processes and individual variability. Two ecological problems with avenues for future work are discussed in particular detail: the role of sea ice and ice algae in the life cycle of copepods and krill, and the adaptive value and ecological consequences of semelparous versus iteroparous reproductive strategies.

KEYWORDS: *Calanus*; dynamic state-variable models; evolutionary ecology; match-mismatch; optimality modelling; reproductive value; seasonality

INTRODUCTION

The seasonal cycling of the environment over the year is among the most pronounced rhythms on planet earth. Plants and animals display many adaptations to these periodicities. Seasons are caused by the earth circling around the sun on a tilted axis, causing irradiance to vary over the year, mostly so at high latitudes. This leads to seasonal cycles in abiotic factors, such as temperature, wind and precipitation which propagate through biological production. The

seasonal primary production starts and is followed by higher trophic levels, such as zooplankton, fish and birds, including seasonal cycles in their distribution, activity and behaviour. Seasonality has resulted in adaptations, such as using particular periods of the year for reproduction, maintenance and growth, often coupled with seasonal migrations, reduced activity and extensive energy storage. Importantly, natural selection forms the combined set of adaptations and their timing, resulting in the annual routine of the organism (McNamara and Houston, 2008).

Annual routines can be viewed as schedules of activities or behaviours over the annual cycle. Trade-offs link these events because certain activities cannot be performed at the same time, and because activities at one point of the year influence the organism's physiology and state and therefore determine the options available, as well as their consequences, at later times of the year (Houston and McNamara, 1999). These temporal trade-offs must be included if we are to predict optimal annual routines (Houston and McNamara, 1999; Varpe *et al.*, 2007; McNamara and Houston, 2008) and animal responses to changes in seasonal environments (Visser and Both, 2005; Fero *et al.*, 2008). Acknowledging trade-offs within the annual cycle, and their state-dependence, raises interesting questions. For instance, how will changes in costs and benefits of spring activities, such as timing or amount of egg production, influence autumn activities such as energy storage or migration?

Here I focus on zooplankton and on the highly seasonal environments of high latitudes, where climate change is expected to be most pronounced, and where proper tools for studies of seasonal ecology are particularly important. I outline the key parts of optimal annual routine models and some of the model possibilities and limitations. McNamara and Houston (McNamara and Houston, 2008) and Fero *et al.* (Fero *et al.*, 2008) provide recent and more complete reviews of the modelling framework. I describe how annual routine models can be used to study life histories and phenology, including responses and adaptations to environmental change. Furthermore, I suggest how these models can guide future field and laboratory investigation. Empirical challenges relating to temporal resolution, state dependence and individual variability are covered. Finally, I deal with two cases of zooplankton ecology in particular detail, with an annual routine perspective being important for both: the role of sea ice and ice algae for zooplankton, and the issue of semelparity versus iteroparity as alternative reproductive strategies.

OPTIMAL ANNUAL ROUTINE MODELS

Optimal annual routine models incorporate the periodicity of the environment and include individual state variables, and therefore allow optimal behaviours or energy allocation decisions to depend not only on time of year, but also on individual characteristics or states, such as size, energy reserves or spatial position (Figs 1 and 2). When studying strategies covering the whole year, long term fitness considerations are needed as optimization criteria. That is, alternative actions must be evaluated in terms of their current and future consequences (Williams, 1966). This approach is incorporated in optimality modelling which uses dynamic programming to find optimal state-dependent strategies by maximizing the number of descendents left far into the future (McNamara and Houston, 1996). Developing an optimal annual routine model involves three main steps. (i) We need to describe the individual and its interactions with the environment. This includes formulating and parameterizing individual processes, such as rates of growth, metabolism and egg production, and to
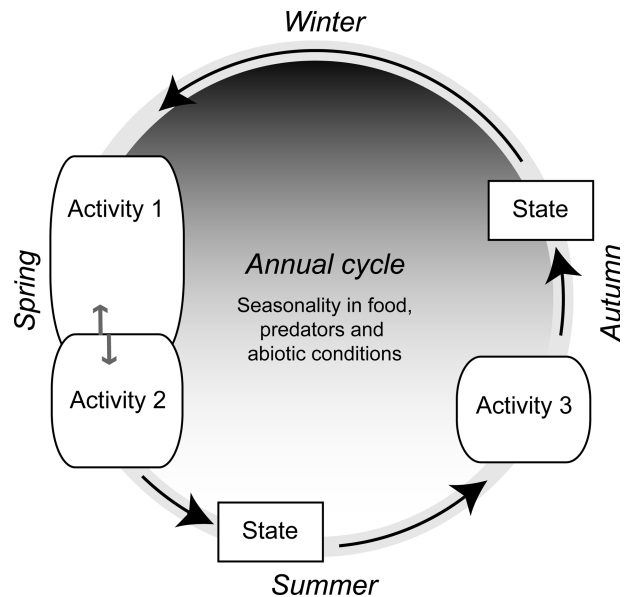
Fig. 1. Key components of annual routines include the scheduling of activities over the annual cycle and the role of the organism's state in linking activities and generating temporal trade-offs. Optimal annual routine models analyse these trade-offs and predict optimal state-dependent strategies using long-term fitness considerations as optimization criteria (Houston and McNamara, 1999; McNamara and Houston, 2008). Adaptations to seasonality are shaped by the complex interactions between activities, whether they can be performed simultaneously or not (cf. grey arrows), how the timing of one activity influence the optimal timing of others and how one activity, through its influence on state, has delayed consequences and determines the options available later in the cycle. See Fig. 2 for annual routines in a zooplankton context.
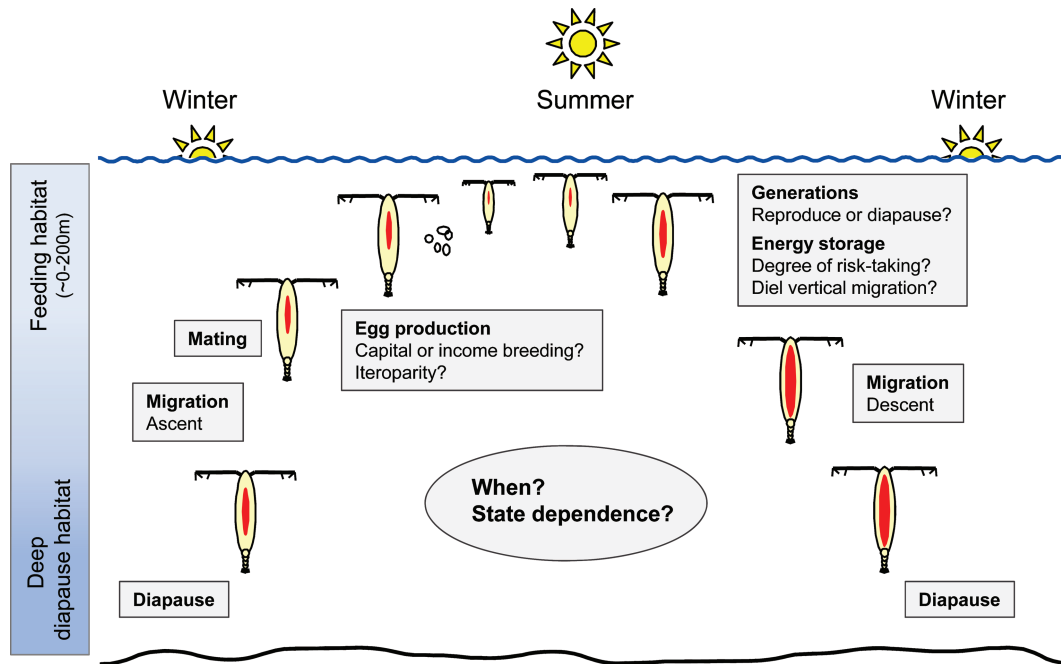
Fig. 2. A zooplankton annual routine, exemplified by a herbivorous copepod in an oceanic environment. Some key life-history traits and behaviours are indicated, along with the phenology question of when to perform a given activity. Energy reserve is a central physiological state variable, here represented by a lipid sac (red colour). The reserves vary over the year and with developmental stage. Egg production and development takes place in association with the spring phytoplankton growth. Mode of egg production (capital- versus income-breeding) differs between species, and can be state-dependent within a species (Varpe *et al.*, 2009). Some capital breeders, such as *C. hyperboreus* or *Neocalanus* spp., produce and release eggs at depth. Diapausing copepods spend the winter in the deep, dark and safer interior of the ocean. Development from egg to adult includes six nauplie stages and six copepodite stages (simplified here). Factors shaping the costs and benefits of alternative annual routines include predation risk relative to food through the year and the role of energy reserves at different times of the year. Models that have dealt with these and related topics include work by Fiksen and Carlotti (Fiksen and Carlotti, 1998) and Varpe *et al.* (Varpe *et al.*, 2007, 2009).

choose which states to include. One must also characterize the periodic environment (e.g. food availability, predation risk and temperature) and define the actions to optimize, that is the alternative behaviours and allocation decisions included (e.g. migration and reproduction). (ii) The second step is to implement the optimization to find optimal state-dependent strategies. The emerging arrays of state-dependent strategies and fitness (expected reproductive value as a function of state and time of year) are the central output from the optimization. They can provide interesting results, such as predictions on the variable value of offspring born at different times of the year (Houston and McNamara, 1999; Barta *et al.*, 2006; Varpe *et al.*, 2007). (iii) Finally, a very useful third step is to assume that population members use the predicted optimal strategies and then compute population dynamics by forward iterations. This can be done by matrix projections (Mangel and Clark, 1988; Houston and McNamara, 1999). The population dynamics offer predictions on quantities such as population growth rate, egg production and mortality, and importantly, on abundances, state distributions and habitat use of the population members over

the annual cycle. Fiksen and Carlotti (Fiksen and Carlotti, 1998) and Varpe *et al.* (Varpe *et al.*, 2007, 2009) provide examples of such population simulations for zooplankton.

Fero *et al.* (Fero *et al.*, 2008) compare optimal annual routine models with alternative individual-based models, such as models using empirically derived strategies (or rules). Predetermined strategies, for instance a fixed date for migration, are of limited value in novel circumstances, where modified strategies are likely to be followed. Optimal annual routine models offer a mechanistic basis for the strategies and a link to long-term fitness considerations, which allow optimality derived strategies to emerge and the possibility of new solutions to new conditions. Therefore, these models can predict possible new strategies or adaptations to conditions not yet observed in the field (Fero *et al.*, 2008), and numerical experiments can contrast the performance of a strategy that evolves in response to change with a strategy that does not evolve (McNamara and Houston, 2008).

Optimal annual routine models come with limitations and challenges. The complexity increases rapidly as states are included. This requires careful consideration of

which states to include, with the risk of excluding states that are important. Adding states may increase the phenotypic plasticity of the modelled organism (McNamara and Houston, 1996). Also, testing and analysing the direct output from the optimization, the fitness array and the optimal state-dependent strategies, is a complex task. It can also be difficult to test these prediction from an empirical perspective, for instance to measure the state of individuals. The population level predictions are often easier to compare with observations. Furthermore, there are also conceptual challenges. The fitness criteria used in optimal annual routine models, maximization of expected number of descendants left far into the future, is not well suited for situations with large interannual variability in environmental conditions (McNamara and Houston, 1996). Additionally, the optimality models do not capture dynamic interactions with feedback, for instance, between predator and prey, but see Alonzo et al. (Alonzo et al., 2003) for one solution. In-depth treatments of opportunities and limitations of optimality modelling, dynamic programming and models of optimal annual routines are available (e.g. Houston and McNamara, 1999; Clark and Mangel, 2000; Fero et al., 2008).

SEASONALITY AND ZOOPLANKTON ANNUAL ROUTINES

The biosphere displays an impressive variability of environments, some towards the extreme endpoints on gradients in abiotic (and biotic) conditions. Polar habitats are viewed as extreme, not by the organisms evolved to live there, but by those who investigate their ability to live under such conditions. Low temperatures, sea ice and strong seasonality in light and primary production are among the characteristics of polar ecosystems. Seasonality in solar irradiance is the key driver, and the seasonality of the environment therefore typically increases with latitude.

With limited ability of horizontal movement (in contrast with many fishes, birds and mammals), high latitude zooplankton species have evolved a range of adaptations to allow permanent residence in highly seasonal environments. These adaptations include: diapause (Hirche, 1996; Fiksen, 2000); seasonal vertical migrations (Andrews, 1966; Conover, 1988); resting eggs (Marcus, 1996); long lifespan, slow growth and low metabolism (McLaren, 1966); shrinkage (Ikeda and Dixon, 1982); and extensive energy storage (Lee et al., 2006; Falk-Petersen et al., 2009). The scheduling of these

traits is a key characteristic of life histories and annual routines. Most of these traits, and their timing, are explained as adaptations of herbivores to a highly pulsed food source (Ji et al., 2010), the phytoplankton bloom, including the need to minimize mortality and metabolism during the non-feeding season. The role of omnivory and predation risk may on the other hand deserve more attention as explanatory variables.

Several species and groups of zooplankton are omnivorous (e.g. Ohman and Runge, 1994), some are also specialized predators, for which seasonality in food is less pronounced. Activity may therefore be higher for a larger proportion of the year (Hagen, 1999). For instance, *Oithona similis* produce eggs all year round in the Arctic (Lischka and Hagen, 2005). A challenge regarding less seasonal strategies is to understand to what degree egg fitness (the likelihood that an egg contributes to future generations) nevertheless varies over the year. Maximum egg fitness is not necessarily at the time of highest population level egg production, as predicted in a copepod annual routine model (Varpe et al., 2007). Parents may maximize their long-term fitness by producing eggs at a time with sub-optimal offspring fitness, a parent-offspring conflict referred to as an "internal life-history mismatch" (Varpe et al., 2007). This adds complexity to the match-mismatch concept (cf. Cushing, 1990) because the difference between a match in terms of offspring and parental fitness is revealed.

Despite the importance of predators as a selective force (Verity and Smetacek, 1996; Alonzo and Mangel, 2001), top-down processes are less studied compared with effects operating through food availability or the physical environment. However, predation risk can be highly seasonal, well-documented in freshwater copepods (Hairston and Munns, 1984) and predicted to be a central factor in shaping zooplankton phenology and annual routines (Fiksen and Carlotti, 1998; Varpe et al., 2007). In the oceans, migrating predators can cause seasonality in predation risk (Kaartvedt, 2000; Varpe et al., 2005) as can constraints operating on visually searching predators whose efficiency depends on the seasonal cycle in irradiance (Varpe and Fiksen, 2010).

With this multifaceted role of seasonality, it is unfortunate that most experiments, field studies and models consider single seasonal events at the time. This concern is particularly relevant at high latitudes, where a seasonal perspective on ecology is crucial and where logistic challenges most often prevent seasonal coverage, with some notable exceptions (e.g. Dawson, 1978; Tande, 1982; Kosobokova, 1999; Madsen et al., 2001; Nygård et al., 2010). Achieving seasonal coverage

through automated data collection is one recent and promising development (Berge *et al.*, 2009).

Field studies can benefit from interactions with theoretical modelling. Models serve as thinking tools and generate explicit hypotheses (Hilborn and Mangel, 1997). In optimal annual routine models, the predictions are on the scheduling of activities over the year (Fig. 2), and how state-dependence influences which behaviours or energy allocations that are optimal at a given time. Model predictions are useful for planning and designing field studies that aim at efficient seasonal coverage. Importantly, models can provide theoretical and seasonal context also for observational snap shots, studies with limited seasonal coverage. In this article, most examples and much of the focus are on relatively long-lived species (Fig. 2). However, multiple generations per year are common in many zooplankton species (Allan, 1976). Models of annual routines can also be developed for these shorter lived species, with the number of generations per year predicted by the model. For instance, a model for *Calanus finmarchicus* predicted two generations per year (Fiksen and Carlotti, 1998).

STATE VARIABLES AND STATE-DEPENDENT STRATEGIES

Individuals differ in behaviour and in their ability to reproduce and survive. One explanation for this variability is that the state of individuals also varies and that strategies are state-dependent (McNamara and Houston, 1996). States are often linked to physiological processes. Energy reserves (or other reserves such as proteins), body size, immune function and parasite load are examples of states. In optimal annual routines, states are important because a given activity can induce lagged effects through a change in state (Fig. 1). For instance, whether to feed or not will affect the level of reserves, which may not have immediate effects but instead influence future activities (such as maturation or egg production) and their value. In other words, an activity has consequences, at other times of the year and for other activities, a key argument for why events in an annual routine should not be studied in isolation (McNamara and Houston, 2008).

Modelling studies predict state-dependent strategies (Houston and McNamara, 1999; Clark and Mangel, 2000), and observations support these predictions, particularly in organisms where repeated measurements and observations of the same individual are easier than for small plankton. One example is how energy reserves

may determine breeding in seabirds (Chastel *et al.*, 1995; Olsson, 1997). Examples of observed state-dependent behaviour and life-history strategies in zooplankton include lipid-dependent diel vertical migration (DVM) (Hays *et al.*, 2001), seasonal migrations and diapause (Ohman *et al.*, 1998; Rey-Rassat *et al.*, 2002) and rates of egg production (Hirche and Kattner, 1993), as well as sex-specific activity levels and timing of maturation and seasonal migrations (Gilbert and Williamson, 1983). Furthermore, different developmental stages behave differently, causing stage-dependent distributions (Dawson, 1978; Sameoto, 1984). Also, the state of the gonads may offer valuable insight into the reproductive phenology and its links to the energy reserves of the female (Hagen and Schnack-Schiel, 1996), and detailed studies of gonads allow estimation of past reproduction (Kosobokova, 1999). Below I point at how state-dependence draws attention to at least two particular challenges for empirical zooplankton work.

Seasonal state-dependence

Models can incorporate high temporal resolution and therefore be useful for studies of annual routines and phenology. A key challenge for empirical work is to achieve some of the same resolution, for instance by studying how state-dependent responses vary over the year and depend on the life-history context. We may distinguish between short-term state-dependent behaviours, such as DVM, and responses linked to longer term activities, such as state-dependent initiation of diapause, reproduction or seasonal migrations. However, there is a continuum of time scales and important links between short-term behaviours and life-history decisions, suggesting that these should be studied in relation. Model examples include zooplankton work where DVM is included in addition to life-history decisions, such as reproduction and diapause (Fiksen, 1997; Fiksen and Carlotti, 1998). Long-term fitness maximization is used in these models and a key prediction is that behaviour depends on state as well as the life-history context and season. It would be exciting to see more field studies having a seasonal perspective on state-dependence in zooplankton. Hays *et al.* (Hays *et al.*, 2001) elegantly documented how feeding and DVM in *Metridia pacifica* depended on body condition. At other times of the year, with different risks and food availability, the state-dependence is likely to be different, as shown for condition-dependent partial-migration in freshwater fish (Brodersen *et al.*, 2008). Wallace *et al.* (Wallace *et al.*, 2010) used acoustic techniques to characterize different DVM patterns over the entire year in Arctic zooplankton, but could not ascribe these patterns

to species or states, a key challenge for future studies using acoustics. DVMs are central in determining trophic interactions and vertical fluxes in the water column (Bollens et al., 2011). It is therefore important to expand our studies of DVM to include better treatments of how the role of state varies with environmental conditions, life-history stage and time of year. Understanding state-dependent responses, and how they vary over the year, is one key to predict how organisms may respond to new and altered environments (Fero et al., 2008).

Individual-based zooplankton ecology

Individuals respond to their environment and their responses vary, depending both on individual state and the environment. It is important to quantify processes at the level of individuals in order to predict behaviour, annual routines and the resulting population dynamics and trophic interactions. State-dependence, as described above, draws attention to individuals as a study unit. Many zooplankton studies include measurements of body mass, carbon and nitrogen contents, and composition of proteins and fatty acids. The motivation is often to quantify production or species differences in feeding and life-history strategies, less often to investigate individual variability in behaviour, growth or reproduction in relation to these states. Also, due to their small size, individuals are often pooled for laboratory analyses. This is unfortunate as the information on individual variability is then lost and unavailable for further analyses. Another challenge for empirical work is therefore to establish observational techniques and laboratory analyses that prepare ground for an individual-based zooplankton ecology. Promising developments include video analyses for studies of behaviour (Tsuda and Miller, 1998; Kiørboe et al., 2009) and photographic methods for lipid reserve measurements (Vogedes et al., 2010). Measurements of individual enzyme activity (Ohman et al., 1998; Hassett, 2006) and repeated observations of individuals using acoustics (Klevjer and Kaartvedt, 2011) are other promising avenues.

ANNUAL ROUTINES AND TWO CURRENT CHALLENGES IN ZOOPLANKTON ECOLOGY

Annual routines draw attention to the scheduling of activities over the annual cycle and how these activities may be traded against each other. Below I discuss two challenges in zooplankton ecology where this

perspective is central and where both modelling and empirical work are needed: (i) the changing polar oceans and the role of sea ice in the life cycle of zooplankton, and (ii) semelparity and iteroparity as alternative reproductive strategies.

Sea ice, ice algae and zooplankton

Primary production in seasonally ice-covered waters consists of ice algae growing on the under-surface of sea ice, followed by open water phytoplankton (Arrigo et al., 2010). This may lead to a bimodal food distribution (Fig. 3) for herbivores that graze on both ice algae and phytoplankton. Copepods (Runge and Ingram, 1988; Conover and Huntley, 1991) and krill (O'Brien, 1987) are among these grazers. A bimodal food source offers opportunities, such as maturation or egg production
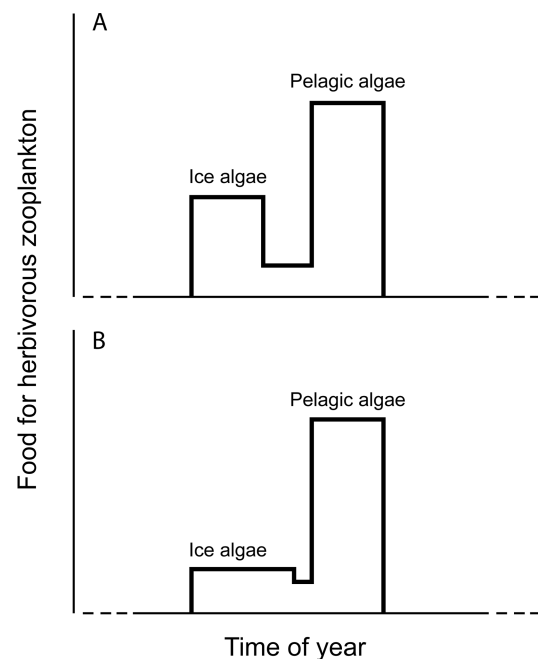
Fig. 3. Two of several alternative generic seasonal distributions of primary producer abundance in seasonally ice-covered waters. An ice algae bloom at the undersurface of the ice precedes a pelagic phytoplankton bloom. The timing of the two blooms and their duration and magnitude are poorly known, including the degree of bimodality. We need an improved understanding of these factors in order to determine food availability and predict annual routines of high-latitude pelagic herbivores. For instance, if the two blooms are separated in time by a period of low food availability, particular zooplankton adaptations may have evolved to deal with this challenge. The shape of the scenarios is deliberately made box like to stress the different blooms and their potential separation. The ice algae production typically occurs sometimes during March–June and the pelagic production sometimes during May–September (Jin et al., 2011; Leu et al., 2011). Useful units for food availability are Chla or carbon per volume or area.

fuelled by feeding on ice algae (Tourangeau and Runge, 1991; Søreide et al., 2010), a head start compared with scenarios with a pelagic bloom only. Relatively rapid life cycles at high latitudes may be the paradoxical consequence. However, a bimodal food source comes with challenges, such as how to handle the period in between the blooms and how different life cycle stages may best match and utilize the blooms. Furthermore, the effects of environmental change gets more complex since the relative change of two food sources must be understood. Rapid changes in the sea ice extent and thickness of the polar oceans, particularly for the Arctic, are predicted and reported, with consequences for both ice algae and phytoplankton (e.g. Jin et al., 2011; Leu et al., 2011; Wassmann, 2011). With declining area and changing distribution of sea ice, the ice algae bloom may become insignificant and adaptations to this food source maladaptive.

There are important questions needing more attention if we are to understand the consequences of reduced sea ice distributions for polar zooplankton. (i) What is the seasonality of the bimodal food source from a grazer's point of view? The relative magnitude and timing of the ice algae and pelagic blooms are poorly known and may take different forms (Gosselin et al., 1997; Jin et al., 2011, Fig. 3). (ii) If waters become ice-free in spring, how will that influence the amount and duration of the pelagic bloom (Hunt et al., 2002; Kahru et al., 2011; Wassmann, 2011)? (iii) What is the predation risk of zooplankton feeding on ice algae? Light levels are low under ice, which reduces the efficiency of visually searching predators. There may therefore be increased predation risk as sea ice thickness declines, allowing an earlier ice algae bloom but causing higher predation risk. (iv) How does the presence of an ice algae bloom modify the value of capital breeding (Varpe et al., 2009)? Is there a benefit of egg production also prior to the ice algae production? If yes, for which species and individuals in which state? (v) How are the copepods feeding on the ice algae? Can they feed on algae attached to the ice, in ways similar to krill (Hamner et al., 1983; Marschall, 1988), or are they, maybe more likely, grazing on algae that are loose from the ice and accessible in the water below? We do not now. Observations and experimentation casting light on feeding mechanisms will help us understand the value of this food source.

Ice algae and the ice habitat are important also for the highly abundant herbivore of the Southern Ocean, the Antarctic krill (Marschall, 1988; Brierley et al., 2002; Atkinson et al., 2004). Some of the questions suggested for copepods above would be valuable to answer also in a krill context. Differences between copepods and krill,

in size, life cycles and longevity, may serve as interesting contrasts.

Iteroparity and semelparity

Life histories and annual routines are intimately linked and synonymous in the case of annual species. Scheduling of reproduction is a key characteristic of life histories. Some species have one reproductive period, while others breed several times during a life time. Cole (Cole, 1954) pinpointed this difference and introduced the terms *semelparity* and *iteroparity*. Cole's simplistic model of semelparity versus iteroparity was followed by more realistic models which included both mortality and age at maturity (reviewed by Stearns, 1992; Brommer, 2000). Theoretical models help us predict in which cases semelparity is likely to be favoured over iteroparity.

An interesting case from zooplankton ecology is that of the relatively long-lived herbivorous calanoid copepods, such as *Calanus* spp. These species are regarded as semelparous in the sense that the reproduction is believed to take place in one breeding season only. Hairston and Bohonak (Hairston and Bohonak, 1998) termed this strategy "iteroparous annual" because of the multiple clutches within a season. Here I refer to semelparity as breeding completed in 1 year, and iteroparity as breeding in two or more years. Some species have constraints that make iteroparity unlikely, such as the *Neocalanus* spp., where the adult stage is unable to feed and therefore cannot refuel for a subsequent overwintering and breeding season (Miller et al., 1984). In species where adults feed, studies of semelparity versus iteroparity are scarce because individuals are difficult to follow over time; age and past signs of breeding are difficult to observe; and because adult mortality will cause second year breeders to constitute a relatively small proportion of the reproducing part of the population. One exception is Kosobokova's (Kosobokova, 1999) study of *C. glacialis* ovaries. She was able to characterize the difference between re-maturing gonads and gonads maturing for the first time. From this, she inferred iteroparity in *C. glacialis*. Compared with a semelparous strategy, new trade-offs must then be considered. These include when to stop producing eggs and rather prioritize energy storage as a preparation for the next winter and breeding season. Recent field studies have found some evidence for the timing of such switches in *C. glacialis* and *C. hyperboreus*, whereas *C. finmarchicus* seemed to proceed according to a semelparous strategy (Swalethorp et al., 2011). There should be continued attempts to document the extent of iteroparity and to understand its adaptive value in this group of plankton.

Previous copepod life-history models have been constrained to semelparity (e.g. Varpe *et al.*, 2007). It would be interesting to see this assumption relaxed and the annual routines predicted in a context where iteroparity may emerge as the optimal strategy. This modifies the temporal trade-offs and it may help us understand the seasonality in egg production. If iteroparity is common, one should expect few eggs to be produced at late and sub-optimal times of the feeding season, hence a more compressed seasonality in egg production than that predicted by Varpe *et al.* (Varpe *et al.*, 2007).

CONCLUDING REMARK

The perspectives provided by optimal annual routines contribute to a firmer theoretical basis for zooplankton ecology and when applied hopefully also to a greater appreciation of zooplankton adaptations as inspiration in evolutionary ecology (cf. Hutchinson, 1951). The logic of theory and evolutionary reasoning can strengthen the predictive power of our toolbox, and models help in generating hypotheses about life-history strategies, phenology and the relations to environmental factors. An understanding of phenology is essential in order to predict responses to environmental change (Visser and Both, 2005) and to further develop central concepts of ecology, such as the match-mismatch hypothesis (Cushing, 1990). If equipped with an understanding covering the scale of annual routines, we can better understand and predict zooplankton responses to perturbations and changes in their seasonal environment.

ACKNOWLEDGEMENTS

FUNDING

REFERENCES

Allan, J. D. (1976) Life history patterns in zooplankton. *Am. Nat.*, **110**, 165–180.

Alonzo, S. H. and Mangel, M. (2001) Survival strategies and growth of krill: avoiding predators in space and time. *Mar. Ecol. Prog. Ser.*, **209**, 203–217.

Alonzo, S. H., Switzer, P. V. and Mangel, M. (2003) Ecological games in space and time: the distribution and abundance of Antarctic krill and penguins. *Ecology*, **84**, 1598–1607.

Andrews, K. J. H. (1966) The distribution and life-history of *Calanoides acutus* (Giesbrecht). *Discov. Rep.*, **XXXIV**, 117–162.

Arrigo, K. R., Mock, T. and Lizotte, M. P. (2010) Primary producers and sea ice. In Thomas, D. N. and Dieckmann, G. S. (eds), *Sea Ice*. Wiley-Blackwell, Oxford, pp. 283–325.

Atkinson, A., Siegel, V., Pakhomov, E. *et al.* (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, **432**, 100–103.

Barta, Z., Houston, A. I., McNamara, J. M. *et al.* (2006) Annual routines of non-migratory birds: optimal moult strategies. *Oikos*, **112**, 580–593.

Berge, J., Cottier, F., Last, K. S. *et al.* (2009) Diel vertical migration of Arctic zooplankton during the polar night. *Biol. Lett.*, **5**, 69–72.

Bollens, S. M., Rollwagen-Bollens, G., Quenette, J. A. *et al.* (2011) Cascading migrations and implications for vertical fluxes in pelagic ecosystems. *J. Plankton Res.*, **33**, 349–355.

Brierley, A. S., Fernandes, P. G., Brandon, M. A. *et al.* (2002) Antarctic krill under sea ice: elevated abundance in a narrow band just south of ice edge. *Science*, **295**, 1890–1892.

Brodersen, J., Nilsson, P. A., Hansson, L. A. *et al.* (2008) Condition-dependent individual decision-making determines cyprinid partial migration. *Ecology*, **89**, 1195–1200.

Brommer, J. E. (2000) The evolution of fitness in life-history theory. *Biol. Rev.*, **75**, 377–404.

Chastel, O., Weimerskirch, H. and Jouventin, P. (1995) Body condition and seabird reproductive performance: a study of three petrel species. *Ecology*, **76**, 2240–2246.

Clark, C. W. and Mangel, M. (2000) *Dynamic State Variable Models in Ecology*. Oxford University Press, New York.

Cole, L. C. (1954) The population consequences of life history phenomena. *Q. Rev. Biol.*, **29**, 103–137.

Conover, R. J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high-latitudes of the northern hemisphere. *Hydrobiologia*, **167**, 127–142.

Conover, R. J. and Huntley, M. (1991) Copepods in ice-covered seas: distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. *J. Mar. Syst.*, **2**, 1–41.

Cushing, D. H. (1990) Plankton production and year-class strength in fish populations: an update of the match mismatch hypothesis. *Adv. Mar. Biol.*, **26**, 249–293.

Dawson, J. K. (1978) Vertical distribution of *Calanus hyperboreus* in the central Arctic Ocean. *Limnol. Oceanogr.*, **23**, 950–957.

Falk-Petersen, S., Mayzaud, P., Kattner, G. *et al.* (2009) Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.*, **5**, 18–39.

Fero, O., Stephens, P. A., Barta, Z. *et al.* (2008) Optimal annual routines: new tools for conservation biology? *Ecol. Appl.*, **18**, 1563–1577.

Fiksen, Ø. (1997) Allocation patterns and diel vertical migration: modeling the optimal *Daphnia*. *Ecology*, **78**, 1446–1456.

Fiksen, Ø. (2000) The adaptive timing of diapause: a search for evolutionarily robust strategies in *Calanus finmarchicus*. *ICES J. Mar. Sci.*, **57**, 1825–1833.

Fiksen, Ø. and Carlotti, F. (1998) A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia*, **83**, 129–147.

Gilbert, J. T. and Williamson, C. E. (1983) Sexual dimorphism in zooplankton (copepoda, cladocera, and rotifera). *Annu. Rev. Ecol. Syst.*, **14**, 1–33.

Gosselin, M., Levasseur, M., Wheeler, P. A. *et al.* (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep-Sea Res. II*, **44**, 1623–1644.

Hagen, W. (1999) Reproductive strategies and energetic adaptations of polar zooplankton. *Invertebr. Reprod. Dev.*, **36**, 25–34.

Hagen, W. and Schnack-Schiel, S. B. (1996) Seasonal lipid dynamics in dominant Antarctic copepods: energy for overwintering or reproduction? *Deep-Sea Res. I*, **43**, 139–158.

Hairston, N. G. and Bohonak, A. J. (1998) Copepod reproductive strategies: life-history theory, phylogenetic pattern and invasion of inland waters. *J. Mar. Syst.*, **15**, 23–34.

Hairston, N. G. and Munns, W. R. (1984) The timing of copepod diapause as an evolutionarily stable strategy. *Am. Nat.*, **123**, 733–751.

Hamner, W. M., Hamner, P. P., Srand, S. W. *et al.* (1983) Behavior of Antarctic krill, *Euphausia superba* chemoreception, feeding, schooling, and molting. *Science*, **220**, 433–435.

Hassett, R. P. (2006) Physiological characteristics of lipid-rich "fat" and lipid-poor "thin" morphotypes of individual *Calanus finmarchicus* C5 copepodites in nearshore Gulf of Maine. *Limnol. Oceanogr.*, **51**, 997–1003.

Hays, G. C., Kennedy, H. and Frost, B. W. (2001) Individual variability in diel vertical migration of a marine copepod: why some individuals remain at depth when others migrate. *Limnol. Oceanogr.*, **46**, 2050–2054.

Hilborn, R. and Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press.

Hirche, H. J. (1996) Diapause in the marine copepod *Calanus finmarchicus*: a review. *Ophelia*, **44**, 129–143.

Hirche, H. J. and Kattner, G. (1993) Egg-production and lipid-content of *Calanus glacialis* in spring: indication of a food-dependent and food-independent reproductive mode. *Mar. Biol.*, **117**, 615–622.

Houston, A. I. and McNamara, J. M. (1999) *Models of Adaptive Behaviour*. Cambridge University Press, Cambridge.

Hunt, G. L., Stabeno, P., Walters, G. *et al.* (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. *Deep-Sea Res. II*, **49**, 5821–5853.

Hutchinson, G. E. (1951) Copepodology for the ornithologist. *Ecology*, **32**, 571–577.

Ikeda, T. and Dixon, P. (1982) Body shrinkage as a possible overwintering mechanisms of the Antarctic krill, *Euphausia superba* Dana. *J. Exp. Mar. Biol. Ecol.*, **62**, 143–151.

Ji, R. B., Edwards, M., Mackas, D. L. *et al.* (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. *J. Plankton Res.*, **32**, 1355–1368.

Jin, M., Deal, C., Sang, L. H. *et al.* (2011) Investigation of Arctic sea ice and ocean primary production for the period 1992–2007 using a 3-D global ice-ocean ecosystem model. *Deep-Sea Res. II*, doi:10.1016/j.dsr1012.2011.1006.1003.

Kaartvedt, S. (2000) Life history of *Calanus finmarchicus* in the Norwegian Sea in relation to planktivorous fish. *ICES J. Mar. Sci.*, **57**, 1819–1824.

Kahru, M., Brotas, V., Manzano-Sarabia, M. *et al.* (2011) Are phytoplankton blooms occurring earlier in the Arctic? *Glob. Change Biol.*, **17**, 1733–1739.

Kiørboe, T., Andersen, A., Langlois, V. J. *et al.* (2009) Mechanisms and feasibility of prey capture in ambush-feeding zooplankton. *Proc. Natl Acad. Sci. USA*, **106**, 12394–12399.

Klevjer, T. A. and Kaartvedt, S. (2011) Krill (*Meganyctiphanes norvegica*) swim faster at night. *Limnol. Oceanogr.*, **56**, 765–774.

Kosobokova, K. N. (1999) The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. *Polar Biol.*, **22**, 254–263.

Lee, R. F., Hagen, W. and Kattner, G. (2006) Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.*, **307**, 273–306.

Leu, E., Søreide, J. E., Hessen, D. O. *et al.* (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Prog. Oceanogr.*, **90**, 18–32.

Lischka, S. and Hagen, W. (2005) Life histories of the copepods *Pseudocalanus minutus*, *P. acuspes* (Calanoida) and *Oithona similis* (Cyclopoida) in the Arctic Kongsfjorden (Svalbard). *Polar Biol.*, **28**, 910–921.

Madsen, S. D., Nielsen, T. G. and Hansen, B. W. (2001) Annual population development and production by *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. *Mar. Biol.*, **139**, 75–93.

Mangel, M. and Clark, C. W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton.

Marcus, N. H. (1996) Ecological and evolutionary significance of resting eggs in marine copepods: past, present, and future studies. *Hydrobiologia*, **320**, 141–152.

Marschall, H. P. (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. *Polar Biol.*, **9**, 129–135.

McLaren, I. A. (1966) Adaptive significance of large size and long life of the chaetognath *Sagitta elegans* in the Arctic. *Ecology*, **47**, 852–855.

McNamara, J. M. and Houston, A. I. (1996) State-dependent life histories. *Nature*, **380**, 215–221.

McNamara, J. M. and Houston, A. I. (2008) Optimal annual routines: behaviour in the context of physiology and ecology. *Phil. Trans. R. Soc. Lond. B*, **363**, 301–319.

Miller, C. B., Frost, B. W., Batchelder, H. P. *et al.* (1984) Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. *Prog. Oceanogr.*, **13**, 201–243.

Nygård, H., Wallenschus, J., Camus, L. *et al.* (2010) Annual routines and life history of the amphipod *Onisimus litoralis*: seasonal growth, body composition and energy budget. *Mar. Ecol. Prog. Ser.*, **417**, 115–126.

O'Brien, D. P. (1987) Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985. *J. Crustac. Biol.*, **7**, 437–448.

Ohman, M. D., Drits, A. V., Clarke, M. E. *et al.* (1998) Differential dormancy of co-occurring copepods. *Deep-Sea Res. II*, **45**, 1709–1740.

Ohman, M. D. and Runge, J. A. (1994) Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St-Lawrence. *Limnol. Oceanogr.*, **39**, 21–36.

Olsson, O. (1997) Clutch abandonment: a state-dependent decision in king penguins. *J. Avian. Biol.*, **28**, 264–267.

Rey-Rassat, C., Irigoien, X., Harris, R. *et al.* (2002) Energetic cost of gonad development in *Calanus finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.*, **238**, 301–306.

Runge, J. A. and Ingram, R. G. (1988) Underice grazing by planktonic, Calanoid copepods in relation to a bloom of ice microalgae in southern Husdon Bay. *Limnol. Oceanogr.*, **33**, 280–286.

Sameoto, D. D. (1984) Vertical distribution of zooplankton biomass and species in northeasterns Baffin Bay related to temperature and salinity. *Polar Biol.*, **2**, 213–224.

Søreide, J. E., Leu, E., Berge, J. *et al.* (2010) Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Change Biol.*, **16**, 3154–3163.

Stearns, S. C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.

Swalethorp, R., Kjellerup, S., Dunweber, M. *et al.* (2011) Grazing, egg production, and biochemical evidence of differences in the life strategies of *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* in Disko Bay, western Greenland. *Mar. Ecol. Prog. Ser.*, **429**, 125–144.

Tande, K. S. (1982) Ecological investigations on the zooplankton community of Balsfjorden, Northern Norway: generation cycles, and variations in body-weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). *J. Exp. Mar. Biol. Ecol.*, **62**, 129–142.

Tourangeau, S. and Runge, J. A. (1991) Reproduction of *Calanus glacialis* under ice in spring in southeastern Hudson Bay, Canada. *Mar. Biol.*, **108**, 227–233.

Tsuda, A. and Miller, C. B. (1998) Mate-finding behaviour in *Calanus marshallae* Frost. *Phil. Trans. R. Soc. Lond. B*, **353**, 713–720.

Varpe, Ø. and Fiksen, Ø. (2010) Seasonal plankton-fish interactions: light regime, prey phenology, and herring foraging. *Ecology*, **91**, 311–318.

Varpe, Ø., Fiksen, Ø. and Slotte, A. (2005) Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia*, **146**, 443–451.

Varpe, Ø., Jørgensen, C., Tarling, G. A. *et al.* (2007) Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Oikos*, **116**, 1331–1342.

Varpe, Ø., Jørgensen, C., Tarling, G. A. *et al.* (2009) The adaptive value of energy storage and capital breeding in seasonal environments. *Oikos*, **118**, 363–370.

Verity, P. G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.*, **130**, 277–293.

Visser, M. E. and Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B*, **272**, 2561–2569.

Vogedes, D., Varpe, Ø., Søreide, J. E. *et al.* (2010) Lipid sac area as a proxy for individual lipid content of arctic calanoid copepods. *J. Plankton Res.*, **32**, 1471–1477.

Wallace, M. I., Cottier, F. R., Berge, J. *et al.* (2010) Comparison of zooplankton vertical migration in an ice-free and a seasonally ice-covered Arctic fjord: an insight into the influence of sea ice cover on zooplankton behavior. *Limnol. Oceanogr.*, **55**, 831–845.

Wassmann, P. (2011) Arctic marine ecosystems in an era of rapid climate change. *Prog. Oceanogr.*, **90**, 1–17.

Williams, G. C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.*, **100**, 687–690.