

Life history adaptations to seasonality

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List of papers

Paper 1

Øystein Varpe, Øyvind Fiksen, and Aril Slotte

Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia* 2005 (146) 443-451

Paper 2

Øyvind Fiksen, Øystein Varpe, and Stein Kaartvedt

Reply to Horizons Article “Some ideas about the role of lipids in the life cycle of *Calanus finmarchicus*” Irigoien (2004): II. *Journal of Plankton Research* 2004 (26) 980-980

Paper 3

Øystein Varpe, Christian Jørgensen, Geraint A. Tarling, and Øyvind Fiksen

Early is better: seasonal egg fitness and timing of reproduction in a zooplankton life-history model. *Manuscript*

Paper 4

Øystein Varpe, Christian Jørgensen, Geraint A. Tarling, and Øyvind Fiksen

The value of capital and income breeding from a life cycle perspective. *Manuscript*

Paper 5

Øystein Varpe and Øyvind Fiksen

A marine perspective on capital and income breeding. *Manuscript*

Paper 6

Øystein Varpe, Torkild Tveraa, and Ivar Folstad

State-dependent parental care in the Antarctic petrel: responses to manipulated chick age during early chick rearing. *Oikos* 2004 (106) 479-488

Abstract

The thesis contains studies of animal life histories at high latitudes. Several topics are covered; from ecosystem consequences of life histories to tests of specific behavioural predictions put forward based on life history arguments. Work on complete life histories is also included in an attempt to understand the evolution of capital and income breeding in marine copepods. My main research questions, followed by main topics and findings, are as follows:

- How are seasonal environments influencing life history traits and phenology?
- What are the roles of storage as a reproductive adaptation?
- How are individual states, particularly energy reserves, influencing optimal life histories and behaviour?

Paper 1 deals with how growth of a high-latitude pelagic fish, the Norwegian spring-spawning herring, is scheduled during the annual cycle. Body mass data reveal a short period of rapid annual increase in body mass at the time when the copepod *Calanus finmarchicus* is the main prey. The food consumption (energy units) of the entire herring population is estimated, using a bioenergetics model, and compared with production estimates of *C. finmarchicus*. Large herring populations, particularly because of their selective predation on older stages, can influence population dynamics of *C. finmarchicus*, and may explain some of the copepod's life history adaptations. Finally, estimates of spatial energy transport are presented; caused by herring migrating from oceanic feeding grounds to coastal overwintering and spawning sites. The large herring stock may be responsible for the world's largest biomass transport caused by a migrating population. This flux of energy and nutrients is important for coastal species, and potentially for interactions not yet studied, such as between herring eggs and benthic invertebrates.

Paper 2 is a short comment on recent studies of copepod life cycles that have suggested that the large lipid stores serve as a means of obtaining neutral buoyancy at a given depth - an ultimate explanation of energy stores. There is, however, a need to understand the use of energy reserves remaining after the winter, before we understand

the ultimate explanation for storage. That is, we must study to what degree copepods are capital breeders (using energy reserves for egg production) as opposed to income breeders (relying on concurrent food intake for egg production).

These ideas were pursued in **papers 3 and 4** which are based on a life history model of the abundant Southern Ocean copepod *Calanoides acutus*. Life history trade-offs arise in the model because bioenergetics, developmental constraints, and interactions with the environment (temperature, food availability and predation risk) are made explicit. Hence, trade offs need not be assumed. The model is state-dependent and reproductive value of individuals with different developmental stage and condition is predicted by dynamic programming. The model predicts the optimal energy allocation and diapause strategies that maximise reproductive value at any time of the year, determining the entire life history strategy. A highly seasonal pattern in optimal egg-laying time is predicted. This optimality is, however, seen from an egg's perspective. Actual egg production, as predicted from population simulations, do not match the seasonal peak in offspring fitness, which suggest that later life cycle stages are subject to trade-offs and constraints causing laying dates sub-optimal from the offspring's perspective. Mechanism behind the mismatch are studied. Eggs from capital breeding have higher fitness than income bred eggs as capital breeding takes place early in the season, even before the phytoplankton bloom. The time an egg is produced influences its probability of: 1) reaching a stage capable of diapause; 2) developing large energy reserves, and; 3) developing to a stage capable of capital breeding next season. We conclude that seasonality in both growth potential and predation risk are key drivers of copepod life histories.

Paper 5 is on the costs and benefits of capital breeding in aquatic environments, including ecosystem consequence that follow from capital breeding strategies such as the lipid transport of herring. Costs and benefits of carrying energy reserves are different for aquatic compared to terrestrial organisms. General analyses of the costs and benefits of capital breeding would improve by incorporating more of the findings from studies of marine organisms. Marine biologists, on the other hand, may better understand and appreciate the life history trade-offs of their study organism if

theoretical concepts from the predominantly terrestrial literature were used more actively. Quantification of pre-breeding costs of a capital breeder strategy is one such issue. These costs may influence how we understand life cycle questions such as timing of diapause and other state-dependent decisions prior to breeding.

Paper 6 is on a long lived seabird whose reproductive strategy includes sophisticated parental care. State-dependent behavioural responses are studied, and as in the papers above, an important state is body condition in terms of stored resources. The petrels are found to adjust chick feeding and guarding according to their own body condition, the body condition of their partner with whom they co-ordinate the chick-rearing period, and finally, adjustments in response to the chick's needs for food and guarding. All these factors are found to play a role in determining individual behaviour. The results are obtained using a field experiment, and are discussed in relation to the life history strategies of seabirds.

Prologue

The herring

Together with thousands of neighbours in the school the herring cruises the ocean in search for food. The menu varies, but for some hectic months, a small copepod is the favourite. Some months later, the same herring is waiting for spring. Spring, or even late winter, means spawning time – the time when the work of last summer is cashed in as thousands of eggs deposited on the bottom of coastal spawning grounds. The challenges of the herring are many – where should it swim to obtain the best food, where should it spend the winter to be safe and not waste the valuable stores acquired through summer, where and when should it spawn, and what effort should be spent on egg production during each annual spawning event?

The copepod

When winter-storms are roaring at the surface and the sun's energetic input reaches the annual minimum, many copepods have retreated to great depths to rest. Just as the herring, the copepod has brought with it a valuable package of resources. These stores fuel the daily needs but are also for maturation and early egg-production next spring. Before that, however, the copepod must respond to some clue telling it to migrate more than thousand meters to the surface. Positioning itself in the water column is one of the main challenges of a copepod and in contrast to the herring, its miniature size allows for little control of its horizontal destiny. There are also other key questions. Many are linked to the temporal patterns of food availability and risk of death: when should it produce offspring; how large should the energy reserves be before the winter; or should it instead reproduce this summer, leaving the winter with the offspring?

The seabird

It is heating up, the snow melts from the nest-sites, and the bird returns to the colony to breed. This is not a new experience; it did so last year and the year before, and will most likely breed next year. Organizing such a long life is in strong contrast to the challenge of the copepod. Also, the offspring are experiencing something very different from that of a young herring or a copepod, a caring parent. The single chick

is fed and guarded and thought many of the crucial skills of life while eager predators circle the skies above. Parents with surplus resources can care well for the chick and respond to its changing needs. Still, the parent must spare resources. It may be next year's breeding conditions that that are ideal.

The common denominator

The great many ways to live a life have been observed by humans at all times. Some of this variation is described in the examples above. Charles Darwin understood that all these patterns of life had a common denominator – they were outcome of a process he termed evolution by natural selection (Darwin 1859). Individuals vary in their characteristics and those with the greatest success (leaving many high quality offspring) leave descendants that harbour many of the same qualities as their parents. Variation is however generated so that new types challenge existing ones. In the long run this leads to adaptations, including speciation. All aspects of life influenced by genetics are subject to this process; both the evolution of a well functioning eye and the evolution of life history characteristics such as clutch size in birds or egg size in herring. Life history theory is the branch of biology dealing with how growth and reproduction of organisms are scheduled through time. Life histories are also the focus of this thesis, in the context of high latitude copepods, fish and seabirds.

Introduction to synthesis

The main actors are now introduced, and a summary of the thesis is given. I will continue with some background on life history theory, including its history and some of the recent developments. Then I present some key concepts of life history theory and illustrate them with relevant cases from the papers (referred to as **P1-P6**, see list of papers page 7). Finally, I give further background and perspectives on some central issues of the thesis. 1) State-dependent life history models and dynamic optimisation; 2) capital and income breeding as a continuum of reproductive strategies; 3) seasonality as a selective force in life history evolution, and; 4) ecosystem consequences of life histories and behaviour.

Life history theory

History and recent developments

Early landmarks

Important landmarks in the studies of life history evolution appeared at increasing rates from the 1950s. One landmark is Cole's (1954) extensive discussion and analyses of population consequences arising from life histories. Another milestone is Williams's (1966a) short and to the point formalisation of what has later been termed the General Life History Problem; how current and residual reproductive value should be balanced. A crucial source of inspiration for both Cole and Williams, as well as today's evolutionary ecologists, was the work by R. A. Fisher, in particular his book entitled *The Genetical Theory of Natural Selection*¹ (Fisher 1930). Here, Fisher gave evolutionary theory a mathematical basis and he contributed to merge Darwin's theory of natural selection with Mendel's theory of inheritance. Life history questions were an important part of Fisher's focus, with one of his major contributions being the

¹ for a digital collection of Fisher's work see:

<http://digital.library.adelaide.edu.au/coll/special//fisher/index.html>

concept of reproductive value. His work undoubtedly paved the way for evolutionary biology in general and for life history theory in particular.

Life history theory is today a separate field of biology (Roff 1992, Stearns 1992, Roff 2002). However, life history studies are at the heart of biology and focus on how patterns of growth and reproduction are scheduled through life. The goal is to understand which factors that have selected for and currently select for observed variation in life history traits both within and between species. A wide range of ecological topics depend on insights from life history studies, including management of harvested resources (Law and Grey 1989), biodiversity (Dieckmann and Ferrière 2004), population dynamics (Saether et al. 2005), and phenological responses to environmental change (Visser and Both 2005). Studies of life histories are much driven by theory developed from models in addition to empirical investigations.

Returning to the early landmarks, Cole's (1954) work is by many considered an important advent of systematic studies of life history characteristics. He discussed the population growth consequences of life histories and emphasised the use of the per capita growth rate r (or as termed by Fisher (1930), the Malthusian parameter) as a fitness measure. One of Cole's key findings was the large influence of age at first reproduction on per capita growth rate. Further, Cole fathered the terms semelparity and iteroparity, introducing the need to understand the benefits of surviving to reproduce several times (iteroparous) compared to only once (semelparous).

Williams' (1966a) work some ten years later dealt with the costs of reproduction and the importance of adult survival (Williams 1966a). Fisher (1930) had postulated that enhanced investment of current reproductive effort would decrease the output from future reproduction, and he raised the question of how an organism should divert available resources to growth vs. reproduction. Williams stated the general solution to Fisher's problem:

“expenditures on reproductive processes must be in functional harmony with each other and worth the costs, in relation to the long-range reproductive interest; and the use of somatic processes is favored to the extent that somatic survival, and perhaps growth, are important for future reproduction” **G.C. Williams (1966a)**

He also formalised the solution mathematically. Williams coined the term *residual reproductive value* for the part of reproductive value that may be realised in the future (Williams 1966a). In doing so, he started a still lasting focus on the consequences of current behavioural and life history decisions on future opportunities and possibilities, and he drew attention to the implications of differential mortality of individuals following different strategies.

William's insights had direct implications for current life history ideas such as Lack's (1947) studies of clutch sizes in birds. Lack predicted optimal clutch size based on the number of chicks that the parents were able to raise, and he assumed that the parents' foraging capability would be limiting. Lack did not consider the interaction between clutch size and parent mortality. Williams did however acknowledge that increased investments at one point may lead to reduced survival later (Williams 1966a). Hence, the future survival of a parent investing in a larger clutch is lower than if the clutch had been smaller. This cost reduces Lack's optimal clutch size as iteroparous parents invest prudently in a single reproductive attempt (Drent and Daan 1980). There are empirical support for the costs of reproduction suggested by Williams (Lindén and Møller 1989, Dijkstra et al. 1990). Williams (1966a) showed how reproductive decisions may serve the interest of the *individual*, and in the same paper he added to his critique of the contemporary ideas that reproductive processes serve the survival of the *species* (Williams 1966b).

Adding realism: individual states and explicit environments

Early analytical models relied on simple assumptions, for instance that fecundity and survivorship are constant with age. More realistic models followed, such as Schaffer's (1974) analyses of coevolution of age specific rates. Pianka and Parker (1975) also modelled age-specific life histories, and the appreciation of age differences raised a general appreciation of individual differences (Pianka and Parker 1975). Studies of phenotypic plasticity (the same genotype expressing different phenotypes depending on the environment) followed (e.g. Stearns and Koella 1986) and plasticity may itself be regarded a genetically determined trait (Houston and McNamara 1992). The focus on individual differences raised the question of which individual characteristics –

states – that indeed influence the optimal life history (McNamara and Houston 1996). Physiological states became viewed as important and were included in population models (Metz and Diekmann 1986), and states other than age, such as size and condition (for instance energy store, nutrient reserve, and parasite load) were suggested to be biologically more meaningful (McNamara and Houston 1996). For instance, there is a clear link between high energy reserves and high fecundity if reproduction depends on internal stores. The fact that increased reproductive effort at one point may have long lasting effects on future survival or reproduction (Gustafsson and Sutherland 1988, Daan et al. 1990) also suggest that condition variables determine reproductive success. Variation in life history traits such as laying date and clutch size may therefore be caused by individuals adjusting behaviour and investments in response to their state (Drent and Daan 1980).

In parallel with the development towards state-dependent life history models, there was a growing appreciation of density dependence, such as its influence on optimal reproductive effort (Charlesworth and Leon 1976). The importance of density dependence has been discussed since, and it is clear that the choice of fitness measure in optimisation studies should depend on the form of density dependence that operates (Mylius and Diekmann 1995). The focus on density dependence, as well as frequency dependence (Heino et al. 1998), created a general interest in how a life history strategy influences its own environment.

Optimisation and adaptation

Optimisation is a search for the combination of life history traits that maximises fitness (an optimization criteria reflecting the success of a strategy). Commonly used fitness measures, r and R_0 , assume a constant environment in the sense that mortality and fecundity rates are constant and that the whole population consists of individuals with the same life history strategy (Stearns 2000). The classical explanations of life history variation are obtained using this optimality approach (Stearns and Schmid-Hempel 1987, Stearns 2000).

Eco-evolutionary feedbacks (Dieckmann and Ferrière 2004) are ignored in the optimization tradition that pervades early life history theory. Critics of *optimization*

suggests *adaptation* as the alternative in the sense that good strategies perform well only relative to the environment they are an integral part of (Dieckmann and Ferrière 2004). Linking life history evolution with population dynamics is a route of current research which attempts to create an explicit environment and population where evolution takes place, thereby allowing both density and frequency dependent effects. This line of research is often called adaptive dynamics (Dieckmann 1997, Waxman and Gavrillets 2005). The focus on adaptation is also central in individual based models where algorithms, such as the genetic algorithm, mimicking evolution are used to search for well adapted life histories (Strand et al. 2002). When used for life history questions, individual based models allow for the eco-evolutionary feedbacks.

The focus on eco-evolutionary feedbacks has been argued to be driven more by logic than evidence against the explanatory power of classical optimisation (Stearns 2000). There are however recent and strong evidence for long term coexistence of several good, but not optimal, life history strategies in the same population. Impressive field studies of lizards have revealed coexistence of three strategies that all perform well when in minority (Sinervo and Lively 1996) and strategies that alternate in abundance because one performs well at low densities, the other at high densities (Sinervo et al. 2000). These field-studies may have been inspired by directions taken by theory as theory sometimes strongly shapes what is studied in the wild.

Elements of life history theory

According to Stearns (2000) a biologist should ask at least three questions when studying life history evolution. First, which factors affect survival and reproduction of individuals of different ages and sizes (or other individual states)? Second, how are life history traits connected to each other? Third, what constraints are there on how a trait can vary? When working on these questions one uses more or less standardised concepts and terminology. The following concepts are important for the subsequent discussion and papers.

Life history traits

A life history trait is a characteristic of an individual (phenotypes are typically studied) that directly influences how growth and reproduction is scheduled through time. Key life history traits are age and size at maturity, juvenile and adult survival, offspring size and offspring numbers. Additional traits include growth patterns (determinate vs. indeterminate growth), migrations, energy storage, energy acquisition tactics and resting stages.

Life history traits dealt with here include seasonal growth patterns and migration (**P1, P3, P4**), diapause (**P2-P4**), capital and income breeding (**P1-P5**) and parental care (**P6**).

Short term behavioural strategies may be seen as the realization of a life history strategy. Whether a mother leaves the offspring alone or guards it one day longer may determine the reproductive success for the entire year (**P6**) and the future survival of the mother (and the offspring). Williams (1966a) used such micro-scale life history traits when dividing reproductive value in a current and residual (future) component. The challenge is to develop a currency where the fitness-consequences of behaviour are realistically related to lifetime fitness (McNamara and Houston 1986).

Fitness

Fitness is a measure of the success of a life history strategy relative to other strategies. Ultimately, success is linked to the ability to leave offspring, grand-offspring and so on. This assures high rate of gene propagation and thereby representation of the parent's genes in future generations (Dawkins 1976). Several quantitative measures of

fitness have been suggested, all are approximations with limitations and assumptions, but some have been used extensively, such as the intrinsic rate of increase r or the reproductive ratio R_0 (cf. Brommer 2000). Both measures focus on age specific patterns of survival and fecundity, two quantities that may indeed be measured in field studies. As it is not only the number of offspring that determine long term success, there is a need for more than simple counts. An ideal fitness measure should include the potential of an offspring resulting in grand-offspring. This potential varies with time of birth (seasonality), the number of co-specifics (density dependence), or the presence of other successful strategies (frequency dependence).

As we have seen, feedback from the environment is not treated using r or R_0 , and it has been argued that an invasion criterion is needed to define a true fitness concept. Mylius and Dieckmann (1995) formulated the master fitness concept as ‘*the average exponential growth rate of the invader, growing in the environment set by the resident*’ (see also Metz et al. 1992). In the case of an evolutionarily stable strategy (ESS) no strategy can in fact invade (Maynard Smith 1982). In adaptive dynamics invaders (or mutants) are tested in the resident strategy’s environment (Dieckmann 1997). A main lesson from the development and use of fitness measures is to be aware of their limitations and implicit assumptions, and to choose accordingly (Mylius and Dieckmann 1995, Pasztor et al. 1996, Brommer 2000).

The optimisation model presented in **P3** and **P4** relies on r as fitness measure, and reproductive value (see below) is maximised to predict optimal daily decisions that in turn determine the optimal life history. **P6** on the other hand is a snapshot from reality where parental care strategies are studied. In this and similar studies, offspring survival or body condition are assumed to measure success. Such simplified measures are used when future success of parents and offspring are logistically difficult to follow (but see Gustafsson and Sutherland 1988, Daan et al. 1990).

Life history trade-offs

Life history traits are combined and in sum make up the entire life history. Changes in one trait may lead to changes in other traits, and trade-offs refer to those cases where a positive change (in terms of fitness) in one trait leads to a negative change in others.

Trade-offs operate simultaneously, and to understand life history variation one needs to understand interactions between trade-offs (e.g. Roff et al. 2006). It is useful to distinguish evolutionary trade-offs from physiological trade-offs (Stearns 1992). Evolutionary trade-offs imply a genetical link between two traits and are defined by the decrease in the value of a given trait as another trait is selected for. Physiological trade-offs are caused by competition for energy or material within a species, such as the trade-off between structural growth and energy reserves (**P3**, **P4**) or between allocation of resources to somatic vs. reproductive functions (**P3**, **P4**, **P6**).

Trade-offs are manifested by the common coexistence of certain life history traits. Fast life histories have short lifespan, rapid development, high fecundity and small offspring. On the slow side, such as for seabirds or ourselves, we find long lifespan, high age at maturation, parental care, and few offspring (**P6**). Yet, there are exceptions, such as the many eggs spawned by the long lived herring during annual spawning-events (**P1**).

Constraints

Constraints are boundaries on possible solutions, such as minimal viable egg-size, growth rates or swimming speeds. The state-space (possible sizes of structure and energy reserves) assumed in the copepod model is one example (**P3**). Similarly, there are constraints on the amount of food gathered during a day, and thereby on growth and the rate of reproduction (**P3**).

Constraints are also set by the evolutionary past as some traits do not contain the variation needed for rapid evolution. The fact that all species in the order Procellariiformes, such as the Antarctic petrel (**P6**), has a clutch size of one, may therefore be a lineage-specific effect (Stearns 1992), where a lineage is a set of species with common ancestry. Other traits, such as the degree of capital vs. income breeding in closely related copepods, seem not to be lineage specific and are instead free to evolve rapidly (**P5**). Lineage specific effects illustrate the limits of adaptation. Traits regarded as adaptations today evolved to yesterday's environment and from genetical raw material that may limit potential solutions. Organisms are adaptation executers

and not fitness maximisers and may sometimes seem maladapted or have characteristics of little importance for fitness (cf. Gould and Lewontin 1979).

Reproductive value

Reproductive value (Fisher 1930) is a measure of how different individuals are expected to contribute to population growth, that is, the remaining number of offspring an individual can expect to have. Hence, subsets of a population such as age classes, take different numerical values, and thereby have different importance in the ongoing evolution. Mathematically, Fisher (1930) defined reproductive value as

$$v_x = \frac{e^{mx}}{l_x} \int_x^{\infty} e^{-mt} l_t b_t dt$$

where l_x is the survival probability until age x , l_t is the survival probability and b_t the fecundity to ages t later in life, m is the population growth rate which he termed the Malthusian parameter. There is discounting for population growth, such that contribution by future offspring are devaluated if the growth rate is positive.

Traditionally, age has been used to categorize individuals, but reproductive values depending on body condition, habitat, time of birth, or other individual states are increasingly popular and biologically more realistic (McNamara and Houston 1996). This focus on state dependence is a development reflected here (**P3**, **P4**, **P6**).

Reproductive value typically increases from the onset of life towards maturation, declining thereafter (Fisher 1930, Stearns 1992). Reproductive value of an individual of given age assumes survival until that age and is by definition independent of the past of the individual, only by its present state.

Reproductive value is used as an optimization-criteria in models of adaptive behaviour and life history (Houston and McNamara 1999) (**P3**, **P4**), but also when analysing data on life histories (Daan et al. 1990, Tinbergen and Daan 1990).

State-dependent life history models and dynamic optimization

Individuals can take a number of actions. Examples include to feed or rest, breed or skip breeding, and migrate or stay. Each action affects the individual's state, for instance body mass, and individuals with different states are affected differently. In addition, the effect of an action may vary within the season or in different habitats. If one seeks to find the optimal actions of individuals, not just at one point in time, but for consecutive time steps, it is apparent that the success of a great many individual trajectories must be calculated. Soon the brute force of computer simulations becomes limiting, and a shortcut is needed.

Future expectations of an individual depend on its present but also future actions. One may therefore start with the future and work backwards. The optimal action at a given time is hence conditional on already determined future actions. Dynamic programming elegantly solves such problems (Mangel and Clark 1988, Houston and McNamara 1999, Clark and Mangel 2000).

For life history problems one starts at the end of a life and proceeds towards birth, or for an annual life cycle (**P3**), starts at mid-winter and works backwards. Individuals alive at his endpoint need a reward, in this case a reproductive value. However, any reward will do as long as the model is run until the set of optimal actions are the same for consecutive years; and therefore independent of the initial reward (Houston and McNamara 1999). State-dependent reproductive values for all states and any day of the year emerges and can be used to predict optimal state-dependent actions.

Dynamic programming have been used extensively for questions in behavioural ecology (Houston and McNamara 1999, Clark and Mangel 2000). Simplified fitness measures are then used, such as being alive on the final day. More recently, the same approach has been used for life histories (Fiksen and Carlotti 1998, Jørgensen and Fiksen 2006) (**P3**, **P4**) and annual routines (McNamara et al. 1998, Barta et al. 2006). The optimal strategy, which is then a sequence of actions through the year, now maximises the number of offspring produced or the reproductive value of descendants left far into the future.

There are limitations to the approach as it is outlined here and applied in **P3** and **P4**. The strategy is optimal only in the defined environment, and there are no feedbacks from the strategy back on the environment, for instance in terms of altered food availability or predation risk. Effects of density dependence on optimal life histories are therefore not tested. As it is not known how the strategy alters the environment, the potential of other strategies as invaders can not be tested, and frequency dependence is not included. Finally, as the environment has no interannual variation, we can not model life history adaptations to fluctuating environments, such as bet-hedging strategies. There exists no equivalent to maximisation of descendants left far into the future when the environment is fluctuating (McNamara and Houston 1996, McNamara 2000).

The limitations must be evaluated against strengths. The method is useful when linking short-term behaviour to life history strategies (e.g. Fiksen 1997). Further, we can elucidate life history trade offs because we link consequences of actions at different points in time (**P3**, **P4**). State-dependence creates focus on the plastic potential of organisms and explicitly acknowledges individual variation (Houston and McNamara 1999) (**P3**, **P4**). Finally, optimization by dynamic programming predicts highly realistic life histories when combined with bioenergetics models (Fiksen and Carlotti 1998, Jørgensen and Fiksen 2006) (**P3**, **P4**), including a condition dependent phenomena such as skipped spawning (Jørgensen et al. 2006). Skipped reproduction would not occur in a purely age structured model, but rely on states more closely linked to physiology, such as energy reserves.

Capital and income breeding as a continuum of reproductive strategies

Life history strategies reflect how an organism's limited resources are allocated to three typically considered purposes, growth, maintenance, and reproduction. This allocation question is the focus of reproductive effort theory (e.g. Williams 1966a), which predicts that resource *allocation* should balance an individual's present effort against its chances of survival and future reproduction. The focus on residual reproductive value has directed much attention to the costs of reproduction paid after the offspring is independent, as when clutch-size is manipulated and the effect on future parental success is followed (Dijkstra et al. 1990). Resource *acquisition* has received less attention in life history studies (Jönsson 1997). One aspect of resource acquisition is storage, which may be viewed as a fourth main purpose to which resources should be allocated (Reznick and Braun 1987). Stores allow organisms to reproduce at times or in areas where food is scarce. Reproduction based on previously acquired stored resources are referred to as *capital breeding*, whereas reproduction based on current food intake is termed *income breeding* (Stearns 1992, Jönsson 1997).

Treating capital breeding as a life history strategy directs attention to costs paid prior to offspring production (Jönsson 1997). The distinction between costs incurred before as opposed to after offspring production was made by Sibly and Calow (1984) and has later been termed pre- and post-breeding costs (cf. Jönsson et al. 1998). Pre-breeding costs must be studied to understand the trade-offs of a capital breeder (Jönsson 1997). For instance, knowing the degree of capital breeding is important when studying short term adjustments of parental care (Chastel et al. 1995). A capital breeder can judge at an early stage if it has the resources needed to complete the necessary care of an offspring, and if necessary, it should defer reproduction at an early stage. For a strategy on the income breeder side, it may pay to reduce own condition for a while, as feeding conditions may soon change, and in turn allow successful reproduction (see also **P6**). Furthermore, studying capital breeding attracts attention to costs of acquiring and carrying resources, which are often intimately linked to predation risk (Jönsson et al. 1995) (**P5**). Clear benefits of capital breeding are expected, as life cycles with mortality costs prior to the release of offspring should

be selected against. Why are there for instance semelparous capital breeders (Sibly and Calow 1986)?

In high-latitude copepods, closely related species are represented along the full range of the capital-income breeder continuum (Lee et al. 2006), but the causes behind this variation is poorly understood (but see Hagen and Schnack-Schiel 1996). A general benefit of capital breeding is that feeding is decoupled from breeding, with the possibility of breeding when the offspring have the highest value. In many seasonal environments peak offspring fitness is early in the feeding season (Nilsson 1999, Reznick et al. 2006), favouring capital breeding. This is also predicted for the copepod studied here (**P3**, **P4**) where the ideal egg should be laid even prior to the feeding season. Other copepods use capital breeding to gain spatial independence from the food source, and produce offspring at depth (Miller et al. 1984). Copepods experience predation risk when storing energy in the surface habitat, and the gathered stores scale directly with next year's fecundity. Hence, the classical trade-off between fecundity and survival is experienced prior to breeding. One should then expect a level of stores maximising a combination of survival and the fecundity realised next spring. At the inter-specific level, differences in predation risk may explain variation in the degree of capital breeding, and intra-specifically, one should expect plastic behavioural and life history responses to the level of predation risk and stores acquired (Fiksen and Carlotti 1998) (**P4**, **P5**). High-latitude copepods constitute an excellent group of study species to further elucidate the costs and benefits of capital and income breeding (**P2-P5**).

Seasonality as a selective force in life history evolution

Phenology is concerned with the dates of natural events in their annual cycle. Many such events are life history events, for instance flowering or arrival of migrating birds. Timing of life history events within the annual cycle are important when there is seasonality, for instance in food availability (Cushing 1990) and predation risk (Vonesh 2005). Life histories of months and longer are exposed to this seasonality and annual events are common in life cycles spanning several years. Timing of breeding, growth, and diapause influence survival and fecundity directly and are therefore life history traits *per se*. Although profound at high latitudes there are also annual environmental cycles at lower latitudes (e.g. Gu and Adler 2004) to which life history adaptations are expected (Watling and Donnelly 2002, Lee et al. 2006).

Life histories in temperate and high-latitude systems have marked fitness gradients related to timing of reproduction (Rowe et al. 1994, Nilsson 1999). This is a recurring topic of the thesis, treated most explicitly when predicting the seasonal variation in reproductive value of a copepod egg (**P3**), patterns that can only be understood in relation to the seasonal environment (food, predation risk and temperature). Timing of reproduction is also a central component of the annual cycle of the Norwegian spring-spawning herring (**P1**), which needs to place eggs at the coast when temperature and food availability render possibilities of efficient larval growth (cf. Cushing 1990). Both the timing (Devold 1963, Varpe et al., unpublished) and area (Holst et al. 2002) of spawning has varied historically, and it is a present challenge to understand the causes of this variation, as well as the impact on the coastal ecosystem (**P1**).

Other factors than food may limit the time-window available for reproduction, such as the availability of ice floes for breeding seals (Lydersen and Kovacs 1999), or nest sites free of snow in birds. The synchronised breeding of the Antarctic petrel studied here (**P6**) may be a consequence of a short period available for nesting or it may be a predator-swamping strategy (Ims 1990, Varpe and Tveraa 2005).

In seasonal environments there are also adaptations to long periods with low food availability. Dormancy and diapause are such adaptations, implying reduced

metabolism, and the use of safe habitats, which may require long seasonal migrations (**P3**). In annual organisms, different life cycle stages may serve as the link between the productive seasons. Many calanoid copepods spend the winter in well developed stages close to maturity (**P3, P4**), whereas others have resting eggs (Uye 1985). Adaptations to seasonal resource depressions also include migration away from the area and to more abundant resources, as seen in efficient travellers such as birds and marine mammals (Alerstam et al. 2003).

Finally, seasonality may act differently on offspring compared to parents with potential for parent-offspring conflicts regarding time of reproduction. In iteroparous life cycles prudence may cause the conflict, because the parent should balance investment in young against its chances to survive and reproduce in the future. When it is energetically costly to reproduce early, although beneficial for the offspring, the prudent parent will delay reproduction until it can justify the cost (Drent and Daan 1980, Daan and Tinbergen 1997). A conflict is also predicted here (**P3, P4**). Eggs are laid later than their time of maximum fitness. This occurs because it pays to delay capital breeding so that income breeding can follow directly. The first eggs do, however, still have markedly higher fitness than the last.

It is important to understand life histories in terms of the reproductive value produced, not simply in terms of the number of offspring. Knowing the reproductive value of an individual has consequences for how we should interpret data and how harvested stocks should be managed. Times of the year when only a few offspring are born may seem unimportant from a managing point of view, but it may in fact be these individuals that contribute most to next generations (**P3, P4**).

Ecosystem consequences of life histories and behaviour

"On coasts long frequented by herring, and favorably situated in other respects, towns gradually spring up."

Bjørnstjerne Bjørnson, first sentence, *The Fisher Maiden* (1869)

Because of trade-offs there are no super-organisms that have solved all challenges of life history evolution. Dieckmann and Ferrier (2004) recently discussed biodiversity in light of the absence of such super-organisms, or “Darwinian Demons” (Law 1979), and drew the attention to life history trade-offs as a fundamental unit of biodiversity. A “Darwinian Demon” would quickly outcompete any other form and leave no diversity behind. Trade-offs, on the other hand, open the existence of niches and diverse communities.

The thesis also deals with life history consequences beyond the optimality of the studied species, for instance the ecosystem consequences of migrations (**P1**, **P5**), and the cascades of effects that a life history may have on other components of a trophic system. State-dependent life histories are one example. The spawning migration of herring along the Norwegian coast is predicted to be state-dependent in the sense that individuals in poor condition undertake a shorter migration than individuals that are better off (Slotte and Fiksen 2000). This individual response may, when average condition of the population is poor, lead to shorter migrations, other spawning habitats, and lower reproductive effort, with many potential effects for coastal species relying on herring eggs and larvae for food. Why then may the herring be in poor condition some years? The answer is most likely related to food-availability. One suggested mechanism is that large herring populations reduce the number of its main copepod prey that enters diapause, and to levels that limit subsequent copepod recruitment (**P1**). There is some recent support for this mechanism (Olsen et al. in press). The herring’s selective feeding on large copepod stages (Dalpadado et al. 2000), and potentially those with the largest oil sac, strengthens the predation mechanism. It may be added, in line with the flexible responses expected by capital breeders under predation risk, that when the herring is abundant, it may induce earlier

diapause and smaller energy reserves in the copepod. Such responses by the prey would in turn reduce the proportion of early eggs, produced by capital breeding, which may have high value also in this species, *Calanus finmarchicus* (Richardson et al. 1999). Some of these links are highly uncertain and needs further study, but this line of reasoning is an example of how state-dependent life histories influence ecosystem dynamics.

I also discuss other ecosystem consequences, particularly those emerging from storage (**P5**). These include increased accumulation of organic pollutants in trophic systems where capital breeders are common, and where capital breeders migrate between systems with resulting transport of pollutants (Krümmel et al. 2003). Transports are also common in breeding seabirds, but then on shorter timescale. Parental care include feeding of young, and for seabirds this means commuting between sea and land, with a resulting flux of energy with far-reaching consequences for many terrestrial systems (e.g. Ellis 2005, Sekercioglu 2006). However, complex ecological interactions determine the breeding success of the seabirds, including their willingness to breed (Chastel et al. 1995). When breeding is initiated, the state of their prey is important, as it influences the net transport of energy to the chick (Wanless et al. 2005). The prey's state is, as illustrated above, a result of complex interactions between the environment and the life history, including our own harvesting strategies (Österblom et al. 2006). It is a challenge to understand the role of life history strategies in determining such ecological dynamics. The theory of evolution by natural selection has, however, given biology predictive power, providing us with some of the tools (Sutherland 2005).

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