

Growth strategies of ectothermic animals in temperate environments

Karl Gotthard

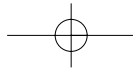
1. Introduction

Individual growth is a fundamental biological process and a typical component of juvenile development. The study of juvenile growth and development has long been of interest for a range of biological sub-disciplines including physiology, ecology and evolution. This chapter mainly concerns evolutionary aspects of juvenile growth, and in particular I will try to relate empirical findings to recent advances in life history theory. I will focus on how the evolution of growth strategies may be influenced by time constraints that are caused by seasonality. To keep this a manageable review I have restricted it to ectothermic animals, mainly because they share physiological features that are important in environments where temperature varies seasonally. I will first review the relevant theory and then discuss empirical results from three major groups of ectothermic animals (insects, fish, amphibians) in the light of the theoretical framework.

2. Theory

2.1 *Life history theory and growth*

Life history theory sees the scheduling of events such as growth, sexual maturation and reproduction as the result of strategic decisions over an organism's life (Roff, 1992; Stearns, 1992; McNamara and Houston, 1996). The theory attempts to define organisms by relatively few demographic traits, called life history traits, that show a close relationship with fitness (i.e. size at birth, growth patterns, age and size at maturity, age- and size-specific investments in reproduction, number and quality of offspring). Life history theory tries to explain how natural selection has shaped these traits to produce life cycles that fit the requirements of the environment. Life history analysis is also a tool for investigating hypotheses of evolutionary causes and of adaptations in general (Stearns, 1986; McNamara and Houston, 1996; Nylin and Gotthard, 1998). This is because any heritable



feature of an organism, be it behavioural, morphological or physiological, that affects the traits listed above will be under some type of selection.

Juvenile growth, age and size at maturity. The onset of reproduction is a key event in the life of most organisms, and in evolutionary terms it divides life into preparation and fulfilment (Stearns, 1992). Age and size at first reproduction are fundamental life history traits that often have a strong influence on fitness. A short juvenile period is beneficial because it reduces the risk of being killed before reproduction and entails a short generation time, while a large adult size is often correlated with high female fecundity and competitive ability in both males and females (Roff, 1992; Stearns, 1992). At some level a trade-off between these traits is expected since, all other things being equal, it will take longer to grow to a larger size. Nevertheless, the range of possible combinations of age and size at maturity for a particular individual is determined by its juvenile growth trajectory (*Figure 1*). Consequently, variation in growth patterns will affect the age and size at maturity and the study of juvenile growth may be crucial for understanding life history evolution in general. Variation in growth trajectories may be due to inevitable variation in the quality of the environment but, as will be argued in this chapter, it may also be the result of an adaptive balancing of benefits and costs associated with different patterns of growth.

Growth rate is a pivotal aspect of growth trajectories and most life history models have assumed that selection should favour a maximization of juvenile growth rate. The rationale for this assumption is quite intuitive; individuals that maximize their juvenile growth rates will have the potential to reach the largest possible size in the shortest possible time. Growth rate will then be directly determined by the quality of the environment that in turn depends on factors such as food availability and ambient

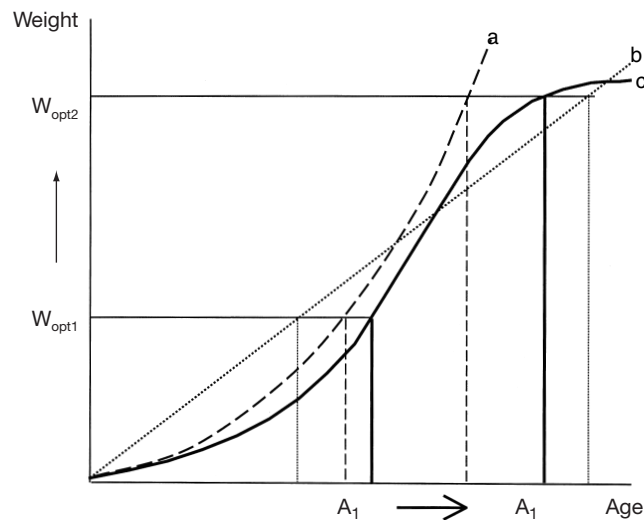
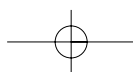
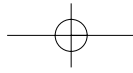


Figure 1. Three hypothetical growth trajectories where growth rates are constant, increasing or decreasing at large sizes (i.e. they differ in how the slope of the growth trajectories change with size). When the optimal size of maturation for some reason changes from W_{opt1} to W_{opt2} the age at maturation increases in all three cases but the time sequence of maturation of the three growth trajectories is altered (from $a - b - c$ to $b - c - a$).





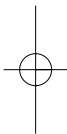
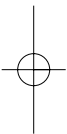
temperature. Despite these arguments there is a growing body of evidence that individual organisms are often growing at a lower rate than they are physiologically capable of (Case, 1978; Arendt, 1997; Nylin and Gotthard, 1998). Moreover, genetic variation within and between populations has frequently been identified (Case, 1978; Arendt, 1997; Blanckenhorn, 1998a; Simons *et al.*, 1998). These observations suggests that the *optimal* growth rate of an individual organism in a particular environmental setting is not necessarily the same as the *maximal*, and that high growth rates might be associated with fitness cost. Consequently, much of the observed variation in growth rate may be the result of an adaptive balancing of costs and benefits associated with growth, which may result in different optima in different populations. Alternatively, individuals within a population may adjust their growth rates in relation to environmental conditions that influence the balance between costs and benefits of a particular growth pattern. In other words individual growth may be determined by a genetically imprinted *growth strategy* that can be modified by natural selection (Gotthard, 1999).

State-dependent life history theory. State-dependent life history theory is emerging as one of the major conceptual and theoretical tools for understanding the evolution of life histories (McNamara and Houston, 1996). The basic idea of this approach is that the outcome of life history decisions (i.e. when and how to grow, mature and reproduce) depends on the *state* of the organism. In any particular case the relevant individual state may include different aspects of the organism's physiological condition but also external circumstances. A life history strategy is seen as a genetically coded decision rule that specifies how an individual should respond to its internal state and its environment. These decision rules are the targets of natural selection (Houston and McNamara, 1992; McNamara and Houston, 1996). To some extent, state-based approaches have been used to model strategic decision-making during development and growth of individuals (Rowe and Ludwig, 1991; Hutchinson *et al.*, 1997). Moreover, state-dependent decision making may serve as a conceptual model for finding mechanisms of strategic growth (Gotthard, 1998; Metcalfe *et al.*, 1998; Gotthard *et al.*, 1999, 2000).

2.2 The costs of juvenile development

The costs of growing fast. An important result of theoretical and empirical studies of adaptive growth adjustment is that high juvenile growth rates are likely to carry fitness costs, and in certain circumstances it is beneficial for individuals to avoid these costs by growing more slowly (Sibly and Calow, 1986; Werner, 1986; Lima and Dill, 1990; Stockhoff, 1991; Werner and Anholt, 1993; Gotthard *et al.*, 1994; Skelly, 1994; Anholt and Werner, 1995, 1998; Abrams *et al.*, 1996; Abrams and Rowe, 1996; Arendt, 1997; Blanckenhorn, 1998a; Nylin and Gotthard, 1998; Gotthard, 2000). The costs of high growth rates that have been proposed can roughly be divided into three categories: physiological, developmental and ecological costs.

Physiological costs. Arguments for the presence of physiological costs are based on the notion that high growth rates are associated with physiological conditions that entail a lower ability to endure adverse environmental conditions. This could, for instance, be periods of starvation or sub-optimal temperatures (Sibly and Calow, 1986; Conover



and Present, 1990; Stockhoff, 1991; Gotthard *et al.*, 1994; Arendt, 1997). A possible mechanism for this trade-off is that high growth rates are associated with high metabolic rates that would more quickly deplete stored resources during, for example, a period of starvation (Conover and Present, 1990; Stockhoff, 1991; Gotthard *et al.*, 1994). Alternatively, fast growing individuals are allocating more resources to growth processes and relatively less to energy storage that could be used during periods of food shortage (Chippindale *et al.*, 1996).

Developmental costs. It has been suggested that a high juvenile growth rate may be associated with lower degree of developmental 'quality control' and thus with a higher probability of developmental error (Sibly and Calow, 1986; Arendt, 1997). This mechanism may explain observations of negative phenotypic and genetic correlations between growth or developmental rates and various measures of both juvenile and adult viability (see references in Arendt, 1997; and in Nylin and Gotthard, 1998).

Ecological costs. In animals a high growth rate typically necessitates high foraging activity, which increases the encounter rate with, and detection by, predators. This relationship leads to a fundamental trade-off between growth rate and predation risk (Lima and Dill, 1990; Werner and Anholt, 1993). It is clear that a wide range of animals lower their foraging activity in response to perceived increases in predation risks and that this lowers their growth rates. Moreover, there is direct observational and experimental evidence that high levels of activity and high growth rates increase the risk of predation (Bernays, 1997; Anholt and Werner, 1998; Gotthard, 2000).

The cost of a long juvenile period. Although slow juvenile growth may reduce mortality rate a slowly growing individual will typically have a long developmental period, which will increase the risk of being killed before sexual maturity *per se*. This is in fact the most commonly assumed cost of juvenile development in life history theory (Roff, 1992; Stearns, 1992). Hence, there are two fitness costs of juvenile growth that exert opposing selection pressures and it will be important to determine, which of these costs are likely to be most important.

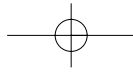
The chance of a juvenile to survive to reproduction (S_{juv}) can be expressed as a function of the daily survival chance (s) and the juvenile period in days (t):

$$S_{juv} = s^t \quad (1)$$

Equation (1) shows that, in the simplest possible case, differences in development time (t) will typically be more important than differences in daily survival rate (s) and, consequently, the *costs of growing fast* might be less important than the *costs of growing for a long time*. However, in temperate areas the seasonal timing of life history events is of great importance and this is likely to influence the simple equation of juvenile survival presented above. In the next section I will discuss how seasonality might influence the relative importance of a high survival rate (s) and a short development time (t).

2.3 Seasonality – time horizons

Time horizons. Practically all environments are seasonal in that there is predictable variation in climatic variables over the year. In temperate regions a large proportion of

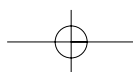
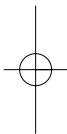
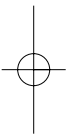


the year is unsuitable for growth and reproduction for most organisms, and for ectotherms this is particularly true. The life cycles of temperate ectotherms must be completed within the limits set by seasonality, and the timing of life history events will have a strong influence on fitness. For example, reproductive success typically depends on the occurrence of resources that vary seasonally (i.e. food and temperatures that allow activity). Moreover, in sexually reproducing species it is indeed of crucial importance to start reproductive activities (mate searching, establishing mating territories, mating etc.) at a time of year when sexually mature potential mates are likely to be present. As a consequence, populations in temperate regions typically show a pattern of strong seasonal synchronization of generations. The amount of time that is available for growth and reproduction will be limited and therefore organisms will face *time horizons*. A time horizon can be defined as 'a period of time of predictable length' and they are typical components of temperate habitats.

In order to survive the winter most temperate ectotherms have to reach a certain developmental stage or a minimum body size before the onset of bad conditions. If an early maturing genotype has time enough to produce a whole new generation that can reach the overwintering stage/size before the onset of winter, a shortening of the juvenile period (smaller t in equation (1)) is likely to be beneficial. However, if the prevailing time horizon rules out an additional generation it will instead be important to maximize survival rate (s in equation (1)) until the next reproductive opportunity. Hence, when time horizons restricts potential shortenings of the juvenile period (t) it might be beneficial to increase survival rate (s) by lowering juvenile growth rate, and thus, increase the total chance of juvenile survival (S_{juv}).

Consider a semelparous organism with an annual life cycle in a region where time horizons never permit more than one generation per year. The exact length of the time horizon will vary between years due to weather conditions and between individuals within years because of differences in microclimate and time of start. Within a population some individuals are likely to have more time available for growth and development than others, although there is never time enough to shorten the juvenile period. This type of life cycle is common in temperate insects but the logic can easily be extended to populations with either more or fewer than one generation per year, as well as populations where the number of generations varies among years. In fact, most organisms in temperate areas are likely to experience selection for synchronization of the life cycle *simultaneously* as they experience selection for utilizing the available time efficiently. Thus, we might expect to find adaptations that allow organisms to predict time horizons and to adjust their growth and development accordingly.

Predicting time horizons. In temperate areas variation in climatic variables allow organisms to predict time horizons and the most commonly used cue of seasonal change is the photoperiod, which gives relatively noise-free information about the time of year (*Figure 2a*). Photoperiodic sensitivity has been documented in a wide range of temperate organisms (Beck, 1980; Gwinner, 1981; Hoffman, 1981; Saunders, 1981; Tauber *et al.*, 1986; Danks, 1994). Temperature is another important seasonal cue, although a large proportion of the variation in temperatures is non-predictable (*Figure 2b*). Furthermore, the ambient temperature has large direct effects on practically all physiological processes and this is of course particularly important in ectothermic organisms. Hence, in respect to growth and development of temperate ectotherms the ambient temperature has a dual role: to some degree it predicts time



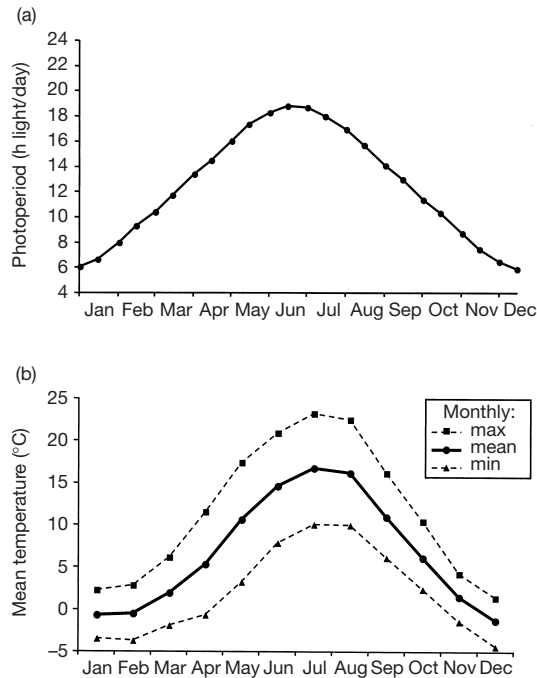
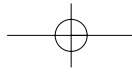


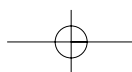
Figure 2. Example of yearly variation in climatic variables in central Sweden that predict time of year. (a) Photoperiod in the Stockholm area excluding twilight, and (b) mean monthly temperature in Målilla (in the region of Småland) flanked by the monthly maximal and minimal temperatures (values are means of daily recordings during the period 1988–1997; the data was provided by the Swedish Meteorological and Hydrological Institute). The difference between minimum and maximum temperatures represents variation that does not predict time of year. In contrast, photoperiod is a relatively ‘noise-free’ predictor of time of year.

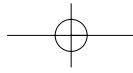
horizons, while at the same time it is an important direct determinant of growth and developmental rates (Atkinson, 1994).

2.4 Life history models

Most models of optimal age and size at maturity have not incorporated the possibility that individuals adaptively adjust their growth by balancing it against juvenile mortality (reviewed in Roff, 1992; Stearns, 1992). Gilliam and Fraser (1987) presented a model including a trade-off between juvenile growth and mortality rate, which suggested that the optimal growth strategy of an individual is to choose habitats that minimise the ratio of mortality rate (μ) and growth rate (g) – the ‘minimize μ/g ’ rule. However, seasonal time horizons were not incorporated into this model. In contrast, Ludwig and Rowe (1990) and Rowe and Ludwig (1991) analysed models of age and size at maturity/metamorphosis that included a growth/mortality trade-off and time horizons due to seasonality. The models assume that the trade-off is mediated by a choice between two habitats that differ in growth and mortality rates. Werner and Anholt (1993), furthermore, investigated adaptive responses in foraging activity (speed of foraging and time spent foraging) when individual growth rate and mortality risk are functions of activity, and time horizons are present. All these models indicate that when there are seasonal time constraints, the optimal age and size at maturity should typically vary with the time horizon for juvenile growth.

This last conclusion is also in line with the work of Abrams *et al.* (1996) and Abrams and Rowe (1996), which represents perhaps the most explicit life history modelling of adaptive growth strategies in a seasonal environment. In some contrast to the previous models Abrams *et al.* (1996) treats juvenile growth rate as an adaptively flexible trait





that individuals can adjust depending on the situation. As in the other models there is a trade-off between growth and mortality rates, as well as a cost of maturing at a sub-optimal time of year. The model also assumes that individuals can predict time horizons by means of seasonal cues (i.e. photoperiod, temperature). The study then focuses on the optimal responses in final size, development time and growth rate when the amount of time available for growth varies. The results show that juveniles should adjust their growth according to information about prevailing time horizon. The model makes the intuitive prediction that with less time available for growth (shorter time horizon) juvenile development time should decrease. Such a shortening of the developmental period can in principle be achieved by maturing at a smaller size, or by growing faster, or by a combination of the two. In essence, the analysis shows that the optimal combination of juvenile growth rate and size at maturity depends on how costly it is to be a small adult, in relation to how costly it is to grow faster as a juvenile. Since these relationships are poorly known and the number of combinations that are theoretically possible is large, the range of predicted life history responses are also large. However, for both biological and theoretical reasons some relationships between final size and fitness and between growth rate and juvenile mortality are less probable than others (Abrams *et al.*, 1996). The authors, therefore, argue that the most likely effect of decreasing the time horizon for growth is that growth rate increases (or stays constant), adult size decreases (or stays constant), as the development time becomes shorter. These life history responses can be viewed as reaction norms in response to some environmental cue of the time horizon such as the photoperiod, and this plasticity would represent an optimal *growth strategy*.

3. Empirical findings

The object of this part is to review empirical data that relates to various aspects of the theory presented above and I have chosen model cases where the development and growth can be clearly linked to the ecological setting of the animals. To show the generality of the phenomena discussed I concentrated on three major groups of ectothermic animals representing a large taxonomic range: insects, fish and amphibians. Rather than finding *all* relevant examples in the literature, I have focused on systems that illustrate some important aspects of the theory. Reviews by Case (1978), Arendt (1997) and Nylin and Gotthard (1998) provide other examples of adaptive growth adjustment.

3.1 Insects

Temperate insects survive the winter in a hormonally controlled diapause that in the typical case can only take place in one species-specific life stage (i.e. egg, larva, pupa or adult). Furthermore, many insect populations produce several, consecutive, generations per year (bivoltine or multivoltine populations). This is possible because these insects have alternative developmental pathways, allowing direct development to reproduction early in the favourable season and development to winter diapause as conditions deteriorate (Tauber *et al.*, 1986; Danks, 1994). Individuals that enter winter diapause then postpone reproduction to the next year. The pathway taken by an individual is typically determined by environmental cues of seasonal progression that are experienced during development (Tauber *et al.*, 1986; Danks, 1994). The amount of

time that is available for growth and reproduction is clearly an important resource for temperate insects, and selection is likely to favour an efficient usage of time (Gotthard, 1999). For example, the start of development for any given generation may vary between years, due to varying weather, and between individuals due to the time of oviposition. Nevertheless, any insect larva must develop in such a way that it, or its offspring, will reach the diapausing stage before the onset of winter, independently of when in the favourable season it finds itself (Reavey and Lawton, 1991). Therefore, several researchers have argued that seasonality should favour phenotypic plasticity in the timing of growth and development also within developmental pathways of insects (Masaki, 1978; Nylin *et al.*, 1989; Leimar, 1996; Nylin and Gotthard, 1998).

This last prediction has been supported by experiments with several species of temperate butterflies that have been shown to adjust their growth in response to information about time horizons as given by photoperiod (Nylin *et al.*, 1989, 1995, 1996; Nylin, 1992; Leimar, 1996; Gotthard, 1998; Gotthard *et al.*, 1999, 2000). Most of the evidence comes from work on species from the tribe Parargini (Satyrinae: Nymphalidae) in which larval growth decisions in response to photoperiod show adaptive variation among species (Nylin *et al.*, 1996; Gotthard *et al.*, 1999) and among populations within species (Nylin *et al.*, 1989, 1995; Gotthard, 1998). There is also evidence that individual growth decisions in response to the photoperiod and ambient temperature depend on the seasonal state of growing larvae (Figures 3 and 4; Gotthard *et al.*, 1999, 2000). This state-dependence of individual growth decisions appears to be

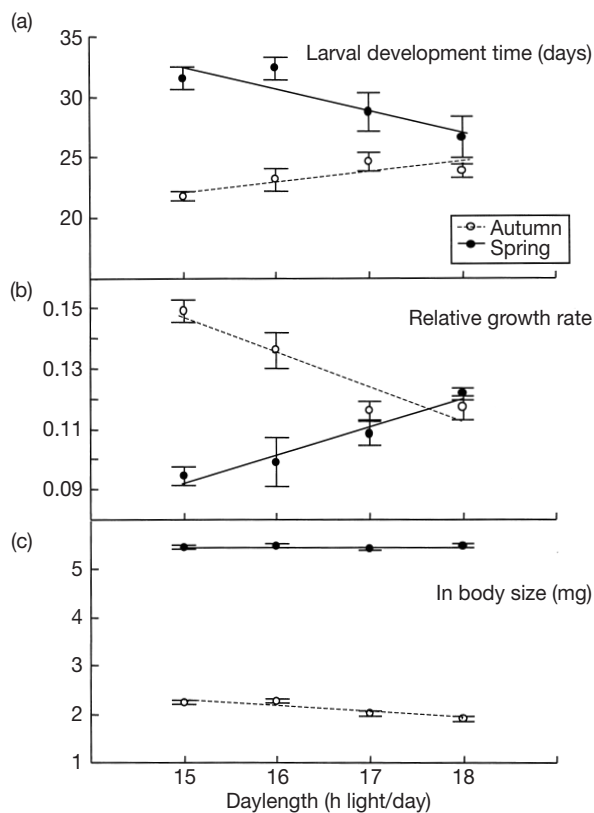
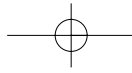


Figure 3. The effect of experimental manipulation of the photoperiod during larval growth on (a) larval development time, (b) growth rate, (c) \ln final size of the butterfly *Lasiommata maera* (Figure 2 in Gotthard *et al.*, 1999, © Oikos, 1999). The same cohort of larvae was reared first in autumn, before the entering winter diapause as half-grown larvae, and then in spring until pupation. Larvae used the photoperiod to adjust their growth patterns both in autumn and spring, but the relationship between photoperiod and time horizon differed between autumn and spring. This difference between the two growth periods seems to be adaptive since the information about time horizons that photoperiod gives is qualitatively different in the two periods (in autumn the photoperiod is decreasing with time while in spring it is increasing with time). This experiment shows that growth decisions of individual larvae in response to information given by the photoperiod are state-dependent.



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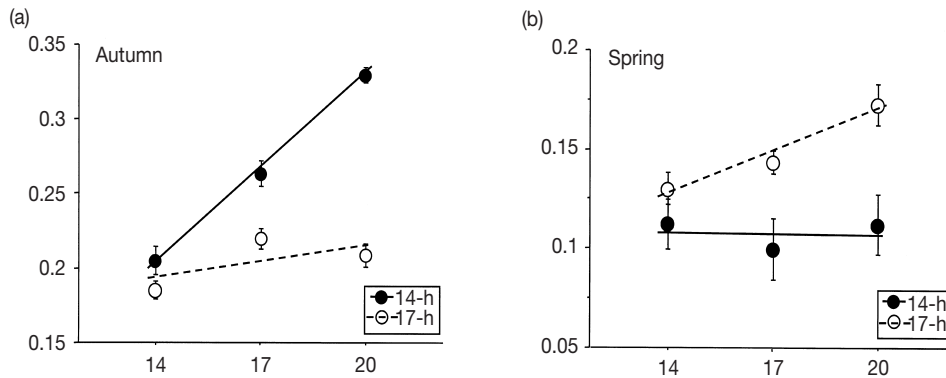
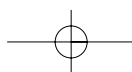
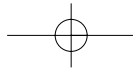


Figure 4. The effect on relative larval growth rate of a combination of experimental variation in photoperiod and temperature in the butterfly *Lasiommata maera*, during (a) autumn and (b) spring (Figure 2 in Gotthard *et al.*, 2000, © 2000 The Royal Society). During both growing seasons larvae increased their growth rates in higher temperatures more if the photoperiod indicated short time horizon, and thus high time stress. In autumn a short photoperiod indicates high time stress, while in spring a relatively long photoperiod indicates a later date of the season.

adaptive to allow larvae to adequately estimate time horizons from the photoperiod both before and after summer solstice (Gotthard *et al.*, 1999, 2000). Moreover, within the Pararginii there is experimental support that high larval growth rates may carry fitness costs both in terms of reduced starvation endurance (Gotthard *et al.*, 1994; Gotthard, 1999) and increased predation rate (Gotthard, 2000). As predicted by most of the theoretical models a shorter time horizon for larval growth in these species had the effect of reducing larval development time (i.e. Figure 3). This reduction in time was always associated with an increase in larval growth rate but only rarely was the final size of the developing larvae affected (Figure 3; Nylin *et al.*, 1989, 1995, 1996; Gotthard, 1998; Gotthard *et al.*, 1999, 2000). This implies that, when there is a shortage of time for growth in these species, the cost of increasing larval growth rate is typically lower than the cost of finishing at a smaller size. On the other hand when there is a surplus of time (that is not long enough to allow an additional generation), the benefit of growing slower is typically larger than the benefit of ending up at larger size (Gotthard, 1999).

In a series of papers Blanckenhorn (1997a,b, 1998a,b) reports on both field and laboratory experiments investigating growth and developmental strategies of the yellow dung fly (*Scatophaga stercoraria*). The populations studied produce several overlapping generations each year. Female dung flies oviposit into cattle dung, which the developing larvae feed on and thereby deplete. In addition to seasonal time constraints, competition for dung imposes food and time constraints on development. In contrast to most cases of insects temperature rather than photoperiod is the most important cue for the induction of diapause in *S. stercoraria* (Blanckenhorn, 1998b). Nevertheless, when the direct effects of temperature variation are controlled, individuals increase their growth rates as the time horizon for development prior to winter diapause becomes shorter. This increase in growth rate allowed late-hatching individuals in the field to maintain large final body sizes even though developmental periods in degree-days were shortened (Blanckenhorn, 1997b, 1998a). On the other





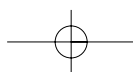
hand, the increase in growth rate also increased larval mortality, indicating a trade-off between growth and mortality rates (Blanckenhorn, 1998a). The author relates his results to the model of Abrams *et al.* (1996) and concludes that the developmental strategy of *S. stercoraria* can only be fully predicted if larval growth rate varies adaptively and independently of developmental time (Blanckenhorn 1998a).

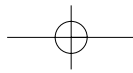
The relationship between the mountain birch (*Betula pubescens czerepanovii*) and its insect herbivores in northern Finland has been studied extensively over several decades (Haukioja *et al.*, 1978, 1988; Hanhimäki *et al.*, 1995; Tammaru, 1997; Kause *et al.*, 1999). The system is characterized by a seasonal decline in the nutritional quality of leaves for a range of insects feeding on the mountain birch. This decline is especially fast in early summer and during this period there is extensive within-canopy variation in leaf quality. Later in the season the quality of leaves is generally low and there is little variation in quality within the foliage of a tree. Early in the season the deterioration of food quality creates time horizons and in 'early season growers' such as the autumnal moth *Epiritta autumnata* selection apparently acts to maximize larval growth rate (Ayres and MacLean, 1987; Tammaru, 1997). Kause *et al.* (1999) showed how the nutritional quality of birch leaves affected larval growth and its physiological and behavioural determinants in six species of sawflies, which ranged from species growing early in the season to those growing later. All species were capable of maintaining relatively stable larval growth rates in a gradient of birch leaf quality (due to known differences among 20 tree genotypes), but the underlying behavioural and physiological mechanism of larval feeding varied among species. Early summer species that were given low-quality leaves typically increased growth effort by dispersing to new feeding sites, which increased the probability of finding young and nutritious leaves that are heterogeneously distributed in the tree canopy. In contrast, the late season species that typically meet little spatial variation in plant quality responded to poor leaf quality by increasing consumption rate. These results also suggest that a high growth effort carries some fitness cost in both seasonal categories since larvae growing on good-quality leaves could apparently have grown faster by altering their growth effort. In other studies, Kause (2000) investigated how the variation in diet-imposed time horizons among birch feeding insects (one butterfly species and six sawfly species) influences the genetic architecture of developmental traits. The genetic correlation between development time and final size was positive only in species feeding on mature leaves of stable quality (mid-season species). However, in species that typically feed on rapidly growing or senescing leaves a longer development time did not lead to a greater final size and the genetic correlation was negative or absent. Hence, variation in time horizons among species seems to have resulted community wide patterns in the genetic architecture of growth and development (Kause, 2000).

3.2 Fish

Most fishes may continue somatic growth after sexual maturation and fish growth is typically described as indeterminate and highly habitat-dependent (Sebens, 1987). Nevertheless, it is likely that juvenile growth and development are strongly correlated to fitness and this review concentrates on the juvenile growth trajectory.

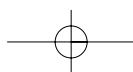
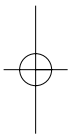
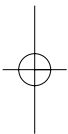
The life history of the Atlantic salmon (*Salmo salar*) has been well studied because of its economic and conservation value (Metcalf, 1998). Juvenile growth and development of Atlantic salmon occur in freshwater streams and after a developmental

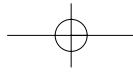




event which transforms juvenile salmon to smolt, most individuals migrate to the sea in late spring. The survival rate of migrants is positively correlated with body size at the time of the seaward migration (Mangel, 1996; Thorpe and Metcalfe, 1998), and therefore there is selection against a small body size at migration (Mangel, 1996). The age at migration to the sea varies between rivers and there is a strong negative correlation between the age at migration and length of the growth season (i.e. populations with a shorter time horizon for growth are on average older at migration; Metcalfe and Thorpe, 1990; Metcalfe, 1998). Moreover, the age at the seaward migration varies between individuals, and within a single river there is often several age classes of smolt (Metcalfe and Thorpe, 1990; Metcalfe, 1998). The developmental decision of whether or not to migrate any given year is made in autumn, some 9 months prior to the migratory event in spring, and the outcome is largely due to the environmental conditions experienced by individual fish. After the decision point in autumn a cohort is divided into those fish that will migrate at the next spring and those that will postpone it for at least another year (Thorpe, 1977; Nicieza *et al.*, 1991; Metcalfe, 1998). During the months between the smolting decision and actual migration the growth rate of early migrants is much higher than that of delayed migrants of the same age (Metcalfe, 1998). This bimodal pattern of growth is most likely adaptive since early migrants will be experiencing size selective mortality in the sea and must grow fast to reach a large size, while the delayed migrants should be more prone to avoid potential costs of high growth rates (Nicieza *et al.*, 1994; Metcalfe, 1998; Metcalfe *et al.*, 1998, 1999; Nicieza and Metcalfe, 1999). Moreover, Nicieza *et al.* (1994) showed that the smolting decision varied adaptively with the time horizon for growth: fish from a southern population (Spain) where post-decision growth is possible for a long period, initiated smolting at a lower threshold size than did a more northern population (Scotland) that has a shorter time horizon for growth after the smolting decision is made. This suggests that developmental decisions and growth patterns of these populations are locally adapted to the typical time horizons at their places of origin. Other studies show that growth decisions of individual juvenile salmon depends on their physiological state (i.e. early or late migrant, body size; Metcalfe *et al.*, 1998), as well as their seasonal state (growing during winter or summer; Bull *et al.*, 1996; Metcalfe, N.B., Bull, C.D. Mangel, M., unpublished results]). These patterns are in line with adaptive predictions from models of state-dependent behaviour and life history (Metcalfe *et al.*, 1998; Metcalfe, N.B., Bull, C.D., Mangel, M., unpublished results). Thus, there is evidence that the growth of juvenile salmon is controlled by a state-dependent decision process that appears to take into account both the costs and the benefits of high growth rates at several points in juvenile development.

The relationship between seasonal time horizons and growth has also been the subject for several studies in the Atlantic silverside (*Menidia menidia*; i.e. Conover and Present, 1990; Present and Conover, 1992; Schultz and Conover, 1997; Billerbeck *et al.*, 2000). The species inhabits shallow waters along the east coast of North America from northern Florida (30°N) to the Gulf of St Lawrence (46°N) and throughout this geographical range the entire life cycle is completed in one year: all fish are sexually mature at age one and a very low proportion reaches a second breeding season. The length of the first growing season decreases by a factor of 2.5 going northwards along the latitudinal gradient, yet there is no decline in the final body size with increasing latitude. Body size at the end of the first growing season is related to fitness since larger fish survive the winter better than smaller fish (Conover and Present, 1990). Common

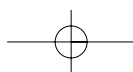
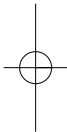
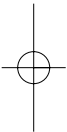


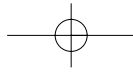


garden experiments in the laboratory revealed that more northern populations of *M. menidia* had a greater capacity for growth, and that this latitudinal clime in growth rate had a genetic basis. Unexpectedly, fish from northern populations primarily grew faster than fish from southern populations in the high temperatures that southern populations are more often exposed to. The faster growth of high latitude fish was due to behavioural and physiological differences (Present and Conover, 1992; Billerbeck *et al.*, 2000). This latitudinal pattern is interpreted as a result of strong selection in northern populations that favours a rapid elevation in growth rate during the brief period of the year when temperatures are favourable (Conover and Present, 1990). The authors argue that the lower growth rates of the southern populations are most likely due to some costs of high growth rates, one of which may be a reduced swimming performance (Billerbeck *et al.*, 2000). Thus, it seems that the optimal growth strategy of these fish changes with the prevailing time horizons, which vary with latitude.

3.3 Amphibians

Most studies of growth and development of amphibians have analysed juvenile development to the metamorphosis of aquatic larvae (reviewed by Wilbur, 1980; Werner, 1986; Newman, 1992), while relatively few have investigated the entire juvenile development to sexual maturity (Berven, 1982b; Werner, 1986; Smith, 1987; Semlitsch *et al.*, 1988; Goater, 1994). However, these latter studies all suggest that phenotypic variation induced in the larval stage influence adult fitness. Metamorphosing early and at a large size was typically positively associated with both juvenile and adult components of fitness (i.e. juvenile survival, age and size at maturity, reproductive output; Smith, 1987 Q64; Semlitsch *et al.*, 1988; Goater, 1994). While these studies indicate that high growth rates in larval amphibians may be positively associated with adult fitness, other studies have shown that the high activity needed to achieve a high larval growth rate is also costly in terms of higher predation risk (Werner and Anholt, 1993; Skelly, 1994, 1995; Anholt and Werner, 1995, 1998). Hence, the mode of growth and development of amphibian larvae is likely to affect important fitness components and many studies have focused on how variation in time horizons may influence the balance between larval growth- and survival-rates. For example, many amphibians breed and grow as larvae in temporary ponds that are occasionally filled by rain and then dry out (at a rate that depends on pond characteristics and weather conditions). As a pond dries out the larvae in it are exposed to a high mortality risk and in order to survive they must complete metamorphosis and enter the terrestrial phase of life (Newman, 1992). A large number of studies have investigated the relationship between pond duration and larval development with the adaptive expectation that individuals in short-duration ponds should metamorphose earlier than individuals in ponds of longer duration (Semlitsch and Gibbons, 1985; Petranka and Sih, 1987; Newman, 1988a,b; Semlitsch and Wilbur, 1988; Semlitsch *et al.*, 1990; Semlitsch, 1993; Tejedo and Reques, 1994). This prediction is also often supported by field observations and experimental studies of species that inhabit temporary ponds, but not in species that inhabit more stable aquatic environments (Newman, 1992). The within-species variation in development time is typically associated with variation in growth and developmental rates and, to a lesser degree, with changes in the size at metamorphosis (Semlitsch and Gibbons, 1985; Petranka and Sih, 1987; Newman, 1988a,b; Semlitsch and Wilbur, 1988; Semlitsch *et al.*, 1990; Semlitsch, 1993; Tejedo and Reques, 1994).



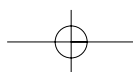
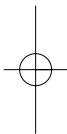
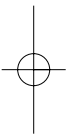


The work of Berven and colleagues (Berven *et al.*, 1979; Berven, 1982a,b) provides examples of a geographic variation in growth strategies of frog tadpoles that most likely represents adaptation to altitudinal variation in time horizons for growth. Wood frog larvae (*Rana sylvatica*) from high altitude populations grew and developed faster than lowland larvae in a range of rearing temperatures in the laboratory (Berven, 1982a). Consequently, in a common environment the mountain larvae completed metamorphosis both faster and at a larger size than their low-elevation conspecifics, and this difference had a clear genetic basis. The growing season is almost 50% longer in the lowlands compared to the mountain conditions (Berven, 1982b), and despite their lower genetic growth capacity the lowland populations metamorphose earlier in the field (Berven, 1982a). The higher growth capacity of mountain larvae is most likely due to the shorter time horizon for growth, while a different body size–fitness relationship may explain the relatively lower growth rates of the low-altitude larvae (Berven, 1982a,b). Moreover, recent evidence indicate that costs of fast larval growth may also be an important factor for explaining variation in growth strategies in wood frogs (Anholt and Werner, 1998).

4. Conclusions

Organisms in temperate environments are likely to experience selection for synchronization of the life cycle, as well as selection for utilizing the available time efficiently. Life history analysis of the optimal age and size at maturity predicts that growth and developmental strategies of ectotherms should covary with time horizons for growth (Rowe and Ludwig, 1991; Abrams *et al.*, 1996; Abrams and Rowe, 1996). This correlation can be expected when there is variation in time horizons for growth among populations. Moreover, since time horizons for growth are bound to vary between individuals, we should expect that organisms estimate time horizons and adjust their growth and development accordingly. The predictions are supported by empirical evidence from a taxonomically large range of ectothermic animals, which emphasizes the generality of these phenomena. When time horizon for growth decreases the juvenile period is typically becoming shorter and this is often associated with a higher juvenile growth rate and a smaller size at maturity. The optimal growth strategy will depend on how fitness is related to adult body size, juvenile development time and juvenile growth rate. The notion that high juvenile growth rates may carry fitness costs is a relatively new and important finding that has emerged from studies of adaptive growth strategies. State-dependent life history theory is emerging as a promising tool for analysing adaptive growth strategies. Within this framework a growth strategy can be viewed as a set of decision rules that specify how an individual should respond to its internal state and its environment. The decision rules have a genetic basis and this is the target for natural selection.

The presence and nature of growth strategies are of central importance for understanding the evolution of age and size at maturity. However, there is still a lack of basic empirical information such as quantitative estimates of how fitness depends on body size, development time and juvenile growth rate in a more natural setting (Abrams *et al.*, 1996; Leimar, 1996; Tammaru *et al.*, 1996; Tammaru, 1997; Blanckenhorn, 2000). Unfortunately, such estimates are often difficult to obtain and they are also likely to vary among organisms. Nevertheless, a combination of carefully designed field and laboratory experiments could produce adequate estimates. If so, it would add pieces of



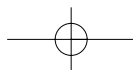
information that would increase the predictive power of models of the optimal age and size at maturity and thereby enhance our understanding of the evolution of developmental strategies and life histories.

Acknowledgements.

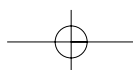
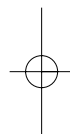
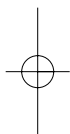
I thank David Atkinson for inviting me to the Annual Meeting of The Society for Experimental Biology. I also thank W. Blanckenhorn, N. Metcalfe and A. Kause for supplying me with their unpublished manuscripts.

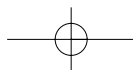
References

- Abrams, P.A., Leimar, O., Nylin, S. and Wiklund, C. (1996) The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *Am. Nat.* **147**: 381–395.
- Abrams, P.A. and Rowe, L. (1996) The effects of predation on the age and size of maturity of prey. *Evolution* **50**: 1052–1061.
- Anholt, B.R. and Werner, E.E. (1995) Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology* **76**: 2230–2234.
- Anholt, B.R. and Werner, E.E. (1998) Predictable changes in predation mortality as a consequence of changes in food availability and predation risk. *Evol. Ecol.* **12**: 729–738.
- Arendt, J.D. (1997) Adaptive intrinsic growth rates: An integration across taxa. *Q. Rev. Biol.* **72**: 149–177.
- Atkinson, D. (1994) Temperature and organism size – a biological law for ectotherms? *Adv. Ecol. Res.* **25**: 1–58.
- Ayres, M.P. and MacLean S.F. Jr (1987) Development of birch leaves and the growth energetics of *Epiritta autumnata* (Geometridae). *Ecology* **68**: 558–568.
- Beck, S.D. (1980) *Insect Photoperiodism*. Academic Press, New York.
- Bernays, E.A. (1997) Feeding by lepidopteran larvae is dangerous. *Ecol. Entomol.* **22**: 121–123.
- Berven, K.A. (1982a) The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* II. An experimental analysis of larval development. *Oecologia* **52**: 360–369.
- Berven, K.A. (1982b) The genetic basis of altitudinal variation in the wood frog *Rana sylvatica* I. An experimental analysis of life history traits **Q65**.
- Berven, K.A., Gill, D.E. and Smith-Gill, S.J. (1979) Countergradient selection in the green frog, *Rana clamitans*. *Evolution* **33**: 609–623.
- Billerbeck, J.M., Schultz, E.T. and Conover, D.O. (2000) Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. *Oecologia* **122**: 210–219.
- Blanckenhorn, W.U. (1997a) Altitudinal life history variation in the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea*. *Oecologia* **109**: 342–352.
- Blanckenhorn, W.U. (1997b) Effects of temperature on growth, development and diapause in the yellow dung fly – against all the rules? *Oecologia* **111**: 318–324.
- Blanckenhorn, W.U. (1998a) Adaptive phenotypic plasticity in growth, development, and body size in the yellow dung fly. *Evolution* **52**: 1394–1407.
- Blanckenhorn, W.U. (1998b) Altitudinal differentiation in the diapause response of two species of dung flies. *Ecol. Entomol.* **23**: 1–8.
- Blanckenhorn, W.U. (2000) The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* (in press). **Q66**
- Bull, C.D., Metcalfe, N.B. and Mangel, M. (1996) Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. *Proc. R. Soc. Lond. B* **263**: 13–18.
- Case, T.J. (1978) On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *Q. Rev. Biol.* **53**: 243–282.

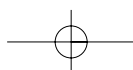
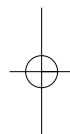
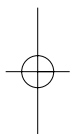


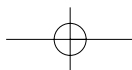
- Chippindale, A.K., Chu, T.J.F. and Rose, M.R. (1996) Complex trade-offs and the evolution of starvation resistance in *Drosophila melanogaster*. *Evolution* **50**: 753–766.
- Conover, D.O. and Present, T.M.C. (1990) Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia* **83**: 316–324.
- Danks, H.V. (1994) Diversity and integration of life-cycle controls in insects. In: *Insect life-cycle polymorphisms* (ed H. V. Danks). Kluwer Academic, Dordrecht, pp5–40.
- Gilliam, J.F. and Fraser, D.F. (1987) Habitat selection under predation hazard: a test of a model with foraging minnows. *Ecology* **68**: 1856–1862.
- Goater, C.P. (1994) Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. *Ecology* **75**: 2264–2274.
- Gotthard, K. (1998) Life history plasticity in the satyrine butterfly *Lasiommata petropolitana*: investigating an adaptive reaction norm. *J. Evol. Biol.* **11**: 21–39.
- Gotthard, K. (1999) Life history analysis of growth strategies in temperate butterflies. Ph.D. thesis, Stockholm University.
- Gotthard, K. (2000) Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. *J. Anim. Ecol.* **69**: 896–902
- Gotthard, K., Nylin, S. and Wiklund, C. (1994) Adaptive variation in growth rate – life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* **99**: 281–289.
- Gotthard, K., Nylin, S. and Wiklund, C. (1999) Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength. *Oikos* **84**: 453–462.
- Gotthard, K., Nylin, S. and Wiklund, C. (2000) Individual state controls temperature dependence in a butterfly (*Lasiommata maera*). *Proc. R. Soc. Lond. B* **267**: 1–5.
- Gwinner, E. (1981) Circannual Systems. In: *Handbook of Behavioral Neurobiology* (ed J. Aschoff). Plenum Press, New York, pp. 391–410.
- Hanhimäki, S., Senn, J. and Haukioja, E. (1995) The convergence in growth of foliage-chewing insect species on individual mountain birch trees. *J. Anim. Ecol.* **64**: 543–552.
- Haukioja, E., Niemelä, P., Iso-Iivari, L., Ojala, H. and Aro, E.-M. (1978) Birch leaves as a resource for herbivores. I. Variation in the suitability of leaves. *Rep. Kevo Subarctic Res. Station* **14**: 5–13.
- Haukioja, E., Neuvonen, S., Hanhimäki, S. and Niemelä, P. (1988) The autumnal moth in Fennoscandia. In: *Dynamics of Forest Insect Populations. Patterns, Causes, Implications* (ed A. A. Berryman). Plenum Press, New York, pp. 163–178.
- Hoffman, K. (1981) Photoperiodism in Vertebrates. In: *Handbook of Behavioral Neurobiology* (ed J. Aschoff). Plenum Press, New York, pp. 449–473.
- Houston, A.I. and McNamara, J.M. (1992) Phenotypic plasticity as a state-dependent life-history decision. *Evol. Ecol.* **6**: 243–253.
- Hutchinson, J.M.C., McNamara, J., Houston, A.I. and Vollrath, F. (1997) Dyar's rule and the investment principle: optimal moulting strategies if feeding rate is size-dependent and growth is discontinuous. *Phil. Trans. R. Soc. Lond. B* **352**: 113–138.
- Kause, A. (2000) Environmental and genetic determination of phenotypes in insects feeding on mountain birch. Ph.D. thesis University of Turku.
- Kause, A., Haukioja, E. and Hanhimäki, S. (1999) Phenotypic plasticity in foraging behavior of sawfly larvae. *Ecology* **80**: 1230–1241.
- Leimar, O. (1996) Life history plasticity: Influence of photoperiod on growth and development in the common blue butterfly. *Oikos* **76**: 228–234.
- Lima, S. and Dill, L.M. (1990) Behavioral decision made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.
- Ludwig, D. and Rowe, L. (1990) Life history strategies for energy gain and predator avoidance under time constraints. *Am. Nat.* **135**: 686–707.
- Mangel, M. (1996) Computing expected reproductive success of female Atlantic salmon as a function of smolt size. *J. Fish Biol.* **49**: 877–882.





- Masaki, S. (1978) Seasonal and latitudinal adaptations in the life cycles of crickets. In *Evolution of Insect Migration and Diapause*. (ed. H. Dingle). Springer, New York, pp. 72–100.
- McNamara, J.M. and Houston, A.I. (1996) State-dependent life histories. *Nature* **380**: 215–221.
- Metcalfe, N.B. (1998) The interaction between behavior and physiology in determining life history patterns in Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **55** (Suppl. 1): 93–103.
- Metcalfe, N.B. and Thorpe, J.E. (1990) Determinants of geographical variation in the age of seaward-migrating salmon, *Salmo salar*. *J. Anim. Ecol.* **59**: 135–145.
- Metcalfe, N.B., Fraser, N.H.C. and Burns, M.D. (1998) State-dependent shifts between nocturnal and diurnal activity in salmon. *Proc. R. Soc. Lond. B* **265**: 1503–1507.
- Metcalfe, N.B., Fraser, N.H.C. and Burns, M.D. (1999) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *J. Anim. Ecol.* **68**: 371–381.
- Newman, R.A. (1988a) Adaptive plasticity in development of *Scaphiopus couchii* tadpoles in desert ponds. *Evolution* **42**: 774–783.
- Newman, R.A. (1988b) Genetic variation for larval anuran (*Scaphiopus couchii*) development time in an uncertain environment. *Evolution* **42**: 763–773.
- Newman, R.A. (1992) Adaptive plasticity in amphibian metamorphosis. *BioScience* **42**: 671–678.
- Nicieza, A.G. and Metcalfe, N.B. (1999) Costs of rapid growth: the risk of aggression is higher for faster growing salmon. *Funct. Ecol.* **13**: 793–800.
- Nicieza, A.G., Brana, F. and Toledo, M.M. (1991) Development of length-bimodality and smolting in wild stocks of Atlantic salmon, *Salmo salar* L., under different growth conditions. *J. Fish Biol.* **38**: 509–523.
- Nicieza, A.G., Reyes-Gavilan, F.G. and Brana, F. (1994) Differentiation in juvenile growth and bimodality patterns between northern and southern populations of Atlantic salmon (*Salmo salar* L.). *Can. J. Zool.* **72**: 1603–1610.
- Nylin, S. (1992) Seasonal plasticity in life history traits: growth and development in *Polytonia calbum* (Lepidoptera: Nymphalidae). *Biol. J. Linn. Soc.* **47**: 301–323.
- Nylin, S. and Gotthard, K. (1998) Plasticity in life history traits. *Annu. Rev. Entomol.* **43**: 63–83.
- Nylin, S., Wickman, P.-O. and Wiklund, C. (1989) Seasonal plasticity in growth and development of the speckled wood butterfly, *Pararge aegeria* (Satyridae). *Biol. J. Linn. Soc.* **38**: 155–171.
- Nylin, S., Wickman, P. O. and Wiklund, C. (1995) Life-cycle regulation and life history plasticity in the speckled wood butterfly: are reaction norms predictable? *Biol. J. Linn. Soc.* **55**: 143–157.
- Nylin, S., Gotthard, K. and Wiklund, C. (1996) Reaction norms for age and size at maturity in Lasiommata butterflies: predictions and tests. *Evolution* **50**: 1351–1358.
- Petranka, J.W. and Sih, A. (1987) Habitat duration, length of larval period, and the evolution of a complex life cycle of a salamander, *Ambystoma texanum*. *Evolution* **41**: 1347–1356.
- Present, T.M.C. and Conover, D.O. (1992) Physiological basis of latitudinal growth differences in *Menidia menidia*: variation in consumption or efficiency? *Funct. Ecol.* **6**: 23–31.
- Reavey, D. and Lawton, J.H. (1991) Larval contribution to fitness in leaf-eating insects. In: *Reproductive Behaviour of Insects* (eds W. J. Bailey and J. Ridsdill-Smith). Chapman & Hall, London, pp. 293–329.
- Roff, D.A. (1992) *The Evolution of Life Histories*. Chapman & Hall, New York.
- Rowe, L. and Ludwig, D. (1991) Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* **72**: 413–427.
- Saunders, D.S. (1981) Insect photoperiodism. In: *Handbook of Behavioral Neurobiology*. (ed J. Aschoff). Plenum Press, New York.
- Schultz, E.T. and Conover, D.O. (1997) Latitudinal differences in somatic energy storage: adaptive responses to seasonality in an estuarine fish (Atherinidae: *Menidia menidia*). *Oecologia* **109**: 516–529.





- Sebens, K.P. (1987) The ecology of indeterminate growth in animals. *Annu. Rev. Ecol. Syst.* **18**: 371–407.
- Semlitsch, R.D. (1993) Asymmetric competition in mixed populations of tadpoles of the hybridogenetic *Rana esculenta* complex. *Evolution* **47**: 510–519.
- Semlitsch, R.D. and Gibbons, J.W. (1985) Phenotypic variation in metamorphosis and paedomorphosis in the salamander *Ambystoma talpoideum*. *Ecology* **66**: 1123–1130.
- Semlitsch, R.D. and Wilbur, H.M. (1988) Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. *Copeia* **1988**: 978–983.
- Semlitsch, R.D., Scott, D.E. and Pechmann, J.H.K. (1988) Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. *Ecology* **69**: 184–192.
- Semlitsch, R.D., Harris, R.N. and Wilbur, H.M. (1990) Paedomorphosis in *Ambystoma talpoideum*: maintenance of population variation and alternative life-history pathways. *Evolution* **44**: 1604–1613.
- Sibly, R.M. and Calow, P. (1986) *Physiological Ecology of Animals: an Evolutionary Approach*. Blackwell Science, Oxford.
- Simons, A.M., Carrière, Y. and Roff, D. (1998) The quantitative genetics of growth in a field cricket. *J. Evol. Biol.* **11**: 721–734.
- Skelly, D.K. (1994) Activity level and the susceptibility level of anuran larvae to predation. *Anim. Behav.* **48**: 465–468.
- Skelly, D.K. (1995) A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog larvae. *Ecology* **76**: 150–164.
- Smith, D.C. (1987) Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* **68**: 344–350.
- Stearns, S.C. (1986) Natural selection and fitness, adaptation and constraint. In: *Patterns and Processes in the History of Life* (eds D. M. Raup and D. Jablonski). Springer, Heidelberg, pp. 23–44.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stockhoff, B.A. (1991) Starvation resistance of gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae): tradeoffs among growth, body size, and survival. *Oecologia* **88**: 422–429.
- Tammaru, T. (1997) Size and time for a geometrid moth: evolutionary forces and consequences for population dynamics. Ph.D. thesis, University of Turku.
- Tammaru, T., Ruohomaki, K. and Saikkonen, K. (1996) Components of male fitness in relation to body size in *Epirrita autumnata* (Lepidoptera, Geometridae). *Ecol. Entomol.* **21**: 185–192.
- Tauber, M.J., Tauber, C.A. and Masaki, S. (1986) *Seasonal Adaptations of Insects*. Oxford University Press, Oxford.
- Tejedo, M. and Reques, R. (1994) Plasticity in metamorphic traits of natterjack tadpoles: the interactive effects of density and pond duration. *Oikos* **71**: 295–304.
- Thorpe, J.E. (1977) Bimodal distribution of length in juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *J. Fish Biol.* **11**: 175–184.
- Thorpe, J.E. and Metcalf, N.B. (1998) Is smolting a positive or a negative developmental decision? *Aquaculture* **168**: 95–103.
- Werner, E.E. (1986) Amphibian metamorphosis: growth rates, predation risk and the optimal size at transformation. *Am. Nat.* **128**: 319–341.
- Werner, E.E. and Anholt, B.R. (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am. Nat.* **142**: 242–272.
- Wilbur, H.M. (1980) Complex life cycles. *Annu. Rev. Ecol. Syst.* **11**: 67–93.

