Eco-evolutionary Dynamics: Experiments in a model system

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Abstract (208 words)

Understanding the consequences of environmental change on both long and short term ecological and evolutionary dynamics is a basic prerequisite for any effective conservation or management programme but inherently problematic because of the complex interplay between ecological and evolutionary processes. Components of such complexity have been described in isolation or within conceptual models on numerous occasions. What remains lacking are studies that characterise effectively the coupled ecological and evolutionary dynamics, to demonstrate feedback mechanisms that influence both phenotypic change, and its effects on population demography, in organisms with complex life-histories. We present a systems-based approach that brings together multiple effects that "shape" an organism's life history (e.g. direct and delayed life history consequences of environmental variation) and the resulting eco-evolutionary population dynamics. Using soil mites in microcosms we characterise ecological, phenotypic and evolutionary dynamics in replicated populations in response to experimental manipulations of environment (e.g. the competitive environment, female age, male quality). Our results demonstrate that population dynamics are complex and are affected by both plastic and evolved responses to past and present environments, and that the emergent population dynamic itself shaped the landscape for natural selection to act on in subsequent generations. Evolutionary and ecological effects on dynamics can therefore be almost impossible to partition, which needs to be considered and appreciated in research, management and conservation.

Keywords: eco-evolutionary, parental effects, maternal, phenotype, body size, offspring, population dynamics, life histories, harvesting, natural selection, evolutionary rescue

Contents

1. Introduction

A fundamental goal in evolutionary ecology is to understand the mechanisms responsible for generating the phenotypic variation upon which selection acts. Similarly, a fundamental goal in population ecology is to understand the role that individual phenotypic variation, created by density independent and/or density dependent processes, plays in shaping population dynamic patterns. Thus, understanding between-individual phenotypic variation is key to understanding both ecological and evolutionary dynamics (Benton et al., 2006). Traditionally, an individual's phenotype has been considered a consequence of interaction between its genes and the environment in which they are expressed. Phenotypic variation has thus been envisaged as the sum of direct environmental and genetic effects, plus their interactions. Despite this recognition, for most of the history of ecology it has been assumed that the ways in which genes and environments interact are relatively unimportant for population dynamics (i.e. the trait changes from life history evolution are either small or take too long to influence short-term dynamics). Two major conceptual advances have recently occurred that casts doubt on this traditional view. First, we now recognize that the environment experienced in previous generations can have consequences for contemporary phenotypes (Beckerman et al., 2002), reflecting the importance of non-genetic modes of inheritance that relate parental and offspring life-histories (Qvarnstrom and Price, 2001, Bonduriansky and Day, 2009, Rasanen and Kruuk, 2007).

Second, there is a growing realisation that evolutionary change can occur over ecological timescales which has highlighted the need to better understand how ecological and evolutionary processes interact to drive population dynamics and demographic change (Coulson et al., 2010, Stockwell et al., 2003, Olsen et al., 2004, Bassar et al., 2010, Carroll et al., 2007, Coulson et al., 2006, Ellner et al., 2011, Ezard et al., 2009, Hairston et al., 2005, Schoener, 2011, Pelletier et al., 2007, Pelletier et al., 2009).

Teasing apart parental, plastic, ecological and reversible responses from evolved and irreversible responses of life-histories to environmental change is inherently problematic, as it is rarely possible to study parental environment effects, genetics, life histories and population dynamics simultaneously and in sufficient detail (Coulson and Tuljapurkar, 2008, Coulson et al., 2010, Morrissey et al., 2012, Andersen and Brander, 2009a, Andersen and Brander, 2009b, Bonenfant et al., 2009, Darimont et al., 2009, Becks et al., 2012, Ozgul et al., 2009, Ozgul et al., 2012, Uller, 2008). However, this is exactly what is required to understand how, or even if, populations will be able to respond to rapid anthropogenic environmental stressors such as selective harvesting (Andersen and Brander, 2009a, Andersen and Brander, 2009b, Coltman et al., 2003, Kinnison et al., 2009, Law, 2007, Ezard et al., 2009, Browman et al., 2008), the potential for species to respond to environmental change through evolution (Bell and Gonzalez, 2009, Ezard et al., 2009, Stockwell et al., 2003), and the role that parental effects have in those adaptive responses to environmental change (Uller, 2008).

Our research with an invertebrate model system has gone some way towards understanding the role of parental environments, and the significance of plastic responses and rapid evolution in delimiting individual phenotypic variation. Here we describe how we have approached these challenging questions by presenting our conceptual framework of eco-evolutionary population dynamics (**Figure 1**), and reporting on what progress we have made in determining each process within this framework. To this end we review previously published material, and report new results from ongoing empirical studies. We use our findings to identify new avenues for research necessary to properly understand how contemporary, historical, and evolutionary determinants of individual life histories interact to shape population level responses.

2. Aims and scope

The aim of this chapter is to introduce the mite model system, a soil invertebrate microcosm based experimental system, and show how it has been used to test and develop our understanding of individual phenotypes, how they form, and how they scale up to population dynamics (i.e. **Figure 1**). We will begin by introducing our study organism, its general biology and the various experimental methods we have used to explore individual and population biology (section 3). In section 4 we will review our previously published work on the development of individual phenotypes as a function of resource availability. This has been a key empirical proof-of-principle of the L-shaped reaction norms predicted to arise when developmental thresholds determine age and size at maturity (Day and Rowe, 2002). Again referring to our published works, using this L-shaped age and size at maturity reaction

norm as a background measurement, we will describe our current understanding of when and how parental environments shape offspring phenotypes. The role of non-genetic inheritance of parental traits is important in the development of our later arguments that describe how current and historical environmental effects interact with natural selection to create eco-evolutionary population dynamics. If, and how, parental effects manifest themselves beyond effects on individual offspring will be presented in section 5. Here we will present our published work on the magnitude and longitude of detectable effects of ancestral environments on soil mite population dynamics.

In section 6 we will present a new analysis of how selection on individual phenotypes, caused by feedbacks from population dynamics in the form of strong density dependent competition, leads to the evolution of population dynamics. This extends the analysis of soil mite populations living in periodically fluctuating resource environments and subject to experimental harvesting (Cameron et al., 2013). Here we are able to present data across constant, randomly variable and periodically variable resource environments. Crucially, it is the imposition of experimental harvesting that reveals that the environmental variation is important in the evolutionary responses of populations to environmental change. Finally, in section 7 we summarise what we have presented in the form of previously published and new analyses and discuss how the different routes we have found to influence population dynamics through changes in individual phenotypes might interact. The overall scope of this contribution therefore, is to stress that it is by understanding how the different routes that lead to phenotypic variation interact that we will come to a more than conceptual understanding on eco-evolutionary population ecology.

3. Model system and methods

The soil mite *Sancassania berlesei* (Michael) is common in soil, poultry litter, and stored food products. Populations of *S. berlesei* have been collected from a variety of sources in different years since 1996 and have been kept in separate stock lines ever since (stock cultures kept in 10 cm diameter containers maintained at 24°C in unlit incubators, number c1–2.5 × 10^5 individuals).

3.1 *The mite model system and generic methods*

The life cycle consists of five stages, beginning with eggs (length: 0.16 ± SD 0.01mm), continuing through a six-legged larvae (length: 0.22 ± 0.01mm), a protonymph, tritonymph, and then to adulthood (female length at maturity: 0.79 ± 0.17mm, range 0.47 (low food) to 1.17 (high food), n = 64; males: 0.72 ± 0.11mm, range 0.55 (low food) to 1.02 (high food), n = 39). As indicated by the standard deviations of the adult lengths, there is considerable variation in the life history and much of it is governed by intake rates of food (Plaistow et al., 2004). An individual's intake rate is a function of a number of factors: population density, stage structure, and the amount of food supplied and its spatial

configuration; together these factors create the individual's competitive environment (Benton and Beckerman, 2005)

Eggs hatch 2 to 5 days after being laid. Juveniles can mature from as little as 4 to 50+ days after hatching (Beckerman et al., 2003), depending on food and density. The longevity of the adults can also vary from ç10 to ç50 days. Thus, total longevity varies from 3 weeks (high food, low density) to 7+ weeks (low food, high density). Fecundity is related to resources, and so to body size, and to survival. The relationship between fecundity and the growth-survival trade-off is in itself dependent on resources (Plaistow et al., 2006, Plaistow et al., 2007).

3.2 General Experimental Procedures

Generally, mite cultures are supplied food in the form of powdered or granulated yeast. Different feeding regimes were used in different experiments and consisted of controlled feeding of balls or rods of dried baking yeast, filtered to minimise variation in their size (diameter of 1.25-1.40 mm for standard size balls). Experimental vessels are either glass tubes (20mm in diameter and 50mm in height) or small non-static plastic vials (3-7ml). These are half-filled with plaster of Paris, which, when kept moist, maintains humidity in the tubes. The tops of the tubes are sealed with a circle of filter paper held in place by the tubes' cap with ventilation holes cut into it. For some shorter experiments (24hr) the plastic vials were sealed with clingfilm. For population experiments, the mites are censused using a Leica MZ8 binocular microscope and a hand counter. In each tube, a sampling grid is etched into the plaster surface to facilitate more accurate counting and observation. All adults are counted in the tube, but juveniles and eggs are counted in a randomly chosen quarter.

3.2.1 Common garden environments

Common garden tubes were used to both standardise and manipulate parental and offspring environments prior to carrying out life history assays or population dynamic experiments. A common garden was created by placing standardised numbers of eggs (from either stock culture females or experimental animals) into identical tubes with controlled food access/competitor density and rearing them until maturation. Upon maturation these individuals are paired and either placed in a new common garden or in egg laying tubes for the collection of eggs for life history assays, reproduction allocation measurements or population dynamic experiments i.e. (Plaistow and Benton, 2009, Plaistow et al., 2004).

3.2.2 Life history assays

Life history assays are used to quantify the life history or phenotype of an individual, full-sib family or population from a given treatment. Life history assays are conducted by placing individuals or groups

of random or full-sib eggs in a small vial that is half-filled with plaster (7-20ml plastic or glass vials). These individuals are observed daily, either with density being standardised by replacement of dead individuals or not. At maturation, individuals are photographed for later measurement and then removed from the vial. We can collect data on age and size at maturity, fecundity at maturity or any other stage of development (e.g. egg size, hatching, protonymphs). Reproductive allocation is a measure of the differences between mite eggs laid by mothers from different parental environments i.e. (Plaistow et al., 2007). We have measured reproductive allocation in terms of numerical, (e.g. total eggs, eggs-at-age), physical (e.g. length, volume) and biochemical properties of eggs laid (e.g. total protein). Measurements of individuals and eggs are made from digital images captured from the microscope (e.g. Leica MZ8, Nikon SMZ15) and measured using ImageJ 1.28u (http://rsb.info.nih.gov/ij) or Nikon Elements D software (v3.2 64bit).

3.2.3 Population dynamic experiments

Population dynamic experiments involve monitoring free-running populations over multiple generations. Such experiments have been started in different ways depending on the purpose of the experiment. Where the purpose was to investigate the timescale of parental effects, populations were started with controlled numbers of eggs from parents of different environmental backgrounds or ages (Plaistow et al., 2006, Plaistow et al., 2007, Pinder, 2009). To investigate the interplay between population and phenotypic dynamics, populations were initiated with a mix of sexed adults (n=75-150/sex) and juveniles (n=500-1000), approximately at stable stage distribution to minimise transient dynamics. To investigate the links between ecological plasticity and life history change, populations were initiated with mites recently collected from the wild to maximise genetic diversity (n=150 adult /sex and 1000 juveniles).

In the population experiments, we have often manipulated stochasticity by varying the timing and amount of food supplied, while trying to maintain other factors as close to constant as possible. Our rationale for this is that many natural environmental factors will either vary the absolute food supply (e.g., the weather), the requirement for food (e.g., temperature), or the availability of food (e.g., patchiness, territoriality, inter-specific competition). Each treatment supplied food at the same mean daily rate (equivalent to one or two balls of yeast per day), but at a variable amount on different days. The algorithms we developed were to supply balls of yeast randomly, or periodically, within each window of time, such that over repeating window lengths, the cultures received a constant number of balls of yeast. Other populations were maintained on constant food regimes either to act as contrasts to those in the variable environments, or on their own for some parental effect experiments. Effects of the different distributions of food supply on variation in population abundance are described elsewhere (Benton et al., 2002).

4. Within and between individual phenotypic variation

In this section we review our previously published work explaining how environment induced changes in the growth rate and maturation decisions are responsible for generating a L-shaped age and size at maturity reaction norm. We then summarise our previously published work explaining how variation in age and size at maturity alters the provisioning of individual offspring and the developmental environment of those same offspring, leading to intergenerational phenotypic variation.

4.1 Age and size at maturity reaction norms

Population growth rates are intrinsically linked to the trade-off between the age and size at which individuals mature because age at maturity determines how quickly individuals start to reproduce and because fecundity is often closely associated with age and body size (Roff, 2002, Plaistow et al., 2006, Plaistow et al., 2007). Consequently, understanding how populations respond to environmental change is likely to depend upon how individuals, within those populations, respond to environmental change. Organisms that live in variable environments, due to environmental forcing or density dependence, for example, are expected to evolve plasticity in age and size at maturity because of fluctuations in resource availability (DeWitt et al., 1998, Via et al., 1995). We demonstrated that in soil mites, the trade-off between age and size at maturity is extremely plastic in response to food availability. Offspring reared on high food matured five times faster and at double the body size of offspring reared in a poor food environment. Moreover, the age and size at maturity reaction norm is L-shaped (Plaistow et al., 2004)**(Figure 2)**. This pattern arises because an individual's decision to mature is controlled by a developmental threshold, which is the minimum size below which maturation cannot occur (Day and Rowe, 2002). Fast growing individuals in good food environments overshoot the minimum threshold size considerably by the time maturation is complete. In contrast, slow-growing individuals in poor food environments have to delay maturation until the minimum threshold size is reached. Consequently, in good food environments all individuals mature at young age but individual differences in growth rates translate into variation in size at maturation. In contrast, in poor food environments, all individuals mature at the same minimum threshold size but individual differences in growth rates translate into differences in age at maturity (Plaistow et al., 2004). As we will see later, this fundamental difference in how environmental variation is translated into phenotypic variation has important implications for understanding how individual plasticity influences population dynamics.

4.2 Intergenerational parental effects on individual phenotypic variation

Parental effects are defined as any effect that parents have on the development of their offspring over and above directly inherited genetic effects (Uller, 2008). Two types of mechanisms can be involved in the transmission of parental effects to offspring phenotypes. In the first mechanism, parental effects

can arise from alterations of the developmental environment experienced by offspring through variation in allocation of non-genetic resources such as nutrients, e.g. (Benton et al., 2005, Plaistow et al., 2007), immune factors, e.g., (Hasselquist and Nilsson, 2009) and hormones e.g., (Meylan et al., 2012). Traditionally, studies of environmental parental effects have focused on maternal influences on her offspring's developmental environment because, in most species, females invest more resources in offspring than males. However, a few examples of paternal effects arising from variation in food provisioning, e.g. (Isaksson et al., 2006) and transmission of immune factors, e.g. (Jacquin et al., 2012, Roth et al., 2012) exist in the literature. In addition, females can alter their investment in offspring in response to males' characteristics, e.g. (Pinder, 2009, Gil et al., 1999), leading to indirect paternal effects. In the second mechanism, parental effects can arise from alterations of gene expression through epigenetic modifications of regulatory regions of the genome in the germline, for instance mediated by DNA methylation and histone modifications, and without changes in DNA sequences (Bonduriansky and Day, 2009). Transgenerational inheritance of epigenetic modifications have been suspected to be involved in some parental age effects, e.g., (Bonduriansky and Day, 2009, Perrin et al., 2007), in some heritable disorders, e.g. (Champagne, 2008, Olsen et al., 2012), and, more generally in paternal effects transmitted through variation in allocation of non-genetic resources, e.g. (Rando, 2012). In addition, there is increasing evidence that maternal and paternal effects arising from variation in offspring's provisioning or from epigenetic modifications are context-dependent, e.g. (Badyaev and Uller, 2009), and can interact to shape offspring phenotype, e.g. (Ducatez et al., 2012). In soil mites, we have explained how age and size at maturity is critically dependent on food availability in the offspring's current environment (Plaistow et al., 2004). However, we have also demonstrated how variation in the maternal provisioning of offspring and the age of the mother can influence both offspring growth rates (Plaistow et al., 2006) and their decision to mature (Benton et al., 2008). In this contribution, we are specifically dealing with the first mechanism described above (i.e. alterations of the developmental environment). Consequently, individual variation in developmental or somatic growth is not just a result of the environment that the individual experiences, but also the environment experienced by its ancestors e.g. (Pinder, 2009) **(Figure 3a)**. From a population dynamic perspective, these effects are important because they mean that a population's response to environmental change may be time-lagged to some degree, with intergenerational effects operating as a source of intrinsic delayed density dependence (Beckerman et al., 2002, Rossiter, 1994).

4.3 Understanding the context dependence of parental effects

Our results have suggested that the importance of parental environments for the variation of offspring phenotypes in soil mites is trait-dependent and may be highly context-dependent (Beckerman et al., 2006, Plaistow et al., 2006). For instance, in low-food current environments, variation in egg size produced by different parental food environments altered the trade-off between age and size at maturity, but had little effect on the size of eggs produced in subsequent generations. Consequently,

the variation in egg size that affected intergenerational effects decreased over time. In contrast, in high-food environments, variation in egg size predominantly influenced a trade-off between fecundity and adult survival and generated increasing variation in egg size (**Figure 3b**). As a result, maternal effects transmitted through variation in egg provisioning persisted and we have observed great grand-maternal effects on descendant's life histories (Plaistow et al., 2006). We therefore predicted that the persistence and significance of intergenerational effects for population dynamics would itself be context-dependent. However, it is important to realize that in an eco-evolutionary sense 'context' is itself something that is derived from the traits and maternal strategies that have evolved in the population.

In viscous populations with overlapping generations, mothers and offspring are forced to compete for the same resources and may, therefore, directly influence each other's probability of survival and future reproductive success. The close covariation between the quality and number of offspring produced and maternal survival means that any change in one offspring provisioning trait may have consequences for the others (Beckerman et al., 2006). It is necessary, therefore, to understand how females change their offspring provisioning strategy as a whole (e.g. egg numbers, egg size, maternal survival) in order to interpret the adaptive significance of maternal responses to changes in their environment. We have shown that in soil mites, offspring provisioning strategies are dynamic, switching from investment in many small eggs in young females to fewer, better provisioned eggs in older females (Plaistow et al., 2007). This strategy may be adaptive if it increases the survival of younger offspring that must compete with older, larger siblings that had been laid previously. This age-related dynamic shift in egg provisioning was greater in high food environments in which females lived longer, creating a greater asymmetry in offspring competitive abilities. Such conditions are likely to be common in an opportunistic species such as soil mites that have evolved a life history that specializes in strong competition between individuals exploiting patchily distributed resources, such as carcasses and dung (Houck and Oconnor, 1991). In the following section we examine the effects that these complex environmentally driven parental effects have on patterns of population dynamics.

5. From phenotypic variation to population dynamics

Parental effects may be especially important from a population dynamic perspective because they generate a lag in the response of a population to an environmental change (Beckerman et al., 2006, Beckerman et al., 2002, Benton et al., 2005). This could make it harder to predict changes in population size, but may also theoretically lead to long-term deterministic population dynamic patterns, such as population cycles (Ginzburg, 1998, Ginzburg and Taneyhill, 1994, Inchausti and Ginzburg, 1998). Consequently, we have been interested in how parental effects might influence population dynamics (Benton et al., 2001). This is not easy to study in the wild, or in many laboratory systems, due to the difficulty of measuring parental effects and following population dynamics in sufficient demographic detail. However, it is possible in the soil mite system because replicated

populations can first, be initiated with different numbers of eggs, changing the initial environment experienced by offspring; but also initiated with eggs from different types of mothers, enabling us to experimentally manipulate parental effects e.g. (Benton et al., 2005, Benton et al., 2008, Plaistow and Benton, 2009).

5.1 Transient population dynamics and parental effects

In the first of these types of experiments, all replicated populations were initiated with 250 eggs. However, half the populations were set-up with large eggs from mothers experiencing low food, the other half were set-up with small eggs from well-provisioned mothers (see Benton et al., 2005 for details). This manipulation of the maternal effect alone was sufficient to generate differences in the transient population dynamics of the populations that were still present after three generations, even though the populations were experiencing the same constant environment with respect to the food supplied to them each day. Such deviations in population dynamics arise because differences in the hatching success, growth rate, size and fecundity and survival in the initial cohort generate differences in the competitive environment experienced by offspring produced in the second cohort. Changes in the competitive environment creates further phenotypic variation between individuals from the two treatments that ultimately leads to large differences in the population dynamics of the populations sustained over multiple generations (Benton et al., 2005).

In a second experiment, but this time using similarly sized eggs that either came from young (3 days) or old (9 days) mothers, the effects on transient population dynamics again lasted three generations (Benton et al., 2008) (**Figure 4**). The results clearly demonstrate that deterministic differences in eggs, which are not obviously related to their size, and so may be undetectable in a population setting, may have a significant effect on population dynamics. Comparing these two experiments, the effects of parental background or age were of a similar magnitude. However, as we discussed earlier, our individual-level studies of maternal effects in soil mites suggested that the exaggeration and the transmission of maternal effects from one generation to the next increased in high-food environments, but decreased in low-food environments (Plaistow et al., 2006). Consequently, we hypothesized that maternal effects would be more likely to persist, and have a bigger influence on population dynamics, in high-food environments compared to low-food environments. In order to test this hypothesis we created maternal effects by initiating populations with eggs from young mothers or old mothers but we also simultaneously manipulated the initial resource environment by changing the initial density from high (500 eggs, low food) to low (50 eggs, high food) (see Plaistow *et al*., 2009 for details). The results clearly supported our hypothesis that the importance of maternal effects for population dynamics is context-dependent. An influence of maternal age treatment on both population and egg and body-size dynamics was only observed in the populations initiated under low density rather than high density (Plaistow and Benton, 2009).

In summary, we have explained how an interaction between current and historical maternal states (transmitted as parental effects) interact to shape patterns of individual phenotypic variation (e.g. size-at-hatch, growth rate to maturity, size-at-maturity, offspring's own egg provisioning patterns) and how this phenotypic variation is then translated into fluctuations in population size. Understanding the various factors that can determine such fluctuations is crucial for predictive modelling of populations for management purposes. From an eco-evolutionary perspective, it is also critical because it is those fluctuations in the number, size and age structure of populations that determine the temporal resource heterogeneity that ultimately shape how individual traits and life history strategies evolve (Roff, 2002). In the following section we summarise our current understanding of how differences in temporal resource heterogeneity, created by environmental variation and harvesting, influence the evolution of mite life histories and, in turn, how this evolution influences population dynamics.

6. Eco-evolutionary population dynamics – the full loop

Debate on the role of genetic change in ecological dynamics is not new (Lenski, 1984, Pimentel, 1961, Pimentel et al., 1978, Pimentel and Stone, 1968, Wilcox and Maccluer, 1979), and includes predictions of cyclic consumer-resource dynamics caused by evolution (Lenski, 1984, Abrams and Matsuda, 1997). It is only more recently that the search for the role of the gene in ecology has been termed "eco-evolutionary dynamics".

It has largely been assumed that this emerging field of eco-evolutionary dynamics has demonstrated that evolutionary "loops" exist in nature, where loops are defined as genetic selection pressures placed on populations from ecological interactions that have significant effects on population dynamics, additive to that of the ecological interaction itself (Kinnison and Hairston, 2007). For example, while a predator can reduce population growth by killing individuals, does it have an additional detectable effect on prey population growth rate by causing the average somatic growth rate to maturation to evolve? Such an evolutionary response of the prey life history, causing a feedback to prey population dynamics, and subsequently predator dynamics would be an evolutionary loop (Post and Palkovacs, 2009).

There is however a dearth of robust empirical evidence for such evolutionary loops. An early study by Nelson Hairston Jr. described the pattern of rapid evolution of toxin resistance in *Daphnia galeata* in Lake Constance in response to eutrophication (Hairston et al., 2001, Hairston et al., 1999). While not evidence of a loop *per se*, the Lake Constance study led to a series of experiments on zooplankton-phytoplankton interactions that demonstrated that rapid evolution in response to an ecological interaction can alter predator-prey cycles (Yoshida et al., 2003), that rapid evolution can mask interactions normally identified through changes in predator and prey abundance (Yoshida et al., 2007) and that rapid prey evolution can affect predator dynamics more than changes in prey abundance (Becks et al., 2012). Other studies on microcosm based asexual communities have followed to show the generality of the importance of rapid evolution on ecological dynamics e.g. (Friman et al., 2014).

A common thread across all these aquatic predator-prey studies, with few exceptions e.g. (Fussmann et al., 2003), is the evolution of traits associated with either defence from predators or digestion of prey. This is clearly important in a community setting, but it is difficult to make the jump from proof of principle in these systems to studies that consider the role of environmental change (e.g. trends in mean annual temperature) or high rates of harvesting against life history traits such as somatic growth rate in well-studied populations of fishes, birds and mammals (Darimont et al., 2009). Other differences between demonstrated eco-evolutionary dynamics in freshwater microorganisms and proposed eco-evolutionary dynamics in larger animals exist, not least of which is asexual vs. sexual reproduction and *more* complex life histories based on significant growth from birth. Experimental studies have shown that rapid life history evolution in vertebrates is possible, through response to selection caused by predation (Reznick et al., 1996) and harvesting (van Wijk et al., 2013), but trait change from selection on vertebrates in itself is not an eco-evolutionary loop. Analyses of empirical data demonstrates that eco-evolutionary feedback from an environmental change to population dynamics could explain observed trait distributions and population sizes (Coulson et al., 2010, Ozgul et al., 2010, Ozgul et al., 2012), but this generally lacks evidence of genetic selection, but see similar studies of trait demography in birds (Charmantier et al., 2008, Nussey et al., 2005). Other studies have identified where eco-evolutionary dynamics are likely to occur, for example by demonstrating how changes in selection have led to changes in animal behaviour and/or distribution (Strauss et al., 2008). Fewer studies, however, have been able to manipulate the eco-evolutionary loop in more complex organisms and ask what role ecological conditions have on selection on traits, and does this trait change feed-back to influence population dynamics (Cameron et al., 2013, Walsh et al., 2012).

The role of predation in life history evolution has long been recognised (Law, 1979, Michod, 1979, Reznick, 1982, Stenson, 1981), and remains a contemporary interest (Beckerman et al., 2013). There has been a fever of interest in the role of high rates of trait-selective exploitation on shifts in the trait distributions of many harvested animal populations, in particular of body size or age and traits that would otherwise be under sexual selection, such as male ornamentation (Biro and Post, 2008, Bonenfant et al., 2009, Bunnefeld et al., 2009, Ciuti et al., 2012, Darimont et al., 2009, Hamilton et al., 2007, Milner et al., 2007, Olsen et al., 2009, Pelletier et al., 2007, Coltman et al., 2003). There has also been a concomitant interest in the role that these shifts in trait distributions may play in eco-evolutionary dynamics (Coulson et al., 2006, Coulson et al., 2010). In those animal species that we exploit at some of the highest rates, specifically the marine and freshwater fishes, there is an ongoing debate about the mechanisms that lead to these shifts in body size distributions (Andersen and Brander, 2009a, Andersen and Brander, 2009b, Anderson et al., 2008, Browman et al., 2008, Kinnison et al., 2009, Kuparinen and Merila, 2007, Kuparinen and Merila, 2008, Law, 2007). There are several more robust explanations for reduced mean body size-at-age in exploited fishes including body condition effects (Marshall and Browman, 2007), size structured community interactions (De Roos et al., 2003, Persson et al., 2007, Van Leeuwen et al., 2008, Anderson et al., 2008), and fisheries-induced evolution (Jorgensen et al., 2007). Intuitively these more prominent explanations are not mutually exclusive and have each been more plausible an explanation for responses to harvesting in different

case studies. Here, we will investigate the role of evolutionary responses of phenotypes to exploitation, and in particular to stage-selective harvesting.

Stage-selective harvesting, occurring at times of the year or in places where particular life history stages dominate the harvest (e.g. adult Barents Cod at spawning ground), or where there are other stage-based vulnerabilities in likelihood of harvest mortality (e.g. in cryptic selection of hunted birds (Bunnefeld et al., 2009), or killing only adults or juveniles of pest species) is predicted to lead to shifts in growth rate to maturity that are distinct from size-selection harvesting. Here it is expected that life histories will evolve such that individuals who minimise their time in the most vulnerable stages will be selected for (Stearns, 1992). So we expect that harvesting of juveniles will lead to faster developmental growth to maturity, while harvesting adults will reduce developmental growth via a trade-off with increased juvenile survival and adult fecundity (Ernande et al., 2004).

Previous investigations with soil mites in seasonal environments where we exposed populations to adult or juvenile mortality resulted in statistically different growth rates to maturity in harvested populations, and compared to unharvested populations, the shifts in growth rate were exactly as predicted by theory (Cameron et al., 2013). Here we extend this analysis to the evolved responses of growth rate to maturity when harvesting juveniles or adults across constant, random and periodic environments. Mite populations were harvested at a rate of 40% per week (proportional harvest) or as an additional threshold harvest treatment in randomly variable environments of all adults above 60% of the long term adult population size. We estimated these rates to be close to the maximum soil mite populations can sustain without collapsing (Benton, 2012). We report the life history results on Low food conditions as we assume this is most representative of the conditions in long term experimental populations e.g. (Cameron et al., 2013).

In summary of this introduction we present new empirical data from the mite model system where we have investigated the role evolution plays in the contemporary responses of population dynamics to environmental change. We will summarise our main finding on the role of phenotypic evolution on population responses to highly competitive environments and building on this we will discuss the roles of environmental variation (i.e. variation in food availability) and harvesting on the development of the eco-evolutionary feedback loop.

6.1 Methods

Soil mites were collected from several wild populations and allowed to mate for two generations in the laboratory before being placed in our standard microcosm population tubes (see section 3)(Cameron et al., 2013). Sixty populations were started with 150 of each sex of adult and approximately 1000 juveniles in order to minimise transient dynamics. Each population received the same average access to resources of 2 balls of yeast per day, but was randomly assigned to one of three experimentally induced levels of resource variability (i.e. environmental variation): constant (replicates (n) =18); periodically variable (n=18) and randomly variable (n=24). The periodically variable treatment was

designed to represent seasonality as best as possible by having a 28 day cycle e.g. (Cameron et al., 2013). The randomly variable treatment was designed to be entirely unpredictable with daily food provisions being chosen from a random distribution with mean of two balls over a 56 day window, with a maximum daily provision of 12 balls (Benton et al., 2002). The mite populations were censused each week for 2 years, where a generation is approximately 5 weeks (Ozgul et al., 2012).

From week 13 to 83 the populations from each environmental variation treatment were subjected to a factorial stage-structured harvest treatment where: populations were either unharvested; juveniles were proportionally harvested (where 40% of juveniles were removed each week) or adults were proportionally harvested (where 40% of adults were removed each week). In the randomly variable treatment there was an additional treatment of a threshold adult harvest, sometimes called a fixed-escapement harvest (Fryxell et al., 2005), where all adults above 60% of the long term mean number of adults were removed. This number was set to 176 adults based on 60% of the long term mean adult population size from previous studies on the same mean resources (Benton and Beckerman, 2005). Threshold harvest strategies have been said to be more conservative in affecting the variance in population size and therefore minimise extinction risks to harvested populations (Lande et al., 1997), but such claims have not been tested experimentally in variable environmental conditions.

In tandem with the population census, we conducted less frequent common garden life history assays to measure the development to maturation of seven full sib families for two of the six replicate populations per treatment combination. For the common garden, 100 juveniles were removed from populations and reared to the F2 generation on fixed per-capita resources to standardise parental effects e.g. (Plaistow et al., 2006). Single F2 male-female pairs were allowed to mate and their eggs were collected. Twenty offspring from each pair were each reared collectively in either High or Low food resource availability. Only the results from the Low food life history assay will be presented in this paper as this was found to best represent the competitive conditions in experimental populations. Age (days) and body sizes (body length in mm) at maturity were recorded for each adult individual of each sex. Daily survival rates until maturity of the cohort of 20 juveniles were calculated using standard methods (e.g. Mayfield estimates). Fecundity at maturity was estimated for each female individual using a linear regression of the age and size at maturity with cumulative fecundity from day 3-7 post eclosion from existing data (Plaistow et al., 2006, Plaistow et al., 2007). These data led to average trait values representing family and treatment phenotypes.

Twenty four adult females per population were sampled from the common garden F3 generation in weeks (i.e. time-points) 0, 18, 37, 63 and 95 and their genotype characterised using amplified fragment length polymorphisms (AFLP). The assay used 299 loci and the methodology has been described in detail elsewhere (Cameron et al., 2013), but here incorporated the constant, periodic and random environmental variation treatments.

6.1.1 Quantitative methods and statistical analysis

Life history trait data on age and size at maturity are presented in the text as full-sib female or treatment means with standard deviations at the beginning (week 0) and end (week 95) of the experiment (e.g. Plaistow et al. 2004). Statistical differences in daily Mayfield survival estimates between environmental or harvesting treatments was most appropriately tested using a generalised linear model with a quasipoisson error distribution. Significance of treatments was tested while correcting for the highly overdispersed distribution using F tests (Crawley, 2007). The significance of environmental variation and harvesting treatments on the mean female phenotype and the age and size at maturity of each family per treatment at the end of the study was assessed using MANOVA to jointly model log(age) and log(size) in Low food conditions while controlling for population density in the life history assay tubes by using tube covariates (weighted density, median density and total tube survival), see Cameron et al. (2013). Owing to the extra threshold harvest treatment in random variation treatments, a full model was first built without this one treatment to independently test for an environment*harvest interaction. Following this, and for predictions of treatment means, a separate MANOVA was built for each environmental variation treatment. Age and size at maturity trait values were then plotted as model predicted means with associated standard errors of the model estimates.

To test for any link between Low food phenotypic change and changes in observed population growth, we estimated the mean and confidence intervals of the basic reproductive rate per treatment, R_0 ($R_0 = \exp((\ln (l_x * m_x))/T_c$, where l_x is the chance of an individual surviving to age x, m_x is the number of offspring produced during age x-1 to x and T_c is the average generation time) (Stearns, 1992). R_0 was corrected by the average generation time due to the overlapping generations. For further details of this method refer to supplementary material associated with Cameron et al. (2013). Average population growth rate (pgr = Nt + 1/Nt) was calculated from a smoother fitted across replicate population time series per treatment (observed population growth = change in total population size from week to week, over a 10 week window around assay time-points), and a Pearson's correlation test between the two estimates of population growth were undertaken.

For each environmental variation treatment, genetic diversity in age-at-maturity in a Low food assay was apportioned using an analysis of molecular variation (AMOVA) approach into: 1) differences among individuals within replicate populations; 2) differences among replicate populations within time-points within harvesting regimes; 3) differences among time-points within harvesting treatment; and 4) differences among harvesting treatments across time-points (AMOVA, Arlequin Version 3.5 (Excoffier and Lischer, 2010)). The relative magnitude of differences can highlight the effects of deterministic and stochastic microevolution acting across the populations. It is expected that drift would cause significant differences to accumulate among replicates within time-points for any treatment, whereas selection would cause significant differences across time-points within a treatment or among the treatments themselves.

6.2 Results- Evolution of population dynamics in variable environments

548 All mite populations initially declined across all three environments and then recovered (**Figure 5**).
549 Before the recovery, the mean population growth rate of the populations was 0.980 (=2% decline per
550 week), 0.978 and 0.980 at week 20 for the constant, periodic and random environments respectively.
551 During the recovery, the population growth had increased to 1.010 (= 1% increase per week), 1.013
552 and 1.012 respectively by week 60. At the start of the experiment, in low food and hence highly
553 competitive conditions, soil mites took an average of 12.3 days to mature. By the end of the
554 experiment we observed a large reduction in the growth rate to maturity of the average mite family
555 from all three environments, equating to a 35%, 76% and 83% delay in age-at-maturity in the constant
556 (16.6±2.6s.d. days), periodic (22.1±3.6s.d. days) and variable environments (21.6±4.27s.d. days)
557 respectively. The observed increasing delays in developmental growth rate over the course of the
558 experiment in resource poor conditions are positively correlated with increases in fecundity in adult
559 mites (Cameron et al., 2013, Plaistow et al., 2006, Plaistow et al., 2007). This is suggestive that the
560 delays in maturity are adaptive. There was no significant difference in daily survival rate between
561 families from the three environments (Quasipoisson GLM:$F_{env}=0.29_{2,123,}$ $P>0.7$). Consequently, while
562 the earlier maturation phenotype we see in constant environments would have reduced fecundity
563 compared to other environment phenotypes, this appears to be offset by increased overall survival to
564 maturity. The question of interest, that separates our experiment from only demonstrating that the
565 traits of mites change when they are placed in different laboratory environments, was to determine if
566 the change in growth rates observed were caused by selection and if that selection led to the recovery
567 of the populations after only eight generations.

568 The basic reproductive rates R_0 estimated from the common garden life history data at weeks 0, 18,
569 37, 63 and 95 were highly correlated with the average of observed population growth rates estimated
570 from replicated experimental time series (Pearson's = 0.88, $t_{2,13}$ = 4.81, $P<0.001$). Furthermore, there
571 is no significant difference between the estimates of population growth from life history data or the
572 time series (e.g. R_0 vs pgr, paired t-test, p=0.34). Given that the phenotype data used to estimate R_0
573 (i.e. age and size at maturity, survival to maturity, reproduction at maturity) are collected in similar
574 competitive conditions to those in the population experiments but after 3 generations in a common
575 garden environment, this is very strong evidence that we are observing evolved changes in mean life
576 history that lead to changing population dynamics; a requirement for the demonstration of an eco-
577 evolutionary feedback loop (Schoener, 2011). However, it does not prove that the phenotypic change
578 observed is being caused by genetic evolution e.g. (Chevin et al., 2010). The AMOVA analysis on
579 AFLP variation confirms that both genetic drift and selection are operating in concert to affect the
580 levels and distribution of genetic variation in growth rates within the microcosm system (**Figure 6**).
581 All of the partitions explained a significant proportion of the variation observed (e.g. more than 5%)
582 except for the difference among harvesting treatments within the constant food environment. This
583 need not reflect a lack of selection caused by harvesting acting on growth rates in constant
584 environments, but that among individual variation is likely masking its importance in this treatment.
585 This highlights that within each environmental variation treatment, genetic drift is acting to force
586 populations into different evolutionary trajectories (given that replicate populations within harvesting

treatments within time-points and within environments accumulated significant genetic differences). It also demonstrates that selection operates to generate differences in the growth rate to maturity across time-points, within harvesting regimes, in the different environment treatments as well as between environments across time-points.

6.3 Results - Life history responses to harvesting in variable environments

We found a significant interaction between environmental variation and harvesting treatment on the age and size at maturity (MANOVA: age-at-maturity $F_{env:har}=2.45_{4,123}$ $P<0.05$; size-at-maturity $F_{env:har}=3.15_{4,123}$ $P<0.02$). To understand this interaction, and by controlling for stochastic differences in mite densities between life history assay tubes, we standardised survival and density covariates to the mean values per environmental treatment and predicted the mean and variance of trait values from a MANOVA for each environment. In both constant and randomly variable environments harvesting adults or juveniles led to a significant delay in maturation in comparison to unharvested controls (**Figure 7**, left and centre panels). This contrasts with what was observed in periodic environments where harvesting juveniles reduced age at maturity in line with reducing risk of increased harvesting mortality (**Figure 7**, right panel). In both constant and randomly variable environments there was no significant effect of harvesting on size at maturation (constant: $F_{har}=2.25_{2,28}$ $P>0.1$; random: $F_{har}=0.76_{3,40}$ $P>0.5$), unlike the small but significant increase in size at maturity in adult harvested phenotypes from periodic environments originally described in Cameron et al. (2013). As we discussed in the previous section, we detected a statistically significant effect of selection caused by harvesting on the variation in developmental growth rates in both random and periodically variable environments (**Figure 6**). It is surprising that given the clear phenotypic differences found between unharvested and harvested constant environment populations at the end of the experiment, that the AFLP response was not more pronounced. However, selection was observed, and this assay method is a blunt tool given that we only have a snapshot of phenotype and genotype differences from a small number of individuals from two of six replicate populations at the F3 generation.

6.4 Discussion of Evolution of life histories in response to environmental variation and harvesting

Life history research increasingly focusses on understanding the links between environmental variation and population demography. Stochastic demography is a matrix based approach to estimate optimum life histories that maximise fitness averaged over variable environments, when variable environments lead to variation in vital rates (Caswell, 2010, Haridas and Tuljapurkar, 2005, Trotter et al., 2013, Tuljapurkar et al., 2009, Tuljapurkar et al., 2003). Not all such approaches have focussed or presented the same traits we have considered here, i.e. developmental growth. However, stochastic demographic approaches have shown that the generation time, measured variously as cohort generation time (T_c) or longevity, buffers against the negative effects of environmental variation on fitness (Morris et al., 2008, Tuljapurkar et al., 2009). Shertzer & Ellner present a dynamic energy

budget approach that, while not strictly evolving per se, sought out optimum energy allocation strategies to growth, storage or reproduction that maximised R_0 in a genetic algorithm model of a rotifer population (Shertzer and Ellner, 2002). In the Shertzer & Ellner study, what is relevant is that environmental variation was experienced over the time scale of an individual's lifetime, as in soil mites (e.g. day-to-day variation instead of between generation or inter-annual variation). Life history strategies that delayed age to maturity were optimum in more variable environments and/or environments with periods of resource limitation (Shertzer and Ellner, 2002). Tenhumberg and colleagues also focussed on stochastic variation in prey availability within a predators lifetime that led to a negative relationship between growth rate and mortality arising from the physiological constraints of 'digestion and gut capacities' in syrphids (Tenhumberg et al., 2000). The negative relationship led to increased fitness of those strategies that delayed growth rate to maturity in variable environments. Negative relationships between vital rates have been suggested to increase fitness in variable environments in other analytical approaches (Tuljapurkar et al., 2009). In *Caenorhabditis elegans*, mutants that aged slower were also found to have higher fitness in more stressful environments, including when food availability was variable. This is suggested to lead to altered allele frequencies in more heterogeneous environments in ecological time that feeds into evolutionary dynamics (Savory et al., 2014). All these predictions fit with our main result that strong competition and more variable food supply led to larger delays in maturity, which led to increased population growth rates. There is great consistency therefore, across a number of empirical and theoretical approaches that the evolution of slow life histories is likely in variable environments. However the relative importance of the magnitude of environmental variability, its predictability or autocorrelation in the evolution of slow life histories is not yet clear and should be an interesting avenue of future research.

While our experiment was designed to investigate potential links between phenotypic change and population dynamics, it shows the potential for populations to recover from an extinction trajectory through evolution: evolutionary rescue (Bell and Gonzalez, 2009). Across all three of our environmental variation treatments, the initial trajectory of population growth is negative (i.e. an extinction trajectory), but becomes positive after evolution in response to laboratory conditions leads to delayed maturity and increased fecundity.

It is a key result that increased juvenile mortality can generate faster or slower life histories relative to controls depending on the temporal variability in the strength of resource competition. The constant and random environments produced more similar juvenile harvested mite life histories when compared to the periodic treatment. While the variation in food provision in the constant and random treatments was different (Coefficient of Variation (CV): zero vs. 0.36), the resulting variation in mite abundance was more similar due to demographic noise in constant populations (Benton et al., 2002, Cameron, Submitted)(CV_{adults}:0.20 vs. 0.34; $CV_{juveniles}$:0.46 vs. 0.50). In periodic environments the variation of food provision, and therefore adult and juvenile mite abundance is much greater (CV = 0.86, 0.46 and 0.76 respectively). However, the greatest difference between constant, random and periodic variation is that periodicity is caused by highly autocorrelated resource provisioning. We predict that this is where the different life history responses to harvesting arise, in the interaction between density

dependent demographic responses to mortality and evolutionary responses to more (periodic) or less (noisy-constant and random) predictable resource pulses between harvesting events. Such interactions could increase the positive relationship between age-at-maturity and fecundity if the increase in risk of harvesting mortality from delaying maturity was less than the potential gains to lifetime fitness from receiving a glut of resources just before maturation. Theoretical understanding of the interaction between intra-generation environmental noise and selective mortality at this temporal scale is currently lacking, largely due to the taxonomic bias in evolutionary demography studies towards long lived mammals and birds.

What we have presented in section 6 by describing ecological dynamics of a wild population adapting to a controlled laboratory environment, provides a much higher level of resolution on the consequences of ecological and evolutionary interaction. We demonstrate how individuals maximise their lifetime fecundity in response to resource poor conditions, or high selective mortality and highlight how complex population dynamics can be maintained despite long term erosion of genetic diversity caused by both stochastic and deterministic processes. The latter is difficult to reconcile with classical ideas of extinction debt in conservation population genetics e.g. (Fagan and Holmes, 2006) whereby positive feedback occurs between reduced population growth rate and loss of genetic diversity that leads to an inevitable extinction. Clearly there is a need to address how evolutionary rescue can interrupt an on-going extinction vortex, and the limits to the recovery of populations in relation to extant and introduced genetic variation.

7 Summary

The aim of this contribution was to explore the complexity of the route from individual phenotypic variation to population dynamics and back again in a model system: the eco-evolutionary loop. The mite model system has provided a rich series of experiments that have highlighted the level of information on individual life histories we require to make predictions about transient population dynamics following environmental perturbations is often considerable. The study of ecology has been described as the investigation of variation in space and time of the abundance and density of organisms (Begon et al., 2005), and while demography may be a main objective of ecology, it is clear from our work and others in this volume that the proposal that all evolutionary biologists should be demographers goes both ways (Metcalf and Pavard, 2007).

We have presented the study of three distinct pathways between environments, phenotypes and population dynamics: the role of current and historical environments on offspring phenotypes; the multigenerational effects of environmentally determined phenotypes on short term population dynamics and finally the feedback between population abundance and resource availability to selection on phenotypes and evolution of population dynamics. In our diagram of eco-evolutionary interactions (Figure 1), we have represented those pathways as independent routes. It is, however,

clear from the context dependency of our results that the selection on life histories that determines population dynamics will very much depend on the interaction between historical (parental effects) and current environments (growth rate to developmental thresholds).

Through our demonstration that soil mite population trends are determined by their life histories, which evolve in response to density dependent competition and predation (the eco-evolutionary loop), we have shown that in populations in which density-dependent competition is common, there is selection for individuals with life-history strategies that permit individuals to mature later in low food conditions, but still retain the ability to mature early when conditions improve (Cameron et al., 2013). If this is evidence of eco-evolutionary dynamics selecting for increased phenotypic plasticity, it highlights the potential importance of the parental effects we previously found to shape reaction norms such that selection can act on novel phenotypes e.g. (Plaistow et al., 2006). Selection on more novel phenotypes would have the potential to allow more rapid feedbacks between natural selection and population dynamics. This is particularly relevant in light of the interest in rapid evolutionary responses to environmental change. Our current research in the mite model system is examining how variation in the population dynamic patterns created in different environments influences the evolution of offspring provisioning strategies and epigenetic variation in gene expression during development and the effect that this has on later population dynamic patterns. This should lead to a less conceptual, and more mechanistic, understanding of eco-evolutionary population dynamics.

While we have identified much complexity, we have also shown when the role of environmentally determined phenotypic variation is less important in a population dynamics context (e.g. when resources are low), but it was only through experimentation that we were able to say this. This is in some ways the most important conclusion of this review, that carefully planned experiments in well-studied systems are what is required to separate potential consequences of eco-evolutionary dynamics from those which are likely to have important consequences in natural populations.

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Figure Legends

Figure 1. A diagramatic representation of eco-evolutionary dynamics based on the results of mite model system experiments. The eco-evolutionary loop is moving between the three circled states: from (a) population structure is dependent on life history transition rates, and interacts with the environment (b) via an interaction between density depedent and independent mechanisms and parental effects to determine per capita resources (c). Per capita resources interact with genetic and environmental determinants of individual life histories (d), which leads to a closure of the eco-evolutionary loop by creating population structure. We consider here the effects of predation and harvesting as external to the loop (orange boxes and arrows), affecting the loop directly by selecting against life histories or changing population size and structure.

Figure 2. A model of the L-shaped developmental threshold model predicting growth rates to maturation along an environmental gradient of food availability (i.e. norm of reaction). This model, developed by Day and Rowe (2002), is supported by our results in the mite model system and captures the feedback caused by the interaction between population size and environmental quality on per-capita resources, and the resulting density dependent effects on individual phenotype (based on Beckerman et al. 2004, Plaistow et al. 2004).

Figure 3. A. Male age and condition influences female allocation patterns. 16 different males were mated to virgin females at each of 5 time-points during their lifetime ("time"). Males (subpanels) were well fed (males 11-18) or poorly fed (males 1-8) and are presented in the order of the two male conditions. Graphs show egg size (mm) as a function of male age. Lines are fitted values from mixed effects' model. Time, food and male are all significant. Virgin females mating with "prime" males (time class 3) laid larger eggs (Pinder, 2009). **B.** Vector plots of the factor loadings from a factor analysis of parental effects (variation in egg length) between life history traits for individuals reared in high- or low-food current environments. In high current food environments, variation in egg length predominantly influenced a negative trade-off between fecundity and adult survival and had little effect on recruitment or age and size at maturity. In contrast, in low-food environments variation in egg length translated into differences in the probability of recruiting and variation in age and size at maturity. Modified from Fig. 4 in Plaistow et al. 2006 with the kind permission of University of Chicago Press.

Figure 4. The intergenerational effects of variation in parental investment in offspring on population dynamics. The graphs show the transient dynamics of populations initiated with eggs that were laid by either younger 3 day old (white points) or older 9 day old mothers (black points). The error bars represent bootstrapped 95% confidence intervals. The individual cohorts are marked approximately on the figures as F1, F2 and F3 and were identified by inspection of the age-structured dynamics. Modified from Benton et al. 2008 with permission from Wiley and the British Ecological Society.

Figure 5. Mean age and size at maturity of full-sib females (top panel), and of harvesting treatment means and twice standard error bars predicted from MANOVA when controlling for differences in tube densities (bottom panel). Panels represent constant (left panels), randomly variable (centre panels) and periodically variable resource environments (right panels). Colours represent juvenile (green), adult (red), threshold adult (orange) and unharvested harvesting treatments (black).

Figure 6. Analysis of molecular variance for 299 AFLP loci for (black) differences among individuals within replicate populations; (back hatching) differences among replicate populations within time-points; (forward hatching) differences among time-points within harvesting regimes; (waves) differences among harvesting regimes. ***** indicates statistical significance of treatment group at $P<0.05$.

Figure 7. Adult population size (±95%CI) from GAM fits across a 5 week centred moving average of replicate weekly counts per treatment (6 d.f., minimum model across all environments). All other stage

counts show a similar pattern of initially decreasing in abundance then increasing. Arrows at weeks 13 and 83 mark start and end of harvesting period respectively.