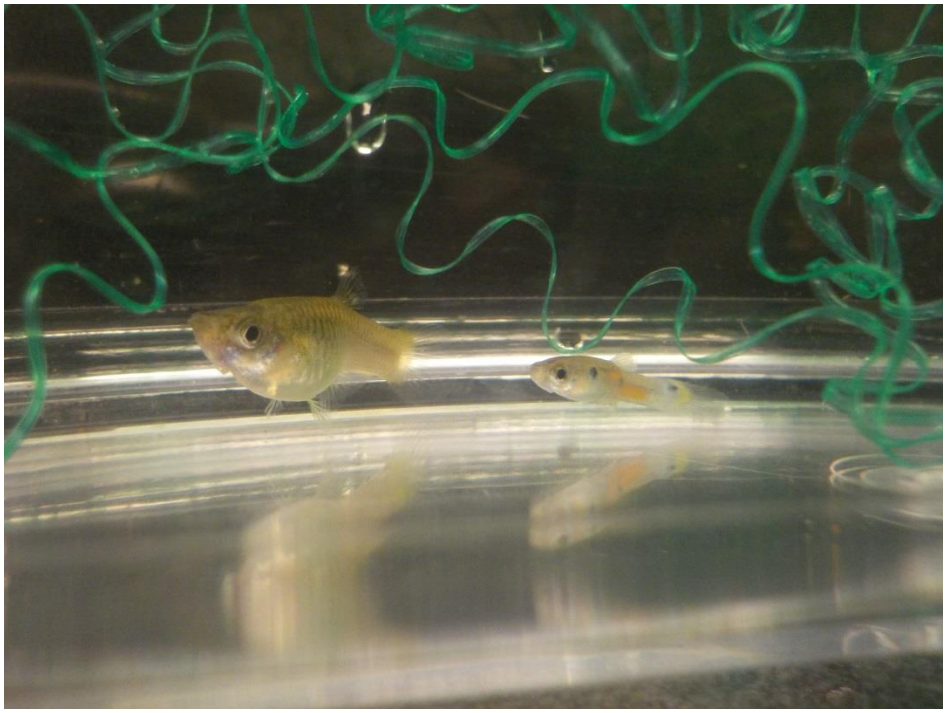
Drivers of eco-evolutionary dynamics in model systems - the role of harvest mortality and intraspecific competition



Matthew Neil Bond

A thesis submitted for the degree of Doctor of Philosophy (Ph.D)

Department of Biological Sciences

University Of Essex

September 2018

The Guppy (by Ogden Nash)

Whales have calves,
Cats have kittens,
Bears have cubs,
Bats have bittens,
Swans have cygnets,
Seals have puppies,
But guppies just have little guppies.

Acknowledgements

I would firstly like to thank my supervisors Dr Alex Dumbrell and Dr Tom Cameron for the support they have given me over the past three years. It is difficult to stress enough how fortunate I have been to have two highly supportive supervisors, both academically and personally, with such complimentary supervisory styles.

It would be remiss of me not to thank Dr Michael Steinke, whose support during my undergraduate dissertation gave me the confidence I needed to pursue a PhD.

In addition, I would like to thank Dr Etienne Low-Decarie, my board member, who has prepared me well for both my viva and future career.

Finally, I have relished the opportunity to work with Professor Robert Arlinghaus, a leading expert in his field who's given invaluable advice on making my work high impact and robust.

To name all friends who have supported me during the process of this PhD is difficult, there are so many. Therefore apologies for any omissions I make. Drs David Clark, James Fox, Rob Ferguson, Kate Randall, having done it so recently your selves, your support through the final stages of this PhD have been invaluable. Amy Sing-Wong, Ben Archer, Beth Greenwood, Phillip Pichon, Rameez Subhan, Yazen Al-Salman and others I have missed who have put up with me for so long.

I extend special thanks to all those who helped me look after the shed load of Guppies, without whose help my PhD would have been near impossible. To name but a few of these special people, thank you Amelia, Jess, Lydia, Hartley, and Louise, you've been awesome, and I hope I haven't put you off fish for life. Thanks again to my two best friends from home, Tom and Sam, whose support reminds me all the time of why we're

still friends 14 years on. Jason, the man who sparked my interest in fish, it would be amiss if you weren't included in my thanks. Apologies to anyone I've missed, as I've said, too many to count.

Finally I send all my Love and thanks to my extremely supportive family. Without their continual support, I would not have got through my time here at Essex University overall, and I'm extremely lucky to have them there for me every step of the way, always ready to lend a helping hand or support during the times that have been tough.

Contents

Table of figures

Thesis Abstract

Populations exist under a range of selective pressures, and the relative importance of natural (e.g. environmental change) and anthropogenic pressures (e.g. fishing mortality) remains hotly contested. Such external pressures can affect a population directly – for example when environmental change reduces the number of territories available in a population, and indirectly – when fishing pressure alters the gene frequencies for slow growth to large maturation size in a population. Understanding how populations the individuals within them, are likely to change in the face of growing pressures, both environmental and anthropogenic, remains of utmost importance if we are to manage populations for the future, particularly in the context of harvesting. In this thesis, I utilise model systems to explore the roles of competition and harvesting in regulating population growth, structure and phenotypic variation of individuals. As well as addressing broad theoretical questions of how individuals adapt to differing environmental pressures, and how such adaptation can feedback to population dynamics - I also address the outcomes of real world pressures on populations and in chapter IV offer a potential solution to one of those pressures, specifically fishing. This thesis therefore represents an exciting addition, not only to the field of eco-evolutionary dynamics but also has implications for the future management of exploited populations.

Chapter I – Introduction

Organisms and populations are under continuous selective pressure to adapt from exterior influences, such as climate change, human exploitation, predation (Reznick, Bryga and Endler, 1990; Reed, Schindler and Waples, 2011; Heino, Díaz Pauli and Dieckmann, 2015). Additionally, organisms are all subject to density dependent competition to lesser or greater extents (Amundsen, Knudsen and Klemetsen, 2007). Individual fitness is always selected for and therefore individual's variation in traits is the avenue by which adaptation operates. All individuals are unique in the trait space that they occupy, and these traits can influence the transfer of biomass through populations (De Roos *et al.*, 2007). Almost all populations on the planet are influenced by selective pressure from humans. However, very few management strategies of population dynamics incorporate the potential for adaptation to those pressures. This thesis investigates the feedback loop of individual variation / adaptation on population cycling and vice versa.

Avenues of Adaptation

Traditionally adaptation by organisms and populations has been considered to occur over millennial timescales, based on initial ideas set out in Darwin and Wallace's work(Darwin and Wallace, 1858). However, the idea of organisms requiring 1000s of generations to adapt to and fill differing niches has been challenged in recent years(Carroll *et al.*, 2007). Observations of the natural world show that changes in

organism's phenotypes, i.e. the traits they express, can occur over very few generations in response to environmental pressures (Reznick, Bryga and Endler, 1990). A classic example which first highlighted this to natural historians was the changes in coloration observed in the peppered moth *Biston betularia* (Kettlewell, 1958). Human induced changes in their environment (pollution changing the physical characteristics of the tree bark they had adapted to), elicited a response that occurred over relatively few generations, which in turn reversed to "natural" coloration when the pollution had been removed (Clarke, Mani and Wynne, 1985). This highlighted the possibility of rapid phenotypic change over ecologically relevant timescales, but required multiple generations for the population to adapt.

Evolution via natural selection is favoured in response to a consistent selective pressure when a single trait value is optimal for fitness (Sereda, Wilke and Schultheiß, 2014). Selection requires genetic mutation and is facilitated by sexual reproduction (Crow, 1992). Expressed phenotypes have corresponding genes that code for their expression which are called alleles. These can vary between individuals of the same population, which we would term genetic variation, which then manifests as phenotypic variation within a population. Sexual reproduction promotes the variation in alleles during the formation of gametes and fertilisation (Bateson and Saunders, 1902).

Natural selection acts on genetic variation, as only individuals that express phenotypes that are adaptive survive to pass on their alleles to their offspring. Mean traits expressed within populations then change as a result of selective pressure that removes maladapted individuals, i.e. changing the frequency of adaptive alleles within a population (Maynard Smith and Haigh, 1975).

As such, it can require multiple generations to generate a testable mean change in trait values, and therefore it is time limited (Hairston *et al.*, 2005). That said, many studies now show the number of generations that are required for such adaptation to occur is lower than previously thought and can occur over “ecologically relevant” time scales(Cameron *et al.*, 2014). Examples of this have now been investigated across taxa, from microbial selection experiments (Fischer *et al.*, 2014), invertebrates (Tribolium, Soil Mites, Drosophilia etc) to transplantation experiments with vertebrates (Arendt and Reznick, 2005).

In contrast, simple observations of organisms show that adaptive responses can occur over an individual organism’s life time or over a single generation. Humans can produce more melanin in response to increased UV exposure. Leaf number, shape and size; can change in response to light level in many species of vascular plants (Gratani, 2014). Therefore if there are differing avenues of adaptive responses, it is intuitive to assume there are differing conditions that select for them.

Phenotypic plasticity is the ability of a given genotype to express a differing phenotype according to the environment they experience (Price, Qvarnström and Irwin, 2003). This can occur within an organism’s life time (Chevin and Lande, 2015), or it can occur across generations, i.e. transgenerational plasticity (Walsh *et al.*, 2016). Transgenerational plasticity can occur when the parental environment drives a response in an offspring’s phenotype (Allen *et al.*, 2008). An example of this is when mothers adjust reproductive investment in response to population density, conferring competitive advantage on their offspring (Leips *et al.*, 2009) – often referred to a maternal or parental environment effects. Plasticity may also be behavioural, whereby organisms

adjust behavioural patterns to respond to environmental cues experienced (Bhat, Greulich and Martins, 2015).

Phenotypic variation is underpinned by variation in the genetic structure that codes for expressed phenotypes. Although it is this variation that natural selection acts upon, phenotypic change often occurs far too quickly for genetic mutation to be the driving force behind it, a.k.a. evolution by natural selection (Thorson *et al.*, 2017). Although the exact mechanisms remain unclear, plasticity is suggested to be controlled by "epigenetic alterations" rather than mutation, which in turn alters the expression of phenotypes. When these alterations are triggered by environmental cues, we can say that they form the basis of adaptive phenotypic plasticity (Duncan, Gluckman and Dearden, 2014). As such, phenotypic plasticity is said to be reliant on the environmental cues a whole organism experiences in order to express an adaptive phenotype (Bonamour *et al.*, 2019).

Phenotypic Plasticity can therefore facilitate rapid responses to changes in environmental pressures, and subsequently can facilitate persistence (Chevin and Lande, 2011; Ashander, Chevin and Baskett, 2016). Theory on plasticity dictates that it is selected for by variable strengths of selection, e.g. fluctuating temperature (Hoving *et al.*, 2013), and also the reliability of environmental cues that trigger a phenotypic response, e.g. chemical cues of predators eliciting a defence response (Boersma, Spaak and De Meester, 1998). In the absence of reliable cues, other responses to variable environments are sometimes favoured, such as bet-hedging (Furness, Lee and Reznick, 2015). Examples of this include diversified bet-hedging, where offspring are specifically adapted to a range of specific conditions in the hope that a portion will be well adapted to their environment (Einum and Fleming, 2004). Bet-hedging means long term fitness is maximised by sacrificing fitness in the short term (i.e. temporarily wasting

energy to maximise long term reproductive success). Bet-hedging is beyond the scope of this thesis but it's importance as an avenue of adaptation should be recognised.

Although the prevalence of "rapid" adaptation has become mostly accepted in recent years, fundamental knowledge gaps still exist on what specific trait responses might be to environmental pressures that populations experience. While there has been many demonstrations of the potential for ecologically relevant evolution in laboratory studies of population trends – there remain significant knowledge gaps on the ecological condition that will select for plasticity. In addition, consideration of the role of evolution will improve or diminish the likelihood of many existing laboratory approaches to understanding harvesting and ontogenetic development. To date, much work on multicellular and vertebrate populations is limited by observational data where exact mechanisms of evolutionary response are difficult to identify (Fuller, Baer and Travis, 2005). Therefore, there is great value in empirical laboratory collected data for identifying the responses of populations to simulated real-world pressures (Benton *et al.*, 2007; Cameron *et al.*, 2013; Van Wijk *et al.*, 2013).

Eco-evolutionary dynamics

Ecological conditions lead to selection in populations that drive evolution of trait values within populations, sometimes over “ecologically relevant” timescales (Carroll *et al.*, 2007). The use of “ecologically relevant” is key here, as a growing body of work explores the idea that trait change can affect ecological dynamics, such as population cycling and community dynamics (Fischer *et al.*, 2014; Post and Palkovacs, 2014). This in turn may feedback on traits expressed, which forms what is termed by some as a full eco-evolutionary loop (Cameron *et al.*, 2014).

Eco-evolutionary dynamics are determined by traits which directly influence size structure and growth e.g. life history traits such as growth, survival and reproduction. Population growth and structure are extrinsically linked to traits associated with individual growth (Stearns, 1989; Reznick, 1990). How fast individuals grow, and when and what size they mature determines when individuals start reproducing. This then will naturally impact biomass transfer and population density (Plaistow, Lapsley and Benton, 2006). Full eco-evolutionary loops, where evolved phenotypic change has a full feedback loop to influence population density, have only rarely been demonstrated empirically (Yoshida *et al.*, 2007; Cameron *et al.*, 2013, 2014). Many studies have demonstrated part of loop – for example where population dynamics results in an evolved change in the phenotypes (e.g. altered reproductive investment due to size structure and density) (Leips, Helen Rodd and Travis, 2013) what might this mean for populations

Alternatively, phenotypic change can be linked to changing population dynamics (e.g. differences in life history traits driving demographic changes in guppy populations) (Rodd and Reznick, 1997).

Pressures on populations, size as size-selective mortality or high competition for resources can select fordiffering investment in reproductive strategies such as investing in fewer large offspring during periods of high population density(Reznick, Bryant and Bashey, 2002). This has traditionally been viewed through the r vs K spectrum, i.e. do you invest in many lower quality offspring or fewer high quality offspring (Reznick, Bryant and Bashey, 2002). What is more recently considered is the idea that this can occur over short time scales to create these feedback loops with population growth and structure (Plaistow and Benton, 2009; Barneche *et al.*, 2018). Observations of guppy populations with differing strategies of reproductive investment show drastically different size structure and growth in wild settings (Bashey, 2006, 2008). These strategies are largely determined by predation regime and environmental productivity – for example in a high predation regime, individuals may invest in smaller-bodied offspring (Walsh and Reznick, 2009). When adapted organisms are transplanted to novel environments with differing predation regime, phenotypic changes are observed in reproductive investment alongside changes in population size structure and maturation size (Reznick, Bryga and Endler, 1990).

What is often unknown about these feedback loops is the mechanism by which they are occurring: whether by plasticity or directional selection (Torres-Dowdal *et al.*, 2012). Phenotypic plasticity is observed to have feedback loops in simple microbial systems, where rapid generation times and growth rate make observations of such dynamics simpler (Fischer *et al.*, 2014). However, understanding if plasticity is relevant to eco-evolutionary feedbacks in more complex organisms over ecological timescales is as yet,

relatively understudied. Given the evidence placed on rapid and relevant changes in mean trait values, and how this affects populations, it is also unclear how ecologically relevant selection would simultaneously affect both mean traits and the PP associated with those traits. If so do such feedbacks exist, and do they occur on similar timescales?

The newly understood prevalence of eco-evolutionary dynamics has wider implications for the way that we manage and understand how populations are likely to respond in the face of future environmental change (Dunlop, Eikeset and Stenseth, 2015). Climate change, pollution, and exploitation of natural populations are all factors that can influence life history traits, and therefore eco-evolutionary dynamics within them (Kuparinen and Hutchings, 2012; Hoving *et al.*, 2013). Understanding how realistic pressures impact individual fitness and therefore phenotypic variation is of paramount importance if we are to understand how populations of the future will look.

Fisheries and evolution

Global fishing produces 90.9 million tonnes of animal protein annually, comprising 17% of the world's total protein intake in (Food and Agriculture Organisation of the United Nations, 2018). As such, fishing represents a selective pressure on global fish stocks/populations that is unlikely to go away. This selective removal of individuals from fisheries drives shifts in size structure and the production of new biomass within populations (Svedäng and Hornborg, 2014; Siskey *et al.*, 2016). Fisheries are inherently size selective, and for the most part in fished populations, the likelihood of removal increases with body size (Law, 2000). This is driven both by the yield based demands, but also by regulations imposed in order to protect the sustainability of fish populations (Suuronen and Sardà, 2007).

Regulations dictating minimum take size limits, and therefore the technical regulations of fishing gears, are specified to protect smaller individuals in a fishery (Jusufovski and Kuparinen, 2014). This is designed so that maturing individuals are able to "spawn at least once", whilst maintaining yield expectations of a fishery (Vasilakopoulos, Neill and Marshall, 2014).

Counterintuitively, removal of biomass from a population can positively affect new biomass production through the release from density dependent competition for resources (Cameron and Benton, 2004; Schröder, Persson and De Roos, 2009; Svedäng and Hornborg, 2014). However, consistent high removal of biomass from the largest size classes of a population could affect population size and age structure (Wikström, Ripa and Jonzén, 2012). The removal of spawning stock biomass, (the actively reproducing portion of a population) will ostensibly reduce reproductive

capability, particularly if the largest individuals are removed (Hixon, Johnson and Sogard, 2014). In fish, reproductive output is found to disproportionately scale with body size, highlighting the importance of large bodied individuals for recruitment and population persistence (Barneche *et al.*, 2018). Therefore, fishing is evidenced to affect short term population size structure and maturation size, long term yields, extinction risk (Kuparinen and Hutchings, 2012) and as is increasingly considered, evolutionary dynamics.

Humans are inherently selective when they exploit wild populations. Animals are often selected for in terms of their value: either as trophies for recreational hunting; or for their body size when hunting for food (Allendorf and Hard, 2009). This artificial selective pressure acts on fitness related phenotypic traits, and therefore steadily removes individuals with maladapted phenotypes from the population (Kuparinen and Festa-Bianchet, 2017). This has been shown to result in observable changes in trait values in hunted animal populations, i.e. Harvest-induced selection (Strickland *et al.*, 2001). Examples include reduction in adult body size and horn size in sheep (Hengeveld and Festa-Bianchet, 2011; Pigeon *et al.*, 2016), reduced tusk size in African Elephants (Chiyo, Obanda and Korir, 2015) and reduced antler size in deer (Strickland *et al.*, 2001). These changes have all been observed over what is termed “ecologically relevant” scales, i.e. over the space of a few generations, affecting population size, cycling and size structure (Kuparinen and Festa-Bianchet, 2017). This has been paralleled in fish populations where harvest-induced selectivity for size leads to changes in mean trait values in pops over as little as 4 generations (Conover and Munch, 2002).

The potential for harvesting induced phenotypic responses of fish populations to affect long term sustainability of fisheries is gaining increasing attention (Heino, Díaz Pauli and Dieckmann, 2015). As previously discussed, fish populations show evidence of phenotypic adaptation in the face of size-selective mortality (Ernande and Dieckmann, 2004; Okamoto *et al.*, 2009; Hunter, Speirs and Heath, 2015). This is reflected in multiple species of commercially harvested fish populations, showing phenotypic responses in life history traits over 50 years of sustained industrial fishing (Marty, Rochet and Ernande, 2014). Exploited fish populations can be selected for faster growth, reduced size at maturation, and shifts in reproduction towards many smaller offspring / eggs through the increased mortality of slower growing, late and large maturing individuals (Kuparinen *et al.*, 2016). This is termed fisheries induced evolution (FIE) and is gaining increasing attention due to potential lasting effects on size structure, extinction risk and therefore yield of fisheries (Uusi-Heikkilä *et al.*, 2015). If we were to look at fishing from the same perspective as the farming of livestock, the negative effects of selectively breeding smaller individuals would be obvious.

Experimental work on this topic has demonstrated trait change in populations in response to size selective harvesting (Van Wijk *et al.*, 2013; Cameron *et al.*, 2014). Phenotypic responses range from behavioural responses in boldness, to changes in rates of maturation (Lindstro *et al.*, 2016; Andersen, Marty and Arlinghaus, 2017). Such empirical studies of FIE are inevitably criticised for their limitations due to the difficulty of accurately replicating realistic fishing pressure. Current work that evidences phenotypic change, often lacks density dependent competition due to the experimental design and/or the study species used (Van Wijk *et al.*, 2013; Lindstro *et al.*, 2016). Indeed, long term criticisms of FIE as a cause for concern are: how prevalent is it in wild systems?

and How strong is the selective pressure in real world fisheries (Marshall and Browman, 2007; Andersen and Brander, 2009).

The concept of “balanced” harvesting approach, has been gaining traction as a way of negating the effects of ecological and evolutionary pressure on fisheries (Froese *et al.*, 2016; Law and Plank, 2018). Balanced harvesting is defined by modifying the level of exploitation of a fish stock according to how productive it might be (Jacobsen, Gislason and Andersen, 2014). Typically, “balanced” harvesting is designed to reduce the selective pressure on fish populations, particularly on large bodied individuals. Additionally, there is heightened concern to adequately compromise between the societal, economic and conservation related demands on fisheries (Brown *et al.*, 2018).

A relatively new example of balanced fisheries regulation involves the use of “slot windows”, whereby individuals that fall within a given size range or “slot” are subject to harvest, and the individuals that fall outside of this range are protected from harvest (Gwinn *et al.*, 2015). Theoretical predictions of “harvest slots” are yields that compete with traditional size regulations, and importantly, also preserve size structures with reduced extinction risk across a range of fish life history strategies (Arlinghaus, Matsumura and Dieckmann, 2010; Gwinn *et al.*, 2015). These studies however are limited in scope due to studying relatively short-term consequences, and also do not investigate the phenotypic responses to “harvest slots”.

Therefore, fundamental knowledge gaps are present in empirical studies of fisheries dynamics. The relative importance of FIE (compared to other threats that fish populations face),_is undecided due to the practical difficulties of measurement in wild populations (Audzijonyte, Kuparinen and Fulton, 2013). The ability of novel harvesting regulations to compete with demands in yield while also protecting long term fisheries is

also unknown, and difficult to test due to similar reasons. Therefore, this presents exciting opportunities to test fisheries dynamics in a robust laboratory setting, which could have exciting implications for fish populations in the future.

Ontogenetic Asymmetry

Beyond mortality, one certain demographic process that all individual organisms undergo is ontogenetic development, i.e. all organisms grow and change state as they age. Therefore, the energetic demands of individuals can inevitably change throughout their lifetime (Sibly *et al.*, 2015). The energetic cost of maintaining more somatic and reproductive material will increase with age (Harshman and Zera, 2007). Organisms can also undergo niche shifts between different life history stages, utilising differing resources or habitats which alter the energetic demands on individuals (ten Brink and de Roos, 2017).

Differences in energetic requirements throughout an individual's lifetime can impact intraspecific competition, where there is "ontogenetic asymmetry" in energy efficiency between life history stages (Schröder, Persson and De Roos, 2009). When scaled up to whole population dynamics, this inefficiency may result in bottlenecks of biomass transfer (Persson *et al.*, 2007). Depending on what life history stage is competitively weaker, we find the bottlenecks in biomass transfer to occur in that weaker stage limited by either maturation (development control) or reproductive output (reproduction control) (Persson and De Roos, 2013).

Development control, where juveniles are competitively weaker than adults, results in a build-up of biomass in the juvenile cohort, as reduced food acquisition limits maturation into the adult cohort (Cameron and Benton, 2004). This is observed in invertebrate model systems, for example where adults out compete juveniles for clumped food resources.

Reproduction control, where adults are competitively weaker than juveniles, results in a build-up of biomass in the adult cohort, as reduced fitness reduces reproduction and therefore recruitment into the juvenile cohort (Reichstein, Persson and De Roos, 2015). This has been observed in fish populations, where adults become stunted and invest less in reproduction due to competitive stress (Persson *et al.*, 2007).

Release from these bottlenecks has been achieved in experimental populations through either culling the competitively weaker stage (Persson *et al.*, 2007; Schröder, Persson and De Roos, 2009), or biasing food ratios towards the competitively weaker stage (Reichstein, Persson and De Roos, 2015). Additionally, these controls have been observed in wild populations, where bottlenecks in biomass production result in increase in stunted mature individuals (Persson *et al.*, 2007).

Wild observations of stage structured, stunted fish populations often manifest due to the loss of external controls on populations. These controls often take the form of predators that regulate prey population dynamics (Persson *et al.*, 2007). The loss of predators due to overfishing has been observed to have knock-on effects on prey populations which then become subject to the above bottlenecks. This can then have further consequences for community dynamics, where relative abundances of different cohorts may prevent the reestablishment of predators into an ecosystem (Schröder *et al.*, 2009; ten Brink *et al.*, 2015).

The ubiquity of biomass bottlenecks caused by an emergent property of mass – specific energy efficiencies has been presented as a potential unifying theory of community ecology (de Roos, Metz and Persson, 2013; Persson and De Roos, 2013). However, as previously stated, the few wild examinations of population regulation arising from asymmetric energy efficiency throughout life history are as a result of the removal of a

control mechanism, e.g. a predator. A basic hypotheses emerges that challenges this emerging theory, as unless some external control maintains the symmetry of biomass transfer in a population, then evolution would act to minimise asymmetry. Selection would act to limit the low likelihood of maturing or reproducing, making juveniles and adults more symmetrical. Understanding how ontogenetic asymmetry and life history evolution might interact to regulate population cycling and individual fitness is therefore a knowledge gap that is yet to be investigated, and has implication for the management of populations.

Use of model systems in population ecology

The study of wild systems in ecology or evolution presents inherent challenges to those who investigate them. Unknown random effects may mask significant results (Stewart *et al.*, 2013), or the discovery of regulating processes may take longer than is practical for a field experiment to achieve results. Many processes investigated in population ecology may take place over years or decades, even for seemingly the simplest questions (Benton *et al.*, 2007; Conover and Baumann, 2009). Studies of wild large mammal populations do show significant results in terms of trait and demographic change, however are limited in respect of the time and effort taken to yield such results (Childs *et al.*, 2011). If rapid response to arising issues in population management is required, the need for short-term, robust, and easy to collect datasets is high.

Model systems often refer to particular study species that are used by different disciplines within biology to answer particular sets of research questions. These model systems are used for their reliability to produce results, increased replication, and improved ability to control for confounding variables (Fuller, Baer and Travis, 2005). When examining population ecology and evolutionary ecology, ideal model systems have fast generation times, ease of culture / husbandry, and are relatively small sized for ease of replication.

The use of model systems is not without criticism. The ease of not being measured under stochastic real word conditions raises questions about the relevance of findings from model systems (Carpenter, 1996; Srivastava *et al.*, 2004). Furthermore, many believe that the findings of model systems are overstretched in their interpretation and

usage to real world problems. This said model systems are ideal as a way of drawing reliable outcomes to the specific problems that you might be trying to address. In addition, the cumulative knowledge of given model systems that have been studied for a long time allows for increasingly more complex questions to be asked in the safer knowledge of obtaining significant results.

Studying individual variation in traits, adaptation through phenotypic change, and then scaling this to population dynamics in wild populations is inherently costly and time consuming (Cadotte, Drake and Fukami, 2005). Model systems used to test these questions must achieve the right balance of fast generation time in order to detect responses, and also be relevant enough to real world populations that are exploited. Here we strike a balance between the use of an invertebrate model system and a vertebrate fish model system. The soil mite, *Sancassania berlesei,* allows for short-term, reliable detection of evolution and population dynamics with high replication (Cameron *et al.*, 2014). However, small closed microcosms of invertebrates are arguably limited when trying to infer evolution about wild, commercially important populations. In contrast, populations of Trinidadian Guppies, *Poecilia reticulata*, are consumptive of time and space, but have dynamics that are more comparable to fisheries (Reznick and Ghalambor, 2005). As such, the use of both in this thesis allows for the capture of mechanisms of adaptation and population regulation under differing yet realistic environmental pressures.

Thesis Scope

This thesis aims to investigate the consequences of environments on life histories – specifically phenotypic plasticity in an invertebrate model system and also and the consequences of adaptation in life history traits on population dynamics in a vertebrate model system. Populations that humans utilise are under increasing pressure, both through direct human interventions such has harvesting, and indirectly from increasingly unpredictable and variable environmental conditions (Benton *et al.*, 2007; Fenberg and Roy, 2008). These pressures undoubtedly drive changes density dependent competition within populations, which in turn feeds back on individual fitness (Schrader and Travis, 2012a). Knowledge gaps exist in the exact mechanisms of how organisms and populations respond to realistic environmental pressures, and also what particular trait responses there might be to those pressures.

Chapter Objectives

Chapter III – Plasticity is a locally adapted trait with consequences for ecological dynamics in novel environments

- Does environmental variation drive the evolution of Phenotypic Plasticity in age and size at maturation?
- To empirically test if environmental variation can select for Phenotypic Plasticity as a trait in and of itself
- If Plasticity is an evolved trait then are more plastic populations better at adapting to novel environments than less plastic ones

Chapter IV – Protecting large bodied individuals alleviates negative eco-evolutionary responses of size selective fishing

- How does novel harvest regulation compare to traditional minimum sized based harvesting in terms of size structure, biomass, spawning biomass and yield?
- Do we observe evidence of selection on life history traits after a sustained period of harvesting?
- Does traditional harvest regulation result in greater phenotypic responses than novel harvest regulation?
- Do populations still show significant differences from each other after a period of recovery from harvest?

Chapter V – Asymmetry in energy efficiency throughout ontogeny: changes in resource allocation drive changes in population size and structure

- Do we observe bottlenecks in biomass transfer within guppy populations when juveniles and adults have equal access to food?
- If so, does biasing food to the competitively weaker stage drive overall increases in biomass?
- Can food bias towards the competitively weaker stage push a population towards symmetric maturation and reproductive rates?
- Do we see indication of phenotypic responses of life history traits in response to asymmetric conditions?

Chapter II - General Methodology

Study Species

Model systems have long been used to study ecological and evolutionary population dynamics (e.g. *Drosophila*, *Paramecium*, *Daphnia*, etc) (Gill and Hairston, 1972; Promislow *et al.*, 1998; Nilsson, Persson and van Kooten, 2010). Use of model systems in controlled laboratory experiments allow for complete characterisation of whole populations – which is difficult or unachievable in the wild. Whole population ecological studies on fish in aquaria are relatively new - where often fish are only used in shorter term behaviour or physiological studies (Lindstro *et al.*, 2016; Thambithurai *et al.*, 2018). But there has been an increase in the use of guppies, zebrafish and least killifish in ecological and evolutionary research both in the field and lab (Leips *et al.*, 2009; Schröder, Persson and De Roos, 2009; Bassar *et al.*, 2012; Schrader and Travis, 2012a). The relevance of utilising fish in lab experiments is obvious, in light of the strong selective pressure humans impose on wild fish populations, controlled experiments are allowing tests of specific and controversial hypotheses such as fisheries induced evolution (Van Wijk *et al.*, 2013) and ontogenetic asymmetry (Reichstein, Persson and De Roos, 2015), where previously only invertebrate models have been used (Cameron and Benton, 2004; Nilsson, Persson and van Kooten, 2010).

Zebrafish, *Danio rerio*, are commonly used in heritance and selection experiments, due to high reproductive output, fast generation time and ease of culture (Lindstro *et al.*, 2016). However, high rates of cannibalism on eggs results in high levels of experimenter intervention to maintain populations – where density dependence feedbacks are minimised. This means that any experiments will be unrepresentative of

the kinds of density dependent selection one expects in wild fish populations due to eggs, juveniles and adults being reared separately.

Other studies have utilised the Least Killifish, *Heterandria formosa* (Schrader and Travis, 2012a, 2012b). Given that previous studies investigating ontogenetic asymmetry have utilised this species, my initial experimental set up conducted for this thesis was meant to focus on this species. The benefits of this species are reported as high levels of reproduction and very short generation times (Travis *et al.*, 1987; Leips, Helen Rodd and Travis, 2013). This is particularly valuable in a study seeking evidence of evolutionary feedbacks to population dynamics. As a livebearerit has similar properties to the more widely known guppy but smaller body size, and birth of offspring is spread over the course of several days (Travis *et al.*, 1987). However, *H.formosa* was found to have poor reproductive rates in the Essex lab and required supplementary feeding of live foods to thrive. Despite six months of 10+ populations it was decided to not continue with this model.

Trinidadian guppies, *P.reticulata*, have been commonly utilised as model species to detect selection and population dynamics (Reznick, Bryga and Endler, 1990; Schröder *et al.*, 2009; Van Wijk *et al.*, 2013). Guppies are an ovoviviparous (livebearing) tropical fish found in streams in Trinidad, which show cannibalism on early stage juveniles. Commonly known, both in research and colloquially, for it's high reproductive output and rapid generation times (Reznick, Callahan and Llauredo, 1996; Travis, Reznick and Bassar, 2014), guppies lend themselves to addressing ecological questions in laboratory mesocosms. Previous studies of guppies have shown evidence of selection on guppies over relatively short time scales (Reznick, Bryga and Endler, 1990). As

such, in light of previous research conducted, guppies were chosen for my examinations of long term ecological and evolutionary dynamics.

Owing to the significant delays in starting my own fish populations a decision was made to incorporate analysis of existing unpublished data into my studies - for my first chapter. The soil mite, *Sancassania berlesei*, is a hardy, short-lived (3-7 weeks) invertebrate with relatively short generation time (4-50 days to maturation) (Beckerman *et al.*, 2003; Cameron *et al.*, 2014). Small body size means that microcosms can maintain high population size, with density dependent competition. This allows for high power, high replication studies of population dynamics and selection on life histories. Data analysed in chapter III was collected from experimental mite populations prior to the beginning of this PhD studentship, and as such general methods pertaining to that chapter were not undertaken by myself. Previous analyses of these data only considered the evolution of mean trait values – focussing predominately on low food environment phenotypes and the link to trends in population size (Cameron *et al.*, 2013). In this study I focused on the evolution of plasticity, independently of evolved changed in mean trait values- and a new experiment that assayed the role of evolved plasticity on responses to novel environments. Due to delays to set up a new laboratory with a guppy model system, this data analysis based chapter allowed me to get started on work during the first year of my PhD.

Overview of Mite model system methodology

Soil mites were collected from 4 different UK locations, mixed together and reared in excess food for a generation to maximise genetic diversity. Mite microcosms were then each inoculated with 150 males, 150 females and 1000~ juveniles to minimise transient dynamics. Microcosms were standardised glass tubes, 25mm in diameter, 50mm tall each half filled with a standardised density calcium sulphate substrate (plaster of paris). Substrate when kept moist maintained humidity within microcosms. Data from mites, analysed in chapter III, were collected in 2005-2008 by T.Cameron. The data collected from individual measurements of female mite size and age at maturation for wild mites and of mites originating from treatment populations. In addition, relative abundance of individuals in each stage and in total were measured as a time series of reintroduced populations (see figure 2 for details). No analysis had previous been undertaken with the data provided in any way.

Mite populations were counted using a Leica MZ8 binocular microscope and hand counter. Selection was measured using a multi-generation, common garden rearing experiment to remove the potential for maternal effects on trait measurements. Outlined in the figure 1 (used with permission from Cameron et al, 2013), size and age at maturation were assessed in high and low food environments, following 2 generations in a common environment to minimise maternal effects(Plaistow, Lapsley and Benton, 2006).

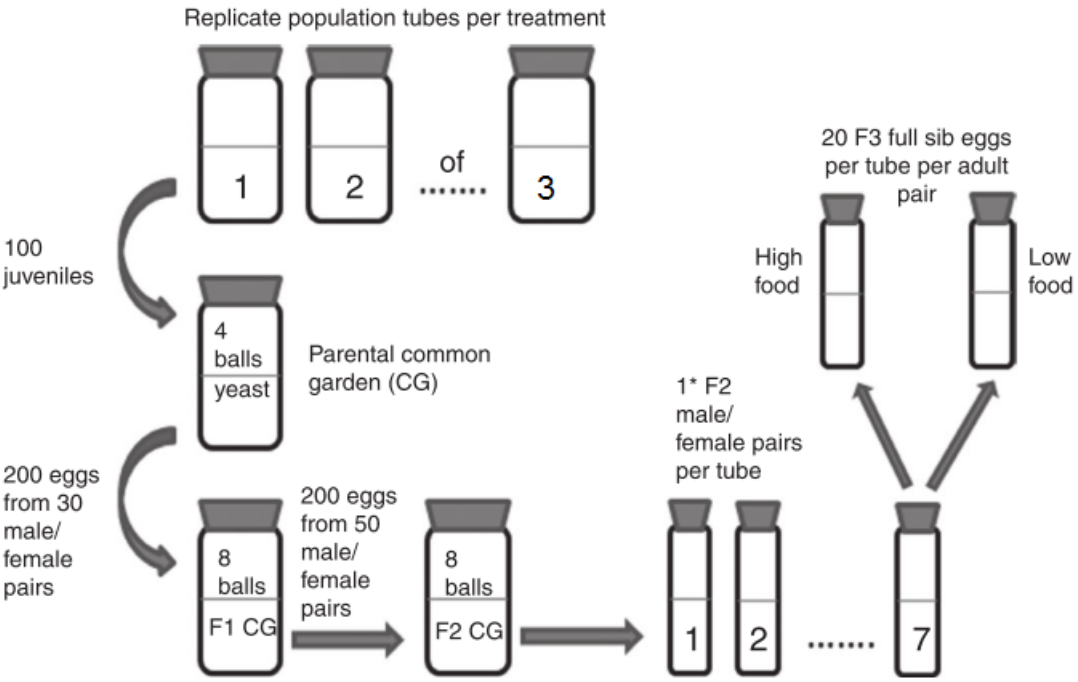


Figure 1: Schematic of 3 generation common garden experiment with soil mites (top) and adult female soil mite S.*berlesei (bottom).* Schematic taken with permission from Cameron et al (2013) and Photo Credit to Tom Cameron.

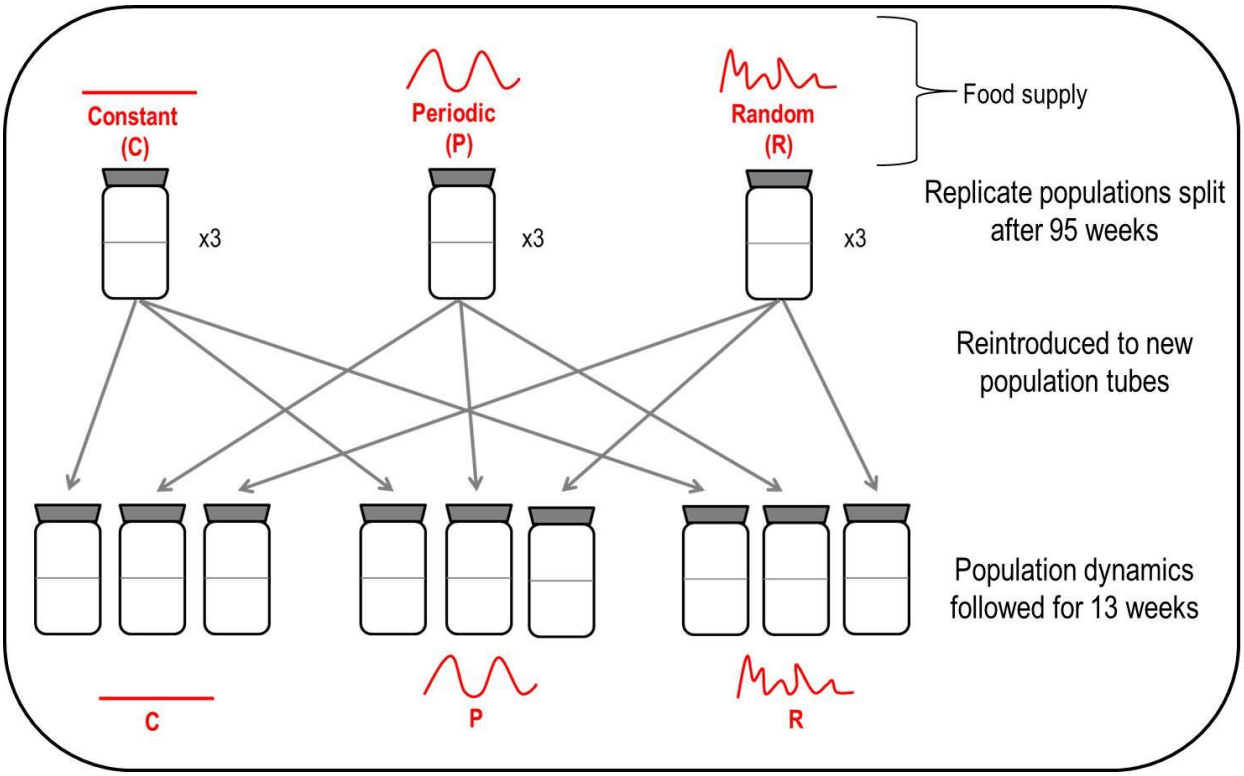


Figure 2: Schematic of population reintroduction experiment with soil mite microcosms. Populations were split and reintroduced to new tubes with either one of three food treatments, and regularly censused for total abundance, juvenile and adult abundance.

Outline of general aquarium protocol

Guppies for experiments listed in chapters IV and V were kept in controlled temperature freshwater aquaria within the same laboratory. Temperature was maintained at 26^0C±0.7, by both an air conditioning unit within the lab, and each tank also had individual heaters as an additional precaution.

All guppies were maintained in standardised water that was used for set up and water changes. Reverse Osmosis (RO) water was mixed with Reef Salt (D and D H2ocean Pro+ salt) to 2ppt to protect against ectoparasites, and buffered with aquarium buffer to 250 mg/L (Waterlife 8.3 aquarium buffer) to maintain pH of 8.

Food supplied to all treatment tanks and stock populations was Zm-400 granulated fry feed (ZM-systems). Food was supplied daily for 6 days a week, with one day off feeding on the weekend to prevent overfeeding / polluting of aquaria. Occasional additional feeding of defrosted copepods and *Daphnia sp* was undertaken to promote stock health, equally supplied to all treatment populations whenever required.

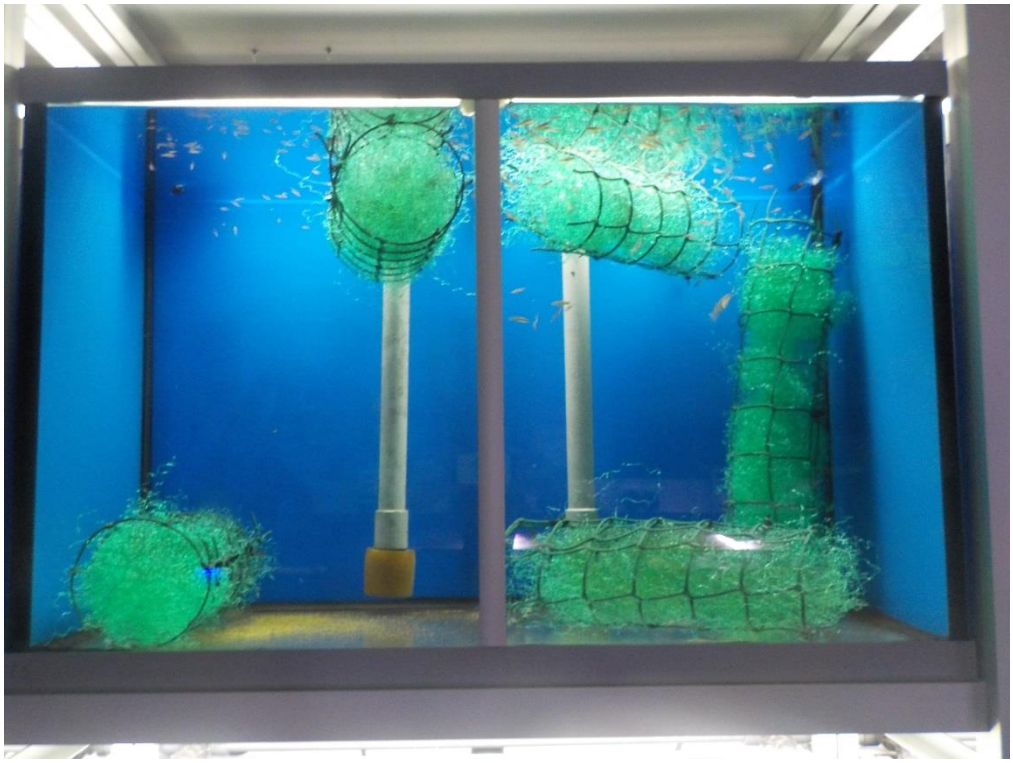
Refugia were supplied in all treatment and stock population tanks to reduce cannibalism on fry from adults, and reduce stress on females from male harassment. Refugia were standardised 30cm tall cylinders made from green plastic garden mesh with 50mm^2 gaps, each loosely stuffed with 1-2 litres green plastic thread filter medium (EHFIFIX - Ehiem) (See figures 3 and 4). Each experimental population had three standard refugia, one laying flat horizontally, the other two vertical.

Guppy stocks were transported from two separate locations to start experimental work: one from Umea University and the other from the University of Exeter. Umea guppies originated from a Low Predation (LP) site on the Quare River in Trinidad. Exeter guppies originated from a High Predation (HP) site on the Aripo River in Trinidad. These stocks were maintained in separate stock aquaria. All experimental populations were inoculated with a mix of individuals from both stocks to maintain as high a genetic diversity as possible.

A “mixed-stock aquarium” was maintained to house any individuals removed (see chapter IV), and for any individuals of unspecified origin. This prevented any potential contamination of original stock populations.

Mortality was recorded for biosecurity purposes. Fish health was also checked and reported daily in the same diary. Sickness or injured individuals were either treated with a broad range aquarium treatment (Tetra Medifin) or removed and dispatched in accordance with Home Office guidelines.

Population censuses were conducted on a monthly basis for both chapters IV and V at the same time as general aquarium maintenance. Tank sides were scraped of algae, refugia removed and rinsed, and 25% of water was removed and replaced with fresh RO water, salted and bufferedas per the above recipe. For censuses, all individuals were netted from populations into small 2 litre plastic tanks, and then sorted into life history stage: mature males, mature females and juveniles. Each stage was then placed in a plain white tray with a plastic ruler for scale, and then photographed for later image analysis (see figure 5).



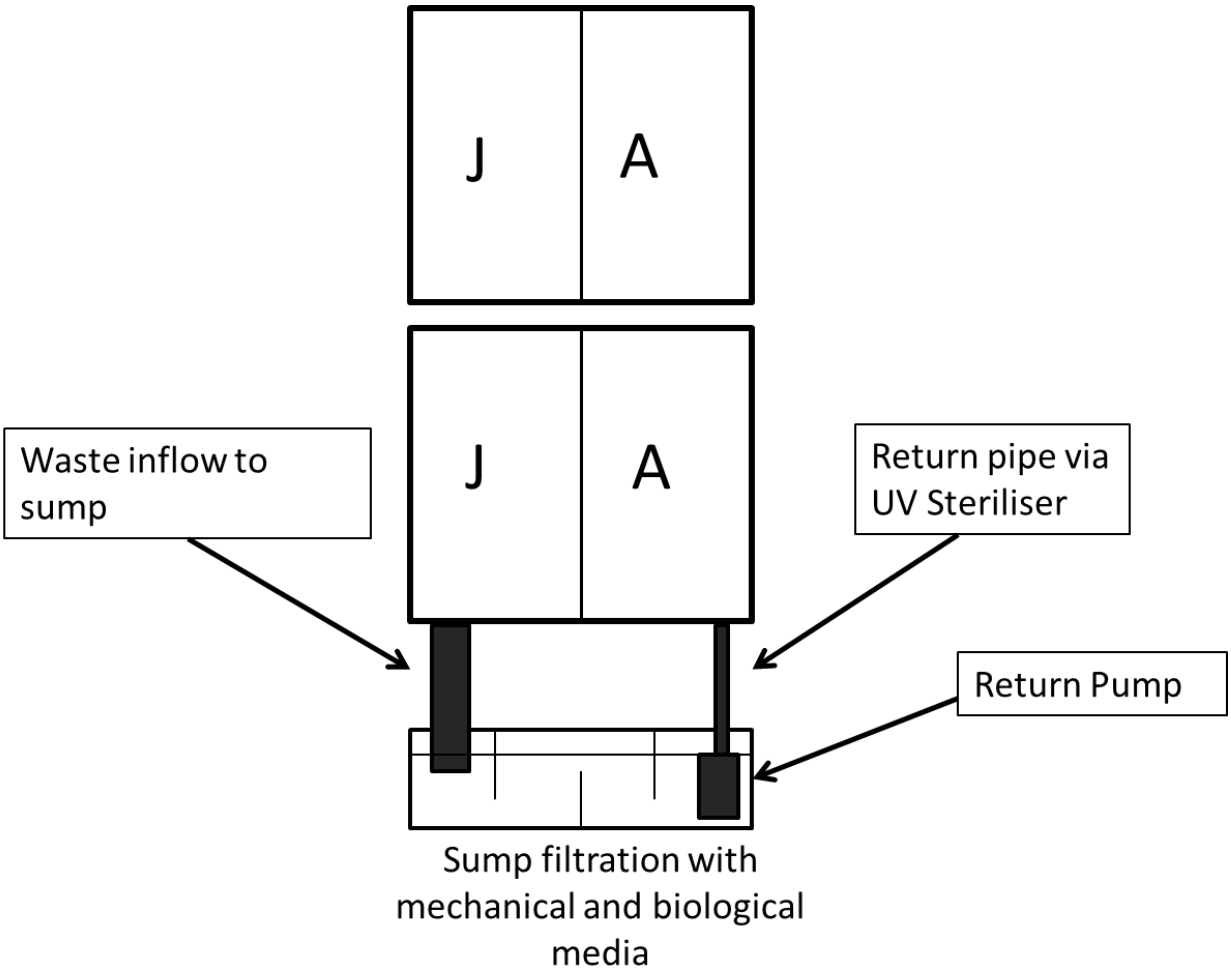


Figure 3: Front on photo of aquaria utilised in chapter V (top) and schematic for systems used (below). Juvenile and adult populations were kept on the left and right hand sides respectively.

Figure 4: Front on views of experimental population tanks, stacked, semi-closed system 210 litre aquaria for chapter V (top image) and stand-alone 110 litre aquaria for chapter IV (bottom image).

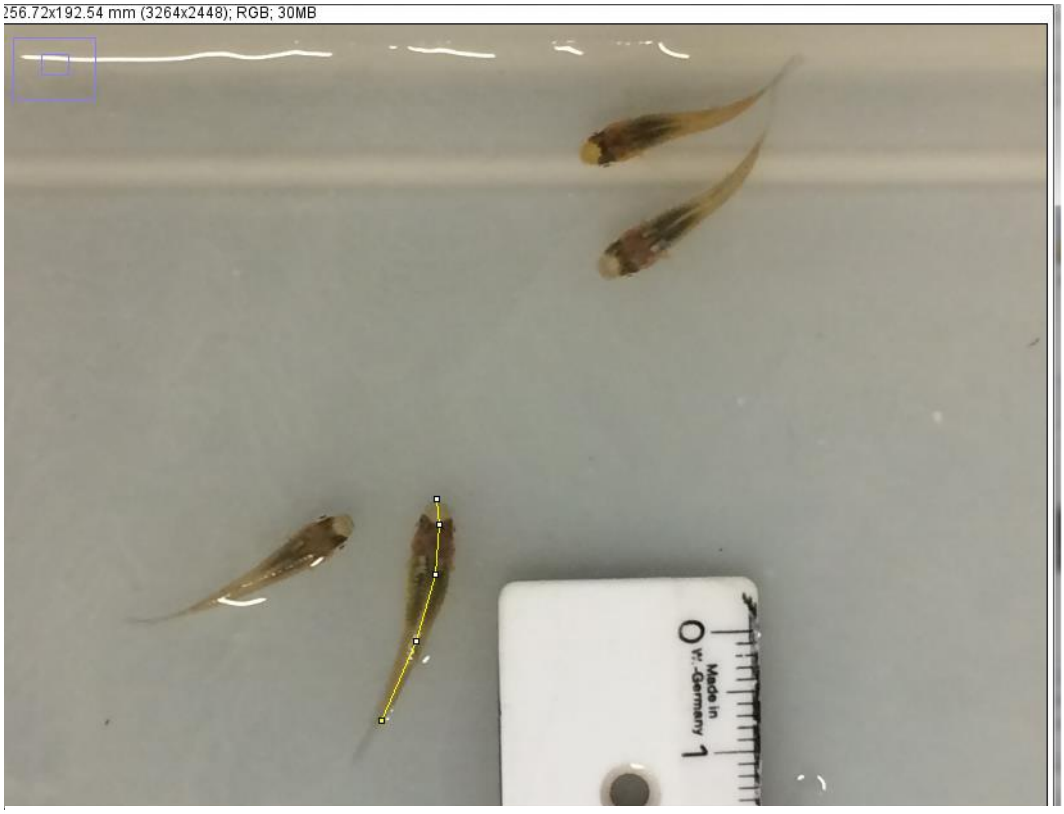


Figure 5: Example of image analysis technique used for both population censuses, measuring maturation and reproduction, and life history assays. Image analysis software (imageJ) was used to calculate standard length in mm.

Life history assay – development and set up

In order to investigate phenotypic change in experimental fish populations, I designed and created a circulating system and protocol for measuring life history traits. Water was circulated at 3000 litres per hour through a sump filter, through a TMC Vectron UV steriliser, and then pumped up into individual 2litre plastic aquaria, which overflowed into a tray and back to the sump (see photos and schematic in figures 6-8). Each tank contained a small amount of Ehiem fix as refuge. Temperature and water chemistry were maintained as above.

Methods development is a significant part of the development of a new research laboratory. As the first researcher in a new group developing a life history assay to assess evolutionary divergence in development traits in fish, in a common garden framework, was a significant objective to help me reach my research goals in Chapters IV to V. The purpose of the life history assay I wanted to develop was to measure changes in reproductive investment, age and size at maturity, to allow me to assess changes in mean and plasticity of development traits. Maturity was visually assessed without any dissections of individuals: females were identified as mature by presence of a gravid spot and shape of the abdomen; males by the full development of the gonopodium fin.

This was motivated by approaches taken on my other study system used in chapter III, using the soil mite *Sancassania berlesei* (Cameron *et al.*, 2014). However, published literature that measures life history traits in Guppies (Reznick, 1997; Van Wijk *et al.*, 2013; Pauli *et al.*, 2017) is not without its limitations.

Numerous studies investigating life history evolution in livebearing fishes utilised liver paste as a food source (Riesch *et al.*, 2016). Liver paste is a high protein food utilising beef liver, a standard food that has been used in fish experiments since 1943 (Reznick, 1983). Given the high nutritional quality of this food, it is arguable that even small portions of liver paste would effectively be *ad libitum*. Comparatively, the natural food of juveniles is well below this in terms of nutritional quality. Providing food *ad libitum* is unlikely to help differentiate development traits between treatment populations, particularly given the ability of many organisms including guppies to use compensatory growth (Auer *et al.*, 2010; Sundström *et al.*, 2013). It is often discussed that life history assays should use a range of food availabilities that capture the food supply experienced in either experimental or wild populations under density dependence (Beckerman *et al.*, 2003). Another concern of using ad lib food is the magnification of parental environment effects that common garden approaches are usually thought to minimise. For example in soil mites, high food experienced by ancestors drove intergenerational effects on life histories up to 3 generations later (Plaistow, Lapsley and Benton, 2006).

Following initial trials with counting out very small numbers of pellets from our population scale food (ZM-400, www.zmsystems.co.uk), which we found to take too long on feeding days we experimented with Interpet Liquifry no 2. This can be bought in bulk and used with a syringe for precise dosing of food levels. To develop our pilot assay we based our “Low” and “High” food levels off estimated per capita levels of ***protein*** received by individuals within populations. To do this we first divided the total weight of protein in the daily total food provided by the number of adult individuals in a long term population at high equilibrium density. This provided our first estimate of “Low” food life history assay treatment level of 0.04ml per day *per capita*. However this

0.04ml per capita resulted in slow growth and high mortality of juveniles. We then divided the population food by only the average of the highest observed juvenile tank densities to estimate 0.1ml per day *per capita.* This resulted in high survival (compared to early pilots), but with slower growth to maturity than previously published literature (Van Wijk *et al.*, 2013; Pauli *et al.*, 2017).

High food levels were set at 0.3 ml per day per capita and was found to result in significantly greater growth rates (figure 8) These two feeding rates, 0.1 and 0.3 per day per capita was therefore determined to be the low and high guppy life history assay treatments.

Results using this method are shown in chapter IV. Mean growth rates for both food levels from the two successful life history assays (pilot and chapter IV) are also shown in figure 8, using data produced with permission of Bemrose and Cameron (2017, unpublished manuscript).

For the Chapter IV life history assay, gravid females were removed from experimental populations, fed ZM-400 *ad libitum* until birth. Females were checked for birth daily to minimise any risk of cannibalism. Females that gave birth were separated from their offspring, and then measured before being returned to their original population. Reproductive output per female was assessed through the measurement of two traits: Brood size (number of offspring per litter) and body size of offspring. To assess these, newborn litters were photographed together for later analysis.

Individuals from litters were then separated and grown in groups on either high or low food (0.3ml or 0.1ml *per capita* respectively). Juveniles were grown to maturity and

photographed for later image analysis so that both age and size at maturity can be estimated.

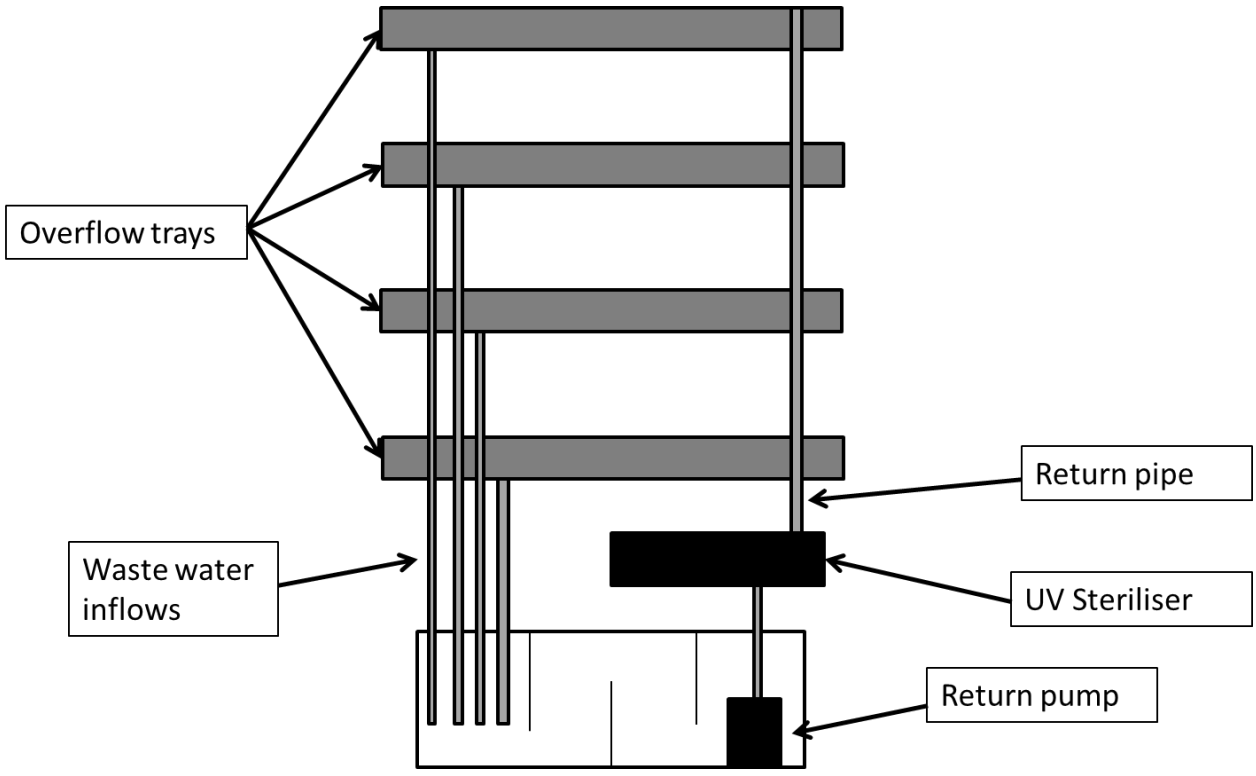


Figure 6: Schematic for circulating rack for measuring life history traits in fish. Water was circulated through a sump filter and UV steriliser before being supplied to individual plastic tanks which overflowed into a tray before draining to the sump.

Figure 7: Side on view of life history rack (top image), showing overflow trays which drained waste water to sump filter, and close up view of individual tanks that housed mothers / juveniles for trait measurement (bottom).

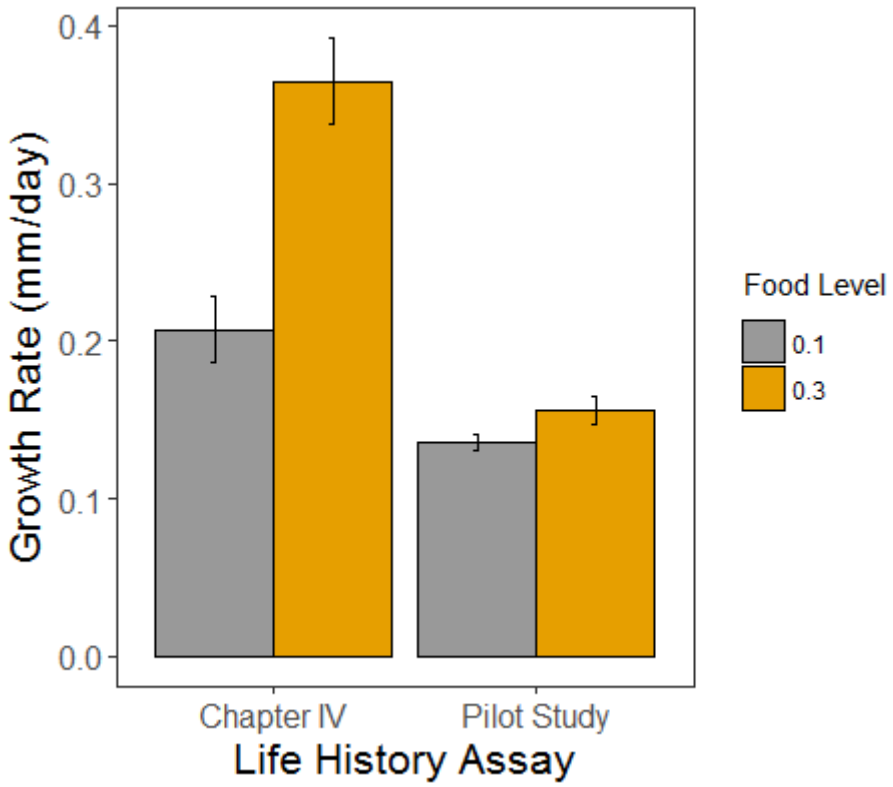


Figure 8: Growth rates of juveniles (mm/day) in both pilot studies and eventual life history assay in response to high and low food levels, Error bars show ±1 standard error.

Chapter III - Plasticity is a locally adapted trait with consequences for ecological dynamics in novel environments

Abstract

Phenotypic plasticity is predicted to evolve in more variable environments, conferring an advantage on individual lifetime fitness. However, experimental evidence for the evolution of plasticity in response to environmental variation is rare. Additionally, the potential consequence of evolved changes in plasticity for ecological population dynamics is unknown. Here we use an invertebrate model system to examine the effects of environmental variation (food) on the evolution of phenotypic plasticity in life history traits – age and size at maturation. Plasticity in both traits initially declined in all microcosm environments, but then evolved increased plasticity for age-at-maturation, significantly so in more environmentally variable environments. We also demonstrate how plasticity affects ecological dynamics by reintroducing mites with plastic-phenotypes into new microcosms that had either familiar or novel environments. Populations originating from periodically variable environments had lowest variation in population abundances in novel environments than those from constant or random environments. In the first study of its kind, we fully characterise the evolution of phenotypic plasticity from environmental variation and demonstrate its effects on population dynamics - a eco-evolutionary feedback loop.

Introduction

Phenotypic plasticity (hereafter plasticity) is the ability of a given genotype to express different phenotypes according to the environment they experience (Price, Qvarnström and Irwin, 2003; Fusco and Minelli, 2010). Plasticity, therefore, facilitates organisms to persist in environments that vary across a range of conditions (DeWitt, Sih and Wilson, 1998; Murren *et al.*, 2015).

Given that organisms are not infinitely plastic, and not all organisms exhibit similar plasticity in response to environment, being plastic must therefore have inherent costs(DeWitt, Sih and Wilson, 1998; Relyea, 2002). When an optimum phenotype maximises fitness, as might be expected in a constant environment, assuming it incurs an energetic cost we expect that plastic genotypes should be eroded from the population (Chevin, Lande and Mace, 2010; Chevin *et al.*, 2013). Conversely, if environments are variable because they shift between otherwise constant conditions on a regular basis, plasticity could be considered a by-product or legacy of fluctuating selection pressure (Furness, Lee and Reznick, 2015). Predictability of environmental variation could also enhance the development of plasticity, as more unpredictable stochastic environments would increase the likelihood of non-adaptive plasticity and phenotypic mismatch, resulting in reduced mean fitness (Reed *et al.*, 2010; Ashander, Chevin and Baskett, 2016). Here we experimentally examine the role of environmental variation in food availability on the evolution of developmental trait plasticity in microcosm populations of a soil invertebrate, the mite *Sancassania berlesei*.

Comparative studies have found that plasticity is linked to environmental variation. Increased plasticity is found in plant species in response to seasonality of temperature (Frei, Ghazoul and Pluess, 2014; Trunschke and Stöcklin, 2017) or when corals experience more regular fluctuations in light stress (Salih *et al.*, 2000; Ow and Todd, 2010). Plasticity in life history traits have been shown to be greater in those populations that inhabit more variable environments, such as growth and reproduction traits in cephalopod populations subjected to more regular El Nino events (Hoving *et al.*, 2013). Transgenerational plasticity, where variation in the parental environment can influence offspring phenotypes, is also well documented in both plants and animals (Plaistow *et al.*, 2004; Furness, Lee and Reznick, 2015). For example, maternal adjustments in offspring body size are common, allowing mothers to produce more competitive offspring (Plaistow *et al.*, 2007; Leips *et al.*, 2009). Such transgenerational plasticity, that creates offspring phenotypes via plastic expression, suggests plasticity can be considered adaptive and should evolve, for example in response to variation in population density and competition for resources (Allen *et al.*, 2008). There is also a diverse theoretical framework that predicts multiple ways in which plasticity could evolve in populations (Forsman, 2014). This body of work proposes that environmental variation would affect the selection on plasticity, for example variability of rainfall driving drought resistant traits in plant species (Richter, Wohlgemuth and Moser, 2012), but overall what remains lacking is clear empirical evidence that variable environments lead to the evolution of more plastic life histories (de Jong, 2005; Murren *et al.*, 2015; Hendry, 2016).

Shifts in life history traits can have rapid consequences on population dynamics over ecologically relevant timescales (Carroll *et al.*, 2007; Fussmann, Loreau and Abrams, 2007; Cameron *et al.*, 2013). However the broad focus of literature has been conducted

on directional selection on life histories by local environmental conditions (Bassar *et al.*, 2013), or whether, how and for how long plasticity is maintained following changes in local environments (i.e. transplant experiments) (Ghalambor *et al.*, 2007; Handelsman *et al.*, 2013). Given that most populations are not under a constant intensity of selection (Reed, Schindler and Waples, 2011), due to the ubiquity of environmental variation, it is important to understand the effects of variable environmental pressure on the evolution of plasticity in life history traits in tandem with selection on mean trait values (Fischer *et al.*, 2014).

In this study I present data from two experiments. In the first, I analysed the evolutionary response of plasticity in two linked life history traits from populations experimentally held in constant, periodically or randomly variable environments that otherwise receive the same average amount of food on a daily basis (but which varies over time). Previous research has shown that wild-caught soil mites transferred into closed, laboratory populations with strong density-dependence creates the conditions for reductions in average population size over time (an “extinction trajectory”), but this then rebounds as the population adapts to the novel conditions (Cameron *et al.*, 2013). In addition, it is also shown that speed and magnitude of evolution in mean life history trait values is driven mostly by density dependent competition for food. Environmental variation therefore affects mean trait values in a predictable way by altering the likelihood of periods of intense density-dependent resource competition (Cameron *et al.*, 2014).

Here I present new analyses of those data which examine the plasticity in life-history traits across a resource gradient (e.g. from high to low food availability in a common garden experiment). Following on from the previous experiment, where populations were selected for ~25 generations, mites were transferred to novel environments. I present the results and show strong evidence for selection for increased plasticity in life

history traits in more variable environments. This has consequences for variance in population size as organisms experience environmental change. This chapter therefore demonstrates the role of plasticity in adaptation to a novel ecological environment. Therefore plasticity in life history traits influences size structure, which in turn feeds back and influences selection pressure on the same traits, i.e. a full eco-evolutionary loop.

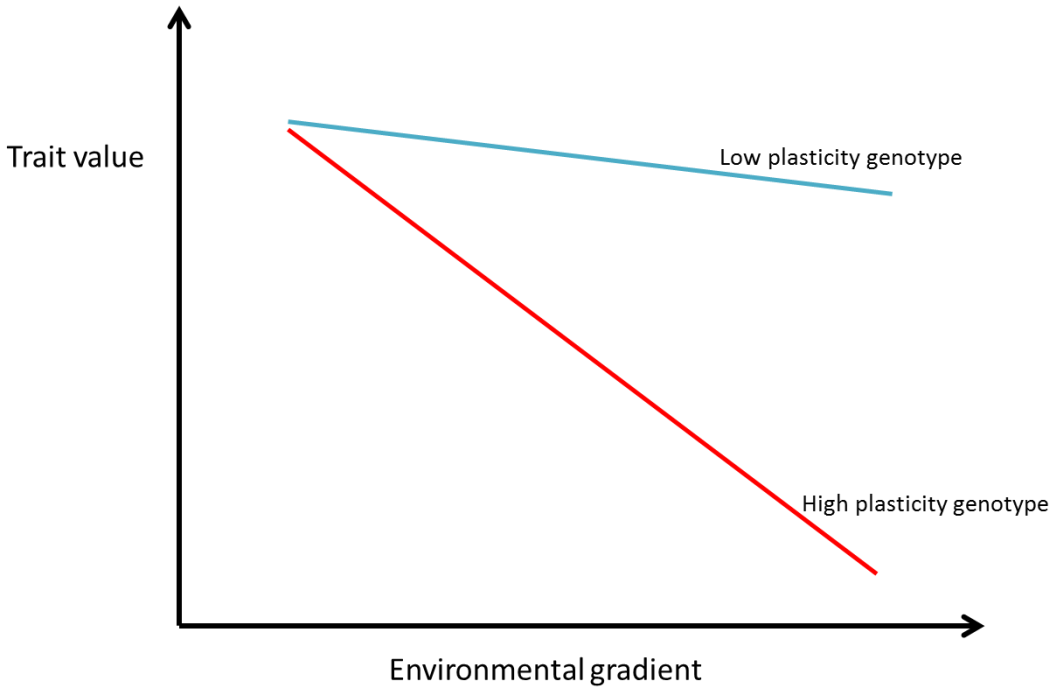


Figure 9: Reaction norms – the more plastic a phenotype gives a greater slope value. This slope is a widely used index of plasticity

Methods

Experimental set up

Wild soil mites (*S*. *berlesei*) were collected from four UK locations, mixed and reared with ad lib food for ca. 2 generations. Mites were then transferred to population tubes with a standardised inoculum of 300 adults (50:50 gender ratio) and 1000 juveniles. Population tubes consisted of 25mm diameter x 50mm tall glass tubes half filled with standardised calcium sulphate substratum. All populations were maintained at 24^{o}C in unlit incubators. Each population tube was subject to an environmental variation treatment: Constant, periodic, or random food supply, with six replicate tubes per treatment level.

Populations were fed with dried balls of activated yeast and 2 drops of distilled water per day to maintain humidity levels. All populations received the same mean food over a 28day period at a rate of two 0.0015g balls of yeast per day, but the rate at which this was supplied defined the environmental treatment. Periodic food treatment followed a repeating pattern: 9 days 0 balls, 3 days 1 ball, 2 days 3 balls, 9 days 4 balls, 3 days 3 balls and 2 days one ball. Daily food supply in the random treatment was taken from a random distribution between 0-12 balls/day over 56 days constrained to no more than 112 balls in that period. The constant food supply consisted of two 0.0015g balls per day. Further information on this experiment can be found in (Cameron *et al.*, 2013, 2016). This experiment lasted 95 weeks (~ 13 - 30 generations).

Assessing Evolution of Plasticity: Life history assay

An assay was designed to assess evolved changes in life history trait plasticity throughout the course of the experiment by use of a multi-generation common garden rearing environment to minimise maternal environment effects e.g. (Plaistow, Lapsley and Benton, 2006). Assays were conducted on weeks 0 (initial wild-type assay), 18, 37, 63 and 95. Details of the assay are published elsewhere, e.g. (Cameron *et al.*, 2013), but in summary, standardised density F3 eggs (n=20) from single family matings (n=7, one family per tube) were reared in either high or low food availability representing low and high competition conditions from population environments respectively. The age and size of female mites at maturation was recorded in addition to the female and male survival to maturity and daily counts of juveniles and emerging adults. Unlike in Cameron *et al.* (2013) & Cameron *et al.* (2014) where the focus was on the mean life history trait values in low food conditions, here we are focussing on the difference in trait expression across high and low levels of resource availability: phenotypic plasticity in age-at-maturation (days) and size at maturation (mm) (hereafter referred to as age plasticity and size plasticity respectively).

Phenotypic plasticity is most often measured through the use of indices, with one most commonly utilised in ecology being the slope value of a reaction norm (Stearns and Koella, 1986). Reaction norms allow for plasticity to be captured through the slope value obtained from trait values at two ends of an environmental gradient, e.g. food availability (see figure 8)(Valladares, Sanchez-Gomez and Zavala, 2006). We used reaction norms in this study to estimate size-plasticity and age-plasticity. Common garden (CG) assays allowed us to generate trait plasticity values at the family level where families are

replicates nested in source populations nested within treatments. We also considered variation between family slopes to also ask if environmental variation selects for, or against, phenotypic diversity in a density-dependent population as this could also affect how populations respond to novel environments.

Population responses to novel environments

In order to assess the ecological consequences of c20 generations of selection in variable environments under either constant, periodic or random environments, we undertook a second experiment where new population tubes were inoculated with individuals from the original treatment populations. Individuals from these original populations' tubes (3 per treatments group, 9 in total) were split equally across 3 new tubes creating 18 tubes in total. These new population tubes were assigned one of the three original environmental treatments and two novel treatments (see figure x in methods for details). This created nine treatments, for example Constant-Constant, Constant-Periodic, Constant-Random and the same with the other original treatments. Censuses were conducted weekly for 13 weeks, counting population size of juveniles, adults and therefore total population size each week for 13 weeks. The coefficient of variation of abundance of each stage and of the total population was calculated from each time series for each replicate population. This then meant that each replicate population had a value for population variation (for stage abundance and total abundance), which was then analysed using linear models to determine the role of measured plasticity on the variation in population dynamics.

Data analysis

The significance of temporal trends in age and size plasticity and effects of environmental variation on that plasticity were determined using linear mixed effects models (lme, R package nlme), with repeated measures of life history traits nested within population tubes as a random effect on the intercept (Cameron *et al.*, 2013). Posthoc comparisons are taken from the summary table of coefficients from each lme with associated student t statistics or comparison of mean differences between treatments.

To assess whether there are differences in phenotypic diversity between treatments, a 95% confidence interval was generated around the arithmetic mean of the Coefficient of Variation (CV) between family slopes per treatment, by bootstrap resampling with replacement (n=1000). Where mean CV is overlapped by confidence intervals from other treatments we do not consider them to be different.

The relative importance of the original environment in which mite populations evolved and the new novel environments to which they were exposed in effecting the variation in abundance of different life history stages (e.g. juveniles, adults) was analysed using a linear model (ANOVA, CV ~Original*Novel). A model was built for each of total, adult and juvenile mite variation in abundance. A series of model simplification deletion tests were undertaken to find the minimum adequate model.

All statistical analyses were conducted in R studio (R: A language and environment for Statistical Computing, R core team, 2016).

Results

Evolved changes in plasticity over time

There was a significant change in the life history trait plasticity expressed by F3 offspring throughout the course of the experiment (figure 9). Initial assessment of phenotypic plasticity in both age and size showed high levels of phenotypic plasticity in wild mites prior to imposing environmental treatments (Age plasticity: -15.84 ± 0.32 (this and all values that follow are mean ± standard error), Size plasticity: 0.53 ± 0.0059). We observed an initial reduction in age and size plasticity, from these initial wild genotypes after a period of 18 weeks across all treatments.

No further change in size plasticity after the 18 week time point was observed between any of the treatment populations (size plasticity ~ assay timepoint * environmental variation: $F_{2,132} = 0.15$, $P > 0.05$; figures 9B & 10B, table 3). Age plasticity recovered in all environment treatments over time, however no significant difference was observed between treatments until the final assay at the end of the experiment in week 95 (lme: age plasticity~ assay timepoint * environmental variation: $F_{8,233} = 5.187$, $P < 0.05$; figure 10B + x and tables 2 and 4). While age plasticity in both random and periodically variable populations was found to be greater by the end of the experiment than in constant environment populations (random – $t_{2,233}$=-4.2, P<0.01; period - $t_{2,233}$=-3.8, P<0.01, figure x and table 2), they did not differ from each other in their age plasticity (mean difference =0.5±1.25 s.e.).

Table 1: ANOVA output table of a linear mixed effects model, showing the effect of environmental variation on Size Plasticity at the end of the experiment.

	numDF	denDF	F-value	p-value
(Intercept)	1	36.00	637.17	0.00
env	2	3.00	0.65	0.58

Table 2: ANOVA output table of a linear mixed effects model, showing the effect of environmental variation on Age Plasticity at the end of the experiment.

	numDF	denDF	F-value	p-value
(Intercept)	1	36.00	679.69	0.00
env	2	3.00	9.44	0.05

Table 3: ANOVA output table of a linear mixed effects model, showing the effect of environmental variation over time on Size Plasticity.

	numDF	denDF	F-value	p-value
(Intercept)	1	233.00	5557.82	0.00
assay	4	233.00	219.82	0.00
env	2	6.00	0.09	0.91
assay:env	8	233.00	0.51	0.85

Table 4: ANOVA output table of a linear mixed effects model, showing the effect of environmental variation over time on Age Plasticity.

	numDF	denDF	F-value	p-value
(Intercept)	1	233.00	4709.93	0.00
assay	4	233.00	123.11	0.00
env	2	6.00	1.29	0.34
assay:env	8	233.00	5.19	0.00

Genotypic diversity

Both random and periodic populations had a higher degree of interfamily variation in age plasticity reaction norm slopes than populations from constant environments (16.9%± 0.13 and 8.3 %± 0.19 respectively, figure 11). Conversely, interfamily variations in size plasticity reaction norm slopes were lowest in populations from variable (random and periodic) environments than populations from constant environments (14.1% ± 0.003 and 14.9% ± 0.004 less than constant).

Population responses to novel environments

Populations of mites that had been raised in one of three levels of original environmental variation (e.g. constant, random or periodic) were inoculated into new population tubes assigned to one of those same environments. As such, each original population produced three new populations, one in the same environmental condition as before and two novel environments. Differences in population variability were assessed as a function of the original environmental treatment that the mite lines had come from and the novel environment.

The environmental treatment that populations originated from had a significant effect on total population variation (CV ~ original environments: $F_{2,24}$=5.534, P<0.05, table 5), unlike the novel environment they were introduced to (CV ~ Novel Environments: $F_{2,24}$ = 3.222, P>0.05, table 8). Total population size had lowest variation in populations that originated from periodically variable environments (0.266±0.022) in comparison to those that originated from constant (0.354±0.025) or random environments (0.351±0.014).

Variation in juvenile population abundance was also found to be significantly affected by the original treatment but not the novel (Original: $F_{2,24}$= 8.43 P<0.05 vs Novel: $F_{2,24}$ = 0.849, P=0.44, figure 12, tables 7 and 10). Populations that originated from periodic environments had 72 % less variation in juvenile population size than those from constant, and 70% less variation than random environments.

A common pattern observed was that populations originating from periodic environments had observed variation in abundance that was significantly lower than those populations that originated from constant or random environments when exposed to novel environments (see figure 12 and figure 2 in methods for clarity). However, there was not found to be a significant effect on the adult portion of the population. There was no interactive effect of the original and novel environments on population variability in total or stage abundance (ANOVA, CV ~ Original*New, F4, 18 = 0.54, P>0.05). Novel environments showed no effects on total population variability or juvenile population variability but did for variability in the adult population size (as shown in figure a, tables 8 -10).

Table 5: ANOVA output table of a linear model, showing the effect of ancestral environments on the variation in total population size when introduced to new environments.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
OrigTrt	2	0.05	0.02	5.53	0.0106
Residuals	24	0.10	0.00		

Table 6: ANOVA output table of a linear model, showing the effect of ancestral environments on the variation in the adult population size when introduced to new environments.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
OrigTrt	2	0.01	0.01	0.48	0.6222
Residuals	24	0.32	0.01		

Table 7: ANOVA output table of a linear model, showing the effect of ancestral environments on the variation in the juvenile population size when introduced to new environments.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
OrigTrt	2	0.08	0.04	8.43	0.0017
Residuals	24	0.11	0.00		

Table 8: ANOVA output table of a linear model, showing the effect of novel environments on the variation in total population size.

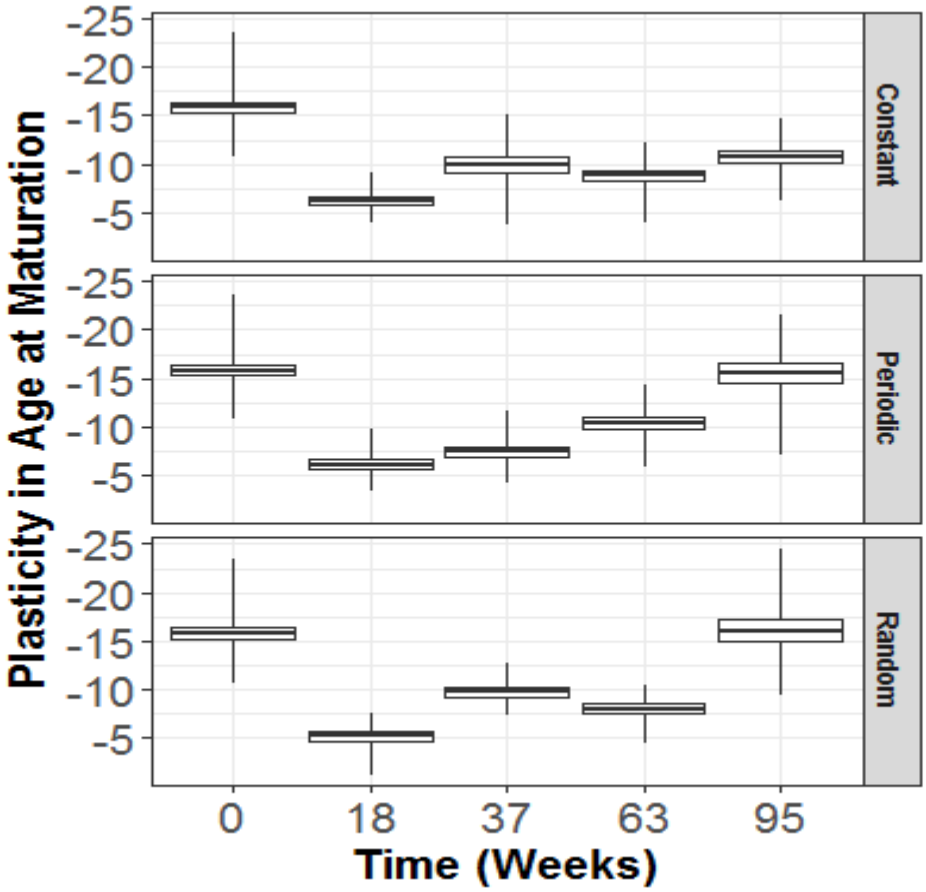
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
NewTrt	2	0.03	0.02	3.22	0.0576
Residuals	24	0.11	0.00		

Table 9: ANOVA output table of a linear model, showing the effect of novel environments on the variation in the adult population size.

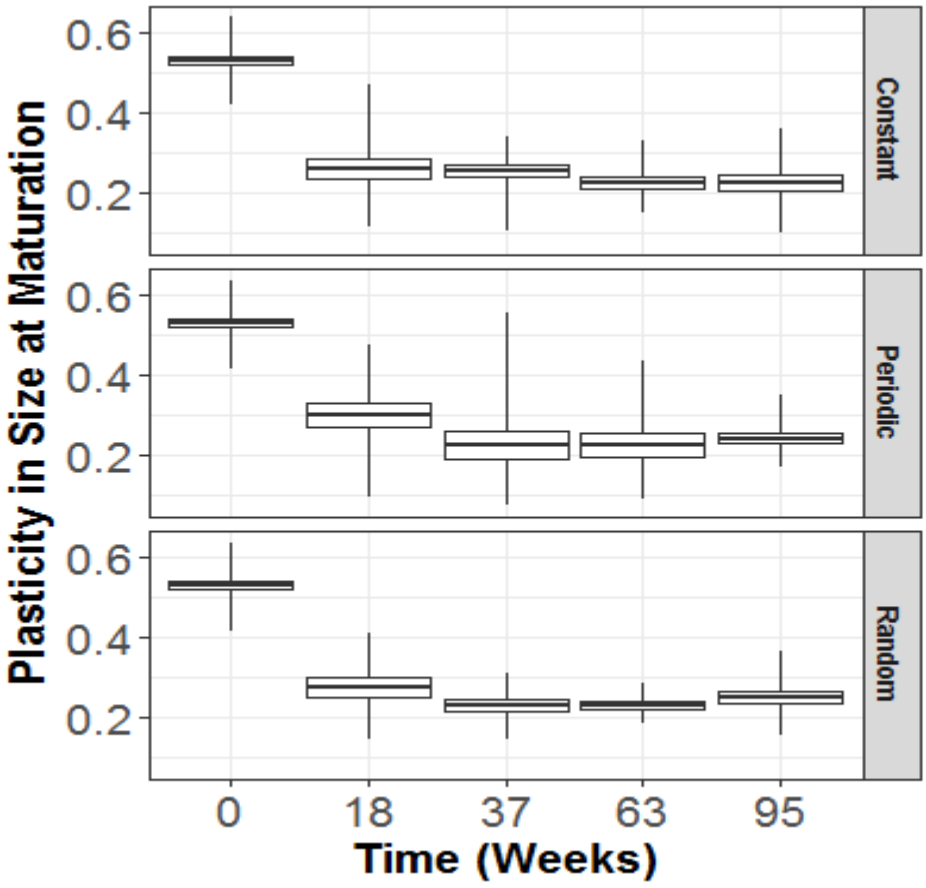
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
NewTrt	2	0.24	0.12	31.66	0.0000
Residuals	24	0.09	0.00		

Table 10: ANOVA output table of a linear model, showing the effect of novel environments on the variation in the juvenile population size.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
NewTrt	2	0.01	0.01	0.85	0.4402
Residuals	24	0.17	0.01		



A



B

Figure 10A and B: Changing prevalence of plasticity over time, facets showing families raised in constant, periodic and random environments. Figure 9A indicates changing plasticity for age at maturity; 9B indicates changing plasticity for size at maturity. Boxplots show, mean, +/- 1* standard error, max and min

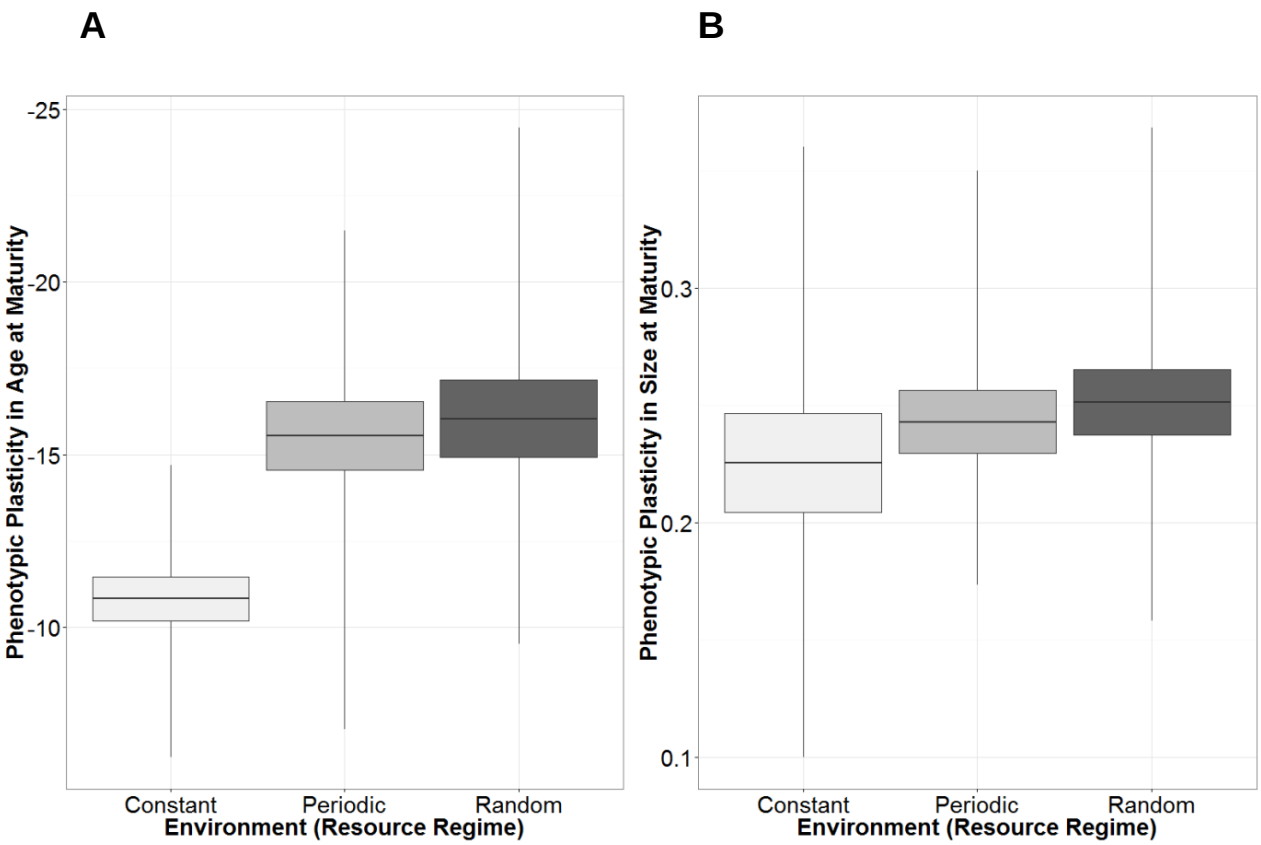


Figure 11A + B: Phenotypic plasticity from common garden rearing in age-at-maturity (10A) and in size-at-maturity (10B) at week 95 (experiment's end) Boxplots show +/-1 standard error, min and max

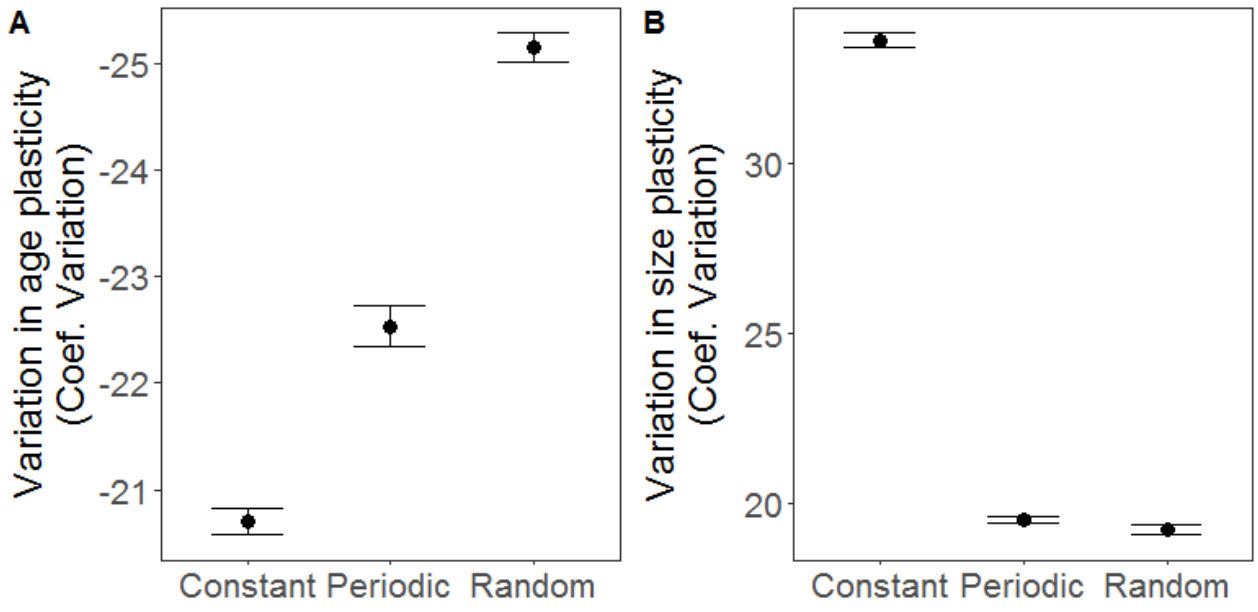


Figure 12A and B: Diversity in plasticity for both age (11A) and size (11B) plasticity at week 95 (experiments end). Each point represents the variation in plasticity from 14 families from 2 treatment populations (7 families each).

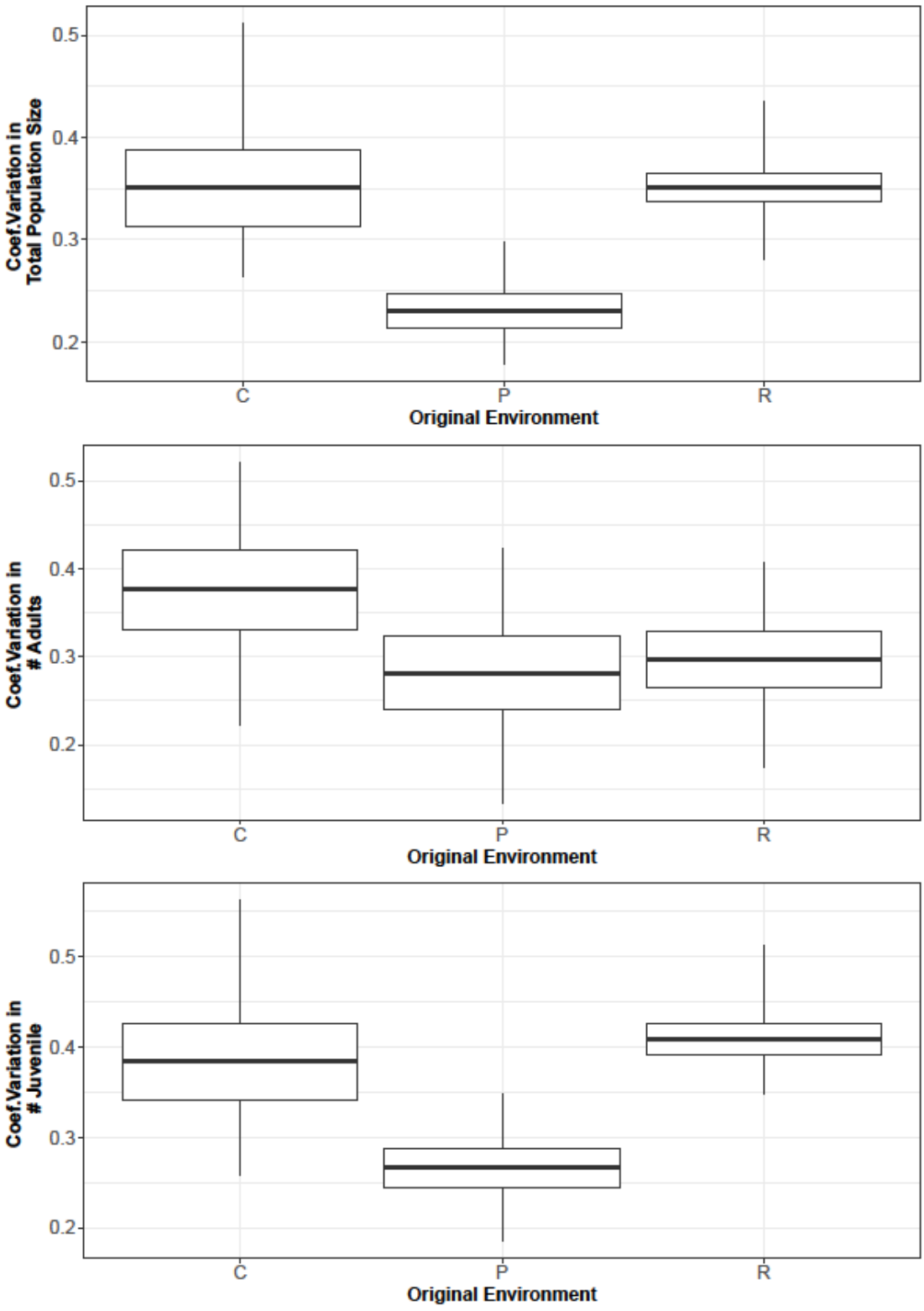


Figure 13: Variation in total population size, adult and juvenile population size in populations that originated from constant, periodic and random environments. These are shown as C, P and R respectively. Plots show variation without control populations e.g. Control into Control. Boxplots show ±1 standard error, min and max

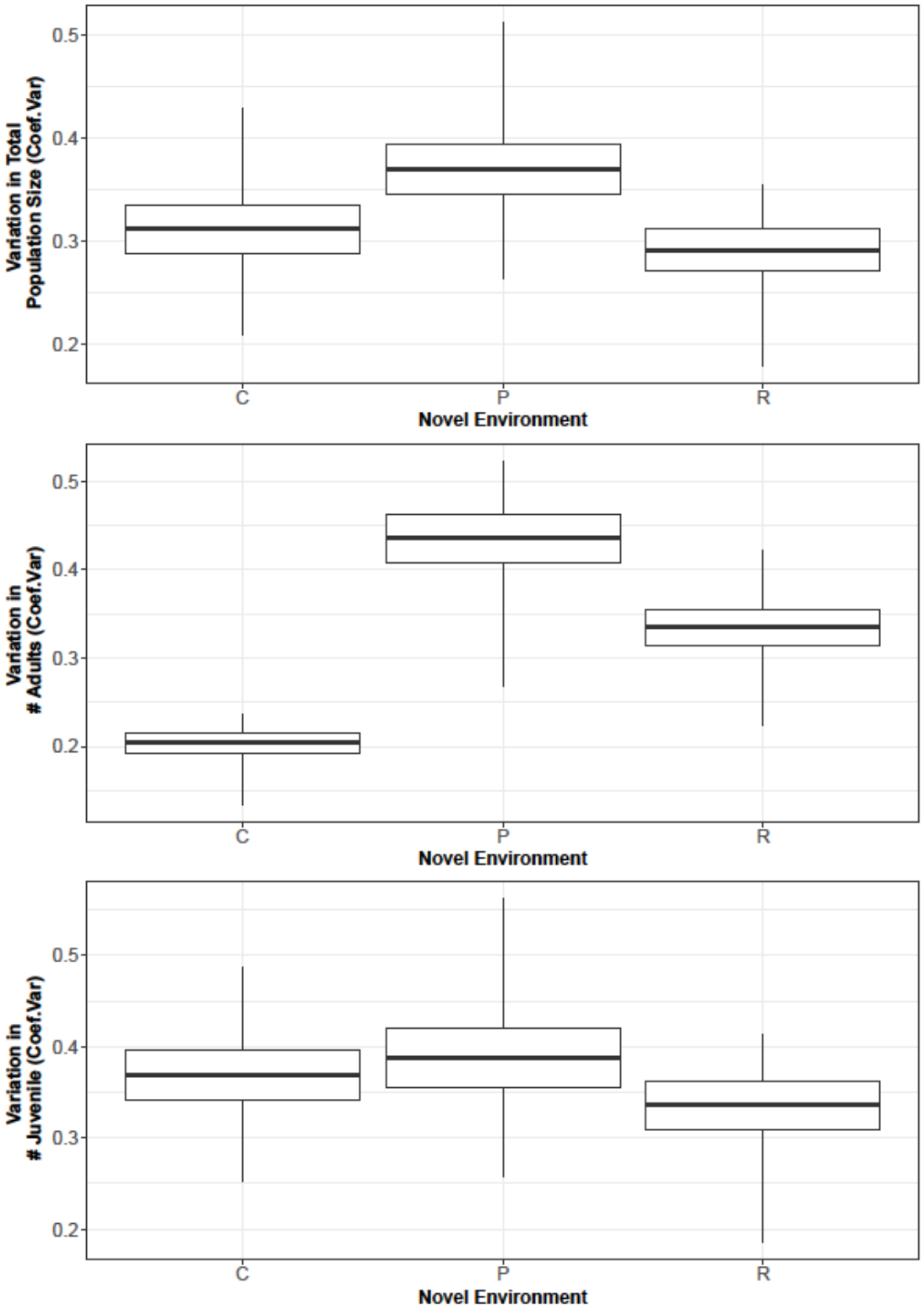


Figure 14: Variation in total population size, adult and juvenile population size in populations introduced to constant, periodic and random environments. These are shown as C, P and R respectively. Boxplots show +/-1 standard error, min and max

Discussion

I have shown a clear effect of both environmental change from wild to a novel laboratory setting and environmental variation on phenotypic plasticity. Through the use of a three generation common garden rearing environment – rearing soil mites from birth at low (High food) to high (Low food) competition – we have demonstrated that higher levels of environmental variation in density dependent resource competition selects for greater plasticity in developmental growth rate to maturity. We have also shown that despite no differences in the effect of environmental variation on genotypic diversity, populations that have retained greater plasticity in developmental traits have more constant population dynamics when exposed to novel environments. This is an interesting proof of concept where we have shown a full eco-evolutionary loop (Cameron *et al.*, 2013; Post and Palkovacs, 2014), and this loop is simultaneously selecting on components of life history trait plasticity as we have demonstrated here and also on mean trait values as we have demonstrated previously.

Investigating the development of both life history traits and plasticity is often problematic in wild systems due to logistical constraints and also time required to observe responses. Use of invertebrate model systems have long been used to examine population dynamics and selection on trait values due to their short generation time (Beckerman, Rodgers and Dennis, 2010; Robinson and Beckerman, 2013). Soil mites (*Sancassania berlesei*), small sexually reproducing detritivores commonly found in compost bins, have been used as a model organism in several studies of population ecology and evolution (Benton, Lapsley and Beckerman, 2001; Cameron and Benton, 2004). Previous analysis of time series and mean trait values from experimental soil mite populations has shown that evolution of development rate has significant

consequences for feedbacks to mean trends in population dynamics, including preventing extinction in novel environments (Cameron *et al.*, 2013). This result was driven by selection for maintaining highest potential fecundity at sexual maturity, by slowing development in highly competitive environments.

Previous studies show that the life history traits of mites, when moved from their wild type conditions to highly competitive laboratory condition, evolve a delayed age at maturation. The average trait values expressed in high food common garden conditions would also have been maladaptive in these wild-type mites at the start of the experiment. As such, we found declines in both age and size plasticity as population size declines, driven by intense directional selection during the initial stage of the long term experiment.

After this initial decline in plasticity for both examined traits, in all environments, we see an increase of families that are highly plastic in their age at maturation in all subsequent life history assays. The effect of this increase in plasticity is greatest in the most variable environments. We found no change in plasticity for size at maturation in any environment. We can place these results in the context of previously reported evolution of the mean trait values of age and size at maturity, where significant evolution of increased age-at-maturity (in low food environments) is observed over the course of the experiment, but not in body size (Cameron *et al.*, 2013, 2014). This was driven by density dependent competition, where on average all individuals are experiencing food shortage. Delaying growth to maturity was associated with increased fecundity in low food environments – i.e. those common garden conditions that are more likely to represent the density dependent microcosm conditions in which the mites evolved during the experiment (Cameron *et al.*, 2013, 2014). While larger adult mites can have far greater fecundity (Plaistow *et al.*, 2007), this does not apply in low food conditions

where body size confers no such advantage (Plaistow *et al.*, 2007; Cameron *et al.*, 2013). More generally, given the mean competitive conditions, investment in body size may be detrimental due to starvation risks as larger individuals have larger metabolic requirements (Bystrom, Persson and Wahlstrom, 1998). Assuming that there was sufficient genetic diversity associated with body size, this perhaps explains why we saw little selection on the mean or plasticity of size–at-maturity in this study.

Variable environments have been found to correlate with variable life histories when observed in a natural setting (Hendry, 2016). Aquatic invertebrates have been found to exhibit plasticity in life histories in response to variable cues of predation pressure (Beckerman, Rodgers and Dennis, 2010). Indeed, plastic responses in maturation and growth have been observed in environments that are characterised by their variability, such as in rainfall events (Furness, Lee and Reznick, 2015) and in thermal regimes (Hoving *et al.*, 2013). However, direct empirical evidence demonstrating that the variability of environments are selecting for flexibility in life history strategies is lacking (Hendry, 2016). In this study we observed pronounced effects of environmental variation on the evolution of phenotypic plasticity in age at maturation, allowing populations to regain what was lost during the initial stage of the experiment. In this instance, flexibility in growth rate allows an individual to capitalise on resources when they are high but also facilitates persistence when resources are low. These observations have been observed in comparative studies of aquatic invertebrate (Zhang, 2006) and fish populations (Gale *et al.*, 2013) in response to altered resource availability suggesting that our results are more generalised and that environmental variation may maintain plasticity in a variety of taxa.

In contrast to our expectations, we did not see any difference in the evolution of plasticity values between the random and periodic environments, i.e. the stochastic and

predictable variable environments. Stochastic environments that are unpredictable in nature are said to favour bet-hedging strategies as opposed to plasticity in development (Furness, Lee and Reznick, 2015). Diversified bet-hedging allows a female to produce offspring that can express a range of specific phenotypes, i.e. many offspring, each expressing phenotypes optimal for a particular environment so that at least a portion of offspring survive (Einum and Fleming, 2004). However, given our methodology, it is difficult to differentiate between the two strategies, as the allocation of female eggs to either high or low food conditions was entirely randomised.

Evolved changes in maturation life history traits are well documented to have feedbacks on population dynamics that may promote persistence or productivity of systems (Reznick, Butler Iv and Rodd, 2001; Cameron *et al.*, 2013; Quetglas *et al.*, 2016). Given that altering plasticity may be selected for if it impacts on fitness, a consequence of this is that populations made of plastic individuals to respond more rapidly. Therefore, the role of plasticity in life history traits is increasingly relevant in examining eco-evolutionary dynamics (Richter, Wohlgemuth and Moser, 2012; Torres-Dowdal *et al.*, 2012). In rotifer-algae predator-prey systems, predator induced plastic responses in prey defence and growth rate were found to feedback on population cycles (Fischer *et al.*, 2014). By reintroducing mites from given background environments to novel environments we have shown the role that plasticity can play in eco-evolutionary dynamics. Variation in population sizes, total population and specific life history stage, indicated the original environment that mite populations experienced influenced the ability of individuals to respond to novel environments and therefore the dynamics of those populations. Mite populations originating from periodic environments showed lowest overall variation in total population size when moved to a novel environment, indicating that the plasticity selected populations were better at adapting to new

environments than those from constant conditions. This was driven by a similar result (low variation in periodic mites) in juvenile populations, indicating that the ability to delay growth to maturity also led to reduced variation in juvenile abundance. This may have been caused by a feedback from adult reproduction rates – the more juveniles alive, the more severe competition for food, and the lower adult fecundity becomes - as well as through survival-growth trade-offs of juveniles. However variation in adult population size remained high regardless of the environment that mites had originated from. This can also be explained by the high age plasticity we observed in our final life history assay, in that the aforementioned age plasticity combined with the food regime would result in high variation in the number of recruits into the adult stage. As such, our results support previous work highlighting the potential importance of plasticity in maturation rates for the persistence of populations (Aratayev and Raft, 2015). Intriguingly while overall plasticity in age-at-maturation evolved to similar levels in both the periodic and random environments, this did not transfer into similar results in population variation when mites were moved to novel environments. Mites from random environmental backgrounds did not experience the same range of positive effects of reduced variation in abundance in novel environments that those originating from periodic environments. This points to all plasticity *not being equal* and further research on this lack of equality is warranted.

We propose that these results shed light on the role of environmental variation in maintaining plasticity even when strong directional selection is operating. Environments are never entirely constant, random or periodic – even our constant environment results in an experience of environmental variation due to demographic stochasticity (Cameron et al. 2014) – and as such the role of plasticity in reducing the likelihood of environmentally induced extreme population densities can help explain its maintenance.

Conclusion

I have analysed a large dataset from an experiment that used an established invertebrate model system to empirically confirm environmental variation in resources can result in evolved changes in phenotypic plasticity in two key life history traits, age and size at maturation. Additionally, we have shown how this plasticity affects the response of a population to a novel environment and how the response of the population dynamics help explain the maintenance of phenotypic plasticity even in the presence of strong directional selection. Combined, these two main results evidence the importance of considering selection on phenotypic plasticity when predicting the eco-evolutionary dynamics of populations in a changing world.

Chapter IV – Protecting large bodied individuals alleviates negative eco-evolutionary responses of size selective fishing

Abstract

Fisheries and aquaculture provide 17% of animal protein consumed by the global population, yet current estimates suggest that at least 33% of wild populations are overfished. Current approaches to reduce impact on fisheries include size selective harvest regulations, which aim to only target fish above a minimum size. However, this has been shown to truncate population age/size structure and select for faster life-histories, affecting the reproductive potential of exploited stocks. Alternatively, a new balanced form of regulation, harvest slots (HS), has been suggested to balance conservation, societal and economic objectives of fishing regulation. HS targets only intermediate-sized individuals, and protects large bodied individuals, thus preserving individuals with high spawning potential and reducing size selection on individuals . Although theoretical and limited field testing of harvest slots suggest that HS achieve this whilst still preserving adequate yield, it has yet to be empirically tested. Here I use a guppy model system (*P. reticulata*) to empirically test the effectiveness of HS relative to traditional minimium-sized limit harvesting, on size structure, abundance, biomass and yield. HS maintain a size structure and biomass very similar to the unharvested control populations, while facilitating less variable yield than traditional harvest (32.4% lower Coef of Variation in Biomass yield). By contrast, populations exposed to minimum-length limits show a highly truncated size structure, lower biomass more variable yield in both biomass and numbers of individuals removed. We further evaluate feedback from the 3-4 generations of harvesting to life history differentiation between harvested and

unharvested populations. We find HS do not differ from unharvested populations in any examined life history traits. Comparatively, traditional harvest drove reduced size of offspring at birth, reduced size at maturity and increased age at maturity. While costs to yield and technical challenges exist to deploy HS regulations, this chapter provides much needed evidence to support the development of HS regulations for a variety of exploited fisheries. Additionally, Harvest slot approaches may be particularly relevant for populations where targets are to prioritise conservation or stability over shorter term economic objectives – for example in recovering stocks or in smaller coastal fisheries As such, this work represents an exciting new avenue not just for research but as a practical solution to many issues facing contemporary fisheries.

Introduction

Global fisheries supply approximately 17% of global intake of animal protein (Food and Agriculture Organisation of the United Nations, 2018), and approximately two thirds of harvested fish stocks are being fished unsustainably (Costello *et al.*, 2016). Important and well recognised feedbacks from the exploitation of larger individuals, often sexually mature adults, include reduced recruitment to the larger adult classes over time through reduction in densities of adult spawning stock (Swain, Sinclair and Mark Hanson, 2007; Fenberg and Roy, 2008) and changes in the composition of ecological communities (Benoît and Swain, 2008).

Size selective harvesting is the preferential targeting of individuals in a population of a given body size, or other associated trait. Size-selectivity ordinarily targets the largest individuals in a population – where individuals above a minimum size are vulnerable to harvest (Radomski *et al.*, 2001; Suuronen and Sardà, 2007). In fishing, this is undertaken for a variety of technical and biological reasons. Technical motivation for catching large individuals in commercial fishing include simplicity of the approach to catch larger individuals using nets of a given width or hooks and baits of a given size (Andersen, Marty and Arlinghaus, 2017). Biological reasons include the production of new biomass through reduced competition, and protecting a “standing stock” of a fishery, i.e. leaving some individuals behind so the population is preserved (Jusufovski and Kuparinen, 2014). In addition, societal pressure exists for harvesting large individuals, both for the purposes of consumption (more meat to sell) and for the motivation of catching larger trophy fish in recreational fishing (Beardmore *et al.*, 2015).

Demographic changes also ensue with truncation of size and age structures, driving relative higher abundance in small younger fish (Levin *et al.*, 2006; Hixon, Johnson and Sogard, 2014). Truncation of age/size structures lead to social pressures to increase fishing effort to compensate for reduced biomass in catches (Anticamara *et al.*, 2011). This compounds to increased pressure on fish stocks, as increased fishing effort is applied in order to catch the largest individuals remaining (Siskey *et al.*, 2016) The value of large bodied individuals for recruitment in fisheries is well recognised, as reproductive output is expected to scale with body size (Hixon, Johnson and Sogard, 2014). Recent work illustrates that large bodied females contribute disproportionately more to population recruitment, thus effecting fisheries productivity (Barneche *et al.*, 2018).

Harvest mediated age truncation has been linked to other important feedbacks from fishing onto population and evolutionary dynamics (Cameron et al. 2013, 2016; Heino et al. 2015; Laugen et al. 2014). Consistent selective removal of older, larger individuals has been linked to evolved changes in the life histories of commercially important fish stocks (Kuparinen, Kuikka and Merilä, 2009). This leads to selection for life history strategies that favour early reproduction over growth, as overall likelihood of mortality has increased (Reznick and Ghalambor, 2005). This manifests as reduced size and age at maturation, and shifts in reproductive investment (Reznick, Bryant and Bashey, 2002). Observed shifts in life history trait expression have long lasting effects on fish populations, in terms of both recruitment and size structure (Uusi-Heikkilä *et al.*, 2015). Simulations of fisheries induced evolution show that evolved changes in population growth rate persist long after harvesting ceases (Enberg *et al.*, 2009; Dunlop, Eikeset and Stenseth, 2015). These shifts are suggested to threaten future productivity of fish

populations as recovery to pre-harvest levels is found to take far longer than the sustained fishing period that has occurred (Enberg *et al.*, 2009; Laugen *et al.*, 2014).

The challenges of traditional selective harvesting regulations have led to the development of alternative harvest regulations. Any new regulations must be able to meet realistic trade-offs between conservation and yield objectives (Brown *et al.*, 2018). Initial theoretical papers suggest that targeting of intermediate sized individuals and protecting large more fecund individuals represents a solution to existing fisheries mismanagement (Arlinghaus, Matsumura and Dieckmann, 2010). Most prominently this has been termed Harvest Slots (Gwinn *et al.*, 2015). Harvest slots protect large-bodied fecund fish; preserving the capacity to “replenish” the population by maintaining a high spawning stock biomass (SSB). Furthermore, regular removal of biomass reduces competition and still allows for production of new biomass, a desirable characteristic of a commercial fishery.

However, challenges in field studies of medium body size catch in commercial fisheries mean that thus far empirical testing of harvest slots is rare, particularly in comparison to traditionally harvested populations (Gwinn *et al.*, 2015). Experiments in lake systems suggest that targeting of medium size classes preserve natural age/size and reducing extinction risk and therefore meets conservation objectives (Arlinghaus, Matsumura and Dieckmann, 2010). However use of large field systems (e.g. lakes) rarely allows for requirements of replication or full population characterisation. Model systems in the laboratory are ideal for measuring population dynamics as they allows for relatively high levels of replication and full counts of populations as opposed to survey data/catch reconstructions (Cameron *et al.*, 2014; Travis, Reznick and Bassar, 2014).

In this chapter, I utilised the Guppy model system to address the following objectives:

i) How does novel harvest slot fishing compare to traditional minimum sized based fishing in terms of size structure, biomass, spawning biomass and yield?

ii) Do we observe evidence of selection on life history traits after a sustained period of harvesting?

iii) Does traditional harvest regulation result in greater phenotypic responses than novel harvest regulation?

iv) Do populations still show significant differences from each other after a period of recovery from harvest?

I hypothesised that over a period of ecologically relevant harvest (3-4 generations), HS would not significantly differ from unharvested controls in terms of population size structure. In contrast, ML would result in a truncated size structure and reductions in mean body size. Additionally, this would drive similar results in terms of overall population biomass and spawning stock biomass. In line with theory, I expected that yield would not significantly differ between harvesting strategies.

After a period of recovery, I hypothesised that HS populations would not significantly differ from unharvested controls in terms of life history traits examined: age and size at maturation, size of offspring at birth and brood size. In contrast I expected reductions in size and age at maturation, reduced size at birth and greater numbers of fry per brood. This in part would drive a truncated size structure, even after a period of recovery, as is

suggested to occur in wild fish populations that have been fished (Uusi-Heikkilä *et al.*, 2015).

Methods

Study system

Trinidadian guppies (*P.reticulata*) are viviparous poecilid sexually dimorphic fish inhabiting freshwater and brackish streams and ponds in the coastal regions of northern South America and Trinidad. Much like commercially exploited fish stocks, guppy populations are subject to resource competition and cannibalism (Barlow, 1992). Additionally, short generation times exhibited by guppies allows for measurement of adaptation over ecological time (Reznick and Ghalambor, 2005). As such, guppies were chosen as an optimal model species for studying fisheries exploitation as they allow for replicate, density-dependent populations that are known to show significant phenotypic responses over relatively short time scales.

Newborn juveniles are born at approximately 5-6mm. Males mature around 13-14mm and show largely determinate growth, i.e. little or no somatic growth post maturation. Females conversely show indeterminate growth and matures at around 15-16mm (Arendt and Reznick, 2005). Populations were started with an equal ratio of adult male and female guppies, from stocks originating from either high or low predation adapted populations (Aripo high and Quare Low)(Reznick, 1982), assigning equal numbers and demographics from each population to minimise founding effects.

Nine Independent 100l aquaria were inoculated with 20 adult guppies (1:1 male-female ratio) from stock populations. Each had internal bio-filters (Eheim Aquaball 130), 200w thermostat heaters, and 11w LED lights (12:12 Light/Dark regime). Aquaria were filled with reverse osmosis water with added salt to prevent ectoparasites and buffer to

maintain pH (standard recipe detailed in chapter II). All aquaria had standardised refuges (see chapter 2 for details) of cylindrical plastic mesh stuffed with green plastic threads (Eheim fix). Water temperature was standardised to 26^0C±0.7, using Ehiem 100w glass aquarium heaters. All populations received equal food of 160mg per day of ZM-400 granular fry food 6/7 days a week (ZM-Systems). In addition all tanks received fixed volumes of defrosted copepods at irregular intervals. This, combined with a biannual application of a general aquarium medicine (Tetra Medifin) was conducted to maintain stock health.

Experimental design

After inoculation, all population tanks were allowed 10 months to grow and acclimate to novel conditions. Aquaria were divided into high, medium or low productivity by assessing relative population sizes. Populations were then randomly assigned one of three harvest treatments: Minimum Length (ML), Harvest Slot (HS) or unharvested control (CO), with each treatment having a replicate population of high, medium or low productivity.

All populations were harvested and censused monthly. Harvesting was a set daily mortality rate applied to the number of individuals that fell within the vulnerable size range. The vulnerable size range for the ML treatment was defined as all individuals above 17mm, i.e. recorded size at first parturition for guppies. This was to replicate a “spawn at least once” policy that current regulations aim for. Given that guppies are sexually dimorphic (as described above); ML treatments have an inherent sex biased removal. This is designed to reflect what occurs in commercial fisheries, where sexual dimorphism means that harvest disproportionately impacts individuals of one sex over

the other, as seen in Pacific Herring (Ward *et al.*, 2019) ,Sockeye salmon (Kendall and Quinn, 2013) and several Gadoid species (Keyl, Kempf and Sell, 2015).

For HS, the lower slot limit was set at 17mm and the upper slot limit was set at 21mm. Upper limit was set at 2/3 of approximate asymptotic length (estimated from previous work on guppy populations) in order to maximise yield as indicated by Gwinn et al (2015). As such HS results in reduced sex biased removal of females, as both males and females fell within the slot window.

Monthly harvest was calculated from the previous month's census data. Harvest treatments were subjected to equal daily harvest rates (F) of 0.017 individuals per day. If the number of individuals in the vulnerable size class was 3 or less then populations were left unharvested for that month. This allowed for adaptive harvest such that there is no harvest to extinction.

The number of individuals removed each harvest was calculated as follows:

$$Nremoved = Fvulnerable * (1 - e^{(-harvest\ rate\ *28days)}). \qquad Equation\ 1.$$

Where Nremoved is the number of individuals removed each month and Fvulnerable is the number of individuals that fell within the targeted size range in the previous month's census.

All populations were harvested for a period of 12 months. After this period populations were monitored for signs of recovery for a further 6 months.

Population censuses to monitor changes in population size and structure over time were conducted every four weeks, with harvesting occurring at the same time. Populations were sorted into different life history classes of juveniles, mature males and mature females, and photographed on a white tray with a scale. These photographs were then analysed using image analysis software (ImageJ) to obtain the length of every individual in each population. All populations were censused in the same week but not always on the same day.

Life History Assay

Populations were allowed to recover for 6 months after harvesting ceased before collection of females for life history assays. Individual females were fed zm-400 granulated fry food *ad libitum* until birth. Litters were photographed together to determine female brood size and size-at birth. Individuals were then raised in groups of at least 3 in 2 litre plastic aquaria in a constantly circulating system complete with sump filtration. Temperature and water was maintained at the same parameters as population tanks above*. Groups of fry were assigned either high or low food common garden rearing environments, using Interpet's Liquifry no2™. High and low food was set at 0.3ml and 0.1ml per capita per day respectively based on previous pilot study (detailed in chapter II). Fry were grown to maturation and photographed for later image analysis to assess both age and size at maturation.

Data analysis

Image analysis software (ImageJ) was used to determine individual body sizes, measured in standard length (in mm). This software was used to analyse population census photographs, photographs of *Nremoved* individuals and photographs from life history assays.

Census photos allowed characterisation of the body size of all individuals within populations. This allowed visualisation of temporal changes in population size structure, mean body size, and abundance.

I used length*weight regression equations from previously published research on guppies (Nilsson and Persson, 2013) to calculate dry biomass for each individual in all populations. Total population biomass was calculated by summing all calculated individual biomass data. SSB was calculated by summing the biomass of all individual females over 17mm.

Yield was calculated using images of individuals removed from the population to calculate harvested biomass over a 10 month period.

The significance of temporal trends in population metrics (e.g. total biomass, spawning stock biomass, number of individuals) and size structure were determined using linear mixed effects models using the nlme package in R (Pinheiro J et al, 2018), with repeated measures nested within replicate population tanks as a random effect (Cameron *et al.*, 2013).

Juveniles photographed during life history assay were also assessed for standard length at birth and at maturation. Photos of new-born individuals and maturing individuals were also used to assess brood size and age at maturation (in days). The effect of harvest treatments on life history traits were determined using standard linear models.

All statistical analyses were conducted in R studio (R: A language and environment for Statistical Computing, R core team, 2016).

Results

Total Population, Spawning Stock Biomass and Stock-Recruitment relationships

Population biomass declined in all harvested and unharvested treatments over time (LME: Population biomass ~ time, F_2=153.77, P < 0.05 see figure). During harvesting, the greatest decline in overall population biomass was observed in tanks under traditional, minimum length (ML) based harvesting, on average being 3% lower biomass than unharvested controls. In comparison, Harvest slot regulated tanks on average had 2% lower biomass. After a period of 12 months harvest, populations under ML had 54% lower population biomass than unharvested controls. In comparison, HS regulated populations had 30% lower biomass than unharvested controls, but did not significantly differ from one another (P>0.05).

Following this 12 month harvest period, population recovery was tracked for 6 months with all harvesting ceased. During this time, unharvested control populations continued to decline in overall population biomass, but still maintained the highest biomass. After this 6 month recovery period, HS populations did not differ from controls, only showing on average 12% less biomass in comparison to 40% less biomass observed in ML populations at the end of the study period.

Spawning stock biomass (SSB) was total biomass of all females of reproductive potential in a population, i.e. all females above previously recorded measures of first parturition. Harvest treatment was found to significantly affect SSB over time (LME: SSB ~ time*treatment, $F_{2,139}$=6.43, P < 0.05, see figure). Harvest slot populations

maintained on average 18% more SSB than minimum length over time and did not significantly differ from unharvested controls (LME: P<0.05).

Table 11: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on total population biomass over time.

	numDF	denDF	F-value	p-value
(Intercept)	1	141.00	369.81	0.00
Census	1	141.00	153.77	0.00
treatment	2	6.00	10.20	0.01
Census:treatment	2	141.00	2.64	0.07

Table 12: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on population biomass after a recovery period of 6 months.

	numDF	denDF	F-value	p-value
(Intercept)	1	105.00	345.99	0.00
Census	1	105.00	104.28	0.00
treatment	2	6.00	8.61	0.02
Census:treatment	2	105.00	7.85	0.00

Table 13: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on spawning stock biomass over time.

	numDF	denDF	F-value	p-value
(Intercept)	1	139.00	235.06	0.00
Census	1	139.00	79.77	0.00
treatment	2	6.00	24.36	0.00
Census:treatment	2	139.00	6.43	0.00

Size structure and demography

Traditional harvest regulations (ML) altered population size structure (see figure 15). This was evidenced by significant changes in mean body size within populations (LME: Body Size ~ Harvest treatment * time, $F_{2, 11452}$ =69.10, P<0.05). Over the course of the experiment, ML harvesting resulted in an average reduction of 29.7% in body size over unharvested control populations. In comparison, populations under HS regulations resulted in 14.5% reductions in overall body size. Before harvest treatment was imposed, mean body size was not found to significantly differ between populations (LM: F_2=2.604, P< 0.05, as shown in figure 17 and table 15).

Body size was still found to significantly differ between treatments after a 6 month period of recovery after harvesting ceased (LM: Body Size ~ Harvest treatment, $F_{2, 6}$ =24.89, P < 0.05). Mean body size in ML harvested populations was on average 32% smaller than individuals from unharvested control populations. In comparison, unharvested controls and HS populations that did not differ from one another in terms of mean body size at this same time point.

Sex ratios were found to be significantly affected by harvesting treatments. Female numbers were on average 31.7% lower in ML populations than unharvested controls and 23.5% lower in HS populations (LM: F_2=12.11, P<0.05, figure x). Male numbers also differed in response to harvest treatments (LM: F_2= 58.36, P<0.05, figure x), with ML being 76% greater on average than unharvested control populations. Male numbers in HS populations did not significantly differ from control populations.

Table 13: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on body size over time.

	numDF	denDF	F-value	p-value
(Intercept)	1	12219.00	1762.55	0.00
Census	1	12219.00	202.86	0.00
treatment	2	6.00	26.98	0.00
Census:treatment	2	12219.00	69.10	0.00

Table 14: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on body size after a recovery period of 6 months.

	numDF	denDF	F-value	p-value
(Intercept)	1	472.00	1387.90	0.00
treatment	2	6.00	24.89	0.00

Table 15: ANOVA output table of a linear mixed effects model comparing body size between populations before treatment began.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
treatment	2	153.36	76.68	2.60	0.0746
Residuals	764	22493.77	29.44		

Table 16: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on female abundance over time

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
treatment	2	1582.60	791.30	12.11	0.0000
Residuals	150	9801.18	65.34		

Table 17: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on male abundance over time

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
treatment	2	9123.88	4561.94	58.36	0.0000
Residuals	150	11724.59	78.16		

Yield

The number of fish taken at each census was calculated from Fvulnerable at the previous census. Individuals removed from each tank were photographed, biomass for each individual was measured and summed to calculate yield changes over time. Harvest treatment was not found to significantly affect biomass yield (LM: Yield ~ Harvest Treatment, $F_{1,70}$=2.87, P>0.05). Biomass yield was found on average to be 45.3.% greater in populations under ML regulation than HS over 10 months of harvest. (see figure 16).

Additionally, there was no significant difference between the two harvest treatments over time in the numbers of fish harvested at each census (LM: # of Fish ~ Harvest Treatment, $F_{1,}$ = 6.20, P>0.05) (See figure 1).

Table 18: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on numbers of fish removed

	numDF	denDF	F-value	p-value
(Intercept)	1	70.00	183.81	0.00
census	1	70.00	101.96	0.00
treat	1	4.00	6.20	0.07
census:treat	1	70.00	3.47	0.07

Table 19: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on biomass of fish removed

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
treatment	1	0.39	0.39	2.87	0.0945
Residuals	70	9.61	0.14		

Phenotypic responses of Life History traits

Life history assays to measure trait responses were conducted after a 6 months recovery period with no harvesting, 18 months since the harvest treatments were first imposed. Significant differences were observed in the phenotype of both female reproductive traits and juvenile life history traits associated with growth, i.e. rates of maturation, between fish from different harvesting treatments. Size of offspring at birth was significantly affected by the harvest treatment mothers originated from (LM: Size at Birth ~ Harvest treatment, F_2=40.68, P<0.05). Females originating from populations under ML produced offspring 22.4% smaller on average than those from unharvested pops. Conversely, females originating from populations under HS did not significantly differ from unharvested pops in offspring size at birth (see figure 18). Harvest treatment was not found to significantly affect the clutch/litter size (see figure 18).

Age and size at maturation of juveniles were both found to be affected by the harvest treatment that their parents originated from. Size at maturation was found to be significantly affected by harvest treatment (LM: size at maturation ~ Harvest treatment, F_2=5.13, P<0.05). On average we found that juveniles from ML lineages were found to matured 11% smaller than those that were from unharvested lineages. Conversely juveniles from HS lineages showed less than 1% difference from unharvested individuals and as such did not significantly differ from those (see figure 19).

Age at maturation was also significantly affected by harvest treatment (LM: age at maturation ~ Harvest treatment, F_2=4.5, P<0.05). Juveniles that originated from both harvested populations took longer to mature than those from unharvested populations. On average HS and ML lineage juveniles took 30% and 28% longer to mature than

juveniles from unharvested populations, but did not significantly differ from one another (figure 19).

Table 20: ANOVA output table of a linear model showing the effect of harvesting treatment on size of offspring produced by females.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
treatment	2	34.87	17.43	40.68	0.0000
Residuals	134	57.42	0.43		

Table 21: ANOVA output table of a linear model showing the effect of harvesting treatment on brood size of females.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
treatment	2	5.70	2.85	0.63	0.5403
female_size	1	43.60	43.60	9.63	0.0043
treatment:female_size	2	0.95	0.48	0.11	0.9006
Residuals	28	126.72	4.53		

Table 22: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on age at maturation

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
food_level	1	17854.77	17854.77	57.95	0.0000
treatment	2	2769.90	1384.95	4.50	0.0138
food_level:treatment	2	761.04	380.52	1.24	0.2957
Residuals	90	27727.61	308.08		

Table 23: ANOVA output table of a linear mixed effects model showing the effect of harvesting treatment on size at maturation

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
treatment	2	21.09	10.55	5.13	0.0077
Residuals	93	191.12	2.06		

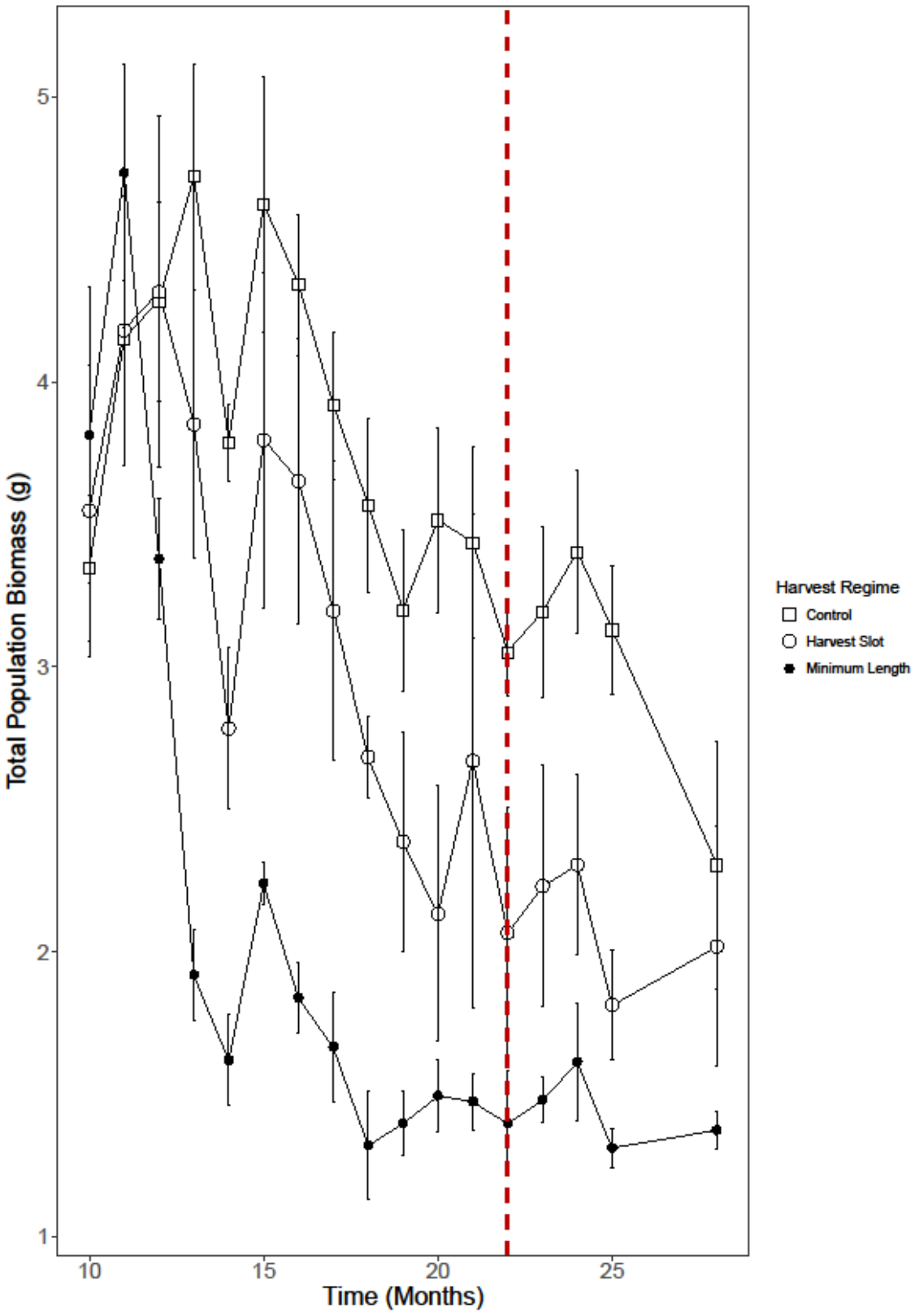


Figure 15: Total Population Biomass in dry-mass over time from the start of harvest (month 10). Red dashed line indicates the last harvest before a 6 month recovery period. Error bars are +/- 2* standard error.

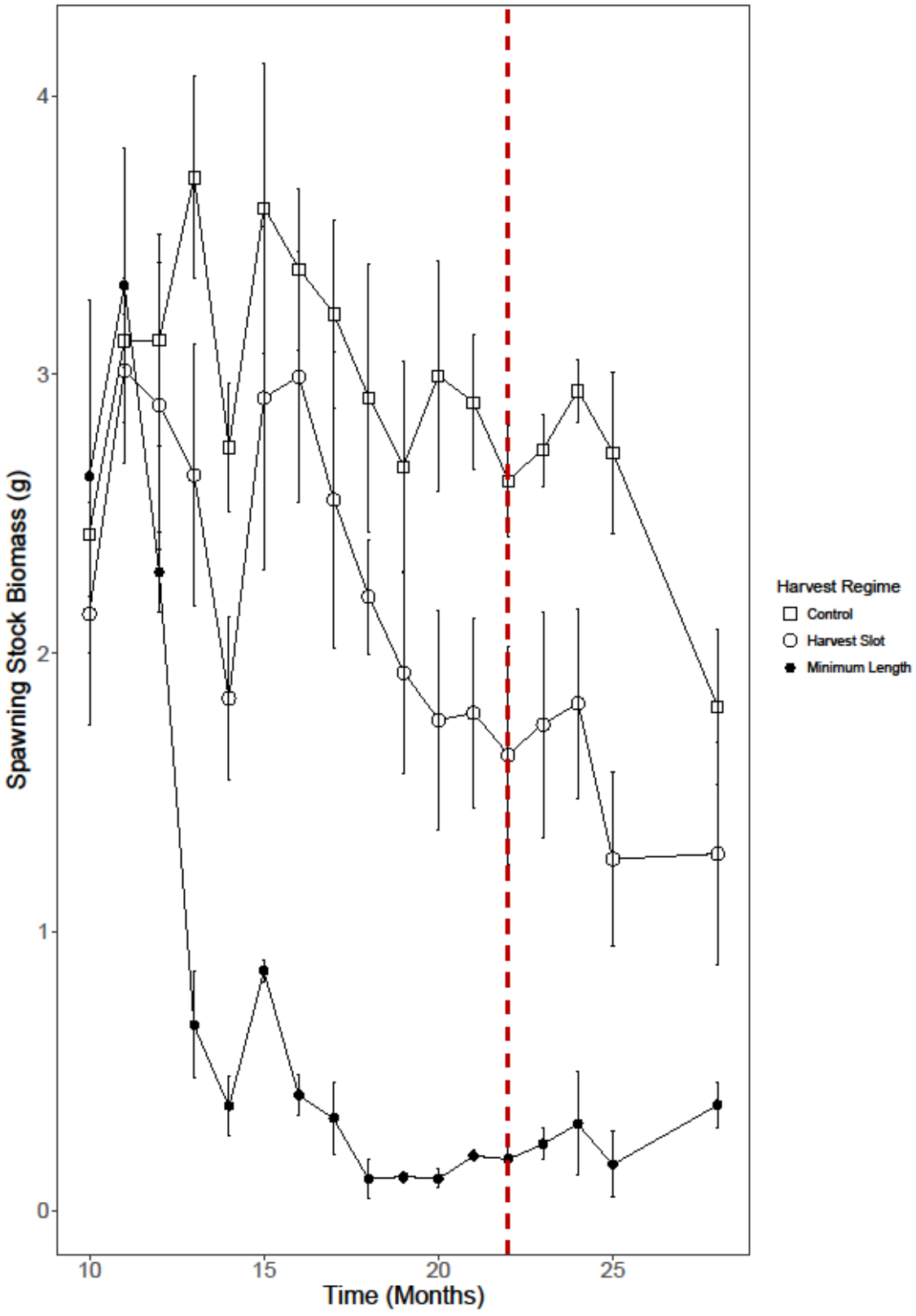


Figure 16: Spawning Stock Biomass in dry-mass over time from the start of harvest (month 10). Red dashed line indicates the last harvest before a 6 month recovery period. Stock Biomass was calculated by the sum of all spawning individuals in a population. Error bars are +/- 2* standard error.

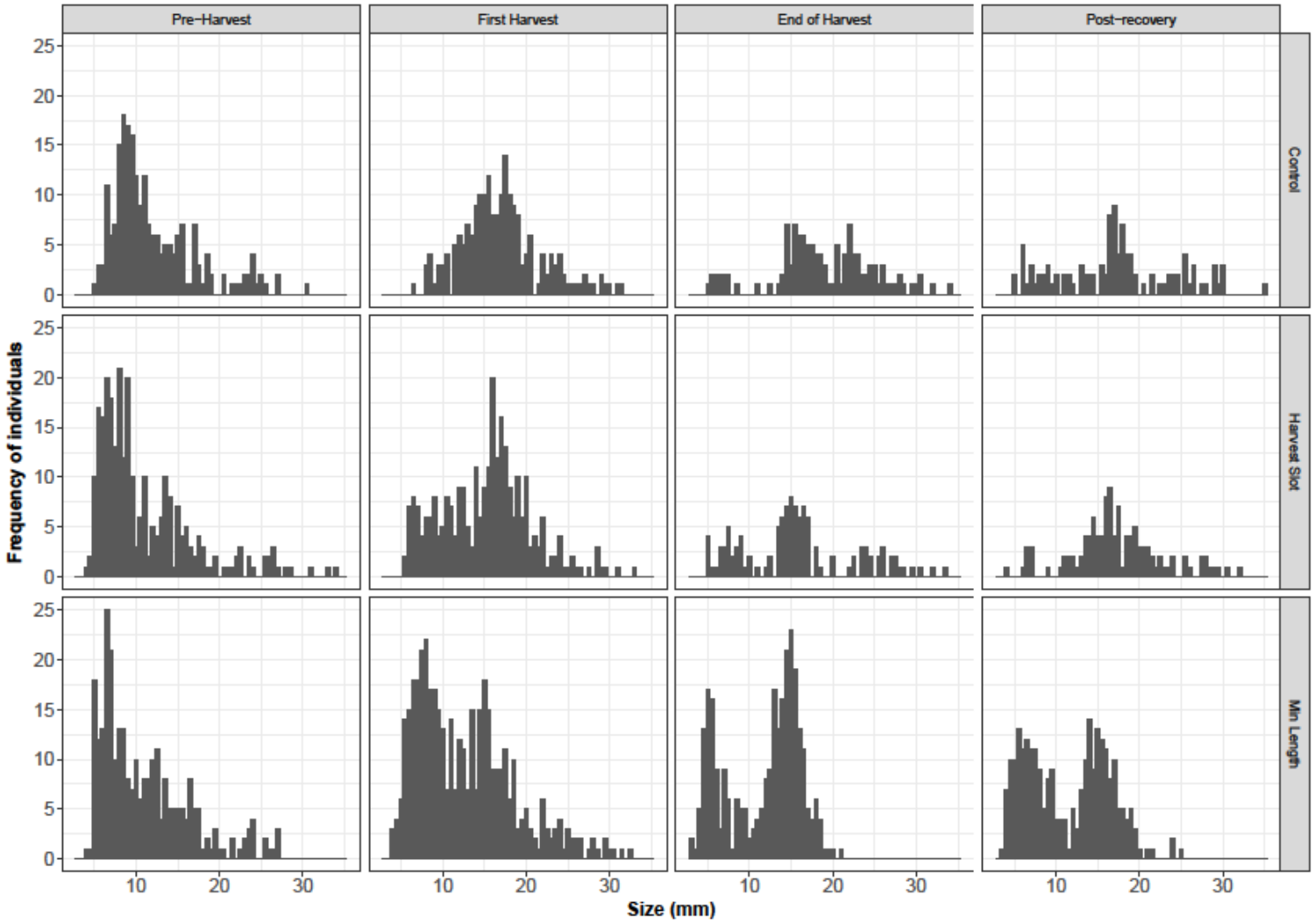


Figure 17: Summed population size structure over time. Facets show (from left to right): before harvest treatment, after first month of harvest, at the end of harvesting, and after six months recovery.

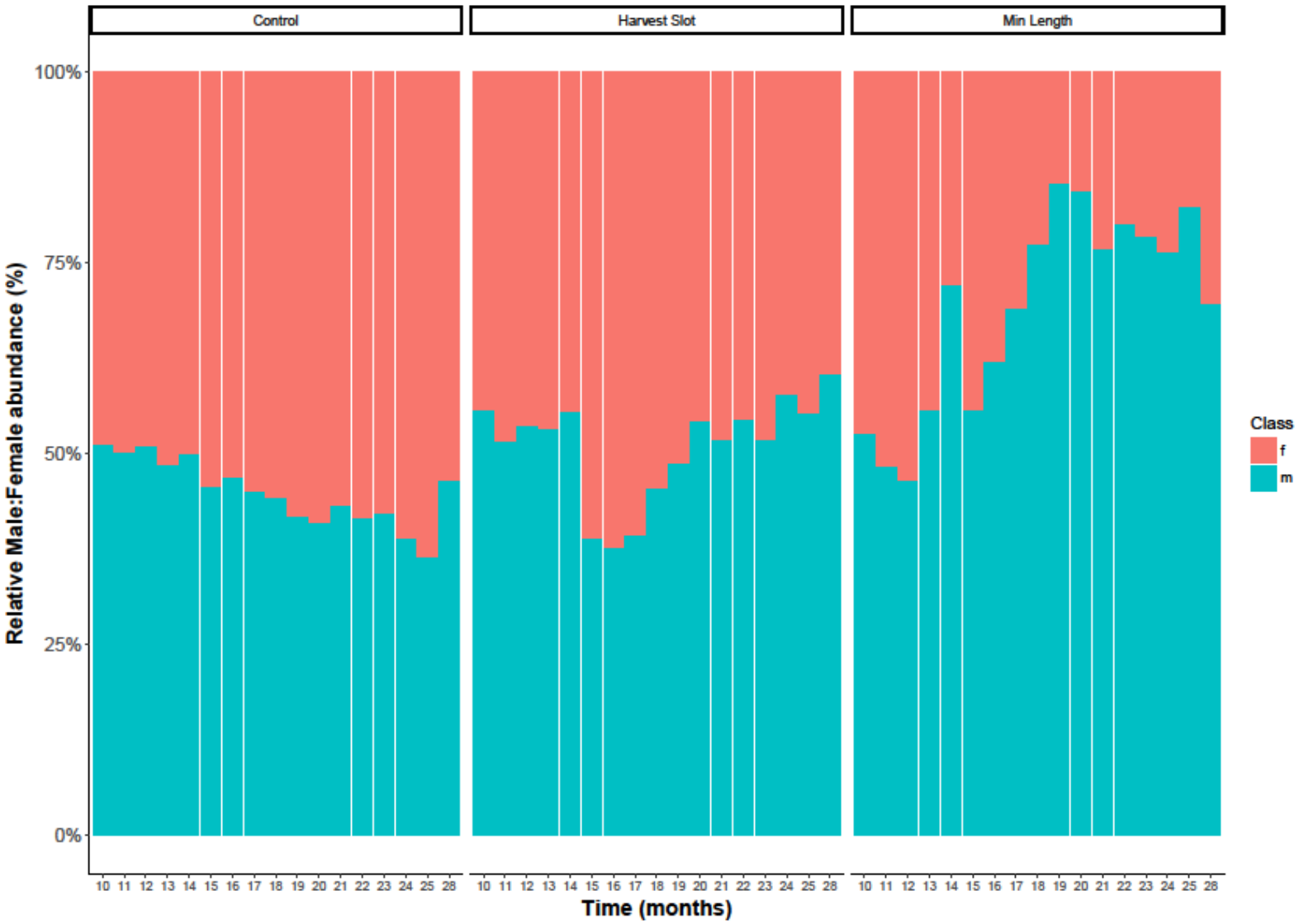


Figure 18: Average sex ratios over time from the start of harvest to the end of recovery (as detailed above). Bars indicate the proportion of males to females in the adult portion of populations.

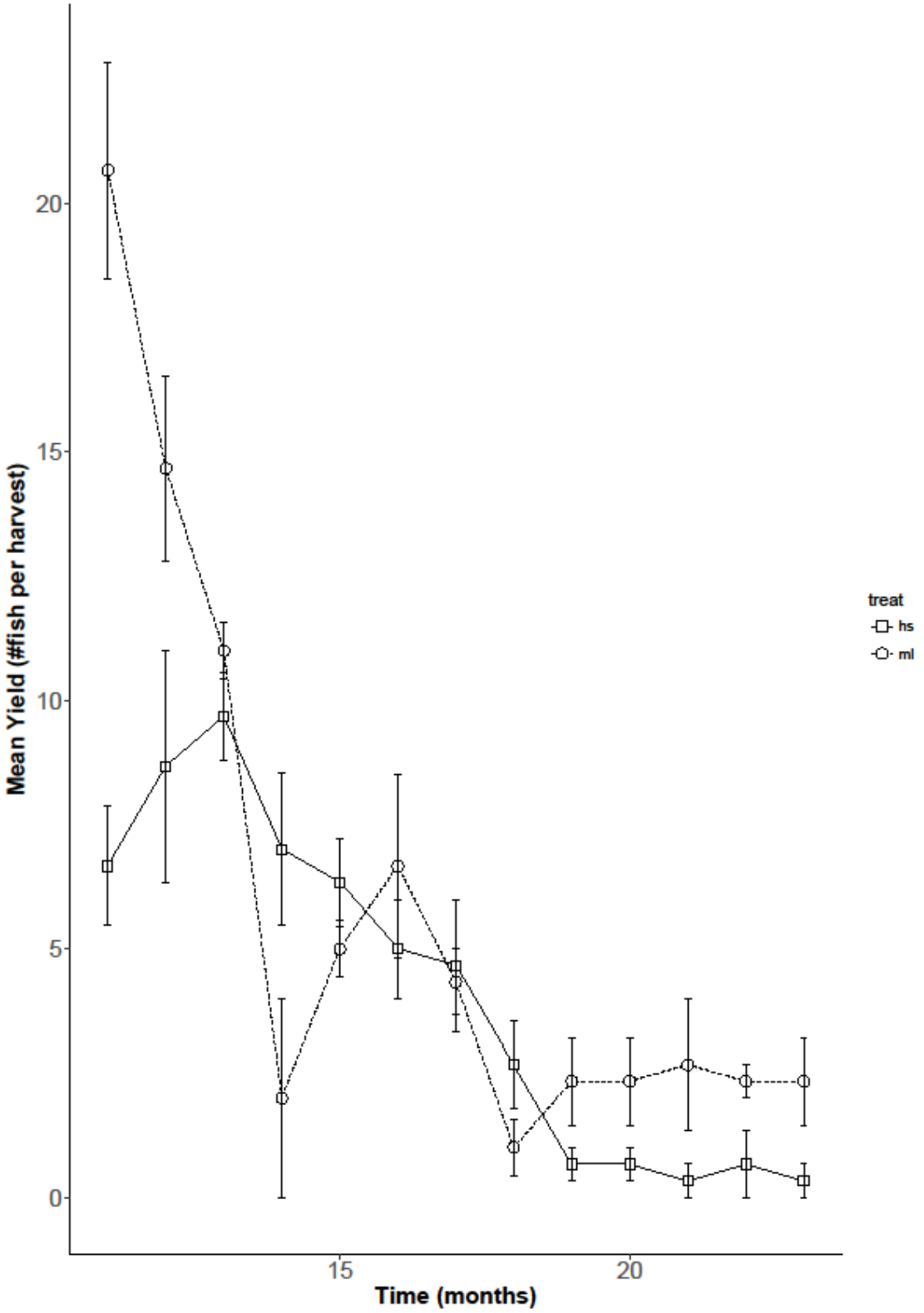


Figure 19: Yield in numbers of individuals removed (bottom) over harvest period. Error bars are +/- 2* standard error.

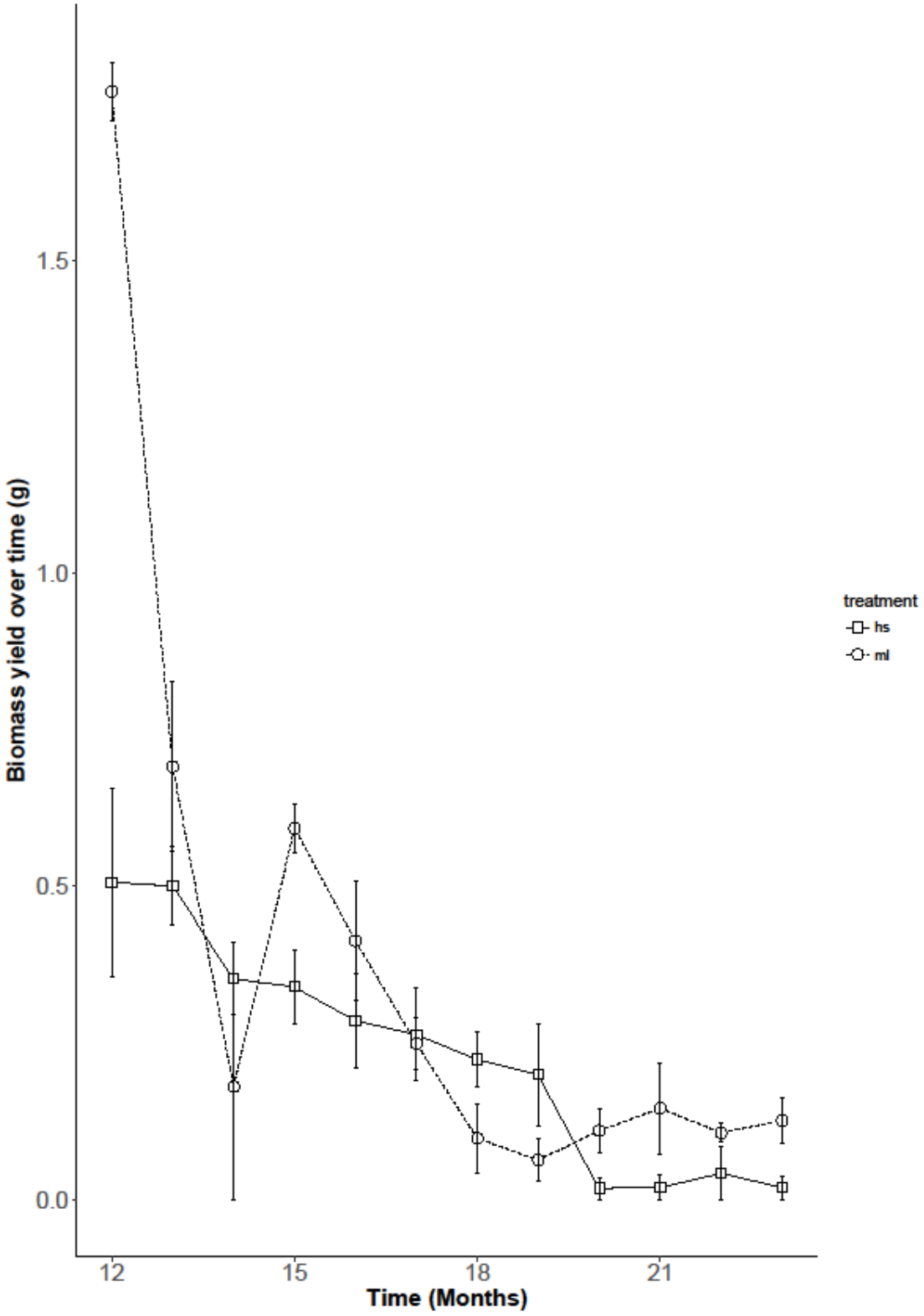


Figure 19: Yield in biomass removed (bottom) over harvest period. Error bars are +/- 2* standard error.

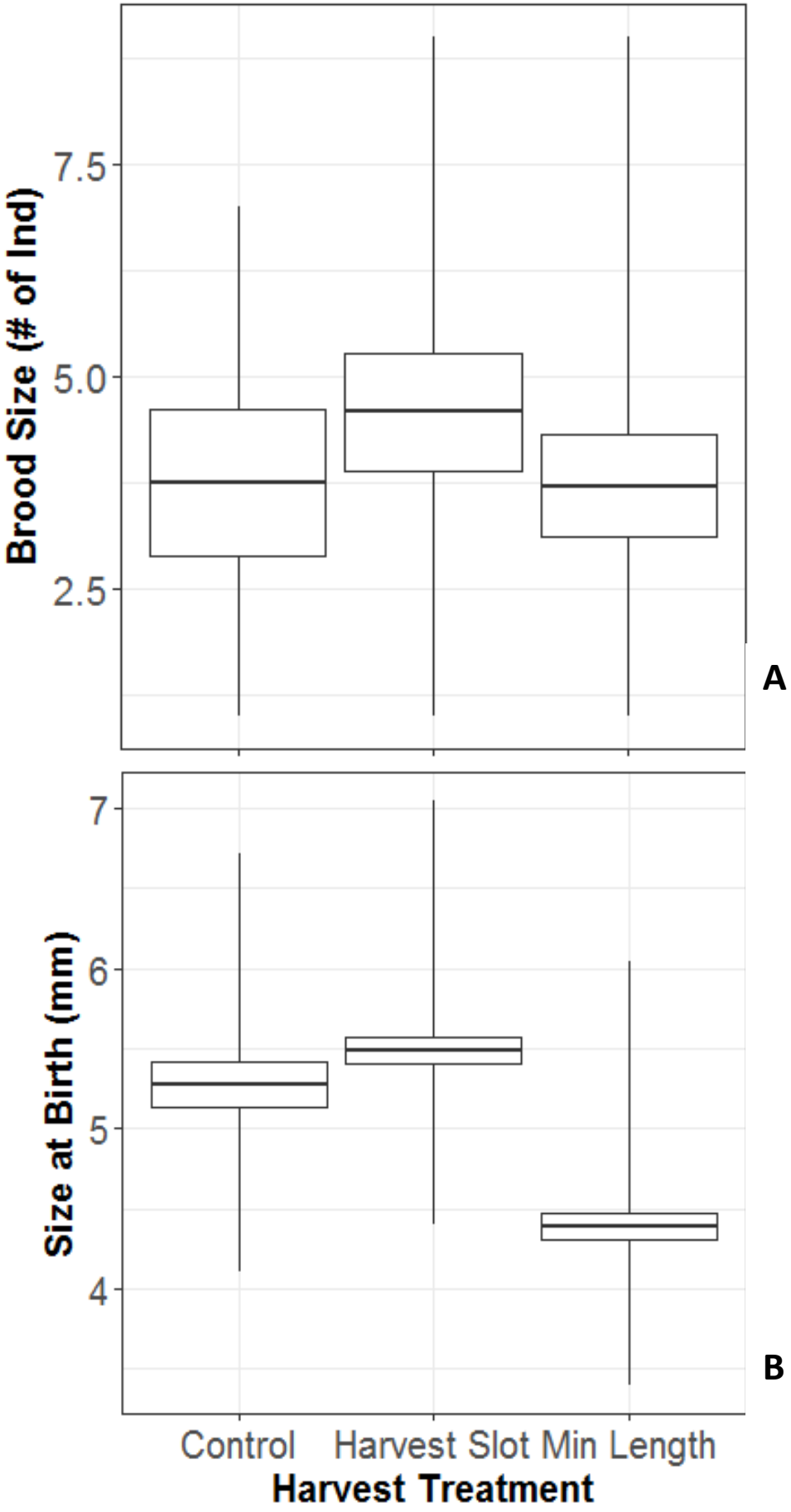


Figure 21A and B: Reproductive investment of females. 18A (top) shows mean number of offspring per brood. 18B (bottom) shows mean size of offspring at birth in mm. Boxplots show +/-1 standard error, min and max

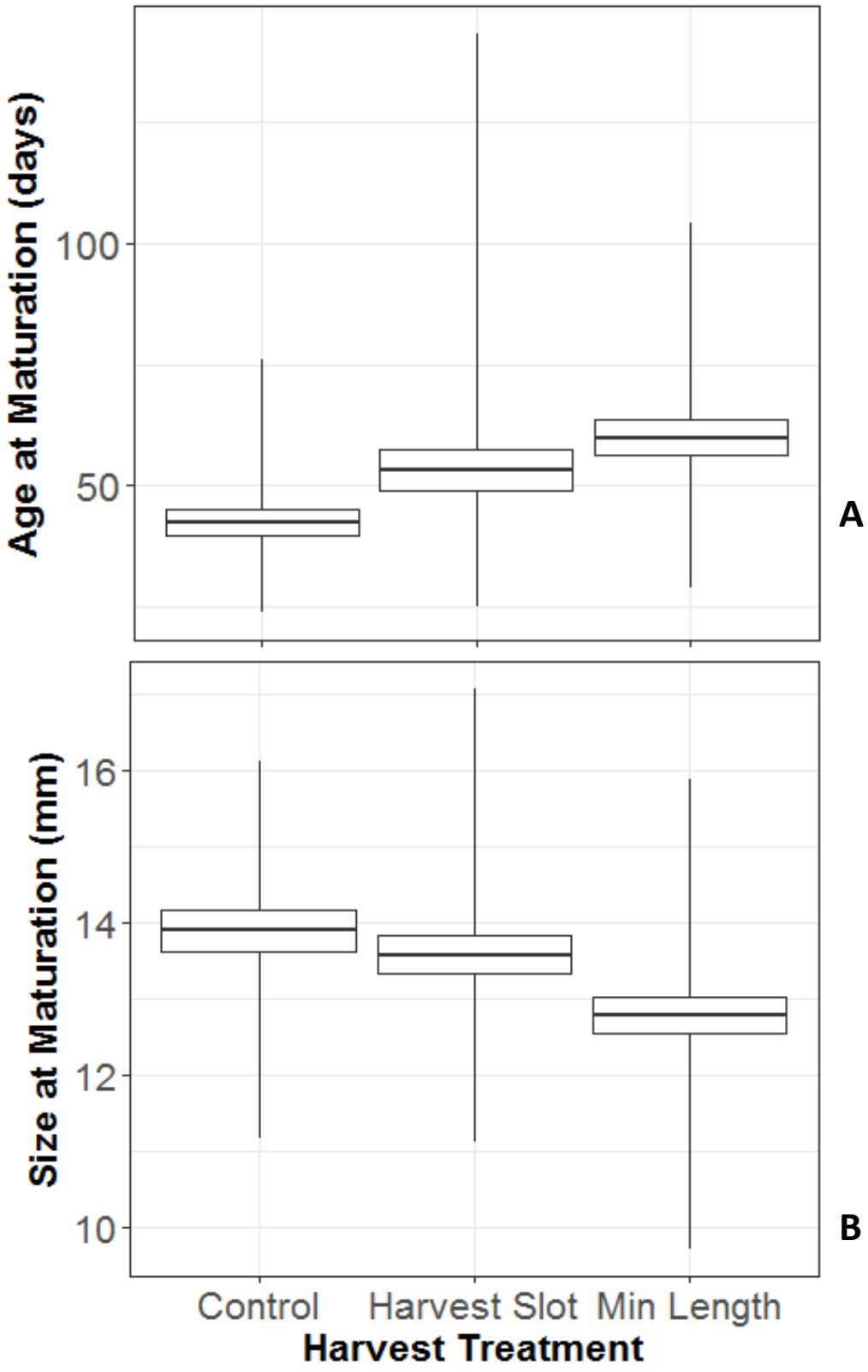


Figure 22A and B: Mean age at maturation in days (top) and mean size at maturation in mm (bottom). Boxplots show +/-1 standard error, min and max

Discussion

I found traditional minimum length based harvest regulations have pronounced effects on size structure and biomass both during harvest and after a period of recovery. Phenotypic change in key life history traits after 6 months recovery suggests longer term consequences for the value of fish populations that have been traditionally harvested. In contrast, I found that HS regulation promotes populations with greater overall and spawning stock biomass, more "natural" size structure and reduced effects on life histories in comparison to traditional harvest. However, HS was not found to provide comparable levels of yield that traditional ML regulations did.

Size selectivity that occurs in traditional fisheries has been known to cause short term changes in ecological dynamics, i.e. changing size structure and therefore productivity. I observed that traditional ML harvesting results in the greatest reductions in biomass. In contrast, we observed that HS populations do not significantly differ from unharvested control populations in terms of overall biomass. These trends in biomass can be explained by observations of size structure and sex ratios I make both during and post-harvest. Erosion of large bodied size classes in ML drives reductions in mean body size and therefore biomass, driven by the biased removal of females that are able to attain larger body sizes. Removal of biomass results in reduced competition of resources (Zipkin *et al.*, 2008; Svedäng and Hornborg, 2014), facilitating greater investment in reproduction by the remaining adults. This however is limited by skewed sex ratios, with high numbers of small bodied males dominating the adult cohort. This inadvertent effect of selective fishing is increasingly observed in several commercially harvested fish populations (Kendall and Quinn, 2013; Kell *et al.*, 2016; Ward *et al.*, 2019).

This size selectivity is also theorised to drive phenotypic change in key life history traits (Kuparinen, Kuikka and Merilä, 2009). Selection against large body size is evidenced here by reduced size at birth in ML population, as well as reduced size at maturation. As observed in commercial fish stocks (Uusi-Heikkilä *et al.*, 2015), the legacy of selective fishing is still present in size structure, sex ratio and phenotypes months after fishing has ceased (figures 15, 18 and 19).

In contrast HS don't differ from unharvested populations in terms of mean body size, and maintain similar population size structure. Regular removal promotes production of new biomass in a population (Arlinghaus, Matsumura and Dieckmann, 2010), facilitating growth and reproductive output, particularly as selective removal of fecund females is reduced. Additionally, life history assays show HS do not show the same evidence of phenotypic change, with the comparatively reduced selective pressure resulting in comparatively smaller differences in life histories than ML populations.

Current size selective fishing drives declines in catches and by association population biomass in targeted fish species. Excessive removal of the largest individuals is found to drastically reduce the reproductive potential of a population (Hixon, Johnson and Sogard, 2014). The capacity of a population to replenish itself is significantly affected by the number of mature reproducing individuals in a population. In a fisheries context this is determined by the spawning stock biomass (Arlinghaus, Matsumura and Dieckmann, 2010; Koehn and Todd, 2012). Failure to protect reproductive potential of a fishery has been shown to result in fisheries collapse e.g. the Newfoundland cod fishery (Xu, Schneider and Rideout, 2012) where targeting of largest valuable fish resulted in demography dominated by smaller, more vulnerable size classes. Recent work highlights the disproportionate importance of large bodied individuals for recruitment,

where increasing body size results in increased reproductive output (Olsson and Gislason, 2016; Barneche *et al.*, 2018).

Contemporary fisheries are suggested to be the world's largest artificial selection experiment, with size selective fishing expected to select for fast life histories and shifts in reproductive investment (Reznick and Ghalambor, 2005). Theoretical papers project reductions in maturation size in several commercially important fish species as a result of cumulative fishing pressure (Kuparinen, Kuikka and Merilä, 2009). This is backed up further by observed data of fish stocks, where reductions in individual body size have been observed over the past 50 years (Audzijonyte *et al.*, 2013). Criticism of fisheries induced evolution is that selection is not particularly fast or strong enough to be observed in the real world (Andersen and Brander, 2009). However, evidence of evolutionary change of life history traits over "ecological timescales" have been observed in in invertebrate model systems (Cameron *et al.*, 2013), as well as in wild fish populations (Reznick, Bryga and Endler, 1990). In the field of fisheries induced evolution, the limited empirical evidence proving the role of size selective harvesting on phenotypic change is limited, often by lack of density dependence or realistic harvesting pressure (Van Wijk *et al.*, 2013; Lindstro *et al.*, 2016). Although we cannot categorically say that fisheries induced evolution is occurring in our harvested populations, we can say that traditional ML harvest results in pronounced phenotypic change in life history traits associated with body size and growth long after selective harvesting has ceased. In contrast we find that HS regulation does not significantly differ from unharvested populations in the same traits, therefore showing that HS also negates the potential phenotypic effects of size selective fishing.

However, real world fisheries are often subject to harvest levels beyond what scientists and managers suggest is sustainable (Piracha, 2015). In this theme, I elected to impose a “realistically high” daily F rate that previous studies suggest guppy populations can just sustain without resulting in complete extinction (Barlow, 1992; Schröder, Persson and De Roos, 2009). In this context, I observe that in whilst both harvesting treatments result in declining yields, HS yields are lower overall than those of ML. . The concept of a triple bottom line plan for fisheries is increasingly discussed, whereby a compromise between social, economic and conservation objectives is sought when deciding on appropriate regulations for a fishery (Brown *et al.*, 2018). Previous simulations on Harvest Slots indicate that they should be superior to traditional Minimum size/length based fishing on all of the above metrics when applied correctly (Gwinn *et al.*, 2015). In this empirical study I find that economic yield (biomass removed) is compromised by the usage of harvest slots. Given the results of Gwinn et al (2015) and other results presented here, I propose that future work on the viability of harvest slots could include more extensive testing of slot size and also mortality rate. That said, HS regulated populations here result in populations with greater numbers of large bodied individuals and are less liable to phenotypic changes in life history traits, indicating longer term societal and conservation benefits of utilising harvest slots.

My results demonstrate the potential of HS to maintain a more sustainable fishery meeting the demands of conservation of fish stocks by maintaining high population and spawning stock biomass. That said, given that the primary reason for fisheries regulations is to maintain a desirable output in terms of food and economic benefit, more development on HS approaches is needed before it is able to match traditional regulations in terms of yield. In addition, I empirically show evidence for fisheries

induced phenotypic change in a realistic density dependent setting, and suggest that HS reduces the selective pressure on fish life histories. As such, I suggest that HS presents a possible solution to sustainable fisheries that combats current issues of size selective fishing, and warrants further exploration in a field setting with a view to implementation in fisheries policy.

Chapter V – Asymmetry in energy efficiency throughout ontogeny: linking responses in size structure to individual adaptation

Abstract

The efficiency at which organisms utilise resources can change throughout their ontogeny. Inevitably, when both juvenile and adult organisms share the same resources, this can result in an inequality between life history stages in how effectively they compete against one another. This asymmetry between life history stages is observed to result in bottlenecks in biomass transfer within populations, by either reproduction or maturation rates, often resulting in imbalances in the relative biomasses of different stage or age groups. However life history evolution by selection dictates that growth rates should evolve to avoid the negative effects of intraspecific competition on individual fitness. This is complex as we are asking how selection will influence the life history and development of an organism at different parts of its journey from birth to maturation and to subsequent reproduction events. Wild populations also experience a range of potential controls on their life history and competitive abilities through ontogeny – such as predation and interspecific competition. It is difficult to separate out which of several potential driving forces is driving the evolution of competitive asymmetries that are found to be dominant in nature when we might expect them to be selected against. Here we use a model vertebrate system, Trinidadian Guppies, to test whether the life history of the average individual is selected to be more or less competitively asymmetric in a controlled intraspecific competition population experiment. I undertook a population study where I controlled the environmental productivity and therefore the inter-stage competition of a separated juvenile or adult stage through biasing food to the

competitively weaker stage (e.g. adults). As juveniles were born in the adults' environment or juveniles matured – they were transferred to their respective environments. Feedbacks between the demographic rates and intra-stage density dependent competition can then occur. If for example, fecundity increases, it increases the competition for maturation in the juvenile habitat. In addition, I followed temporal changes in per capita reproductive investment. If selection acts to minimise competitive asymmetry we should expect differences between maturation and reproduction rates, and in stage biomasses, to decline over time.

I find that populations that have greater food bias towards adults are released from bottlenecks in recruitment, and therefore have subsequent biomass increases without any overall increase in resources. However, I do not find conclusive evidence that adaptation in life history traits has occurred in response to food treatments, and that more experimental work is needed to confirm whether this is the case.

Introduction

Individuals are sources of variation within populations and individual variation underpins evolution. Individuals vary throughout their lifetime, by virtue of ontogenetic development, or put simply, they change as they grow (Persson and De Roos, 2013). Indeed while all individuals are born and die, growth is much more probable than reproduction and in much of ecological theory has appeared to be less considered (Persson and De Roos, 2013). Small changes at the level of individuals (mortality, changes in reproductive output, growth) can multiply to alter growth rate of populations as a whole (Benton, 2012; Sæther *et al.*, 2013), which in turn feeds back on individual trait variation through selection (Travis, Reznick and Bassar, 2014).

The efficiency at which resources are utilised change throughout an organism's life time (De Roos *et al.*, 2007). The resources utilised may change throughout an individual's life time (i.e. ontogenetic niche shift)(Osenburg, Mittlebach and Wainwright, 1992; ten Brink and de Roos, 2017) or the energy gained whilst utilising the same resource might change throughout its life time (Nakazawa, 2015). All organisms grow to some extent, and with increased body size will logically incur increasing costs of maintenance. So even if an individual's resource efficiency is maintained, they will need more resources to deal with increased costs. Organisms that sexually mature will also incur additional costs of maintenance of reproductive organs (Audzijonyte and Richards, 2018). With this in mind, a single unit of food that might sustain a juvenile's growth for a day might be barely enough to sustain a sexually mature adult of the same species, even if corrected for body weight. Conversely, an adult might be more effective at utilising a resource than a juvenile due to its increased size, e.g. larger gape size meaning less energy is wasted due to handling time (Vincent *et al.*, 2006).

This inequality in energy efficiency between different life history stages is under increasing scrutiny has been termed ontogenetic asymmetry (de Roos, Metz and Persson, 2013; Persson and De Roos, 2013). When studied, very few organisms are equally good throughout their life time at utilising a resource, which would be called ontogenetic symmetry. When species are studied in isolation, equal resource distribution can result in stage structured populations, with bottlenecks in biomass production caused by the reduced resource use, capture or utilisation by one or more stages relative to another (Schröder, Leeuwen and Cameron, 2014). These bottlenecks can be characterised by the demographic process that is limiting population growth (Cameron and Benton, 2004). Reproduction control, where juveniles are better competitors than adults, results in a build-up of biomass in the adult stage, and a lack of resources to invest in reproduction (see figure 20). Development control, where adults are better competitors than juveniles, results in a build-up of biomass in the juvenile stage, and juveniles lack the resources to mature into adults (see figure 21). Reproduction control is a common feature in many animal systems that have been examined due to the magnitude of body size differences between life history stages, and therefore energetic costs of maintenance (as outlined above) (Schröder, Leeuwen and Cameron, 2014).

However if such controls exist that limit individual growth and fitness, It is logical to predict that evolution by natural selection should select against individuals with traits that limit their competitive ability at some stage in their development. Individual asymmetries that lead to population asymmetries will result in evolution away from asymmetry towards a population where juveniles are no better/worse competitors than adults. Therefore, evolution would counteract the negative effects of these asymmetries that lead to bottlenecks on populations (Bassar *et al.*, 2016). However it is

not clear what the fitness consequences are of more symmetric or asymmetric environments. Does evolution maintain population asymmetries solely because average lifetime fitness benefits from either I. adult investment in reproduction > juvenile investment in maturation? Or II. Does size structure as a result of inequality in energy efficiency between life history stages, affect individual fitness?

In line with evolution by natural selection, growth rates to maturation could shift to counteract the reduction in mean fitness that occurs with ontogenetic asymmetry (Myrvold and Kennedy, 2015). This, and our understanding that species exist in a web of interactions with other species and their environment, means that it is intuitive to assume that species naturally exist with exterior controls to their populations (Campbell *et al.*, 2012). Organisms rarely exist in isolation, and population dynamics are often determined by the presence of competitors or predators (Hik, 1995; Stenseth *et al.*, 1997; Huss and Nilsson, 2011). If these modulate the inefficiency between life history stages, it is reasonable to suggest that organisms have evolved to require them to avoid bottlenecks in biomass production while in the presence of these external interactions. In their absence we observe asymmetry – which could suggest symmetry breaking is observed only in simple or experimental systems. However little work exists to explore how populations might adapt toward or to avoid asymmetry. This is the knowledge gap that will be addressed by the current chapter.

In the absence of exterior controls, how has asymmetry been manipulated and what were the consequences for biomass production, population and community dynamics? Previous work has focussed on experimental manipulation through culling experiments (Persson *et al.*, 1996; Schröder, Persson and De Roos, 2009) or more recently bottom

up controls of biasing resources (Reichstein, Persson and De Roos, 2015). Limitations of these studies are often that they are not carried out for particularly long periods of time, and therefore adaptation to experimental conditions is less likely. Additionally, little work exists that has pushed an asymmetric population to symmetry through its manipulations (Reichstein, Persson and De Roos, 2015). This opens fundamental knowledge gaps in our understanding of ontogenetic asymmetry. If populations have evolved to be asymmetric – can we push rates towards symmetry through manipulating the relative fitness's of juveniles and adults? In addition, how far apart is symmetry in numbers of individuals from symmetry in biomass? And finally, when studied long enough, do populations that are asymmetric modify their life histories to become symmetric?

In this chapter, I utilised the guppy model system to address the following objectives:

i) Does equal food supply to adult and juvenile populations reveal asymmetry in energy efficiency between life history stages?
ii) Can resource bias towards the competitively weaker stage promote more symmetrical transfer of biomass/individuals via maturation and reproduction?
iii) If so does this drive increases in overall population productivity?
iv) Do asymmetric conditions affect individual fitness, and if so is there evidence of adaptation to counteract this?

I hypothesised that the guppy model system used here would show reproduction control (figure 20), in line with previous work with similar fish populations (Schröder, Leeuwen and Cameron, 2014). As such, I also hypothesised that overall population productivity / biomass would increase win line with food bias towards the adult portion of the population. This would be driven by a release from competition within the adult

environment, facilitating greater investment in reproduction. Therefore, populations with greatest adult food levels would see more symmetric levels of maturation and reproduction.

In line with evolutionary theory, I also hypothesised that assymetric conditions would impact individual fitness, and as such there would be evidence of emerging adaptation to counteract this. Specifically, this would manifest as observable differences in life history strategies between populations under assymetric conditions.

Here I unpick how the “ubiquity” of ontogenetic asymmetry in population cycling, is potentially regulated by more longer term responses of life histories, utilising a model species who’s eco-evolutionary dynamics are well documented.

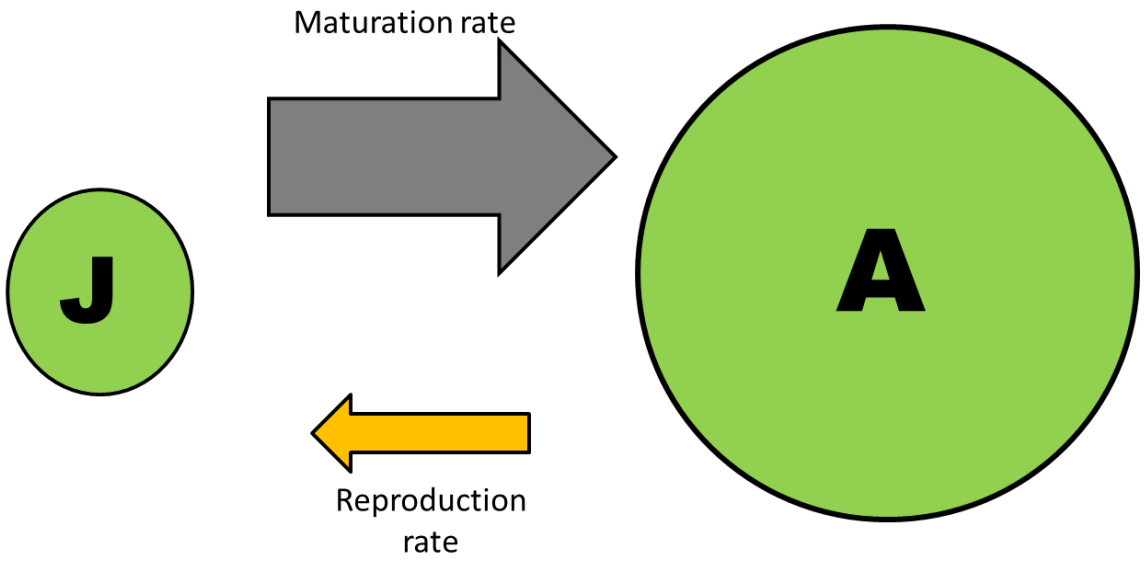


Figure 23: Reproduction control: where juveniles are superior competitors, rates of maturation are high, and competition between adults reduces reproductive investment

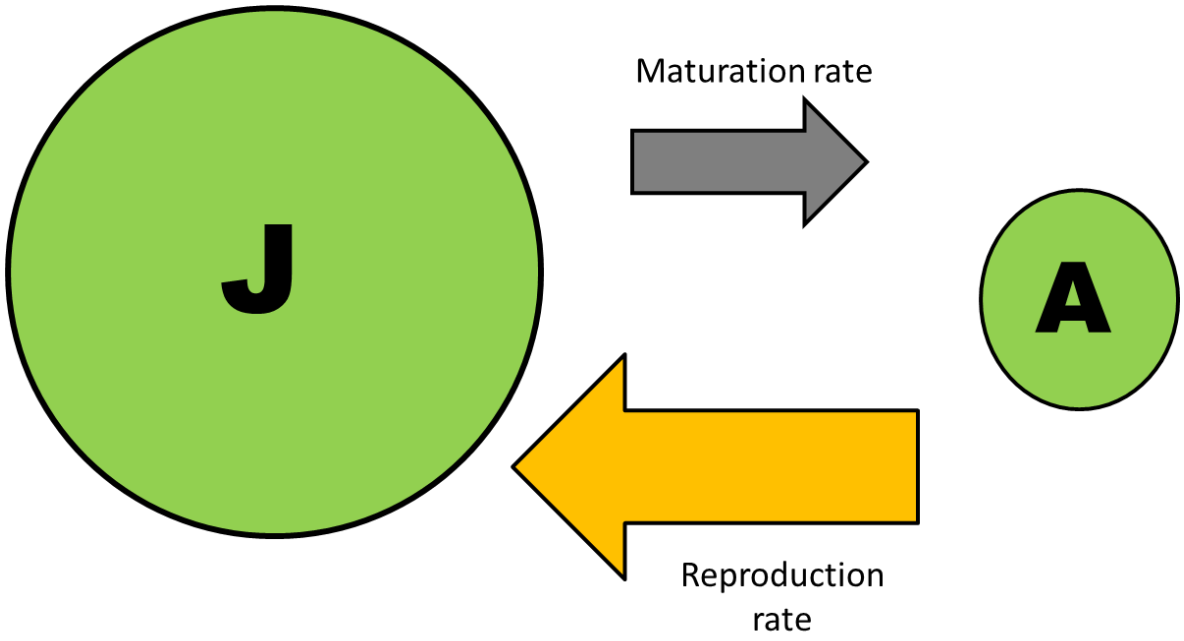


Figure 21: Developmental control: where adults are superior competitors, rates of reproduction are high, and competition between juveniles reduces growth to maturation

Methods

Study system

Trinidadian Guppies (*P.reticulata*) are viviparous poecilid sexually dimorphic fish inhabiting freshwater and brackish streams and ponds in the coastal regions of northern South America. Guppy populations are observed to experience resource competition and are cannibalistic (Barlow, 1992).

Newborn juveniles are born at approximately 5-6mm. Males mature around 13-14mm and females around 15-16mm. Populations were started with an equal ratio of adult male and female guppies, from stocks originating from either high or low predation adapted populations (Aripo high and Quare Low)(Reznick, 1982), assigning equal numbers and demographics from each population to minimise founding effects. Twelve 210 litre aquaria were inoculated with 20 adult guppies (1:1 male-female ratio) from multiple stock populations to maximise genetic diversity. Aquaria were part of a closed circulating system, with filtration and heating by sump and each tank had 2x t8 fluorescent tubes to supply lighting (12:12 Light/Dark regime). Aquaria were filled with reverse osmosis water with additional salt to prevent infection from ectoparasites (2ppt marine reef salt). All aquaria had standardised refuges as outlined in chapter II. Water temperature was standardised to 26^{o} C. All tanks would receive irregular fixed volumes of defrosted copepods and biannual application of a general medical and health treatment (Tetra Medifin). During set up of aquaria, a cull of all moribund individuals was undertaken to maintain stock health in accordance with home office guidelines.

Experimental design

Each aquarium was divided by clear acrylic panels to form two separate environments: the left hand side for the juvenile population, the right hand side for the adult population. All individuals born into the right hand side were transferred to the juvenile environment. All maturing individuals in the left hand side were transferred to the adult environment. These transfers were conducted on a bi-weekly basis, either during monthly censuses or half-way between. Populations were maintained with equal food supply to both adults and juveniles for 10 months before treatments (outlined below) were applied to minimise founding effects.

Full censuses characterising all individuals in populations were conducted on a monthly basis. Populations were netted and sorted into: mature males, mature females, juveniles, new-born individuals (to measure reproduction) and maturing individuals from the juvenile environment. Sorted fish were then photographed in a white tray with a standardised scale for later image analysis. All populations were censused in the same week but not always on the same day. Usual aquarium maintenance (outlined in chapter II) was conducted to maintain water quality and stock health in the aquaria. In addition, regular cleaning of algal films on glass and removal of detritus build up was conducted to reduce guppies feeding on alternative sources to supplied food treatments.

Treatment was applied through differential supply of food to juveniles and adult environments. Control populations received equal food supply to both environments. The other two treatments were at a 1:2 or 1:4 food ratios with the larger amount of food biased towards the adult side. These ratios were chosen in line with those utilised in previous published literature (Reichstein, Persson and De Roos, 2015), as symmetry in

livebearing fish populations (*H.formosa*) was not fully achieved with 1:2 food bias. Based on personal communication with the authors of that study, 1:2 and 1:4 were suggested as appropriate for the model system we were using. All populations received the same total daily food level of 160mg per day of ZM-400 granular fry food 6/7 days a week (ZM-Systems).

Data analysis

Image analysis software (ImageJ) was used to determine individual body sizes (in mm) from population census photographs and photographs of individuals transferred between environments (i.e. maturations and reproductions). We used existing length*weight regression equations from published work on guppies (Nilsson and Persson, 2013) to calculate individual dry biomass for each individual in all populations. Using individual size and stage data we were able to measure changes in mean, min and max body size and observe changes in population size structure through time. Using calculated individual biomass data we were able to measure changes in total population biomass over time and biomass transferred between juvenile and adult populations (e.g. biomass production rates).

The significance of temporal trends in maturation, reproduction and population biomass were determined using linear mixed effects models (R package nlme), with repeated measures nested within replicate population tanks as a random effect (Cameron *et al.*, 2013). Maturation and reproduction were assessed both in terms of numbers of individuals moved from one environment to another and also the summed biomass

moved. Temporal changes in per capita reproductive output were also measured, estimated from bi-weekly reproduction data and demographic data (all females over known size at first parturition). All statistical analyses were conducted in R studio (R: A language and environment for Statistical Computing, R core team, 2016).

Results

Population biomass was found to significantly change over time (LME: Population biomass ~ time, $F_{2,169}$ =4.063, P<0.05, see figure 22). 1:4 treatments were shown to increase in biomass over time, which by the final month had on average 63.8% greater total biomass (g) over control 1:1 populations. 1:4 populations significantly differed (LME: Population biomass ~ Food treatment * time, $F_{2,69}$ =6.88, P < 0.05) from both 1:1 and 1:2 but 1:1 and 1:2 did not differ from one another in terms of overall biomass over time (see figure 22).

Maturation rate was not found to be significantly affected by food treatment, either in terms of numbers of individuals maturing (LME: # of Individuals maturing ~ Food treatment * time, $F_{2,160}$=1.39, P > 0.05, figure 24), or the biomass transferred (LME: Biomass transferred ~ Food treatment * time, $F_{2,127}$ 2.29, P > 0.05, figure 23).

Reproductive rate was influenced by food treatment both in terms of numbers of individuals being born (and therefore moved to the juvenile environment) and also the biomass of new born individuals. The number of new individuals born was significantly affected by food treatment, with 1:4 showing on average 65.45% more juveniles produced over time than 1:1 controls (LME: # of Individuals born ~ Food treatment * time, $F_{2,154}$= 8.43, P < 0.05, figure 24). 1:2 food treatments did not significantly differ from 1:1 controls (P>0.05).

The biomass of new born individuals as a proportion of total tank biomass was not significantly affected by the food treatments applied over the course of the experiment (LME: Biomass transferred as a proportion of total biomass ~ Food treatment * time,

$F_{2,129}$=0.61, P > 0.05, figure 23). However, 1:4 treatments on average had 13.15% greater reproduction in biomass than controls over the course of the experiment.

The per capita reproductive output, i.e. per female reproductive output, was not found to be significantly affected by the food treatment or over time This is observed in figure x, where reproductive output is highly variable over the course of the experiment, but does show an increase in all treatments in the final assay.

Table 24: ANOVA output table of a linear mixed effects model showing the effect of food treatment on population biomass over time.

	numDF	denDF	F-value	p-value
(Intercept)	1	69.00	195.34	0.00
treatment	2	9.00	1.66	0.24
census	1	69.00	4.06	0.05
treatment:census	2	69.00	6.88	0.00

Table 25: ANOVA output table of a linear mixed effects model showing the effect of food treatment on the biomass of maturing individuals

	numDF	denDF	F-value	p-value
(Intercept)	1	127.00	47.32	0.00
treatment	2	127.00	0.70	0.50
census	1	127.00	1.20	0.28
treatment:census	2	127.00	2.29	0.11

Table 26: ANOVA output table of a linear mixed effects model showing the effect of food treatment on the amount of reproductive biomass produced

	numDF	denDF	F-value	p-value
(Intercept)	1	129.00	39.01	0.00
treatment	2	9.00	3.64	0.07
census	1	129.00	6.52	0.01
treatment:census	2	129.00	2.96	0.06

Table 27: ANOVA output table of a linear mixed effects model showing the effect of food treatment on the number of maturing individuals

	numDF	denDF	F-value	p-value
(Intercept)	1	160.00	58.42	0.00
treatment	2	160.00	1.77	0.17
census	1	160.00	0.10	0.76
treatment:census	2	160.00	1.39	0.25

Table 28: ANOVA output table of a linear mixed effects model showing the effect of food treatment on the number of newborn individuals

	numDF	denDF	F-value	p-value
(Intercept)	1	154.00	22.20	0.00
treatment	2	154.00	2.98	0.05
census	1	154.00	8.99	0.00
treatment:census	2	154.00	8.43	0.00

Table 29: ANOVA output table of a linear mixed effects model showing the effect of food treatment on the amount of reproductive biomass produced as a proportion of total population biomass

	numDF	denDF	F-value	p-value
(Intercept)	1	129.00	43.15	0.00
treatment	2	9.00	1.33	0.31
census	1	129.00	5.70	0.02
treatment:census	2	129.00	0.61	0.55

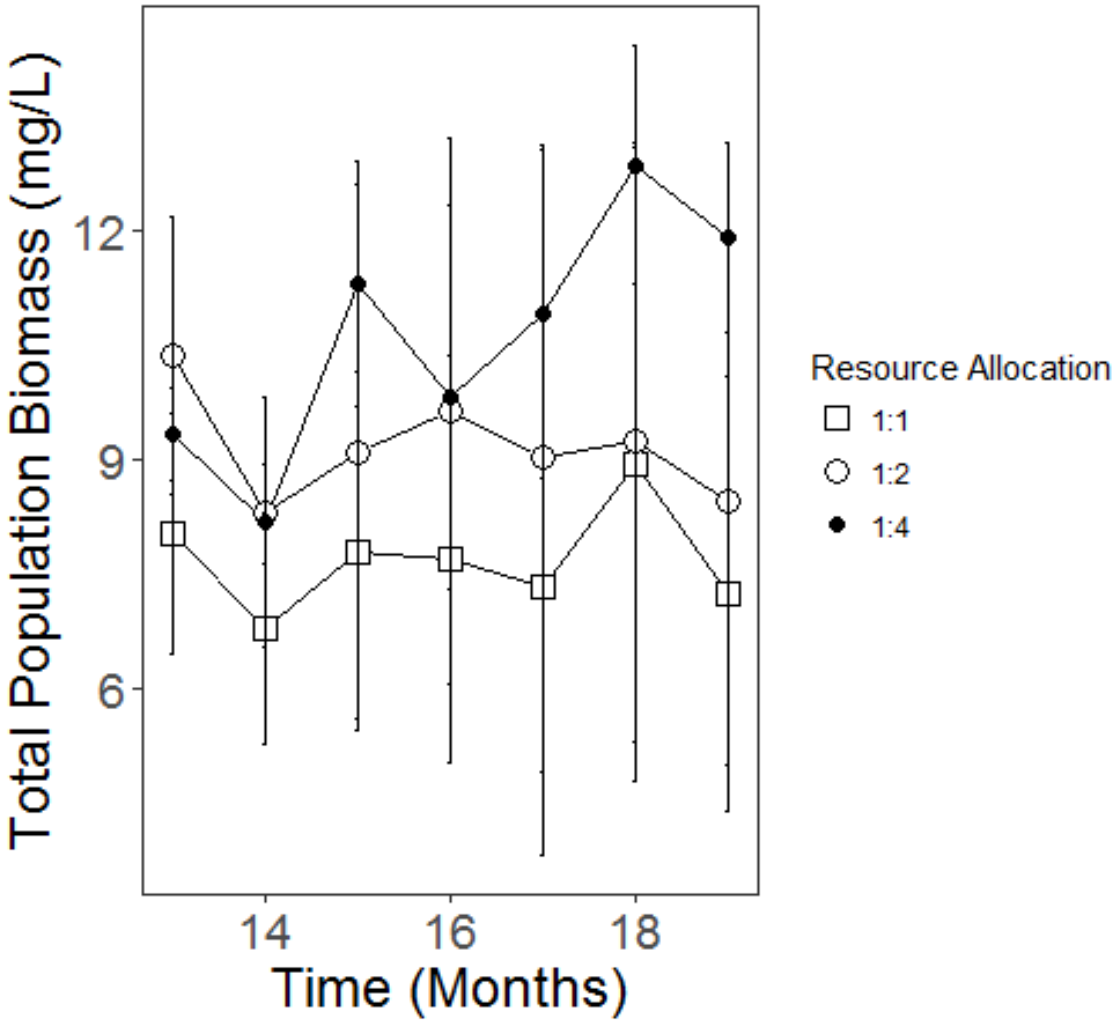


Figure 22: Mean (+/- 2* standard error) total population biomass in response to differing levels of food bias towards adults

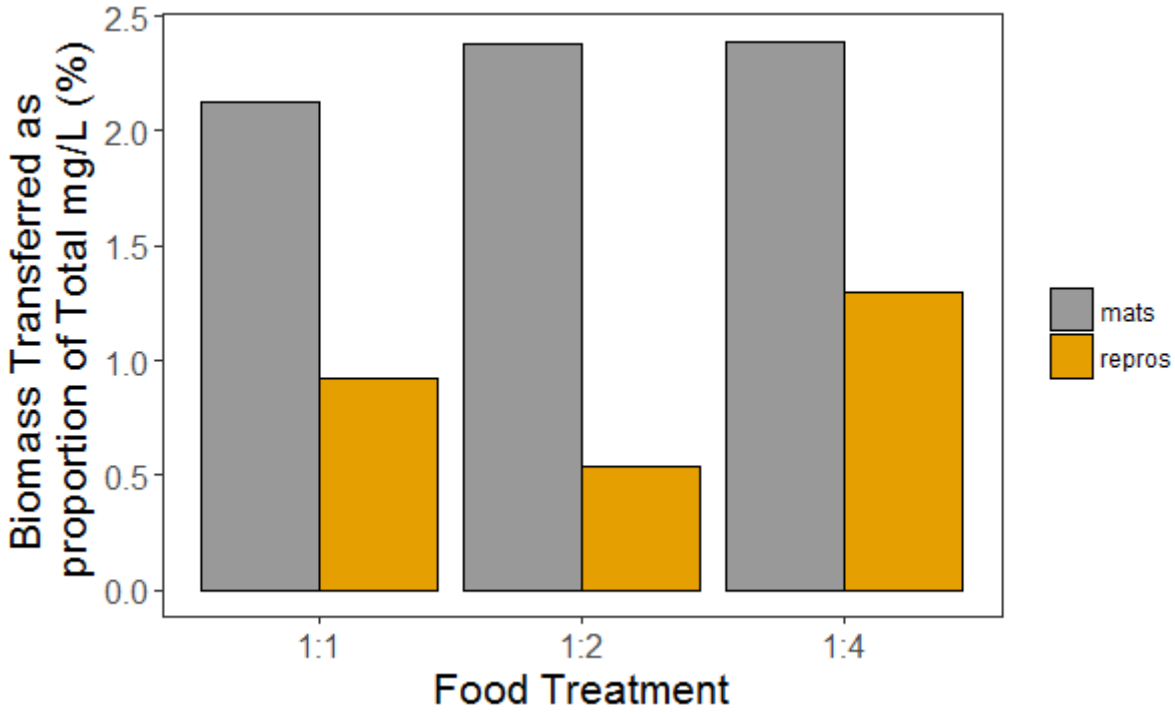


Figure 25: Biomass transferred as a proportion of total biomass, in maturation (grey) or reproduction (orange) in response to food bias

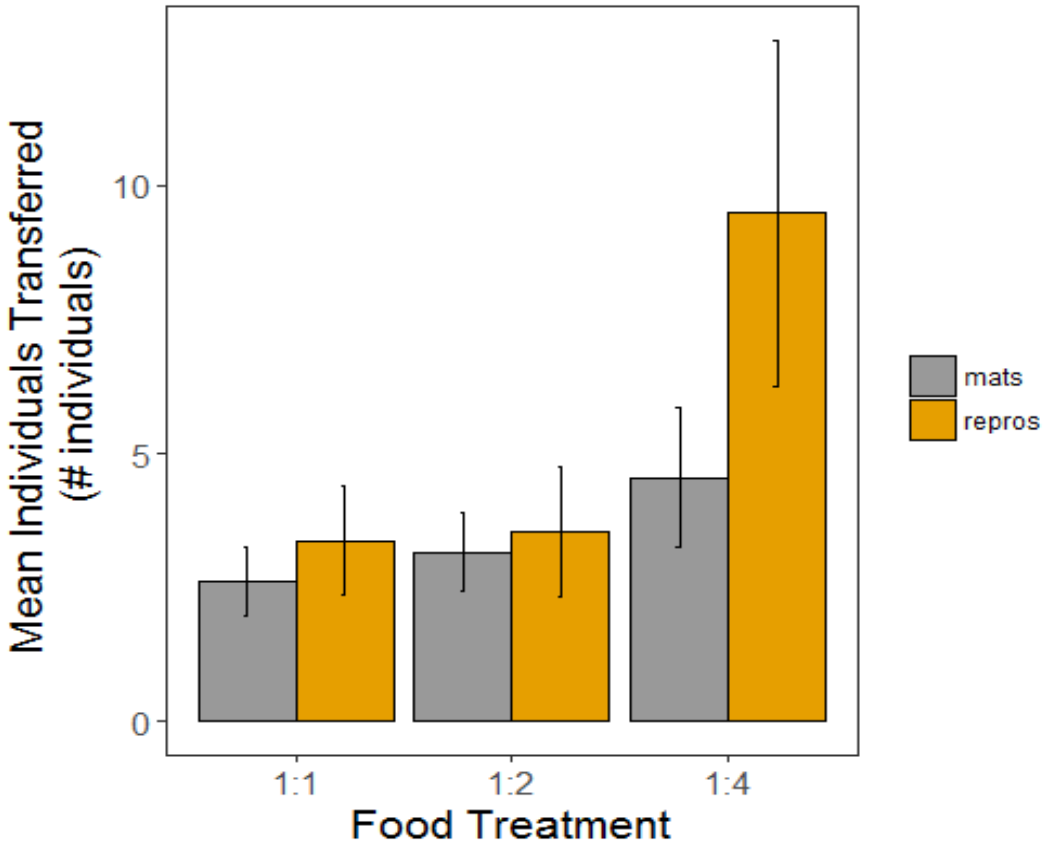


Figure 26: Mean (+/- 2* standard error) number of individuals transferred as maturation (grey) or reproduction (orange) in response to food bias

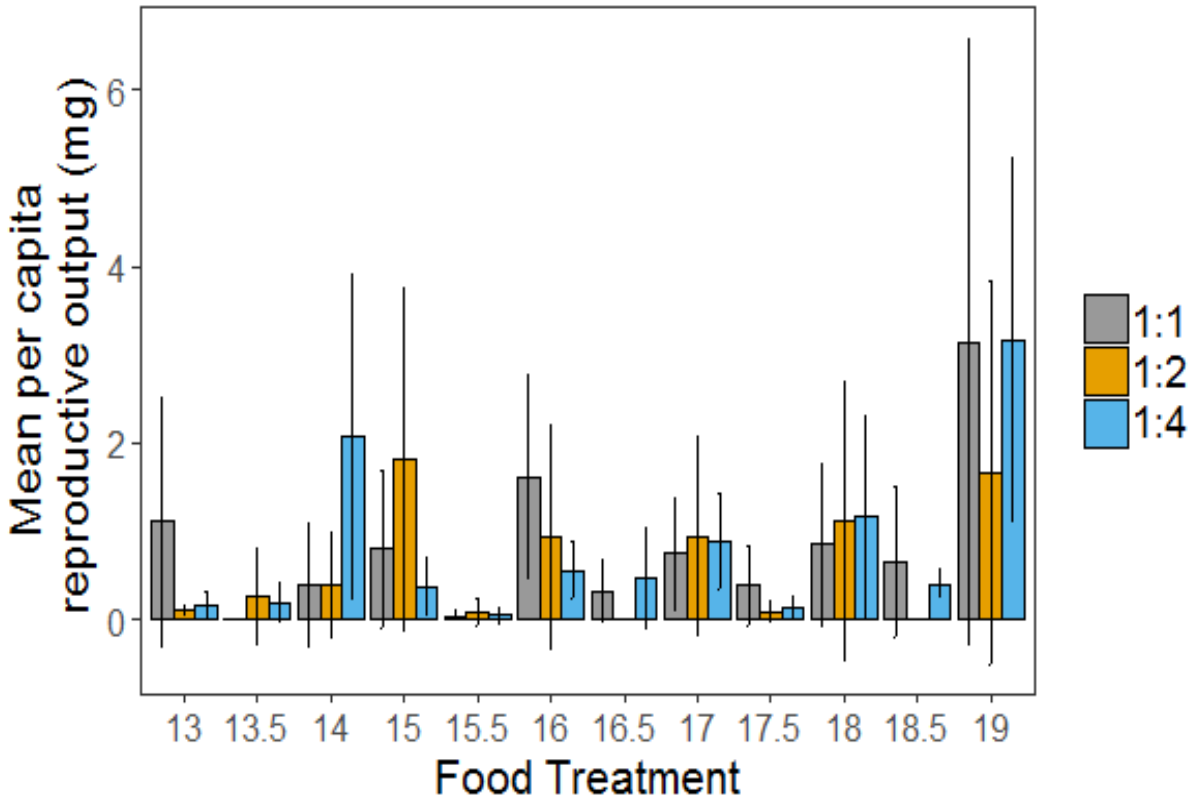


Figure 26: Mean (+/- 2 * standard error) per capita reproductive output over time in response to food bias

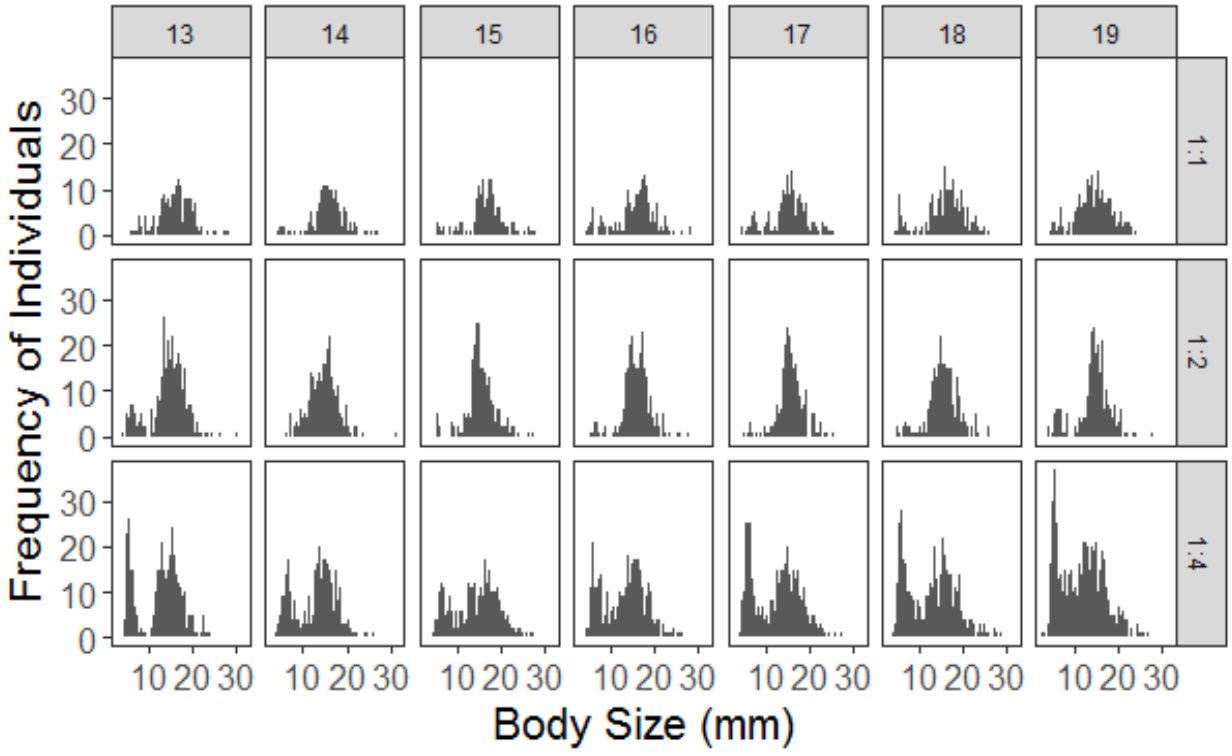


Figure 27: Summed population size structure over time in response to food bias

Discussion

Changes in energy efficiency and habitat use occur in all organisms as they grow and mature (Miller and Rudolf, 2011). As such, understanding how these changes scale up to population level dynamics is important for understanding how populations cycle and should be managed (Reichstein, Persson and De Roos, 2015). We demonstrate how the inequality between adults and juveniles in energy efficiency impacts the transfer of biomass through populations. Furthermore through biasing food supply to the competitively weaker ontogenetic stage, we are able to release populations from its reproductive bottleneck and results in overall biomass increases.

Investigations of ontogenetic asymmetry in energy efficiency are often conducted in the short term and make little reference to the potential role of adaptation in counteracting population bottlenecks. Here I show indications of adaptation to asymmetric conditions in our model species, *P.reticulata*, through changes in per capita reproductive output. Although there are no significant differences between food treatments, we see reproductive output increase in all populations over time (see figure 25). The implication here is that populations that are “more asymmetric”, such as those with equal food supply to juveniles and adults, are overcoming the reproductive bottleneck they are initially under. To lend further credence to this suggestion, the populations shown here were all kept under control 1:1 conditions for 6 months prior to the experiment’s start. This therefore means the scope of this entire experiment covers 6-7 generations, which as previous work with this species shows, is ample time for adaptation in life history traits (Reznick *et al.*, 1997). As such, further work on the life history responses to asymmetric conditions is warranted and planned for future manuscripts.

As our and previous other work shows, guppies are found to be subject to reproduction control when adults and juveniles have equal access to the same resources (Persson and De Roos, 2013; Schröder, Leeuwen and Cameron, 2014). Adults are competitively weaker than juveniles and therefore investment in reproduction is reduced (Schröder, Persson and De Roos, 2009). Whilst maturation is not shown to be effected; either in terms of biomass or numbers of individuals' maturing; reproduction is found to respond to biased food supply to competitively weaker adults. We find that although biomass of reproductive output does increase in response to 1:4 food biases, this does quite appear to be statistically significant. Conversely, numbers of new-born individuals does significantly increase in response to 1:4 food biases. As previous work with other live bearing fish species shows, bias of 1:2 despite resulting in increases in overall biomass, does not break a pattern of asymmetry between ontogenetic stages. These results show that to achieve symmetry in maturation and reproductive rates would require further biasing of food levels towards the competitively weaker stage. This therefore also warrants further testing of the role of resources in modulating bottlenecks in reproduction.

. We identify that this model species exists under reproduction control according to original theory outlined with regards to ontogenetic asymmetry. This asymmetry in alternative circumstances (i.e. wild populations), may well be regulated by exterior interactions, such as predators, competitors, alternative resource usage or a combination of the above (de Roos, Persson and Thieme, 2003; Persson *et al.*, 2007). By virtue of our experimental design, we also remove another mechanism that could regulate asymmetry in wild populations. Cannibalism has long been recognised as a regulating factor in population dynamics (Claessen, De Roos and Persson, 2004; Wise, 2006; Nilsson *et al.*, 2011) and is observed in our model species. However, through

regular transfer of new born individuals into a protected juvenile environment and high levels of refuge we drastically reduce the potential for this to occur, potentially impacting the fitness of adults.

In conflict with this prediction of ontogenetic asymmetry, the length of our study in terms of generation time means that there is potential for adaptation in life history traits and therefore eco-evolutionary dynamics. Our results for per capita reproductive output (a proxy for changing reproductive investment), show change over the course of several generations but are quite variable over this period. This suggests that although there is potential for adaptive responses in life history, simple assessments of population demography are not enough to detect them. As such, any trait changes that act to counteract the negative effects on fitness that reproduction control has on these populations would have to be detected through a multi-generational common garden as outlined in chapters II and IV.

This work therefore gives us early indication of how eco-evolutionary dynamics interact with “eco-developmental” dynamics to regulate biomass transfer through populations. This allows us to better understand and predict how populations will behave in “wild” settings when exterior controls are removed (Persson *et al.*, 2007). Early work on asymmetry has demonstrated negative societal impacts as a result of ontogenetic asymmetry. The removal of regulating organisms, such as predators has resulted in stunted populations that are of less value to people that relying upon them (Persson *et al.*, 2007). By integrating eco-evolutionary findings this allows us to predict how long a population in the absence of regulating factors might take to recover / adapt to asymmetry and therefore informs our management of said populations.

Chapter VI - Thesis discussion

This thesis aimed to investigate how variation in individual level life history traits affects population dynamics which in turn can feedback on those same traits. Research interest in eco-evolutionary dynamics has increased greatly over the past 20 years or more (see figure 27). Understanding the feedback loop between adaptation, population dynamics and structure not only is important for the preservation of populations but also has consequences for communities and ecosystem functioning (Bassar *et al.*, 2012; El-Sabaawi *et al.*, 2015). Specifically I aimed to see how realistic environmental pressures of harvesting or changing resource availability influence population density and structure that would influence selection on life history traits and lead to eco-evolutionary dynamics.

Managing populations in the face of future environmental pressures is of societal and economic importance. Increasingly it is accepted, that effective population management should incorporate the possibility that individuals within populations will adapt to the pressures that they face, thus effecting size structure, productivity, extinction risks (Davies and Baum, 2012; Kuparinen and Hutchings, 2012), on ecological timescales.

Here, I utilised laboratory model systems to test some emerging and specific hypotheses at the interface of ecology and evolution. Firstly, does plasticity evolve independently of mean trait evolution and does it affect population response to environmental change? Secondly, does novel selective mortality affect size structure, productivity and phenotypic variation any differently from traditional selective mortality of fishing? Finally, do emerging theories on controls of population and community

dynamics, by differences in energy efficiency throughout ontogeny, a.k.a ontogenetic asymmetry, persist in an eco-evolutionary framework?

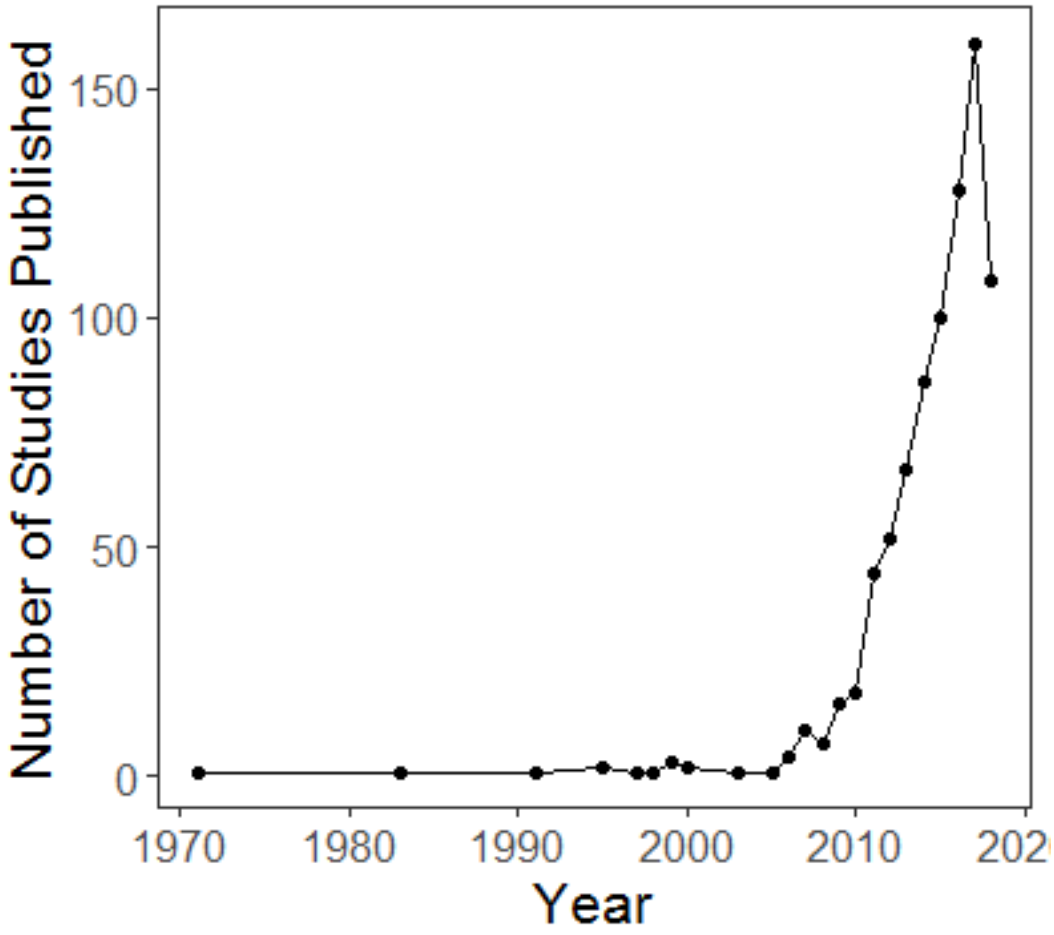


Figure 27: Yearly studies using “eco-evolutionary dynamics” as a key word– data used from Web of Science

Summary of findings

Does plasticity evolve despite directional selection as it minimises demographic stochasticity?

Phenotypic plasticity (PP) is a mechanism of adaptation that can occur within or across generations, facilitating a rapid response to an altered environment (Chevin and Lande, 2011). Plastic responses in life history traits are shown to drive changes in size structure and dynamics over short times scales (Reed, Schindler and Waples, 2011). As such, understanding the conditions that promote the evolution of PP is important for predicting population persistence (Ashander, Chevin and Baskett, 2016). Here, I evidenced that PP in individual's growth rate can evolve in populations in response to environmental change.

Importantly, and for the first time as an experimental test in a complex organism, I have shown that high levels of plasticity had consequences for population dynamics in subsequent environmental change. Environmental variation led to evolution of plastic phenotypes, which in turn was related to reduced population level variation when experiencing future environmental shifts. Populations that had originated from periodically variable environments, with greatest plasticity in growth rate, were found on average to have the lowest variation in population size over time when introduced to novel environments. This result of long term impacts for whole population dynamics in novel environments evidences a full eco-evolutionary feedback loop mediated by PP.

This chapter links the role of environmental variation to levels of competition between individuals within a population. For example in microcosms with clumped food patches, I

suggest that body size will be under directional selection, but the ability to be plastic about when you mature would be advantageous if food availability and hence competitive pressure is variable (Benton, 2012). I present the case that it is strong intraspecific competition for food which either promotes or limits the evolution of plasticity within populations. PP therefore represents a very conceivable response within populations to environmental pressures, which could have knock on implications for size structure and persistence.

Can the benefits of harvest slots be captured more widely in fisheries?

Size selective fishing, even when clearly ecologically sustainable, truncates population size structure and reduces productivity of fish populations (Kuparinen and Hutchings, 2012). The strong selective pressure of fishing, and other forms of harvesting, is widely considered to drive evolved changes in life histories within harvested populations (Heino, Díaz Pauli and Dieckmann, 2015). Across a range of studies in harvested vertebrates changes in body size, growth rate and reproductive output of individuals has been attributed to harvesting induced selection (Cameron *et al.*, 2013; Van Wijk *et al.*, 2013; Lindstro *et al.*, 2016; Pauli *et al.*, 2017), with potential long term negative consequences for yield and population persistence.

However, direct empirical evidence for phenotypic change in fishes in response to realistic fishing mortality is lacking due to the complex drivers of life history traits (e.g. Maternal x Genetic x Environmental effects) (Plaistow *et al.*, 2004, 2007). There are growing calls for harvest regulation that balances both conservation and food security objectives. Harvest slot management has been proposed to do this as it protects large individuals with high spawning potential (Arlinghaus, Matsumura and Dieckmann, 2010), and preserves a more natural size structure, which provides a more consistent level of yield (Gwinn *et al.*, 2015).

In this chapter, I investigate both the short term ecological responses and long term phenotypic responses of fish populations to realistic levels of fishing mortality. Specifically, this chapter compares these responses between two forms of harvest regulation: traditionally selective fishing versus a novel harvest regulation called Harvest Slots. HS targets an intermediate size range of individuals for harvest, whilst protecting the largest and smallest fish either side of the “slot window”.

Fishing of all kinds drove reductions in biomass and yield over a period of sustained fishing pressure. However, harvest slots did not differ from unharvested controls in terms of overall or spawning stock biomass. In addition, after a period of recovery, traditionally fished populations still showed truncated size structure, which in part was driven by stark phenotypic differences in life history from control and HS populations. However, given that harvest slots was unable to compete with traditional harvest regulation in terms of yield, it is clear that there is further research warranted on the execution of harvest slots in real world fisheries.

This chapter therefore evidences not only the role of harvesting in altering eco-evolutionary dynamics, but also presents a novel solution to combat the negative repercussions of traditionally regulated fisheries.

Does environmental productivity mitigate bottlenecks in biomass production rising from differences in energy efficiency throughout ontogeny?

Besides mortality, a certainty for most organisms is that they will grow / develop as they age. Therefore, it is intuitive to suggest that the efficiency at which individuals utilise resources might change as they grow (Auer *et al.*, 2010). This chapter aimed to explore how individual variation throughout ontogeny in energy efficiency, can scale up to alter the transfer of biomass within a population and subsequently a populations structure (Schröder, Leeuwen and Cameron, 2014). Using split aquaria to create distinct environments for both juveniles and adults, I identified that juveniles were better competitors than adults, which resulted in bottlenecks in biomass transfer within populations. This inequality in energy efficiency between life history stages is referred to as ontogenetic asymmetry, and is observed across taxa (Persson and De Roos, 2013).

In this chapter, I aimed to explore some knowledge gaps associated with ontogenetic asymmetry. Firstly, I aimed to see if populations showing ontogenetic asymmetry can be pushed towards equal rates of biomass transfer between life history stages. In addition, I wanted to explore if populations kept in conditions that promoted Ontogenetic asymmetry, would adapt in any way to reduce the fitness costs of the environment they were in.

I showed how differing levels of biased resources towards adult populations could push populations towards symmetrical levels of maturation and reproduction within a population. This in turn resulted in increases in overall biomass without any changes in overall resource input.

As discussed in Chapter II, assays of life history in fish populations presented many challenges and development of methods. Although a working protocol for measuring life

history had been developed by the end of the data collection period, time limitations meant that the assessment of life history for this chapter was postponed to after the thesis submission date. Details are outlined below as future work for the purposes of turning the findings of this chapter into a publication.

However, utilising data from overall population censuses allowed for measurements of per capita reproductive output over time. Increases observed in all treatments in this metric give indication of adaptation to reduced fitness arising from ontogenetic asymmetry.

Broad findings of this thesis

Individuals within populations are subject to external changes in their environment. These environmental pressures drive changes in population density and therefore competition among individuals for resources (Cameron *et al.*, 2007). Individual fitness and the variation of traits expressed are therefore dependent on prevailing environmental conditions.

In the event of a change in environmental pressure; be it a new predator, hunting, changes in food availability; selection will act on variation in traits expressed, selecting for appropriate life history strategies (Reznick, Bryant and Bashey, 2002; Arendt and Reznick, 2005; Walsh and Reznick, 2009). Shifts in life history traits drive changes in size structure, density and therefore effect how productive populations can be (Bassar *et al.*, 2013).

With wild populations under a myriad of environmental pressures, management of them requires reasonable knowledge of how populations might look in the future. Understanding the adaptive responses of individuals within populations is key to their conservation and in the case of fisheries, their continued exploitation.

This thesis provides evidence of the feedback loop between individual adaptation and population cycling. Under a range of realistic scenarios, I demonstrate how responses of individual life histories to direct or indirect to selective pressure, drives changes in size structure and density which in turn can impact on individual fitness. Competition impacted fitness of individuals in all experiments, resulting in adaptive responses both of mean trait values but also the flexibility in expressing those trait values. In addition,

direct selective pressure on body size was shown to select for specific life history strategies, although this was not fully in line with theoretical expectations. In particular, selective pressure of harvesting was shown to select for individuals that matured smaller and LATER, as opposed to expectations of smaller faster maturing young. I rationalise this as an adaptive response of individuals to have optimal condition for reproduction by the time that they reach maturation size, therefore maximising offspring quality and individual fitness.

Realistic fishing pressure in replicate populations resulted in expected shifts in size structure, productivity and life history strategies, but in resolution that would be unfeasible to obtain in wild fisheries. Additionally, a novel method of harvest regulation preserved a more “natural” size structure and life history strategies. An effort to maintain realism through high harvest mortality drove reductions in yield in all fished populations. However, the legacy of size structure and life histories after recovery, dictates that HS regulations may have longer term benefits for population productivity and preservation.

Population regulation rising from differences in energy efficiency throughout ontogeny has been claimed to be ubiquitous in recent literature (Persson and De Roos, 2013). However, many studies that prove this to be the case are in simple systems, and often take place over “relatively” short time scales. Where ontogenetic asymmetry is observed in the wild, it is often due to the removal of controls on populations, which then drive reductions in fitness due to asymmetric conditions. Intuition would dictate that organisms then evolve in the presence of controls to maximise fitness, and therefore they could adapt out of asymmetric conditions in the same way. I evidence that indeed, asymmetry may regulate size structure and dynamics in the short term, but also evidence emerging responses of individual reproductive investment that evidences adaptation to asymmetric conditions. I therefore cautiously suggest that asymmetry

might well be widespread in its prevalence but it's effects on size structure may be mitigated by responses in life history. This said, the work conducted here does not definitively prove this suggestion, and that planned examination of phenotypic values in a common garden environment would have provided more clarity on the interplay between eco-evolutionary and eco-developmental regulation of population cycling.

Future work

The work conducted here is both illuminating in terms of the findings of each chapter, but also for avenues for further research to explore. Whilst the data in chapter III was already completely collected prior to the start of this thesis, both laboratory experiments yield great scope for further reinforcement of findings.

As previously touched on, the experimental results shown here for chapter V only scratch the surface of what could be discovered from this system. In particular, the early evidence of adaptation due to uniform increases in reproductive output across treatments lends even more credence to the need for accurate measurement of life histories in these populations. As it stands, data collection and treatments have been ongoing in this experiment, and as such the possibility to bolster future publication from this experiment with new data is present. After submission of this thesis, further work to investigate life history adaptation to the differing treatments is planned.

Chapter IV is unique, not only in terms of its novelty but also in terms of its real world application to fisheries management. However, implementation of new fisheries regulation demands robust testing of those regulations. Populations under the different harvest treatments have been maintained in the lab – allowing for further testing of life histories a long time after the commencement of harvest, confirming the long term lasting consequences of fisheries induced selection. Declining yield over time is not the result of successful fisheries regulation. As such, further work to investigate how to select the optimal sized “slot” for the take limit, and the appropriate mortality rate should and undoubtedly will be covered in future research of HS. The scope for this work to be conducted exists both in the existing Guppy model system (which this thesis has further

justified its usage), and for future field testing on commercially relevant species. Implementation in the field undoubtedly presents a range of challenges, due to the technical difficulty of selectivity that HS requires. The theoretical paper that this chapter is largely based off initially focusses on the potential of usage in recreational fisheries (Gwinn *et al.*, 2015). Given our results and recent work highlighting the importance of preserving large individuals in commercial stocks (Barneche *et al.*, 2018), the role of HS for preserving commercially important fish stocks should be considered. The identification of fisheries that currently are, or have the potential to be, highly selective of individuals taken would therefore be a necessity if HS was to be trialled as an alternative to a minimum size limit fishing. In addition, given that HS is designed to promote higher biomass, there is potential for implementation in facilitating the recovery of over-exploited fish populations, whilst still providing societal objectives of yield.

Chapter VII – Conclusion

Most populations in the world are subject to anthropogenic induced environmental stressors. This can be direct, for example in the form of harvesting, or indirect, such as climate change. Given that we rely on populations for societal, cultural, health or economic benefits, their appropriate management for the future is of paramount importance. Knowing that these stressors will affect population density, competition for resources and therefore individual fitness means that effective population management must take all of the above into account. This thesis investigates the feedback between individual adaptation and size structure/density - termed a full eco-evolutionary loop. Although all data chapters do not fully identify a full feedback loop (shown in chapter III), observations within experimental fish populations indicate similar processes occurring. Demand from fisheries for food is only going to increase with human population, and therefore the need to understand and mitigate the impact on fisheries dynamics has never been higher. This thesis identifies realistic stress on fish populations, their responses and where possible, identifies ways to mitigate that stress.

References

Allen, R. *et al.* (2008) 'Offspring Size Plasticity in Response to Intraspecific Competition : An Adaptive Maternal Effect across Life - History Stages', *The American naturalist*, 171(March), pp. 225–237. doi: 10.1086/524952.

Allendorf, F. W. and Hard, J. J. (2009) 'Human-induced evolution caused by unnatural selection through harvest of wild animals', *Proceedings of the National Academy of Sciences*, 106, pp. 9987–9994. doi: 10.1073/pnas.0901069106.

Amundsen, P.-A., Knudsen, R. and Klemetsen, A. (2007) 'Intraspecific competition and density dependence of food consumption and growth in Arctic charr', *Journal of Animal Ecology*, 76(1), pp. 149–158. doi: 10.1111/j.1365-2656.2006.01179.x.

Andersen, K. H. and Brander, K. (2009) 'Expected rate of fisheries-induced evolution is slow', *Proceedings of the National Academy of Sciences of the United States of America*, 106(28), pp. 11657–11660. doi: 10.1073/pnas.0901690106.

Andersen, K. H., Marty, L. and Arlinghaus, R. (2017) 'Evolution of boldness and life history in response to selective harvesting', *Canadian Journal of Fisheries and Aquatic Sciences*, 11(April), pp. 1–11. doi: 10.1139/cjfas-2016-0350.

Anticamara, J. A. *et al.* (2011) 'Global fishing effort (1950-2010): Trends, gaps, and implications', *Fisheries Research*. Elsevier B.V., 107(1–3), pp. 131–136. doi: 10.1016/j.fishres.2010.10.016.

Aratayev, V. A. K. and Raft, C. E. K. (2015) 'Racing through life : maturation rate plasticity regulates overcompensation and increases persistence', *Ecosphere*, 6(October), pp. 1–12.

Arendt, J. D. and Reznick, D. N. (2005) 'Evolution of juvenile growth rates in female guppies (Poecilia reticulata): predator regime or resource level?', *Proceedings. Biological sciences / The Royal Society*, 272(August 2004), pp. 333–337. doi: 10.1098/rspb.2004.2899.

Arlinghaus, R., Matsumura, S. and Dieckmann, U. (2010) 'The conservation and fishery benefits of protecting large pike (Esox lucius L.) by harvest regulations in recreational fishing', *Biological Conservation*. Elsevier Ltd, 143(6), pp. 1444–1459. doi: 10.1016/j.biocon.2010.03.020.

Ashander, J., Chevin, L. M. and Baskett, M. L. (2016) 'Predicting evolutionary rescue via evolving plasticity in stochastic environments', *Proceedings of the Royal Society B: Biological Sciences*, 283(1839). doi: 10.1098/rspb.2016.1690.

Audzijonyte, A. *et al.* (2013) 'Ecological consequences of body size decline in harvested fish species : positive feedback loops in trophic interactions amplify human impact', *Biology letters*, 9(20121103), pp. 1–5. doi: 10.1098/rsbl.2012.1103.

Audzijonyte, A., Kuparinen, A. and Fulton, E. A. (2013) 'How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies', *Evolutionary Applications*, 6(4), pp. 585–595. doi: 10.1111/eva.12044.

Audzijonyte, A. and Richards, S. A. (2018) 'The Energetic Cost of Reproduction and Its Effect on Optimal Life-History Strategies', *The American Naturalist*, 192(4), pp. E000–E000. doi: 10.1086/698655.

Auer, S. K. *et al.* (2010) 'Juvenile compensatory growth has negative consequences for reproduction in Trinidadian guppies (Poecilia reticulata)', *Ecology Letters*, 13(8), pp. 998–1007. doi: 10.1111/j.1461-0248.2010.01491.x.

Barlow, J. (1992) 'Nonlinear and Logistic Growth In Experimental Populations of Guppies', *Ecology*, 73(3), pp. 941–950. doi: 10.2307/1940170.

Barneche, D. R. *et al.* (2018) 'Fish reproductive-energy output increases disproportionately with body size', *Science*, 360(May), pp. 642–645.

Bashey, F. (2006) 'Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy Poecilia reticulata.', *Evolution; international journal of organic evolution*, 60(2), pp. 348–361. doi: 10.1111/j.0014-3820.2006.tb01111.x.

Bashey, F. (2008) 'Competition as a selective mechanism for larger offspring size in guppies', *Oikos*, 117(1), pp. 104–113. doi: 10.1111/j.2007.0030-1299.16094.x.

Bassar, R. D. *et al.* (2012) 'Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian guppy (Poecilia reticulata).', *The American naturalist*, 180(2), pp. 167–85. doi: 10.1086/666611.

Bassar, R. D. *et al.* (2013) 'Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories.', *The American naturalist*, 181(1), pp. 25–38. doi: 10.1086/668590.

Bassar, R. D. *et al.* (2016) 'The effects of asymmetric competition on the life history of Trinidadian guppies', *Ecology Letters*, (March). doi: 10.1111/ele.12563.

Bateson, W. and Saunders, E. R. (1902) 'The Facts of Heredity in the Light of Mendel's Discovery', *Evolution Committee of the Royal Society*, 1(1), pp. 125–160.

Beardmore, B. *et al.* (2015) 'Effectively managing angler satisfaction in recreational fisheries requires understanding the fish species and the anglers', *Canadian Journal of Fisheries and Aquatic Sciences*, 72(4), pp. 500–513. doi: 10.1139/cjfas-2014-0177.

Beckerman, A. P. *et al.* (2003) 'Talkin' 'bout My Generation: Environmental Variability and Cohort Effects', *The American Naturalist*, 162(6), pp. 754–767. doi: 10.1086/381056.

Beckerman, A. P., Rodgers, G. M. and Dennis, S. R. (2010) 'The reaction norm of size and age at maturity under multiple predator risk.', *The Journal of animal ecology*, 79(5), pp. 1069–1076. doi: 10.1111/j.1365-2656.2010.01703.x.

Benoît, H. P. and Swain, D. P. (2008) 'Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community', *Canadian Journal of Fisheries and Aquatic Sciences*, 65(10), pp. 2088–2104. doi: 10.1139/F08-112.

Benton, T. G. *et al.* (2007) 'Microcosm experiments can inform global ecological

problems', *Trends in Ecology and Evolution*, 22(10), pp. 516–521. doi: 10.1016/j.tree.2007.08.003.

Benton, T. G. (2012) 'Individual variation and population dynamics: lessons from a simple system', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1586), pp. 200–210. doi: 10.1098/rstb.2011.0168.

Benton, T. G., Lapsley, C. T. and Beckerman, A. P. (2001) 'Population synchrony and environmental variation: An experimental demonstration', *Ecology Letters*, 4(3), pp. 236–243. doi: 10.1046/j.1461-0248.2001.00225.x.

Bhat, A., Greulich, M. M. and Martins, E. P. (2015) 'Behavioral plasticity in response to environmental manipulation among zebrafish (Danio rerio) populations', *PLoS ONE*, 10(4), pp. 1–13. doi: 10.1371/journal.pone.0125097.

Boersma, M., Spaak, P. and De Meester, L. (1998) 'Predator-mediated plasticity in morphology, life history, and behavior of Daphnia: the uncoupling of responses.', *The American naturalist*, 152(2), pp. 237–248. doi: 10.1086/286164.

Bonamour, S. *et al.* (2019) 'Phenotypic plasticity in response to climate change: The importance of cue variation', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374(1768). doi: 10.1098/rstb.2018.0178.

ten Brink, H. *et al.* (2015) 'Do intraspecific or interspecific interactions determine responses to predators feeding on a shared size-structured prey community?', *Journal of Animal Ecology*, 84, pp. 414–426. doi: 10.1111/1365-2656.12305.

ten Brink, H. and de Roos, A. M. (2017) 'A Parent-Offspring Trade-Off Limits the Evolution of an Ontogenetic Niche Shift', *The American Naturalist*, 190(1), pp. 45–60. doi: 10.1086/692066.

Brown, C. J. *et al.* (2018) 'Trade-offs in triple-bottom-line outcomes when recovering fisheries', *Fish and Fisheries*, 19(1), pp. 107–116. doi: 10.1111/faf.12240.

Bystrom, P., Persson, L. and Wahlstrom, E. (1998) 'Competing Predators and Prey : Juvenile Bottlenecks in Whole-Lake Experiments', *Ecology*, 9658(May 2014). doi: 10.1890/0012-9658(1998)079.

Cadotte, M. W., Drake, J. A. and Fukami, T. (2005) 'Constructing Nature: Laboratory Models as Necessary Tools for Investigating Complex Ecological Communities', *Advances in Ecological Research*, 37(04), pp. 333–353. doi: 10.1016/S0065-2504(04)37011-X.

Cameron, F. T. C. *et al.* (2014) 'Eco-Evolutionary Dynamics : Experiments in a Model System', *Advances in Ecological Research*, 50, pp. 171–206.

Cameron, T. C. *et al.* (2007) 'Two-species asymmetric competition : Effects of age structure on intra- and interspecific interactions', *Journal of Animal Ecology*, 76(June), pp. 83–93. doi: 10.1111/j.1365-2656.2006.01185.x.

Cameron, T. C. *et al.* (2013) 'Eco-evolutionary dynamics in response to selection on life-history', *Ecology Letters*, 16, pp. 754–763. doi: 10.1111/ele.12107.

Cameron, T. C. *et al.* (2016) 'Harvested populations are more variable only in more

variable environments', *Ecology and Evolution*, pp. 1–14. doi: 10.1002/ece3.2164.

Cameron, T. C. and Benton, T. G. (2004) 'Stage-structured harvesting and its effects: An empirical investigation using soil mites', *Journal of Animal Ecology*, 73, pp. 996–1006. doi: 10.1111/j.0021-8790.2004.00886.x.

Campbell, E. W. *et al.* (2012) 'Do predators control prey species abundance? An experimental test with brown treesnakes on Guam', *Ecology*, 93(5), pp. 1194–1203. doi: 10.1890/11-1359.1.

Carpenter, S. R. (1996) 'Microcosm experiments have limited relevance for community and ecosystem ecology', *Ecology*, 77(3), pp. 677–680. doi: 10.2307/2265490.

Carroll, S. P. *et al.* (2007) 'Evolution on ecological time-scales', *Functional Ecology*, 21, pp. 387–393. doi: 10.1111/j.1365-2435.2007.01289.x.

Chevin, L.-M., Lande, R. and Mace, G. M. (2010) 'Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory', *PLoS Biology*, 8(4), p. e1000357. doi: 10.1371/journal.pbio.1000357.

Chevin, L. M. *et al.* (2013) 'Phenotypic plasticity in evolutionary rescue experiments', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1610). doi: 10.1098/rstb.2012.0089.

Chevin, L. M. and Lande, R. (2011) 'Adaptation to marginal habitats by evolution of increased phenotypic plasticity', *Journal of Evolutionary Biology*, 24(7), pp. 1462–1476. doi: 10.1111/j.1420-9101.2011.02279.x.

Chevin, L. M. and Lande, R. (2015) 'Evolution of environmental cues for phenotypic plasticity', *Evolution*, 69(10), pp. 2767–2775. doi: 10.1111/evo.12755.

Childs, D. Z. *et al.* (2011) 'Predicting trait values and measuring selection in complex life histories : Reproductive allocation decisions in Soay sheep', *Ecology Letters*, (July). doi: 10.1111/j.1461-0248.2011.01657.x.

Chiyo, P. I., Obanda, V. and Korir, D. K. (2015) 'Illegal tusk harvest and the decline of tusk size in the African elephant', *Ecology and Evolution*, 5(22), pp. 5216–5229. doi: 10.1002/ece3.1769.

Claessen, D., De Roos, A. M. and Persson, L. (2004) 'Population dynamic theory of size-dependent cannibalism', *Proceedings of the Royal Society B: Biological Sciences*, 271(1537), pp. 333–340. doi: 10.1098/rspb.2003.2555.

Clarke, C. A., Mani, G. S. and Wynne, G. (1985) 'Evolution in reverse: clean air and the peppered moth', *Biological Journal of the Linnean Society*, 26(2), pp. 189–199. doi: 10.1111/j.1095-8312.1985.tb01555.x.

Conover, D. O. and Baumann, H. (2009) 'The role of experiments in understanding fishery-induced evolution', *Evolutionary Applications*, 2(3), pp. 276–290. doi: 10.1111/j.1752-4571.2009.00079.x.

Conover, D. O. and Munch, S. B. (2002) 'Sustaining fisheries yields over evolutionary time scales.', *Science*, 297(5578), pp. 94–96. doi: 10.1126/science.1074085.

Costello, C. *et al.* (2016) 'Global fishery prospects under contrasting management regimes', *Proceedings of the National Academy of Sciences*, 113(18), pp. 5125–5129. doi: 10.1073/pnas.1520420113.

Crow, J. F. (1992) 'An advantage of sexual reproduction in a rapidly changing environment', *Journal of Heredity*, 83(February), pp. 169–173.

Darwin, C. and Wallace, A. (1858) 'The Tendancy of Species to Form Varieties'. Linnean Society.

Davies, T. D. and Baum, J. K. (2012) 'Extinction risk and overfishing: Reconciling conservation and fisheries perspectives on the status of marine fishes', *Scientific Reports*, 2, pp. 1–9. doi: 10.1038/srep00561.

DeWitt, T. J., Sih, A. and Wilson, D. S. (1998) 'Cost and limits of phenotypic plasticity', *Trends in Ecology & Evolution*, 13(97), pp. 77–81. doi: 10.1111/j.1558-5646.2009.00647.x.

Duncan, E. J., Gluckman, P. D. and Dearden, P. K. (2014) 'Epigenetics, plasticity, and evolution: How do we link epigenetic change to phenotype?', *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 322(4), pp. 208–220. doi: 10.1002/jez.b.22571.

Dunlop, E. S., Eikeset, A. M. and Stenseth, N. C. (2015) 'From genes to populations: How fisheries-induced evolution alters stock productivity', *Ecological Applications*, 25(7), pp. 1860–1868. doi: 10.1890/14-1862.1.

Einum, S. and Fleming, I. A. (2004) 'Environmental unpredictability and offspring size: Conservative versus diversified bet-hedging', *Evolutionary Ecology Research*, 6(3), pp. 443–455.

El-Sabaawi, R. W. *et al.* (2015) 'Assessing the effects of guppy life history evolution on nutrient recycling : from experiments to the field', *Freshwater Biology*, 60, pp. 590–601. doi: 10.1111/fwb.12507.

Enberg, K. *et al.* (2009) 'Implications of fisheries-induced evolution for stock rebuilding and recovery', *Evolutionary Applications*, 2(3), pp. 394–414. doi: 10.1111/j.1752-4571.2009.00077.x.

Ernande, B. and Dieckmann, U. (2004) 'The evolution of phenotypic plasticity in spatially structured environments: implications of intraspecific competition, plasticity costs and environmental characteristics', *Journal of Evolutionary Biology*, 17(3), pp. 613–628. doi: 10.1111/j.1420-9101.2004.00691.x.

Fenberg, P. B. and Roy, K. (2008) 'Ecological and evolutionary consequences of size-selective harvesting: How much do we know?', *Molecular Ecology*, 17(1), pp. 209–220. doi: 10.1111/j.1365-294X.2007.03522.x.

Fischer, B. B. *et al.* (2014) 'Phenotypic plasticity influences the eco-evolutionary dynamics of a predator-prey system', *Ecology*, 95(11), p. 140527085017003. doi: 10.1890/14-0116.1.

Food and Agriculture Organisation of the United Nations (2018) *The State of World Fisheries and Aquaculture 2018*. doi: issn 10.

Forsman, a (2014) ‘Rethinking phenotypic plasticity and its consequences for individuals, populations and species.’, *Heredity*. Nature Publishing Group, 115(August), pp. 1–9. doi: 10.1038/hdy.2014.92.

Frei, E. R., Ghazoul, J. and Pluess, A. R. (2014) ‘Plastic responses to elevated temperature in low and high elevation populations of three grassland species’, *PLoS ONE*, 9(6). doi: 10.1371/journal.pone.0098677.

Froese, R. *et al.* (2016) ‘Minimizing the impact of fishing’, *Fish and Fisheries*, 17(3), pp. 785–802. doi: 10.1111/faf.12146.

Fuller, R., Baer, C. and Travis, J. (2005) ‘How and When Selection Experiments Might Actually be Useful 1’, *Integrative and Comparative Biology*, 45, pp. 391–404.

Furness, A. I., Lee, K. and Reznick, D. N. (2015) ‘Adaptation in a variable environment: Phenotypic plasticity and bet-hedging during egg diapause and hatching in an annual killifish’, *Evolution*. doi: 10.1111/evo.12669.

Fusco, G. and Minelli, A. (2010) ‘Phenotypic plasticity in development and evolution: facts and concepts’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1540), pp. 547–556. doi: 10.1098/rstb.2009.0267.

Fussmann, G. F., Loreau, M. and Abrams, P. a. (2007) ‘Eco-evolutionary dynamics of communities and ecosystems’, *Functional Ecology*, 21, pp. 465–477. doi: 10.1111/j.1365-2435.2007.01275.x.

Gale, B. H. *et al.* (2013) ‘Effects of predation environment and food availability on somatic growth in the Livebearing Fish Brachyrhaphis rhabdophora (Pisces: Poeciliidae)’, *Ecology and Evolution*, 3(2), pp. 326–333. doi: 10.1002/ece3.459.

Ghalambor, C. K. *et al.* (2007) ‘Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments’, *Functional Ecology*, 21, pp. 394–407. doi: 10.1111/j.1365-2435.2007.01283.x.

Gill, D. E. and Hairston, N. G. (1972) ‘The Dynamics of a Natural Population of Paramecium and the Role of Interspecific Competition in Community Stucture’, *The Journal of Animal Ecology*, 41(1), p. 137. doi: 10.2307/3509.

Gratani, L. (2014) ‘Plant Phenotypic Plasticity in Response to Environmental Factors’, *Advances in Botany*, 2014, pp. 1–17. doi: 10.1155/2014/208747.

Gwinn, D. C. *et al.* (2015) ‘Rethinking length-based fisheries regulations: The value of protecting old and large fish with harvest slots’, *Fish and Fisheries*, pp. 1–23. doi: 10.1111/faf.12053.

Hairston, N. G. *et al.* (2005) ‘Rapid evolution and the convergence of ecological and evolutionary time’, *Ecology Letters*, 8, pp. 1114–1127. doi: 10.1111/j.1461-0248.2005.00812.x.

Handelsman, C. a. *et al.* (2013) ‘Predator-Induced Phenotypic Plasticity in Metabolism and Rate of Growth: Rapid Adaptation to a Novel Environment’, *Integrative and Comparative Biology*, 53(6), pp. 975–988. doi: 10.1093/icb/ict057.

Harshman, L. G. and Zera, A. J. (2007) ‘The cost of reproduction: the devil in the

details', *Trends in Ecology and Evolution*, 22(2), pp. 80–86. doi: 10.1016/j.tree.2006.10.008.

Heino, M., Díaz Pauli, B. and Dieckmann, U. (2015) 'Fisheries-Induced Evolution', *Annual Review of Ecology, Evolution, and Systematics*, 46(1), pp. 461–480. doi: 10.1146/annurev-ecolsys-112414-054339.

Hendry, A. P. (2016) 'Key Questions on the Role of Phenotypic Plasticity in Eco-Evolutionary Dynamics', *Heredity*, pp. 25–41. doi: 10.1093/jhered/esv060.

Hengeveld, P. E. and Festa-Bianchet, M. (2011) 'Harvest regulations and artificial selection on horn size in male bighorn sheep', *Journal of Wildlife Management*, 75(1), pp. 189–197. doi: 10.1002/jwmg.14.

Hik, D. S. (1995) 'Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares', *Wildlife Research*, 22(1), pp. 115–129. doi: 10.1071/WR9950115.

Hixon, M. A., Johnson, D. W. and Sogard, S. M. (2014) 'BOFFFFs: on the importance of conserving old-growtg age structure in fishery populations', *ICES Journal of Marine Science*, 71, pp. 2171–2185.

Hoving, H. T. *et al.* (2013) 'Extreme plasticity in life-history strategy allows a migratory predator (jumbo squid) to cope with a changing climate', *Global Change Biology*, 19, pp. 2089–2103. doi: 10.1111/gcb.12198.

Hunter, A., Speirs, D. C. and Heath, M. R. (2015) 'Fishery-induced changes to age and length dependent maturation schedules of three demersal fish species in the Firth of Clyde', *Fisheries Research*. Elsevier B.V., 170, pp. 14–23. doi: 10.1016/j.fishres.2015.05.004.

Huss, M. and Nilsson, K. a. (2011) 'Experimental evidence for emergent facilitation: Promoting the existence of an invertebrate predator by killing its prey', *Journal of Animal Ecology*, 80, pp. 615–621. doi: 10.1111/j.1365-2656.2011.01810.x.

Jacobsen, N. S., Gislason, H. and Andersen, K. H. (2014) 'The consequences of balanced harvesting of fish communities.', *Proceedings. Biological sciences / The Royal Society*, 281(1775), p. 20132701. doi: 10.1098/rspb.2013.2701.

de Jong, G. (2005) 'Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes.', *The New phytologist*, 166(1), pp. 101–17. doi: 10.1111/j.1469-8137.2005.01322.x.

Jusufovski, D. and Kuparinen, A. (2014) 'Contrasting evolutionary and ecological management objectives in the context of sustainable harvesting', *Evolutionary Ecology Research*, 16, pp. 133–142.

Kell, L. T. *et al.* (2016) 'Is spawning stock biomass a robust proxy for reproductive potential?', *Fish and Fisheries*, 17(3), pp. 596–616. doi: 10.1111/faf.12131.

Kendall, N. W. and Quinn, T. P. (2013) 'Size-selective fishing affects sex ratios and the opportunity for sexual selection in Alaskan sockeye salmon Oncorhynchus nerka', *Oikos*, 122(3), pp. 411–420. doi: 10.1111/j.1600-0706.2012.20319.x.

Kettlewell, H. B. D. (1958) ‘A survey of the frequencies of *Biston betularia* (L.)(Lep.) and its melanic forms in Great Britain’, *Heredity*, 12, pp. 51–72. doi: 10.1038/hdy.1958.4.

Keyl, F., Kempf, A. J. and Sell, A. F. (2015) ‘Sexual size dimorphism in three North Sea gadoids’, *Journal of Fish Biology*, 86(1), pp. 261–275. doi: 10.1111/jfb.12579.

Koehn, J. D. and Todd, C. R. (2012) ‘Balancing conservation and recreational fishery objectives for a threatened fish species, the Murray cod, Maccullochella peelii’, *Fisheries Management and Ecology*, 19, pp. 410–425. doi: 10.1111/j.1365-2400.2012.00856.x.

Kuparinen, A. *et al.* (2016) ‘Fishing-induced life-history changes degrade and destabilize harvested ecosystems’, *Scientific Reports*. Nature Publishing Group, 6, pp. 1–9. doi: 10.1038/srep22245.

Kuparinen, A. and Festa-Bianchet, M. (2017) ‘Harvest-induced evolution: Insights from aquatic and terrestrial systems’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1712). doi: 10.1098/rstb.2016.0036.

Kuparinen, A. and Hutchings, J. A. (2012) ‘Consequences of fisheries-induced evolution for population productivity and recovery potential’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1738), pp. 2571–2579. doi: 10.1098/rspb.2012.0120.

Kuparinen, A., Kuikka, S. and Merilä, J. (2009) ‘Estimating fisheries-induced selection: Traditional gear selectivity research meets fisheries-induced evolution’, *Evolutionary Applications*, 2, pp. 234–243. doi: 10.1111/j.1752-4571.2009.00070.x.

Laugen, A. T. *et al.* (2014) ‘Evolutionary impact assessment: Accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management’, *Fish and Fisheries*, 15(1), pp. 65–96. doi: 10.1111/faf.12007.

Law, R. (2000) ‘Fishing, selection, and phenotypic evolution’, *ICES Journal of Marine Science*, 57(3), pp. 659–668. doi: 10.1006/jmsc.2000.0731.

Law, R. and Plank, M. J. (2018) ‘Balanced harvesting could reduce fisheriesinduced evolution’, *Fish and Fisheries*, (February), pp. 1–14. doi: 10.1111/faf.12313.

Leips, J. *et al.* (2009) ‘Adaptive maternal adjustments of offspring size in response to conspecific density in two populations of the least killifish, heterandria formosa’, *Evolution*, 63(Spitzer 2004), pp. 1341–1347. doi: 10.1111/j.1558-5646.2009.00631.x.

Leips, J., Helen Rodd, F. and Travis, J. (2013) ‘The adaptive significance of population differentiation in offspring size of the least killifish, Heterandria formosa’, *Ecology and Evolution*, 3(4), pp. 948–960. doi: 10.1002/ece3.509.

Levin, P. S. *et al.* (2006) ‘Shifts in a Pacific Ocean Fish Assemblage : the Potential Influence of Exploitation’, *Conservation Biology*, 20(4), pp. 1181–1190. doi: 10.1111/j.1523-1739.2006.00400.x.

Lindstro, K. *et al.* (2016) ‘Altered trait variability in response to size-selective mortality’, *Biology letters*, 12(October). doi: 10.1098/rsbl.2016.0584.

Marshall, C. T. and Browman, H. I. (2007) ‘Disentangling the causes of maturation trends in exploited fish populations’, *Marine Ecology Progress Series*, 335(April 2007),

pp. 249–251. doi: 10.3354/meps335249.

Marty, L., Rochet, M. J. and Ernande, B. (2014) ‘Temporal trends in age and size at maturation of four North Sea gadid species: Cod, haddock, whiting and Norway pout’, *Marine Ecology Progress Series*, 497(February), pp. 179–197. doi: 10.3354/meps10580.

Maynard Smith, J. and Haigh, J. (1975) ‘Hitch-Hiking Effect of a Favourable Gene’, *Genetics Research*. University of Sussex, 23(1974), pp. 23–35. doi: 10.1007/978-1-4613-3924-3_7.

Miller, T. E. X. and Rudolf, V. H. W. (2011) ‘Thinking inside the box: Community-level consequences of stage-structured populations’, *Trends in Ecology and Evolution*, 26(9), pp. 457–466. doi: 10.1016/j.tree.2011.05.005.

Murren, C. J. *et al.* (2015) ‘Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity’, *Heredity*. Nature Publishing Group, (November 2014), pp. 1–9. doi: 10.1038/hdy.2015.8.

Myrvold, K. M. and Kennedy, B. P. (2015) ‘Density dependence and its impact on individual growth rates in an age-structured stream salmonid population’, *Ecosphere*, 6(12), pp. 1–16. doi: 10.1890/ES15-00390.1.

Nakazawa, T. (2015) ‘Ontogenetic niche shifts matter in community ecology: a review and future perspectives’, *Population Ecology*, 57(2), pp. 347–354. doi: 10.1007/s10144-014-0448-z.

Nilsson, K. a. *et al.* (2011) ‘Guppy populations differ in cannibalistic degree and adaptation to structural environments’, *Oecologia*, 167, pp. 391–400. doi: 10.1007/s00442-011-1990-4.

Nilsson, K. a. and Persson, L. (2013) ‘Refuge availability and within-species differences in cannibalism determine population variability and dynamics’, *Ecosphere*, 4(August), pp. 1–15. doi: 10.1890/ES13-00105.1.

Nilsson, K. a., Persson, L. and van Kooten, T. (2010) ‘Complete compensation in Daphnia fecundity and stage-specific biomass in response to size-independent mortality’, *Journal of Animal Ecology*, 79, pp. 871–878. doi: 10.1111/j.1365-2656.2010.01679.x.

Okamoto, K. W. *et al.* (2009) ‘Mitigating fisheries-induced evolution in lacustrine brook charr (Salvelinus fontinalis) in southern Quebec, Canada’, *Evolutionary Applications*, 2(3), pp. 415–437. doi: 10.1111/j.1752-4571.2009.00095.x.

Olsson, K. H. and Gislason, H. (2016) ‘Testing reproductive allometry in fish’, *ICES Journal of Marine Science*.

Osenburg, C. W., Mittlebach, G. G. and Wainwright, P. C. (1992) ‘Two-Stage Life Histories in Fish : The Interaction Between Juvenile Competition and Adult Performance’, *Ecology*, 73(1), pp. 255–267.

Ow, Y. X. and Todd, P. A. (2010) ‘Light-induced morphological plasticity in the scleractinian coral Goniastrea pectinata and its functional significance’, *Coral Reefs*, 29(3), pp. 797–808. doi: 10.1007/s00338-010-0631-4.

Pauli, B. D. *et al.* (2017) 'Effects of ambient oxygen and size-selective mortality on growth and maturation in guppies', *Conservation Physiology*, 5(1). doi: 10.1093/conphys/cox010.

Persson, L. *et al.* (1996) 'Size-Specific Interactions in Lake Systems : Predator Gape Limitation and Prey Growth Rate and Mortality', *Ecology*, 77(3), pp. 900–911.

Persson, L. *et al.* (2007) 'Culling prey promotes predator recovery--alternative states in a whole-lake experiment.', *Science (New York, N.Y.)*, 316, pp. 1743–1746. doi: 10.1126/science.1141412.

Persson, L. and De Roos, A. M. (2013) 'Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults', *Ecology*, 94(7), pp. 1487–1498. doi: 10.1890/12-1883.1.

Pigeon, G. *et al.* (2016) 'Intense selective hunting leads to artificial evolution in horn size', *Evolutionary Applications*, 9(4), pp. 521–530. doi: 10.1111/eva.12358.

Plaistow, S. *et al.* (2004) 'Age and size at maturity : Sex , environmental variability and developmental thresholds', *Proceedings of the Royal Society B*, (June). doi: 10.1098/rspb.2004.2682.

Plaistow, S. *et al.* (2007) 'How to Put All Your Eggs in One Basket : Empirical Patterns of Offspring Provisioning throughout a Mother ' s Lifetime How to Put All Your Eggs in One Basket : Empirical Patterns of Offspring Provisioning throughout a Mother ' s Lifetime', (January 2017). doi: 10.1086/521238.

Plaistow, S. J. and Benton, T. G. (2009) 'The influence of context-dependent maternal effects on population dynamics: An experimental test', *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1520), pp. 1049–1058. doi: 10.1098/rstb.2008.0251.

Plaistow, S. J., Lapsley, C. T. and Benton, T. G. (2006) 'Context-Dependent Intergenerational Effects: The Interaction between Past and Present Environments and Its Effect on Population Dynamics', *The American Naturalist*, 167(2), pp. 206–215. doi: 10.1086/499380.

Post, D. M. and Palkovacs, E. P. (2014) 'Eco-evolutionary feedbacks in community and ecosystem ecology : Interactions between the ecological theatre and the ... Eco-evolutionary feedbacks in community and ecosystem ecology : interactions between the ecological theatre and the evolutionary play', *Philosophical Transactions of the Royal Society B: Biological Sciences*, (July 2009). doi: 10.1098/rstb.2009.0012.

Price, T. D., Qvarnström, A. and Irwin, D. E. (2003) 'The role of phenotypic plasticity in driving genetic evolution.', *Proceedings. Biological sciences / The Royal Society*, 270(February), pp. 1433–1440. doi: 10.1098/rspb.2003.2372.

Promislow, D. E. L. *et al.* (1998) 'Adult fitness consequences of sexual selection in Drosophila melanogaster', *Proceedings of the National Academy of Sciences of the United States of America*, 95(September), pp. 10687–10692. doi: 10.1073/pnas.95.18.10687.

Quetglas, A. *et al.* (2016) 'Contrasting responses to harvesting and environmental

drivers of fast and slow life history species', *PLoS ONE*, 11(2), pp. 1–15. doi: 10.1371/journal.pone.0148770.

Radomski, P. J. *et al.* (2001) 'Visions for Recreational Fishing Regulations', *Fisheries*, 26(5), pp. 7–18. doi: 10.1577/1548-8446(2001)026<0007:vfrfr>2.0.co;2.

Reed, T. E. *et al.* (2010) 'Phenotypic plasticity and population viability: the importance of environmental predictability.', *Proceedings. Biological sciences / The Royal Society*, 277(June), pp. 3391–3400. doi: 10.1098/rspb.2010.0771.

Reed, T. E., Schindler, D. E. and Waples, R. S. (2011) 'Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate.', *Conservation biology : the journal of the Society for Conservation Biology*, 25(1), pp. 56–63. doi: 10.1111/j.1523-1739.2010.01552.x.

Reichstein, B., Persson, L. and De Roos, A. M. (2015) 'Ontogenetic asymmetry modulates population biomass production and response to harvest', *Nature Communications*, 6, p. 6441. doi: 10.1038/ncomms7441.

Relyea, R. a (2002) 'Costs of phenotypic plasticity.', *The American naturalist*, 159(3), pp. 272–282. doi: 10.1086/338540.

Reznick, D. (1983) 'THE STRUCTURE OF GUPPY LIFE HISTORIES: THE TRADEOFF BETWEEN GROWTH AND REPRODUCTION', *Ecology*, 64(4), pp. 862–873.

Reznick, D., Bryant, M. J. and Bashey, F. (2002) 'r- and K-Selection Revisited: The Role of Population Regulation in Life-History Evolution', *Ecology*, 83(6), p. 1509. doi: 10.2307/3071970.

Reznick, D., Butler Iv, M. J. and Rodd, H. (2001) 'Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments.', *The American naturalist*, 157(2), pp. 126–140. doi: 10.1086/318627.

Reznick, D., Callahan, H. and Llauredo, R. (1996) 'Maternal effects on offspring quality in poeciliid fishes', *American Zoologist*, 36(2), p. 147. doi: 10.1093/icb/36.2.147.

Reznick, D. N. (1982) 'The impact of predation on life history evolution in Trinidadian guppies: genetic basis of observed life history patterns', *Evolution*, 36(1), pp. 1236–1250. doi: 10.2307/2408156.

Reznick, D. N. (1990) 'Plasticity in age and size at maturity in male guppies (*Poecilia reticulata*): An experimental evaluation of alternative models of development', *Journal of Evolutionary Biology*, 3(3–4), pp. 185–203. doi: 10.1046/j.1420-9101.1990.3030185.x.

Reznick, D. N. *et al.* (1997) 'Evaluation of the Rate of Evolution in Natural Populations of Guppies (Poecilia reticulata) Evaluation of the Rate of Evolution in Natural Populations of Guppies (Poecilia reticulata)', *Science*, 1934(275), pp. 1934–1937. doi: 10.1126/science.275.5308.1934.

Reznick, D. N. (1997) 'Evaluation of the Rate of Evolution in Natural Populations of Guppies (Poecilia reticulata)', *Science*, 275(1997), pp. 1934–1937. doi: 10.1126/science.275.5308.1934.

Reznick, D. N., Bryga, H. and Endler, J. A. (1990) 'Experimentally induced life history

evolution in a natural population', *Letters To Nature*, 346, pp. 183–187. doi: 10.1038/346183a0.

Reznick, D. N. and Ghalambor, C. K. (2005) 'Can commercial fishing cause evolution? Answers from guppies (*Poecilia reticulata*)', *Canadian Journal of Fisheries and Aquatic Sciences*, 62(4), pp. 791–801. doi: 10.1139/f05-079.

Richter, S., Wohlgemuth, T. and Moser, B. (2012) 'Phenotypic plasticity facilitates resistance to climate change in a highly variable environment', *Oecologia*, 169(November 2011), pp. 269–279. doi: 10.1007/s00442-011-2191-x.

Riesch, R. *et al.* (2016) 'Sex-specific local life-history adaptation in surface- and cave-dwelling Atlantic mollies (Poecilia mexicana)', *Scientific Reports*. Nature Publishing Group, 6(March), p. 22968. doi: 10.1038/srep22968.

Robinson, M. R. and Beckerman, A. P. (2013) 'Quantifying multivariate plasticity: Genetic variation in resource acquisition drives plasticity in resource allocation to components of life history', *Ecology Letters*, 16(3), pp. 281–290. doi: 10.1111/ele.12047.

Rodd, F. H. and Reznick, D. N. (1997) 'Variation in the demography of natural populations of guppies: the importance of predation and life histories.', *Ecology*, 78(2), pp. 405–418. doi: 10.1890/0012-9658

De Roos, A. M. *et al.* (2007) 'Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation.', *The American naturalist*, 170(3), pp. E59–E76. doi: 10.1086/520119.

de Roos, A. M., Metz, J. a J. and Persson, L. (2013) 'Ontogenetic symmetry and asymmetry in energetics', *Journal of Mathematical Biology*, 66, pp. 889–914. doi: 10.1007/s00285-012-0583-0.

de Roos, A. M., Persson, L. and Thieme, H. R. (2003) 'Emergent Allee effects in top predators feeding on structured prey populations.', *Proceedings. Biological sciences / The Royal Society*, 270, pp. 611–618. doi: 10.1098/rspb.2002.2286.

Sæther, B.-E. *et al.* (2013) 'How Life History Influences Population Dynamics in Fluctuating Environments', *The American Naturalist*, 182(6), pp. 743–759. doi: 10.1086/673497.

Salih, A. *et al.* (2000) 'Fluorescent pigments in corals are photoprotective.', *Nature*, 408(6814), pp. 850–853. doi: 10.1038/35048564.

Schrader, M. and Travis, J. (2012a) 'Assessing the roles of population density and predation risk in the evolution of offspring size in populations of a placental fish', *Ecology and Evolution*, 2, pp. 1480–1490. doi: 10.1002/ece3.255.

Schrader, M. and Travis, J. (2012b) 'Variation in offspring size with birth order in placental fish: A role for asymmetric sibling competition?', *Evolution*, 66, pp. 272–279. doi: 10.1111/j.1558-5646.2011.01422.x.

Schröder, A. *et al.* (2009) 'Invasion success depends on invader body size in a size-structured mixed predation-competition community', *Journal of Animal Ecology*, 78, pp.

1152–1162. doi: 10.1111/j.1365-2656.2009.01590.x.

Schröder, A., Leeuwen, A. Van and Cameron, T. C. (2014) 'When less is more : positive population-level effects of mortality', *Trends in Ecology & Evolution*, 29(11). doi: 10.1016/j.tree.2014.08.006.

Schröder, A., Persson, L. and De Roos, A. M. (2009) 'Culling experiments demonstrate size-class specific biomass increases with mortality.', *Proceedings of the National Academy of Sciences of the United States of America*, 106, pp. 2671–2676. doi: 10.1073/pnas.0808279106.

Sereda, S. V. E., Wilke, T. and Schultheiß, R. (2014) 'Changes in selection regime cause loss of phenotypic plasticity in planktonic freshwater copepods', *PLoS ONE*, 9(2). doi: 10.1371/journal.pone.0090010.

Sibly, R. M. *et al.* (2015) 'Fundamental insights into ontogenetic growth from theory and fish', *Proceedings of the National Academy of Sciences*, 112(45), pp. 13934–13939. doi: 10.1073/pnas.1518823112.

Siskey, M. *et al.* (2016) 'Forty years of fishing : changes in age structure and stock mixing in northwestern Atlantic bluefin tuna (Thunnus ... Forty years of fishing : changes in age structure and stock mixing in northwestern Atlantic bluefin tuna (Thunnus thynnus) associated ', (July). doi: 10.1093/icesjms/fsw115.

Srivastava, D. S. *et al.* (2004) 'Are natural microcosms useful model systems for ecology?', *Trends in Ecology and Evolution*, 19(7), pp. 379–384. doi: 10.1016/j.tree.2004.04.010.

Stearns, S. C. (1989) 'Trade-offs in Life-History Evolution', *Functional Ecology*, 3(3), pp. 259–268.

Stearns, S. C. and Koella, J. C. (1986) 'The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity', *Evolution*, 40(5), pp. 893–913. doi: 10.2307/2408752.

Stenseth, N. C. *et al.* (1997) 'Population regulation in snowshoe hare and Canadian lynx: Asymmetric food web configurations between hare and lynx', *Proceedings of the National Academy of Sciences*, 94(10), pp. 5147–5152. doi: 10.1073/pnas.94.10.5147.

Stewart, R. I. A. *et al.* (2013) *Mesocosm Experiments as a Tool for Ecological Climate-Change Research*. 1st edn, *Advances in Ecological Research*. 1st edn. Elsevier Ltd. doi: 10.1016/B978-0-12-417199-2.00002-1.

Strickland, B. K. *et al.* (2001) 'Effects of Selective-Harvest Strategies on White-Tailed Deer Antler Size', *Wildlife Society Bulletin*, 29(2), pp. 509–520. doi: 10.2307/3784175.

Sundström, L. F. *et al.* (2013) 'Density-Dependent Compensatory Growth in Brown Trout (Salmo trutta) in Nature', *PLoS ONE*, 8(5). doi: 10.1371/journal.pone.0063287.

Suuronen, P. and Sardà, F. (2007) 'The role of technical measures in European fisheries management and how to make them work better', *ICES Journal of Marine Science*, 64(4), pp. 751–756. doi: 10.1093/icesjms/fsm049.

Svedäng, H. and Hornborg, S. (2014) 'Selective fishing induces density-dependent

growth', *Nature communications*, (June). doi: 10.1038/ncomms5152.

Swain, D. P., Sinclair, A. F. and Mark Hanson, J. (2007) 'Evolutionary response to size-selective mortality in an exploited fish population.', *Proceedings. Biological sciences / The Royal Society*, 274(1613), pp. 1015–1022. doi: 10.1098/rspb.2006.0275.

Thambithurai, D. *et al.* (2018) 'Shoal size as a key determinant of vulnerability to capture under a simulated fishery scenario', *Ecology and Evolution*, 8(13), pp. 6505–6514. doi: 10.1002/ece3.4107.

Thorson, J. L. M. *et al.* (2017) 'Epigenetics and adaptive phenotypic variation between habitats in an asexual snail', *Scientific Reports*. Springer US, 7(1), pp. 1–11. doi: 10.1038/s41598-017-14673-6.

Torres-Dowdal, J. *et al.* (2012) 'Local adaptation and the evolution of of phenotypic plasticity in Trinidadian guppies (Poecilia reticulata)', *Evolution*, 66, pp. 3432–3443. doi: 10.5061/dryad.84gf5.

Travis, J. *et al.* (1987) 'Testing Theories of Clutch Overlap with the Reproductive Ecology of Heterandria Formosa', 68(3), pp. 611–623.

Travis, J., Reznick, D. and Bassar, R. D. (2014) *Eco-Evolutionary Dynamics*, *Advances in Ecological Research*. doi: 10.1016/B978-0-12-801374-8.00001-3.

Trunschke, J. and Stöcklin, J. (2017) 'Plasticity of flower longevity in alpine plants is increased in populations from high elevation compared to low elevation populations', *Alpine Botany*, 127(1), pp. 41–51. doi: 10.1007/s00035-016-0176-4.

Uusi-Heikkilä, S. *et al.* (2015) 'The evolutionary legacy of size-selective harvesting extends from genes to populations', *Evolutionary Applications*, 8(6), pp. 597–620. doi: 10.1111/eva.12268.

Valladares, F., Sanchez-Gomez, D. and Zavala, M. a. (2006) 'Quantitative estimation of phenotypic plasticity: Bridging the gap between the evolutionary concept and its ecological applications', *Journal of Ecology*, 94, pp. 1103–1116. doi: 10.1111/j.1365-2745.2006.01176.x.

Vasilakopoulos, P., Neill, F. G. O. and Marshall, C. T. (2014) 'Misspent youth : Does catching immature fish affect fisheries sustainability ? Misspent youth : does catching immature fish affect fisheries sustainability ?', *ICES Journal of Marine Science*, (January). doi: 10.1093/icesjms/fsr075.

Vincent, S. E. *et al.* (2006) 'Do juvenile gape-limited predators compensate for their small size when feeding?', *Journal of Zoology*, 268(3), pp. 279–284. doi: 10.1111/j.1469-7998.2005.00014.x.

Walsh, M. R. *et al.* (2016) 'Local adaptation in transgenerational responses to predators', *Proceedings of the Royal Society B: Biological Sciences*, 283(1823). doi: 10.1098/rspb.2015.2271.

Walsh, M. R. and Reznick, D. N. (2009) 'Phenotypic diversification across an environmental gradient: A role for predators and resource availability on the evolution of life histories', *Evolution*, 63(Wootton 1994), pp. 3201–3213. doi: 10.1111/j.1558-5646.2009.00785.x.

Ward, E. J. *et al.* (2019) 'Assessing long-term changes in sex ratios of Pacific herring in Prince William Sound, Alaska', *Fisheries Research*. Elsevier, 211(December 2018), pp. 300–308. doi: 10.1016/j.fishres.2018.10.031.

Van Wijk, S. J. *et al.* (2013) 'Experimental harvesting of fish populations drives genetically based shifts in body size and maturation', *Frontiers in Ecology and the Environment*, 11(4), pp. 181–187. doi: 10.1890/120229.

Wikström, A., Ripa, J. and Jonzén, N. (2012) 'The role of harvesting in age-structured populations: Disentangling dynamic and age truncation effects', *Theoretical Population Biology*. Elsevier Inc., 82(4), pp. 348–354. doi: 10.1016/j.tpb.2011.12.008.

Wise, D. H. (2006) 'Cannibalism, Food Limitation, Intraspecific Competition, and the Regulation of Spider Populations', *Annual Review of Entomology*, 51(1), pp. 441–465. doi: 10.1146/annurev.ento.51.110104.150947.

Xu, C., Schneider, D. C. and Rideout, C. (2012) 'When reproductive value exceeds economic value : An example from the Newfoundland cod fishery', *Fish and Fisheries*, (January 2012). doi: 10.1111/j.1467-2979.2012.00464.x.

Yoshida, T. *et al.* (2007) 'Cryptic population dynamics: Rapid evolution masks trophic interactions', *PLoS Biology*, 5(9), pp. 1868–1879. doi: 10.1371/journal.pbio.0050235.

Zhang, Y. (2006) 'Balancing food availability and hydrodynamic constraint: Phenotypic plasticity and growth in Simulium noelleri blackfly larvae', *Oecologia*, 147(1), pp. 39–46. doi: 10.1007/s00442-005-0243-9.

Zipkin, E. F. *et al.* (2008) 'Overcompensatory response of a smallmouth bass (Micropterus dolomieu) population to harvest: release from competition?', *Canadian Journal of Fisheries and Aquatic Sciences*, 65, pp. 2279–2292. doi: 10.1139/F08-133.

Appendices

Appendix I – Additional statistical results for Chapter III

```
Linear mixed-effects model fit by REML
 Data: grouped_age_slope
       AIC      BIC    logLik
  1235.884 1294.984 -600.9421

Random effects:
 Formula: ~1 | pop
         (Intercept) Residual
StdDev: 0.0001186318 2.741478

Fixed effects: slope ~ assay * env
                 Value Std.Error  DF   t-value p-value
(Intercept) -15.835390 0.5005231 233 -31.63768  0.0000
assay1        9.654747 0.8873326 233  10.88064  0.0000
assay2        5.958227 0.8873326 233   6.71476  0.0000
assay3        6.978162 0.8873326 233   7.86420  0.0000
assay4        5.021218 0.8873326 233   5.65878  0.0000
env2          0.000000 0.7078466   6   0.00000  1.0000
env3          0.000000 0.7078466   6   0.00000  1.0000
assay1:env2   0.046152 1.2900353 233   0.03578  0.9715
assay2:env2   2.440239 1.2548778 233   1.94460  0.0530
assay3:env2  -1.514527 1.2548778 233  -1.20691  0.2287
assay4:env2  -4.728630 1.2548778 233  -3.76820  0.0002
assay1:env3   0.963083 1.2712252 233   0.75760  0.4495
assay2:env3   0.104809 1.2712252 233   0.08245  0.9344
assay3:env3   0.773192 1.2548778 233   0.61615  0.5384
assay4:env3  -5.225763 1.2548778 233  -4.16436  0.0000
 Correlation:
            (Intr) assay1 assay2 assay3 assay4 env2   env3   ass1:2 ass2:2 ass3:2
assay1      -0.564
assay2      -0.564  0.318
assay3      -0.564  0.318  0.318
assay4      -0.564  0.318  0.318  0.318
env2        -0.707  0.399  0.399  0.399  0.399
env3        -0.707  0.399  0.399  0.399  0.399  0.500
assay1:env2  0.388 -0.688 -0.219 -0.219 -0.219 -0.549 -0.274
assay2:env2  0.399 -0.225 -0.707 -0.225 -0.225 -0.564 -0.282  0.310
assay3:env2  0.399 -0.225 -0.225 -0.707 -0.225 -0.564 -0.282  0.310  0.318
assay4:env2  0.399 -0.225 -0.225 -0.225 -0.707 -0.564 -0.282  0.310  0.318  0.318
assay1:env3  0.394 -0.698 -0.222 -0.222 -0.222 -0.278 -0.557  0.480  0.157  0.157
assay2:env3  0.394 -0.222 -0.698 -0.222 -0.222 -0.278 -0.557  0.153  0.494  0.157
assay3:env3  0.399 -0.225 -0.225 -0.707 -0.225 -0.282 -0.564  0.155  0.159  0.500
assay4:env3  0.399 -0.225 -0.225 -0.225 -0.707 -0.282 -0.564  0.155  0.159  0.159
            ass4:2 ass1:3 ass2:3 ass3:3
assay1
assay2
assay3
assay4
env2
env3
assay1:env2
assay2:env2
assay3:env2
assay4:env2
assay1:env3  0.157
assay2:env3  0.157  0.310
assay3:env3  0.159  0.314  0.314
assay4:env3  0.500  0.314  0.314  0.318

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-3.07683124 -0.46439729  0.08925154  0.46547575  3.10093160

Number of Observations: 254
Number of Groups: 9
```

Table 30: Summary table of a Linear mixed effects model of age plasticity ~ environment * time

```
Linear mixed-effects model fit by REML
 Data: grouped_size_slope
       AIC       BIC   logLik
  -490.6111 -431.5112 262.3055

Random effects:
 Formula: ~1 | pop
         (Intercept)   Residual
StdDev: 7.931069e-07 0.07402017

Fixed effects: slope ~ assay * env
                 Value  Std.Error  DF   t-value p-value
(Intercept)  0.5310185 0.01351417 233  39.29345  0.0000
assay1      -0.2716692 0.02395807 233 -11.33936  0.0000
assay2      -0.2765380 0.02395807 233 -11.54258  0.0000
assay3      -0.3057499 0.02395807 233 -12.76188  0.0000
assay4      -0.3056197 0.02395807 233 -12.75644  0.0000
env2         0.0000000 0.01911193   6   0.00000  1.0000
env3         0.0000000 0.01911193   6   0.00000  1.0000
assay1:env2  0.0416769 0.03483108 233   1.19654  0.2327
assay2:env2 -0.0293123 0.03388182 233  -0.86513  0.3879
assay3:env2 -0.0005870 0.03388182 233  -0.01732  0.9862
assay4:env2  0.0175229 0.03388182 233   0.51718  0.6055
assay1:env3  0.0162394 0.03432320 233   0.47313  0.6366
assay2:env3 -0.0234299 0.03432320 233  -0.68263  0.4955
assay3:env3  0.0058941 0.03388182 233   0.17396  0.8620
assay4:env3  0.0259103 0.03388182 233   0.76473  0.4452
 Correlation:
            (Intr) assay1 assay2 assay3 assay4 env2   env3   ass1:2 ass2:2 ass3:2
assay1      -0.564
assay2      -0.564  0.318
assay3      -0.564  0.318  0.318
assay4      -0.564  0.318  0.318  0.318
env2        -0.707  0.399  0.399  0.399  0.399
env3        -0.707  0.399  0.399  0.399  0.399  0.500
assay1:env2  0.388 -0.688 -0.219 -0.219 -0.219 -0.549 -0.274
assay2:env2  0.399 -0.225 -0.707 -0.225 -0.225 -0.564 -0.282  0.310
assay3:env2  0.399 -0.225 -0.225 -0.707 -0.225 -0.564 -0.282  0.310  0.318
assay4:env2  0.399 -0.225 -0.225 -0.225 -0.707 -0.564 -0.282  0.310  0.318  0.318
assay1:env3  0.394 -0.698 -0.222 -0.222 -0.222 -0.278 -0.557  0.480  0.157  0.157
assay2:env3  0.394 -0.222 -0.698 -0.222 -0.222 -0.278 -0.557  0.153  0.494  0.157
assay3:env3  0.399 -0.225 -0.225 -0.707 -0.225 -0.282 -0.564  0.155  0.159  0.500
assay4:env3  0.399 -0.225 -0.225 -0.225 -0.707 -0.282 -0.564  0.155  0.159  0.159
            ass4:2 ass1:3 ass2:3 ass3:3
assay1
assay2
assay3
assay4
env2
env3
assay1:env2
assay2:env2
assay3:env2
assay4:env2
assay1:env3  0.157
assay2:env3  0.157  0.310
assay3:env3  0.159  0.314  0.314
assay4:env3  0.500  0.314  0.314  0.318

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.74420059 -0.57638150 -0.01293441  0.41961379  4.47792604

Number of Observations: 254
Number of Groups: 9
```

Table 31: Summary table of a Linear mixed effects model of size plasticity ~ environment * time

```
Linear mixed-effects model fit by REML
 Data: slopes_har_zero_t4
       AIC      BIC    logLik
  226.5996 234.9174 -108.2998

Random effects:
 Formula: ~1 | pop
         (Intercept) Residual
StdDev: 0.0001640167 3.513024

Fixed effects: slope ~ env
                 Value Std.Error DF    t-value p-value
(Intercept) -10.814172 0.9388952 36 -11.517976  0.0000
env2         -4.728630 1.3277983  3  -3.561256  0.0378
env3         -5.225763 1.3277983  3  -3.935660  0.0292
 Correlation:
     (Intr) env2
env2 -0.707
env3 -0.707  0.500

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.40108372 -0.68508412  0.07033175  0.42629848  2.41989105

Number of Observations: 42
Number of Groups: 6
```

Table 32: Summary table of a Linear mixed effects model of age plasticity ~ environment at 95 weeks

```
Linear mixed-effects model fit by REML
 Data: slopes_har_zero_size_t4
        AIC       BIC   logLik
  -88.81624 -80.49843 49.40812

Random effects:
 Formula: ~1 | pop
         (Intercept)   Residual
StdDev: 1.282166e-06 0.06158631

Fixed effects: slope ~ env
                 Value  Std.Error DF   t-value p-value
(Intercept) 0.22539878 0.01645964 36 13.694033  0.0000
env2        0.01752291 0.02327744  3  0.752785  0.5063
env3        0.02591034 0.02327744  3  1.113110  0.3468
 Correlation:
     (Intr) env2
env2 -0.707
env3 -0.707  0.500

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.03962636 -0.56203123 -0.06306735  0.50610615  2.18711664

Number of Observations: 42
Number of Groups: 6
```

Table 33: Summary table of a Linear mixed effects model of size plasticity ~ environment at 95 weeks

Appendix II – Additional statistical results for Chapter IV

```
Linear mixed-effects model fit by REML
 Data: grouped_tank_biomass
       AIC      BIC    logLik
  339.9971 363.9206 -161.9986

Random effects:
 Formula: ~1 | Tank
        (Intercept)  Residual
StdDev:   0.4191892 0.6221166

Fixed effects: dry_mass_g ~ Census * treatment
                        Value Std.Error  DF   t-value p-value
(Intercept)          5.276589 0.4019819 141 13.126435  0.0000
Census              -0.090106 0.0170504 141 -5.284695  0.0000
treatmenths          0.126730 0.5684882   6  0.222925  0.8310
treatmentml         -0.754035 0.5684882   6 -1.326387  0.2330
Census:treatmenths  -0.047020 0.0241129 141 -1.950009  0.0532
Census:treatmentml  -0.048876 0.0241129 141 -2.026962  0.0446
 Correlation:
                    (Intr) Census trtmnth trtmntm Cnss:trtmnth
Census              -0.768
treatmenths         -0.707  0.543
treatmentml         -0.707  0.543  0.500
Census:treatmenths   0.543 -0.707 -0.768  -0.384
Census:treatmentml   0.543 -0.707 -0.384  -0.768   0.500

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-1.90703905 -0.67968461 -0.09220954  0.53703251  3.57296331

Number of Observations: 153
Number of Groups: 9
```

Table 34: Summary table of a Linear mixed effects model of total population biomass ~ harvest treatment * time

```
Linear mixed-effects model fit by REML
 Data: decline
       AIC     BIC    logLik
  283.8431 306.143 -133.9215

Random effects:
 Formula: ~1 | Tank
        (Intercept)  Residual
StdDev:    0.458416 0.6153906

Fixed effects: dry_mass_g ~ Census * treatment
                        Value Std.Error  DF   t-value p-value
(Intercept)          5.126338 0.4797200 114 10.686104  0.0000
Census              -0.080751 0.0235559 114 -3.428056  0.0008
treatmenths          0.626687 0.6784265   6  0.923736  0.3913
treatmentml          0.307876 0.6784265   6  0.453810  0.6659
Census:treatmenths -0.079673 0.0333131 114 -2.391639  0.0184
Census:treatmentml -0.119687 0.0333131 114 -3.592792  0.0005
 Correlation:
                    (Intr) Census trtmnth trtmntm Cnss:trtmnth
Census              -0.810
treatmenths         -0.707  0.573
treatmentml         -0.707  0.573  0.500
Census:treatmenths  0.573 -0.707 -0.810  -0.405
Census:treatmentml  0.573 -0.707 -0.405  -0.810   0.500

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-2.1146654 -0.6603755 -0.1330419  0.5376326  3.1620233

Number of Observations: 126
Number of Groups: 9
```

Table 35: Summary table of a Linear mixed effects model of total population biomass ~ harvest treatment over 12 months harvest

```
Linear mixed-effects model fit by REML
 Data: recovery
       AIC      BIC    logLik
  267.8527 289.5289 -125.9263

Random effects:
 Formula: ~1 | Tank
        (Intercept)  Residual
StdDev:   0.4630867 0.6212053

Fixed effects: dry_mass_g ~ Census * treatment
                        Value Std.Error  DF   t-value p-value
(Intercept)          5.083907 0.5121629 105  9.926348  0.0000
Census              -0.077720 0.0265851 105 -2.923444  0.0042
treatmenths          0.758819 0.7243077   6  1.047647  0.3352
treatmentml          0.703460 0.7243077   6  0.971217  0.3689
Census:treatmenths -0.089111 0.0375971 105 -2.370154  0.0196
Census:treatmentml -0.147943 0.0375971 105 -3.934959  0.0001
 Correlation:
                    (Intr) Census trtmnth trtmntm Cnss:trtmnth
Census              -0.831
treatmenths         -0.707  0.587
treatmentml         -0.707  0.587  0.500
Census:treatmenths  0.587 -0.707 -0.831  -0.415
Census:treatmentml  0.587 -0.707 -0.415  -0.831   0.500

Standardized Within-Group Residuals:
        Min           Q1          Med           Q3          Max
-2.14683104 -0.63843144 -0.09577655  0.59034979  2.99925213

Number of Observations: 117
Number of Groups: 9
```

Table 36: Summary table of a Linear mixed effects model of total population biomass ~ harvest treatment after 6 months recovery period

```
Linear mixed-effects model fit by REML
 Data: grouped_tank_BOFFFs
       AIC      BIC    logLik
  334.5386 358.3525 -159.2693

Random effects:
 Formula: ~1 | Tank
        (Intercept)  Residual
StdDev:   0.3491124 0.6228417

Fixed effects: dry_mass_g ~ Census * treatment
                       Value Std.Error  DF   t-value p-value
(Intercept)         3.729050 0.3793191 139  9.830905  0.0000
Census             -0.044818 0.0170703 139 -2.625482  0.0096
treatmenths         0.006083 0.5364382   6  0.011339  0.9913
treatmentml        -0.577128 0.5366323   6 -1.075462  0.3235
Census:treatmenths -0.043219 0.0241410 139 -1.790270  0.0756
Census:treatmentml -0.086568 0.0241448 139 -3.585354  0.0005
 Correlation:
                   (Intr) Census trtmnth trtmntm Cnss:trtmnth
Census             -0.815
treatmenths        -0.707  0.577
treatmentml        -0.707  0.576  0.500
Census:treatmenths  0.577 -0.707 -0.815  -0.408
Census:treatmentml  0.576 -0.707 -0.408  -0.815   0.500

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.20183486 -0.66617670 -0.04103645  0.53701068  3.86522107

Number of Observations: 151
Number of Groups: 9
```

Table 37: Summary table of a Linear mixed effects model of spawning stock biomass ~ harvest treatment * time

```
Linear mixed-effects model fit by REML
 Data: HS_size_str
       AIC     BIC    logLik
  76626.11 76685.4 -38305.06

Random effects:
 Formula: ~1 | Tank
        (Intercept) Residual
StdDev:    1.069657 5.534503

Fixed effects: Length_mm ~ Census * treatment
                       Value Std.Error    DF    t-value p-value
(Intercept)        14.127038 0.6896132 12219  20.485452  0.0000
Census              0.253127 0.0181786 12219  13.924414  0.0000
treatmenths        -1.777714 0.9677310     6  -1.836991  0.1159
treatmentml        -2.681257 0.9523264     6  -2.815481  0.0305
Census:treatmenths -0.046435 0.0249587 12219  -1.860459  0.0628
Census:treatmentml -0.232358 0.0222611 12219 -10.437828  0.0000
 Correlation:
                   (Intr) Census trtmnth trtmntm Cnss:trtmnth
Census             -0.418
treatmenths        -0.713  0.298
treatmentml        -0.724  0.303  0.516
Census:treatmenths  0.305 -0.728 -0.404  -0.221
Census:treatmentml  0.342 -0.817 -0.243  -0.376   0.595

Standardized Within-Group Residuals:
         Min           Q1          Med           Q3          Max
-2.958256591 -0.777768915 -0.009355348  0.653746528  4.059201198

Number of Observations: 12231
Number of Groups: 9
```

Table 38: Summary table of a Linear mixed effects model of individual body size ~ harvest treatment * time

```
Linear mixed-effects model fit by REML
 Data: HS_recent_census
       AIC      BIC    logLik
  3017.671 3038.519 -1503.836

Random effects:
 Formula: ~1 | Tank
        (Intercept) Residual
StdDev:   0.8807232 5.508925

Fixed effects: Length_mm ~ treatment
                Value Std.Error  DF   t-value p-value
(Intercept) 17.076694 0.7420448 472 23.013022  0.0000
treatmenths  0.138950 1.0397196   6  0.133642  0.8981
treatmentml -5.603315 0.9630768   6 -5.818139  0.0011
 Correlation:
            (Intr) trtmnth
treatmenths -0.714
treatmentml -0.770  0.550

Standardized Within-Group Residuals:
        Min          Q1         Med          Q3         Max
-2.48520674 -0.74974442 -0.04788897  0.66201622  3.30462985

Number of Observations: 481
Number of Groups: 9
```

Table 39: Summary table of a Linear mixed effects model of individual body size ~ harvest treatment after 6 months recovery period.

```
lm(formula = dry_mass_g ~ treatment, data = grouped_biom_yield)

Residuals:
    Min      1Q  Median      3Q     Max
-0.3787 -0.2307 -0.1087  0.1449  1.4654

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  0.23073    0.06174   3.737 0.000377 ***
treatmentml  0.14800    0.08732   1.695 0.094535 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.3705 on 70 degrees of freedom
Multiple R-squared:  0.03942,    Adjusted R-squared:  0.0257
F-statistic: 2.873 on 1 and 70 DF,  p-value: 0.09454
```

Table 40: Summary table of a Linear model of yield in biomass ~ harvest treatment

```
lm(formula = yield ~ treat, data = no_of_fish_stats)

Residuals:
   Min     1Q Median     3Q    Max
-5.949 -3.949 -1.949  2.013 19.051

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   4.1026     0.8031   5.109 2.34e-06 ***
treatml       1.8462     1.1357   1.626    0.108
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 5.015 on 76 degrees of freedom
Multiple R-squared:  0.0336,    Adjusted R-squared:  0.02089
F-statistic: 2.642 on 1 and 76 DF,  p-value: 0.1082
```

Table 41: Summary table of a Linear model of yield in fish numbers ~ harvest treatment

```
lm(formula = size_mm ~ treatment, data = birth_data)

Residuals:
    Min      1Q  Median      3Q     Max
-1.1754 -0.4632 -0.1032  0.4607  1.6538

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   5.2754     0.1195  44.139  < 2e-16 ***
treatmenths   0.2122     0.1486   1.428    0.156
treatmentml  -0.8891     0.1501  -5.924  2.5e-08 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.6546 on 134 degrees of freedom
Multiple R-squared:  0.3778,    Adjusted R-squared:  0.3685
F-statistic: 40.68 on 2 and 134 DF,  p-value: 1.563e-14
```

Table 42: Summary table of a Linear model of size at birth ~ harvest treatment

```
lm(formula = juv_id ~ treatment * female_size, data = brood_size)

Residuals:
    Min      1Q  Median      3Q     Max
-4.9898 -0.9689 -0.0836  0.9304  4.1327

Coefficients:
                          Estimate Std. Error t value Pr(>|t|)
(Intercept)               -8.19237    6.74584  -1.214   0.2347
treatmenths                4.80983    7.98619   0.602   0.5518
treatmentml                4.04367    8.10013   0.499   0.6215
female_size                0.47323    0.26564   1.781   0.0857 .
treatmenths:female_size   -0.14548    0.31759  -0.458   0.6504
treatmentml:female_size   -0.09717    0.34032  -0.286   0.7773
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 2.127 on 28 degrees of freedom
Multiple R-squared:  0.2839,    Adjusted R-squared:  0.1561
F-statistic: 2.221 on 5 and 28 DF,  p-value: 0.08022
```

Table 43: Summary table of a Linear model of brood size ~ harvest treatment

```
lm(formula = size ~ treatment, data = hs_mat_df)

Residuals:
    Min      1Q  Median      3Q     Max
-3.0609 -1.0123 -0.0270  0.9829  3.4825

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  13.8951     0.2989  46.485  < 2e-16 ***
treatmenths  -0.3236     0.3848  -0.841  0.40252
treatmentml  -1.1202     0.3787  -2.958  0.00393 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.434 on 93 degrees of freedom
Multiple R-squared:  0.09939,   Adjusted R-squared:  0.08002
F-statistic: 5.132 on 2 and 93 DF,  p-value: 0.00769
```

Table 44: Summary table of a Linear model of size at maturation ~ harvest treatment

```
lm(formula = age ~ food_level * treatment, data = hs_mat_df)

Residuals:
    Min      1Q  Median      3Q     Max
-30.600 -10.589  -1.500   8.142  71.400

Coefficients:
                       Estimate Std. Error t value Pr(>|t|)
(Intercept)              61.238      9.084   6.741 1.46e-09 ***
food_level              -84.603     37.496  -2.256   0.0265 *
treatmenths              26.362     11.515   2.289   0.0244 *
treatmentml              24.540     11.021   2.227   0.0285 *
food_level:treatmenths  -75.397     48.005  -1.571   0.1198
food_level:treatmentml  -48.175     47.106  -1.023   0.3092
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 17.55 on 90 degrees of freedom
Multiple R-squared:  0.4354,    Adjusted R-squared:  0.4041
F-statistic: 13.88 on 5 and 90 DF,  p-value: 4.761e-10
```

Table 45: Summary table of a Linear model of age at maturation ~ harvest treatment

Appendix III – Additional statistical results for Chapter V

```
Linear mixed-effects model fit by REML
 Data: assym_biomass
       AIC      BIC    logLik
  109.5398 128.3934 -46.76988

Random effects:
 Formula: ~1 | Tank
        (Intercept)  Residual
StdDev:   0.4606052 0.3225758

Fixed effects: dry_mass_g ~ treatment * census
                        Value Std.Error DF    t-value p-value
(Intercept)         1.4369736 0.5427668 69  2.6474971  0.0100
treatmentB          0.9575679 0.7675882  9  1.2475021  0.2437
treatmentC         -1.2041221 0.7675882  9 -1.5687085  0.1512
census              0.0111211 0.0304805 69  0.3648580  0.7163
treatmentB:census  -0.0405654 0.0431060 69 -0.9410606  0.3500
treatmentC:census   0.1136244 0.0431060 69  2.6359295  0.0104
 Correlation:
                   (Intr) trtmnB trtmnC census trtmB:
treatmentB         -0.707
treatmentC         -0.707  0.500
census             -0.899  0.635  0.635
treatmentB:census   0.635 -0.899 -0.449 -0.707
treatmentC:census   0.635 -0.449 -0.899 -0.707  0.500

Standardized Within-Group Residuals:
          Min            Q1           Med            Q3           Max
-1.887383904 -0.696611535  0.003557508  0.655524572  2.033933727

Number of Observations: 84
Number of Groups: 12
```

Table 46: Summary table of a Linear mixed effects model of total population biomass ~ food treatment * time.

```
Linear mixed-effects model fit by REML
 Data: mat_biomass
        AIC       BIC   logLik
  -352.5504 -329.1323 184.2752

Random effects:
 Formula: ~1 | tank
        (Intercept)   Residual
StdDev:  0.01569647 0.05648283

Fixed effects: dry_mass_g ~ treatment * census
                          Value  Std.Error  DF    t-value p-value
(Intercept)       -0.00294787 0.07025364 128 -0.0419604  0.9666
treatmentb         0.21130484 0.09933304 128  2.1272363  0.0353
treatmentc         0.06398037 0.09939560  10  0.6436942  0.5343
census             0.00235961 0.00430411 128  0.5482225  0.5845
treatmentb:census -0.01242506 0.00608661 128 -2.0413765  0.0433
treatmentc:census -0.00280859 0.00608661 128 -0.4614381  0.6453
 Correlation:
                  (Intr) trtmntb trtmntc census trtmntb:
treatmentb        -0.706
treatmentc        -0.707  0.499
census            -0.987  0.698   0.698
treatmentb:census  0.698 -0.987  -0.493  -0.707
treatmentc:census  0.698 -0.493  -0.987  -0.707  0.500

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.3660163 -0.6235665 -0.2748868  0.3817208  3.9328587

Number of Observations: 144
Number of Groups: 12
```

Table 47: Summary table of a Linear mixed effects model of maturing biomass ~ food treatment * time.

```
Linear mixed-effects model fit by REML
 Data: repro_biomass
       AIC       BIC   logLik
  -543.721 -520.3029 279.8605

Random effects:
 Formula: ~1 | tank
        (Intercept)  Residual
StdDev: 0.005913975 0.0284799

Fixed effects: dry_mass_g ~ treatment * census
                         Value  Std.Error  DF    t-value p-value
(Intercept)       -0.02167808 0.03535568 129 -0.6131427  0.5409
treatmentb         0.03208816 0.05000048   9  0.6417571  0.5370
treatmentc        -0.06702225 0.05000048   9 -1.3404321  0.2130
census             0.00228319 0.00217000 129  1.0521620  0.2947
treatmentb:census -0.00227458 0.00306884 129 -0.7411880  0.4599
treatmentc:census  0.00502188 0.00306884 129  1.6364108  0.1042
 Correlation:
                  (Intr) trtmntb trtmntc census trtmntb:
treatmentb        -0.707
treatmentc        -0.707  0.500
census            -0.990  0.700   0.700
treatmentb:census  0.700 -0.990  -0.495  -0.707
treatmentc:census  0.700 -0.495  -0.990  -0.707  0.500

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.4543113 -0.4354297 -0.2982735  0.2297669  4.8833711

Number of Observations: 144
Number of Groups: 12
```

Table 48: Summary table of a Linear mixed effects model of new reproductive biomass ~ food treatment * time.

```
Linear mixed-effects model fit by REML
 Data: mat_numbers
       AIC      BIC    logLik
  958.8899 984.0232 -471.445

Random effects:
 Formula: ~1 | tank
        (Intercept) Residual
StdDev:    1.291594 3.391017

Fixed effects: ind ~ treatment * census
                       Value Std.Error  DF    t-value p-value
(Intercept)         0.049619  3.001561 161  0.0165312  0.9868
treatmentb          7.159758  4.151775 161  1.7245052  0.0865
treatmentc          4.376741  4.298301  10  1.0182492  0.3326
census              0.167277  0.188852 161  0.8857546  0.3771
treatmentb:census  -0.433459  0.263898 161 -1.6425281  0.1024
treatmentc:census  -0.155547  0.269869 161 -0.5763793  0.5652
 Correlation:
                   (Intr) trtmntb trtmntc census trtmntb:
treatmentb         -0.717
treatmentc         -0.698  0.501
census             -0.967  0.701   0.676
treatmentb:census   0.689 -0.968  -0.481  -0.717
treatmentc:census   0.677 -0.490  -0.967  -0.700  0.501

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.5476670 -0.5119579 -0.2190202  0.2092856  5.2753364

Number of Observations: 177
Number of Groups: 12
```

Table 49: Summary table of a Linear mixed effects model of number of maturing individuals ~ food treatment * time.

```
Linear mixed-effects model fit by REML
 Data: repro_biomass
       AIC      BIC    logLik
  548.6542 572.0722 -266.3271

Random effects:
 Formula: ~1 | tank
        (Intercept) Residual
StdDev:   0.2793715 1.494061

Fixed effects: percentage ~ treatment * census
                        Value Std.Error  DF    t-value p-value
(Intercept)       -1.3619386 1.8535391 129 -0.7347774  0.4638
treatmentb         0.8316897 2.6213001   9  0.3172814  0.7583
treatmentc        -1.4103688 2.6213001   9 -0.5380417  0.6036
census             0.1435260 0.1138384 129  1.2607867  0.2097
treatmentb:census -0.0678947 0.1609918 129 -0.4217273  0.6739
treatmentc:census  0.1078780 0.1609918 129  0.6700840  0.5040
 Correlation:
                  (Intr) trtmntb trtmntc census trtmntb:
treatmentb        -0.707
treatmentc        -0.707  0.500
census            -0.990  0.700   0.700
treatmentb:census  0.700 -0.990  -0.495  -0.707
treatmentc:census  0.700 -0.495  -0.990  -0.707  0.500

Standardized Within-Group Residuals:
       Min         Q1        Med         Q3        Max
-1.1336291 -0.5255492 -0.3281258  0.1027517  4.4984496

Number of Observations: 144
Number of Groups: 12
```

Table 50: Summary table of a Linear mixed effects model reproductive biomass as a proportion of total population biomass ~ food treatment * time.