Contemporary evolution caused by fisheries

Contributions from experimental studies.

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Scientific environment

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I love fools' experiments. I am always making them.
Charles R. Darwin,
as quoted by E. Ray Lankester

Abstract

Evolutionary change is occurring within tens of generations or fewer in nature. This contemporary evolution is commonly caused by human activities, as they alter the selective pressures that the populations experience. Human harvesting activities (plant gathering, hunting and fishing) are imposing particularly high selective pressure on natural populations and thus, inducing great changes in the populations. In the case of fishing, the selection is commonly imposed on size, as large fish are more valuable commercially. However, fishing can also be selective on other traits, such as behaviour, morphology, sex, etc. Thus, theoretically fishing can cause evolutionary change in the exploited populations, which may not only affect population viability, but also productivity for fisheries.

Exploited stocks are experiencing phenotypic change in life history traits, mainly age and size at maturation, growth, and fecundity. These observed changes occurred in the expected direction if fishing would be causing evolutionary change, referred to as fisheries-induced evolution (FIE). Evidence for FIE is accumulating from three different research areas, theoretical modelling, empirical evidence from the field, and experimental studies. Each one of these areas of research has contributed to establishing the current knowledge on FIE. However, it is still not clear whether the changes observed have a genetic basis, whether fishing selectivity is the main driver, and whether the changes are occurring at a fast enough pace to be considered in fisheries management plans. This thesis contributes to clarifying some of these questions using an experimental approach.

Most evidence for FIE comes from analysing field data using the Probabilistic Maturation Reaction Norm (PMRN) approach. This method infers genetic change from phenotypic data, but its approach has been questioned. *Chapter I* is an experimental evaluation of the PMRN. We estimated PMRN from male guppies differing in growth rate and the social environment they were reared in. We found that the PMRN could not completely account for these environmental effects, but the PMRN method performed better when a measurement of maturation closer to the maturation decision (initiation of maturation, rather than completion) was considered. Moreover, the analyses of empirical data have focused on studying the effect of size-selectivity on maturation schedules, as this is the data readily available. Thus, the assessment of other effects of fishing selectivity has been scarce. *Chapter II* shows that fishing has potential to cause selection on traits other than size and

such selectivity has broader consequences than changes in the time of maturation. In *Chapter II*, we studied the selectivity of passive and active fishing gears on fish personality (shy-bold axis). Shy individuals were caught less by the passive trap, while they were caught more often by the trawl. Shy individuals seem to grow faster than bold ones. We discussed that such selectivity may alter the population structure, but also the fishery productivity, as personality can be associated with productivity traits (e.g., growth).

Evidence that fishing selectivity can cause genetic change comes from experimental studies. However, the applicability of such results has been questioned, due to the experimental conditions not being comparable to natural populations (reviewed in *Chapter IV*). In *Chapter V*, we aimed to study the effect of size-selective fishing in experimental guppy populations. Our populations were created intending to be more comparable to natural populations. Fishing pressure mimicked that of exploited populations in the oceans and in our experimental conditions ecological feedbacks and natural selection were allowed in self-renewing and age- and size-structured experimental populations. We compared three different harvesting regimes (removing large individuals, removing small ones and size-independent harvest), which resulted in different growth rates, size at maturation and fecundity. Density-dependent processes heavily influenced these changes, but size-selective fishing also played a role. Unfortunately, the experiment described in *Chapter V* is in a too early phase to conclude whether the changes observed are genetic or phenotypic.

I believe dissemination of scientific goals and results, particularly to the general public, is a very important aspect of research. *Chapter III* describes a savoury approach on how to present the ecological and evolutionary consequences of fishing to schools or undergraduate students. In this experiment, we used fish-shaped candies as a common resource that was exploited by university employees. Even with such a simple experimental setting, we observed the processes commonly present in a real fishery, overexploitation, the tragedy of the commons vs. close access, and evolutionary effects.

This thesis aimed at contributing to the knowledge on the evolutionary effects of fishing. Particularly, it addressed the potential that the experimental approach has on studying contemporary evolution in a broad range of traits, caused by selective fishing. Additionally, it focused on several aspects of FIE that are currently on debate, as it intended to fill up some of the gaps that still remain in the study of FIE.

List of publications

I. Diaz Pauli, B. and Heino, M. The importance of social dimension and maturation stage for the probabilistic maturation reaction norm in *Poecilia reticulata*. *Submitted manuscript*

II. Diaz Pauli, B., Wiech, M., Heino, M. and Utne-Palm, A. C. Do personality types differ in vulnerability to fishing gear? *Submitted manuscript*

III. Diaz Pauli, B. and Heino, M. Ecological and evolutionary consequences of fishing. The candy fish experiment as an educational tool. *Submitted manuscript*

IV. Diaz Pauli, B. and Heino, M. What can selection experiments teach us about fisheries-induced evolution? *Submitted manuscript*

V. Diaz Pauli, B., Savolainen, H., Utne-Palm, A. C., Reznick, D. and Heino, M. Phenotypic changes in growth and maturation and dynamics of exploitation of experimental populations of guppies (*Poecilia reticulata*). *Manuscript*

Contents

Contemporary evolution caused by fisheries

1. Contemporary evolution

Contemporary evolution refers to microevolutionary change that takes place in hundreds of generations or fewer (Hendry and Kinnison 1999, Carroll et al. 2007). This concept contrasts with the idea that evolution is a slow process that requires the pass of many centuries to take place (Darwin 1859). However, since the 1990s there has been increasing awareness about the common occurrence of contemporary evolution and its consequences for populations and ecosystems (see Carroll et al. 2007 for a historical review). The evolutionary changes observed within humanly observable time scales range from changes in the specialization to new hosts (e.g. adaptation of apple maggot fly to introduced apples), the acquisition of resistance to antibiotics or insecticides in bacteria or pests, to the loss of colouration of guppies in the presence of predators (for more comprehensive reviews see Thompson 1998, Hendry and Kinnison 1999, Palumbi 2001, Reznick and Ghalambor 2001, Carroll et al. 2007). These evolutionary changes do not only allow the populations to adapt to the new environment, but in turn these changes can affect the ecology of populations by altering reproductive success and community structure resulting in eco-evolutionary dynamics (Kinnison and Hairstone 2007, Fussmann et al. 2007, Hendry et al. 2007).

Recent studies show that contemporary evolution is a common response to human-induced changes of selection pressures or population structures (Palumbi 2001, Ashley et al. 2003, Rice and Emery 2003). This can be due to human selection being stronger than natural selection, as already Darwin (1859) considered and Hendry et al. (2008) calculated. It is unclear whether human-induced is more common than natural rapid evolution, as this impression might be simply caused by biased sampling (Reznick and Ghalambor 2001). Either way, human-induced contemporary evolution is a widespread phenomenon and the main drivers of it are habitat fragmentation or degradation, the introduction of exotic species and harvesting of natural populations as they entail large selection pressures (Stockwell et al. 2003).

Harvesting, by plant gatherers, hunters and fishers, has been shown to produce the

largest changes in wild populations, and these changes are greater in life history traits than in morphological ones (Darimont et al. 2009, Devine et al. 2012); although not restricted to those (e.g., see Conrad et al. 2011). The selection imposed by harvest is directly targeted at the phenotypes of human interest (e.g. large roots or leaves, horn size, body size) and remains constant over long periods of time. Other human-induced and natural selection pressures are not that stable over time and do not focus on certain phenotypes, which results in lower strength of selection (Darimont et al. 2009).

Commercial harvest results in bigger changes, relative to recreational and scientific harvest (Darimont et al. 2009). Commercial exploitation of natural populations differs from exploitation and breeding of domestic species (agriculture and cattle farming) in its selectivity. The former is prone to remove all valuable individuals from the stock, while the latter deliberately keeps some individuals with those valuable traits in order to ensure future production. This thesis focuses particularly on the selection pressures imposed by commercial fishing and its potential to cause evolutionary changes in the fish stocks, referred to as fisheries-induced evolution (FIE).

2. Fisheries-induced evolution

Most aquatic areas are exposed to fishing activities, 89% of those areas are marine ecosystems. Only 15% of marine fish stocks are moderately exploited or underexploited, while 32% are overexploited, depleted or recovering (FAO 2010). Fishing imposes an increased mortality on the exploited population, altering the abundance and thus, the population (size distribution, interspecific competition, etc.). Fishing activities also alter the community structure through the removal of individuals (e.g. altering the food web; Pauly et al. 1998) or by disturbing the habitats (e.g. trawl on macrobenthos; Moran and Stephenson 2000). All these changes in the environmental conditions may shift the selective pressure the exploited populations are experiencing. Fishing intentionally selects those individuals with more valuable traits (e.g. large fish are more economically valuable; Zimmermann et al. 2011), but thereby often also unintentionally selects for a certain sex, behaviour, activity, physiology or morphology (Heino and Godø 2002; Enberg et al. 2012). The effects of fishing on the population can be categorized as 1) demographic effects, affecting population density and structure, 2) ecological effects, influencing the
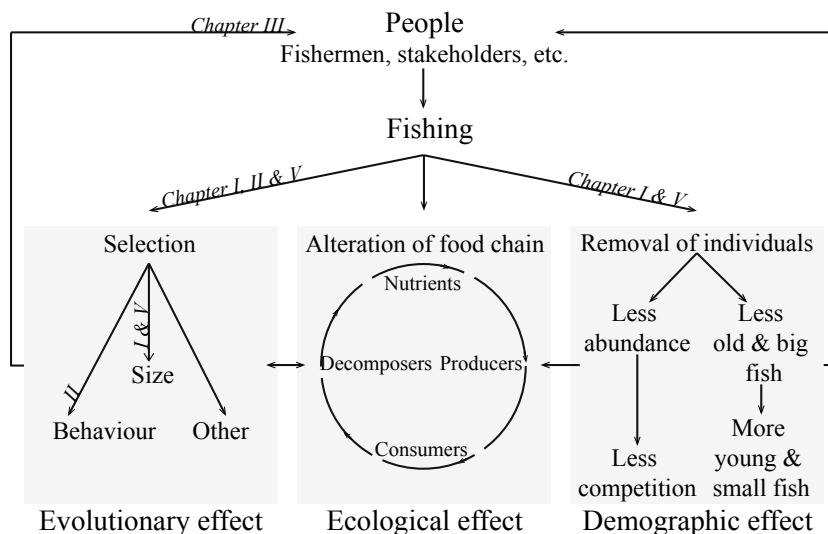
Figure 1. General overview of the different effects that fishing activities cause on the exploited stocks. Text in italics refers to the chapters from this thesis that handle those topics.

communities, and 3) evolutionary effects, when the selective pressure is altered, either directly by removing individuals with specific traits or indirectly by altering the environmental conditions (Figure 1).

Several studies show that marine and freshwater stocks are experiencing phenotypic changes in life history traits (for reviews see for example, Miller 1957, Trippel 1995, Sharpe and Hendry 2009). It was previously thought that the main driver of such changes was the release of competition through the reduction of stock biomass (Law 2000), i.e. fishing had only demographic and ecological effects on the populations. However, this demographic effect alone cannot explain all the changes observed (Law 2000). Currently, it is

considered that the evolutionary effect of fishing (due to its selective nature) has a major role in changing the life history of exploited fish (Law 2000, Jørgensen et al. 2007, Dunlop et al. 2009a, Sharpe and Hendry 2009). However, it is not the sole player, other factors such as environmental change and the previously mentioned demographic and ecological effects of fishing also contribute.

Evolution is defined as a change in allele frequencies in a population over time. Besides neutral evolution through genetic drift, a selective pressure imposed on a genetically variable population causes evolutionary change. Therefore, for an evolutionary change induced by fishing pressure to occur, there has to be a genetic

basis for the phenotypic variation under selection. There is evidence that traits under fishing selection, such as life history, morphological and behavioural traits, are heritable (Mousseau and Roff 1987, Merilä and Sheldon 2000). Moreover, breeding programs (Fjalestad et al. 2003, Gjedrem et al. 2012) and selection experiments (Reznick et al. 1990, Conover and Munch 2002, Philipp et al. 2009) have shown that selection of certain traits can result in genetic change of commercially interesting traits. Therefore, theoretically the potential for fisheries-induced evolution should not be doubted.

Evidence for fisheries-induced evolution

The study of FIE has been based on three different areas of research: empirical field studies, theoretical modelling and experiments. Most of the evidence comes from the empirical studies, which have been focused on phenotypic changes in maturation and growth (Dunlop et al. 2009a). Only recently, the potential for an evolutionary basis in those traits has been investigated with the implementation of probabilistic maturation reaction norms (PMRNs; Box 1; Heino et al. 2002, Dieckmann and Heino 2007) to these empirical data. PMRNs can infer genetic shifts from phenotypic data due to their

formulation (Box 1; Heino et al. 2002, Heino and Dieckmann 2008). These studies suggested evolutionary trends towards maturation at lower age, size and condition, reduced growth and increased fecundity (see supplementary material from Jørgensen et al. 2007).

Many theoretical models have been developed to study different aspects of the evolutionary effect of selective fishing (see Dunlop et al. 2009a for a review). Recently, complex models have been developed, which incorporate ecological and evolutionary processes to the simulation of age- and size-structured populations (Dunlop et al. 2009b). These models not only allow to study when fishing-induced evolution can take place, but estimate the rate at which it happens and the rate of reversal to initial conditions. Most importantly, they strengthen the theoretical evidence that selective fishing can be a main driver of the trends observed empirically (Dunlop et al. 2009b). It has been shown that phenotypic changes occurred rapidly, while genetic changes happened gradually during the size-selective harvesting period. The reversal of those changes during a moratorium period occurred at a much lower rate, due to natural selection pressure being weaker than the harvesting

Box1: Probabilistic Maturation Reaction Norms

A *reaction norm* describes the full distribution of the different phenotypes produced in different environments by a single genotype. Thus, they are genetically determined. However, perfect reaction norms cannot be easily obtained to study genetic changes, because considering all the environmental conditions is not possible. Thus, inference about genetic changes can only be done when the key environmental effects are included.

A *reaction norm for age and size at maturation* (or *maturation reaction norm*) (Stearns and Koella 1986) is represented as a curve in a diagram with age and size as coordinate axes. By measuring size and age, information on growth and survival is obtained, which capture the environmental conditions. Thus, a *maturation reaction norm* captures the effects of environmental variation (in conditions for growth and survival) on maturation. Maturation occurs when a growth trajectory hits the reaction norm. The environmental changes (reflected by changes in the slope of growth and in the probability of survival) are represented as maturation events (i.e., points) along the reaction norm. The genetic changes are represented by the shape and position of the reaction norm. Thus, reaction norms of maturation offer more information than mean ages and sizes at maturation (Figure B1a). Maturation is assumed to be a deterministic process.

A *probabilistic maturation reaction norm (PMRN)* includes a probabilistic nature to the maturation reaction norm (Figure B1b). Therefore, maturation is no longer deterministic and the allowed stochasticity represents that the maturation process cannot be solely explained with age and size (Heino et al. 2002). Thus, PMRN is defined by the probability of maturing at a certain age and size, given that the individual has survived to that point and is still immature. A shift in the PMRN can be interpreted as an evolutionary change, because environmental effects are represented in changes in growth rates and the PMRN already accounts for them (Figure B1b).
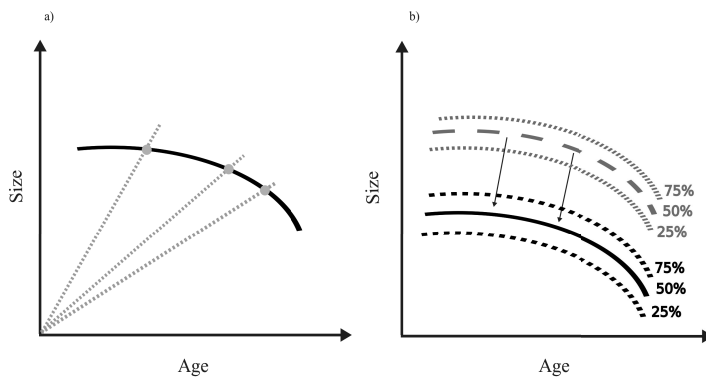
Figure B1. a) Maturation reaction norm curve (solid line) maturation occurs when the growth trajectory (dotted grey lines) hits the curve (grey dots). b) PMRN midpoint (black solid line) and maturation envelope (black dotted lines) describe age and size at which 50%, 25% and 75% of the individuals mature. Downward shift (arrows) from grey PMRN curves to black PMRN is interpreted as evolutionary change.

selection (Dunlop et al. 2009b, but see Andersen and Brander 2009).

Experimental studies allow FIE to be assessed empirically and under more controlled settings compared to studies based on field data. The experimental set-up can account for confounding factors and thus, unequivocally determine the drivers of the change and whether the change is phenotypic or genetic. In addition, experiments enable us to account

for trade-offs and genetic covariances and to study a broader range of traits than field-based data, as selection can be focused deliberately on traits other than size, growth and maturation.

Several studies have shown the evolvability of traits under different selection pressures. These studies were mainly based on comparing different populations that occur along environmental gradients and rearing them under common garden conditions (Reznick and Ghalambor 2005, Conover et al. 2009, Conover and Baumann 2009). Selection experiments have demonstrated that a selective agent can cause evolutionary change (Fuller et al. 2005). Experiments designed to study different aspects of FIE have shown that selective fishing can cause genetic changes in growth (Edley and Law 1988, Conover and Munch 2002), age and size at maturation (Edley and Law 1988), fecundity (Edley and Law 1988, Walsh et al. 2006), vulnerability to be caught (Philipp et al. 2009), larval viability, food consumption (Walsh et al. 2006), and metabolic rate (Redpath et al. 2009).

There is a fourth approach that has recently begun to be applied to study adaptive evolution (Naish and Hard 2008, Nielsen et al. 2009a). It is based on studying genetic changes based on molecular markers and quantitative traits. In order to determine that adaptive change has occurred, caused by certain selection pressure, six criteria should be fulfilled: 1) genetic variation exists, 2) genes assessed are relevant to the environmental stress of interest, 3) genes are analysed over time, 4) selection is tested, 5) shifts in allele frequency agree with expectations, and 6) simple replacement by a genetically different population is not adaptive genetic change (Hansen et al. 2012). Evidence from this area of research is only starting to accumulate for general evolutionary change studies (Hansen et al. 2012) and is still scarce for fisheries-induced genetic changes.

Criticisms of fisheries-induced evolution

Despite the evidence for FIE described above, there is still a debate on whether FIE is occurring in natural populations and whether it should be included in fisheries management plans (Jørgensen et al. 2008, Browman et al. 2008, Kuparinen and Merilä 2008, Andersen and Brander 2009).

Field based evidence has been criticised for inferring genetic changes from phenotypic data and not being directly based on genetic observations (Marshall

and Browman 2007, Kuparinen and Merilä 2008). Moreover, the roles of other drivers (environmental, physiological, etc.) are not clearly taken into account (Marshall and Browman 2007, Browman et al. 2008, Andersen and Brander 2009). This issue is also discussed in this thesis (*Chapter I*).

Experimental evidence of FIE has been critiqued for 1) imposing extremely high knife-edge selection (Hilborn and Minte-Vera 2008, Brown et al. 2008), 2) not allowing density-dependent processes, 3) describing semelparous life histories with discrete generations (Hilborn and Minte-Vera 2008, *Chapter V*), and thus representing simple experimental conditions that cannot be compared to wild conditions (Hilborn 2006, Hansen et al. 2012). *Chapter V* aimed at studying FIE circumventing some of these criticisms.

Most research has been focused on size-selectivity's direct effects on size and its consequences on growth and maturation. However, fishing may be affecting the populations in a multitude of ways. It has been suggested that fishing can be directly selective on fast growth (Biro and Post 2008) and both directly (Philipp et al. 2009) and indirectly selective on behaviour (Walsh et al. 2006). *Chapter II*

also showed how fishing pressure could be selective towards behaviour.

3.   Aims of the thesis

From the above it should be clear that FIE could be caused by several direct and indirect mechanisms. Therefore this thesis was aimed to study different aspects of FIE using an experimental approach. The main issues assessed were:

1)   Experimental evaluation of the probabilistic maturation reaction norm method (*Chapter I*). Can PMRN account for all environmental variability under experimental conditions? Which factors are more important drivers of maturation? How does considering different maturation stages influence PMRN?

2)   Assessment of the fishing gear selectivity on behaviour (*Chapter II*). Are passive and active fishing gears selective towards personality types? What are the consequences of the selectivity?

3)   Dissemination of ecological and evolutionary consequences of fishing to the general public (*Chapter III*). How selective fishing consequences can be taught in a simple and savoury way? Can we harvest in an ecologically and evolutionary sustainable way? Can fisheries scientists harvest sustainably?

4) Experimental approach to the study of FIE (*Chapters IV and V*). What are the strengths and limitations of experimental studies considering FIE? How is the phenotypic response to size-selective fishing of a size- and age-structured experimental population?

4.   Model species

The Trinidadian guppy, *Poecilia reticulata*, has been used as model species for this thesis (*Chapters I, II and V*). The guppy is a small, freshwater, live-bearing fish native from NE South America and Trinidad and Tobago (Magurran 2005). Guppies present sexual dimorphism, with males being more colourful and smaller than females (approximately 16 mm standard length for mature males and 18-35 mm for mature females). It is a member of the Poeciliidae family and as all members it has internal fertilization (Wourms 1981) with the help of the gonopodium (modified anal fin in males). The external development of the gonopodium is correlated with the maturation of the gonads (Kallman and Schreibman 1973, Schreibman and Kallman 1977). Thus, the maturation stage of males can be visually determined (Turner 1941) in vivo. Females can mate multiply and they can store sperm in their ovaries for months (Constantz 1984).

Insemination can occur during consensual mating, after courtship behaviour, or during forced inseminations (Liley 1966). Males reach maturity when they are seven weeks old or younger, while females are between ten and twenty weeks old at the time of their first parturition and they reproduce continuously thereafter, producing litters every three to four weeks (Reznick et al. 2001).

Naturally occurring populations differ in life history, behavioural and morphological traits depending on their locality of origin. There is substantial research on the differences between populations subjected to high and low predation in the Northern Range Mountains of Trinidad (Haskins et al. 1961, Seghers 1973, 1974, Endler 1980, Reznick et al. 1990). The guppies used for this thesis belong to the Yarra River in Trinidad, which is a low predation site. Low predation guppies were chosen to avoid any natural adaptation to size-selective mortality. This was of concern for *Chapter V*. Low predation individuals relative to high predation individuals present weaker anti-predator responses, later maturity, reduced reproduction, more intense sexual selection, and males are larger and more colourful (for a summary see table 2.2 in Magurran 2005).

Guppies are an excellent model species for a wide range of studies, due to their amenability, small size, short generation time, and high probability of survival in the lab, and continuous reproduction. In addition, several well-developed techniques to assess maturation (Turner 1941, Reznick 1990), mating behaviour (Liley 1966), personality (Burns 2008), and life history evolution (Reznick and Bryga 1987) make its use as model species easy and comparable between studies.

Besides guppies, we also used in *Chapter III*, employees at the University of Bergen, Institute of Marine Research and Fisheries Directorate in Bergen (Norway), as well as, fish-shaped candies (Malaco Salt Sild and Brynild Jordbær Fisker) as model species.

5. Main results

Experimental evaluation of the PMRN method (Chapter I)

The probabilistic maturation reaction norm (PMRN) is the main method to infer genetic changes from long-term field data induced by fisheries pressure, as it can disentangle phenotypically plastic from genetic changes (Heino and Dieckmann 2008). Its strengths and limitations have

been debated (Marshall and Browman 2007, Dieckmann and Heino 2007).

PMRN improves the deterministic estimation of maturation (Box 1) by including probabilistic growth and maturation and removes the environmental effects on varying survival and juvenile growth from the maturation schedules. Therefore, it is possible to account for and infer phenotypic plasticity in maturation and genetic adaptation (Dieckmann and Heino 2007).

However, they have been criticised for not considering other environmental factors that might affect maturation (Kraak 2007, Morita et al. 2009). Although these could be included in the estimation (Heino and Dieckmann 2008), and for describing the maturation stage instead of the maturation decision, which is controlled by physiological stages, rather than age and size (Wright 2007). Therefore, it has been suggested that the power of PMRNs should be tested under controlled experimental conditions (Heino and Dieckmann 2008), which has only been done once by Uusi-Heikkilä et al. (2011).

Here we present results from our experimental assessment of PMRN under different food availabilities, similar to Uusi-Heikkila et al. (2011). However, we used the direct estimation (Heino et al.

2002), instead of the demographic estimation of PMRN (Barot et al. 2004), and expanded the assessment to 1) extra environmental variability in the form of different social contexts, and 2) included two estimates of maturation stage, which might differ in their proximity to the maturation decision.

Our results agree with Uusi-Heikkila et al. (2011), that differential growth rate was not completely accounted for by the PMRN in experimental settings, but the differences are reduced when condition (Fulton condition index) is included in the analysis. Variation in the social environment was neither completely accounted for by the PMRN, but its effect was lower than food availability. The most interesting result was that the outcome of the analysis changed when initiation of maturation was considered as maturation stage, instead of completion of maturation (see *Chapter I* for details). The effects of food availability and social cues were always lower in the PMRN estimated for initiation of maturation. We hypothesised that initiation of maturation might be closer to the maturation decision, and thus PMRN for initiation describes better the maturation schedule in male guppies.

Assessment of the fishing gear selectivity on behaviour (Chapter II)

The study of FIE has been mainly focused on the adaptive change in life history traits. Studies concerned with behavioural changes have been scarce (Uusi-Heikkilä et al. 2008), despite the fact that there has been awareness that fishing can also be selective towards certain behaviours (Heino and Godø 2002) and fish behaviour has long been considered for improving fishing gears (Fernö and Olsen 1994).

Behaviour is the first response to most human-induced changes (Sih et al. 2011) and fishing should be no exception. This first response may be plastic, but over time it can become an evolutionary response if the behaviour is heritable (already shown for angling vulnerability by Philipp et al. 2009; for examples on heritabilities in behaviours, Mousseau and Roff 1987). This evolutionary change in behaviour might or might not affect the viability of the population, but it eventually will have implications for fishery productivity, as the populations will become harder to catch. Moreover, behaviour selectivity can be indirectly selective towards other traits, such as life history and physiology, which might

influence even further the population and the fishery.

We studied the selectivity towards personality type (in the shy-bold axis) of two types of fishing gear, a trawl and a trap. Selectivity of passive gears towards behaviours have been already studied (Suski and Philipp 2004, Cooke et al. 2007, Biro and Post 2008), but the effect of active gears has generally been ignored (but see Wilson et al. 1993) even though it is known that behaviour affects the capture process of active gears such as trawls (Engås and Godø 1989, Heino and Godø 2002). Moreover we studied the relationship between personality and activity, growth, and metabolic rate to uncover possible indirect selectivity of the different gears.

We showed that an experimental trawl and trap were selective towards female guppies' personality. The trap caught bold individuals more often, while these escaped the trawl more often. Personality was weakly correlated with growth rate; shy individuals presented higher growth. We found no correlation between metabolic rate and activity with personality.

Our results indicate that fishing can impose selection towards personality in the fished populations. If this differential

vulnerability has a genetic basis (Wohlfarth et al. 1975, Philipp et al. 2009), gear selectivity can affect the population structure and might make the capture process less effective as populations are becoming less vulnerable to capture. We could show only weak indirect selection of growth rate in our experimental setting. However, other studies showed that disrupting the personality distribution of the population has effects on many aspects of the structure and viability of the population (schooling behaviour, Budaev 1997; resistance to stress, Budaev and Zhuikov 1998; female choice, Godin and Dugatkin 1996; and feeding motivation and swimming, Dyer et al. 2008). Moreover, selectivity on personality may alter the productivity of the fishery when personality types are correlated with productivity traits (e.g., growth and fecundity).

Dissemination of FIE to the general public (Chapter III)

Fisheries management is a challenging issue and thus not all management plans are successful (for a review Dankel et al. 2008). It has been suggested that it is easier to put a man on the moon than to achieve economically and biologically sustainable fisheries (Hilborn 2007). The

main challenge is that fisheries management is about managing people and their complex behaviour (Larkin 1988, Hilborn 2007). On the one hand, fisheries seem to be stuck in the *tragedy of the commons* (Hardin 1968). On the other hand, *public goods game* experiments result in people acting better than expected and overcoming the *tragedy* (Kraak 2010). The *tragedy of the commons* refers to the idea that overexploitation will always occur when a common resource is exploited, because people tend to behave selfishly and the costs of such behaviour are shared by all exploiters (Hardin 1968).

The fishery is a complex system where ecological and evolutionary processes interplay with human behaviour. We wanted to test whether this complexity was reflected in a very simple system (candies, as a common resource, and fisheries scientists, as exploiters) and to determine its consequences. Our results indeed resembled the complexity observed in fisheries systems.

Some of the populations suffered the tragedy of the commons and went extinct, while others circumvent the tragedy when a 'stock manager' arose independently of the experimental set-up and ensure more cautionary exploitation. There were even incidents of introduced 'alien' species.

Evolutionary changes occurred in the populations, as the higher selectivity towards the tastiest clone resulted in almost complete removal of that clone from the population. However, the ecological consequences overshadowed the evolutionary, as extinction was the most common outcome. In addition, fisheries scientists did not seem to harvest the populations more cautiously than the other participants.

We believe our candy experiment is a very valuable tool for disseminating the complex nature of fisheries systems in schools and undergraduate students. It is open to many variations that allow shifting the focus to different issues in fisheries management, 1) tragedy of the commons vs. cooperative behaviour, 2) FIE, as in our case, and 3) other ecological consequences (e.g. how species that differ in productivity are affected when they are harvested in the same manner).

Experimental approach to the study of FIE (Chapters IV and V)

The main focus of this thesis was the experimental study of FIE. After reviewing the literature on how experiments contributed to the knowledge on FIE, we concluded that selection experiments had a major role. Selection

experiments allow controlling the selection strength and disentangling phenotypic from genetic changes. Additionally, selection experiments enable us to study the response of a broader range of traits to the selective pressure (*Chapter IV*). However, we also pointed out some limitations in the set-up of previous studies. Lack of ecological realism and thus, difficulty to compare to natural populations, was the main one. 1) The use of model species (clonal or semelparous species) that differ from typical exploited species, and 2) absence of density-dependent feedbacks and natural selection, are the main issues that reduced the realisms of the experimental set-ups.

We designed a selection experiment aimed at overcoming some of the limitations mentioned (*Chapter V*). This selection experiment started in October 2010, when the selective harvest started, and it is planned to continue until October 2012, with the same settings, but until end of 2014 in slightly different settings (selective harvest will continue in some populations, but assessment of recovery will also be performed). We aim at studying how size-selective harvest affects life history (maturation, growth, and fecundity), morphological (body shape and colouration) and, behavioural (mating, personality, and gear vulnerability) traits,

as well, as changes in yield. Phenotypic responses are assessed from *census fish* (representative samples of the population; see *Chapter V* for details), while genetic responses are assessed from annual common garden experiments and molecular analyses. Once a year four females from each population are removed from aquaria and maintained isolated under common garden conditions (light, temperature, water quality and, food availability) to rear their second-generation offspring. From these second-generation individuals, growth, maturation, fecundity, morphology, mating behaviour, personality and, gear vulnerability are measured. This process lasts for approximately nine to twelve months. At the time of writing this thesis, the first common garden was finished and the second one was in progress. The molecular analyses have not been performed yet. Thus, no genetic responses could be presented.

In *Chapter V*, we present the initial phenotypic responses of guppy populations under different size-selective harvesting regimes. Positive size-selective fishing (*positive harvest*) consisted of removing large individuals; negative size-selective fishing was the removal of small individuals (*negative harvest*), while size independent-selective fishing, was the

removal of both large and small individuals (*random harvest*). We showed how these different harvesting regimes resulted in different growth rate, male age and size at maturation, female size at maturation, fecundity, and generation time in the populations. The driver of these changes is certainly a combination of selective harvest and density-dependent feedbacks, mainly resource competition and cannibalism. At the end of the study it was difficult to differentiate the role of each factor.

Chapter V represents only the initial stage of a long-term experiment, but it was included in the thesis to highlight the complex response of the populations. Even though the populations were created and maintained under equal and controlled conditions, different ecological processes arose in each population, which led to different outcomes. Growth, age and size at maturation, and fecundity differed between fishing regimes. These differences were partly due to the fishing regimes, and partly due to density-dependent processes, such as competition for resources and cannibalistic pressure. This complex experimental set-up certainly masks the effect of selective harvest, but when the harvest pressure is imposed for longer time, the density-

dependent differences will be easier to account for and interpret.

6. Conclusions and future perspectives

Fishing is an important selective pressure that may be causing contemporary evolution in marine and freshwater systems. Despite the large amount of studies performed, there are still important gaps in our knowledge of FIE. The main issues are 1) whether the phenotypic changes observed have a genetic basis, 2) whether fishing selectivity is the major driver of the changes, and 3) is the rate of change fast enough to be considered in management plans.

Chapter I focused on how to disentangle genetic from plastic effects. PMRNs have been used as tool to infer genetic changes from phenotypic data, and *Chapter I* was an experimental assessment of such tool for our model species. The PMRNs estimated in *Chapter I* could not completely account for growth and social environment effects on maturation. However, when the PMRN was estimated for initiation of maturation, the effects of growth and social environments were reduced. PMRN will also be estimated for the populations in our selection experiment at a later stage, when phenotypic changes are more obviously

observed. Thereby, we will be able to compare the performance of PMRN under different experimental conditions (isolated vs. population individuals).

Chapter II dealt with how fishing can be the driver of phenotypic and genetic changes. It addressed behaviour-selective effect of fishing, compared to the size-selective effect most commonly considered. We found that the trap caught bold individuals more often, while they escaped the trawl more, compared to shy individuals. The trap and the trawl indirectly selected on growth rate, as shy individuals grew more in our experiment. Thus, *Chapter II* contributed to broaden our knowledge of the process of how fishing selectivity can affect different traits. Additionally, *Chapter II* served as pilot study to establish the experimental routines to assess gear vulnerability and personality that will later be applied to individuals from the selection experiment.

I believe the major contribution to the study of FIE is *Chapter V* or will be in its final version, as it addresses the three main questions posed above. Moreover, it addressed those questions with an experimental set-up more complex than previously done. Ecological processes were allowed and could be accounted for, which may make the results be more readily comparable to natural populations.

Size-selectivity, competition for resources and cannibalism jointly contributed to the changes in growth, maturation and fecundity observed in our populations.

The public dissemination of results is a very important part of the research process, especially to a broad audience, as done with *Chapter III*. It has been shown that experimental studies reach wider audiences and stimulate more interest, as exemplified by Conover and Munch's (2002) study. This and the previously mentioned advantages of experimental studies over correlative studies make me believe more effort should be put in studying FIE from an experimental point of view. Rutter (1902) raised attention to the potential deleterious effects of size-selective fishing as early as in 1902. Much theoretical and empirical development has been done since, but Conover and Munch's (2002) experiment remains one of the most cited studies.

Molecular analyses have begun to be applied to the study of FIE (Nielsen et al. 2009b) and when those techniques are further developed, empirical studies of field data will gain importance again. However, experimental studies, when appropriately designed, will still be of great importance to study the processes and proximate causes that lead to adaptive responses to fishing pressure.

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