EVOLUTIONARY EFFECTS OF FISHING AND IMPLICATIONS FOR SUSTAINABLE MANAGEMENT: A CASE STUDY OF NORTH SEA PLAICE AND SOLE

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Summary

Exploited resources might genetically evolve as a consequence of exploitation by adapting their life history to the imposed mortality regime. Although evolution favors traits for survival and reproduction of the fittest, human-induced evolution might have negative consequences for the exploiter. In general, a shift towards lower growth rate, earlier maturation and increased reproductive investment might be expected from increased (unselective) mortality and these changes might lead to generally smaller exploited individuals. Hence, the evolution might negatively affect the productivity of the resource and thus the sustainable exploitation and furthermore, genetic changes might be slow to reverse. If selection forces are high, evolution might occur fast and be observable within a few decades. Fisheries provide a large scale experiment for fisheries-induced evolution (FIE) since fishing mortality rates, typically being size-selective, exceed natural mortality rates by a multiple and data samples are available for decadal time scales. This thesis aims to assess the potential importance of FIE for sustainable exploitation by empirical evidence as well as evolutionary modeling, illustrated for the North Sea flatfish plaice and sole.

In empirical studies the problem of inferring on genetic changes from phenotypic observations lies in the disentangling of the phenotypic plasticity caused by environmental variations from the potential genetic change. This is at least partly achieved by constructing norms of reaction that account for this environmental variation. The probabilistic maturation reaction norm for instance disentangles phenotypic plasticity in maturation caused by variation in growth. Because growth, maturation and reproductive investment are correlated due to tradeoffs on the individual level, a method was developed that fits an energy allocation model to individual growth trajectories, obtained by the back-calculation of otoliths. This method provides size-specific estimates of the mechanistic individual life history tradeoffs and of the selection differentials imposed by the fishery. Because the correlation of estimated life-history traits is captured, temporal changes could (for the first time) be analyzed conditionally on the correlation and on potential environmental effectors, thus disentangling not only environmental variability but also effects from changes in another trait. The results suggest that maturation shifted to occur earlier, surplus energy and reproductive investment increased partly due to environmental factors, but that all changes also bear a genetic component, indicative for FIE.

Species-specific individual-based eco-genetic models were developed to explore the evolutionary causes of reverse sexual size dimorphism in the case of flatfish. The hypothesis that males are smaller than females because of an energy loss through behavioural reproductive investments has to be rejected in this evolutionary perspective, since a higher demand on reproductive investment is compensated by increased energy acquisition. In contrast, the results show that males are smaller because increasing reproductive investment pays off less in males than in females. The finding can likely be generalized to many cases where mating opportunities are limited in space and time. Since eco-genetic models include the inheritance of traits with frequency-dependent selection, they are therefore a powerful tool to study FIE and the model is therefore fitted to the estimated evolution of plaice and the evolutionary impact of different management scenarios is assessed. The so called maximum sustainable yield MSY and the corresponding maximal fishing mortality F_{MSY} evolve along with the population life history and occur both at lower levels after a while. The currently estimated reference points are thus not sustainable but slipping targets. By a dome-shaped exploitation pattern being protective for larger fish the evolutionary trends could be reversed and with it the negative evolutionary impact. However, the evolutionary impact trades off against the short term loss in yield: by protecting the large fish the evolutionary impact is minimized but the instantaneous yield is decreased too – the optimal strategy for a given time horizon is somewhere in between. In summary, the thesis provides evidence that FIE should be taken into account for sustainable management.

Contents

Introduction 9

I: Empirical evidence from single traits 31

Chapter 1: Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea* 33

Chapter 2: Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.) 45

II: Empirical evidence from correlated traits 55

Chapter 3: Multiple growth-correlated life history traits estimated simultaneously in individuals 57

Chapter 4: The study of plastic and evolutionary responses in correlated life history traits 75

III: Modeling adaptation evolutionarily 107

Chapter 5: An evolutionary explanation of sexual size dimorphism: predictions from a quantitative model calibrated to North Sea plaice 109

Chapter 6: A reconstruction of the fisheries-induced evolution of North Sea plaice (*Pleuronectes platessa*) 141

IV: Implications for management 159

Chapter 7: Evolutionary impact assessment of commercial fisheries: a case study of North Sea flatfish fisheries management 161

Synthesis 181

Acknowledgements 199

Introduction

DIVERSITY AND EVOLUTION

Since the introduction of the concept of natural selection (Darwin 1859), science has been based on the assumption that individual traits that define individual biological fitness, i.e. the ability to survive and produce offspring, are inherited from parent to offspring. Individuals with higher fitness are more likely to survive and produce more offspring, and consequently have greater relative representation in a population. The individual fitness depends on the environment and thus, because the environment is shaped by other organisms inhabiting it, on the distribution of other trait variants in the environment, i.e. fitness is frequency-dependent (Metz, et al. 1992). The optimal strategy therefore always depends on the environment and its changes in space and time. Since the environment is always changing, the trait variants unlikely ever reach evolutionary equilibrium. They rather steadily evolve towards always changing evolutionary optima. This is how species adapt to the changing environment and evolve into other species, and this mechanism has supposedly generated all biodiversity we observe.

With the discovery of the DNA (Watson and Crick 1953), the unit of inheritance of traits could be analyzed more closely. The phylogenetic relatedness or distance between organisms could thereafter be defined more precisely by their genetic similarity or dissimilarity respectively obtained from genome sequencing. However, this revealed contradictions with the former classification of species, which was mainly based on morphology, making the classification of species ambiguous and giving raise to various concepts of taxonomy (e.g. Kullander 1999, Domis, et al. 2003, Staley 2006). A main insight was that genetic diversity between species is continuous or gradual, most visibly revealed by the simpler organisms, and it is on this continuous gene pool that natural selection acts and shapes the genetically discrete beings.

The formulation of evolutionary processes depends on what is considered to be the unit of selection and the unit of evolution. The gene might be the selfish instance operating as if aiming to reproduce itself as much as possible, using individuals as vehicles of transport (Dawkins 1976). However, the fitness of the individual determines whether genes survive and to which extent they are reproduced along with the individual in the selection process (Dover 2000). For the traceability of the selfish gene view one would therefore need to know the functioning of the genes up to their effects on reproduction and survival in individual phenotypes. Because this information is usually not available, the individual, being defined as a combination of certain traits which are in turn determined by certain genes, is adopted in this thesis as the unit of selection. Since the phenotype determines the fitness of traits which are inherited by genes, the translation from genotype to phenotype becomes irrelevant for the definition of fitness. Evolution thus refers to changes in the prevailing composition of traits, based on an continuous genetic diversity, in locally separated interbreeding groups of individuals.

HUMAN-INDUCED EVOLUTION

Humanity has taken an increasingly important role in the modification of the environment, with a steep increase in the last century due to industrialization. Climate change, changes in habitat and connectivity due to changes in land use, harvest, disease control, are all anthropogenic effects that create new niches and affect the survival and reproduction of organisms, resulting in direct or indirect anthropogenic evolution. The problem with this anthropogenic evolution is that it is almost never anticipated and might go into undesirable directions. Famous examples are the resistance of pathogens towards antibiotics, the resistance of agricultural pests towards pesticides or the continuous evolution of the HIV virus to evade the immune system (review in Palumbi 2001). These adaptations might be irreversible or hardly reversible, since the selection force in one direction, typically forcing organisms to adapt to assure survival until reproduction or otherwise being penalized by death, might be stronger than in the opposite direction.

Only with the knowledge of the functioning of these potentially undesired evolutionary effects, the management of resources can be adjusted trying to reduce the rate with which they spread. As any change in the environment of a resource will have an effect on its genetic diversity, the general question is not whether anthropogenic evolution occurs but how fast and important it is. The higher the rate of the induced environmental change is, the less time is expected for the evolutionary responses to occur. Concerns had been raised that evolution caused by the increased impact on natural systems of humans through industrialization might be contemporary, i.e. may be observable within a human lifetime (review in Reznick and Ghalambor 2001). The potential for human-induced contemporary evolution provides the background of this thesis.

LIFE-HISTORY EVOLUTION

Life history theory addresses the age-specific schedules of growth, reproduction and survival (Stearns 1992, Roff 2002). The genetic basis for life-history traits is poorly understood as it seems nowadays obvious that life-history traits are mostly determined by complex interactions of several genes (e.g. Roff 2007). Life-history theory is therefore constrained to focus on the phenotypic expression of life-history traits instead of focusing on their genetic basis. Fitness can be understood as the cumulative reproductive output of an individual, i.e. the number of offspring produced over its entire life, weighted by the fitness of this offspring in turn. Growth, maintenance, maturation and reproductive investment are key life functions and are tightly linked to determine this lifetime reproductive output. Because the energy resources of an individual in any particular environment will be finite, these life functions are competing and the allocation of energy resources thus involves several tradeoffs between the life-history traits. For instance, the energy spent for growth is not available for reproduction. Because fecundity generally increases with body size, individuals also experience a tradeoff between current and future reproduction in case of indeterminate growth, i.e. if an organism continues to grow after maturation (Heino and Kaitala 1999). Growth and reproduction furthermore trade off against survival. Searching for food often increases the exposure to predators and reproduction is often associated with increased mortality risks due to the depletion of energy resources (Stearns 1992, Roff 2002). The timing of the onset of maturation is crucial because it determines the number of reproductive events until death and the size at which energy is no longer used solely for growth but also for reproduction after which growth consequently decreases. If survival probability is high, investment in growth to a relatively large size before maturation may therefore be favored because fecundity relative to size typically increases with size, at the cost of delayed maturation. If survival probability is on the other side low, it will not pay off to postpone maturation because it is less likely to survive until future reproductions and therefore using all energy for the present reproduction will result in a relatively higher fitness. Consequently, earlier maturation and using relatively more surplus energy for reproductive investment than for growth will result in a relatively higher fitness. With earlier maturation and increased reproductive investment less energy is available for somatic growth and hence a smaller size at age can be expected if survival is low. Varying the allocation of time and energy between growth, maintenance and reproduction has thus interlinked consequences for fitness. The cumulative reproductive output depends on cumulative survival and fecundity. These are largely determined by the size of an organisms, the size reflecting the combined effect of life history "decisions". Predicting life history is often not straight forward because changes in size might have opposite consequences for fitness components. If mortality is size-selective for instance, increasing size might reduce survival but increase fecundity and *vice versa*.

HARVESTING-INDUCED EVOLUTION

Harvesting natural populations means to apply additional mortality and occurs typically in a specific manner. In most cases, the additional mortality affects the priciest individuals and as consequence has reduced the traits in the population that made these attractive. Trophy hunt has reduced body weight and horn size of bighorn rams *Ovis canadensis* by 25% over three decades (Coltman, et al. 2003). In the Himalayan snow lotus *Saussurea laniceps* plant height has been decreasing the last century in areas where there is intense harvest for use in traditional medicine (Law and Salick 2005). The marine environment is an example where anthropogenic influence has dramatically increased over the last century: The mortality due to fishing may exceed the natural mortality typically by about fourfold (Mertz and Myers 1998).

FISHERIES-INDUCED EVOLUTION (FIE) OF LIFE HISTORY

Fisheries provide a large-scale experimental framework to study life-history evolution (Rijnsdorp 1993). Fishing pressures have substantially increased with industrialization in the last century, the landings from the world's capture fisheries increased fivefold between 1950 and 2000 (FAO 2008). Furthermore, fishing is almost always size-selective, most commonly used gears are selective for large size (trawl nets, seine nets), a few might be selective for intermediate size (e.g. gillnets). As size determines survival and reproduction, the exploited resource will therefore respond by adjusting its life history to the increase in mortality. In the natural unexploited situation, the larger individuals have a higher survival probability because predation decreases with size and a higher fecundity, since the efficiency of allocating energy for reproduction increases with size (Fig. 1). Under exploitation however, the selection of natural mortality is reversed (Conover 2007): the survival probability of the large fish might decrease below the one of the smaller fish, starting to reproduce at a large size might not pay off because the probability to reach this size is low, and since survival between the events of reproduction is low, it might not pay off to save energy for future reproductive events (Fig. 1). A shift towards decreased growth, earlier maturation at consequently smaller size and increased reproductive investment might therefore be expected from evolution due to increased fishing mortality (Law and Grey 1989, Stokes, et al. 1993, Heino 1998, Law 2000).

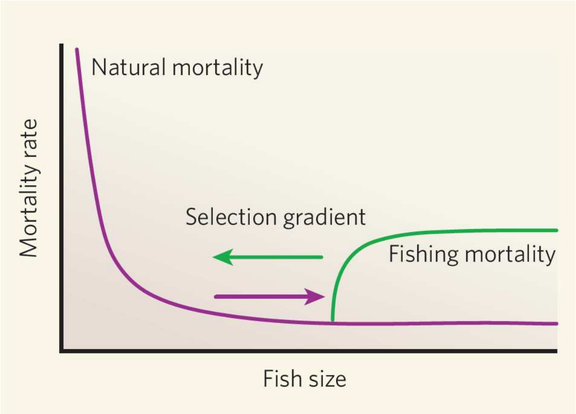


Figure 1: Illustration of the opposite selection gradients for size from natural and fishing mortality. With courtesy from Conover (2007).

The rate of evolutionary change will be affected by the strength of selection, i.e. by the level of the fishing mortality rate, and by the selectivity of the fishery. A mortality for instance that only targets mature individuals would affect also the older and larger fish as in the typical size-selective fishery, but in this case they could not escape the mortality by maturing earlier. Because of the positive relationship between size and reproductive output, evolution will in this situation favor later maturation.

Fisheries-induced evolution (FIE) might have negative long-term effects on the productivity of stocks and thus on their sustainable exploitation and furthermore, evolutionary changes might be hard to reverse or might even be irreversible (see below). Scientists have therefore warned of FIE and its potential negative effects for sustainable exploitation for decades (Borisov 1978, Ricker 1981, Edley and Law 1988, Law and Grey 1989). In 1991 a symposium was dedicated to FIE (Stokes, et al. 1993) but without attracting the deserved attention. Only 10 years later the subject was taken up again in various studies. Two European networks, “FishACE” http://www.iiasa.ac.at/Research/EEP/FishACE/ and “FinE” http://www.iiasa.ac.at/Research/EEP/FinE/ starting in 2005 and 2007 respectively, aim to provide evidence for FIE, to understand its functioning through modeling and to provide advice for sustainable exploitation. The research of this thesis was conducted under these two projects.

CONSEQUENCES OF FISHING POLICIES AIM TO CONSIDER

Landings from the world's capture fisheries increased fivefold between 1950 and 2000 but have now leveled off (Fig. 2, FAO 2008). The proportions of overexploited, depleted and recovering stocks have remained relatively stable in the last 10–15 years, after the noticeable increasing trends observed in the 1970s and 1980s with the expansion of fishing effort. In 2007, about 28 % of stocks were either overexploited (19 %), depleted (8 %) or recovering from depletion (1 %) and thus yielding less than their maximum potential owing to excess fishing pressure. A further 52 % of stocks were fully exploited and, therefore, producing catches that were at or close to their maximum sustainable limits with no room for further expansion. Most of the stocks of the top ten species, which together account for about 30 % of world marine capture fisheries production in terms of quantity, are fully exploited or overexploited (FAO 2008).

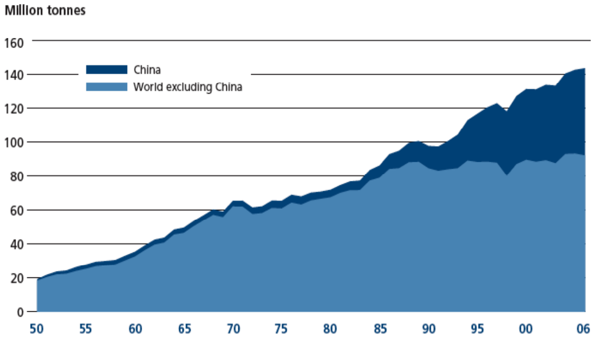


Figure 2: Worldwide capture and aquaculture production (in 106 tonnes) from 1950 to the early 2000s, with courtesy from FAO (2008). Of this total, aquaculture accounted for 47%. Outside china, per capita supply has shown a modest growth rate of 0.5% yr^{-1} since 1992, following a decline from 1987.

The catch per unit effort therefore has reduced significantly (Myers and Worm 2003). Removing species changes and simplifies marine food webs and in conjunction with the truncation of age-classes that commonly results from harvest it couples the abundance of fish stocks more tightly to fluctuations in the environment (Pauly, et al. 2002). Large, long-lived predatory fish are driven to collapse (Hutchings 2000, Myers and Worm 2003) and are replaced by fish further down the food chain (Pauly, et al. 1998). The stocks driven to collapse have been slow to recover or have not recovered at all (Hutchings 2000). Reduced predation has lead to increasing invertebrates, phytoplankton, and macroalgae, as well as higher turnover in the microbial loops (Jackson, et al. 2001).

The productivity of a stock is difficult to predict because the food availability might increase or decrease due to fishing the predator and/or prey communities. If there is no change in the prey and predator community of a certain stock, an increased food availability might be expected because after the removal of a part of the population there will be less intraspecific competition for resources and thus *per capita* more food available. Furthermore fishing affects the habitat, especially by demersal trawling, which might banish a species by destruction of its habitat (Worm, et al. 2006) but might also increase its food availability. By regular disturbance of the seabed, long-lived species will disappear and be replaced by short-lived species with high turnover loops. This might increase the productivity of the smaller benthic pray organisms thus also the food availability for species that feed on them (Hutchings 2000, Hiddink, et al. 2008).

There were furthermore important environmental changes occurring in the last century that are not directly related to the activity of fishing. Industrialization had impacts on the climate and caused pollution. The life history of exploited resources might have been affected or, if the perturbations were persistent, even have adapted to such changes. Global surface temperatures have increased in the past century by 0.74 ± 0.18 °C and climate model projections indicate that the global surface temperature will probably rise a further 1.1 to 6.4 °C during the coming century (Solomon, et al. 2007). Land temperatures increase about twice as fast as ocean temperatures (0.25 °C per decade against 0.13 °C per decade) because of the larger effective heat capacity of the oceans and more evaporation (Sutton, et al. 2007), but might still be sufficient to have an impact on fish life history. Growth in fish is strongly affected by temperature (Pepin 1991, Brown, et al. 2004) and there might be also direct growth-independent effects of temperature on maturation and reproductive investment (Kurita, et al. 2003, Dhillon and Fox 2004).

Pollution in the sea increased due to atmospheric pollution, river discharges and spills. The marine ecosystem might become more or less productive if pollution is organic and discharges limiting factors such as nitrate or phosphate, or if pollution is toxic. Endocrine disrupting agents might furthermore interact in the reproductive cycle of fish and mainly affect maturation and fecundity (Oberdörster and Cheek 2001, Den Hond, et al. 2002).

The productivity of a stock will thus not only be affected by the level of exploitation of a stock but also by indirect effects of fishing, fishing of other stocks, habitat impacts of fishing and abiotic changes in the environment. For decades stocks were however assessed independently of each other by their mere estimated abundance without taking account of species-environment interactions. Because fishing and environmental impacts are tightly interlinked, the management started to aim in recent years for an action plan in which all potential impacts of a fishing activity together with other environmental changes are considered on the ecosystem level. There is however not yet a formal framework to do so.

CONSEQUENCES OF FISHING POLICIES NEGLECT

Policy makers and fisheries managers have thus many reasons to worry about the effects of fishing and FIE is another component that a policy encompassing all potential impacts on the ecosystem might need to consider. So far, FIE is not considered in fisheries management, partly because the concern that life histories might adapt and that they might adapt quickly is rather young, and partly because in the view of the public, observed changes are rather attributable to environmental changes to which the fish respond with phenotypic plasticity without affecting the genetic diversity. The non-evolutionary impacts of fishing on the ecosystem to which species react with phenotypic plasticity would not affect the underlying genetic diversity in life history. These changes might be dramatic but have raised little concern because there is a long tradition for the belief that altering the abundance of a species represents a mere numeric change and is readily reversed (Myers, et al. 1995). On the ecosystem level one might assume too that by reversing the environmental conditions that had changed a system, i.e. by the deregulation of fishing, the ecosystem would accordingly reverse to its initial state (Worm, et al. 2006). The recovery potential depends on the resilience of the system which in turn depends on its biodiversity (Worm, et al. 2006), i.e. its genetic diversity. But there might also be the case where a recovery to the initial state is not possible because by changing the relative abundances of its communities a system might switch to an alternative stable state (Scheffer, et al. 2001).

There is however an important difference in evolutionary and non-evolutionary impacts. First, the FIE due to the traditional exploitation of marine resources tends to move in an undesired direction because it likely negatively affects the productivity of the stock and hence the long-term sustainable yield (Law and Grey 1989, Heino 1998, Conover and Munch 2002). If mortality is selective for larger sizes, a shift in maturation towards earlier age and size, an increased reproductive investment and a decreased growth rate is expected (see above). Under a constant realized fishing mortality rate (being defined in terms of numbers and not biomass) the yield will be smaller if the size distribution of the population moves towards lower size at age. Due to the shift towards earlier maturation, the proportion of matures might increase and thus positively affect recruitment and yield. However, because the evolving mature individuals are smaller, the spawning stock biomass and the stock fecundity might be disproportionally smaller. It seems therefore unlikely that FIE will lead to an increased recruitment. If there is a severe negative effect of the smaller sizes and lower fecundities on recruitment, stocks might even collapse due to these evolutionary effects (Williot, et al. 1997, Hutchings and Reynolds 2004, Olsen, et al. 2004). Second, if populations undergo genetic changes, the recovery of populations and ecosystems might be affected (Heino 1998), as the evolutionary force of fishing in one direction might be much stronger than the evolutionary force without fishing in the opposite direction. Evolution in direction to adapt to high fishing pressures is fast because the lack of adaptation is penalized by death and the genotypes of the initial populations therefore quickly disappear. The evolution towards earlier maturation, increased reproductive investment and smaller size at age consequently may occur within a few decades. The reversal of these evolutionary changes by releasing fishing mortality might however occur much slower (Law and Grey 1989, Law 2000, De Roos, et al. 2006, Jørgensen, et al. 2007). Adaptation to the evolutionary optimum without fishing is rewarded with the benefit of increased size at age but lack of adaptation is not penalized with death. With increased size at age the fecundity and hence the reproductive fitness increases and there might be a benefit to survive predation mortality. But this natural mortality favoring larger size is typically small relative to fishing mortality favoring smaller size (Mertz and Myers 1998). Modeling work therefore suggests that the selection force to reverse a fisheries-induced change is likely less important and adaptation might take longer (Law and Grey 1989, De Roos, et al. 2006, Enberg, et al. 2009). A controlled experiment on a captive wild population, which was formerly used to demonstrate that life-history evolution can occur within a few generations (Conover and Munch 2002), suggests that evolutionary changes are reversible but that recovery would take at least 2-3 times longer (Conover, et al. 2009). However, because the biological fitness is frequency-dependent (Metz, et al. 1992) it might also occur that the evolutionary optimum without fishing is no longer represented by the initial population (Law and Grey 1989, Law 2000, Scheffer, et al. 2005, De Roos, et al. 2006) and that a recovery might consequently no longer be possible. The failure of some fish stocks to recover after a collapse might be due to FIE (Hutchings 2000, Hutchings and Reynolds 2004, Walsh, et al. 2006). Marked changes in key life-history traits such as the maturation schedule occurred for instance in the northern cod off Newfoundland and Labrador before its collapse (Olsen, et al. 2004). Around the same time, other cod stocks in the region showed changes in growth that are interpreted as being indicative of evolution (Swain, et al. 2007).

MITIGATION

Because of the decreased productivity and the slow or impossible recovery, policy makers and managers should be alerted by the findings of studies on FIE. As to prevent overfishing or undesired effects on the ecosystem, reducing the fishing mortality would also help to mitigate the evolutionary effects. Fishing less in the present might thus guarantee better yields in the future due to less severe evolutionary effects. While non-evolutionary effects might be more prone to stochastic processes resulting in a natural random variation of an ecosystem response, the FIE response is always directional and rather easily predictable. Because of the predictability, the advice for the mitigation of FIE might prove to be quite straight forward compared to advice for the mitigation of other effects of fishing. An alternative to reducing fishing mortality might be to change the selectivity of the fishery to potentially reverse the evolutionary effects that reduce the stocks productivity. This might involve to protect the larger fish and the short-term yield might therefore decrease to the benefit of the long-term yield.

Scientifically at least, the suggestion that fisheries can produce genetic change should not cause too much bother. However, some people have conflicting views, due to a conservative personality and reluctance towards new developments or maybe due to religious beliefs, as they might neglect or not believe that evolution is the mechanism that created and creates the biodiversity we observe. The first step in the mitigation of FIE therefore involves to convince people about its credibility and potential importance. Since we assume evolution to be the mechanism to create biodiversity throughout this thesis (as there is no scientific reason to assume anything else), there is little basis for a religious argument. But although some people might not believe that evolution suffices to explain speciation, they might believe that genetic shifts within a species towards different characteristics of that same species might occur. This belief already would suffice to provide a basis for the mitigation of FIE. (Of course new species might evolve due to the high selective force of the fishery, but the problems of FIE will likely emerge much before that).

On a scientific basis the theoretical expectation of FIE is undoubted. The scientific debate on FIE extends to the empirical level on whether the observed phenotypic changes reflect a genetic change (Browman, et al. 2008, Kuparinen and Merilä 2008), on whether FIE could be as fast as suggested in experimental and empirical studies (Andersen and Brander 2009) and furthermore whether FIE is as important compared to other effects of fishing to deserve to be considered in management. Experimental evidence quite unambiguously confirms that FIE can occur within a few generations if the selective pressure is relatively high (Reznick, et al. 1997, Conover and Munch 2002, see below). These findings lead to the question how FIE occurs in natural populations. Since the genetic basis of life history is not well known and genetic data is not readily available, usually phenotypic data has to be used to infer on genetic changes. The difficulty therein is that genetic changes and phenotypic plasticity are confounded in the phenotypic traits. Life history is in fish particularly plastic, and a change in the phenotype might therefore just be the consequence of a change in the environment (see below), and in the wild the environmental effects can not easily be statistically accounted for. If genetic and plastic changes trend in opposite directions and the plastic effects overshadows the genetic change, a genetic change might therefore not be recognized, or, if genetic and plastic changes trend in the same direction the change might be overestimated or falsely diagnosed. The challenge in providing empirical evidence for FIE lies therefore in disentangling genetic from phenotypic changes (Rijnsdorp 1993). Further evidence for FIE might be provided by evolutionary models, in which the outcome of the optimal life history strategy is not a consequence of convenient assumptions but of the species fundamental biology. If all the elementary processes leading to certain phenotypes could be simulated, FIE could be perfectly predicted and its importance evaluated quantitatively.

EXPERIMENTAL EVIDENCE

Experiments confirmed that changes in the mortality regime might induce contemporary evolution in life history. Guppies (*Poecilia reticulate*) that are relocated in an environment with higher predation evolved towards earlier maturation and lower asymptotic size within a few generations and in the opposite direction if predation in the new environment was lower (Reznick, et al. 1990). The observed rates of evolution and the heritabilities were similar to those obtained in artificial breeding experiments (Reznick, et al. 1997). In an experiment with Atlantic silverside (*Menidia menidia*) changes in size at age, growth rate and fecundity were obtained within only 4 generations by implementing strong size-selective mortality, i.e. by harvesting 90% of the largest or of the smallest fish (Conover and Munch 2002). In both examples heritabilities were around 0.2 which is within the expected range in natural populations and artificial breeding (Law 2000, Roff 2002).

EMPIRICAL EVIDENCE:
DISENTANGLING GENETIC FROM ENVIRONMENTAL EFFECTS

Based on experimental evidence we can expect life-history evolution to occur within decades if fishing mortality rates clearly exceed natural mortality rates. It is however not obvious that the phenotypic change in the wild would be similar to the one observed in the controlled experiments because in the wild many other factors could affect the observed traits. Variation in the environment (e.g. temperature, food resources, natural mortality) also affect life history and since fish life history is highly plastic, life history variation due to environmental variation might overshadow the life history variation due to genetic effects. For instance we might expect a genetic shift towards earlier maturation due to exploitation but also increased temperatures, increased growth or increased predation mortality might lead to earlier maturation. Since population numbers decrease due to fishing the intraspecific competition for food resources decreases and therefore *per capita* growth might increase, leading to an earlier maturation independently of the potential genetic response. It is therefore necessary to disentangle the phenotypic plasticity from the genetic response in the observed phenotypic variation by controlling for the plasticity caused by environmental variation. The timing of maturation for instance likely depends mainly on the combination of age and size (Stearns and Koella 1986, Bernardo 1993). If we assume that environmental variability mainly affects growth, the variation in the growth curve is representative for different environments. The onset of maturation might therefore be defined by a maturation reaction norm – a line defining the transition from juvenile to adult (Fig. 3) - in the age-size plane across different environments given by different growth curves (Stearns and Koella 1986).

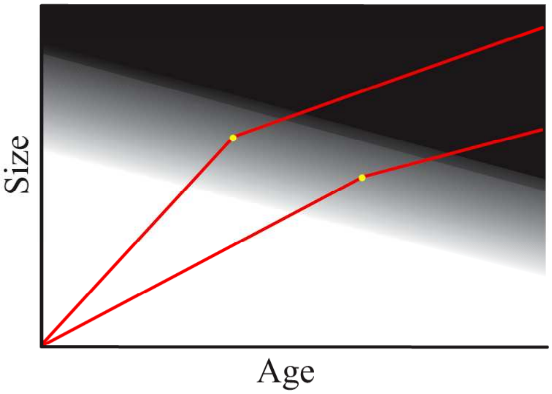


Figure 3: Concept of the probabilistic maturation reaction norm (PMRN) with courtesy from Heino and Dieckmann (2003). Depending on the environment (food availability, competition for resources, temperature), individuals grow at a different pace and become mature at different ages and sizes (dots), and thereafter decrease growth rate due to energy expenditures for reproduction. The faster growing type in the more favorable environment likely becomes mature earlier. The connecting line between the onset of maturation between individuals across all environments reflected by different growth types, defines the maturation reaction norm. Since the onset of maturation is understood stochastically, there is not a deterministic point of this onset but a probability that increases with age and with size. The gray shading indicates how this probability of maturing might increase with age and sizes and thus defines the PMRN. To illustrate an estimated PMRN, often a line representing a certain probability of maturing (e.g. 50%) is given.

To disentangle the plastic variation in maturation due to changes in growth from the underlying genetic maturation, one has therefore to evaluate the maturation reaction norm by accounting for the different maturation-determining environments, supposedly represented by the different growth curves (Reznick 1993, Rijnsdorp 1993). A probabilistic formulation of the maturation reaction norm (PMRN, Heino, et al. 2002) has been applied to several fish stocks to evaluate the hypothesis of FIE (Fig. 3). Most of these studies found that the maturation shifted towards younger ages and smaller sizes (review in Jørgensen, et al. 2007, Kuparinen and Merilä 2007, Allendorf and Hard 2009). If fishing mortalities substantially increased and no environmental factor can sufficiently explain the variation in the PMRN, a shift in the PMRN towards younger ages and smaller sizes is by the principle of exclusion suggestive for an evolutionary change.

Reproductive investment might be mainly affected by the energy acquisition and accordingly a reproductive investment reaction norm could disentangle the plasticity in reproductive investment due to variable energy acquisition (Rijnsdorp, et al. 2005). Measuring reproductive investment and energy acquisition is however more complicated than maturity and size and age. Fecundity provides the most direct estimate, but is restricted to females of species in which the fecundity is determined at the start of the spawning season (determinate spawners). Alternatively, reproductive investment is often estimated by the gonad weight. However, it is difficult to get an accurate estimate since the gonad weight changes substantially in the weeks before the spawning season due to the continuous growth of the ripening oocytes (Rijnsdorp 1991, Kennedy, et al. 2007). More importantly, gonad weight might not be a reliable estimator of reproductive investment because energy continues to be re-allocated from the soma to ripening oocytes during spawning, and because reproductive investment also includes a behavioural cost of activities related to spawning (Rijnsdorp, 1990; Kjesbu et al., 1991). Therefore, estimates of reproductive investment are usually highly variable, consistent estimates over longer time series are rather scarce and with it conclusions about potential temporal changes. Furthermore, energy acquisition can not be directly measured without following a fish and measuring its ingestion. Reaction norms for reproductive investments (reproductive investment as function of energy acquisition) were therefore not yet formally established so far.

Growth might be considered as a representative for energy acquisition, all other life history characteristics being constant. Age and size are usually determined in sampling programs and estimates of growth rates are thus available by population estimates of size at age. If annual body growth is marked in hard structures of a fish such as otoliths or scales and the relation between body growth and growth of the hard structure is known, even individual growth curves may be obtained. From the distribution of the individual size at age and the change in this distribution along the cohort, estimates of the selection differentials of size at age due to the size-selective mortality can be obtained (Sinclair, et al. 2002, Sinclair, et al. 2002). The correlation of the selection differentials with the change in mean size at age in Atlantic cod (*Gadus morhua*) confirms the FIE hypothesis and indeed reveals that a mortality selective for large sizes selects for a smaller size at age (Swain, et al. 2007). Controlling for environmental effects affecting growth and reproduction in Windermere pike (*Esox lucius*) also revealed a correlation of lower size at age and increased reproductive investment with increased size-selective mortality (Edeline, et al. 2007), which is also suggestive for FIE in growth. Furthermore, there might be a selection for growth rate which is independent of size, because the fast growing fish are more exposed to the fishing gear through their feeding behaviour (Biro and Post 2008). However, several life-history traits are confounded in the growth rate or size at age. An individual acquires energy and can spend it either on somatic growth, maintenance or reproductive investment (Von Bertalanffy and Pirozynski 1952, West, et al. 2001, Banavar, et al. 2002). Growth therefore depends on the energy acquisition but also on the allocation of energy to reproduction and is thus also affected by the onset of maturation.

In summary, an impressive number of studies over the past 10 years analyzed changes in life history and most of them corroborate the hypothesis that evolution can occur over contemporary time scales if the recent human-induced selection force of fishing mortality is high compared to the natural selection forces (review in Jørgensen, et al. 2007, Kuparinen and Merilä 2007, Allendorf and Hard 2009). So far studies on FIE focused on the analysis of single traits such as onset of maturation, reproductive investment and growth separately. However, because these are intrinsically linked as they trade off against each other in the individual energy balance they are correlated and can not be considered independently. A fish investing a lot in reproduction will have less energy available to invest into somatic growth. Earlier maturation will have the same effect. And the other way around, if a fish acquires less energy there will be less energy available to invest in somatic growth and/or reproduction. A selection on one trait therefore also has consequences for another trait and it would therefore be desirable to assess all correlated traits at once. Since the tradeoffs apply over the individual energy balance, precise individual information would be necessary.

MODELING

Evolutionary modeling can be used to understand the intricate mechanisms causing life history variation to corroborate the empirical evidence of FIE and to predict human activities on natural populations. Common theoretical tools are optimization models, quantitative genetics models and adaptive dynamics models. However, optimization models, optimizing a certain measure of fitness, can predict only evolutionary endpoints under frequency dependent selection and include no genetic detail (e.g. Smith 1978). Quantitative genetics models include genetic detail but are not apt to predict over longer time-scales due to the inevitable evolution of genetic variances (e.g. Gomulkiewicz and Kirkpatrick 1992). Adaptive dynamics sacrifice genetic in favor of ecological detail by modeling evolution as the successful invasion of a variant type in a resident population (Dieckmann and Law 1996, Geritz, et al. 1998). Selection thereby becomes a density- and frequency-dependent process taking into account the changes of the fitness landscape in the course of evolution. This seems most accurate if individual fitness is a function of the phenotype and the environment, since the latter will be affected by the other phenotypes in a population (Metz, et al. 1992). However, by loosing the detail of the genetic variance, adaptive dynamics are not useful to predict evolution in real time. A sound model to simulate FIE would include both, frequency-dependent selection and genetic variance, and additionally a realistic model would also include density-dependent growth and phenotypic plasticity in a variable stochastic environment. These properties can be combined in the recently developed individual-based eco-genetic models (Fig. 4, Dunlop, et al. 2009). Since the life-history traits trade off at the individual level, the individual is considered as entity of selection. Individuals inherit quantitative trait values from parent to offspring that determine their life history (genetic part) and the structure of the model allows to account for population dynamics, phenotypic plasticity, environmental stochasticity and ecological feedback (ecological part). The modeling framework is rather flexible, individual somatic and gonadic growth may be expressed by energy allocation (West, et al. 2001, Lester, et al. 2004, and as a function of the environment, e.g. population density), maturation by a probabilistic maturation reaction norm (PMRN, Heino, et al. 2002) and the reproductive fitness determining the relative contribution to the offspring as a function of reproductive effort and output, depending on the modeled species in question. Offspring traits are sampled from a distribution defined by the parental traits with a genetic variance that might itself evolve. Since the model is age and size structured, phenotypic traits can plastically respond to a stochastic environment and mortalities can be modeled in dependence of age and/or size. In summary, eco-genetic models (Fig. 4) allow the simultaneous analysis of density-dependent and frequency dependent ecological feedback, predictions of evolutionary rates, transients and endpoints and genetic detail such as the model of inheritance, genetic variance and phenotypic plasticity, and provide therefore a powerful tool to study FIE.

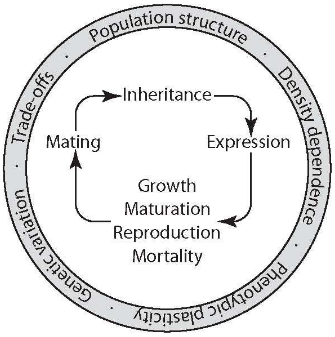


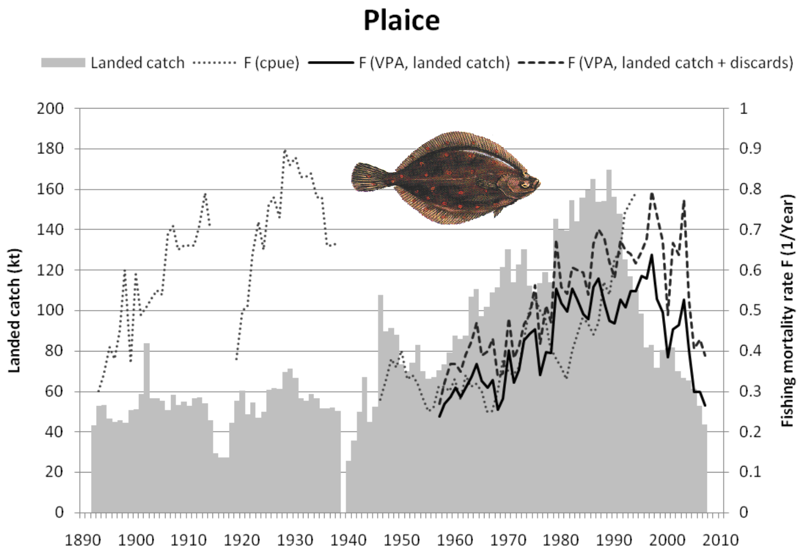
Figure 4: Concept of an eco-genetic model, with courtesy from Dunlop, et al. (2009). The model consists of individuals carrying quantitative life-history traits and grow, mature, reproduce and inherit their traits and die. These processes are shaped by the environment they experience.

As the genetic trait distributions are determined by the eco-genetic dynamics, as trait values promoting survival and reproductive success are demographically favored, eco-genetic models do not assume any fitness function *a priori* (like many traditional life-history models) but allow fitness to emerge naturally as a consequence of the underlying population dynamics. Hence, if the modeled mechanisms of eco-genetic dynamics that determine the life history variation are derived from empirical evidence of these mechanisms and if the model is able to reproduce the observed life-history, the prediction of the model might even be considered as an independent source of evidence. The problem therein is of course that there is hardly quantitative evidence for all mechanisms to be included (e.g. growth-survival trade-off, reproduction-survival trade-off, density-dependence of growth). But optimizing the unknown parameters by fitting the model prediction to empirical data might in this case provide unique solutions.

THE NORTH SEA FLATFISH FISHERY

The North Sea flatfish fishery offers a great opportunity to study FIE. The dutch fleet catches about 75% of the total international landings (ICES 2008) in a mixed demersal fishery with a minimum mesh size of 80 mm. The catches are dominated by plaice but the fishery targets the more valuable sole (Fig. 5, Gillis, et al. 2008, Quirijns, et al. 2008). Whereas plaice mortality rates were already high in the late 19th century (Rijnsdorp and Millner 1996), fishing mortality rates for sole did not increase before the 1960s, when the fishery switched from the otter trawl to the more efficient beam trawl (Fig. 5, Rijnsdorp, et al. 2008). Since 1957 the commercial catches were sampled extensively on a monthly basis and since 1970 surveys dedicated to sample the younger age classes which would not show up in the commercial samples were conducted. For plaice also some historical records of the early 20th century are available (Heincke 1908, Masterman 1911, Wallace 1914). The distribution of the Lusitanian sole ranges from the Mediterranean and north-west coast of Africa to the south coast of Norway, whereas the Boreal plaice ranges between the Bay of Biscay in the south to Iceland and the Barents Sea in the north (Gibson 2005). In the North Sea, sole has a more southern distribution than plaice but the juvenile stages co-occur in shallow coastal waters (Rijnsdorp and Van Beek 1991).

Plaice are larger than sole, become nowadays mature on average at age 4 and grow to a maximal age of 25cm and an average asymptotic size of about 50cm, whereas sole become on average mature at age 3 and grow to a maximal age of 40 years and an average asymptotic size of about 40cm (see chapter 1 and 2 of this thesis). Plaice and sole differ in the minimum size caught in the commercial fisheries: about 22cm (age 2-3) in sole and 18cm (age 2) in plaice. Hence, the difference between the minimum size or age at capture and the size or age at maturation is larger in plaice (>12cm, >2 years) than in sole (<4cm, <1year). Because fishing pressure substantially increased in the last century, FIE can be expected in both species.



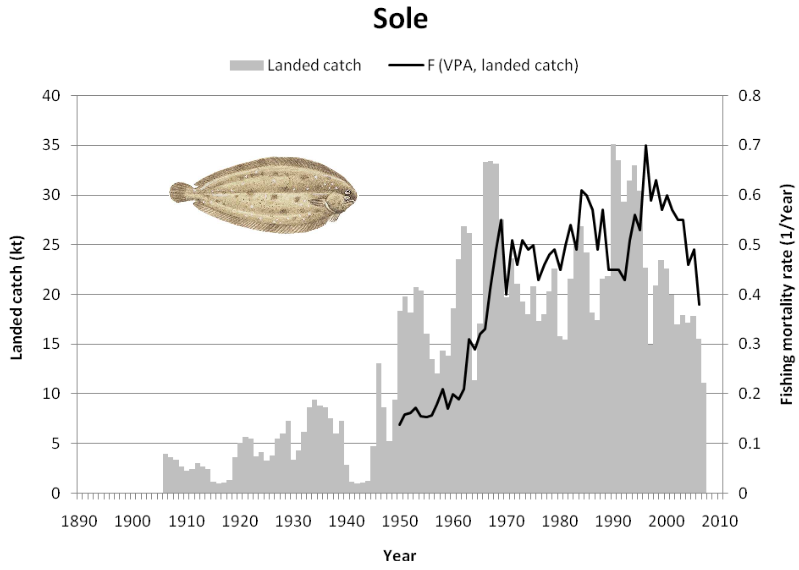


Figure 5: Landings (gray bars in kt) and estimated fishing mortality rates F (black lines) in plaice and sole over the past century (notice the different scales). The fishing mortality is estimated for each age from the observed difference in abundance and an assumed natural mortality by virtual population analysis (VPA) and then averaged over some ages, typically ages 2-6. Estimates based on the catch per unit effort F(cpue) might differ from estimates obtained from the landed catch (VPA) but cover the time series back to the early 1900s in plaice. Furthermore, in plaice also the number of fish that are discarded at sea because they are smaller than the minimal allowed landing size, is estimated. Together with the landings the total number of fish that die due to fishing can thus be given, resulting in more accurate and obviously higher estimates of F. For sole only the VPA estimates from the landed catch was available.

OVERVIEW

This thesis comprises four parts. Part I deals with the empirical evidence of FIE for single traits, part II introduces a new method to analyze multiple traits simultaneously accounting for their correlation, part III deals with the development and the application of an eco-genetic model to simulate the observed life history and the corresponding FIE, and part IV utilizes the model to address the implications of FIE for management. It has been previously shown that maturation in plaice had shifted towards younger ages and smaller sizes since the 1960s (Grift, et al. 2003). **Chapter 1** analyses the potential FIE in maturation of sole. Since exploitation rates for sole substantially increased in the 1960s, a major evolutionary change might be expected thereafter. In plaice exploitation rates were already relatively high in the late 19th century (Rijnsdorp and Millner 1996). Chapter 2 extends the maturation analysis of plaice from the present to the start of the century and includes also males, whereas before only females were considered. **Chapter 2** furthermore estimates reproductive investment in males and females as a function of size and interprets the results in combination with the temporal changes in the patterns of the average growth curve. Like many others, these are studies considering the traits separately estimated on the population level and therefore fail to estimate the individual tradeoffs between these traits, i.e. the correlation between them. Aiming to estimate the individual trait correlations, a method has been developed to estimate multiple size-specific traits simultaneously on the individual level, which is presented in **chapter 3**. To estimate the individual traits, an energy allocation model – a model defining growth as a function of energy acquisition and energy expenditure for maintenance and reproductive investment – is fitted to individual growth trajectories that were obtained from the back-calculation of otoliths. Since the estimated traits are size-specific, they provide the best estimates for individual life history “decisions”. The method is applicable to any other kind of data where individual growth can be obtained. It is applied to time series of plaice and sole otoliths in **chapter 4**, to compare the life history of the two species, to analyze temporal trends in their respective life history in the light of FIE, to estimate tradeoffs and selection differentials and to offer new possibilities for disentangling phenotypic plasticity from genetic effects. Since the correlation of traits can be captured, this study for the fist time disentangles not only environmental effects but also effects due to life-history correlation in temporal phenotypic changes.

To understand the species’ life history and the mechanisms of FIE, individual-based eco-genetic models (see above) are developed. The here considered species plaice and sole are sexually size dimorphic, the females being larger, maturing later and investing more in reproduction than males. The causes of this sexual size dimorphism (SSD) are however unclear and also, whether it might matter for the fisheries-induced evolution observed in the recent decades. Since the SSD itself represents an evolutionary optimal strategy, possible causes taking account of the difference in reproductive behaviour between the sexes are explored in an eco-genetic model (see above) presented in **chapter 5**. The model uses the same energy allocation rule as is assumed in the empirical estimations in chapter 3 and 4 and defines maturation probabilistically with an age and size dependent reaction norm as is assumed in the empirical estimation in chapter 1 and 2. The reproductive fitness in females is given by the gonad size whereas in males this relationship is different and depends also on behavioural traits (spawning duration, time for growth, mortality experienced due to spawning activity, efficiency of reproductive investment). The traits that are inherited, i.e. the evolving traits, are the size-specific energy acquisition rate, the size-specific reproductive investment rate – in males proportional to the behavioural investment rate – and the maturation reaction norm level. Comparing the emergent evolutionary optima of life history for different mechanisms between males and females, chapter 5 aims to give an evolutionary explanation of SSD. The model is fitted to North Sea plaice, because for plaice the most detailed life history estimates are available, but could be used also for any other species with a similar biology of reproduction (e.g. sole). This model furthermore provides a powerful tool to analyze FIE. In **chapter 6** the model is fitted to the empirically estimated life-history evolution of plaice in respect to size at age, maturation and reproductive investment, simulating the historical exploitation over the past century. Within 100 years, the modeled population evolves from an unexploited state to the current population, still evolving in its life-history traits. The pace of evolution is adjusted by optimization of the additive genetic variance (of which little is known in reality) and for simplicity the results are shown only for females. According to the model, the evolutionary endpoint has not yet been reached and the next question thus is what the implications for management are, i.e. what the consequences of FIE for the long-term sustainable exploitation are and how its undesired effects could be mitigated. Although FIE might have many other undesired effects, "sustainable exploitation" in management mainly refers to the stability of the yield. **Chapter 7** therefore evaluates the consequences of different management scenarios, implemented at the current population, on the short-term and long-term yield. The management options are to vary 1) the realized fishing mortality rate, 2) the mesh size or 3) the exploitation pattern (size-selectivity of mortality). The size-selectivity of fishing mortality is typically sigmoidal but might also be dome-shaped, i.e. exerting maximal mortality rates for intermediate sized fish. In the North Sea flatfish fishery a dome-shaped exploitation pattern is realistic because the spatial distribution of fish depends on their age and size and the intensity of exploiting a certain age or size class thus depends on the space to which fishing effort is directed. The loss in yield which is due to FIE is determined by comparing the yield of an evolving population to the yield of a hypothetic population with a presumably constant life history. This comparison defines the impact of FIE on the yield and might be called evolutionary impact assessment or EvoIA (see Jørgensen, et al. 2007). The maximal yields are no longer sustainable if life history evolves and are therefore called maximal yields (MY) instead of maximal sustainable yields (MSY). Only after 1000 years of life-history evolution the traits stabilize and could thus be called sustainable at this time horizon.

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Fisheries-induced evolutionary changes in maturation reaction norms in North Sea sole *Solea solea*

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ABSTRACT: Age and size at maturation decreased in several commercially exploited fish stocks, which, according to life history theory, may be due to fisheries-induced evolutionary change. However, the observed changes may also represent a plastic response to environmental variability. To disentangle phenotypic plasticity from evolutionary change, the probabilistic reaction norm approach was applied to 43 cohorts (1960 to 2002) of female sole *Solea solea* from market samples. The reaction norm for age and size at first maturation has significantly shifted towards younger age and smaller size. Size at 50% probability of maturation at Age 3 decreased from 28.6 cm (251 g) to 24.6 cm (128 g). This change was even stronger when condition was included as a third dimension in the reaction norm estimation. The influence of alternative factors was tested on the population level by regression of reaction norm midpoints on annual estimates of condition, temperature and competitive biomass. Although effects of temperature and competitive biomass were significant, the variation in the midpoints was best explained by the decreasing time trend. Therefore, the results provide strong evidence for a fisheries-induced evolutionary change in the onset of sexual maturity.

KEY WORDS: Life history evolution · Probabilistic maturation reaction norm · Phenotypic plasticity · Growth · Condition

INTRODUCTION

Changes in life history traits such as age and size at first maturation have been reported in several commercially exploited fish stocks (Jørgensen 1990, Rijnsdorp 1993a). These changes may be due to either (1) phenotypic plasticity in response to environmental change or (2) fisheries-induced evolutionary change (Stokes et al. 1993). If mortality increases, earlier maturation and higher reproductive investment will result in a higher fitness (Law 2000). These predictions have been confirmed experimentally (D. A. Reznick et al. 1990, Conover & Munch 2002); the challenge is to examine how these processes occur in exploited wild populations.

Evolutionary changes, however, may be overshadowed by phenotypic plasticity (Stokes et al. 1993). For instance, changes in age and size at first maturity can be caused by changes in growth rate (Reznick 1993, Rijnsdorp 1993b). Since fishing typically is accompanied by a decrease in stock biomass, it may weaken density-dependent effects and cause a change in the onset of maturity simply through its effect on growth rate (Law 2000). For sole, there is evidence for density-mediated compensatory growth, although other factors such as temperature and changes in food availability might also play a role (Rijnsdorp & Van Beek 1991).

The effect of phenotypic plasticity can be disentangled from genetic effects by the reaction norm approach. By definition, a reaction norm describes which phenotypes will be expressed by a genotype under a certain range of environmental conditions (Stearns & Koella 1986). The probabilistic maturation reaction norm (PMRN) has been developed recently to estimate the reaction norm for the onset of maturity conditional on age and size (Heino et al. 2002, Barot et al. 2004). Environmental variability is assumed to be reflected in differences in somatic growth, so that any

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environmental factor that has its effect through growth can be disentangled. This growth conditional PMRN has been applied to several stocks supporting a fisheries-induced evolutionary change in the onset of maturity (reviewed in Dieckmann & Heino 2007). Although the method has been criticized, as it does not disentangle genetic effects from environmental factors affecting maturation other than through size at age (Kraak 2007, Marshall & McAdam 2007), it can easily be extended to incorporate other variables as a third or higher dimension (Grift et al. 2007).

In this paper we investigate the extent to which the change in maturation in North Sea sole can be attributed to (1) phenotypic plasticity in response to the observed variations in growth, or (2) fisheries-induced evolutionary change using the PMRN approach. As environmental variation may affect maturation through more than variations in somatic growth, we explore the possible influence of condition by including it as a third dimension in the reaction norm approach, and analyse the influence of temperature and population density.

MATERIALS AND METHODS

Distribution and exploitation. The common sole *Solea solea* is distributed from the northwest African coast and the Mediterranean to the Irish Sea through the English Channel and the North Sea up to Skagerrak and Kattegat (Rijnsdorp et al. 1992). Spawning of North Sea sole occurs in the southern North Sea, with local concentrations in the German Bight, along the Belgian Coast and in the Thames estuary and the Wash (Fig. 1). Young sole are distributed in coastal waters and migrate to deeper offshore waters when they grow older but return every year in spring for spawning. North Sea sole is mainly caught by the Dutch fleet, which takes about 75% of the total international landings (ICES 2006) in a mixed demersal fishery with a minimum mesh size of 80 mm. The exploitation of sole has increased substantially since the 1960s following the introduction of the beam trawl (De Veen 1976).

Data. Fish samples have been collected monthly since 1957 from commercial landings covering the distribution area of sole in the North Sea and from autumn surveys since 1970. Market samples of individual fish are stratified into 5 market size categories and record date, position, length (mm), weight (g), sex, gonad weight (g), maturity stage and age (yr). Age is determined from the pattern of growth rings in the otolith taking 1 January as birth date. Only females from samples collected in the southeastern North Sea (Areas 1 to 5; Fig. 1) were selected, and the analysis was restricted to Ages 1 to 6 of the Cohorts 1960 to 2002. In total, 21 969 observations were used for the analysis in the first seasonal sampling window, and 12 808 in the second (see below, Table 1).

Maturation. Maturity is determined by macroscopic inspection, and 8 maturity stages are distinguished that represent the seasonal development of the immature and mature gonad (Table 2; De Veen 1970): the immature gonad is classified as Stages I to II; developing ovaries as Stages III to IV representing the vitellogenic phase; the spawning stage when hyaline eggs

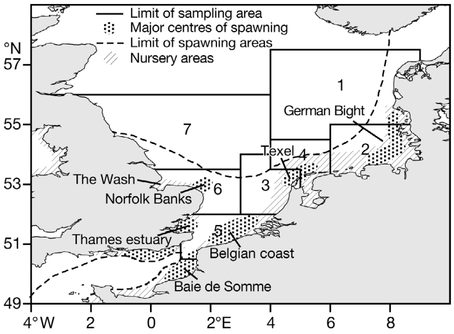

Fig. 1. Distribution of North Sea sole in sampling Areas 1 to 7. Spawning areas, indicated as the main centres of egg production, the limits of spawning activity and the nursery areas are based on Rijnsdorp et al. (1992)

Table 1. Sampling information for the data sets of female sole used a moving time window around the peak of spawning (2 mo before and 1 mo after the estimated maximum relative GSI) and a fixed time window (Nov, Dec and Jan)

	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Total
Moving time window							
Total number	139	1226	7079	6490	4117	2918	21 969
Areas 3 & 4	131	1004	5195	4560	2885	2094	15 869
Areas 1 & 2	8	222	1884	1930	1232	814	6100
Average number per cohort	3	29	165	151	96	68	
Average percentage mature	3	10	78	97	98	99	
Fixed time window							
Total number	299	3870	3783	2531	1629	696	12 808
Areas 3–5	280	2908	2711	1788	1072	466	9225
Areas 1 & 2	19	962	1072	743	557	230	3583
Average number per cohort	0	7	90	88	59	38	
Average percentage mature	0	14	66	92	96	94	

Table 2. Macroscopic maturity stages of female sole. Stages I and II are interpreted as juvenile stages (–). Stages III to VIII are considered adult stages (+). After spawning is completed, the adult sole cycles from maturity Stage VIII to maturity Stage II into the growing phase of the following season

Stage	Interpretation	Observation
I	Juvenile (–)	Transparent and homogenous ovary, tight walls and small lumen, eggs indistinguishable
II	Resting (–)	Reddish translucent ovary, tight walls, eggs are distinguishable, lumen is filled with liquid
III	Vitellogenic (+)	Reddish gray to dark orange mostly opaque ovary, bigger and less tight than in II, rich in blood vessels, vitello-genesis (VTG) has started and some eggs contain yolk, lumen is big
IV	Vitellogenic (+)	Orange to reddish white, completely opaque and stiff ovary at half of its definite size, eggs are polygonal and all contain yolk
V	Ripe (+)	Orange to reddish white opaque ovary in its definite size, lumen is squeezed, eggs are round
VI	Spawning (+)	Mostly grayish-red translucent hyaline but partly still opaque ovary, resilient when pressed together, lumen contains spawn
VII	Half spent (+)	Gray to dark red completely translucent hyaline ovary, walls are very slack and bloody, lumen is big and filled with spawn and liquid
VIII	Spent (+)	Dark red translucent ovary, walls are very slack, lumen is very big mostly filled with liquid, very similar to II or in a transition towards II

are visible as Stages V to VI; and spent fish as stages VII to VIII. The start of vitellogenesis (VTG) ranges in North Sea sole from July to December (Fig. 2), varying between years, areas and also among individuals (Ramsay & Witthames 1996). Some fish might undergo abortive maturation, meaning that VTG has started but ovaries are not developed further than Stages III or IV (De Veen 1970, Ramsay & Witthames 1996).

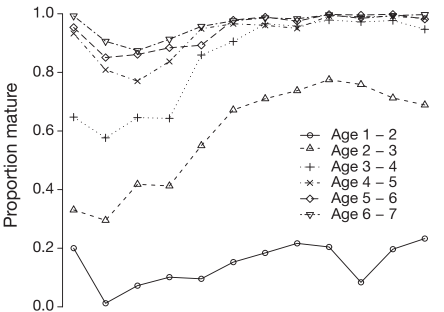

Fig. 2. Seasonal development of the average proportion of mature females by age-group in market samples between July in one year and June in the following year

Moving observation window. The ovary of a spent female (Stages VII to VIII) may look quite similar to the immature ovary (Stages I to II). Hence, the distinction between immature and mature females is more accurate in the time period when all mature females have started VTG or are in spawning stage (Stages III to VI), while none of them is spent. Consequently, the proportion of mature females is most reliably estimated in the period of peak spawning (Fig. 2; De Veen 1976, Ramsay & Witthames 1996). For an unbiased estimate of the proportion of mature fish, a moving time window around the peak of spawning was used to select data (Table 1). Because the timing of the spawning season varies annually in response to ambient water temperature (Van der Land 1991), peak spawning was determined as the date of the maximum ovary weight and was estimated for each year using the model

$$\log(o) = \beta_0 + \beta_1 \log(l) + \beta_2 d + \beta_3 d^2 + \beta_4 d^3 + \varepsilon \qquad (1)$$

where o is the ovary weight, l is fish length and d is the day in the year on which the individual fish was caught. β represents the regression parameters and ε a normal error term (applies to all following equations).

Fixed observation window. The effects of weight and condition (i.e. relative weight: weight × length$^{-3.18}$) on maturation should ideally be analysed at the start of VTG (Wright 2007) because fish improve their condition as a consequence of readying to spawn in the subsequent season (Rijnsdorp 1990). However, because of the ambiguity in detecting maturation macroscopically at the start of VTG, a fixed window comprising the months November, December and January was used as a compromise between the moment where VTG starts and the moment where detection of maturity becomes reliable (Table 1, Fig. 2).

Probabilistic maturation reaction norm. The PMRN is defined as the probability that an immature individual becomes mature at a particular age and size (Heino et al. 2002) and thereby overcomes the confounding effects of growth and mortality. For sole, first time and repeat spawners cannot be distinguished, therefore the probability of becoming mature (p) was estimated by a refinement of the PMRN method (Barot et al. 2004) and is estimated on a yearly basis as:

$$p(a,s,x) = \frac{m(a,s,x) - m(a-1, s-\Delta s, x-\Delta x)}{1 - m(a-1, s-\Delta s, x-\Delta x)} \quad (2)$$

where m is the probability of being mature, a is age, s is size, x is any other additional factor possibly affecting maturation (e.g. condition, see Grift et al. 2007), Δs is the age specific growth increment (in length or weight) and Δx is the age specific change in x. Eq. (2) relies on the simplifying assumption that the growth and mortality rates are the same for immature and mature individuals. Although this is not expected to apply accurately, Barot et al. (2004) confirmed that the method is robust to the relaxation of this assumption. The probability of being mature $m(a,s,x)$ was estimated from individual data by logistic regression. Model selection was done by forward selection of variables based on the Akaike information criterion (AIC) allowing for all possible 1- and 2-way interactions. Two-way interactions were considered when both components of the interaction had been selected:

$$\text{logit}(m) = \beta_0 + \beta_c c + \beta_a a + \beta_l l + \beta_{ca} c \times a + \beta_{cl} c \times l + \beta_{al} a \times l + \varepsilon \quad (3)$$

$$\text{logit}(m) = \beta_0 + \beta_c c + \beta_a a + \beta_w w + \beta_{ca} c \times a + \beta_{cw} c \times w + \beta_{aw} a \times w + \varepsilon \quad (4)$$

$$\text{logit}(m) = \beta_0 + \beta_c c + \beta_a a + \beta_l l + \beta_k k + \beta_{ca} c \times a + \beta_{cl} c \times l + \beta_{al} a \times l + \beta_{lk} l \times k + \varepsilon \quad (5)$$

where m is the probability of being mature, c is cohort as a categorical variable, a is age, l is length, w is weight and k is condition. Because of differences in the interpretation of the timing of effects of length, weight and condition on maturation (see 'Moving observation window' and 'Fixed observation window' above) Model 3 (Eq. 3) was applied to the moving window, and Models 4 (Eq. 4) and 5 (Eq. 5) to the fixed window data set (Table 1).

Growth increments. Annual length increments were estimated by fitting Von Bertalanffy growth curves per cohort. Curves were fitted to mean length at age data, after accounting for length stratification of market samples (Age > 3), survey and backcalculation data (Age ≤ 3). For age groups up to Age 3, the mean length from market samples will be biased because small individuals may escape through the mesh or may be discarded if below minimum marketable size. Therefore, pre-recruit survey data and back-calculation data of Millner & Whiting (1996) were used (see Fig. 3a). The mean growth increments did not differ substantially between the German Bight and the Dutch-Belgian Coast spawning stocks (r = 0.98, R^2 = 0.96).

Weight and condition increments per cohort were estimated as follows. First, the length–weight relationship was modeled assuming a fixed seasonal pattern:

$$\log(w) = \beta_0 + \beta_1 \log(l) + \beta_2 \text{yr} + \beta_3 d + \beta_4 d^2 + \beta_5 d^3 + \varepsilon \quad (6)$$

where d is the day in year and year (yr) is a factor. The length–weight scaling factor was β_1 = 3.18 and has been used throughout the analysis to define the condition factor as $k = 100\ w\ l^{-3.18}$. The mean weight at age per cohort was then calculated from the mean length and corrected for the bias introduced when estimating mean weight from mean length. Given the observed coefficient of variation in length at age, a correction factor was estimated from an empirically derived relationship between the bias and the coefficient of varia-

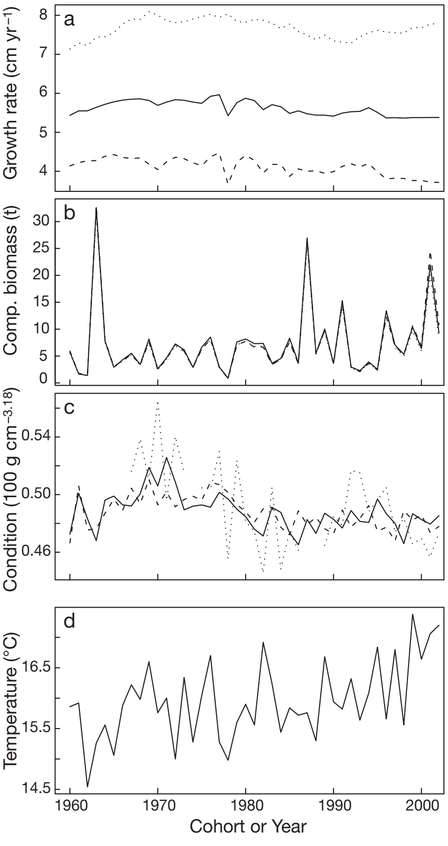

Fig. 3. Time trends per cohort in (a) growth rate as yearly length increments; (b) individually experienced competitive biomass; and (c) condition. (d) Temperature per year. Panels (a) to (c): ··· Age 2; — Age 3; --- Age 4

tion assuming a normal distribution. Because growth increments depend on size rather than age, the annual increments in length, Δl, and weight, Δw, (see Δs in Eq. 2) realized when reaching age *a*, were estimated separately for each cohort as

$$\Delta l_a = l_a - l_{a-1} = \beta_0 + \beta_1\, l_a + \varepsilon \qquad (7)$$

$$\Delta w_a = w_a - w_{a-1} = \beta_0 + \beta_1 w_a + \beta_2 w_a^{2/3.18} + \varepsilon \qquad (8)$$

The so-modeled increments are in line with the theoretical expectation given Von Bertalanffy growth and the length–weight scaling used here.

Diagnostics. To visualize the reaction norm and its change over time we use the reaction norm midpoints in length (Lp50) and weight (Wp50) at which the probability of becoming mature is 0.5. Reaction norm midpoints were obtained by linear interpolation. In the case of the 3-dimensional reaction norm, the midpoints were estimated for a fixed level of the third dimension (condition). Because the reaction norm midpoints are obtained after various steps of calculation, it is not possible to obtain confidence intervals directly and, therefore, they were bootstrapped by resampling the individuals in the original data set with replacement 1000 times, for each cohort. To test for a trend in the Lp50 and Wp50 at a given age, the reaction norm midpoints were regressed to cohort as a variable, weighted by the inverse of the bootstrap variance of each midpoint. Confidence intervals were estimated from the 95% percentile in the bootstrap replicates. Because the onset of maturation might differ between subpopulations, the analysis was run separately for the spawning subpopulation of the German Bight (sampling Areas 1 and 2; Fig. 1) and the Dutch and Belgian coast (Areas 3, 4 and 5; Fig. 1) as well as for the pooled data of the 2 stocks. Because the results of the subpopulations were similar, only results for the pooled data set representing the whole southern North Sea are presented here. Because 95% of the sole matured at Ages 2, 3 and 4 (see Table 1) we only consider these ages for diagnostics.

Alternative factors. To evaluate alternative variables, which could not be incorporated on the individual level PMRN methodology, the Lp50 and Wp50 estimates were regressed against annual estimates of condition, temperature and competitive biomass (Fig. 3). Condition was estimated as the average condition in the third and fourth quarters. Temperature was measured at a coastal station at 53° N, 5° E and averaged from June to October (Van Aken 2003). Competitive biomass, i.e. the biomass with which an individual fish has to compete for resources, was estimated per age group from virtual population analysis stock numbers and weights (ICES 2006) and indices of mean crowding following Rijnsdorp & Van Beek (1991).

Combinations of alternative factors were regressed for age class (*a*) to explain the estimated reaction norm midpoints over cohorts, weighted by the inverse of the corresponding bootstrap variances:

$$Sp50_{c,a} \sim cohort + \Sigma_\Delta T_{c+a-\Delta} + \Sigma_\Delta K_{c,a-\Delta} + \Sigma_\Delta B_{c,a-\Delta} + \varepsilon_{c,a} \qquad (9)$$

where *Sp50* is either Lp50 or Wp50, *cohort* is cohort as a variable, $T_{c+a-\Delta}$ is the average temperature in year $c + a - \Delta$, $K_{c,a-\Delta}$ is the average condition in cohort *c* at age $a - \Delta$, and $B_{c,a-\Delta}$ is the estimated competitive biomass in cohort *c* at age $a - \Delta$. Σ_Δ denotes the time lagged variables with a lag Δ being an element of $\{1, 2, \ldots, a\}$. Model selection was based on the smallest prediction error and the number of parameters was increased forwards-wise. For a given number of parameters, the combination of time lagged variables giving the lowest predicted mean squared error (MSE) in a leave-one-out cross-validation is considered to be the most meaningful model.

RESULTS

Model properties

Cohort, age and size (length or weight), as well as all the 2-way interactions, significantly affected the probability of being mature (Table 3). The length-based Model 3, using a moving time window, gave a better fit and prediction than the weight- and condition-based models (Models 4 & 5) that used a fixed time window. Model 3 explained about 14% more of the null deviance than the fixed window models (Table 3). Considering length and condition as explanatory variables (Model 5) instead of weight (Model 4) results in a lower AIC (Table 3). All models had similarly high classification performance. The sensitivity, i.e. the proportion of correctly classified individuals among matures, was high, but specificity, i.e. the proportion of correctly classified individuals among immatures, was relatively low (Table 3).

Length- and weight-based reaction norms

The estimated reaction norms are close to linear and tend to have negative slopes, suggesting that the size at which sole attains a certain probability to mature decreases with age. This age effect is weaker in the weight reaction norm, such that the probability of becoming mature is determined by weight rather than age. The width of the reaction norm is narrower for length than for weight. The distance between Lp10 and Lp90 is on average 23% of the Lp50

Table 3. Model properties: Akaike information criterion (AIC), proportion of null deviance explained by the model, proportion of correctly classified observations, sensitivity (proportion of correctly classified positives, i.e. matures) and specificity (proportion of correctly classified negatives, i.e. immatures) of Models 3, 4 and 5. Model 3 was built on data from the moving window data selection, Models 4 and 5 were built on data from the fixed window data selection. AIC should not be compared between models obtained from different data sets

	Moving window	Fixed window	
	Model 3	Model 4	Model 5
AIC	8425	7086	7015
Explained deviance	0.54	0.40	0.41
Correct classification	0.92	0.89	0.89
Sensitivity	0.98	0.97	0.97
Specificity	0.59	0.49	0.51

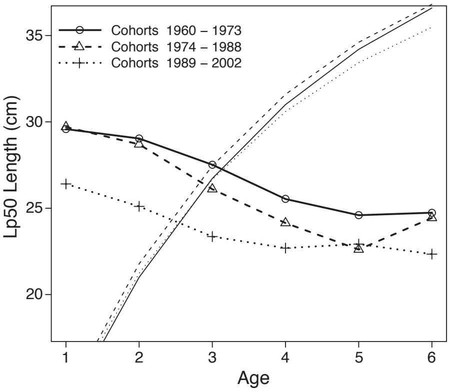

Fig. 4. Reaction norms for Cohorts 1960 to 1973 (—), 1974 to 1988 (---) and 1989 to 2002 (···) estimated as the average Lp50. Thin lines without symbols show mean length at age (cm) of the corresponding cohorts

(Model 3), whereas the distance between Wp10 and Wp90 is on average 65% of the Wp50 (Model 4). Over time, the reaction norms shifted towards younger ages and smaller sizes, with the largest change occurring in the 1980s (Figs. 4 & 5). The intersection of average growth with the reaction norm shows that the age and length at which 50% of the females became mature shifted from about 3.1 yr and 27.3 cm in the 1960s to about 2.5 yr and 24.1 cm in the 1990s (Fig. 4). The Lp50 and Wp50, reflecting the intercepts of the reaction norm, have typically decreased significantly over time at all ages (Fig. 5). The decrease in the Lp50 and Wp50, weighted by the inverse bootstrap variances, is significant for all ages ($p < 10^{-4}$ for all ages in Fig. 5). Inter-annual variation was too large to detect a significant trend in the reaction norm slopes (data not shown). Since most individuals become mature at Age 3 (Table 1), the method is most precise for this age group. For 3 yr old females, the weighted regressions predict that the size at which 50% become mature decreased from 28.6 cm (251 g) in the 1960 cohort to 24.6 cm (128 g) in the 2002 cohort ($p < 10^{-5}$). This trend corresponds to a change of –0.10 cm yr^{-1} in the Lp50 and –3 g yr^{-1} in the Wp50. For the Lp50 values, the minimal marketable size of 24 cm seems to operate as an attractor: the decline of the midpoints ends with an Lp50 of about 24 cm at all ages.

Three-dimensional reaction norm

Condition in the 3-dimensional reaction norm (Model 5) is positively associated with the probability of becoming mature. The Lp50 of the reaction norms, estimated for all values within the 95% CI of observed condition (0.408 to 0.604), indicated that a change of 10% in condition results in a change of about 1 cm in the Lp50. The decrease in Lp50 over time for any given value of condition factor, and, thus, the changes in condition observed in the study period, could not explain the observed decrease in the 2-dimensional Lp50s. The weighted regression on midpoints of the 3-dimensional reaction norm, bootstrapped for the median condition of $k = 0.5$, predicts a decrease in Lp50 from 28.9 cm in 1960 to 23.2 cm in 2002. The decline of –0.14 cm yr^{-1} is stronger than in the 2-dimensional reaction norm. The reaction norm width (21% of the midpoints for condition of $k = 0.5$, Model 5) is similar to the width in the length reaction norm (23% of the midpoints, Model 3) and much smaller than the width in the weight reaction norm (65% of the midpoints, Model 4).

Alternative factors

The alternative factors analysed for their effect on the maturation all showed significant trends over the study period (Fig. 3). Growth rates have decreased significantly (Age 2: –0.045 cm yr^{-2}; Age 3: –0.032 cm yr^{-2}; Age 4: –0.022 cm yr^{-2}; all $p < 10^{-7}$) as does condition (Age 2: –0.13 g $cm^{-3.18}$ yr^{-1}; Ages 3 & 4: –0.04 g $cm^{-3.18}$ yr^{-1}; all $p < 10^{-2}$). Temperature increased significantly (0.03°C yr^{-1}, $p < 10^{-3}$), while competitive biomass showed a peak in the early 1960s, and also around 1990 and 2000. Table 4 presents the variables for the time series in Model 9 (Eq. 9) that give the lowest predicted MSE in a leave-one-out cross-validation for Age 3. The general

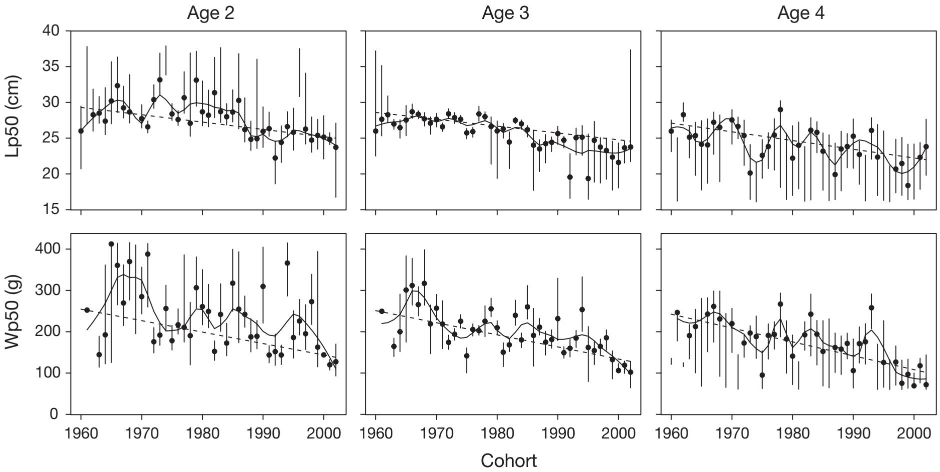

Fig. 5. Reaction norm midpoints Lp50 and Wp50 over time (●), bootstrapped 95% percentiles (vertical bars), trend regression weighted by the inverse bootstrap variances (---) and fit with a non-parametric smoother (—). All trends are significant on a level of $\alpha = 10^{-4}$

pattern of variable selection is consistent for Lp50 and Wp50 for all ages and for all time lags Δ: cohort is always selected as the first variable, while the variables to be selected next are temperature in the year of birth, if this year is included in the analysis, competitive biomass otherwise (Table 4). The MSE only weakly improves by further introduction of variables after cohort, and would increase again by introducing more variables than those displayed in Table 4 (results not shown).

Table 4. Selected models to explain the variation in the Lp50 and Wp50 of Age 3, alternative variables based on the lowest predicted mean square error (MSE) in a leave-one-out cross-validation by allowing the effectors to act on a particular age (Δ fixed) or on all ages together before maturation (Δ element of {1, 2, 3}). Best models were determined by comparing the MSEs from all possible combinations of variables for a given number of variables. Only models for which the cross-validated MSE is lower than it would be if a further variable was introduced are displayed. *: significant at $\alpha = 0.05$. T, B, K: See Eq. 9

Impact period	Number of variables	Selected variables in model	Signs of parameters	MSE
Lp50 at Age 3				
–	0			5.278
Age 0, Δ = 3	1	Cohort*	–	2.320
	2	Cohort*+$T_{age\ 0}$*	– –	2.172
Age 1, Δ = 2	1	Cohort*	–	2.320
Age 2, Δ = 1	1	Cohort*	–	2.320
All ages,	1	Cohort*	–	2.320
Δ = {1, 2, 3}	2	Cohort*+$T_{age\ 0}$*	– –	2.172
Wp50 at Age 3				
–	0			2818
Age 0, Δ = 3	1	Cohort*	–	1816
Age 1, Δ = 2	1	Cohort*	–	1816
	2	Cohort*+ B_{age1}*	– –	1719
	3	Cohort*+ B_{age1}*+ K_{age1}	– – +	1452
Age 2, Δ = 1	1	Cohort*	–	1816
	2	Cohort*+ B_{age2}*	– –	1709
All ages,	1	Cohort*	–	1816
Δ = {1, 2, 3}	2	Cohort*+ B_{age2}*	– –	1709
	3	Cohort*+ B_{age2}*+ K_{age1}	– – +	1448
	4	Cohort*+ B_{age1}*+ K_{age1} + K_{age2}	– – + –	1430

DISCUSSION

Evidence for evolutionary change

This study shows that the PMRN in North Sea sole shifted downwards since the 1960 cohort, which is in agreement with the expectation of a fisheries-induced evolutionary change. In an evolutionary fitness optimization framework, the reaction norm intercept is predicted to decrease and the slope is predicted to increase slightly if exposed to size-selective harvesting

(Ernande et al. 2004). The changes in the reaction norm intercepts found here are consistent with this theoretical expectation (see Fig. 5), but noise in our data was too high to detect a trend in the slopes. Based on the assumption that environmental variation affecting maturation is reflected in variations in the growth rate (Heino et al. 2002), a genetic change in maturation can thus be disentangled from the phenotypic plasticity in maturation. The length-based reaction norm is more reliably estimated than the weight-based reaction norm because of the ambiguity in data selection and corresponding interpretation for the weights (see below) resulting in a smaller data set and higher uncertainty in the reaction norm estimates. However, other factors in addition to size, such as body condition (Kjesbu et al. 1991, Trippel & Neil 2004) or temperature (Dhillon & Fox 2004, Kraak 2007), may affect the probability of becoming mature.

Including condition in the analysis as a third dimension revealed that a higher condition is associated with lower Lp50 values, thus fish in good condition have a higher probability of becoming mature than fish of the same age and length in poor condition. The same effect has been suggested in numerous other species (Kjesbu et al. 1991, Trippel & Neil 2004) and is likely to be (partly) related to the storage of energy during the feeding period that can be metabolized later for reproduction (Rijnsdorp 1990). Although condition contributed significantly to variation in maturation, it could not explain the trends in the midpoints of the 2-dimensional maturation reaction norm over time: the decrease in Lp50 at any given value of condition (see Fig. 6) indicates that the earlier maturation is not due to a time trend in the condition factor. Given the positive association between condition and the probability to become mature, the pattern of observed conditions (Fig. 3c) suggests that by not taking condition into account, the midpoints of the 2-dimensional reaction norm might have been underestimated in the first decades, when condition was high, and overestimated in the last decades when condition was low. Indeed, the estimated shift of the midpoints in the 3-dimensional reaction norm (–0.14 cm yr^{-1}, Fig. 6) is stronger than in the 2-dimensional reaction norm not accounting for condition (–0.10 cm yr^{-1}, Fig 5). The effect of condition in sole seems to be very weakly age-dependent, but it is changing as the maturation reaction norm shifts downwards. Hence, for an early maturing fish, it is getting more important to be in good condition. However, the interpretation of the results in terms of the role of condition in the maturation process is not straightforward (Wright 2007). The role of condition was tested in winter when all maturing females have started VTG, several months after the maturation 'decision' was made. Although we used a fixed window as close as possible to the start of VTG, the positive effect of weight and condition on the probability to become mature is not necessarily affecting the 'decision' to become mature, but is more likely a consequence of it, because fish seem to improve their condition as a consequence of the 'decision' to become mature in the subsequent season (Rijnsdorp 1990). In addition to the different proportions of maturity at age between the 2 data sets, this may also explain the better fit and performance of Model 3 in comparison to Models 4 and 5 (Table 3). Also, the higher uncertainty of the Wp50 estimates might be at least partly due to inter-annual differences in the seasonal ovary development. Unfortunately, this ambiguity has no practical solution.

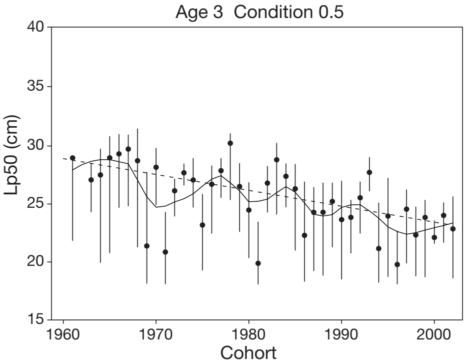

Fig. 6. Reaction norm Lp50 midpoints estimated with Model 5 for Age 3 and condition 0.5 (●), bootstrap 95% percentiles (vertical bars), trend regression weighted by the inverse bootstrap variances (- - -), fit with a non-parametric smoother (—). The trend is significant on a level of $\alpha = 10^{-5}$

Rate of evolutionary response

Because of the difficulty of measuring selection differentials (Sinclair et al. 2002) and heritabilities, especially in the wild, the rate of evolution is not well understood. Experiments have shown that a change in the pattern and rate of size-selective mortality caused major evolution of life history characteristics in 18 generations of guppies *Poecilia reticulate* (D. A. Reznick et al. 1990) and the growth rate of Atlantic silverside *Menidia menidia* evolved within just 4 generations (Conover & Munch 2002). Genetic analyses of rapid life history changes following introduction to novel environments are also well established in several species in the wild (D. N. Reznick et al. 1997, Quinn et al. 2001), and hence, the hypothesis of a rapid fisheries-induced evolution in sole is feasible. The rate of change in the length maturation reaction norm (Model 3) does not seem to be linear, as stepwise change in its reaction norm midpoints seems to occur in the 1980s (Fig. 5). Possible reasons are that: (1) the pattern is due to a change in condition; (2) there was still a considerable proportion of old individuals in the population that contributed to the next generations, reducing the evolutionary response; (3) the selection differential increased after the 1970s; or (4) gene flow between subpopulations affected the changes in reaction norms. Explanation (1) is plausible since the trend in midpoints of reaction norms including weight or condition does not show the same stepwise pattern (Figs. 5 & 6). Explanation (2) is likely since larger fish have a relatively higher fecundity and may contribute disproportionately to reproductive success (Trippel & Neil 2004). Explanation (3) is likely since fishing mortality has increased over time. Since the increase in fishing mortality is not synchronized between subpopulations (ICES 2006), a delay in the evolutionary response due to gene flow (Explanation [4]) may also have played a role (see Conover et al. 2005). The downward trend in the reaction norm is expected to stop, once it falls below the size threshold where selection no longer has any effect (Ernande et al. 2004), e.g. below the minimum size of capture that is close to the minimum landing size of 24 cm. In recent years, the Lp50 in all age groups came close to this threshold and therefore the trend might weaken in the following years.

Alternative factors

It is known that the onset of maturation may be affected by condition (Kjesbu et al. 1991, Trippel & Neil 2004) or other factors such as temperature (Dhillon & Fox 2004, Kraak 2007), in the juvenile period 1 or more years prior to first maturity. The influences of average temperature, condition and competitive biomass were analysed on the population level in the years before maturation. The results show clearly that none of these possible factors could explain the variance in the midpoints better than the trend variable *cohort* (Table 4). Hence, the evolutionary interpretation is the most plausible explanation of the observed shifts in the maturation reaction norm. On top of this trend, temperature in the year of birth and competitive biomass contribute to further reduce the prediction error. Condition, having a considerable effect if introduced as a third dimension in the reaction norm, does not seem to play an important role in the population level, because condition might be much more affected by individual behavior than, for example, either temperature or experienced competitive biomass.

Temperature is known to affect early life history stages, as it may affect age at maturity through its effect on juvenile growth rates (Charnov & Gillooly 2004). However, growth-independent effects of temperature on maturation have also recently been suggested (Dhillon & Fox 2004). Temperature can accelerate developmental rates other than growth (Baynes & Howell 1996, Fuiman et al. 1998) and, therefore, the onset of maturation might be affected by temperature in early life. Since the temperature in the year of birth acting on the larval stage, metamorphosis and early juvenile stages explains most of the variance in addition to the intrinsic trend for the Lp50 (Table 4), our results support such an early life history stage effect.

Similarly, competitive biomass likely has its main effect on maturation through density-dependent growth. However, the significance of competitive biomass in explaining variance in the weight reaction norm midpoints in addition to the intrinsic trend suggest that it may also have a growth-independent effect, driving the fish to accept an earlier maturation at a smaller size if population densities are high (sign of parameter is negative, Table 4). Maturation may be influenced by social factors, e.g. the probability to encounter conspecifics, as shown in the coral-dwelling fish *Gobiodon erythrospilus* (Hobbs et al. 2004). This mechanism might explain a negative correlation of competitive biomass with the reaction norm midpoints (Table 4). By contrast, the presence of dominant adults might suppress maturation of subordinate juveniles as shown in males of the freshwater platyfish genus *Xiphophorus* (Borowsky 1978), hermaphrodites of the coral reef anemone fish genus *Amphiprion* (Fricke & Fricke 1977) and females of the temperate wrasse *Pseudolabrus celidotus* (Jones & Thompson 1980). This would result in a positive correlation of competitive biomass with the reaction norm midpoints.

Another possible cause for changes in the reproductive cycle is that fish might accumulate increased levels of vitellogenin in their tissue due to endocrine disrupting agents present in sewage effluents (Oberdörster & Cheek 2001). Estrogenic pollution (oestradiol or analogues) was found to be associated with elevated concentrations of vitellogenin in flatfish species in the Dutch Wadden Sea (Janssen et al. 1997) and also in samples taken offshore at the Dogger Bank in the North Sea, leading to intersex (Stentiford & Feist 2005). However, since the reproductive effects of increased vitellogenin concentrations in fish are often associated with reproductive impairment and reduced fecundity (Oberdörster & Cheek 2001), it is not clear if increased vitellogenin would accelerate or delay maturation or how these effects would become manifest on the population level. Nevertheless, increased levels of vitellogenin in female *Solea solea* could lead to misclassification of immatures as matures in the macroscopic maturity staging. Therefore, exposure to high concentrations of contaminants during the early juvenile phase in coastal nursery grounds may have influenced the results presented here.

Sources of error

Our results may be influenced by the assumption made to estimate reaction norms: that mature and immature fish have similar growth and mortality rates. However, a sensitivity analysis has shown that the PMRN methodology is robust with respect to differences in growth rate (Barot et al. 2004) and furthermore, these biases would apply to all cohorts equally and thus would not qualitatively change the trends over time. Macroscopic staging of maturity could be erroneous by misclassifying spent or unripe females as juveniles. However, by selecting data around the peak spawning period and applying a moving time window, this error will be negligible. Abortive maturation, in the sense that fish develop until maturity Stage III but not further (De Veen 1970, Ramsay & Witthames 1996), could have biased the PMRN. However, considering maturity Stages I, II and III as juveniles instead of only Stages I and II changed neither our results (not shown) nor our conclusions.

Implications for management

The evidence for fisheries-induced evolution is strong and persistent. Fisheries-induced evolution is likely to decrease maximum sustainable yield (Law & Grey 1989, Heino 1998) and finding practical strategies to reverse the decreasing trend in age and size at maturation will be increasingly difficult. Recovery from a genetic change will be much slower than could be expected from just lower abundance, since selection pressure toward the original genotype in the absence of fishing may be much weaker than selection caused by intensive fishing (Law 2000). If directional selection is strong, the original genotype may have been lost, and surviving genotypes might have a lower fitness in an environment with a lower exploitation rate (Conover et al. 2005). Advanced maturation will result in a reduced size at age of mature fish and thus in a lower biomass per age group (Heino 1998). Whether the reduced growth rates observed in North Sea sole (Fig. 3a) are a direct consequence of the observed shift in the onset of maturation or due to a general deterioration of the growing conditions needs to be analysed in more detail. A direct selection on growth rates, however, seems less likely because in iteroparous species with indeterminate growth, the improved survival through slower growth is unlikely to offset the loss in fecundity (Heino & Kaitala 1999). Even if earlier maturation will positively affect the spawning stock biomass, this may not necessarily translate to an increase in recruitment, since fecundity and egg viability are positively correlated with maternal size (Trippel & Neil 2004), and therefore earlier maturing, smaller individuals will contribute less to reproduction.

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Chapter 2

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Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.)

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ABSTRACT

Changes in the onset of sexual maturation, reproductive investment and growth of North Sea plaice are studied between three periods: 1900s, 1980s and 2000s. Probabilistic maturation reaction norms of both males and females, describing the probability of becoming mature conditional on age and size, shifted towards smaller sizes and younger ages, indicating a fisheries-induced evolutionary change. A higher rate of change was observed during the past 20 years, which may be related to higher temperature conditions. Reproductive investment was estimated from the decrease in lipid, protein, dry weight content and condition factor of the whole body between pre- and post-spawning adults. Reproductive investment expressed as the energy loss over the spawning period increased with body size from 19% at 20 cm to 30% at 40 cm in males and from 35% at 30 cm to 48% at 50 cm in females. No change in reproductive investment could be detected between the 1980s and the 2000s. Von Bertalanffy (VB) growth parameters showed a decrease in L_∞ the asymptotic size and an increase in K, the velocity to reach L_∞, in both males and females. The changes in VB growth are consistent with an increase in energy acquisition and reproductive investment. The observed changes in maturation, reproductive investment and growth are consistent with fisheries-induced evolution, but the changes in reproductive investment and growth need further investigation to disentangle the role of phenotypic plasticity.

1. Introduction

Since fishing mortality is often several times higher than natural mortality and size-selective due to minimum mesh size or minimum landing size regulations, evolutionary changes in the life history traits, such as a decrease in the size and/or age of first maturity, an increase in reproductive investment and a change in growth rate, may be expected (Heino, 1998; Law, 2000; Ernande et al., 2004). Depending on the specific selection pattern, growth rate may evolve towards slower growth, e.g. to remain smaller than the size at first capture as long as possible, or towards faster growth, to reach the size of maturity and start reproducing as quick as possible and thereby ‘outpace’ cumulative (fishing) mortality by higher reproductive fitness (Dunlop et al., in press).

Evidence for fisheries-induced evolution (FIE) has been reported in a number of different species (see reviews in Jørgensen et al., 2007; Kuparinen and Merila, 2007). The main problem in the study of FIE is to disentangle genetic changes from the phenotypic plasticity in traits values (Rijnsdorp, 1993a; Law, 2000; Heino et al., 2002a). Most studies of FIE have focused on changes in sexual maturation, applying the probabilistic maturation reaction norm (PMRN) method of Heino et al. (2002a). This method studies the probability to become mature as a function of the size and age. Assuming that all environmental variability affects maturation indirectly via variation in growth, a downward shift of the reaction norm in the size — age plane provides support for FIE. Most of the studies reported a downward shift in the reaction norm supporting the hypothesis of FIE (reviews in Dieckmann and Heino, 2007; Jørgensen et al., 2007).

Studies of FIE in reproductive investment in natural populations are scarce since the estimation of reproductive investment is complicated. Fecundity provides the most direct estimate, but is restricted to females of species in which the fecundity is determined at the start of the spawning season (determinate spawners). Alternatively, reproductive investment is often estimated by the gonad weight. However, it is difficult to get an accurate estimate since the gonad weight changes substantially in the weeks before the spawning season due to the continuous growth of the ripening oocytes (Rijnsdorp, 1991; Kennedy et al., 2007). More importantly, gonad weight might not be a reliable estimator of reproductive investment because energy continues to be re-allocated from the soma to ripening oocytes during spawning, and because reproductive investment also includes behavioural cost of activities related to spawning (Rijnsdorp,

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1990; Kjesbu et al., 1991; Tyler and Sumpter, 1996). Gonad weight consequently underestimates the total reproductive investment. In capital spawning fish, where the energy reserves for reproduction are stored in the body, reproductive investment can therefore be estimated more reliably from the energy loss over the spawning period (Rijnsdorp and Ibelings, 1989; Rijnsdorp et al., 2005). But also if an accurate estimate of reproductive investment can be made, it will remain difficult to disentangle the effect of environmental conditions such as food or temperature from a potential genetic effect on changes in reproductive investment (Rijnsdorp et al., 2005; Kjesbu and Witthames, 2007). A few studies, which attempted to disentangle phenotypic plasticity in reproductive investment, have provided support for a FIE increase in reproductive investment (Yoneda and Wright, 2004; Wright, 2005; Edeline et al., 2007; Thomas et al., 2009).

Fisheries may select for a change in growth rate by a direct selection on intrinsic growth rates (Ricker, 1981; Sinclair et al., 2002a, b), or indirectly by selection on maturation or reproductive investment, which may typically result in a decrease in growth rate of adults as fish mature earlier and invest more into reproduction under size-selective fishing (Law, 2000; Dunlop et al., in press). Evidence for a FIE change in intrinsic growth rate is reported for a number of natural populations (Edeline et al., 2007; Biro and Post, 2008; Swain et al., 2007), although the interpretation remains controversial (Heino et al., 2008; Dutil et al., 2008).

In this paper we analyse FIE in North Sea plaice. This flatfish species has already been exploited intensively since the mid 19th century (Rijnsdorp and Millner, 1996) and has been studied intensively since the birth of fisheries science in the late 19th century (Wimpenny, 1953; Rijnsdorp, 1993a). FIE in maturation of plaice is suggested by the downward shift in the reaction norm of female cohorts since 1960 (Grift et al., 2003, 2007), but the evidence for a FIE increase in female reproductive investment is equivocal (Rijnsdorp et al., 2005), while the observed changes in growth have been interpreted in relation to changes in the environment (Rijnsdorp and Van Leeuwen, 1996; Bolle et al., 2004). These earlier studies are extended to include males and include data collected in the first decade of the 1900s. Specific objectives are to estimate changes in (i) PMRNs, (ii) reproductive investment and (iii) Von Bertalanffy (VB) growth parameters in males and females between three time periods: I — 1900s (female maturation and male and female growth), II — 1980s and III — 2000s. Results are discussed against the background of differences in environmental condition (temperature, eutrophication, population density) between the time periods.

2. Methods

2.1. Maturation

2.1.1. Data selection

Maturity data for period I were taken from Wallace (1914), where length distributions of immature and mature females were tabulated by age group as recorded from samples taken on the commercial fishing grounds during the spawning season (January–March). For period II and III, we used samples of the commercial landings from the south-eastern North Sea collected between December and February and providing information on the fish length (cm), body weight (g), age (assuming the 1st of January as birthday), sex and maturity stage. Maturity stage was determined by macroscopic inspection of the gonads (Rijnsdorp, 1989). Market samples cannot be used to study the maturation in males because most males mature already below the minimum landing size of 27 cm. Therefore, results of a dedicated maturity survey (Rijnsdorp, 1989) carried out in 1985 and 1986 (period II), and samples collected during the discard monitoring programme on board of commercial fishing vessels and research vessel surveys between September and November in the south-eastern North Sea in 2007 and 2008 (period III) were used. Maturity data of males as reported by Wallace (1914) could not be used because these were collected on the spawning grounds where mature males are known to predominate (Rijnsdorp, 1989). Sampling levels are shown in Table 1.

2.1.2. Probabilistic maturation reaction norms (PMRNs)

The changes in maturation were analysed by comparing the probabilistic reaction norm (PMRN) estimated for the three time periods. PMRNs were estimated according to the method of Heino et al. (2002a) and Barot et al. (2004), which describes the probability to become mature as a function of size and age. The method assumes that environmental variability is reflected in differences in somatic growth, so that any change in an environmental factor that has its effect on maturation through changes in growth can be disentangled (Dieckmann and Heino, 2007). However, changes in the PMRN can not completely control for phenotypic plasticity in maturation, as it does not disentangle genetic effects from environmental factors affecting maturation other than through size and age (Dieckmann and Heino, 2007; Kraak, 2007; Marshall and Browman, 2007). Nevertheless, by incorporating other variables as a third or higher dimension, the role of other environmental variables can be tested, potentially strengthening the interpretation of FIE (Grift et al., 2007; Mollet et al., 2007; Vainikka et al., 2009).

The estimation is based on individual data to yield a PMRN estimate on the population level. Since the aim is to compare three periods, fish from the different periods are treated as distinct populations. For each period, the probability of being mature $m(a,l)$ was estimated from individual data by logistic regression by

$$\mathrm{logit}(m) = \beta_0 + \beta_a a + \beta_l l + \beta_{al} a \times l + \varepsilon \qquad (1)$$

where m is the proportion of mature fish per age and length class, a is age in decimal years, l is length (cm), the β's are the regression parameters and ε is a normally distributed error term. As the data was aggregated by age and 1 cm length classes, the regression was weighted by the number of observations. As first time spawners in plaice can not be distinguished from repeat spawners, the probability of becoming mature p was calculated from the probability of being mature at a certain age a and length l, conditional on the probability of being immature in the previous year by taking account of the length increment (Δl) grown in the course of this year of age group a (Barot et al., 2004):

$$p(a,l) = \frac{m(a,l) - m(a-1, l-\Delta l)}{1 - m(a-1, l-\Delta l)} \qquad (2)$$

This approach relies on the simplifying assumption that the growth rate and mortality rate at a certain size and age are the same for immature and mature individuals. Although this may not be true in reality, Barot et al. (2004) confirmed that the method is robust to the relaxation of this assumption. *Lp50* is used to denote the length

Table 1
Number of observations (N) and percentages of matures (mat) that were used in the maturation analysis per sex, period and age.

			Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
♀	1900s	N	0	263	1199	1831	1125	378
		mat	n.a.	2%	9%	17%	38%	75%
	1980s	N	0	3	555	605	628	439
		mat	n.a	1%	8%	45%	93%	n.a.
	2000s	N	8	44	410	764	915	644
		mat	0%	25%	82%	97%	100%	100%
♂	1980s	N	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
		mat	1%	50%	74%	95%	100%	100%
	2000s	N	44	155	76	14	11	1
		mat	0%	78%	92%	100%	100%	100%.

For males in the 1980s only the ogives per age and size class were available.

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at a given age at which the probability of becoming mature is 50%. Estimation of length increments was based on the Von Bertalanffy fit to the mean length at age (see Section 2.3.2).

2.1.3. Randomization tests

We used a randomization approach to test for statistical differences of *Lp50s* at age between the three periods. For this purpose the data from all three periods were merged and the three periods were permutated randomly to generate a new randomly created data set. From such a randomly created data set the PMRNs and differences between *Lp50s* at age were calculated for each period and this process was repeated 10^5 times. To indicate how likely the observed differences between sex and period might have arisen randomly, the *p*-value of the test was calculated as the proportion of sampled permutations for which the difference in *Lp50s* at age was greater than or equal to the observed differences.

2.2. Reproductive investment

2.2.1. Data selection

Energy content was determined by chemical analysis of the body constituents (%dry weight, %lipid, %ash, %protein). A total of 28 grouped samples of pre-spawning fish ($n = 193$ individual fish), collected between 5 and 20 December 2007, and 26 grouped samples of post-spawning fish ($n = 113$ individual fish), collected between 11 and 29 February 2008, were analysed. Samples were collected by commercial vessel and RV Tridens in the south-eastern North Sea. Maturity stages were classified according to Rijnsdorp (1989). Pre-spawning fish comprised ripening (stage 2) or early spawning (stage 3 or 4) males ($n = 98$) and ripening (stage 2) females ($n = 95$). The post-spawning fish comprised of spent (stage 6 or 7) males ($n = 58$) and females ($n = 55$). In order to study the relationships of reproductive investment with body size, between 3 and 19 fish were pooled in 3–4 size groups representing the full size range. Fish were selected to minimize the size variation within a group. The standard deviation of the groups ranged from 0.41 cm to 3.69 cm.

2.2.2. Sample processing

Fish were stored on ice immediately after being caught, except for the February samples of RV Tridens, which were frozen in sealed polythene. At the laboratory, samples were sorted by sex, maturity stage and length. The frozen samples were thawed slowly at 4 °C before processing. Food, sand or shell particles were removed from the gut to prevent bias in body energy content. The grouped samples were then minced in a commercial meat grinder, thoroughly mixed and a subsample of 300 g was stored in sealed polythene bags for later analysis at -20 °C.

The fraction of dry weight was determined by weighing the samples before and after freeze drying, and by drying samples in an oven for 3 h at 105 °C. The ash content was obtained by heating the samples in a muffle furnace at 550 °C for 22 h. Lipid content was determined using the method of Bligh and Dyer (1959). As the amount of carbohydrates in fish is generally very small (<0.14%; Craig, 1977; Dawson and Grimm, 1980) it was assumed zero. The fraction of protein was not measured but estimated as the difference between the dry weight and the sum of the ash and lipid content.

2.2.3. Estimation of the reproductive investment

Reproductive investment *R* was estimated from the decrease in energy content of the whole body from pre-spawning E_1 to post-spawning E_2 fish,

$$R = E_1 - E_2 \tag{3}$$

The energy density (E, kJ/cm^3) can be estimated as

$$E = \delta\, \varphi\, \alpha \tag{4}$$

where δ is the dry weight percentage, φ is the energy density per gram dry weight, and α is Fulton's condition factor $\alpha = w/l^3$. The energy density per gram dry weight (φ) is estimated from the %lipid and %protein per gram dry weight and the energy values 39.5 kJ/g for lipids and 23.6 kJ/g for protein. The Fulton's condition factor was estimated for the pre-spawning and post-spawning stages from Dutch market samples from December and January–February, respectively.

The size-dependence of the reproductive investment was studied by estimating the size-dependence of the parameters δ, φ, α and body constituents using a GLM:

$$Z = \beta_0 + \beta_l l + \beta_S S + \beta_P P + \beta_{Sl} S \times l + \beta_{Pl} P \times l + \beta_{PS} P \times S + \beta_{PSl} P \times S \times l + \varepsilon \tag{5}$$

where *Z* stands for the dependent variables (δ, φ, α, %lipid, %ash, % protein, %dry weight) and *l* is body length (cm) in the pooled samples or individual fish, *S* is sex and *P* is spawning stage (pre-spawning, post-spawning). Starting from this model with all interactions, we evaluated all other possible models consisting of combinations of these parameters and selected then the model with lowest AIC and significant parameter estimates ($p < 0.05$). For illustration of the selected model, the dependent variable was predicted as a function of body size for males and females in the pre-spawning and post-spawning stage. The selected model was therefore transformed in a simple linear regression with an intercept incorporating the effect of sex and spawning stage and a slope giving the size-dependence. If the size variable was not selected to explain variation in the dependent variable, the slope is 0 and the expectation is given by the intercept.

For the period II, estimates of reproductive investment were available from pooled samples of the commercial fisheries (Rijnsdorp and Ibelings, 1989). Because the sizes of the fish in the pooled samples were not available, the reproductive investment between the period II and period III was compared for the average size of adult fish in the market samples in period II (males: 31.6 cm; females: 41.2 cm).

2.3. Growth

2.3.1. Data selection

For period I, the mean length at age reported by Herwig (1908) was used for the ages 1–4. For the older age groups, mean length at age were reported by Masterman (1911) and Wallace (1914). Averages were weighted by the number of observations per area and 0.5 was added to the age to account for sampling throughout the year.

For period II and III, the survey data of ages ≤6 and commercial data of ages ≥6 were merged because the commercial data is biased towards larger sizes due to the minimal mesh and landing size regulations. To account for the length stratification of the sampling, observations were weighted by their relative frequency in the population.

2.3.2. Analysis

To analyze the changes in growth over time, Von Bertalanffy (VB) growth curves were fitted for each period separately:

$$l_t = L_\infty - (L_\infty - L_0)\mathrm{e}^{-Kt} \tag{6}$$

where l_t is length at age *t*, L_∞ is the asymptotic length, *K* the velocity to reach this asymptotic length and L_0 the length at $t = 0$. For the interpretation of changes in growth, the function was fitted to all age groups and forced to go through the origin ($L_0 = 0$). Since for the maturation estimation only ages 1–6 are relevant, the function was fitted to the survey data of only these ages and the annual length increments Δl used in the PMRN estimation (see Section 2.1.2.) were derived directly from this fit.

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3. Results

3.1. Maturation

The PMRN shifted over the three periods to a smaller size and younger age in both male and female plaice (Fig. 1). The change in female PMRN over the last 20 years was about as important as the change in the 80 years before. The *Lp50* of 4 year old females decreased from 41.6 cm in the 1900s, to 33.3 cm in the 1980s and 22.9 cm in the 2000s. The negative slope of the female reaction norm reflects that the probability of becoming mature at a given length increases with the age of the fish. The male PMRN, which was well below the female PMRN, decreased from 1980s to 2000s: the *Lp50* of 2 year olds decreased from 19.5 cm to 16.0 cm.

The randomization tests indicate that the observed differences are mostly significant at the age where most of the plaice become mature (Table 2). The differences between the female *Lp50*s of the 1900s and the 1980s were significant for all ages ($p<0.01$), while the differences between the 1980s and the 2000s were only significant for the maturation relevant ages 3 and 4, i.e. the ages at which the population growth trajectory hits the PMRN midpoints (Fig. 1). For the males, differences in the *Lp50*s between the 1980s and the 2000s were only significant for age 2 when most males mature. The large difference in male PMRNs at age 3 is not significant and can be considered an artefact due to the very low number of males maturing at this age.

3.2. Reproductive investment

Parameter estimates of the linear regressions of the energy density and body constituents with body size are given in Table 3 and the corresponding regressions (Eq. (5)) are plotted in Figs. 2 and 3. The energy density (kJ/cm^3) of pre-spawning plaice showed a significant positive relationship with body size. In post-spawning plaice, no relation with fish size was observed. Pre-spawning females had a slightly higher energy density than males, whereas in the post-spawning stage, they had a lower energy density (Fig. 2a). The decrease in the energy density between the pre- and post-spawning stage reflects the reproductive investment. Reproductive investment increases with body size in both sexes. Females lose more energy than males, also relative to their larger body size (Fig. 2b).

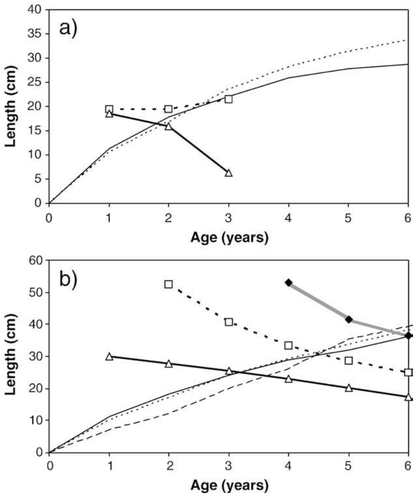

Fig. 1. Probabilistic maturation reaction norms (PMRNs, thick lines) for (a) males and (b) females showing the length (cm) at which the probability of becoming mature is 50% (*Lp50*) in relation to age (years) for three study periods: period I (♦), period II (□) and period III (Δ) and the average growth curves (thin lines): period I (dashed), period II (dotted) and period III (solid).

Table 2
Significance of the differences (cm) in the probabilistic reaction norm midpoints *Lp50*s by age between the periods for females and for males based on 10^5 permutations.

		Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
♀	I – 1900s	n.a.	n.a.	12.4**	8.3**	7.9**	8.4*
	II – 1980s			$p=0.003$	$p=0.003$	$p=0.007$	$p=0.017$
	II – 1980s	n.a.	24.7	15.1**	10.4**	8.3	7.7
	III – 2000s		$p=0.056$	$p=0.001$	$p=0.003$	$p=0.145$	$p=0.291$
♂	II – 1980s	0.9	3.5*	15.2	n.a.	n.a.	n.a.
	III – 2000s	$p=0.335$	$p=0.048$	$p=0.596$			

For some ages the *Lp50*s could not be obtained (n.a.). Level of significance: *$p<0.05$; **$p<0.01$; ***$p<0.001$.

Comparison of the reproductive investment in period II and period III, estimated for the mean size of adult plaice in the commercial samples in period II, revealed similar results: period II: 27% and 44% (Rijnsdorp and Ibelings, 1989); period III: 26% and 43% in males and females, respectively.

The difference in reproductive investment between males and females is reflected in the body constituents — size relationships (Fig. 3). Lipid content increased with size. Pre-spawning males had a higher lipid content than pre-spawning females, but in the post-spawning stage no difference was apparent (Fig. 3a). Relative protein

Table 3
Relationships with body length *l* (cm) of the energy density (kJ/cm^3), lipids (% dry weight), protein (% dry weight), ash (% dry weight), dry weight (%), and condition factor from the selected models from Eq. (5) with the proportion of deviance explained (r^2) and the *p*-value.

Sex (S)	Spawning stage (P)	Intercept	SE	Slope	SE	n
$\text{Energy density} = \beta_0 + \beta_l l + \beta_S S + \beta_P P + \beta_{Sl} S \times l + \beta_{Pl} P \times l + \beta_{PS} P \times S$ ($r^2 = 0.837$; $p<0.001$)						
♀	1	3.322	0.290	0.065	0.009	12
♀	2	3.404	0.103	0.000	–	9
♂	1	3.872	0.429	0.036	0.015	12
♂	2	3.696	0.101	0.000	–	9
$\%\text{lipid} = \beta_0 + \beta_l l + \beta_S S + \beta_P P + \beta_{PS} P \times S$ ($r^2 = 0.824$; $p<0.001$)						
♀	1	8.140	1.680	0.314	0.047	12
♂	1	11.176	1.451	0.314	0.047	12
♀+♂	2	0.815	1.527	0.314	0.047	18
$\%\text{ash} = \beta_0 + \beta_l l + \beta_P P + \beta_{Pl} P \times l$ ($r^2 = 0.764$; $p<0.001$)						
♀+♂	1	17.543	0.984	−0.181	0.032	24
♀+♂	2	16.844	0.385	0.000	–	18
$\%\text{protein} = \beta_0 + \beta_l l + \beta_S S + \beta_P P$ ($r^2 = 0.667$; $p<0.001$)						
♀	1	75.690	1.552	−0.171	0.044	12
♀	2	76.812	1.658	−0.171	0.044	9
♂	1	72.217	1.335	−0.171	0.044	12
♂	2	79.198	1.321	−0.171	0.044	9
$\%\text{dry weight} = \beta_0 + \beta_l l + \beta_P P$ ($r^2 = 0.521$; $p<0.001$)						
♀+♂	1	20.899	0.803	0.056	0.025	24
♀+♂	2	18.363	0.822	0.056	0.025	18
$\text{Condition factor} = \beta_0 + \beta_l l + \beta_S S + \beta_P P + \beta_{Sl} S \times l + \beta_{Pl} P \times l + \beta_{PS} P \times S$ ($r^2 = 0.655$; $p<0.001$)						
♀	1	0.858	0.035	0.005	0.001	394
♀	2	0.810	0.002	0.000	–	824
♂	1	0.942	0.006	0.000	–	111
♂	2	0.965	0.054	−0.004	0.002	154

To simplify the illustration of the size-dependence, the selected model was transformed for each combination of sex (S) and spawning stage (P = pre-spawning stage 1 and post-spawning stage 2) in a simple linear model consisting only of an intercept and the body size-effect (slope). If the size-effect was not selected in Eq. (5), the slope is consequently 0. n denotes the number of grouped samples, except for condition factor where it refers to the number of individual fish.

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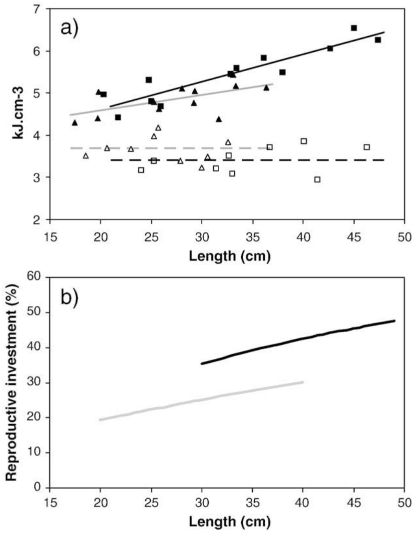

Fig. 2. The energy density (kJ/cm^3) — body size relationship in pre-spawning and post-spawning male and female plaice (a), and the corresponding reproductive investment expressed as the loss of energy density during the spawning period (b). In panel (a), symbols represent estimates of pre-spawning males (closed triangles), pre-spawning females (closed squares), post-spawning males (open triangles) and post-spawning females (open squares). Lines represent significant linear regressions for pre-spawning males (grey), pre-spawning females (black), post-spawning males (grey dashed grey) and post-spawning female (black dashed). In panel (b), the black line represents females and the grey line males.

content increased during the spawning season, in particular in males, and showed a negative relationship with body size (Fig. 3b). No difference in ash content occurred between the sexes. The ash content decreased with body size in pre-spawning fish, whereas in post-spawning fish, the ash content was higher and showed no relationship with fish size (Fig. 3c). The percentage dry weight did not differ between the sexes, but showed a positive relationship with body size and decreased over the spawning period (Fig. 3d). Fulton's condition factor differed between males and females. In males, pre-spawning condition was lower than in females and showed no relationship with body size. In post-spawning males, the condition was higher than in females and showed a slight decrease with body size. Pre-spawning condition factor in females increased with body size, whereas the post-spawning condition factor did not (Table 3).

3.3. Growth

The growth curves of both male and female plaice showed a gradual decrease in the L_∞ since the 1900s, whereas the slope of the curves in the origin or K, the velocity to reach L_∞, increased between period I and period II (Fig. 4). For females, the estimated L_∞ decreased from 90 cm in period I to 53 cm in period II to 48 cm in period III, whereas K increased from 0.087 to 0.200 and 0.232 (Table 4). For the males, the L_∞ decreased from 51.3 to 41.2 cm and 32.6 cm, whereas K increased from 0.155 to 0.281 and 0.393 in period I, period II and period III, respectively.

4. Discussion

4.1. Maturation

Estimating PMRNs for males is difficult because almost all males are currently mature at age 2 (Table 1), making the estimation procedure rather sensitive for the incorrect classification of older males as immature. This may have influenced the estimated relation for the 1980s, in particular the lift in the *Lp50* at age 3, as these data were collected during the spawning period when some of the spent males are not easily distinguished from immature males (Rijnsdorp, 1989) and confident intervals incorporating these uncertainties would be rather large. The randomization test revealed that the difference in the male PMRNs is not significant at age 3. Because in period III samples were collected prior to the spawning period, the results for this period are less affected by the problem of misclassification and therefore more reliable although consisting of much less data. Sampling the male plaice population prior to the spawning season may be advisable to study the maturation process as it may also overcome the differences in spatial distribution of immature and mature fish during the spawning period (Rijnsdorp, 1989) as well as differences in catchability (Rijnsdorp, 1993b, Solmundsson et al., 2003). The difference in spatial distribution between immature and mature plaice during the spawning season rendered the data on males of Wallace (1914) unsuitable to estimate the PMRNs for period I. Nevertheless, the current maturation characteristics of males are quite different from the mean length or age at which Wallace (1914) estimated 50% to be mature: 30–37 cm and 5–6 years of age (Rijnsdorp, 1989). This suggests that also the male PMRN has shifted downwards substantially between period I and II.

As the PMRN disentangles the phenotypic plasticity in maturation caused by variability in growth from an evolutionary genetic effect (Heino et al., 2002a,b), the observed shift in the PMRNs of male and female plaice is indicative for FIE. The decrease in the female PMRN since period II suggests that the decline in the PMRN as observed by Grift et al. (2003) is still continuing (Fig. 5). It is possible, however, that the PMRN may be influenced by other factors that have not been taken into consideration (Kraak, 2007; Marshall and Browman, 2007; Mollet et al., 2007). It has been suggested that the PMRN may shift downward due to increasing temperatures (Grift et al., 2003; Kraak, 2007). The relative large shift over the recent two decades coincided with an increase in sea water temperature on the coastal nursery ground (van Aken, 2008). The average surface temperature during the season when the maturation process occurs (2nd and 3rd quarter, Rijnsdorp, 1989) increased from 13.6 °C in period I, to 14.3 °C (period II) to 15.5 °C (period III). Kraak (2007) showed that the *Lp50* of 4 year old females decreased by 1.0–1.4 cm for an increase in temperature of 1 °C. Hence, the increase in temperature of 1.2 °C between period II and III may explain only a small part (1.2–1.7 cm) of the observed decrease in the *Lp50* of 10.4 cm at age 4 (Table 2). The same conclusion can be drawn about the observed decrease in *Lp50* between period I and II. These results support the conclusion that the observed shifts in the maturation reaction norm are most likely due to FIE and corroborate the conclusions of earlier studies (Rijnsdorp, 1993a; Grift et al., 2003, 2007; Kraak, 2007).

Our results imply that the market sampling database becomes less suitable to monitor the changes in maturation of plaice as an increasing proportion of plaice matures at lengths below the minimum landing size of 27 cm. The problem can be solved for females when discards will be included in the monitoring program. For male plaice, however, this may not be sufficient as the maturation already occurs around the minimum size in the catch (~17 cm). Therefore, a maturation sampling program, for instance during the ongoing flatfish surveys in September and October, is needed to monitor further changes in maturation characteristics.

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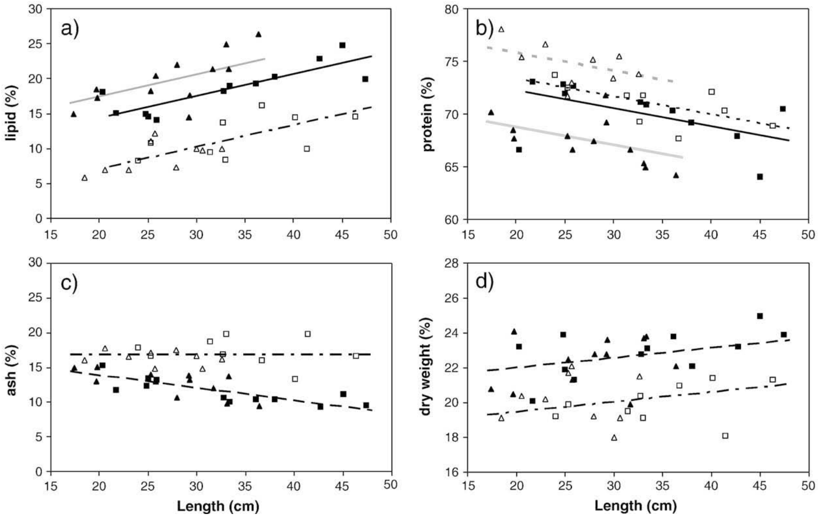

Fig. 3. Relationships of (a) lipid (%dry); (b) protein (%dry); (c) ash (%dry); (d) dry weight (%wet weight) with body size (cm) in male and female plaice. Symbols represent estimates of pre-spawning males (closed triangles), pre-spawning females (closed squares), post-spawning males (open triangles), post-spawning females (open squares). Lines represent significant linear regressions for pre-spawning males (grey), post-spawning males (grey dashed grey), pre-spawning females (black), post-spawning female (black dashed), pre-spawning males and females (long-dashed lines) and post-spawning males and females (dot-dashed).

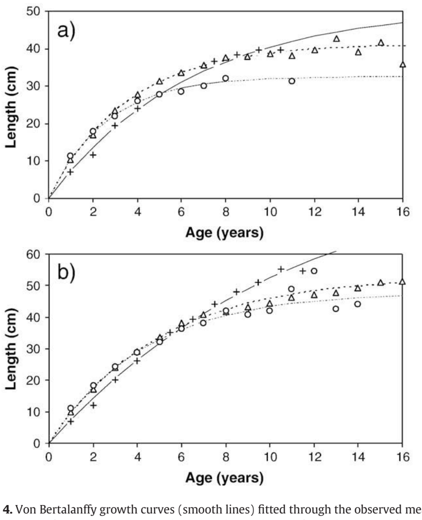

Fig. 4. Von Bertalanffy growth curves (smooth lines) fitted through the observed mean length at age for period I (+), period II (Δ) and period III (o) for males (a) and females (b), assuming that the size at $l(t=0)=0$.

4.2. Reproductive investment

Our study showed that the reproductive investment increased with body size in both males and females. These estimates include both spawning products and activity costs. The increase in reproductive investment with fish size correlates with a longer spawning duration of older fish (Rijnsdorp, 1989; Bromley, 2000), and may reflect the change in the trade-off between current and future reproduction.

Adult male and female plaice, differ in the percentage of lipids and protein. Pre-spawning males have a higher lipid content and lower protein content than females, whereas post-spawning males have a higher protein content than females. This reflects the differences in the chemical demands imposed by the spawning activities of male and female fish. Females require substantial amounts of both protein and lipids to produce eggs, while males will require relatively more lipids for spawning behaviour (Dawson and Grimm, 1980; Rijnsdorp and Ibelings, 1989).

Although the best solution currently available, the approach of estimating reproductive investment from the decrease in the energy density during the spawning period is still crude as it relies on a number of simplifying assumptions: First, it is assumed that during

Table 4
Von Bertalanffy parameters estimates of male and female plaice for three periods assuming that the size at $l(t=0)=0$.

	Period I (1900s)			Period II (1980s)			Period III (2000s)		
	K	L_∞	$K.L_\infty$	K	L_∞	$K.L_\infty$	K	L_∞	$K.L_\infty$
♀	0.087	90.1	7.8	0.2	53.1	10.6	0.232	48.1	11.2
♂	0.155	51.3	8.0	0.281	41.2	11.6	0.393	32.6	12.8

K is a proxy for reproductive investment whereas the product KL_∞ is a proxy of the rate of energy acquisition (see Discussion).

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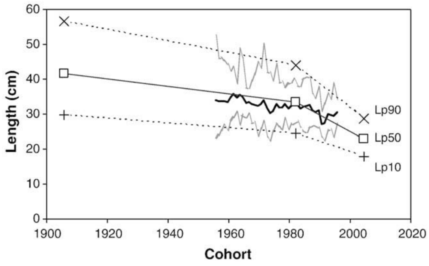

Fig. 5. PMRN midpoints (cm) at which the probability of 4-year old females to become mature is 10% (+ *Lp10*), 50% (□ *Lp50*) and 90% (× *Lp90*) in period I (1900s), period II (1980s) and period III (2000s) as compared to the results of individual cohort (*Lp50* — black line; *Lp10* and *Lp90* — grey lines) from Grift et al. (2003).

the spawning period fish do neither feed or grow in body length. Tagging experiments have shown that body growth stops during the spawning period in winter (Dawson and Grimm, 1980; Rijnsdorp, 1990). Second, it is well established that plaice that are in spawning condition hardly feed. Less than 10% of the spawning males and about 2% of the spawning females were recorded with food remains in their guts in the middle of the spawning period (Rijnsdorp, 1989). Third, the assumption that the fish sampled in February had just ceased spawning, may not be true since the February samples may comprise fish from the eastern English Channel spawning ground that spawned a few weeks earlier than in our study area (Harding et al., 1978). As plaice from this spawning ground migrate through the southern North Sea on their return migration to the northern feeding grounds (Metcalfe and Arnold, 1997; Hunter et al., 2003), it is likely that the spent females caught in the southern North Sea and that were already feeding in January (Rijnsdorp, 1989) originated from this spawning ground. Although fish with food remains in their gut were excluded from our samples we cannot exclude the possibility that some of the fish in our sample may have resumed feeding.

No change in reproductive investment between period II and period III could be detected. Because sampling in the 1980s did not take account of the effect of body size on reproductive investment and the sizes of the sampled fish in period II were not available, the results should be interpreted with caution. Nevertheless, the results are in agreement with a recent study which was unable to detect a change in female gonad weights since 1980 (Rijnsdorp et al., 2005). The lack of support for a change in reproductive investment contrasts the change in the VB growth parameters that suggest an increase in reproductive investment (see below). Further evidence for an increase in reproductive investment in North Sea plaice stems from the increase in potential fecundity between the late 1940s and the 1977–1984 of females up to about 40 cm (Rijnsdorp, 1991; Rijnsdorp et al., 2005). That the evidence for FIE in reproductive investment is sparse (Yoneda and Wright, 2004; Edeline et al., 2007) is partly due to the few studies that have addressed this issue (Jørgensen et al., 2007), but may also be due to the difficulty in disentangling a genetic change from the phenotypic plasticity (Rijnsdorp et al., 2005; Kjesbu and Witthames, 2007).

4.3. Growth

Age reading errors may have affected the accuracy of the growth estimated for the three periods. For period I and II, whole otoliths were analysed, whereas in period III, otolith sections were analysed. The first method may be relatively more prone to the underestimation of the age of older fish, because growth increments become smaller with age. Masterman (1911) discussed that this underestimation occurred in male otoliths with more than seven rings. The estimated L_∞ of the period I and II may therefore be overestimated. The estimated L_∞ of 90 cm for period I was high compared with the maximum size observed in the catch for females of 73 cm, but the L_∞ of 51 cm in males was close to the maximum size of 49 cm observed in the catch (Masterman, 1911; Wallace, 1914). Nevertheless, it is unlikely that age reading errors can fully explain the large change in L_∞ observed and we conclude that K has increased and L_∞ has decreased in both male and females plaice.

In order to interpret the observed changes in the VB growth parameters K and L_∞, we explore how a change in reproductive investment, or a change in the rate of energy acquisition may affect the asymptotic size L_∞ and the growth velocity K. The VB growth model assumes that somatic growth is the result of the rate of energy acquisition and the rate of energy expenditure (Von Bertalanffy and Pirozynski, 1952). Since the VB growth model does not include maturation, a change in the onset of maturation will not affect the VB growth parameters. Integration of the energy allocation model shows that VB parameter K is related to the energy expenditure, L_∞ is related to the ratio of energy acquisition over energy expenditure and the product KL_∞ is related to energy acquisition (Charnov et al., 2001; West et al., 2001; Lester et al., 2004). Assuming that energy expenditure will be mainly determined by reproductive investment, the observed change in K in males and females may suggest that reproductive investment has increased throughout the 20th century. Further, the increase in the rate of energy acquisition (KL_∞) was insufficient to balance the increase in energy expenditure (K) resulting in a decrease in L_∞.

The changes in energy acquisition and energy expenditure may be due to changes in environmental conditions as well evolutionary changes. Earlier studies have shown that density-dependent reductions in growth are restricted to the juvenile phase when plaice are concentrated in restricted coastal nursery grounds. Juvenile growth increased in the 1960s and 1970s coinciding with an increase in eutrophication and bottom trawling, which may have improved the food availability (Rijnsdorp and Van Leeuwen, 1996). Since the mid 1980s, annual growth increments of plaice and sole have decreased, which was interpreted as a decrease in the available food (Rijnsdorp et al., 2004; Philippart et al., 2007). This decrease contrasts with the increase in the indicator of energy acquisition rate KL_∞ between the 1980s (period II) and the 2000s (period III) observed in this study. This suggests that part of the increase in energy acquisition KL_∞ may not be related to the phenotypic plastic response to the environment and may be due to a fisheries-induced evolutionary response to cope with the increasing reproductive investment. A comparison of size specific fecundity revealed an increase since the 1940s, consistent with the change expected from FIE (Rijnsdorp, 1991; Rijnsdorp et al., 2005).

In order to address the changes in growth in more detail, a careful study of changes in growth rate of cohorts in relation to changes in size-selective harvesting, temperature and food availability employing the available otolith collections may help to test the hypothesis of FIE (Sinclair et al., 2002a,b). Swain et al. (2007) adopted this approach and concluded that the mean size at age 4 in Gulf of St Lawrence cod decreased due to FIE, although their conclusion was challenged (Heino et al., 2008; Dutil et al., 2008).

4.4. Conclusion

Our analysis provided support for FIE changes in maturation in males and females over the past century. The higher rate of change observed in the recent two decades might be due to synergistic effects with increasing temperature. The evidence for a FIE increase in reproductive investment is inconclusive. An increase in reproductive investment is suggested by the changes in the VB growth parameters, but the evidence for FIE from the direct measurement of reproductive

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investment is inconclusive as no change in the size-conditional reproductive energy loss could be detected between period II and period III. Literature data suggests that reproductive investment increased between period I and period II in females up to 40 cm, but not in larger sized females. The observed changes in maturation, reproductive investment and growth are consistent with FIE, but the changes in reproductive investment and growth need further investigation to disentangle the role of phenotypic plasticity.

Acknowledgements

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II

Empirical evidence from correlated traits

Chapter 3

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Multiple growth-correlated life history traits estimated simultaneously in individuals

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We present a new methodology to estimate rates of energy acquisition, maintenance, reproductive investment and the onset of maturation (four-trait estimation) by fitting an energy allocation model to individual growth trajectories. The accuracy and precision of the method is evaluated on simulated growth trajectories. In the deterministic case, all life history parameters are well estimated with negligible bias over realistic parameter ranges. Adding environmental variability reduces precision, causes the maintenance and reproductive investment to be confounded with a negative error correlation, and tends, if strong, to result in an underestimation of the energy acquisition and maintenance and an overestimation of the age and size at the onset of maturation. Assuming a priori incorrect allometric scaling exponents also leads to a general but fairly predictable bias. To avoid confounding in applications we propose to assume a constant maintenance (three-trait estimation), which can be obtained by fitting reproductive investment simultaneously to size at age on population data. The results become qualitatively more robust but the improvement of the estimate of the onset of maturation is not significant. When applied to growth curves back-calculated from otoliths of female North Sea plaice *Pleuronectes platessa*, the four-trait and three-trait estimation produced estimates for the onset of maturation very similar to those obtained by direct observation. The correlations between life-history traits match expectations. We discuss the potential of the methodology in studies of the ecology and evolution of life history parameters in wild populations.

The schedule according to which energy is allocated to either somatic growth or reproduction is a cornerstone of life history theory (Kooijman 1986, Roff 1992, Stearns 1992, Kozlowski 1996, Charnov et al. 2001). Energy allocation schedules differ among species as they reflect adaptation to both the environment and internal constraints resulting from sharing a common currency between different functions. Individuals indeed face an energy tradeoff between somatic growth and reproduction (Roff 1992, Stearns 1992, Heino and Kaitala 1999). In case of indeterminate growth, individuals also experience a tradeoff between current and future reproduction since fecundity generally increases with body size. Various energy allocation schedules have been proposed in the literature (Von Bertalanffy and Pirozynski 1952, Day and Taylor 1997, Kooijman 2000, West et al. 2001). They differ mostly in terms of priorities of energy flows to the different functions. Allocation schedules typically comprise four traits, namely energy acquisition, maintenance, onset of maturation, and thereafter reproductive investment, whereas somatic growth arises as a by-product: the energy that remains after accounting for the primary energy flows to maintenance and reproductive investment is available for somatic growth. The study of energy allocation schedules in individual organisms is difficult because of a lack of data at the individual level as this would require monitoring separate individual organisms throughout their life time. Studies therefore have focused on the population level as well as on single traits (Stevenson and Woods Jr. 2006). Studying the four traits together (acquisition, maintenance, onset of maturation and reproductive investment) at the individual level would offer several advantages over the widely used single trait estimation at the population level: (1) phenotypic correlations between traits could be estimated; (2) changes in one trait could be interpreted conditionally on changes in other traits, precisely because of the previous correlations; (3) it would be more consistent with the fact that physiological tradeoffs apply at the individual and not at the population level.

Organisms in which the individual growth history is recorded in hard structures offer a unique opportunity to study energy allocation schedules at the individual level. Fish for instance show indeterminate growth and the growth history of individuals can be reconstructed from the width of the seasonal structures imprinted in hard structures such as otoliths or scales (Runnström 1936, Rijnsdorp et al. 1990, Francis and Horn 1997). Earlier studies have attempted to estimate the onset of maturation using growth history reconstructed from otoliths or scales (Rijnsdorp and Storbeck 1995, Engelhard et al. 2003, Baulier and Heino 2008), but no study has yet attempted to simultaneously estimate several life history traits related to life time patterns of energy allocation at the individual level.

In this study, we estimate simultaneously parameter values at the individual level for energy acquisition, maintenance, onset of reproduction, and reproductive investment by fitting an energy allocation model to individual growth trajectories. The energy allocation model assumes that the onset of maturation is reflected in a discontinuity in the slope of the growth trajectory, while the energy acquisition discounted by maintenance is assessed by the slope of the growth trajectory before maturation, and reproductive investment is translated in the amplitude of the change in the slope of growth trajectory at the discontinuity. The performance of the method and its sensitivity to both model uncertainty and inter-annual environmental variability are explored using simulated data. The method is applied to an empirical data set of individual growth curves back-calculated from otoliths of female North Sea plaice *Pleuronectes platessa*. Maturity status deduced from the age and size at the onset of maturation estimated by our model is compared to direct evaluation of maturity status by visual inspection of the gonads in market sampling (Grift et al. 2003).

Material and methods

Parameter estimation

Energy allocation model

When an animal becomes mature, a proportion of the available energy is channeled towards reproduction and is no longer available for somatic growth (Ware 1982). Hence, a decrease in growth rate can be expected after maturation. We use a general energy allocation model (Von Bertalanffy and Pirozynski 1952, Charnov et al. 2001, West et al. 2001, Banavar et al. 2002) according to which the growth rate of juveniles and adults is given by

$$\frac{\partial w}{\partial t} = \begin{cases} aw^{\alpha} - bw^{\beta} & \text{if } t < t_{mat} \\ aw^{\alpha} - bw^{\beta} - cw^{\gamma} & \text{if } t \geq t_{mat} \end{cases} \tag{1}$$

where w is body weight, t is time, t_{mat} is time at the onset of maturation, aw^{α} is the rate of energy acquisition, bw^{β} is the rate with which energy is spent for maintenance and cw^{γ} is the rate of reproductive investment with which energy is spent for reproductive activity (e.g. gamete production, reproductive behavior). For simplicity we will refer to energy acquisition a, maintenance b and reproductive investment c, although a, b and c describe the size-specific rates for the corresponding processes. There is disagreement about the scaling exponents α, β, and γ involved in the allometries between energy rates and body weight. Metabolic theory of ecology (MTE) suggests that metabolism scales with a quarter power law of body weight (West et al. 1999, Gillooly et al. 2001, Savage et al. 2004). This hypothesis builds on the fractal-like branching pattern of distribution networks involved in energy transport (West et al. 1997) but the generality of this allometric scaling law is contested (Banavar et al. 2002, Darveau et al. 2002, Clarke 2004, Kozlowski and Konarzewski 2004). Nevertheless, we assumed a scaling exponent of energy acquisition $\alpha = 3/4$ (West et al. 1997) as this is close to empirical estimates of α (Gillooly et al. 2001, Brown et al. 2004) including our model species North Sea plaice (Fonds et al. 1992). For the scaling exponent of maintenance β, it is required that $\beta > \alpha$ in order to obtain (1) bounded asymptotic growth, i.e. to reach an asymptotic maximum body weight in the absence of maturation and (2) an energetic reproductive-somatic index (RSI), defined as the ratio of reproductive investment over body weight in terms of energy (in other terms an energetic analogue to the gonado-somatic index), that increases with age and size as commonly observed in empirical data (not shown). MTE suggests $\beta = 1$ since with increasing size, the energy demand becomes relatively more important than its supply (West et al. 1997, 2001) and thus fulfills the required conditions. For the scaling exponent of reproductive investment γ, we assume $\gamma = 1$ for the sake of simplicity. This is in line with the assumption that total brood mass is a constant fraction of maternal body weight (Blueweiss et al. 1978, Charnov et al. 2001), although reproductive investment might be related to a body weight allometry with an exponent higher than 1 (Roff 1991).

By integration of Eq. 1 assuming $\alpha = 3/4$ and $\beta = \gamma = 1$, the somatic weight w can be expressed as a function of time t. To switch from juvenile ($t < t_{mat}$) to adult ($t \geq t_{mat}$) growth in Eq. 1, a continuous logistic switch function S(t) with an inflection point located at the time of the onset of maturation t_{mat} is used (Supplementary material Appendix 1). It results that the lifespan somatic growth curve is obtained as a continuous function of time though a discontinuity in its parameters due to the onset of maturation being introduced by the switch function S(t):

$$w^{1-\alpha}(t) = (1 - S(t))\left[\frac{a}{b} - \left(\frac{a}{b} - w_0^{1-\alpha}\right)e^{-bt(1-\alpha)}\right] + S(t)\left[\frac{a}{b+c} - \left(\frac{a}{b+c} - w_{mat}^{1-\alpha}\right)e^{-(b+c)(t-t_{mat})(1-\alpha)}\right] \tag{3.0}$$

where w_0 is body weight at $t = 0$ and w_{mat} is body weight at $t = t_{mat}$ given by

$$w_{mat}^{1-\alpha} = \frac{a}{b} - \left(\frac{a}{b} - w_0^{1-\alpha}\right)e^{-bt_{mat}(1-\alpha)} \tag{3.1}$$

The growth curve levels off at the asymptotic weight w_{∞},

$$w_{\infty}^{1-\alpha} = a/(b+c) \tag{3.2}$$

Total reproductive investment R (including gonadic and behavioral costs) is obtained by integrating the rate of energy conversion to reproduction from t to $t + \Delta t$:

$$R(t + \Delta t) = \int_{t}^{t+\Delta t} cw(\tau)d\tau \tag{4}$$

where Δt describes the reproductive cycle over which the reproductive products are built up, fertilized and cared until the offspring is autonomous. An analytical expression of $R(t + \Delta t)$ as a function of w(t) and $w(t + \Delta t)$ can be obtained (Supplementary material Appendix 1). Reproduction generally occurs at certain periods during lifespan. Fish for instance are often annual spawners (including North Sea plaice) and hence reproductive investment is given over annual time steps ($\Delta t = 1$). Energy for reproduction is first stored in various body tissues during the feeding period and then re-allocated to the gonad and released during the spawning period. Since the currency of the model is energy, different energy densities of different tissues have to be accounted for when fitting the model to real data.

Fitting procedure

The energy allocation model was fitted using a general-purpose optimization procedure (R 2.6, optim) by restricting all parameters to be positive using box-constraints specification (Byrd et al. 1995). Life history parameters a, b, c and t_{mat} were estimated by using this procedure to minimize the sum of squared residuals of weight at age data versus predicted weight at age. Q–Q-plots indicated that the distribution of residuals is close to normal. The algorithm was given a grid of possible combinations of a, b, c and t_{mat} as starting values and the best solution was selected based on the lowest AIC. A genetic algorithm (<www.burns-stat.com/>) yielded similar results as those presented in this paper (not shown). The estimates of the time at the onset of maturation t_{mat} and the asymptotic weight $w_{\infty}^{1/4} = a/(b+c)$ were constrained to a species-specific range (e.g. North Sea plaice 0.5 year $\leq t_{mat} \leq$ 8.5 year, 400 g $\leq w_{\infty} \leq$ 4000 g).

Confounding

Preliminary analyses of the plaice data set has shown that the estimation of the four life history parameters a, b, c and t_{mat} (four-trait estimation) yields an unimodal distribution for energy acquisition a but a bimodal distribution for maintenance b and reproductive investment c (Fig. 1). The mode in the distribution of b is likely an underestimation at 0, which is related to an overestimation of c reflected in the 2nd mode of its distribution. Selection of observations belonging to the 2nd mode of the b distribution thanks to a Gaussian mixture model (R 2.6, MClust; Fraley and Raftery 2006) also removes the 2nd mode in the c distribution (dotted line, Fig. 1). To remove the confounding between b and c several options were considered: 1) use only observations belonging to the 2nd b-mode – the correlation structure in these observations was considered to be the most representative (Table 3) and was used for simulations – or 2) assume parameter b to be fixed at the population level (three-trait estimation). The rationale for this choice is that maintenance costs are generally acknowledged to be species- rather than individual-specific (Kooijman 2000) and our main interest is in variation in reproductive investment. The population level value of b was estimated by fitting a mean growth trajectory (Eq. 1) to the whole somatic weight-at-age dataset. Confounding between b and c on this level was avoided by fitting concomitantly reproductive investment $R(t+\Delta t)$ to an independent dataset of reproductive investment-at-age (see application to real data). The partitioning of b in the sum $b+c$ could thereby be estimated accurately. The population mean growth trajectory and reproductive investment were fitted simultaneously by minimizing the sum of weighted squared residuals of somatic weight-at-age data and reproductive investment-at-age data versus their predictions.

Performance analysis

Performance

To test its performance, the method was applied to 2000 growth trajectories simulated with known life history parameters. The life history parameters a, b, c and t_{mat} were drawn from a multivariate normal distribution with the co-variance matrix taken from the results of the application to North Sea plaice data, after having selected only observations belonging to the representative b-mode in the distribution of parameter estimates (Table 3). To simulate weight-at-age data, $w(t+\Delta t)$ was expressed as a function of $w(t)$ by using a function similar to Eq. 3 but in which $w^{1-\alpha}(t)$ was replaced with $w^{1-\alpha}(t+\Delta t)$, and $w_0^{1-\alpha}$ (for $t \leq t_{mat}$) and $w_{mat}^{1-\alpha}$ (for $t > t_{mat}$) with $w^{1-\alpha}(t)$. To evaluate the estimation bias on the population level and assess its dependency on life-history strategy and environmental variability, the mean relative bias over all life history parameters (the average absolute difference between estimated and true values relative to true values) was used for each individual i as a measure of accuracy:

$$e_i = \frac{1}{4}\left(\frac{|a_{est} - a_{true}|}{a_{true}} + \frac{|b_{est} - b_{true}|}{b_{true}} + \frac{|c_{est} - c_{true}|}{c_{true}} + \frac{|t_{mat,est} - t_{mat,true}|}{t_{mat,true}}\right) \quad (5)$$

To test performance in the deterministic case, i.e. without environmental variability, the bias e_i was analyzed in dependence of a combination of two of the following

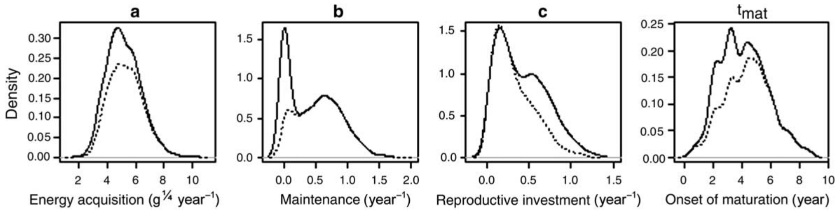

Figure 1. Density distributions of the four estimated parameters on real data. The first mode in the density distribution of maintenance (b) (solid line) is likely an artifact due to confounding and corresponds to the second mode in the distribution of reproductive investment (c). By selecting only observations belonging to the second mode fitted by a Gaussian mixture over parameter b, the first mode in the distribution of b's and the bump to the right in the distribution of c's are removed (dotted thick line).

factors (1) the relative reproductive investment $q = c/(b+c)$, (2) the relative onset of maturation $\tau = t_{mat}(b+c)$, (3) the relative initial size $v_0 = w_0(a/(b+c))^{-4}$, (4) age t and (5) the number of observations in the mature stage y_{mat}. Variation in the three dimentionless parameters q, τ and v_0 accounts for any variation in the parameters they are comprised of, i.e. a, b, c, t_{mat} and w_0, which allows investigating the whole parameter space at a smaller cost.

Effects of temporal variability in environmental conditions

Individual growth trajectories will be affected by environmental variability. To test whether the parameters corresponding to energy acquisition a, maintenance b, reproductive investment c and time at the onset of maturation t_{mat} can be estimated reliably, annual stochasticity was introduced the individuals' life-history traits drawn from the multivariate normal distribution (see deterministic case). As environmental variability is likely to be auto-correlated, for simplicity a first order autoregressive process AR(1) was used to simulate the lifespan series of the energy acquisition parameter a (constrained to be positive):

$$a_t = E(a) + \theta(a_{t-1} - E(a)) + \varepsilon_t \quad \varepsilon_t \sim N(0, \sigma_a^2(1-\theta^2)) \tag{6}$$

where E(a) denotes the expected value of a, θ is the autoregressive parameter and ε_t is a normally distributed noise term with mean 0 and variance $\sigma_a^2(1-\theta^2)$ where σ_a^2 is the variance of a_t. The corresponding series of b_t and c_t were simulated by sampling b_t and c_t from the normal distributions that yielded correlations with the autoregressive a_t series which were the same as those observed among the individual estimations. The rationale here is that we assume that observed correlations between energy acquisition and other life history traits across individuals are mainly due to plastic physiological processes (vs genetic correlations) that therefore can also apply within individuals through time in case of temporal variation in energy acquisition. More precisely, b_t and c_t were sampled from the normal distributions $N(\beta_0+\beta_1 a_t, \sigma)$ that yielded linear regressions of parameters b and c on a that were consistent with observed means, variances and correlations, that is with intercept β_0, slope β_1 and residual variance σ^2 defined as:

$$\beta_0 = \bar{x} - \bar{a}\beta_1 \qquad \beta_1 = \frac{\rho(a,x)\sigma_x}{\sigma_a} \qquad \sigma^2 = \sigma_x^2 - \beta_1^2\sigma_a^2 \tag{7}$$

where x stands for b or c and the means $\bar{x}$ and $\bar{a}$, variances σ_x^2 and σ_a^2, and correlations $\rho(a,x)$ were taken from the empirical results of the application to North Sea plaice r(a,x) (Table 3). Body weight was constrained to be monotonously increasing while prioritizing reproduction over growth. Available surplus energy $aw^{3/4} - bw$ was first allocated to reproduction and the remaining energy thereafter $aw^{3/4} - (b+c)w$ was allocated to growth. If surplus energy happened to be negative $aw^{3/4} - bw < 0$ acquisition a and maintenance b were resampled until obtaining a positive amount. If the remaining energy was negative $aw^{3/4} - (b+c)w < 0$, reproductive investment c was adjusted such that all available surplus energy was used for reproduction and none for somatic growth by setting $c = aw^{-1/4} - b$. The initial conditions of the simulation were chosen such that the realized θ_a of the initial a_t-series was within [0,1], and that the realized CV's in a, b and c where within [0,0.5]. In addition to the relative reproductive investment q, timing of onset of maturation τ and initial weight v_0, the effect of the expected value E(x) of the parameters (x standing for a, b or c), the realized coefficients of variation of the parameters CV_x, the realized degree of auto-correlation θ_x, and the realized correlation $r_{sim}(x,x')$ between the simulated series of a, b and c, the age t and the number of observations in the mature stage y_{mat} on the mean of bias percentages (Eq. 5) was analyzed by a linear model:

$$e = \beta_0 + \beta_1 q + \beta_2\tau + \beta_3 v_0 + \beta_4 t + \beta_5 y_{mat} + \beta_6 CV_x + \beta_7\theta_x + \beta_8 r(x,x') + \varepsilon \tag{8}$$

where the β's are the statistical parameters and ε is a normal error term (also in all subsequent statistical models).

Model uncertainty

The effect of uncertainty about the scaling exponent α of energy acquisition rate with body weight was explored by fitting an energy allocation model to the generated deterministic data set (i.e. without environmental noise) postulating a scaling exponent lower ($\alpha = 2/3$) or higher ($\alpha = 4/5$) than the one used to generate the data ($\alpha = 3/4$). A wrong assumption on α would lead to a different population level estimate of the fixed b and the effect of uncertainty about α in this approach was explored along the same line as above.

Application to data

Data

The method developed was applied to an empirical dataset of individual growth trajectories back-calculated from otoliths of 1779 female North Sea plaice from cohorts from the 1920s to the 1990s, aged at least six years (Rijnsdorp and Van Leeuwen 1992, 1996). This age threshold was chosen as these females then have 90% probability of being sexually mature for at least one year (Grift et al. 2003). Because the otolith samples were length stratified, the observations of each length class were weighted according to its relative frequency in the population to obtain population level estimates.

Length–weight relationship

The back-calculated growth trajectories, which are in body length units (l in cm), were converted into body weight (w in g). We used the relationship between body weight w and length l of post spawning fish, estimated from market sampling data by a linear model. The rationale was that spent fish have a low condition, i.e. there are no energy reserves for reproduction in the post-spawning state:

$$\log(w) = \beta_0 + \beta_1 d^1 + \beta_2 d^2 + \beta_3 d^3 + \beta_3 \log(l) + \varepsilon \tag{9}$$

where d is the day in the year accounting for the high condition early in the year before spawning, the condition low after spawning and the building up of resources thereafter. The body weight at $w_0 = w(t=0)$ was assumed to be constant across individuals and equal to 2.5 mg corresponding to the weight of fish as large as the circumference of an egg with a radius of 2 mm (Rijnsdorp 1991).

Maintenance

To avoid confounding between parameters, maintenance b was assumed to be fixed across individuals at its population level estimate (see section confounding above). To obtain this estimate, the population mean growth trajectory and an independent estimate of reproductive investment were fitted simultaneously by minimizing the sum of weighted squared residuals of somatic weight-at-age data and reproductive investment-at-age data versus their predictions. The population level estimates assuming the scaling exponent $\alpha = 3/4$ were $a = 4.84\ g^{1/4}\ year^{-1}$, $b = 0.47\ year^{-1}$, $c = 0.40\ year^{-1}$, $t_{mat} = 4.00$ year (Fig. 2). The population $b_{\alpha = 3/4} = 0.47\ year^{-1}$ (Results) was used as a constant in the three-trait estimation.

Reproductive investment

Reproductive investment data included the cost of building gonads as well as the cost of migration between the feeding and spawning grounds. Reproductive investment $R_{somatic}$, expressed in units of energy-equivalent somatic weight, was thus obtained as

$$R_{somatic} = p_{adult}(g\kappa + M_{resp}/\delta) \qquad (10)$$

where p_{adult} is the probability of being mature, g is the gonad weight, κ is the conversion factor to account for different energy densities between gonad and soma, M is the energy spent for migration and δ is the energy density of soma. Gonad weight g and the probability of being mature p_{adlt} were estimated as functions of size or age and size, respectively, using linear models fitted to market samples of pre-spawning females:

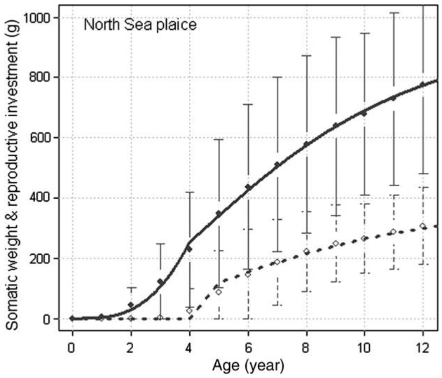

Figure 2. Population fit of life-history on somatic size at age (solid lines) and estimated reproductive investment (dashed lines, see text). Error bars show 5% and 95% confidence intervals for the observations. For the gonads the averages of only mature fish are given whereas the fitted curve represents average population gonadic growth. The estimated life history parameters are $a = 4.84\ g^{1/4}\ year^{-1}$, $b = 0.47\ year^{-1}$, $c = 0.40\ year^{-1}$, $t_{mat} = 4.00$ year.

$$\log(g) = \beta_0 + \beta_1 \log(1) + \varepsilon \qquad (11)$$

Gonad weight was set to zero for females for which the probability of being mature p_{adlt} was less than 50%, given age and size:

$$\mathrm{logit}(p_{adult}) = \beta_0 + \beta_1 t + \beta_2 l + \beta_3 t \times 1 + \varepsilon \qquad (12)$$

The factor used to convert gonad weight g to energy-equivalent somatic weight was $\kappa = 1.75$, corresponding to the ratio between energy densities in pre-spawning gonad and in post-spawning soma (Dawson and Grimm 1980). Migration cost was estimated assuming a cruising speed V of 1 body length per second (Videler and Nolet 1990). The migration distance D is positively related to body size (Rijnsdorp and Pastoors 1995) with an average of about 140 nautical miles for a body length of 40 cm in plaice (Bolle et al. 2005). The energetic cost of swimming is then given by:

$$M_{resp} = (10^{0.3318} V(77.9T + 843.3) w^{3/4}) D/V \qquad (13)$$

where M_{resp} is the respiration rate in J per month (Priede and Holliday 1980), D/V is the duration of active migration (in months) and T is temperature in °C, set to 10°C. The energy spent for respiration M_{resp} was converted into energy-equivalent somatic weight assuming an energy density in post-spawning condition of $\delta = 4.666\ kJ\ g^{-1}$ (Dawson and Grimm 1980).

The resulting size-dependent energy-based reproductive investment relative to the somatic weight, i.e. the reproductive-somatic index RSI, increased with length l, and the resulting gonadic investment relative to the reproductive investment, i.e. the gonado-reproductive index GRI, was minimal for intermediate size classes (Fig. 3). Using this model, an average plaice of 40 cm length had a reproductive investment, expressed as a percentage of the post-spawning body weight, of about 38.0%, of which about 86% is used for gonads and 14% for migration.

Validation

To validate the approach, the estimates of the time at the onset of maturation t_{mat} were compared to independent estimates. Since t_{mat} is estimated in continuous time but reproduction occurs only at the start of the year, the age at first spawning A_{mat} was estimated by rounding up t_{mat} to the next integer, assuming a minimal time interval of four months between the onset of maturation and the actual spawning season ($A_{mat} - t_{mat} \geq 1/3$ year). These four months correspond to the minimal period of time during which gonads are built up in typical annual spawners (Rijnsdorp 1990, Oskarsson et al. 2002). From the estimated A_{mat}, the probabilities of becoming mature at given ages and sizes were estimated and compared to estimates obtained from independent population samples (Grift et al. 2003). Since the individuals' age at first spawning A_{mat} was known, the probability of becoming mature was estimated directly by logistic regression of the ratio between the number of first time spawners and the number of juveniles plus first time spawners (in population samples, first time and repeat spawners can usually not be distinguished and the fraction of first spawners has to be

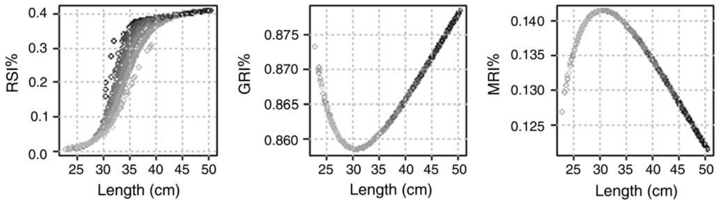

Figure 3. Relationships of reproductive investment relative to size (RSI) and gonadic and migratory investment relative to total reproductive investment (GRI and MRI) as a function of size in the estimation of size-dependent reproductive investment. Because the probability of being mature depends also on age, the RSI slightly changes with age (see gray scale, the darker the older). The GRI has minimal contribution of 86% at a length of about 30 cm and increases thereafter. The cost of migration or MRI is accordingly maximal (14%) at this size.

estimated separately). The probability of becoming mature was modeled as in Grift et al. (2003) using logistic regression:

$$\mathrm{logit}(p_{mat}) = \beta_0 + \beta_{YC}YC + \beta_t t + \beta_l l + \beta_{YCt}YC \times t + \beta_{YCl}YC \times l + \beta_{tl} t \times l + \varepsilon \qquad (14)$$

i.e. the probability of becoming mature p_{mat} depended on the individuals' year class YC (cohort), age t and length l. Year class was treated as a factor while age and length were treated as continuous variables. The probability of becoming mature p_{mat} is also referred to as the probabilistic maturation reaction norm (PMRN, Heino et al. 2002) and is usually visualized using the 50% probability isoline in the age–length plane (also referred to as the PMRN midpoint or L_{P50}).

Results

Performance analysis

Parameter estimation in the deterministic case

When data are simulated deterministically, i.e. without environmental noise, the bias in the life history parameter estimation is negligible over the observed (estimated) range of values for both, the four-trait and the three-trait estimation (Fig. 4). The errors in the b-estimate are positively correlated to errors in the estimates of a and t_{mat} and negatively correlated to errors in the estimate of c (Table 1), but this might not be very meaningful since the averages of biases are about 0. In the three-trait estimation, maintenance b was assumed to be constant to avoid confounding with reproductive investment c. For the four-trait estimation, biases might arise if there are too few observations y_{mat} of the mature status, if the relative onset of maturation τ is early and if the relative reproductive investment q is small (Fig. 4). The trends in the three-trait estimation are similar but relative biases are lower and the relative influence of q on the bias is much less important (Fig. 4).

Parameter estimation in the stochastic case

The suspected confounding between maintenance b and reproductive investment c was confirmed by the results on simulated data with environmental variability: 1) although the co-variance structure used to simulate data was taken from selected modes in the trait distribution estimated from real data, the trait estimates obtained from these simulated data resulted in multimodal distributions (Fig. 5) very similar to those found in the estimates from real data (Fig. 1, 2). The estimation errors of b and c were negatively correlated ($r_e(b,c) = -0.67$, Table 1, Fig. 5), whereas the bias in the sum of b + c was much lower than in its separate compounds b and c (18% vs −32 and 23% average deviation, Table 1, Fig. 5). Hence, the sum b + c is relatively well estimated but its partitioning between b and c is prone to error since an underestimation of maintenance b is compensated by an overestimation of reproductive investment c and vice versa. This correlation between estimation errors of b and c thus results in artifact modes in their trait distributions. If b + c is overestimated, acquisition a has to be overestimated to fit a similar asymptotic weight, therefore the high positive correlation between biases in a and b + c ($r_e(a, b+c) = 0.93$, Table 1, Fig. 5). Overestimation in t_{mat} might compensate for overestimation in a or b + c in the same way (not shown). The confounding could not be removed by simply constraining the b-estimates above a certain positive threshold: the parameter distribution turned out to be bimodal too, with the first mode around the threshold instead of being around 0 (not shown). The unimodal distributions in the deterministic case (not shown) indicate that confounding mainly arises due to the interannual environmental stochasticity in the parameters along the growth trajectory.

Effects of environmental variability on parameter estimation

Environmental noise increases the overall bias (Eq. 5). For four-trait estimation, bias most dramatically increases with variation in the energy acquisition CV_a as shown by the regression against potentially explanatory variables (Eq. 8, Table 2). Furthermore, estimations are more reliable, if relative reproductive investment q, the number of observations (age t), and the correlation between a and b, r(a,b) are high but also if relative onset of maturation τ and the number of mature observations y_{mat} are low (Table 2). In the three-trait estimation, the signs of the effects of age t and relative onset of maturation τ are inversed, relative reproductive investment q and the number of reproductive events do not explain variation in bias but additional

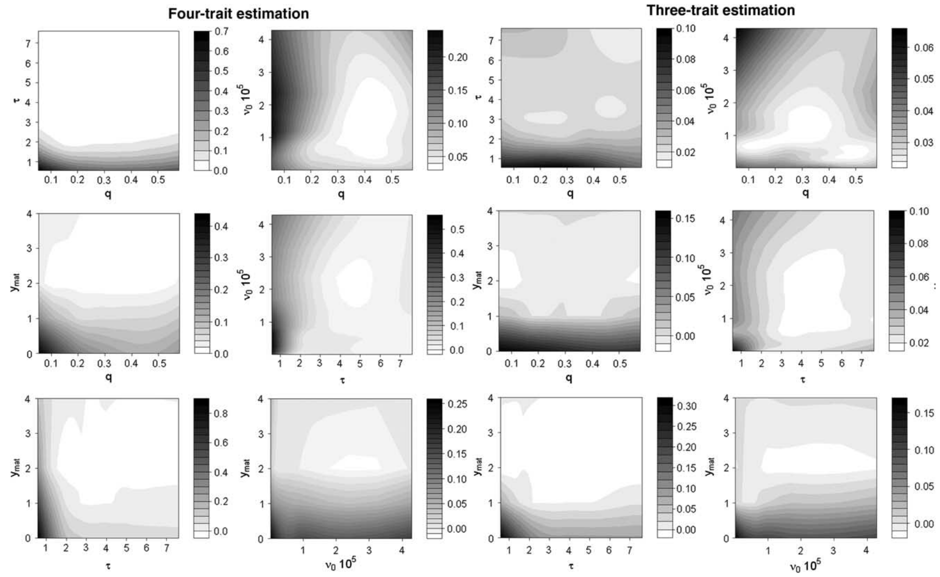

Figure 4. Overall relative bias (Eq. 5) as a function of the true relative reproductive investment q, the true relative onset of maturation τ, the true relative initial size v_0 and the number of years after the first spawning event y_{mat} (rounded up $(A_{max} - t_{mat})$) in the deterministic case of the four-trait and the three-trait estimation. The simulation was based on all possible combinations for the observed ranges of the parameters: a {4,7} $g^{1/4}$ $year^{-1}$, b {0.4,0.9} $year^{-1}$, c {0.05,0.55} $year^{-1}$ and t_{mat} {1.25,5.25} year. Contours were obtained by fitting a non-parametric loess regression to the bias with span = 0.25 for the two explanatory variables to be displayed. Bias becomes considerable if there are few observations y_{mat} of the mature status, if the relative onset of maturation τ is very early and if the relative reproductive investment q is small. Similar trends are found in the three-trait estimation but with lower relative biases and q seems to have no more influence on the bias.

variation is explained by CV_c, the auto-correlations θ_a and θ_c and the correlation r(a,c) instead of r(a,b).

Figure 6 shows the bias in the estimates of the life history parameters against the average realized CV's. As expected, the variance and bias in the estimates typically increase with the overall CV (Fig. 4) and the bias is on average higher in the four-trait estimation than in the three-trait estimation. Generally, the variability in parameters results in an underestimation of a and b and a slight overestimation in t_{mat} relative to their mean (Fig. 6). Reproductive investment c is generally overestimated relative to its geometric mean in the four-trait estimation but slightly underestimated in the three-trait estimation. Recall that the bias is defined relative to the realized geometric mean of the parameter time series, and part of it may therefore not really represent estimation inaccuracy since no real true value can be defined in this case (what is estimated does not necessarily correspond to the geometric mean of the time series). Only the bias in t_{mat} is strictly defined here.

The age at onset of maturation t_{mat} or age at first maturity A_{mat} are generally overestimated for the early maturing individuals (Table 4). This overestimation is smaller in the three-trait estimation but on the other hand, many individuals are assigned to mature at the earliest possible age in this approach. A very early maturation might be the best solution in the energy allocation model fitting if no breakpoint can be detected in the growth curve. The confounding of parameters a, b and c does not seem to influence the accuracy of t_{mat}-estimates significantly, since the similarity between confounded estimates of t_{mat} or A_{mat} and estimates where the confounding has been removed is very high (Table 4).

Effect of model uncertainty on parameter estimation. Figure 7 shows the true against the estimated values of the life history parameters in the deterministic case when the scaling exponent α of energy acquisition rate with body weight was assumed to be lower (α = 2/3) or higher (α = 4/5) in the model fitted to the data than in the one used to simulate the data (α = 3/4). For different scaling exponents, different population level estimates of the parameters are obtained so that the value of fixed maintenance in the three-trait estimation differs: $b_{\alpha=2/3} = 0.33$ $year^{-1}$, $b_{\alpha=3/4} = 0.47$ $year^{-1}$, $b_{\alpha=4/5} = 0.88$ $year^{-1}$. Asymptotic body weight $w_\infty^{1/4} = a/(b + c)$ is always estimated accurately (not shown). If α is assumed too low (α = 2/3), acquisition a and time at the onset of maturation t_{mat} are generally overestimated, whereas maintenance b and reproductive investment c are generally underestimated and vice versa if α is assumed too high (α = 4/5). The effect of an erroneous assumption on the fixed value of maintenance b in the three-trait estimation was also evaluated. It had a negligible effect, resulting in a very small and constant bias in

Table 1. Average of percentage bias μ%, coefficient of variation CV and correlations $r_e(x,x')$ between biases $e(x)$ and $e(x')$ in the estimates of the life history parameters a, b, c and t_{mat} resulting from the four-trait estimation procedure applied to simulated data with (stochastic) and without (deterministic) environmental noise.

	Deterministic				
	e(a)	e(b)	e(c)	e(b+c)	$e(t_{mat})$
μ%	0.00	0.01	−0.02	0.00	0.00
CV	11.91	8.91	5.52	16.84	21.33
$r_e(a,x')$	1				
$r_e(b,x')$	0.47	1			
$r_e(c,x')$	−0.19	−0.40	1		
$r_e(b+c,x')$	0.36	0.18	0.53	1	
$r_e(t_{mat},x')$	−0.09	0.60	−0.07	0.17	1
	Stochastic				
	e(a)	e(b)	e(c)	e(b+c)	$e(t_{mat})$
μ%	−0.15	−0.32	0.23	−0.18	0.30
CV	1.34	2.03	3.85	1.45	2.57
$r_e(a,x')$	1				
$r_e(b,x')$	0.83	1			
$r_e(c,x')$	−0.38	−0.67	1		
$r_e(b+c,x')$	0.94	0.76	−0.21	1	
$r_e(t_{mat},x')$	−0.07	0.17	−0.27	0.00	1

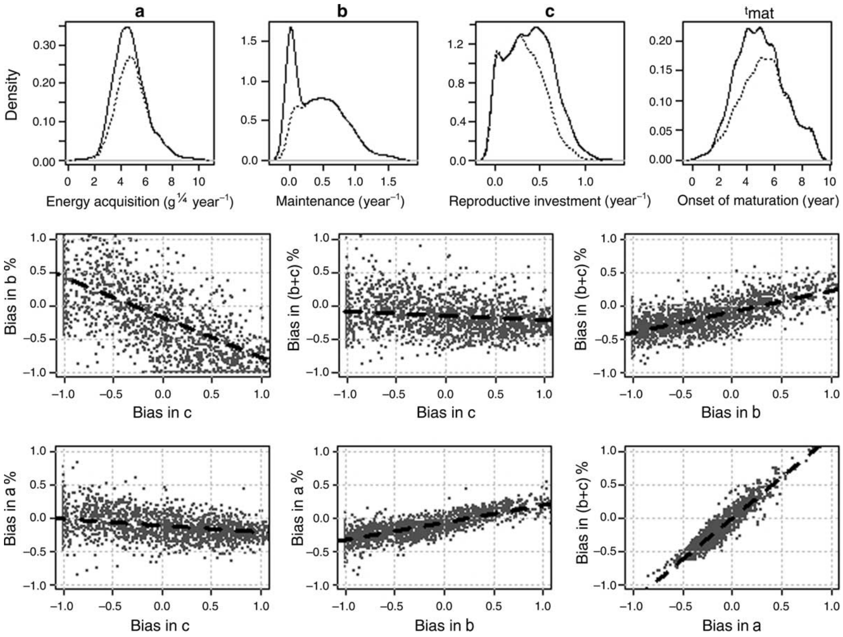

Figure 5. Density distributions of the four estimated life history parameters and relationships between parameter biases estimated on simulated data with environmental noise. Very similar parameter distributions as from real data (Fig. 1) are obtained in the simulation (first row), in which the covariance structure from the selected distribution modes from real data was used. The regressions between parameter biases (dashed lines) show that the biases of b and c are negatively correlated, whereas the bias of (b+c) is on average smaller than bias of each of its components. The strong positive correlation between a and (b+c) is a consequence of fitting to an asymptotic size: the higher a is, the higher (b+c) has to be to reach the same asymptotic size. The same effect translates to b but not to c.

Table 2. Results of the regression analysis of the overall bias in life history parameters (Eq. 5) as a function of the potentially explanatory variables (Eq. 8) from a backward selection. Explanatory variables tested comprised of the coefficients of variation CV_a, CV_b, CV_c, the degree of autocorrelation θ_a, θ_b, θ_c, and the correlations $r_{sim}(a, b)$, $r_{sim}(a, c)$, $r_{sim}(b, c)$ of the simulated time series a_t, b_t, c_t the age t (i.e. the number of simulated data points), the number of experienced spawning events y_{mat}, the relative reproductive investment q, the relative timing of onset of maturation τ, and the relative initial weight ν_0.

Selected variables	4-trait estimation		3-trait estimation	
	coefficient	p-value	coefficient	p-value
Intercept β_0	1.031	$<10^{-3}$	0.475	$<10^{-3}$
CV_a	0.418	$<10^{-3}$	2.092	$<10^{-3}$
CV_c	–	–	−0.245	$<10^{-3}$
θ_a	–	–	0.032	0.087
θ_c	–	–	−0.026	0.066
$r_{sim}(a, b)$	−0.066	0.002	–	–
$r_{sim}(a, c)$	–	–	−0.085	0.001
age t	−0.033	$<10^{-3}$	0.014	$<10^{-3}$
y_{mat}	0.044	$<10^{-3}$	–	–
q	−0.754	$<10^{-3}$	–	–
τ	0.047	$<10^{-3}$	−0.119	$<10^{-3}$
ν_0	–	–	−30540	0.017

parameters estimates for an assumption on b deviating by 10% from the true value (not shown).

Application to North Sea plaice

The algorithm converged in 99% of the cases. The average estimates of life history parameters, after removing the estimations corresponding to the artifact mode in the distribution of b estimates, were $a = 5.31\ g^{1/4}\ year^{-1}$, $b = 0.57\ year^{-1}$, $c = 0.32\ year^{-1}$ and $t_{mat} = 4.45$ year (Table 3). Onset of maturation t_{mat} was negatively correlated with acquisition a, $r(a, t_{mat}) = -0.22$, and reproductive investment c, $r(c, t_{mat}) = -0.63$, but positively correlated with maintenance b, $r(b, t_{mat}) = 0.30$ (Table 3). The correlation between a and b+c was highly positive, $r(a, b+c) = 0.93$. When using the three-trait estimation procedure, i.e. assuming a maintenance fixed at its population level value $b = 0.47$, the following average parameter estimates were obtained: $a = 5.29\ g^{1/4}\ year^{-1}$, $c = 0.41\ year^{-1}$, $t_{mat} = 3.53$ year (Table 3). In this case, the correlation between a and t_{mat}, $r(a, t_{mat}) = -0.68$, and between a and c, $r(a,c) = 0.91$, were stronger. The correlation between a and c equals by definition the correlation between a and b+c under the four-trait estimation (Table 3).

The four-trait and the three-trait estimation give roughly the same results for the timing of maturation t_{mat} or A_{mat} (Table 4). The similarity of the A_{mat} estimate between the two approaches increases slightly, when only the observations belonging to the 2nd b-mode are considered. The elimination of the confounding between maintenance b and reproductive investment c by estimating only three traits or by selecting the 2nd b-mode in the four-trait procedure does not affect the accuracy of the t_{mat} estimate.

The probabilistic maturation reaction norms or PMRNs were derived only for cohorts YC comprising at least 30 observations and showed a good match with those obtained by Grift et al. (2003) averaged over the same cohorts (Fig. 8). For the maturation-relevant ages, i.e. three and four, they are almost identical. The slope of the PMRN estimated here is lower than the one in Grift et al. (2003).

Discussion

Model assumptions

The method developed in this paper is the first to estimate simultaneously the different life history parameters related to the energy allocation schedule (energy acquisition, maintenance, onset of maturation and reproductive investment) from individual growth trajectories. We restricted ourselves to a Von Bertalanffy-like model, but, alternatively, structurally different energy allocation models, such as net production or net assimilation models (Day and Taylor 1997, Kooijman 2000), could be used. The performance analysis shows that the method with a Von Bertalanffy-like model can be expected to give accurate results as long as the scaling exponents of the allometric relationships between the underlying energy allocation processes (energy acquisition, maintenance, reproduction) and body weight applied in the estimation are correct. Even if they are not, the results are still expected to be qualitatively sound, and the resulting biases are predictable.

For the sake of simplicity, the scaling exponents of maintenance β and reproductive investment γ, here assumed to be 1, were neither estimated nor tested for their effects on estimation error, because a value different from 1 would require solving numerically the differential equations describing energy allocation at each iteration. Applying equal scaling exponents for energy acquisition and maintenance, i.e. $\alpha = \beta$, as suggested for instance by Day and Taylor (1997) and Lester et al. (2004), resulted in unrealistic behavior of the energetic reproductive-somatic index RSI, suggesting that the scaling exponent of maintenance needs to be higher than the exponent of energy acquisition. Based on theoretical (West et al. 1997) and empirical case-specific evidence (Fonds et al. 1992), as well as on realistic asymptotic weight and RSI, we conclude that applying scaling exponents following the inequalities $\alpha < \beta$

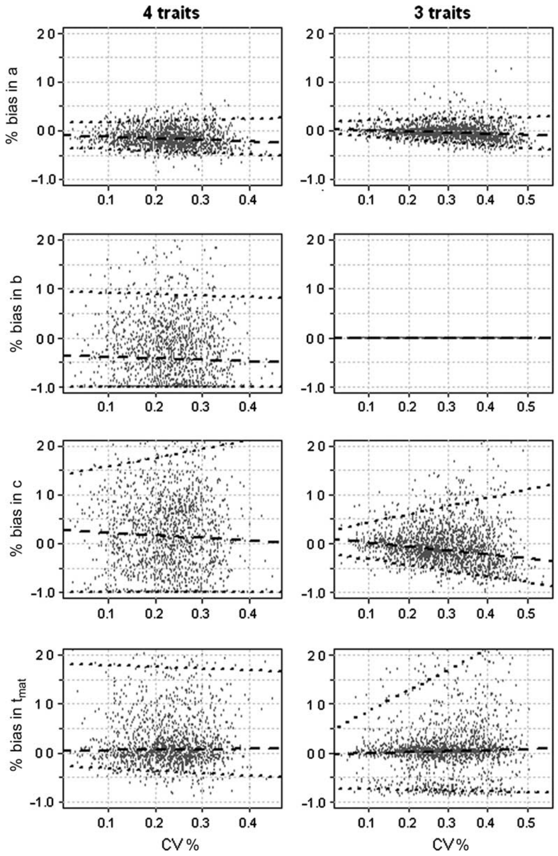

Figure 6. Relative biases in a, b, c and t_{mat} in the four-trait estimation and a, c and t_{mat} in the three-trait estimation, resulting from environmental variation, shown as a function of the CV in the simulated time series of a, b and c (four-trait estimation) or a and c (three-trait estimation). The estimated parameters are given relative to the geometric mean of the time series of a, b and c. The CV is given by the geometric mean of the realized CV's in series of a, b and c. Black lines show a quantile regression through these biases for the 50% (dashed line) and the 5% and 95% quantiles (dotted lines). Notice that the biases are strictly evaluated only for t_{mat}, since the true reference values of the varying a, b and c is not really known. Furthermore the simulated CV's might be higher than those applying in nature.

and $\alpha < \gamma$ are a good starting point for the estimation of individual life history parameters.

Performance analysis

For practical applications, the method should be applied to data on individuals for which two or more observations of the mature state are available. In this case the estimation error is negligible in a deterministic setting over the range of realistic (observed) parameter combinations. Environment variability in life history parameters leads to a slight underestimation of the average parameters for energy acquisition a_t and maintenance b_t and an overestimation of reproductive investment c_t (not in the three-trait estimation) but the onset of maturation t_{mat} is on average correctly estimated. With increasing environmental noise the average biases increase (except for the maintenance b) and estimation precision decreases (Fig. 4). Variability in a_t has the largest impact on bias and the relative reproductive investment q might have to stay above a certain level to minimize the bias (Table 2). The negative effect on the bias of age is balanced by a positive effect of relative onset of maturation τ and of the number of adult observations y_{mat} and the interpretation of the deterministic case, where y_{mat} had a negative effect on the bias, therefore not necessarily falsified. However, these biases should be interpreted with caution because they were

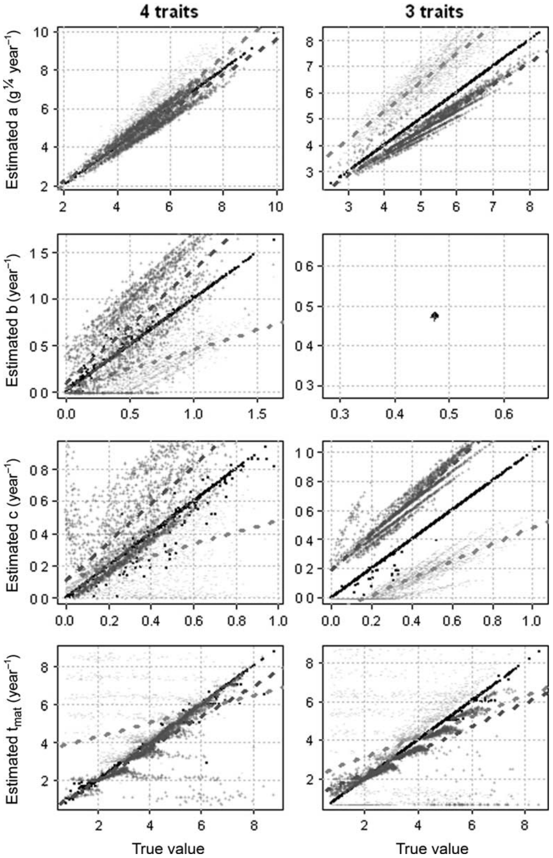

Figure 7. Sensitivity of the parameters estimates a, b, c and t_{mat} to an incorrect assumption about the allometric scaling exponent α ($\alpha_{sim}=3/4$ whereas $\alpha_{fit}=2/3$ or $\alpha_{fit}=4/5$) in the four- and the three-trait estimation. It was accounted for that different allometric scaling exponents would result in different assumptions about the constant maintenance by fitting the energy allocation model to the population growth curve ($b_{\alpha=2/3}=0.175$ year^{-1}, $b_{\alpha=3/4}=0.459$ year^{-1}, $b_{\alpha=4/5}=0.864$ year^{-1}, leading to different solutions of Eq. 4). The estimated against the true parameters are shown, black dots representing the estimates assuming the correct allometric scaling exponent ($\alpha=3/4$), typically on the 45°-line, light gray ' − ' and dark gray ' + ' represent the estimates by assuming falsely a too low ($\alpha=2/3$) or too high ($\alpha=4/5$) scaling exponent respectively, whereas the light grey and dark gray dotted lines represent the regression through these estimated and true data points assuming wrong scaling.

computed relative to the geometric mean of the simulated parameter time series, which does not correspond to a 'true' value as in the deterministic case. In other terms, there is no natural 'true' value to be compared with estimates in the stochastic case, except for t_{mat}.

Life–history correlation

(Co-)variation in (between) life history parameters at the phenotypic level, i.e. as observed across individuals, results from a genetic and an environmental (plastic) source of (co-)variation (Lynch and Walsh 1998). From life history theory (Roff 1992, Stearns 1992) we expect that 1.1) juvenile growth rate $\partial w_{juv}/\partial t$ and age at maturation t_{mat} are negatively correlated $\rho(\partial w_{juv}/\partial t,\ t_{mat})\leq 0$ – the higher the juvenile growth rate is, the earlier the individual will hit a presumably fixed genetically determined PMRN and mature – and 1.2) size-specific reproductive investment RSI and age at maturation t_{mat} are negatively correlated $\rho(RSI, t_{mat})\leq 0$. From the assumptions of our bioenergetic model it is given that 2.1) juvenile growth rate $\partial w_{juv}/\partial t$ increases with size-specific energy acquisition rate a, resulting in a positive correlation $\rho(\partial w_{juv}/\partial t,\ a)\geq 0$; 2.2) juvenile growth rate $\partial w_{juv}/\partial t$ decreases with size-specific maintenance rate b, resulting in a negative correlation $\rho(\partial w_{juv}/$

Table 3. Energy allocation parameters estimated for the1779 individual North Sea plaice growth trajectories using the four-trait and the three-trait model. The table gives the average μ and coefficient of variation CV, as well as the correlation coefficient r(x,x′) between the (four life-history) parameters: energy acquisition a, maintenance b, reproductive investment c, onset of maturation t_{mat}. For the four-trait estimation the results are displayed for only those estimations that belong to the second mode in the distribution of b′s.

	Four-trait estimation: 2nd b-mode				
	a	b	c	(b+c)	t_{mat}
μ	5.31	0.57	0.32	0.90	4.45
CV	0.23	0.62	0.74	0.28	0.37
r(a,x′)	1				
r(b,x′)	0.69	1			
r(c,x′)	−0.06	−0.71	1		
r(b+c,x′)	0.93	0.74	−0.06	1	
r(t_{mat},x′)	−0.22	0.30	−0.63	−0.18	1

	Three-trait estimation: fixed b				
	a	b	c	(b+c)	t_{mat}
μ	5.29	0.47	0.41	0.89	3.53
CV	0.20	–	0.52	0.24	0.49
r(a,x′)	1				
r(b,x′)	–	–			
r(c,x′)	0.91	–	1		
r(b+c,x′)	0.91	–	1	1	
r(t_{mat},x′)	−0.68	–	−0.64	−0.64	1

∂t,b) ≤ 0; and 2.3) size-specific reproductive investment RSI increases with size-specific reproductive investment rate c, resulting in a positive correlation ρ(RSI,c) ≥ 0. Life history theory and our model assumptions together thus lead to the following expectations: 3.1) size-specific energy allocation rate a is negatively correlated with age at maturation t_{mat}, ρ(a,t_{mat}) ≤ 0; 3.2) size-specific maintenance rate b is positively correlated with age at maturation t_{mat}, ρ(b,t_{mat}) ≥ 0; and 3.3) size-specific reproductive investment rate c is negatively correlated with age at maturation t_{mat}, ρ(c,t_{mat}) ≤ 0. The correlations between a, b and c cannot be easily interpreted in terms of life history theory but can be in the light of our model: since the asymptotic size $w_\infty^{1/4} = a/(b+c)$ is roughly constant within a species, increases in size-specific energy acquisition a or in speed of growth (b + c) are reciprocally compensated to stabilize w_∞. The construction of the model therefore imposes ρ(b,c) ≤ 0 and ρ(a,b + c) ≥ 0, the only degrees of freedom being ρ(a,c) and ρ(a,b).

In terms of environmental variation, energy acquisition a might be externally influenced by variable food availability, maintenance b, interpreted here as the resting metabolic rate (i.e. the increase in maintenance due to higher consumption is accounted for by a), might be externally influenced by variability in temperature only and reproductive investment c might vary with the annually stored energy resources. From the environmental co-variation, the correlations ρ(a,c) and ρ(a,b) might be expected across individuals and within the lifespan of an individual: the positive effect of temperature on both food availability due to increased productivity of the system, and hence a, and metabolic rates, hence b may lead to a positive correlation ρ(a,b) ≥ 0; the energy resources available for reproductive investment (gonadic tissue, spawning migration) is determined by the energy which is physiologically made available and hence likely mainly by a, causing a positive correlation ρ(a,c) ≥ 0 on the phenotypic level according to the rule ‘the more resources are available, the more can be spent’.

The signs of the correlations between life history parameters obtained for plaice (Table 3) matched the previous theoretical expectations. Most importantly, we find r(a,t_{mat}) ≤ 0, r(b,t_{mat}) ≥ 0 and r(c,t_{mat}) ≤ 0. These correlations also might be to some degree due to the correlation between estimation errors (Table 1) but not entirely, since the correlations between the traits are higher than between the errors (and the absolute traits are larger than the errors). The correlations r(b,c) and r(a,b + c) are indeed found to be due to the correlations between estimation errors (Table 1) and thereby contribute, by construction of the model, to stabilize the asymptotic weight w_∞. The r(a,b) might also be partly due to the error correlation. However, r(a,c) is not, since the errors in a and c are negatively correlated, whereas the found r(a,c) is about 0. This indicates that the true r(a,c) might in fact be positive. In the three-trait estimation, r(a,c) = 0.91 is indeed highly positive, suggesting that the r(a,c) found in the four-trait estimation might be due to the confounding with maintenance rate b. By assuming a constant b in the three-trait estimation, the co-variances between the three traits a, c and t_{mat} are inflated. The correlation r(a,c) in the three-trait estimation becomes equal to the correlation r(a,b + c) in the four-trait estimation, due to the classical relationship of covariances cov(a,b + c) = cov(a,b) + cov(a,c). In the three-trait estimation cov(a,c) is inflated by artificially fixing b and thereby forcing the covariance cov(a,b) = 0 to nullity so that cov(a,b + c) = cov(a,c).

Application to real data

The method validation was based on the comparison between estimates of the timing of the onset of maturation t_{mat} obtained from back-calculated growth trajectories and

Table 4. Estimated against true age at first maturity A_{mat} in the four- and three-trait estimation. The number of estimations falling in a true A_{mat} class is given as a percentage of the total number of estimations in that true A_{mat} class. The upper panel performances for age at maturation estimation by showing true against estimated A_{mat} in the four-trait (data set in which a, b and c vary stochastically), and the three-trait estimation (data set in which a and c vary stochastically). Performance is slightly better for the three-trait estimation. Notice that the biases might not be representative for the real situation, since the simulated CV's might be higher than those applying in nature. The lower panel presents results of the application to real data by comparing the estimation of A_{mat} between the four-trait and the three-trait estimation (on the real data) for the entire data set and only the observations belonging to the 2nd b-mode (Fig. 2). Agreement between the t_{mat} estimates in the four- and three-trait estimation is very high and does not significantly change between the entire data set and the selected observations belonging to the 2nd b-mode. This indicates that the estimation of t_{mat} or A_{mat} is not affected by confounding.

1) Performance analysis

Four-trait simulated	True A_{mat}					
	2	3	4	5	6	7
Estimated A_{mat}						
2	4	3	2	1	1	0
3	15	16	8	7	2	1
4	17	19	31	19	7	1
5	17	19	21	32	22	5
6	19	15	12	16	37	14
7	13	12	11	11	15	22

Three-trait simulated	True A_{mat}					
	2	3	4	5	6	7
Estimated A_{mat}						
2	30	28	15	10	8	5
3	18	23	3	1	1	0
4	21	29	55	9	2	1
5	15	10	17	59	19	4
6	8	4	4	13	54	15
7	5	2	3	4	14	59

2) Application to real data

2nd b-mode observations	Three-trait A_{mat}					
	2	3	4	5	6	7
Four-trait A_{mat}						
2	30	6	0	0	0	0
3	21	68	7	0	0	1
4	8	13	63	8	0	0
5	0	1	22	64	13	1
6	24	3	4	23	67	12
7	8	1	1	3	17	71

All real data observations	3-trait A_{mat}					
	2	3	4	5	6	7
Four-trait A_{mat}						
2	39	8	0	0	0	0
3	19	76	13	0	0	1
4	7	8	67	12	0	0
5	0	0	15	65	16	2
6	21	2	3	19	65	14
7	7	0	1	3	16	69

independent estimates obtained from biological samples from the spawning population. Both estimation procedures are subject to error but similar patterns should nevertheless indicate the likelihood of both. For the ages at which maturation mainly occurs (around age 4), the PMRN based on our estimates is very similar to the PMRNs based on biological samples from the population (Grift et al. 2003). The relatively higher and lower maturation probability for younger and older ages respectively is likely due to extrapolation to ages at which only few fish become mature and the estimation becomes less reliable. If the interval between the start of energy allocation to reproduction t_{mat} and the subsequent age at first spawning A_{mat} was assumed to be less or more than four months, the resulting reaction norm would be lower or higher respectively in the age-size plane. However, for plaice four months correspond to the time interval between the onset of vitellogenesis (August, September) and the midpoint of the spawning season (Rijnsdorp 1990, Oskarsson et al. 2002). The good correspondence between the two estimation methods of the PMRN suggests that environmental variability is unlikely to have been so high as to result in biases as high as in the simulation analysis (see biases of t_{mat} in Fig. 4).

Reproductive investment

Reproductive investment was modeled including a size-dependent gonadic investment and a size-dependent cost of migration. The modeled energetic reproductive-somatic index RSI (energy-based reproductive investment relative to somatic weight) is increasing with somatic weight as is the modeled gonado-reproductive index GRI (gonadic relative to reproductive investment) and consequently the resulting gonado-somatic index GSI (gonadic weight relative to somatic weight). This is in line with the expectation since data show that GSI increases with size (Rijnsdorp 1991). In contrast, the modeled migration cost relative to reproductive investment (1–GSI) decreases with size. Since migration distance increases with fish size (Rijnsdorp and Pastoors 1995, Bolle et al. 2005), the advantage of feeding offshore must be relatively more important than the migration cost.

Possible extensions

The method proposed here can be applied to a variety of organisms in which the annual pattern in somatic growth is reflected in hard structures: scales or otoliths in fish (Rijnsdorp et al. 1990, Panfili and Tomas 2001, Colloca et al. 2003), shells in bivalves (Witbaard et al. 1997, 1999), endoskeleton in echinoderms (Pearse and Pearse 1975, Ebert 1986, Gage 1992), teeth in mammals (Laws 1952, Godfrey et al. 2001, Smith 2004) or skeleton in amphibians (Misawa and Matsui 1999, Kumbar and Pancharatna 2001) and reptiles (Zug et al. 2002, Snover and Hohn 2004). If a back-calculation method from the hard structures can be validated, the analysis of individual growth trajectories with the method developed in this paper offers the opportunity to study a variety of life history

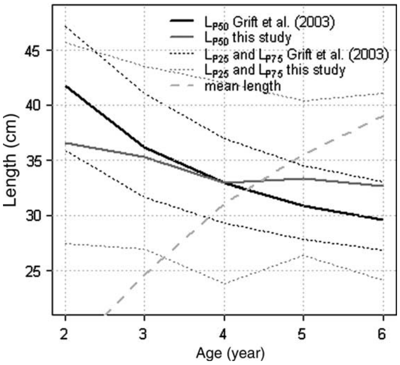

Figure 8. Comparison of reaction norms derived from the three-trait estimation of individual life history in this study (gray lines) with reaction norm estimated by from Grift et al. (2003) averaged over the past five decades by only using cohorts for which more than 30 observations were available. Dotted lines represent the 25%- and 75% probabilities of maturation, the dashed line represents the average length at age. The reaction norm from individual life history estimation is shown for an interpretation of the first spawning event A_{mat} given by t_{mat} plus a minimal period of preparation for spawning of four months, rounded up to the next year.

tradeoffs without the need to follow individuals throughout their lifetime using experiments in controlled conditions or methods such as mark–recapture. The method holds for any other frequency of age and size observations and for any other frequency of spawning than the here illustrated annual observations and annual spawning intervals. Under the assumption that energy is allocated to reproduction continuously between spawning events by storing energy reserves which are then made available later for spawning, the method even applies if spawning intervals are irregular.

Adaptation

Our method could be particularly useful to study changes in life history parameters over time or differences among populations. Concerns had been raised that life history traits of exploited species, may evolve in response to harvesting (Rijnsdorp 1993, Stokes et al. 1993, Heino 1998, Law 2000). Studies on life history evolution in the wild have largely focused on changes in the onset of maturation, although evolutionary changes were also suggested in growth rate and reproductive investment (reviewed by Jørgensen et al. 2007). The analysis of harvesting-induced evolution in the wild has proved to be difficult (Rijnsdorp 1993, Law 2000, Sinclair et al. 2002, Conover et al. 2005). One reason is that growth, maturation and reproductive investment are intricately linked in the energy allocation schedule, another that disentangling phenotypic plasticity from genetic effects in the observed phenotypic response is not evident.

Disentangling plasticity

By estimating the co-variance structure between the life history parameters, our method may prove useful to disentangle phenotypic plasticity from genetic change. Assuming that environmental variability mostly affects the primary energy flow of energy acquisition and that the subsequent energy allocations (maintenance, reproductive investment) are partly determined by this primary energy flow, plastic variation in the other traits due to this process could be accounted for by expressing them conditional on energy acquisition. It is for instance likely that reproductive investment may be affected by feeding conditions during the previous growing season (Rijnsdorp 1990, Stearns 1992, Kjesbu et al. 1998, Marshall et al. 1999). Studies in other taxa than fish (Ernande et al. 2004) have shown that the energy allocation strategy between maintenance, growth, and reproductive investment may vary according to food availability. Expressing reproductive investment conditional on energy acquisition would therefore represent a reaction norm for reproductive investment (Rijnsdorp et al. 2005). Changes in this reaction norm would then reveal genetic change under the assumption that most environmental influence on reproductive investment is accounted for via variation in energy acquisition. It has also been shown here that the PMRN can be estimated directly from the back-calculated ages and sizes and the obtained estimate for the age at first maturity, whereas in other data sources the individual first maturity is typically not known (Barot et al. 2004). By disentangling the plasticity in maturation caused by variation in growth and removing the effect of survival on observed maturation events, the PMRN can also be used to assess genetic changes under the assumption that most environmental influence on maturation is accounted for via growth variation.

Different approaches

In an earlier study, Rijnsdorp and Storbeck (1995) estimated the timing of the onset of maturation in plaice by piecewise linear regression of growth increments on body weight to locate the discontinuity in growth rates expected at maturation. This method might be accurate only for particular combinations of the energy allocation scaling exponents that lead to a linear relationship between growth increments and body weight (not shown). Baulier and Heino (2008) applied an improved version of this method to Norwegian spring spawning herring and obtained relatively accurate estimates (±1 year) of the timing of the onset of maturation. However, this method does not provide estimates of the other life history parameters and it is unlikely that the particular combination of energy allocation scaling exponents leading to the discontinuous linear relationship between growth increments and body weight can be expected to apply in the general case.

The three-trait estimation procedure in the method presented in this paper removes the confounding between parameters by fixing maintenance to its population level average. However, in reality maintenance may be variable since it is affected for instance by temperature and, in addition, assuming a fixed value inflates co-variances between other parameters. A more elegant way to circumvent this problem may be to use generalized linear mixed modeling to estimate the four parameters. Under this approach, the parameters, shown here to be approximately normally distributed after removal of the confounded estimates (Fig. 1), follow a multivariate normal distribution and estimation can thus only lead to unimodal distributions, therefore potentially reducing the confounding between parameters (Brunel et al. unpubl.).

The four-trait method presented in this paper is not practical, since the first mode in the distribution of b estimates would always have to be removed a posteriori. The three-trait estimation gives more stable results (Fig. 4, 5, 6) but a correction for changing temperatures would be needed and due to the inflation of co-variances, results should be considered on a relative scale. If the main interest is on the onset of maturation t_{mat}, then both four-trait and three-trait estimation work similarly well, since the bias in t_{mat} is unlikely due to confounding in the parameters a, b and c (Table 4, Fig. 4).

Maintenance–temperature

The estimated energy allocation parameters here represent average values for the study period. However, assuming a constant maintenance (three-trait estimation) may be incorrect as yearly averaged surface temperatures in the North Sea (Van Aken 2008) suggest that temperature increased from 9.91°C in 1950 to 11.01°C in 2005 ($p < 0.001$). In the interpretation used here, the size-specific maintenance is influenced only by temperature. The Arrhenius description based on the Van't Hoff equation used in dynamic energy budget modeling (Van der Veer et al. 2001) to describe the effect of temperature on physiological rates would predict that an increase from 10°C to 11°C would correspond to an increase in the maintenance rate of about 9% (not shown). If a similar trend occurred in the bottom temperatures, we might expect a change in the average maintenance cost over the study period of about 9%. In the three-trait estimation, the trend in temperature could therefore be accounted for by estimating a separate average b for each cohort. As this paper explores average general patterns, we ignored here the effect of temperature on maintenance by assuming homogeneous temperatures in the demersal zone.

Conclusion

This paper is the first one to present a method to estimate the energy allocation parameters for energy acquisition, maintenance, reproductive investment and onset of maturation of organisms from individual growth trajectories. Performance analysis and the application to real data showed that the method can be successfully applied, at least on a qualitative level, to estimate the relative differences in energy allocation parameters between individuals and to estimate their co-variance structure. Future studies will apply the concept to back-calculated growth curves from otoliths of North Sea sole and plaice and scales of Norwegian spring spawning herring, focusing on the comparison between species and life-history adaptation over the last century.

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Supplementary material (available online as Appendix O17746 at www.ekol.lu.se/appendix). Appendix 1.

Chapter 4

PLASTIC AND EVOLUTIONARY RESPONSES IN CORRELATED LIFE HISTORY TRAITS

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(Manuscript)

Abstract

We present a multivariate analysis of changes in life-history traits – energy acquisition, energy expenditure for maintenance and reproductive investment, and onset of maturation – over more than 6 decades. An energy allocation model, that describes body growth as the difference between energy acquisition and energy expenditure and includes a discontinuity in expenditure at the onset of maturation, is adjusted to individual body growth trajectories of North Sea sole and plaice, back-calculated from the annual marks in archived otoliths. For any given cohort, the method provides individual estimates of the 4 life-history traits together with estimates of their phenotypic mean and covariance structure at the population level. Since the individual rates of energy allocation are size-specific, they represent the unit of the individual tradeoffs better than other proxies, in which these rates are typically confounded (e.g. size, reproductive investment). Sole has a higher pace of life, i.e. has higher rates of energy acquisition, maintenance, reproductive investment and earlier maturation than plaice. Time trends since 1940s show an increase in energy acquisition and reproductive investment and a decrease in the onset of maturation in both species. A part of these observed trend traits is due to a plastic response to population density, eutrophication and temperature and due to effects from correlation between the traits, which is captured in the multivariate response of the analysis. However, a remaining significant time trend suggests a genetic change in the same direction that is consistent with a fisheries-induced evolutionary response. This is the first multivariate analysis of temporal changes in multiple life-history traits based on individual data and accounting for phenotypic correlations. Multivariate viability selection differentials are estimated by comparing trait distributions at age within a cohort over successive sampling ages. Further research is needed to link these selection differentials to the observed evolutionary response accounting for phenotypic correlations and overlapping generations.

Key words: *energy allocation, otolith-size back-calculation, fisheries-induced evolution, energy acquisition, maintenance, onset of maturation, reproductive investment, Pleuronectes platessa, Solea solea, flatfish, life-history correlation*

Introduction

Knowledge of life-history traits (growth rate, onset of reproduction, reproductive investment) is vital for the understanding of a species adaptations to the environment and its resilience to perturbations. Because energy resources will be finite, the basic life functions of growth, maintenance and reproduction are competing for the same resource leading to several life-history trade-offs (Stearns 1992). The energy spent for growth is not available for reproduction thus generating a trade-off between growth and reproduction, and, because fecundity generally increases with body size, individuals with indeterminate growth also experience a trade-off between current and future reproduction (Heino and Kaitala 1999). In addition, the timing of the onset of maturation modulates the schedule of these trade-offs' expression. Estimation of life-history traits at the individual level however is difficult since it requires following individuals throughout their lifetime. Therefore, life-history traits are generally estimated on the population level using proxies such as size-at-age for growth rate, maturity ogives (the probability of being mature as a function of age and/or size) or maturation reaction norms for the timing of the onset of maturation, and the gonado-somatic index (GSI, gonad weight relative to body weight) for reproductive investment. One drawback is that population level proxies do not allow the estimation of phenotypic variation in and co-variation between (phenotypic covariance matrix) these trait and hence overlook life-history trade-offs and their consequences on life-history traits dynamics A recently developed method overcomes this problem by simultaneously estimating four life-history traits (age at onset of maturation, size-specific rates of energy acquisition, maintenance and reproductive investment) from individual growth data and can be applied to individuals separately (Mollet, et al. 2010) or to groups of individuals simultaneously (Brunel, et al. 2010).

Temporal dynamics in life-history traits of natural populations have received increasing attention because of potentially undesired effects of human-induced evolution (Palumbi 2001), in particular life-history evolution due to harvesting (Allendorf and Hard 2009) or climate change (Parmesan 2006, Gienapp, et al. 2007). Empirical studies attempting to disentangle genetic from phenotypically plastic contributions to observed phenotypic trends based on experiments or field observations indeed suggest that genetic changes can occur as quick as within a few decades if selection is strong (Reznick, et al. 1990, Rijnsdorp 1993, Conover and Munch 2002, Grift, et al. 2003, Olsen, et al. 2004). Furthermore, harvest-induced evolutionary changes in life history are likely to have negative effects on the productivity of harvested populations (Law and Grey 1989, Heino 1998) and are difficult, if not impossible, to reverse (De Roos, et al. 2006, Conover, et al. 2009). North Sea plaice (*Pleuronectes platessa*) and sole (*Solea solea*) for instance are two important commercial fish species for which changes in life-history (earlier maturation, increased reproductive investment and lower asymptotic size but increased growth rate) have been reported and related to fisheries-induced evolution (Grift, et al. 2007, Mollet, et al. 2007, Van Walraven, et al. 2010). However, by focusing on a single trait on the population level, these studies ignore possible interactions with phenotypically correlated traits and their potential consequences on trait changes. Furthermore, the association between the actual trait under study and the proxy measured is often doubtful because the environmental effects affecting the proxy can hardly be controlled – for instance size or condition measured at spawning as a proxy for its effect on the maturation 'decision' might not be strongly correlated between the moment of the 'decision' and spawning, when maturity can be assessed (Wright 2007). This is because individual life-history data and associated environmental data are both difficult to obtain - the back-calculation of individuals' size growth from hard structures (otoliths, scales, shells, skeleton, theeth) offers a unique opportunity in this respect.

In this study we simultaneously estimate energy allocation between somatic growth, maintenance and, after the onset of maturation, reproduction on the individual level , by an amended version of the method of (Brunel, et al. 2010), from individual growth curves of the exploited fish stocks of North sea plaice and sole. Capturing the correlation structure between these traits opens the avenue to study the influence of phenotypic co-variation and environmental effects on temporal trait changes. A multivariate analysis of temporal changes in these traits therefore aims to identify the nature of the underlying responsible processes: plasticity and/or evolution. We furthermore present a probabilistic maturation reaction norms (PMRNs), a lifespan reaction norm for reproductive investment and viability selection differentials obtained directly with this method and, if available, compare to independent estimates.

Material and methods

Biology of species and fisheries. Plaice and sole are iteroparous flatfish that spawn in winter and spring and reach a maximum age of about 25 years (pers obs.) and 40 years (Horwood 1993), respectively. The distribution of the Lusitanian sole ranges from the Mediterranean and north-west coast of Africa to the south coast of Norway, whereas the Boreal plaice ranges between the Bay of Biscay in the south to Iceland and the Barents Sea in the north (Gibson 2005). In the North Sea, sole has a more southern distribution than plaice but the juvenile stages co-occur in shallow coastal waters (Rijnsdorp and van Beek, 1991). Both species are caught in a mixed demersal fishery targeting the more valuable sole (Gillis, et al. 2008, Quirijns, et al. 2008). Whereas plaice mortality rates were already high in the late 19th century (Rijnsdorp and Millner 1996), fishing mortality rates for sole did not increase before the 1960s, when the fishery switched from the otter trawl to the more efficient beam trawl (Rijnsdorp, et al. 2008). Further, both species differ considerably in the minimum size caught in the commercial fisheries: about 22 cm (age 2-3) in sole and 18cm (age 2) in plaice. Hence, the difference between the minimum size or age at capture and the size or age at maturation is much larger in plaice (>12cm, >2 years) than in sole (<4cm, <1year). Because this difference will determine the strength of selection of the fishery and because heavy exploitation of sole started only in the 1960s, a stronger evolutionary response in growth, maturation and reproductive investment is expected in plaice than in sole.

Energy allocation model. Once an animal becomes mature, somatic growth is reduced because a fraction of the available energy is channeled towards reproduction and is no longer available for somatic growth. We use a general energy allocation model (Von Bertalanffy and Pirozynski 1952, Charnov, et al. 2001, West, et al. 2001, Banavar, et al. 2002) according to which the growth rate of juveniles and adults is given by

$$\frac{\partial w}{\partial t} = \begin{cases} aw^{\alpha} - bw^{\beta} & \text{if} \quad t < t_{\text{mat}} \\ \\ aw^{\alpha} - bw^{\beta} + cw^{\gamma} & \text{if} \quad t \geq t_{\text{mat}} \end{cases} \tag{1}$$

where w is somatic weight, t is time, t_{mat} is time at the onset of maturation, aw^{α} is the rate of energy intake or acquisition rate, bw^{β} is the rate with which energy is spent for maintenance and cw^{γ} is the rate of reproductive investment with which energy is spent for reproductive activity (e.g. conversion to gonadic tissue, reproductive behavior, gamete production). We assume a scaling exponent of energy acquisition $\alpha = 3/4$ because 1) there is an explanation from metabolic theory of ecology (MTE) which assumes that the rate of energy acquisition is limited by the size of the fractal capillary network that brings energy to cells which scales with a power ¾ of body mass (West, et al. 1999) and 2) this is close to empirical estimates of α (Gillooly, et al. 2001, Brown, et al. 2004) including North Sea plaice (Fonds, et al. 1992). To obtain (i) asymptotic maximum body mass in the absence of maturation and (ii) size-specific relative reproductive investment, i.e. the reproductive investment relative to body size, increasing with age and size, it is required that $\beta > \alpha$ and we therefore assume that $\beta = \gamma = 1$ for the sake of simplicity. By integration of Eq. 1 the size is expressed as a function of time and this function is fitted to individual growth curves (appendix A1). Energy acquisition and maintenance can thereby be assessed by the slope of the growth trajectory before maturation, the onset of maturation is reflected in a discontinuity of this slope and reproductive investment is translated in the amplitude of the change at the discontinuity. Asymptotic weight w_{∞} is related to all metabolic rates by $w_{\infty} = (a/(b+c))^{1/(1-\alpha)}$. As a constant weight-length relationship is assumed, estimated from the post-spawning condition of fish (Mollet, et al. 2010), any weight can be converted into length and *vice versa*.

Individual data. Individual growth curves were back-calculated from individuals' otoliths. Otoliths are accretions of calcium carbonate that develop in the ear canals of the heads of bony fishes and that display annual growth layers or annuli. Assuming a constant log-log relationship between otolith size and body size within a species, individual body growth curves could be reconstructed from otolith growth curves determined by measuring inter-annuli distances (Rijnsdorp, et al. 1990).

Life-history traits estimation. The previous energy allocation model (Eq. 1) was fitted to groups of back-calculated individual growth trajectories using a non-linear mixed effects model (nlme, R 2.9; Brunel, et al. 2010) with random effects defined at the individual level, in order to obtain individual estimates of the allocation model's parameters. The most natural grouping level for model fitting would have been the cohort level but since some cohorts consisted of too few individuals, cohorts were merged into groups of four consecutive cohorts. In a preliminary step, the four life-history parameters a , b , c and t_{mat} were estimated at the individual level (four-trait estimation). However, with this approach some degree of confounding between b and c occured (Mollet, et al. 2010). To avoid confounding, maintenance b was fixed at its population average and only the three parameters a , c and t_{mat} were then estimated at the individual level (three-trait estimation, see Mollet, et al. 2010). The population average of b was estimated by fitting the energy allocation model (Eq. 1) simultaneously to data of size-at-age and size-dependent reproductive investment (see below) using a multivariate non-linear mixed effects model with random effects at the individual level on the dataset consisting of all cohorts. Maintenance rate b , interpreted here as the rate of resting metabolism, will be mainly influenced by temperature, and temperature changed on average from 9.91°C in 1950 to 11.01°C in 2005 at the North Sea surface ($p < 10^{-3}$, Van Aken 2008). Individual maintenance rates b_i were therefore fixed around the estimated population average of b in dependence on the temperatures T_i the individuals on average experienced,

$$b_i(T_i) = b(T_{\mathrm{ref}})\left(\frac{T_A}{T_{\mathrm{ref}}} - \frac{T_A}{T_i}\right) \tag{2}$$

where T_{ref} is a reference temperature (the average of experienced temperatures across individuals), T_{A} is the species-specific Arrhenius temperature (plaice: 7000K, sole: 8500K, Van der Veer, et al. 2001), and $b(T_{\mathrm{ref}})$ was set to the estimated population average of b .

The algorithm of the nlme package for non-linear mixed effects modeling requires being provided with starting values of the parameters to be estimated. Since convergence of the algorithm may depend on the chosen values, a grid of starting values covering a range of potential parameter values was used. The model with the highest likelihood was selected among all model runs. More details about the method can be found in Brunel, et al. (2010), Mollet, et al. (2010) and in the appendix.

Population-level reproductive investment data. Size-dependent reproductive investment data consisted of the cost for egg production and of spawning migration. The cost of egg production was estimated from the fecundity-size relationship ($F = \varphi l^{\phi}$), mean egg size (d_{e}), the egg dry weight-egg size relationship ($w_{\mathrm{e}} = \upsilon d_{e}^{\omega}$, Hislop and Bell 1987) and a conversion factor reflecting the ratio of the energy densities of eggs and soma (ς / ψ). Parameters values used and respective sources are given in Table 1.

	area	Fecundity F		Egg weight w_{e}			Energy densities	
		ϕ [cm-$^{\varphi}$]	φ [1]	d_{e} [mm]	υ [mg.mm$^{-\omega}$]	ω [1]	ς [kJg-1]	ψ [kJg-1]
Sole	IVb east	0.3312	3.966	1.132	0.043	2.941	24.0	4.666
	IVb west	0.1944		1.257				
	IVc	0.3253		1.264				
sources		(Witthames, et al. 1995)		(Rijnsdorp and Vingerhoed 1994)				
Plaice	Southern North Sea	0.6287	3.344	1.871				
sources		(Rijnsdorp 1991)		(Rijnsdorp 1991)	(Hislop and Bell 1987)		(Rijnsdorp and Ibelings 1989)	(Dawson and Grimm 1980)

Table 1: Parameters values used to derivate the relative gonadic cost of reproduction in terms of an energy or somatic weight percentage as described in the text.

The respiratory migration cost M_{resp} was derived from a size-specific cost of swimming (Priede and Holliday 1980) and size-specific migration distance (Mollet, et al. 2010). Whereas a 40cm plaice would migrate 140 miles (Bolle, et al. 2005), a 40cm sole would migrate 60 miles (ICES 1965). The probability of being mature p_{adult} was obtained by a logistic regression as a function of age and size (see Mollet, et al. 2010) and the total reproductive investment R was finally given by $R = p_{\mathrm{adult}}(M_{\mathrm{resp}} + F w_{\mathrm{e}} \varsigma / \psi)$. The size-dependence of the gonadic, migratory and total reproductive cost is given in Figure 1. Since plaice grows faster than sole, the jump in reproductive investment due to the likelihood of maturation occurs at similar ages for sole (3-4 year old) and plaice (4 year old), though at larger size for plaice (30-35 cm) than for sole (20-25 cm).

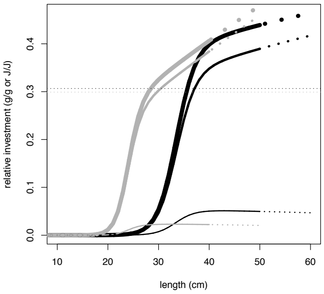

Figure 1: Size-dependent reproductive investment (thick lines) and its composition of gonadic and migratory cost (thin lines) of sole (gray) and plaice (black). The dotted lines represent the reach of the asymptotic lengths.

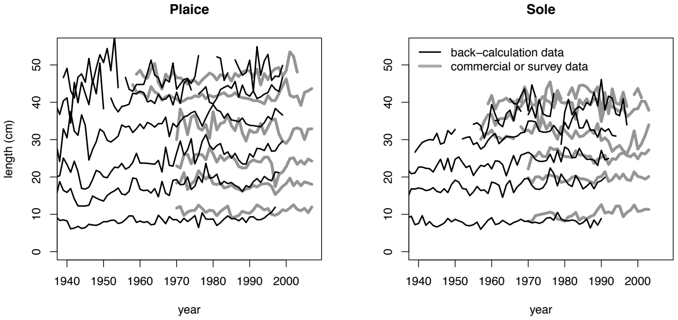

Figure 2: Average size at age in back-calculation data (black) compared to average size at age estimates from surveys and commercial data (gray). The lines represent the average size at age 1,2,3,5,8 and 12 over the years. Below a certain age (in plaice age 6, in sole age 5) the commercial data are biased due to minimal mesh size and minimal landing size, and for these younger ages, data from surveys that started in 1970, are therefore more reliable. The differences between the data sets are not large compared to the interannual variability in size.

Individual size-at-age data. The analyzed data sets comprised of back-calculated growth curves from otoliths of 1723 female plaice (Rijnsdorp and Van Leeuwen 1992, Rijnsdorp and Van Leeuwen 1996) and 935 female soles, consisting of 428 individuals from an earlier study (Millner and Whiting 1996) and a new data set of 507 individuals from market samples. All females were aged 6 or more to restrict the analysis to individuals that were sexually mature for at least one year (last maturing age being 5 for plaice and sole). The back-calculation method was validated for plaice (Rijnsdorp, et al. 1990). For sole, the assumptions about the relationship between body growth and otolith growth were taken from (Millner and Whiting 1996). Because the otolith sampling was length stratified, the frequencies of size classes i in each year y were weighted by their relative frequency $F_{y,i}$ in the size distribution of the sampling year y and rescaled to make the otolith sample representative for the size distribution within the sampling year:

$$q_{y,i} = \frac{(F_{y,i} p_{y,i})}{o_{y,i} \sum_i F_{y,i} p_{y,i}} \sum_i o_{y,i} \qquad (3)$$

where $p_{c,y,i}$ is the proportion of females within sampling year y and size class i estimated from marked samples and $o_{y,i}$ is the number of otoliths sampled in year y and size class i, and hence the sum of these statistical weights per cohort and year over all size classes corresponds to the number of sampled otoliths in that cohort and year, $\sum_i q_{y,i} o_{y,i} = o_y$. Because of non-representative sampling of some cohorts in some years and size classes, variation in these statistical weights was strong, notably because of extremely high values when sample sizes were very low. 5% of the observations corresponding to the upper tail of their weight distribution were removed from the analysis to avoid these extreme weight values. These statistical weights were used in all subsequent average and variance computations and regression models.

The weighted average back-calculated size-at-age was close to independent estimates obtained from pre-recruit surveys (younger age groups) and international commercial data (older age groups, Fig. 1) providing support of the validity of the growth back-calculations. The differences between the data sets are small relative to the interannual variability.

Analysis of temporal trends in life-history traits: multivariate correlated response, environmental effects & trends. The change of life-history traits a and c and t_{mat} estimated from the energy allocation analysis was studied through time and in dependence of potential environmental effects using a multivariate linear mixed effects model (lme, R 2.9). Temporal changes in life history may be due to a phenotypically plastic response to changes in environmental conditions and/or to a genetic change caused by selection, be it natural or fisheries-induced. To separate potential genetic trends in life history from plastic trends caused by trends in environmental conditions, the multivariate life history response was regressed simultaneously on a time variable and relevant environmental variables. As the life-history traits a and c and t_{mat} are phenotypically correlated, a change in one trait can be comprised of an intrinsic change but also of a correlated change due to correlation with another changing trait. To capture this correlation, we carried out a multivariate linear mixed effect analysis by stacking the 3 traits a and c and t_{mat} in a single response variable Y_{xji} and by flagging each trait in this multivariate response variable with a dummy co-variable used as explanatory variable (see Doran and Lockwood 2006 for more technical details). The model included random effects defined on the individual level as life-history traits naturally vary between individuals, so that phenotypic co-variation between life-history traits could be captured and estimated. Environmental variables included in the model were those that had previously been suggested to affect growth rates (population density, eutrophication and temperature;

Rijnsdorp and Van Leeuwen 1996). The proxies used for these environmental variables were the individually experienced average (IEA) number of recruits N_R for population density, the IEA phosphate loads E in the Rhine (www.waterbase.nl) for eutrophication and the IAE sea surface temperature T from May to October (Van Aken 2003) for temperature. According to the life-history trait considered, different parts of the life cycle were relevant for averaging environmental variables : annual levels were averaged over the whole individual life span for a, over the juvenile stage for t_{mat} and over the adult stage for c. The resulting multivariate linear mixed effect model, can be described as follows (with random effects indicated by a tilde)

$$Y_{xji} = \beta_{0,x} + \beta_{1,x} t_j + \beta_{2,x} N_{R,i} + \beta_{3,x} E_i + \beta_{4,x} T_i + \tilde{\delta}_{0,x,ji} + \tilde{\varepsilon}_{xji} \qquad (4)$$

where x indicates a, c or t_{mat}, i.e. the life-history trait considered, i denotes the individual, j identifies the group of cohorts it belongs to, t_j is the weighted average of cohort in group j, and $\beta_{0,x}$, $\beta_{1,x}$, $\beta_{2,x}$, $\beta_{3,x}$, and $\beta_{4,x}$ are the intercept and the regression slopes. The 3-dimensional vector of random effects at the individual level $\tilde{\boldsymbol{\delta}}_{0,ji} = (\tilde{\delta}_{0,a,ji}, \tilde{\delta}_{0,c,ji}, \tilde{\delta}_{0,t_{\mathrm{mat}},ji})$ follows a multivariate normal distribution $N(\mathbf{0}, \boldsymbol{\Sigma}_j)$ for each group j, $\boldsymbol{\Sigma}_j$ being an unstructured co-variance matrix varying with cohort group j. Alternatively, the covariance matrix $\boldsymbol{\Sigma}$ was also considered to be constant among the groups of cohorts. Finally, the within-group errors $\tilde{\varepsilon}_{xji}$ are assumed to be independent and normally distributed, $\tilde{\varepsilon}_{xji} \sim \mathrm{N}(0, \sigma_x)$. The estimated time trends $\beta_{1,x}$ and environmental effects $\beta_{2,x}$, $\beta_{3,x}$, and $\beta_{4,x}$ will thus be conditional on the within-group individual random effects and their covariance structure.

The probabilistic maturation reaction norm (PMRN) is defined as the probability of maturing as a function of age and size (Heino, et al. 2002). It can therefore be used to disentangle the phenotypic plasticity in maturation which is caused by variation in growth. The probability of maturation p_{mat} is estimated by the following logistic regression

$$\mathrm{logit}(p_{\mathrm{mat}}) = \beta_0 + \beta_1 D_{YC} + \beta_2 t + \beta_3 l + \beta_4 D_{YC} \times t + \beta_5 t \times l + \varepsilon \qquad (5)$$

where t is age, l is length and D_{YC} is the average of lumped cohorts (<1960, 1960-1980, >1980) as a factor, fitted to data of back-calculated ages and lengths of immature individuals ($p_{\mathrm{mat}} = 0$) and age and length of first spawning event ($p_{\mathrm{mat}} = 1$) estimated as the next integer age, and the corresponding length, after t_{mat}. Since this age represents the first spawning event, p_{mat} directly estimates the PMRN (compare to the case where first time and repeat spawners cannot be distinguished). The PMRNs are compared to independent reaction norm estimates obtained from the maturity distribution determined by visual inspection of the gonads in samples from commercial catches of plaice (Grift, et al. 2003) and sole (Mollet, et al. 2007).

Reproductive investment is dependent on the energy reserves laid down during the previous growing period and will be affected by feeding conditions (Kjesbu, et al.

1998, Marshall, et al. 1999). Fecundity and somatic growth rate are fine-tuned to the rate of energy acquisition during the feeding season (Kurita, et al. 2003, Van Damme, et al. 2009). Assuming that this annual interaction will be correlated to the interaction of lifespan average reproductive investment and surplus energy, the energy available for either growth or reproduction, a lifespan reaction norm for reproductive investment can be given as function of surplus energy and size. Reproductive investment at any size was calculated for each individual by integrating the allocation rate to reproduction cw from size $w(t)$ to $w(t+1)$:

$$R(t+1)=\int_{t}^{t+1} cw(t)dt\ , \tag{6}$$

(appendix A3). For a given $w(t+1)$, the individual size a year ago $w(t)$ is obtained by inverting the growth function (A2). The surplus energy SP accumulating between $w(t)$ and $w(t+1)$ that could be either used for somatic growth or reproduction is

$$SP(t+1)=R(t+1)+\left(w(t+1)-w(t)\right)=\int_{t}^{t+1}(aw^{3/4}-bw)dt\ , \tag{7}$$

(appendix A4). The individual estimates of annual size-specific reproductive investment R and somatic growth $w(t+1)-w(t)$ relative to size $w(t+1)$ were analyzed as a function of surplus energy SP by a non-parametric smoother (loess, R.2.6.), and on this basis the lifespan reaction norm for reproductive investment was given as a function of surplus energy SP with a log-link,

$$\log(R)=\beta_0+\beta_1 t_j+\beta_2 SP+\beta_3 t_j\times SP+\varepsilon \tag{8}$$

where t_j is the average of cohorts in group j as a factor.

Viability selection differentials. Since the fishery is size-selective, the probability of a fish being caught at a certain age (and size) is dependent on its life history: a fast growing fish will have a higher probability to be caught than a slow growing fish at the same age. Average annual viability selection differentials can be obtained by following the changes of a trait within a cohort as it ages. Average annual viability selection differential in size-at-age were explored by analyzing each length-at-age $l_{t,i}$ as a function of sampling age t_{catch} for each individual i ,

$$l_{t,ji}=\beta_{0,j}YC_j+\beta_{1,j}YC_j\times t_{\text{catch},i}+\varepsilon_{ji} \tag{9}$$

where YC_j is group j of cohorts as a factor. Then, the slope $\beta_{1,j}$ estimates the average annual selection differential on size-at-age l_t for each group j of cohorts. A selection differential of reproductive investment was obtained in the same way by regressing $R_{t,ji}$ (Eq. 6, appendix) instead of $l_{t,ji}$.

Observed viability selection differentials on a, c and t_{mat} might arise from correlated selection due to selection on another correlated trait. Therefore, changes in life-history traits as a cohort ages were again analyzed using a multivariate linear mixed effect model with random effects at the individual level to capture the phenotypic covariance structure,

$$Y_{xji} = \beta_{0,x,j} YC_j + \beta_{1,x,j} YC_j \times t_{\mathrm{catch},i} + \tilde{\delta}_{0,x,i} + \tilde{\varepsilon}_{xji} \tag{10}$$

where x indicates a, c or t_{mat}, YC_j is the group j of cohorts as a factor, $t_{\mathrm{catch},i}$ is the sampling age, $\beta_{0,x,j}$ is the intercept for group j and $\beta_{1,x,j}$ is the slope for group j that estimates the average annual viability selection differential for group j. The 3-dimensional vector of random effects at the individual level $\tilde{\boldsymbol{\delta}}_{0,ji} = (\tilde{\delta}_{0,a,ji}, \tilde{\delta}_{0,c,ji}, \tilde{\delta}_{0,t_{\mathrm{mat}},ji})$ $N(\mathbf{0}, \boldsymbol{\Sigma}_j)$ for each group j, $\boldsymbol{\Sigma}_j$ being an unstructured covariance matrix varying with cohort group j. Finally, the within-group errors $\tilde{\varepsilon}_{xji}$ are assumed to be independent and normally distributed, $\tilde{\varepsilon}_{xji} \sim \mathrm{N}(0, \sigma_x)$.

Results

Energy allocation. The average values of the 4 traits over all cohorts and the covariance structure averaged across groups are presented in Table 2. Sole has a higher pace of life with higher rates of energy acquisition, maintenance and reproductive investment and an earlier maturation. The covariance structure of the traits are similar between the species (except for $r(a,c)$ in the four-trait estimation).

The three-trait estimation with temperature-dependent maintenance rate $b(T)$ reveals that the correlations are positive between energy acquisition rate a and reproductive investment rate c and negative between energy acquisition rate a and the onset of maturation t_{mat} as well as between reproductive investment rate c and the onset of maturation t_{mat}. Since the estimates of b and c are confounded in the four-trait estimation (Mollet, et al. 2010), only the results of the three-trait estimation will be presented.

For both species the rates of energy acquisition a and reproductive investment c have increased, whereas the onset of maturation t_{mat} has decreased across cohorts (Fig. 3). Models analyzing the variation in trait distributions are given in Table 3 for either constant or variable correlation matrices $\boldsymbol{\Sigma}$ among groups of cohorts with either constant maintenance rate b or maintenance rate varying with temperature $b(T)$. The proxies for environmental variables of population density N_R, eutrophication E and temperature T partially explains variation in these life-history parameters. Their effects differ in plaice and sole and depend on the model assumptions ($\boldsymbol{\Sigma}$ constant or variable, $b(T)$).

		Plaice				***Sole***			
		a	***b***	***c***	t_{mat}	***a***	***b***	***c***	t_{mat}
four-trait	μ	5.06	0.58	0.30	4.4	5.38	0.64	0.46	3.22
	CV	0.19	0.43	0.55	0.28	0.18	0.51	0.45	0.19
	$r(a,x)$	1				1			
	$r(b,x)$	0.65	1			0.72	1		
	$r(c,x)$	0.20	-0.55	1		-0.18	-0.76	1	
	$r(t_{\mathrm{mat}},x)$	-0.40	0.19	-0.64	1	-0.37	-0.04	-0.26	1
three-trait	μ	4.88	0.49	0.33	4.10	5.67	0.73	0.42	2.97
	CV	0.15	0.01	0.43	0.28	0.13	0.01	0.35	0.15
	$r(a,x)$	1				1			
	$r(b,x)$	0.19	1			0.21	1		
	$r(c,x)$	0.86	0.03	1		0.82	0.09	1	
	$r(t_{\mathrm{mat}},x)$	-0.68	-0.18	-0.60	1	-0.60	-0.14	-0.62	1

Table 2: Averages, coefficient of variation and correlations of energy allocation parameters from individual estimates across all cohorts of sole and plaice.

Population density N_R has a negative effect on rates of energy acquisition a and reproductive investment c and a positive effect on the onset of maturation t_{mat} (postponed maturation) in plaice, but in sole these effects are almost exactly opposite, the effect on t_{mat} being ambiguous (Table 3). Regarding only significant estimates, eutrophication E has a positive effect on rates of energy acquisition a in both species, has a positive effect on reproductive investment c and a negative effect on the onset of maturation t_{mat} (precocious maturation) in plaice, but in sole these effects are also opposite. The effect of temperature T is most ambiguous between species and among model assumptions. The effect of temperature on energy acquisition rate a might be positive or negative depending on the model assumptions in plaice but is negative in sole, its effect on reproductive investment c is negative in plaice but positive in sole and on onset of maturation t_{mat} the temperature effect is positive in plaice but might be negative or positive in sole depending on the model assumptions (Table 3).

However, these environmental variables only partly explain the observed changes in life history. The time trend variables $\beta_{1,x}$ are significant in all models and tend in the same direction for both species, for all model assumptions considered: rates of energy acquisition a and reproductive investment c increase whereas the onset of maturation t_{mat} decreases over time. Since the models capture the correlation between the life history traits and the phenotypic plasticity in response to the environmental variables included in the model, the remaining temporal trends $\beta_{1,x}$ therefore indicate a genetic change in multivariate life history traits. These trends are illustrated in Fig. 3 by thick light gray lines. Black dots show the observed means of groups of cohorts and the gray dots show the predicted means for constant environmental conditions. The difference between these two indicates the differences due to environmental variability. The deviations of the predicted means from the trend line are due to individual effects within and across the groups of cohorts not captured by environmental variability.

The within group life-history correlations do not tend to change over time and vary around the correlation averages of around $r(a,c)$ =0.85, $r(a,t_{\text{mat}})$ =-0.6 and $r(c,t_{\text{mat}})$ =-0.6 in both species (Fig. 4).

Reaction norms. The estimated PMRNs confirm the downwards shift of maturation age and size over time in both species found in independent studies (Fig. 5). In plaice, most individuals become mature at age 4, whereas in sole most individuals become mature at age 3, and therefore these ages are the most reliable ones in the PMRN estimation. The estimates for the other ages mainly represent the extrapolation from the ogive model (Eq. 5). In plaice, the average maturation given by the interception of PMRN midpoints (size at which the probability of becoming mature is 0.5 in the PMRN for a given age) and the growth curves, decreased from about 35cm at age 5 before the 1960s to about 25cm at age 3.5 after the 1980s. In sole, the average maturation decreased from about 27cm at age >3 around the 1960s to 24cm at age <3 after the 1980s. These changes are less accentuated in the estimated PMRN midpoints from independent estimations (Grift, et al. 2003, Mollet, et al. 2007) but the overall temporal patterns are similar.

The estimated lifespan reaction norm for reproductive investment describes the relationship between reproductive investment and surplus energy (Fig. 6). Reproductive investment increases with size and is therefore illustrated for two size classes (30, and 40cm). In both species, size-specific reproductive investment increases with size-specific surplus energy. While reproductive investment continuously increases with surplus energy, the amount of energy invested into somatic growth levels off after a certain threshold of surplus energy (at higher levels for larger fish, Fig. 6, first panel). The proportion of surplus energy allocated to reproduction therefore increases whereas the proportion invested in somatic growth decreases with surplus energy. A 40cm plaice allocates about 80% to reproduction and 20% to somatic growth, if surplus energy is high, but about 50% to each, if surplus energy is low. In sole the allocation to reproduction is higher: A 40cm sole allocates about 90% to reproduction and 10% to somatic growth, if surplus energy is high, and about 60% to reproduction and 40% to somatic growth, if surplus energy is low. Reproductive investment and surplus energy are highly correlated (plaice $r = 0.91$, sole $r = 0.94$) and changes in one might thus be explained by changes in the other. Relative reproductive investment increased over the studied period by about 50% in plaice and by about 20% in sole (Fig. 6, gray lines in lower panel). However, if this reproductive investment is given conditional on surplus energy for each group of cohorts (Eq. 8), the change over time is weaker in sole and even negative in plaice (Fig. 6, black lines in lower panel), despite the increasing rates of energy allocation to reproductive investment c (Table 3, Fig. 3).

			Σ constant		**Σ variable**		**Σ variable, $b(T)$**	
		description	estimate	p-value	estimate	p-value	estimate	p-value
PLAICE	$\beta_{0,a}$	Averages of a, c and t_{mat}	**5.082**	**$< 10^{-4}$**	**5.106**	**$< 10^{-4}$**	**5.099**	**$< 10^{-4}$**
	$\beta_{0,c}$		**0.345**	**$< 10^{-4}$**	**0.353**	**$< 10^{-4}$**	**0.354**	**$< 10^{-4}$**
	$\beta_{0,t_{\text{mat}}}$		**4.010**	**$< 10^{-4}$**	**4.011**	**$< 10^{-4}$**	**3.983**	**$< 10^{-4}$**
	$\beta_{1,a}$	Temporal change in a, c and t_{mat}	**0.031**	**$< 10^{-4}$**	**0.033**	**10^{-4}**	**0.035**	**$< 10^{-4}$**
	$\beta_{1,c}$		0.005	0.500	**0.005**	**$< 10^{-4}$**	**0.005**	**0.003**
	$\beta_{1,t_{\text{mat}}}$		**-0.044**	**$< 10^{-4}$**	**-0.045**	**$< 10^{-4}$**	**-0.040**	**$< 10^{-4}$**
	$\beta_{N_R,a}$	Density effect on a, c and t_{mat}	**-1.2 10^{-6}**	**$< 10^{-4}$**	**-1.2 10^{-6}**	**$< 10^{-4}$**	**-1.6 10^{-6}**	**$< 10^{-4}$**
	$\beta_{N_R,c}$		**-2.1 10^{-7}**	**$< 10^{-4}$**	**-2.4 10^{-7}**	**$< 10^{-4}$**	**-3.3 10^{-7}**	**$< 10^{-4}$**
	$\beta_{N_R,t_{\text{mat}}}$		2.5 10^{-7}	0.138	**3.9 10^{-7}**	**$< 10^{-4}$**	**5.6 10^{-7}**	**$< 10^{-4}$**
	$\beta_{E,a}$	Eutrophication effect on a, c and t_{mat}	0.224	0.052	0.167	0.223	0.160	0.856
	$\beta_{E,c}$		**0.0488**	**$< 10^{-4}$**	0.003	0.032	**0.026**	**0.004**
	$\beta_{E,t_{\text{mat}}}$		0.1314	0.677	**-0.141**	**$< 10^{-4}$**	**-0.338**	**$< 10^{-4}$**
	$\beta_{T,a}$	Temperature effect on a, c and t_{mat}	-0.009	0.573	**-0.031**	**0.012**	**0.036**	**$< 10^{-4}$**
	$\beta_{T,c}$		**-0.017**	**$< 10^{-4}$**	**-0.029**	**$< 10^{-4}$**	**-0.038**	**$< 10^{-4}$**
	$\beta_{T,t_{\text{mat}}}$		0.158	0.291	**0.008**	**0.047**	**0.119**	**$< 10^{-4}$**

			Σ constant		**Σ variable**		**Σ variable, $b(T)$**	
		description	estimate	p-value	estimate	p-value	estimate	p-value
SOLE	$\beta_{0,a}$	Averages of a, c and t_{mat}	**5.841**	**$< 10^{-4}$**	**5.957**	**$< 10^{-4}$**	**5.812**	**$< 10^{-4}$**
	$\beta_{0,c}$		**0.416**	**$< 10^{-4}$**	**0.449**	**$< 10^{-4}$**	**0.408**	**$< 10^{-4}$**
	$\beta_{0,t_{\text{mat}}}$		**3.046**	**$< 10^{-4}$**	**2.990**	**$< 10^{-4}$**	**3.094**	**$< 10^{-4}$**
	$\beta_{1,a}$	Temporal change in a, c and t_{mat}	**0.016**	**$< 10^{-4}$**	**0.056**	**$< 10^{-4}$**	**0.039**	**$< 10^{-4}$**
	$\beta_{1,c}$		0.002	0.911	**0.008**	**$< 10^{-4}$**	**0.004**	**$< 10^{-4}$**
	$\beta_{1,t_{\text{mat}}}$		**-0.011**	**$< 10^{-4}$**	**-0.021**	**$< 10^{-4}$**	**-0.014**	**$< 10^{-4}$**
	$\beta_{N_R,a}$	Density effect on a, c and t_{mat}	**1.4 10^{-6}**	**10^{-4}**	5.6 10^{-7}	0.665	**1.1-10^{-6}**	**0.043**
	$\beta_{N_R,c}$		9.1 10^{-8}	0.382	**2.0 10^{-7}**	**$< 10^{-4}$**	**2.8 10^{-7}**	**0.013**
	$\beta_{N_R,t_{\text{mat}}}$		-8.0 10^{-7}	0.009	**2.7 10^{-7}**	**0.003**	**-4.2 10^{-7}**	**0.0008**
	$\beta_{E,a}$	Eutrophication effect on a, c and t_{mat}	**0.402**	**$< 10^{-4}$**	-0.255	0.430	-0.389	0.745
	$\beta_{E,c}$		-0.019	0.152	-0.075	0.027	**-0.057**	**0.005**
	$\beta_{E,t_{\text{mat}}}$		**0.252**	**$< 10^{-4}$**	**0.523**	**$< 10^{-4}$**	**0.627**	**$< 10^{-4}$**
	$\beta_{T,a}$	Temperature effect on a, c and t_{mat}	**-0.001**	**$< 10^{-4}$**	-0.023	0.472	**-0.027**	**10^{-4}**
	$\beta_{T,c}$		0.006	0.393	0.016	0.837	**0.050**	**$< 10^{-4}$**
	$\beta_{T,t_{\text{mat}}}$		**-0.200**	**$< 10^{-4}$**	**-0.074**	**$< 10^{-4}$**	**0.028**	**$< 10^{-4}$**

Table 3: Parameter estimates and p-values of models to describe the influence of environmental effects (population density N_R, eutrophication E and temperature T) on and the intrinsic (genetic) temporal trends ($\beta_{1,x}$) in the correlated life history traits of energy acquisition a, reproductive investment c and the onset of maturation t_{mat}, intercepts $\beta_{0,x}$ representing the corresponding averages, in plaice and sole. The correlation matrix $\mathbf{\Sigma}$ between the three life history parameters a, c and t_{mat} is assumed to be either constant ($\mathbf{\Sigma}$ constant) or variable ($\mathbf{\Sigma}$ variable) across groups of cohorts and the otherwise constant maintenance rate b is allowed to vary with temperature $b(T)$.

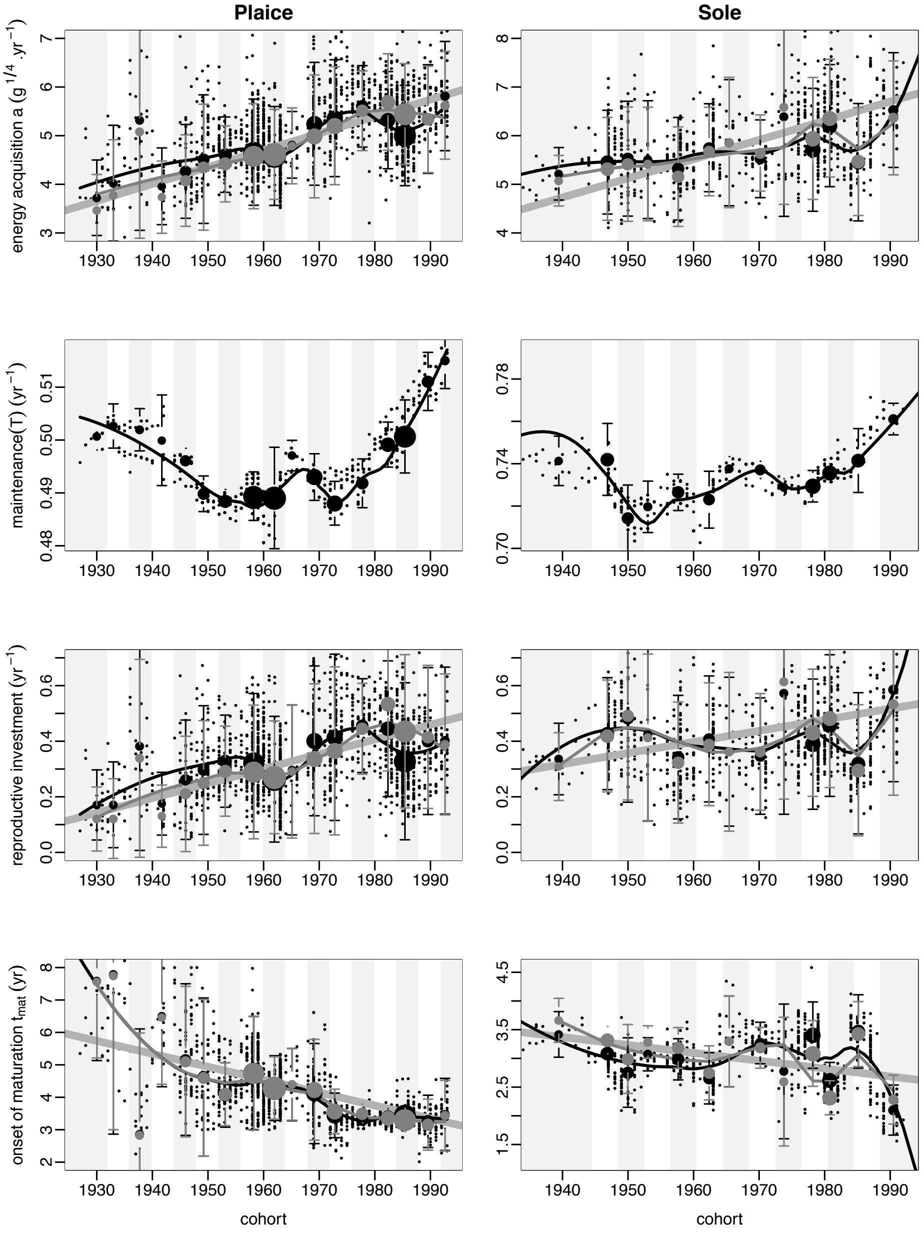

Figure 3: Changes in the estimated energy acquisition a , reproductive investment c and the onset of maturation t_{mat} with a variable correlation matrix $\mathbf{\Sigma}$ and a temperature-dependent maintenance rate $b(T)$ over cohorts in plaice and sole. Dots represent individual estimates, gray background shadings the grouping of cohorts. Black bars indicate observed means and 95% confidence intervals, gray bars the predicted means and intervals for constant averaged environmental variables, the black and gray lines corresponding smoothers through these means, the point thickness being proportional to the number of observations in each group. The thick light gray lines give the remaining temporal trends conditional on environmental effects and life-history correlation.

Viability selection differentials. The expected size at age decreases with sampling age, i.e. the fixed sampling age effect of $\beta_{1,x}$ is negative (Eq. 10, Table 4). For plaice, these effects are significant ($p<0.05$) until age 7, whereas for sole they are significant for all ages (Table 4). The annual viability selection differentials $\beta_{1,x}$ of reproductive investment (see Eq. 6) were also negative (Table 4). For plaice, these effects are significant after age 5, whereas for sole they are significant after age 3 (Table 4).

The viability selection differentials, averaged over the cohorts (fixed effects from linear mixed effect model Eq. 9), are negative for the rates of energy acquisition a (plaice: -0.052/year, sole: -0.066/year) and reproductive investment rate c (plaice: -0.006/year, sole: -0.007/year) and positive for the onset of maturation t_{mat} (plaice: 0.126, sole: 0.024/year) for both species (Table 5). The differentials are stronger in sole for rates of energy acquisition a and reproductive investment rate c but stronger in plaice for the onset of maturation t_{mat}. In certain cohorts the direction of the selection differential might turn around (Fig. 7), but over all cohorts the pattern of the average differentials is consistent.

		Plaice		**Sole**	
	age	$\beta_{1,j}$	p-value	$\beta_{1,j}$	p-value
Size at age	**1**	-0.049	$< 10^{-3}$	-0.146	$< 10^{-3}$
	2	-0.114	$< 10^{-3}$	-0.317	$< 10^{-3}$
	3	-0.179	$< 10^{-3}$	-0.398	$< 10^{-3}$
	4	-0.197	$< 10^{-3}$	-0.410	$< 10^{-3}$
	5	-0.187	$< 10^{-3}$	-0.420	$< 10^{-3}$
	6	-0.167	$< 10^{-3}$	-0.470	$< 10^{-3}$
	7	-0.106	0.034	-0.444	$< 10^{-3}$
	8	-0.070	n.s	-0.464	$< 10^{-3}$
	9	-0.010	n.s	-0.403	$< 10^{-3}$
	10	0.087	n.s.	-0.456	$< 10^{-3}$
Reproductive investment at age	**1**	-	-	-	-
	2	-0.047	n.s.	-1.173	n.s.
	3	0.491	n.s.	-1.146	n.s.
	4	0.282	n.s.	-3.586	$< 10^{-3}$
	5	-1.513	n.s.	-5.091	$< 10^{-3}$
	6	-2.724	0.013	-7.229	$< 10^{-3}$
	7	-3.027	0.023	-8.162	$< 10^{-3}$
	8	-5.301	0.002	-8.812	$< 10^{-3}$
	9	-5.137	0.017	-8.303	$< 10^{-3}$
	10	-5.370	0.037	-8.302	$< 10^{-3}$

Table 4: Average expected length at age in cm as function of sampling age t_{catch}, obtained from the fixed effects in the linear mixed model in Eq. 7 averaged over all groups of cohorts (i.e. without the YC_j interactions). The expected length at age decreases with sampling age, in plaice this effect gets weaker with age, in sole it becomes stronger (see also Eq. 8).

	Plaice		Sole	
	estimate	p-value	estimate	p-value
$\beta_{0,a}$	5.578	$< 10^{-4}$	6.437	$< 10^{-4}$
$\beta_{0,c}$	0.411	$< 10^{-4}$	0.481	$< 10^{-4}$
$\beta_{0,t_{\mathrm{mat}}}$	2.902	$< 10^{-4}$	2.769	$< 10^{-4}$
$\beta_{1,a}$	-0.052	10^{-4}	-0.066	$< 10^{-4}$
$\beta_{1,c}$	-0.006	$< 10^{-4}$	-0.007	0.031
$\beta_{1,t_{\mathrm{mat}}}$	0.126	$< 10^{-4}$	0.024	$< 10^{-4}$

Table 5: Parameter estimates and p–values for the fixed effects changes in energy acquisition a, reproductive investment c and the onset of maturation t_{mat} over sampling ages, averaged over all groups of cohorts (i.e. without the YC_j interactions), taking account of the life-history correlations through random individual effects. The slopes $\beta_{1,x}$ give the cumulative annual viability selection differential of trait x. The slopes for each group of cohorts are illustrated in Fig. 7.

Discussion

Plaice vs. Sole life history. In general, sole has a higher pace of life (higher energy acquisition, maintenance, reproductive investment, earlier maturation) than plaice over the study period (Table 2, Fig. 3). Based on the difference in size at age between the species (see Fig. 2) some difference in energy allocation was expected. A lower size at age could be attained by lower energy acquisition, higher maintenance, higher reproductive investment or earlier maturation, but apparently, all energy allocation parameters differ. The higher energy acquisition and maintenance is in line with the finding of empirical studies that juvenile sole has higher growth rates than plaice (Fonds, et al. 1992, Teal, et al. 2008). The differences in energy acquisition and maintenance might be caused by differences in environmental conditions. Sole has a more southern and shallower distribution and will experience higher summer temperatures (up to 18 - 20°C). Plaice occurs in shallow waters during the juvenile phase, but adults occur in the stratified waters of the central North Sea where temperatures are rather constant around 7-8˚C (Rijnsdorp and Van Beek 1991, Hunter, et al. 2003). The difference in energy acquisition, maintenance and reproductive investment rate may thus be (partly) explained by the difference in temperature environment leading to a higher metabolic rate. The earlier maturation in sole might be a consequence of the higher metabolic rates (see Table 2). Increased food availability might also lead to a higher net energy acquisition rate. Feeding behavior of the two species is similar, both feed on sedentary or slowly moving prey items which do not require swimming at high speed (Rijnsdorp and Vingerhoed 2001), and there is thus no reason to assume that food availability should substantially differ. However, intraspecific competition in sole is smaller than in plaice (Rijnsdorp and Van Beek 1991) consistent with the negative effect of population density on energy acquisition rate in plaice but a positive effect in sole (Table 3). Although the sole dispose of higher surplus energy, the ratio $a/(b+c)$ is lower than in plaice and therefore they grow to smaller asymptotic sizes (see Fig. 2). The life-history correlations are quite similar between the species and differences might be partly due to environmental and genetic differences. To disentangle the relative contribution in the correlation, individual information on the environmental effects would be needed.

Phenotypic plasticity. Energy allocation parameters will be affected by the environmental conditions which an individual fish have experienced during its life. During our study period, important environmental changes have occurred: (i) increase in fishing mortality and a reduction of population biomass (Millner and Whiting 1996, Rijnsdorp and Millner 1996); (ii) increase in temperature (Van Aken 2008); (iii) increase and subsequent decline in primary and secondary productivity coinciding with changes in eutrophication (Beukema and Cadee 1997, Philippart, et al. 2007); (iv) increase in benthic disturbance due beam trawling possibly affecting benthic productivity (Rijnsdorp and Van Leeuwen 1996, Jennings, et al. 2001, Hiddink, et al. 2008); (v) increase in concentrations of pollutants which could affect physiological processes such as endocrine disruptors (Vethaak, et al. 2005).

Population density negatively affected energy acquisition a and reproductive investment c in plaice, whereas a positive effects was found for sole. These results are consistent with the literature on density-dependent growth. In plaice, negative density-dependence in growth has been reported (Rijnsdorp and Van Leeuwen 1996, Bolle, et al. 2004), whereas growth is sole appears to be independent of density (Rogers 1994, Millner and Whiting 1996, Amara 2003, Teal, et al. 2008).

There might be a direct effect of temperature on the onset maturation, which is not captured in the variation in growth, and which is thus not captured in the PMRN (Dhillon and Fox 2004, Dembski, et al. 2006). Furthermore, high population density might favor earlier maturation if the probability of encounter of conspecifics is increased when population density is higher (Hobbs, et al. 2004), or later maturation if dominant adults suppress the maturation of juveniles adults (Fricke and Fricke 1977, Borowsky 1978, Jones and Thompson 1980). Endocrine disrupting agents from sewage effluents that might come in hand with eutrophication, are often associated with increased levels of vitellogenin production but lead to reproductive impairment and reduced fecundity (Oberdörster and Cheek 2001). Anything that accelerates growth would be expected to lead to an earlier maturation (Stearns and Koella 1986).

The increase in energy acquisition a is consistent with the increased food availability and the relaxed intraspecific food competition due to fishing. Accordingly our proxies for eutrophication, the phosphate load in rivers, which is often a limiting biological factor, correlate positively with energy acquisition a in both species and population density, derived from the year class strength, correlates negatively in plaice (Table 3). However, in sole the effect of population density on energy acquisition a is positive and might indicate that growth in sole is not density-dependent confirmed by other studies.

We hypothesized that the primary energy flow of net energy acquisition might determine subsequent energy flows of reproductive investment and hence also maturation. The increase in reproductive investment c rate might therefore be partly the consequence of improved feeding conditions through its correlation with energy intake, $r(a,c)$ being around 0.85. This would also explain why reproductive investment rate c correlates negatively with population density and positively eutrophication (in plaice), namely because these effects act via energy acquisition a on c.

Similarly, the trends towards earlier maturation might be partly explained by increasing net energy acquisition due to improved feeding conditions. There might be a growth-independent effect of population density on postponed maturation in plaice, which might be due to the presence of dominant adults (see above), but not in sole. Higher eutrophication leading to higher food availability is related to earlier maturation as expected in plaice but to later maturation sole. Some of the correlations with temperature are counter-intuitive: temperature might correlates negatively with net energy acquisition rate a and positively with the onset of maturation t_{mat} (postponed maturation, Table 3). Under the constant maintenance assumption this result might be explained by an indirect effect via maintenance b rate: since increased temperatures result in increased maintenance costs, they might decrease the net surplus production, hence the estimated energy acquisition a and therefore delay maturation. When the dependence of maintenance on temperature is accounted for by $b(T)$, the effect of temperature on energy acquisition a changes to the intuitive expectation of being positive in plaice (not in sole). However, the temperature effect on t_{mat} remains positive in both species also accounting for the dependence of maintenance on temperature. From these results it can not be concluded that higher temperatures might have a direct growth-independent positive effect on maturation.

In summary, changes in population density and eutrophication might have partly caused an increase in surplus energy, which in turn partly explain changes in reproductive investment and maturation through correlation. Density-dependent growth seems to play a role in plaice but not in sole, eutrophication attenuates maturation and reproduction in sole, which are more directly exposed to it due to their spatial distribution, but translates to an enhancement of maturation and reproduction for plaice further offshore. The temperature effects remains ambiguous.

However, inference from the average population density, eutrophication and temperature on allocation rates is not straightforward, since individually experienced population density, eutrophication and temperature measurements would be needed to relate to the individual estimates of energy allocation most consistently. Furthermore, caution is needed using a constant, only temperature-dependent maintenance rate $b(T)$. Since no individual effects apply to this $b(T)$ estimate we might miss a part of the individual life-history correlation, which might confound with the environmental effects.

Trends and FIE. The temporal trends indicate that energy acquisition a increases and reproductive investment rate c increase, and the onset of maturation t_{mat} decreases conditional on the environmental variability and the life-history correlation. Due to this conditioning it can be excluded that reproductive investment rate c increases, and the onset of maturation t_{mat} decreases as a mere consequence of their correlation with increasing energy acquisition a, suggesting that these changes are also partly genetic. Even the increasing energy acquisition may thus have a genetic component.

Since the fishery is selective for larger sizes at age, a selection for life histories with lower size at age is expected (see viability selection differentials). Due to fisheries-induced evolution, genetic selection for higher reproductive investment and earlier maturation is expected (Dunlop, et al. 2009). The expectation for energy acquisition might be in both directions and will depend on the size-selectivity: if the likelihood to survive the young ages and small sizes is low, it might be advantageous to increase energy acquisition to sustain higher reproductive investment rates, or if the PMRN has no more flexibility to decrease, earlier maturation can only be achieved by faster growth, otherwise selection would be on lower energy acquisition (Dunlop, et al. 2009). For maintenance there is no theoretical hypothesis how fishing may select for a change. The observed intrinsic changes in life history traits are consistent with the expectations on fisheries-induced evolution.

The reaction norms for maturation and reproductive investment disentangle the phenotypic plasticity caused by variation in somatic growth and surplus energy respectively, from the observed phenotypic traits. The PMRN substantially shifted towards younger ages and smaller sizes from the 1940s to the 1990s for the maturation-critical ages and thus confirms findings of independent studies (Grift, et al. 2003, Mollet, et al. 2007). Since the independent estimates are based on more data points and many more individuals, these might be considered more reliable. Despite the variation in the PMRN midpoints is relatively large, the pattern for the maturation-critical ages is consistent. The sole reaction norm for cohorts before 1960s might differ because this period was dominated by data from another origin (Millner and Whiting 1996) .

The lifespan reproductive reaction norm suggests that while reproductive investment increases with surplus energy, the energy invested into somatic growth levels off. It indicates that reproduction is prioritized over growth, given a certain amount of surplus energy. Since surplus energy likely varies annually, this reaction norm would ideally be given on an annual basis. Since the growth investments levels off with increasing surplus energy, size increments are not a reliable proxy for surplus energy (Rijnsdorp, et al. 2005). Nevertheless, some autocorrelation in metabolic rates is expected over the individual lifespan, which justifies the approach of the lifespan reproductive reaction norm.

The lifespan reproductive investment reaction norm shows that reproductive investment conditional on surplus energy might not have increased importantly over time. In plaice this reaction norm even decreases over time, despite the increasing energy allocation rates c. This is because reproductive investment output relative to somatic energy is not necessarily strongly correlated to the reproductive investment rate c, the first being affected not only by c but also by changes in a, b and the increase in somatic weight between the spawning periods and thus also by t_{mat} (see equation A3 in appendix). Depending on whether the parameters space of a, b c and t_{mat} changes to have a stronger effect on the annual surplus energy or on the reproductive output, the relative reproductive investment might increase or decrease. Empirical studies would typically measure the reproductive output (e.g. given by the energetic difference between pre- and post-spawning fish) relative to body size. As the energy allocation model implies that this measure is confounded with all other metabolic rates and the onset of maturation, the same being the case for surplus energy, our estimate of the size-specific reproductive investment allocation c corresponds best to the object aimed to estimate when estimating “reproductive effort”. The confounding of reproductive output with other life history traits might furthermore be the reason, why empirical studies measuring this output have difficulty in finding evidence for FIE (Yoneda and Wright 2004, Rijnsdorp, et al. 2005). Depending on the evolution of the other life-history parameters, the relative reproductive output is not bound to increase if reproductive allocation rate increases c, as observed here for plaice.

These findings furthermore confirm the integrity of the followed approach by estimating individual size-specific energy allocation rates and the onset of maturation, as these rates represent the units of the life-history tradeoffs. It is therefore better to look at these rates directly to infer on changes in life history than to derive reaction norms based on size, because in size all metabolic rates are confounded. The best reaction norm for reproductive investment is c, because these are not only conditional on size but also conditional on the other life-history traits. The analysis capturing the multivariate distribution of these tradeoff-units over time controlling for environmental effects (Table 3) presented in this study is therefore probably the most integral analysis of FIE done so far.

Viability selection differentials. Since the fishery selectively removes the large, i.e. fast growing individuals, a decrease of the frequency of fast growers with large size is expected from the effect of fishing. A larger size is achieved by either investing more into growth or less into reproduction and thus allocation rates for higher growth or for lower reproduction will be selected against. This might explain why the viability selection differentials for size at age and also for the energy acquisition rate a are positive, but the differentials for reproductive investment and reproductive investment rate c are negative. Part of the cost of growing fast might be due to natural mortality since higher energy acquisition rates are associated to higher foraging rates and thus to a higher exposure risk to predators and diseases. The negative selection differential on reproductive investment and c might also reflect the mortality cost of reproduction. A mortality cost is associated to reproduction in various species (Reznick 1992, Hutchings 1993, Ernande, et al. 2004) because energy resources are depleted during reproduction and the spawners suffer starvation if environmental conditions after spawning are not sufficient to restitute the lost energy. Therefore, the level of reproductive investment and the mortality risk will be correlated. Furthermore, spawning behavior might bear a mortality cost as courting for the other sex and mating exposes the fish to predators or fisheries. In plaice, fishing mortality rates double for females and almost quadruple for males during the spawning season as compared to the rest of the year (Rijnsdorp 1993). These costs of reproduction might explain the positive selection differential in the onset of maturation t_{mat}. A later maturation or higher t_{mat} would also be expected from a selection on lower rates of energy acquisition a and reproductive investment c through life-history correlation (Table 2, Fig. 4). However, since we based our analysis to be conditional on these correlations, the estimates of viability selection differentials should not have been influenced by these correlations.

The applied method may be a novel approach to quantify the trade-offs of energy acquisition and survival, reproductive investment and survival and maturation and survival. These trade-offs are often essential parts in modeling frameworks but since no estimates are available, the parameters used in models are either chosen *ad hoc* or obtained in complicated optimization procedures.

The negative viability selection differentials are opposite to the evolutionary response of increasing a and c and decreasing t_{mat} (Table 3, Fig. 3).

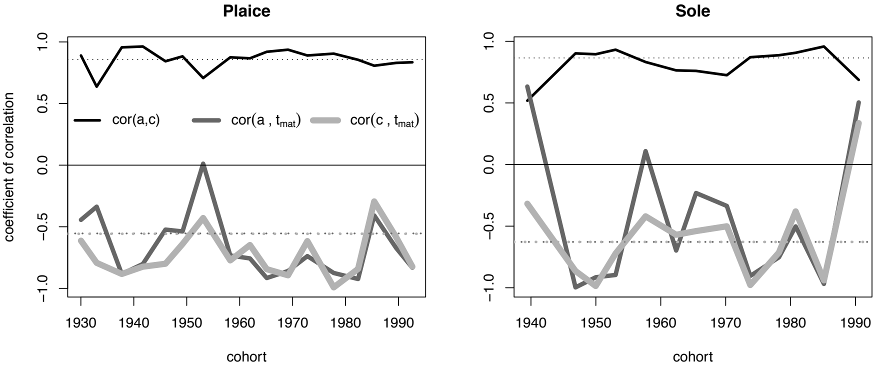

Figure 4: Changes in correlations over time estimated in the model using a variable correlation matrix Σ and temperature dependent maintenance rates $b(T)$. The dotted lines indicate the estimated correlation of the matrix Σ was assumed to be constant across groups of cohorts.

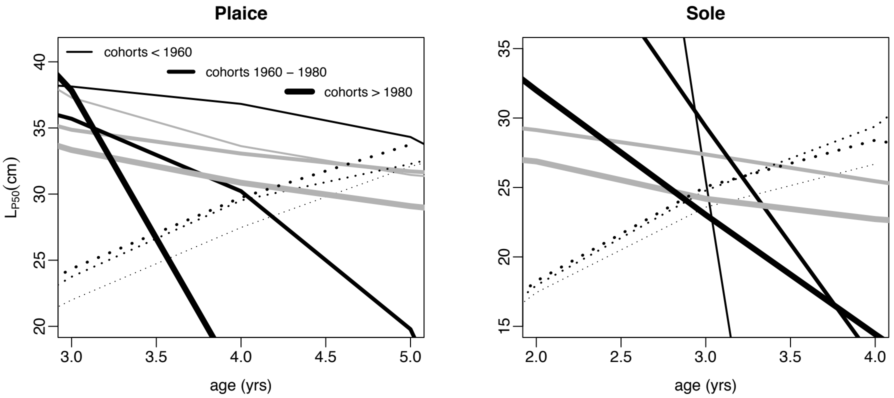

Figure 5: PMRNs obtained from the back-calculated sizes at age and the estimated t_{mat} (black lines), compared to independent estimates (gray lines) in plaice (Grift, et al. 2003) and sole (Mollet, et al. 2007), for three periods (cohorts before 1960, between 1960 and 1980 and after 1980). The dotted lines show the average back-calculated size at age.

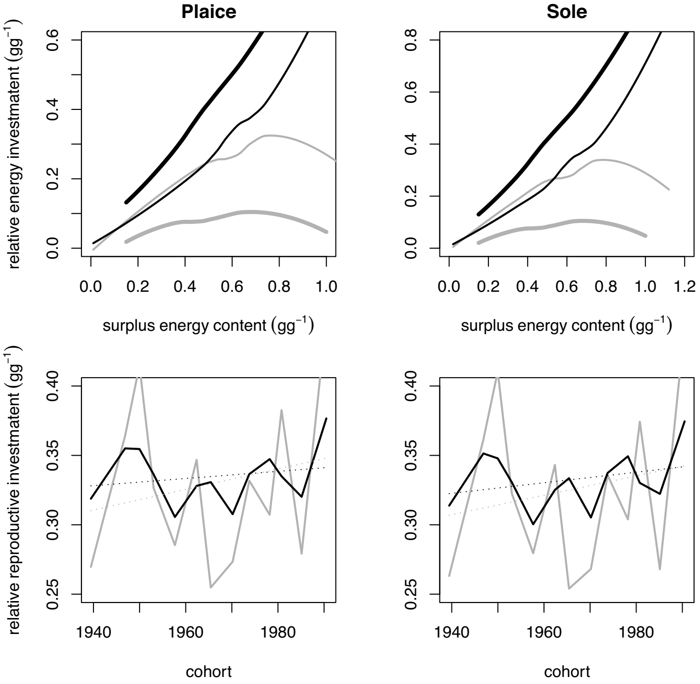

Figure 6: Lifespan reaction norms for size-specific reproductive investment (black lines) and size-specific investment into somatic growth (gray lines) as a function of acquired surplus energy, expressed as allocated energy relative to total body energy, ($g.g^{-1}$) for different sizes (30cm: thin line, 40cm: thick line), in plaice and sole (upper panel). The lower panel shows the observed relative reproductive investment (gray lines) and the predicted relative reproductive investment from the lifespan reproductive investment reaction norm for a constant averaged surplus production (black lines) over groups of cohorts, dotted lines giving linear regressions through these, for fishes between 30 and 40cm.

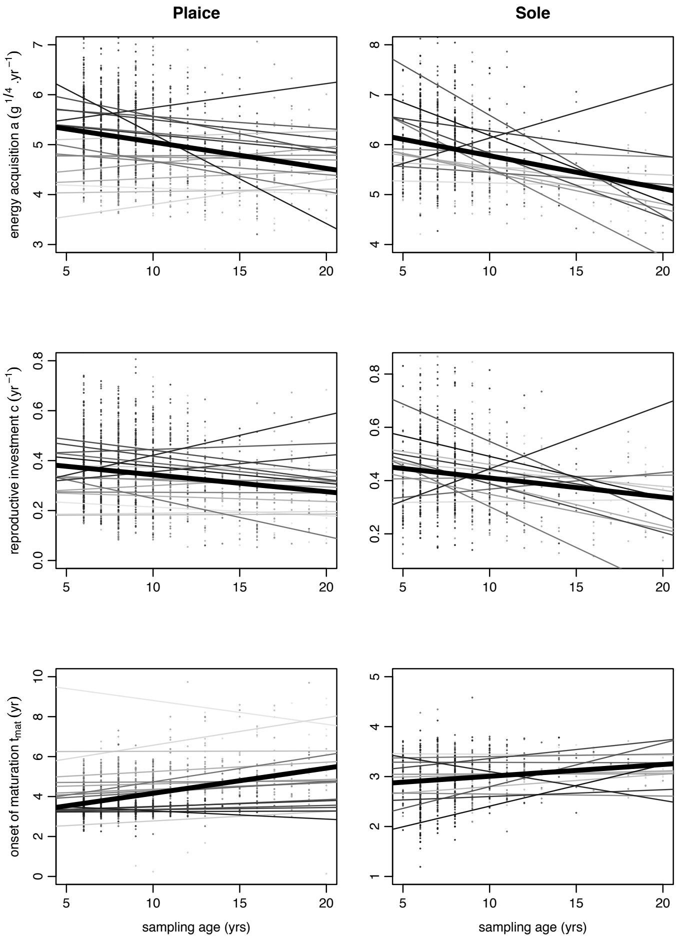

Figure 7: Cumulative annual selection differentials ($\beta_{1,x}$) in energy acquisition a , reproductive investment c and the onset of maturation t_{mat} per group of cohorts (gray lines, the darker the later in time) in plaice and sole. The thick black line shows the change over the sampling ages averaged over all groups of cohorts.

From this it may be expected that the selection differentials for fecundity are opposite to the selection differentials for viability and stronger than these. However, since generations overlap and the traits are correlated, link between selection differentials and the evolutionary response is complex and needs further research (Law 1991).

Origins of different responses. The difference in the response between plaice and sole might be due to several reasons. First, the life history of the two species is different and their response to fisheries selection can be expected to be different. As hypothesized above, sole had a higher pace of life, i.e. higher rates of energy acquisition, maintenance, reproductive investment, and earlier maturation, already before commercial exploitation became substantial. If the sole life history was already adapted to higher mortality rates (predation- or human-induced) it makes the organism less vulnerable to additional mortality (Ernande, et al. 2004). Second, since the difference between size at age, size at onset of maturation and the minimal landing size is smaller, a smaller life history change is expected in sole than in plaice. Third, the fishing mortality for sole only substantially increased in the 1960s due to the introduction of the beam trawl, whereas for plaice it was relatively high already before that. The time series of sole data might thus not yet be long enough to detect fisheries-induced changes of the same magnitude as in plaice. Fourth, for plaice, about twice as many otolith back-calculations were available and the sole data came from different sources. Despite the expected differences, rates of change in the responses between the species are rather similar.

Conclusion. The analysis of changes in the life-history traits over time as a function of environmental factors, taking account of the correlation in life history traits, is new and unique, offering an opportunity to study life-history evolution in free living organisms with indeterminate growth for which individual growth trajectories can be estimated. By including environmental variables known to affect the energy allocation, we could disentangle the phenotypic plasticity in the multivariate response in life history traits from a trend in time reflecting an evolutionary response to fishing. The inferred evolutionary response matched the expected response based on the selection differentials as well as the results of eco-genetic model studies.

Appendix

Growth function. The energy allocation parameters energy acquisition rate a, maintenance b rate and reproductive investment rate c, and the onset of maturation t_{mat} estimated from body weight w as a function of age t given by

$$w^{1-\alpha}(t) = (1-S(t))\left[\frac{a}{b} - \left(\frac{a}{b} - w_0^{1-\alpha}\right)\mathrm{e}^{-b(1-\alpha)t}\right] + S(t)\left[\frac{a}{b+c} - \left(\frac{a}{b+c} - w_{\mathrm{mat}}^{1-\alpha}\right)\mathrm{e}^{-(b+c)(1-\alpha)(t-t_{\mathrm{mat}})}\right] \quad [1]$$

where w_0 is body weight at $t=0$ and w_{mat} is body weight at $t = t_{\mathrm{mat}}$ given by $w_{\mathrm{mat}}^{1-\alpha} = \frac{a}{b} - \left(\frac{a}{b} - w_0^{1-\alpha}\right) e^{-b(1-\alpha)t_{\mathrm{mat}}}$.

To switch from juvenile to adult growth, a switch function is used

$$S(t) = \frac{1}{1+e^{-k(t-t_{\mathrm{mat}})}}$$

where k should be very large relative to the frequency of observable age t data, to result in an almost immediate switch at t_{mat}.

Inverse growth function. To relate a certain size to its corresponding age, the inverse of the growth function is used (e.g. to calculate a size-specific reproductive investment),

$$t = (1-S(w))\left(\frac{1}{b(1-\alpha)}\log\left[\frac{\frac{a}{b} - w^{1-\alpha}}{\frac{a}{b} - w_0^{1-\alpha}}\right]\right) + S(w)\left(t_{\mathrm{mat}} - \frac{1}{(b+c)(1-\alpha)}\log\left[\frac{\frac{a}{b+c} - w^{1-\alpha}}{\frac{a}{b+c} - w_{\mathrm{mat}}^{1-\alpha}}\right]\right) \quad [\mathrm{A2}]$$

where the switch function is now expressed as a function of weight w and weight at maturation w_{mat},

$$S(w) = \frac{1}{1+e^{-k(w-w_{\mathrm{mat}})}}$$

Reproductive investment. The reproductive investment $R(t+\Delta t)$ is given by the rate of energy conversion to reproduction $cw(t)$ integrated over the period from t to $t+\Delta t$, expressed as a function of the somatic weights at the start $w(t)$ and at the end $w(t+\Delta t)$ of the time interval Δt, over which the reproductive events repeatedly occur. Assuming $\alpha = 3/4$ and $\beta = \gamma = 1$,

$$\begin{aligned}
R(t+\Delta t) &= \int_t^{t+\Delta t} cw(\tau)d\tau = \int_{w(t)}^{w(t+\Delta t)} \frac{c}{aw^{\alpha} - (b+c)w}dw = \ldots \\
&= \frac{c}{b+c}\left[w_t - w_{t+\Delta t} + \frac{4a}{3(b+c)}(w_t^{3/4} - w_{t+\Delta t}^{3/4}) + \frac{2a^2}{(b+c)^2}(w_t^{1/2} - w_{t+\Delta t}^{1/2})\right. \\
&\left. + \frac{4a^3}{(b+c)^3}(w_t^{1/4} - w_{t+\Delta t}^{1/4}) + \frac{4a^4}{(b+c)^4}\left(\log(a-(b+c)w_t^{1/4}) - \log(a-(b+c)w_{t+\Delta t}^{1/4})\right)\right] \quad [\mathrm{A3}]
\end{aligned}$$

Surplus energy. The surplus energy $SP(t+\Delta t)$ is given by the rate of energy acquisition accounted for the maintenance cost $cw^{3/4} - bw$ integrated over the period from t to $t+\Delta t$, expressed as a function of the somatic weights at the start $w(t)$ and at the end $w(t+\Delta t)$ of the time interval Δt ,. Assuming $\alpha = 3/4$ and $\beta = \gamma = 1$,

$$SP(t+\Delta t) = \int_{t}^{t+\Delta t} (aw^{3/4}(\tau) - bw(\tau))d\tau = \int_{w(t)}^{w(t+\Delta t)} \frac{aw^{3/4} - bw}{aw^{3/4} - (b+c)w} dw = ...$$

$$\frac{1}{3(b+c)^5}\left[12a^4c\left(\log\left(1-\frac{(b+c)}{a}w_t^{1/4}\right) - \log\left(1-\frac{(b+c)}{a}w_{t+\Delta t}^{1/4}\right)\right) + ...\right.$$
$$+12a^3c(b+c)(w_t^{1/4} - w_{t+\Delta t}^{1/4}) + 6a^2c(b+c)^2(w_t^{1/2} - w_{t+\Delta t}^{1/2}) + ...$$
$$\left. +4ac(b+c)^3(w_t^{3/4} - w_{t+\Delta t}^{3/4}) - 3b(b+c)^4(w_t - w_{t+\Delta t})\right] \qquad [A4]$$

By definition, the surplus energy is also given by
$SP(t+\Delta t) = R(t+\Delta t) + \left(w(t+\Delta t) - w(t)\right)$

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III

Modeling adaptation evolutionarily

Chapter 5

AN EVOLUTIONARY EXPLANATION OF SEXUAL SIZE DIMORPHISM: PREDICTIONS FROM A QUANTITATIVE MODEL CALIBRATED TO NORTH SEA PLAICE

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(Submitted manuscript)

Abstract

Sexual size dimorphism (SSD) is caused by different life-history tradeoffs faced by males and females. Since somatic growth is determined by the difference between energy acquisition and energy expenditures for reproduction, size dimorphism can be expected from different sex-specific energy acquisition or reproductive investment. We therefore hypothesize that SSD might be caused by male-specific behavioral investments into reproduction or by a different male-specific demand on energy acquisition, potentially caused by disparate diminishing returns on reproductive investment. We present a quantitative individual-based eco-genetic model (including life-history trait inheritance and environmental factors) parameterized for North Sea plaice to explore these potential mechanisms. As in many other fishes, but also in many arthropods and certain mammals, male plaice are smaller at age and reach sexual maturation earlier than females (reverse or female-biased SSD). The analysis demonstrates that the demand for a higher reproductive investment through behavioral investments is evolutionarily compensated by increased energy acquisition and delayed maturation, leading thus to larger male size. A mortality or/and a time cost of the behavioral investment has the same effect. In contrast, only a male-specific mechanism of diminishing returns on reproductive investment can sufficiently explain the observed reverse SSD. The logic can be inversed by an increasing return to obtain the opposite SSD. The diminishing return results when sperm competition is relatively weak and mating opportunities are limited in space and time. This is the case for plaice in particular but might be the case for many organisms reproducing in a lek system. Our findings here are therefore likely to be of wider generality.

Key words: *life-history evolution, reverse sexual size dimorphism, energy allocation, growth, behavioural investment, growth-survival tradeoff, diminishing fitness return, phenotypic plasticity*

Introduction

By definition the sexes are dimorphic. Despite the different sexual organs, sexes may differ in coloration, size, and the presence or absence of body parts used in courtship displays or for fights (e.g. feathers, horns, antlers or tusks). Female gametes (eggs), providing the energy reserves for the zygote, are energetically more costly and are thus the limiting resource in reproduction, whereas the males minimize this energetic cost and simultaneously maximize the number of gametes. Hence, as a male has enough sperm to fertilize eggs of several females, males compete for the availability of females. Reproductive success in males is therefore determined by the number of achieved matings, whereas in females it is limited by individual fecundity. The consequence of anisogamy is that males are fundamentally promiscuous and develop traits that are advantageous in competition, whereas females are fundamentally selective and might develop preferences for male traits (Bateman 1948). Sperm competition maintains anisogamy (Parker 1982) and therefore drives the evolution of dimorphism.

In many species including most mammals, the male is larger than the female (Fairbairn, et al. 2007). Larger males evolve because they win male-male combats (Leboeuf and Mesnick 1991, Fleming and Gross 1994) and dispose of larger resources to allocate for reproduction (Fleming and Gross 1994, Schütz and Taborsky 2000), hence monopolize more females and produce more offspring, and additionally suffer less predation mortality (Peterson and Wroblewski 1984, Brown, et al. 2004, Savage, et al. 2004). However, in other species such as many insects (Esperk, et al. 2007, Kelly, et al. 2008), spiders (Foellmer and Fairbairn 2005, Pekar and Vanhara 2006), fish (Pietsch 1975, Henderson, et al. 2003, Rennie, et al. 2008), and certain mammals (Schulte-Hostedde, et al. 2004, Fokidis, et al. 2007), the female is larger than the male (reverse SSD or female-biased SSD). This poses a paradox because smaller males are likely to have an evolutionary disadvantage (combat, energy for offspring production, predation) as long as there is some competition for females. On the individual level acquired energy is channeled towards growth and reproduction (Von Bertalanffy and Pirozynski 1952, Roff 1992, Stearns 1992). Lower energetic costs for sperm than for eggs therefore implies that males would have larger energy resources available that could be used for somatic growth, and one might consequently expect larger males. Assuming that reproduction is prioritized over growth in the individual energy flow, sex-specific differences in growth may result, everything else being equal, from a difference in energy acquisition or reproductive investment. Reverse SSD consequently has to follow from lower energy acquisition, or from higher expenditures on other things than somatic growth, in males. Higher expenditures may be caused by higher reproductive investment or an earlier start of this investment. Indeed, lower energy acquisition and growth efficiency in males have been measured in species with reverse SSD, whereas higher male investment is a potential explanation (Henderson, et al. 2003, Rennie, et al. 2008). In short, the following two mechanisms can be advanced for explaining reverse SSD:

- On one hand, males might have a higher reproductive investment due to higher behavioral activity costs. Males typically have to search and compete for females, trying to maximize the number of matings. Male reproductive success increases with this activity, whereas the energy dissipated in the male reproductive behavior is no longer available for somatic growth and might therefore cause a reverse SSD. There might also be a mortality and a time cost to the behavioral investment: The more a male is active during reproduction, the more likely he is exposed to predators, and the more time he invests for this activity, the less time he has to acquire food.

- On the other hand, males may require less energy than females if male size and reproductive investment are not that important to survive and be successful in reproduction. The male gametic cost, although increasing with sperm competition, is lower, if a few spermatozoa are sufficient to successfully fertilize a female's egg. Furthermore, the limitation of mating partners in space and time might cause increased male investment to pay-off less. In lek systems, reproductive efficiency is maximal at the peak of female availability but decreases with the spatio-temporal distance to the peak. This implies a diminishing return with an increase in male reproductive investment. As a consequence males might benefit from acquiring less energy by foraging less and thereby avoiding mortality due to predation or diseases.

However, no systematic evaluation of the relative merits of these competing mechanisms has been offered so far because the understanding of the implications for evolution of these mechanisms is lacking. In this study we do so by developing a quantitative model for North Sea plaice. A quantitative assessment has several advantages: model predictions can be compared to empirical estimates, a realistic setting accounts for the complexity of a particular life history, capturing which hypothesis applies in practice and not only in principle. North Sea plaice represents a prominent example of sexual size dimorphism, its life history is well documented because it is commercially important. Finally, we discuss the logic of the causality of SSD and how the findings for plaice can be extended to other species. Since plaice has been exploited for centuries (Rijnsdorp and Millner 1996), also the life-history adaptation to the fishing mortality and its effect on SSD are illustrated.

Material and methods

In this section, we will define the specific hypotheses to be evaluated in the study, outline the empirical data used and its sources, specify a full life-cycle model for North Sea plaice, and explain how this model was calibrated using the available empirical data. Equations used in data estimation and modeling are given in Table 1, therein occurring variables are explained in Table 2 and the constant parameter values, either taken from literature or optimized in the calibration, are shown in Table 3.

HYPOTHESES

We develop an individual-based eco-genetic model (see Dunlop, et al. 2009) with annual time increments including sex structure. Male and female individuals inherit both a male- and a female-specific value of each trait but only the value corresponding to their sex is phenotypically expressed (sex-limited expression). The evolving traits in females are energy acquisition rate, reproductive investment rate and the probabilistic maturation reaction norm (PMRN).

We evaluate the differential capacity of the two mechanisms described in the introduction. First, we test whether reverse SSD is caused by higher reproductive investment by considering a male-specific behavioral reproductive activity cost related to gains in reproductive success (hypothesis *H1*). Assuming a constant spawning activity over time, this additional behavioral cost will be proportional to the residence time at the spawning grounds (spawning duration) t_{sg}. As a refinement of *H1* we consider two further mechanisms that may constrain the spawning duration t_{sg} in males: a) since feeding is ceased during spawning, enlarging t_{sg} might be costly by reducing the time available for growth; b) because of the higher mortality rate during spawning, there is a mortality cost to enlarging t_{sg}. These tradeoffs are rather species-specific but likely play a role in many lek systems. We further consider an alternative hypothesis *H2* that the mating possibilities are limited and that male reproductive investment is cheaper than female reproductive investment, so that in males less investment is sufficient for successfully fertilizing the available eggs. In other words we consider a diminishing return on male reproductive investment, i.e. a decreasing marginal gain as male reproductive investment is increased. In summary, we explore the evolutionary consequences of the following mechanisms to affect male life history as potential causes for reverse SSD:

- *H1*: Male reproductive success increases with behavioral investment which is proportional to spawning duration and the rate of reproductive investment.

- *H1a*: The benefits of increased male behavioral investments trade off against the duration of the feeding period.
- *H1b*: The benefits of increased male behavioral investments trade off against survival probability during spawning.
- *H1ab*: The combination of the former three effects.
- *H2*: Male reproductive success gradually saturates with increasing reproductive investment, i.e. male reproductive investment exhibits a diminishing return.
- *H1ab2*: The combination of all likely applicable mechanisms used to calibrate the model.

The ecological and evolutionary consequences of these six settings are explored by application to an initial population with identical male and female life history.

EMPIRICAL DATA

North Sea plaice. Plaice (*Pleuronectes platessa*) are sexually dimorphic: females grow faster and become mature at larger sizes and older ages (Rijnsdorp 1992). Once a year the adults return from the feeding grounds in the central North Sea to the spawning grounds (Rijnsdorp and Pastoors 1995, Hunter, et al. 2004). During spawning the fish cease feeding (Rijnsdorp 1989). The population spawns during a time window of about three months (December-February) with a peak spawning intensity in mid-January. During this spawning window, male plaice remain in spawning condition twice as long as females (Rijnsdorp 1989). The mortality rate during spawning is about twice as high for males than for females, suggesting a difference in behavior that increases their exposure to predators (Beverton 1964, Rijnsdorp and Ibelings 1989) and to the fishing gear (Rijnsdorp 1993, Solmundsson, et al. 2003). Since plaice has been exploited intensively for more than a century (Rijnsdorp and Millner, 1996), its current life-history characteristics are likely affected by fisheries selection: the onset of maturation has decreased in the North Sea plaice stock, whereas growth patterns indicate that growth rates have decreased and reproductive investment increased (Rijnsdorp 1993, Rijnsdorp and Van Leeuwen 1996, Van Walraven, et al. 2009, Mollet, et al. in review.). These observations are in line with predictions from life-history theory (Stearns 1992).

Life-history estimation. Model predictions are fitted to three types of life-history observations:

- size at age
- reproductive investment
- probabilistic maturation reaction norms (PMRNs)

DATA			
maturation	Logistic regression to estimate the probability of being mature as a function of age and size		
	$\mathrm{logit}(m)=\beta_0+\beta_t t+\beta_l l+\beta_{tl} t\times l+\varepsilon$		(D1)
	Estimated probability of becoming mature as a function of the probability of being mature		
	$p_{\mathrm{mat}}(t,l)=\dfrac{m(t+1,l+\Delta l)-m(t,l)}{1-m(t,l)}$		(D2)
	Estimated scaling the width of the maturation probability		
	$\Omega=\dfrac{d}{2\mathrm{logit}(p_{\mathrm{mat}})}$		(D3)
MODEL			
energy allocation and growth	Change in unit of body weight by unit of time given by the difference between energy acquisition and expenditures, comprising of maintenance in juveniles and additionally reproductive costs in adults		
	$\dfrac{\partial w}{\partial t}=aw^{\alpha}-bw$	if juvenile	(1)
	$\dfrac{\partial w}{\partial t}=aw^{\alpha}-(b+c)w$	if adult	
	Body weight as a function of the body weight at a previous time step (here one year) following from the above differential equation		
	$w_{t+1}^{1-\alpha}(t)=\dfrac{a}{b}-\left(\dfrac{a}{b}-w_t^{1-\alpha}\right)e^{-b(1-\alpha)}$	if juvenile	(2)
	$w_{t+1}^{1-\alpha}(t)=\dfrac{a}{b+c}-\left(\dfrac{a}{b+c}-w_t^{1-\alpha}\right)e^{-(b+c)(1-t_{\mathrm{sg}})(1-\alpha)}$	if adult	
	Energy in terms of somatic weight that is channeled (stored or expended) into any investment associated to reproduction, following from the above differential equation		
	$\gamma(t+1)=\int_t^{t+1} cw(x)dx=\dfrac{c}{b+c}\left[w_t-w_{t+1}+\dfrac{4a}{3(b+c)}(w_t^{3/4}-w_{t+1}^{3/4})+\dfrac{2a^2}{(b+c)^2}(w_t^{1/2}-w_{t+1}^{1/2})+\dfrac{4a^3}{(b+c)^3}(w_t^{1/4}-w_{t+1}^{1/4})+\dfrac{4a^4}{(b+c)^4}\left(\log(a-(b+c)w_t^{1/4})-\log(a-(b+c)w_{t+1}^{1/4})\right)\right]$		(3)
	Length-weight relationship		
	$w(t)=k\,l(t)^{\beta}$		(4)
	Population biomass density dependence of individual energy acquisition		
	$a=\dfrac{a_{\mathrm{g}}}{1+(\delta_1 B)^{\delta_2}}$		(5)
maturation	Probability of becoming mature at a certain age and size (analog to PMRN in D1 & D2), with width proportional to PMRN intercept		
	$p_{\mathrm{mat}}=(l,t)=\dfrac{1}{1+e^{-(l(t)-l_{\mathrm{p50}}(t))/\Omega}}$, where $\dfrac{\Omega}{\mu(u)}=\mathrm{const.}$		(6)
	Linear relationship (PMRN intercept and sex-specific slope) of PMRN midpoints with age		
	$l_{\mathrm{p50}}(t)=u+s_{(\mathrm{f,m})}t$		(7)

Table 1: Model equations described in the text. Explanations of variables and constant parameters are given in Tables 2 & 3. By default lower case symbols indicate an individual phenotypic characteristic, subscript g refers to genetic trait values (phenotypic otherwise), subscripts f (female) and m (male) refer to sex-specific characteristics. Population characteristics are in upper case, individual characteristics in lower case.

reproduction	Annual recruitment as a function of total population fecundity	
	$N_\mathrm{r} = \dfrac{r_1}{1 + r_2 w_\mathrm{egg} \left(\sum_{i=1}^{N_\mathrm{f}} \gamma_i\right)^{-1}}$	(8)
	Female reproductive success given by the individual gonadic investment	
	$v_{\mathrm{f},i} = \dfrac{\gamma_i}{\sum_{j=1}^{N_\mathrm{f}} \gamma_j}$	(9)
	Male reproductive success given by the individual gonadic investment and behavioral trait	
	$v_{\mathrm{m},i} = \dfrac{f(\gamma_i) h(t_{\mathrm{sg},i})}{\sum_{j=1}^{N_\mathrm{m}} f(\gamma_j) h(t_{\mathrm{sg},j})}$	(10)
	Effect of behavioral trait on fitness	
	$h(t_\mathrm{sg}) = \dfrac{1}{1 + t_{50} / t_\mathrm{sg}}$	(11)
	Effect of gonadic investment on fitness	
	$f(\gamma) = \dfrac{1}{1 + \gamma_{50} / \gamma}$	(12)
	Proportionality of reproductive investment rate and behavioral trait in males	
	$c_\mathrm{m} = \theta t_\mathrm{sg}$	(13)
mortality	Predation mortality rate decreasing with size but increasing with energy acquisition rate (growth survival tradeoff)	
	$m_\mathrm{p} = \upsilon e^{\omega a_\mathrm{g}} w^{\eta}$	(14)
	Reproduction mortality rate increasing with the energy lost due to reproduction relative to body weight (reproduction survival tradeoff)	
	$m_\gamma = m_0 e^{\chi(\gamma / w)}$	(15)
	Starvation mortality rate if energy intake is too small to cover maintenance costs given by the energetic deficit relative to body size	
	$m_\mathrm{s} = \max\left(0, \rho \dfrac{a w^{3/4} - b w}{w}\right)$	(16)
	Fishing mortality rate determined by fishing effort and the selectivity of the fishing gear	
	$F = \dfrac{F_\mathrm{max}}{1 + e^{-\pi(l(t) - \lambda \psi)}}$	(17)
	Composition of male and female annual natural (*M*) and fishing (*F*) mortality rates	
	$M_\mathrm{m} = m_\mathrm{s} + m_\gamma + m_\mathrm{p} + \varphi_\mathrm{sg} w^{\eta} t_\mathrm{sg}$ $F_\mathrm{m} = F(1 - t_\mathrm{sg}) + \tau_\mathrm{sg} F t_\mathrm{sg}$ $M_\mathrm{f} = m_\mathrm{s} + m_\gamma + m_\mathrm{p}$ $F_\mathrm{f} = F$	(18)
inheritance	Genetic variance of trait *x* in the population assuming a constant *CV*	
	$\sigma_\mathrm{g}^2(x) = (CV \mu_\mathrm{g}(x))^2$	(19)
	Component of phenotypic variance of trait *x* in the population which is due to environmental variability, following from the definition of heritability	
	$\sigma_\mathrm{e}^2(x) = \dfrac{(CV \mu_\mathrm{g}(x))^2 (1 - h^2)}{h^2}$	(20)
fit	Combined bias, consisting of relative biases in size at age, PMRN midpoints and relative reproductive investment RSI=*γ*/*w*, minimized to fit model parameters	
	$\Delta = \sum_{i=1}^{10} \left(\dfrac{\overline{w_i}^{\mathrm{mod}} - \overline{w_i}^{\mathrm{emp}}}{\overline{w_i}^{\mathrm{emp}}} \right)^2 + \sum_{i=1}^{6} \left(\dfrac{\bar{l}_{\mathrm{p50}_i}^{\mathrm{mod}} - \bar{l}_{\mathrm{p50}_i}^{\mathrm{emp}}}{\bar{l}_{\mathrm{p50}_i}^{\mathrm{emp}}} \right)^2 + \sum_{i=6}^{10} \left(\dfrac{\overline{(\gamma / w)_i}^{\mathrm{mod}} - \overline{(\gamma / w)_i}^{\mathrm{emp}}}{\overline{(\gamma / w)_i}^{\mathrm{emp}}} \right)^2$	(21)

		Symbol	Description	Unit
structure		t	Time after birth (age)	yr
		w	Somatic weight	g
		l	Irreversible body length	cm
evolving traits	energy allocation	a a_{g}	Size-specific phenotypic and genetic (potential) energy acquisition rate	$\mathrm{g}^{1/4}\mathrm{yr}^{-1}$
		b	Size-specific (phenotypic) maintenance rate	yr^{-1}
		c	Size-specific (phenotypic) reproductive investment rate	yr^{-1}
		u	Probabilistic maturation reaction norm (PMRN) intercept	cm
		t_{sg}	Spawning duration	
emergent traits	maturation	p_{mat}	Age- and size-specific probability of maturation	-
		l_{p50}	Age-specific reaction norm midpoint or length at which maturation probability is 50%	cm
		Ω	Scaling of d for any length l and probability p_{mat}	cm
	reproduction	γ	Annual size-specific reproductive investment (energy spent for reproduction)	g
		$v_{\mathrm{f},i}$	Female Reproductive success of individual i	-
		$v_{\mathrm{m},i}$	Male Reproductive success of individual i	-
		$f(\gamma_i)$	Fitness return from reproductive energy investment	-
		$h(t_{\mathrm{sg},i})$	Fitness return from reproductive time investment	-
	mortality	m_{p}	Predation mortality rate including baseline predation and predation increasing with foraging (growth survival tradeoff)	yr^{-1}
		m_{γ}	Mortality rate due to reproduction (reproduction survival tradeoff)	yr^{-1}
		m_{s}	Starvation mortality rate	yr^{-1}
		M_{m}	Annual natural mortality rate in males	yr^{-1}
		M_{f}	Annual natural mortality rate in females	yr^{-1}
		F_{m}	Annual fishing mortality rate in males	yr^{-1}
		F_{f}	Annual fishing mortality rate in females	yr^{-1}
population	inheritance	$\mu_{\mathrm{g}}(x)$	Population mean of genetic trait value of x	see x
		$\sigma_{\mathrm{g}}^2(x)$	Genetic variance of trait x in population	see x
		$\sigma_{\mathrm{e}}^2(x)$	Part of phenotypic variance caused by environmental variability of trait x in population	see x
	numbers	B	Biomass of individuals (<25cm) competing for resources	g
		N_{f}	Number of adult females	-
		N_{m}	Number of adult males	-
		N_{r}	Number of recruits	-
	fit	Δ	Bias between model prediction and empirical data summed over certain ages i	-

Table 2: Model variables equations. These are either evolving individual trait values or emergent individual or population characteristics changing as a consequence of the evolving traits and the stochastic environment. Lower case symbols indicate an individual phenotypic characteristic, subscript g refers to underlying genetic trait values, subscripts f (female) and m (male) refer to sex-specific characteristics. Population characteristics are in upper case individual characteristics in lower case.

Size at age was estimated by combining survey, representing the younger age groups, with market data, representing the older age groups, since market data for younger age groups are biased due to minimal mesh and landing sizes. The sampling stratification was accounted for by weighting the observation by their respective representation in the true size distribution (Rijnsdorp 1993, Grift, et al. 2003, Van Walraven, et al. 2009).

The female reproductive investment was estimated from ripening ovary weights, adding 13% for additional migration costs (Mollet, et al. 2010). The model predictions of reproductive investment, given as somatic weight equivalent energy (see below), was converted to the corresponding energy equivalent somatic weight with the ratio κ of gonadic over somatic energy densities (plaice: $\kappa = 1.75$, Dawson and Grimm 1980).

Probabilistic maturation reaction norms (PMRNs) are defined as the individual probability of becoming mature conditional on age and size, (Heino, et al. 2002). Therefore, they can be used to estimate the maturation probability in dependence on the environmental maturation variability caused by variability in growth, in other words, to disentangle the phenotypic plasticity in maturation caused by variation in growth from the underlying genetically determined maturation. First, the maturity ogive m, i.e. the probability of being mature as a function of age t and length l (Eq. D1), is estimated from population level data by logistic regression. Second, the PMRN or probability of becoming mature for the first time is inferred from the ratio of fish that have matured to the ones that could have matured from age t to age $t+1$ (Barot, et al. 2004). The PMRN used here to compare data with model predictions is defined prospectively, i.e. as the probability of becoming mature in the subsequent year, in contrast to the retrospective PMRN, defined by the probability of having become mature in the previous year. The latter is more widely used in empirical studies (Dieckmann and Heino 2007), but since growth depends on maturity, the first is more accurate for modeling. The PMRN midpoints l_{p50}, i.e. the lengths at age at which probability of maturing is 50%, are inferred by interpolation. The PMRN width d, assumed constant across ages, is estimated from the difference between any two complementary probability-specific maturation lengths $d = l_{p_{\mathrm{mat}}} - l_{(1-p_{\mathrm{mat}})}$. Because these are symmetrical around the inflection point l_{p50}, the maturation scaling parameter (see Eq. 6) is proportional to the PMRN width d and can be scaled for any maturation probability p_{mat} (Eq. D3). The sex-specific fixed PMRN slope and width are estimated from the present population state.

MODEL DESCRIPTION

Energy allocation. The energy available for somatic growth in an individual's weight w is given by the difference between its energy acquisition aw^{α} and its energy expenditure bw for maintenance and, if the individual is mature, its energy expenditure cw for reproduction (Von Bertalanffy and Pirozynski 1952, West, et al.

2001, Banavar, et al. 2002). Based on a general life-history framework (West, et al. 1997) and species-specific estimates (Fonds, et al. 1992) we assume the rate of energy acquisition scales with body weight w to the power of $\alpha = 3/4$, whereas the rates of maintenance and reproductive investment scale with a power of 1. The asymptotic body weight is given by the ratio $w_\infty^{1-\alpha} = a/(b+c)$. Assuming equal scaling for rates of energy acquisition and maintenance (e.g. Lester, et al. 2004, $\alpha = 2/3$) does not lead to an asymptotic size without maturation and can not reproduce positive relationships between reproductive investment and size (not shown).

The continuous energy allocation model (Eq. 1) is converted into a discrete annual time step model by expressing body weight w_{t+1} as a function of weight at the start of a growth period w_t and the corresponding elapsing growing season (Eq. 2). Because feeding ceases during spawning (Rijnsdorp 1989), energy used for somatic growth and reproduction is allocated in adults during the period $1\text{yr} - t_{\text{sg}}$ (Eq. 2: juveniles $t = 1\text{yr}$, adults $t = (1 - t_{\text{sg}})$ yr). Reproductive investment γ in terms of somatic weight, given by integration of the rate of conversion of acquired energy to reproduction, is expressed as a function of the weight at the start and the end of the growing season (Eq. 3). Reproductive investment γ consists of a gonadic and a behavioral investment, but as long as we assume a constant proportionality, the partitioning is irrelevant for modeling. The length-weight relationship can be assumed constant (Eq. 4) as it applies only to one moment during the year, namely after reproduction, when all surplus energy has been withdrawn from the body tissue. The individual phenotypic size-specific energy acquisition rate a decreases with population biomass relative to the potential, genetic acquisition rate a_{g} because of intraspecific competition for food (Eq. 5). For North Sea plaice, density dependence is only important on the nursery grounds for fish of a size below 25cm (Rijnsdorp and Van Beek 1991, Bolle, et al. 2004) and thus $a = a_{\text{g}}$ above 25cm.

Size-specific rates of energy acquisition a and reproductive investment c evolve, while maintenance rate b is assumed constant and equal across individuals. In the annually variable trait expression reproduction is prioritized over growth: if no energy is available for growth, i.e., $aw^{3/4} - (b+c)w \leq 0$ (see Eq. 1), the reproductive investment parameter is adjusted to $c = aw^{-1/4} - b$ and the individual does consequently not grow ($\partial w / \partial t = 0$). If the acquired energy is not enough to cover maintenance costs, i.e. $aw^{3/4} - bw \leq 0$, the individual does neither grow nor reproduce and experiences starvation mortality (see section mortality).

Maturation. Sexual maturation is determined by a linear maturation reaction norm in the age-size space (Stearns and Koella 1986). The probability of maturing at a given age t increases logistically with size (Eq. 6). This probability increase is symmetrical around the inflection - or PMRN midpoint l_{p50}, i.e. the age-specific size at which the probability of maturing is 50%. The PMRN is therefore determined by an intercept u and a slope s defining the age-specific PMRN midpoints $l_{\text{p50}}(t)$ (Eq. 7), and the PMRN width d (see data section above), scaling the steepness around the inflection point $l_{p50}(t)$, assumed constant across ages but proportional to the PMRN intercept u when it evolves (see Eq. 6). For simplicity the PMRN slope s is assumed constant (Table 1).

Reproduction. The number of recruits surviving to age 1 is given by a Beverton-Holt-type stock-recruitment relationship depending on the total fecundity of all females that spawn during a season (Eq. 8). In females, reproductive success in terms of the relative offspring contribution is given by the individual fecundity relative to the total population fecundity (Eq. 9). Assuming a constant egg weight, relative fecundity is equivalent to relative gonad weight and hence to reproductive investment γ. In males, reproductive success increases with the reproductive energy investment γ and the spawning duration t_{sg} (Eq. 10), but the return of these might not be linearly increasing: 1) Since mating opportunities are restricted in time (Rijnsdorp 1989) and probability of successful mating decreases before and after peak spawning, there is a diminishing return on increasing spawning duration t_{sg} (Eq. 11); 2) Since the opportunities of total egg fertilizations are limited as such, and male reproductive energy investment for a successful strategy might be less costly, there is a diminishing return on the reproductive energy investment γ (Eq. 12). For simplicity we assume that the energy investment rate c during t_{sg} is constant (Eq. 13), and longer spawning duration therefore results in a higher energy investment γ.

Mortality. Natural mortality rate M includes baseline predation, predation caused by foraging (growth-survival tradeoff), diseases and parasites (constant), reproductive energy depletion (reproduction-survival tradeoff), reproductive behavioral costs (additional reproduction-survival tradeoff in males during spawning) and starvation.
Data and theory suggest that predation mortality rate in marine systems scales with body weight (Peterson and Wroblewski 1984, Brown, et al. 2004, Savage, et al. 2004). Since higher potential energy acquisition rate a_g induce higher foraging rates and therefore lead to higher risk of exposure to predators, the predation mortality rates increase with energy acquisition a_g (Eq. 14). No foraging ($a_g = 0$) results in baseline predation. Due to their spawning behavior males are more exposed to predators during spawning (t_{sg}) and hence suffer a constantly elevated predation mortality rate during spawning (see Eqs. 19).
Depletion of stored energy due to reproduction may result in lower survival probability (Hutchings 1994). Mortality due to reproduction is therefore assumed to increase with stored relative reproductive energy investment γ / w (Eq. 16). No reproduction ($\gamma = 0$) results in the constant baseline mortality for example through diseases.
If individuals do not acquire sufficient energy to cover the maintenance costs, i.e. if $aw^{3/4} - bw \leq 0$, they starve at an instantaneous mortality rate proportional to the rate of energy loss per unit of somatic weight (Eq. 16).

Fishing mortality rate F is described by a logistic curve determined by mesh size selection (Van Beek, et al. 1983), fishing effort and vulnerability to fishing gear (Eq. 17).

Due to their spawning activity, males are more vulnerable during spawning (Rijnsdorp 1993, Solmundsson, et al. 2003) and therefore suffer additional natural predation and fishing mortality. Because these additional rates only apply within the spawning duration t_{sg}, they are multiplied by the yearly fraction t_{sg} in the total annual natural and fishing mortality rate (Eqs 18). The annual survival probability is given for each sex by the exponential survival time expectation $e^{-(M+F)t}$ for the corresponding annual mortality rates and $t=1$.

Inheritance & expression. The evolving traits (a, c, u, t_{sg}) are inherited and expressed with random environmental variation. Parents for each offspring are selected with a von Neumann rejection algorithm (Von Neumann 1951) based on the reproductive success of potential fathers and mothers (Eq. 9 & 10). Offspring trait values are sampled from a normal distribution with the mid-parental values (average of parental traits) as mean and a variance given by a constant coefficient of variation CV (Eq. 19).

Genetic trait values are translated into phenotypically plastic realizations by sampling from a normal distribution with the genetic trait as mean and variance given by the environmental effect of phenotypic variability. Assuming heritability to be constant at a level generally expected for various life-history traits in fish (Roff 1991), the environmental effect of phenotypic variability is given by the narrow sense definition of heritability (Eq. 20).

MODEL CALIBRATION

Evolutionary equilibration. Although the modeled population is likely in a transient evolutionary state, the model is fitted to the historic population state of 100 years ago and to the present population state assuming that these states represent evolutionary equilibria. This has the advantage of avoiding the need for extrapolating available information backward or forward in time and speculating about the population's 'true' ancestral state or its eventual evolutionary fate. The assumption of evolutionary equilibration to the historical fishing pattern is likely to be adequate, since the population has been exploited at relatively low fishing mortality levels already for many centuries before surveys began.

Parameters to be estimated. To account for the changes in exploitation history, different levels of fishing mortalities $F_{\mathrm{max,H}}$ and $F_{\mathrm{max,P}}$ are fitted to the historic and present state, respectively. In addition to $F_{\mathrm{max,H}}$ and $F_{\mathrm{max,P}}$, parameters for which no estimates are available (Table 3) were adjusted to optimize the model's fit to the

	Symbol	Description	Reference	Value	Unit
energy allocation	α	Weight scaling of energy acquisition rate	(Fonds, et al. 1992) (West, et al. 1997)	0.75	-
	b	Size-specific maintenance rate	(Mollet, et al. 2010)	0.6	yr^{-1}
	k β	Length-weight relation (body condition and scaling, Eq. 4)	(Rijnsdorp 1990)	0.01 3.0	$g.cm^{-\beta}$ -
	δ_1 δ_2	Density dependence parameters (Eq. 5)	Optimization	$9.6\ 10^{-7}$ 10.82	g^{-1} -
maturation	Ω	Initial interquantile reaction norm width	(Grift, et al. 2003)	0.11	cm
	s_m s_f	Male PMRN slope Female PMRN slope	Data	-0.5 -1.34	$cm.\ yr^{-1}$
reproduction	w_{egg}	Egg weight	Data	$4.2\ 10^{-3}$	g
	r_1 r_2	Stock-recruitment parameters (Eq. 8)	(ICES 2006)	$8\ 10^3$ $1\ 10^6$	- -
	t_{50}	spawning period resulting in half-maximal male reproductive success	Optimization	0.11	yr
	γ_{50}	Reproductive investment resulting in half-maximal male reproductive success	Optimization	47.0	g
	θ	Proportionality constant for behavioral trait and reproductive investment rate	Optimization	1.45	yr^{-2}
natural mortality	ρ	Starvation mortality rate constant (Eq. 16)	(Schultz and Conover 1999)	-5.0	g^{-1}
	υ	Baseline predation mortality rate constant (Eq. 14)	Optimization	$1.2\ 10^{-4}$	$g^{1/4}.yr^{-1}$
	ω	Acquisition (growth) exposure risk (survival) tradeoff constant (Eq. 14)	Optimization	1.28	$g^{-1/4}.yr$
	η	Weight scaling of predation mortality rate (Eq. 14)	(Beverton 1964) (Peterson and Wroblewski 1984, Brown, et al. 2004, Savage, et al. 2004)	-0.25	-
	φ_{sp}	Male spawning exposure risk (Eqs. 18)	(Beverton 1964)	1.41	$g^{1/4}.yr^{-1}$
	m_0	Baseline mortality rate (Eq. 15)	Optimization	0.009	yr^{-1}
	χ	Reproduction survival tradeoff constant (Eq. 15), adjusted	Optimization	9.4	-
	M_f	Total natural female mortality rate at age 6 (Eqs. 18) constant used to adjust other parameters	(Beverton 1964)	0.1	yr^{-1}
fishing mortality	$F_{max,\ P}$ $F_{max,\ H}$	Fishing effort adjusted in the present (*P*) and historic (*H*) population state assuming evolutionary equilibrium	Optimization Optimization	0.37 0.27	yr^{-1} yr^{-1}
	τ_{sg}	Factor to differentiate male and female fishing mortality rate during spawning	(Rijnsdorp 1993)	1.75	-
	π	Fishing selectivity constant	(Van Beek, et al. 1983)	0.594	cm^{-1}
	λ	Mesh size selection factor	(Van Beek, et al. 1983)	2.2	-
	ψ	Mesh size	(Van Beek, et al. 1983)	8.0	cm
inheritance	CV	Coefficient of variation of evolving traits	(Grift, et al. 2003, Mollet, et al. 2010)	0.1	-
	h^2	Heritability of evolving traits	(Roff 1991)	0.24	-

Table 3: List of constant parameters in text and equations. Parameters for which empirical estimations were not available (i.e. no data available or no reference given) were tuned to optimize the fit to data, sequentially for females and males and for the present and the historic population state (see calibration).

present and historic population state. This included parameters in the mortality rates m_p (Eq. 14) and m_γ (Eq. 15) related to foraging and reproduction, namely υ, ω, m_0 and χ, the male-specific parameters θ (Eq. 12), t_{50} (Eq. 10), and γ_{50} (Eq. 11), and parameters for the density dependence of energy acquisition, δ_1 and δ_2 (Eq. 5).

Fitting procedure. The fitting procedure minimized the overall model bias in growth, maturation, and reproductive investment (Eq. 21), given by the sum of the squared relative deviations between model predictions (mod) and empirical data (emp) in size at age, PMRN midpoints, and reproductive investment relative to body size γ / w, over the ages for which the corresponding data estimates were most reliable (Eq. 21). Parameters were fitted in groups, through three consecutive steps that minimized this bias for (1) the female life history in the present population state (assuming that individual energy acquisition is almost not impaired by population density under heavy exploitation), for (2) the male life history in the present population state (assuming that the shared parameters in m_p and m_γ equally apply to both sexes), and for (3) the density dependence in the historic population state.

Parameters chosen directly. The female annual natural mortality rate M_f (Eqs. 19) for an average fish at age 6 (which corresponds to generation time) was set equal to the average annual mortality rate $M = 0.1\,\mathrm{yr}^{-1}$ used in the ICES stock assessment (ICES 2006). Since density dependence likely plays a minor role in the heavily exploited present population, the ratio $(a / a_\mathrm{g})_\mathrm{P}$ of energy-acquisition reduction for the present population state was set close to 1 (0.98; the absolute value only matters in relation to the subsequently fitted value for the historic state $(a / a_\mathrm{g})_\mathrm{H}$, see below). An accelerating function with two parameters had to be used in the mortality rates m_p and m_γ related to foraging and reproduction, because with linear tradeoffs the life history evolves towards too high trait values in size and reproductive investment (results not shown). Consequently, different combinations of the two parameters in m_p and m_γ can lead to the same realized mortality levels for given trait values. We therefore assumed equal contributions of mortality rates related to foraging and reproduction for average-sized reproducing females at age 6, $m_\mathrm{p} / m_\gamma = 1$, thereby reducing the number of parameters to be estimated by one. Choosing a more extreme partitioning of the natural mortality, such as $m_\mathrm{p} / m_\gamma = 0.1$ or $m_\mathrm{p} / m_\gamma = 10$, did not significantly affect any results of this study (results not shown).

Parameters estimated for female life history. Based on these assumptions, the three parameters $F_{\mathrm{max,P}}$, ω in m_p (Eq. 14), and χ in m_γ (Eq. 15) were optimized (Eq. 21) by an exhaustive grid search with step sizes of 10^{-2}, 10^{-2} and 10^{-2} in the respective units.

Parameters estimated for male life history. Conditional on these parameters, the male-specific parameters t_{50} (Eq. 10), γ_{50} (Eq. 11), and θ (Eq. 12) were optimized by an exhaustive grid search with step size of 1, 10^{-2}, and 10^{-2} in the respective units. There are no reliable estimates for male reproductive investment but for the related behavioral trait (Rijnsdorp 1989). Instead of the relative deviation in relative reproductive investment γ / w (Eq. 21), the relative deviation of t_{sg} from 0.25 (3 months) was therefore used.

Parameters estimated for density dependence. Conditional on these parameters, the ratio $(a / a_{\mathrm{g}})_{\mathrm{H}}$ (which determines the reduction of energy acquisition due to population density; Eq. 5) and the fishing mortality $F_{\mathrm{max,H}}$ were fitted to the historic population state by minimizing the bias in size at age and PMRN midpoints (Eq. 21; other empirical estimates are not available for this period) through an exhaustive grid search with step sizes of 10^{-2} and 10^{-2} in the respective units. The parameters of density dependence, δ_1 and δ_2, were solved from the relative reductions $(a / a_{\mathrm{g}})_{\mathrm{P}}$ and $(a / a_{\mathrm{g}})_{\mathrm{H}}$ in energy acquisition and the corresponding population biomasses (for fish smaller than 25cm, see Eq. 5).

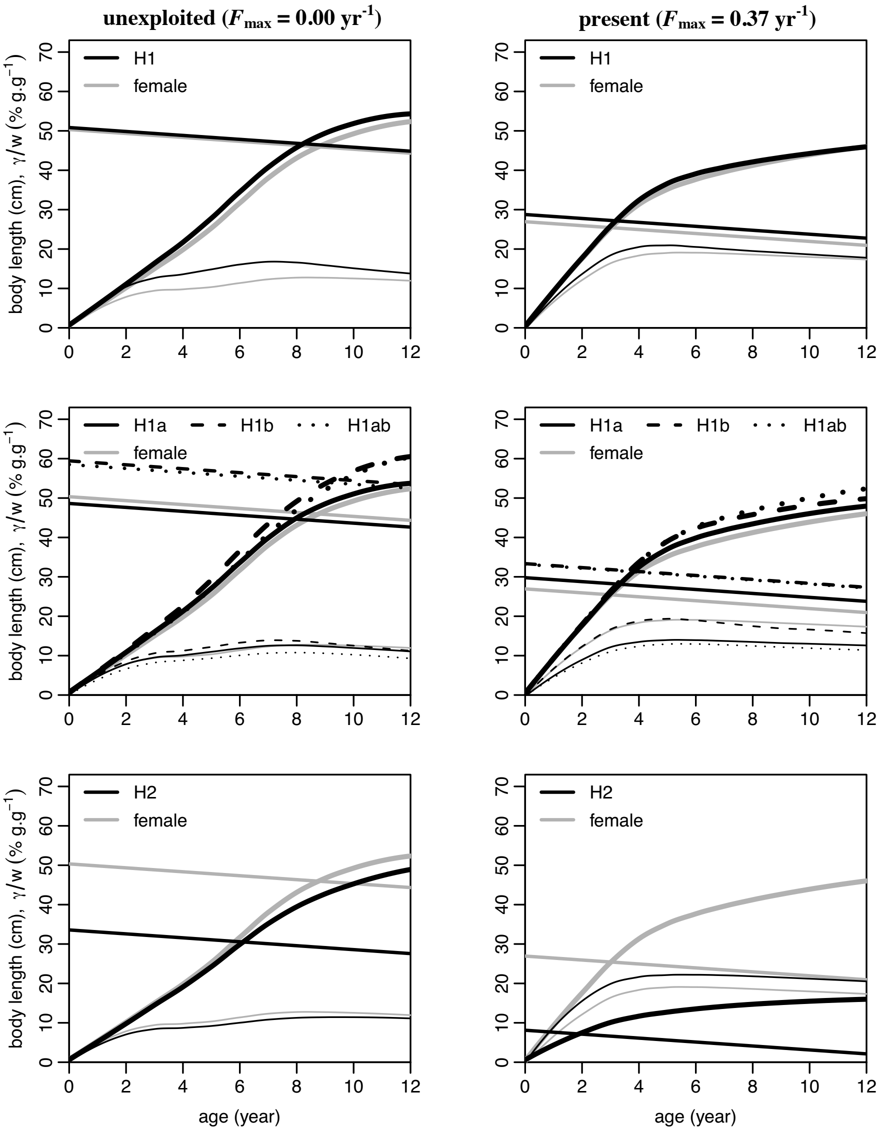
Results

Reconstruction of SSD. The effects on life-history of the respective hypotheses potentially explaining SSD were explored at evolutionary equilibrium with and without fishing. Fig. 1 shows the life history in terms of size at age, PMRN midpoints and relative reproductive investment γ / w for females resulting from the competing hypotheses respectively without ($F_{\max}$ =0.00) and with fishing ($F_{\max}$ =0.37). The values of the corresponding four evolving traits spawning duration t_{sg}, energy acquisition rate a, reproductive investment rate c and PMRN intercept u, are given in Table 4.

- *H1: Higher demand on reproductive investment due to behavior, eventually trading off against growing time (H1a), mortality (H1b) or both (H1ab):*

Assuming a reproductive benefit of enlarging spawning duration t_{sg} (Eq. 11) and accordingly increased reproductive allocation rate c_{m} (Eq. 13, see *H1*) results in a higher relative reproductive investment γ / w (Fig. 1). As a consequence, energy acquisition rate increases and maturation is postponed as reflected in the higher PMRN intercept u (Fig. 1, Table 4). The refinements to this reproductive benefit of increased spawning duration by including a tradeoff against time available for growth (*H1a*) or a tradeoff against increased mortality due to prolonged exposure during spawning to predators and, in the exploited population, to fishing gear (*H1b*), have similar consequences: increased energy acquisition and postponed maturation relative to the female life history. Whereas the male relative reproductive investment

γ / w is typically higher in the unexploited population under the *H1*-hypothesis and its refinements (*H1a*, *H1b* and *H1ab*, Fig. 1), it is typically lower in the exploited population than the female relative reproductive investment γ / w.



unexploited ($F_{\max}$ = 0.00 yr^{-1}) **present ($F_{\max}$ = 0.37 yr^{-1})**

Figure 1: Size at age (thick), PMRN midpoints (medium) and relative reproductive investment γ / w in % (thin), scaled to female gonadic over somatic weight to be comparable with GSI, of females (gray) and mechanisms from hypotheses potentially leading to reverse SSD (black): higher reproductive investment (*H1*), tradeoffs with growing time (*H1a*) and mortality during reproduction (*H1b*, dashed), the combination of these (*H1ab*, dotted) and the diminishing return of male reproductive investment (*H2*). The effects of these mechanism are given for the unexploited ($F_{\max} = 0.00$, left panel) and the exploited ($F_{\max} = 0.37$, right panel) population.

The same applies to the evolving allocation rate to reproduction c_m . Despite these differences the size at age is either on a similar level or higher, and the maturation is postponed relative to the female life history. Also without exploitation, the effects of increased energy allocation rate and higher PMRN intercept, leading to larger sizes and postponed maturation, dominates over the effect of increased energy allocation to reproduction leading to smaller size. In summary, a higher demand by reproductive investment is evolutionarily compensated by increased energy acquisition and postponed maturation leading to larger size at age, and does therefore not lead to a decrease in growth investment as hypothesized.

		female	***H1***	***H1a***	***H1b***	***H1ab***	***H2***
Unexploited $F_{\max}$= 0.00	t_{sg}	0.125	0.282	0.242	0.228	0.191	0.125
	a	5.70	5.77	5.78	5.88	5.89	5.50
	c	0.235	0.288	0.267	0.239	0.214	0.231
	u	41.9	50.8	48.6	59.4	58.5	33.6
Exploited $F_{\max}$= 0.37	t_{sg}	0.125	0.342	0.271	0.314	0.241	0.125
	a	5.88	5.93	5.92	6.00	6.02	2.86
	c	0.421	0.452	0.370	0.411	0.329	0.47
	u	25.3	28.8	29.8	33.3	33.2	8.12

Table 4: Evolutionary stable trait averages of evolving life history traits resulting from respective hypotheses to explain reverse SSD in an unexploited population ($F_{\max} = 0.00$) and under exploitation ($F_{\max} = 0.37$), compared to average female traits. *H1a* and *H1b* represent refinements of the hypothesis *H1* that a higher male reproductive investment would lead to reverse SSD through tradeoffs with time for growing (*H1a*) and mortality during reproduction (*H1b*), *H2* represents the hypothesis of a decreasing relative return from male reproductive investment (see text). The combination of all effects *H1ab2* is used to fit empirical data (see Table 5)

- *H2: Diminishing returns from reproductive investment in males:*

The diminishing return from male reproductive investment into offspring results in decreased energy acquisition rates and precocious maturation (Fig. 1, Table 4). Exploitation amplifies the magnitude of these differences. The effects on energy allocation and maturation lead to significantly smaller size at age and a lower PMRN (Fig. 1). In the unexploited population, the male reproductive allocation rate c_m is higher

than in females, but in the exploited population, the difference is reversed. The higher c_{m} results in a higher relative reproductive investment γ / w in males than in females in the exploited population. Despite the higher investment the male size at age and PMRN are significantly lower than in females (Fig. 1).
The reverse SSD is thus a consequence of reduced energy acquisition and earlier maturation caused by a lower demand on reproductive investment in males than in females, irrespective of the relative reproductive investment γ / w. The *H2*-mechanism is the only cause for reverse SSD and this mechanism alone is sufficient to generate lower size at age and earlier maturation in males.

- *H1ab2: Combined effects*

Because of the empirical evidence for the mechanisms included in the *H1*-hypotheses (Rijnsdorp 1989) and the need to include the mechanism of the *H2*-hypothesis to generate reverse SSD, both mechanisms were combined to fit empirical data (*H1ab2*, Fig. 2).

Fig. 3 shows the average mortality rates per age class in the historic and present population for males and females. Males suffer higher overall mortality because of the exposure to predators and to fishing during spawning but lower foraging- mortality because of lower energy acquisition rates and lower mortality due to reproduction because of lower reproductive investment. The differences in natural mortality caused by exploitation arise mainly from changes in energy acquisition rate affecting the growth-survival tradeoff (Eq. 14) and changes in reproductive investment affecting the reproduction-survival tradeoff (Eq. 15).

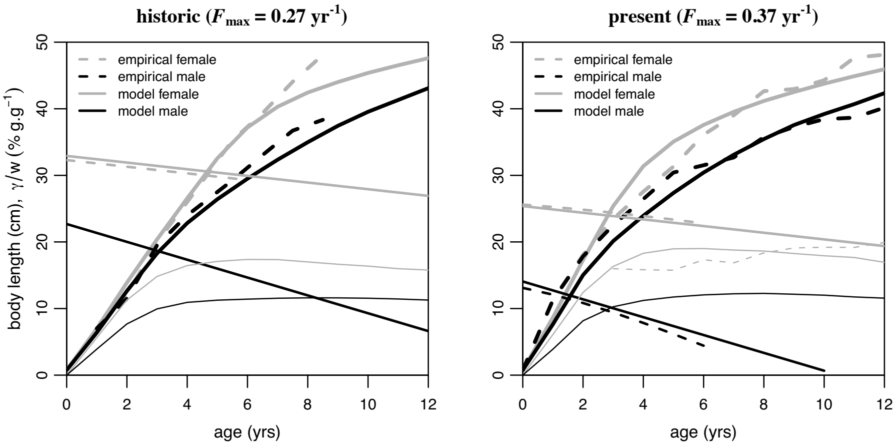


Figure 2: Average size at age (thick), PMRN midpoints (medium) and relative reproductive investment γ / w in % (thin), scaled to female gonadic over somatic weight to be comparable with GSI, from empirical estimation (dashed) and model predictions (solid) for females (gray) and males (black) of the present and the historic population. All potential SSD mechanisms were combined (*H1ab2*) and estimated sex-specific PMRN slopes were used for the fitting.

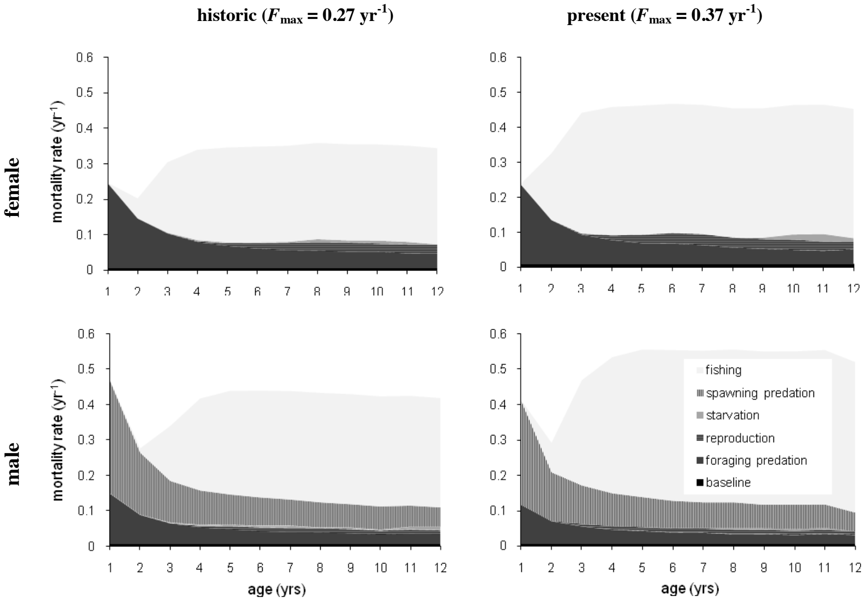


Figure 3: Average mortality rates per age class for males and females in the present and the historic population state. Males suffer higher overall mortality due to the exposure to predators and to the fishing gear during spawning (fishing and spawning), higher predation mortality due to smaller size at age (predation), but lower foraging mortality due to lower energy acquisition rates (foraging) and lower reproduction mortality due to lower reproductive investment (reproduction).

Effects of exploitation. Changes of some life history traits or population characteristics between the historic and present population state are shown in Table 5. The phenotypic energy acquisition rate a increased mainly due to relaxation of density dependence (Eq. 1). Selection on the genetic trait values of energy acquisition a_g was weak (1-2%) and in opposite direction for the sexes, namely towards higher values in females and towards lower values in males (Table 5). Selection is stronger on the reproductive investment rate c and the PMRN intercept u (Table 5). The rate of reproductive investment c increases in both sexes and males correspondingly extend spawning duration t_{sg} under higher exploitation despite the associated higher mortalities in males. Relative reproductive investment γ / w (Eq. 2 & 3), increases in females, but decreases in males. Selection is strongest on maturation traits towards earlier maturation at smaller sizes, and is more important for males than for females (Table 5). The size at younger ages increases (e.g. age 6) but it decrease for older ages (e.g. age 10, Fig. 2, Table 5).

Model fit. Fishing effort set to $F_{\max,P} = 0.37$ and $F_{\max,H} = 0.27\,\mathrm{yr}^{-1}$(Eq.22) maximized the goodness of fit Eq. (21) to the present and historic population state respectively. The model predicts larger size at age for females for the intermediate ages just after

maturation and slightly lower sizes over all younger ages for males than the sizes empirically observed (Fig. 2).
The model suggests that the SSD for certain life stages, especially for younger ages, was less important in the historic than in the present population state (Fig. 2, Table 5), and thus that increased exploitation would have enhanced SSD. For the PMRN, the necessary historic male data was not available for this comparison.

Sensitivity analysis. The effect of a 10% change in parameters on emergent characteristics (size, relative reproductive investment γ / w, size at maturation) is given for those parameters for which the change in at least one of the characteristics is ≥10% for females or males (Fig. 4). The life history is most sensitive for changes in the length-weight scaling exponent β (Eq. 4), maintenance b (Eqs 1-3), weight-scaling of predation mortality η (Eq. 14), growth-survival trade off υ and ω (Eq. 14), and the parameters related to fishing, $F_{\max}$ and $\lambda\psi$ (Eq. 17). Changes that result in larger size at age also result in higher reproductive investment and later maturation and *vice versa.* A 10% increase in each of these parameters results in a lower size, an earlier maturation and a slight increase in relative reproductive investment γ / w and *vice versa* (Fig. 4). For males, the life history is additionally sensitive to the proportionality constant from behavior to reproduction allocation θ (Eq. 13) and the diminishing return constant γ_{50} (Eq. 12). An increase in the proportionality constant θ (Eq. 9) results in lower size, earlier maturation and relatively higher reproductive investment. An increase in the diminishing return constant γ_{50} (Eq. 12) results in larger size and later maturation. The direction of these effects are the same for males and females except for the predation mortality (η) which might be an indirect effect caused by the additional spawning mortality in males (see Eq. 18). Increasing θ increases reproductive investment rate relative to the behavioural trait and thus decreases size at age, increasing γ_{50} increases the importance of having a large reproductive investment and hence the importance of being large.

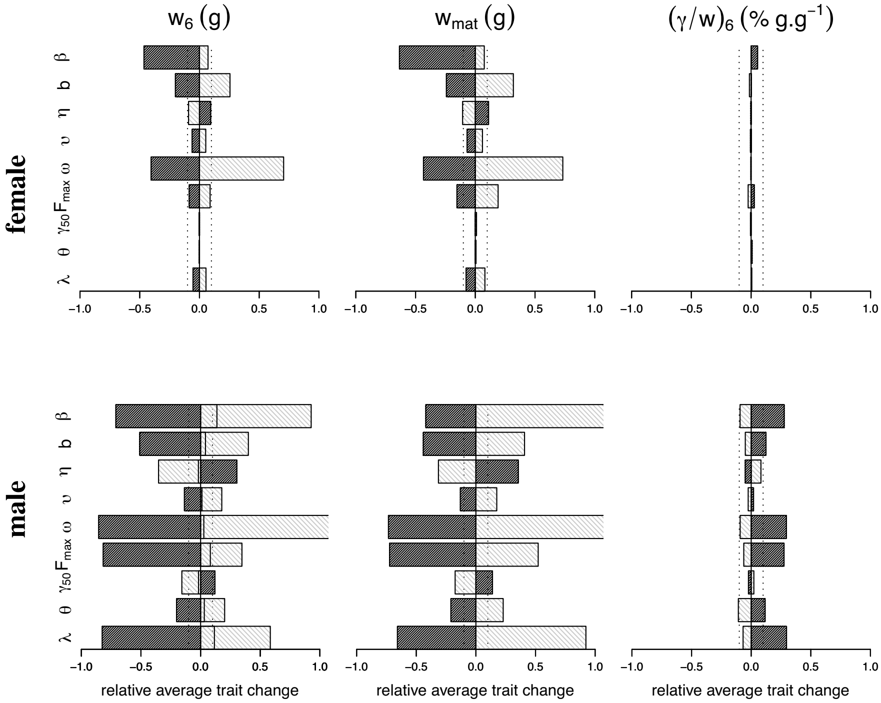


Figure 4: Sensitivity analysis: Effects of 10% changes in model parameters on size at age 6, relative reproductive investment γ / w at age 6, age and weight at first maturity a_{mat} and w_{mat} (light: 10% decrease - dark: 10% increase in the parameter) for females and males. Displayed are only those parameters that have an effect of >10% for at least one of the shown traits in the female or male life history.

	description	symbol	sex	historic	present	% change in time	% change in SSD
Evolving traits	Time spent for spawning	t_{sg} [yr^{-1}]	f m	0.125 0.208	0.125 0.223	+ 0 + 7	+ 18
	Genetic energy acquisition rate	a_{g} [g$^{1/4}$ yr^{-1}]	f m	5.83 5.41	5.91 5.31	+ 1 - 2	+ 43
	Phenotypic energy acquisition rate of fish < 25cm	a [g$^{1/4}$ yr^{-1}]	f m	4.19 4.04	5.72 5.15	+ 37 + 27	+ 280
	reproductive investment rate	c [yr^{-1}]	f m	0.37 0.29	0.42 0.32	+ 14 + 10	+ 25
	PMRN intercept	u [cm]	f m	32.8 22.6	25.6 14.0	- 22 - 38	+ 13
Emergent traits	Population number	N [1]	f m	19320 19888	11776 12114	- 39 - 39	- 40
	fraction of adults	f_{adl} [1]	f m	0.15 0.22	0.22 0.38	+ 47 + 73	+ 128
	Weight (at age 6)	w_6 [g]	f m	564 293	597 309	+ 5 + 5	+6
	Weight (at age 10)	w_{10} [g]	f m	1045 641	900 616	- 14 - 4	- 30
	Length (at age 6)	l_6 [cm]	f m	37.1 29.6	38.2 30.5	+ 3 + 3	+ 3
	Length (at age 10)	l_{10} [cm]	f m	46.0 38.5	44.0 38.6	- 4 + 0	- 28
	Average annual relative growth rate (until age 6)	$(\Delta w/w)_6$ [yr^{-1}]	f m	0.64 0.60	0.58 0.58	- 9 - 3	-100
	Age at 1st maturity	t_{mat} [yr]	f m	5.6 4.4	4.1 3.1	- 27 - 30	- 17
	Length at 1st maturity	l_{mat} [cm]	f m	35.2 24.2	31.2 19.9	- 11 - 18	+ 3
	Weight at 1st maturity	w_{mat} [g]	f m	530 173	352 91	- 34 - 47	- 27
	Relative reproductive investment (at age 6)	$(\gamma/w)_6$ [g.g^{-1}]	f m	0.167 0.112	0.182 0.110	+ 9 - 2	+ 31
	Cumulative juvenile mortality	$\overline{M}_{\mathrm{j}}$ $[t_{\mathrm{mat}}^{-1}]$	f m	0.121 0.082	0.108 0.045	- 11 - 45	+ 62

Table 5: Population averages of evolving traits and other emergent characteristics of males (m) and females (f) at evolutionary and dynamic equilibrium for the historic and the present population and the relative change in these from historic to present population in %.

Discussion

Main finding. Differences in male and female life histories associated with the female-biased SSD, i.e., smaller size and earlier maturation of males, could only be obtained when assuming a diminishing return in offspring contribution of male reproductive investment (hypothesis *H2*). Because increasing reproductive investment pays off relatively less in males than in females, the males acquire less energy, become mature earlier and remain smaller. In contrast, a demand on higher reproductive investment caused by a higher spawning activity cost in males (hypotheses *H1*, *H1a*, *H1b*, *H1ab*), does not lead to the evolution of smaller body size, but to an increased energy acquisition rate, delayed maturation and similar body size. The extend to which a higher demand on reproductive investment will be compensated for by a higher energy acquisition rate will depend on the strength of the growth-survival tradeoff. However, since mortality in this study accelerates disproportionally with energy acquisition rate (see Eq. 14) and since increasing this acceleration did not affect the main finding, we expect that the result that a higher demand on reproductive investment will be compensated by higher energy acquisition rates is general.

Logic of the diminishing return. There are several mechanisms that may explain a diminishing return on male reproductive investment. First, the time window in which fish can reproduce successfully is restricted (Cushing 1990). Therefore, the marginal gain of increasing spawning duration and reproductive investment (assuming a constant spawning intensity) decreases. Second, in the absence of sperm competition the individual reproductive success for a given investment will be increased and hence the the effect of diminishing return of male reproductive investment will be enhanced. Third, if offspring survival is correlated to maternal size (Trippel and Neil 2004), it will also be correlated to reproductive investment. A high number of egg batches, being proportional to body and gonad size, will increase the probability that a batch of larvae will encounter favorable environmental conditions. This would rather correspond to an increasing return of female reproductive investment, but since the sexes are modeled relatively to each other, this would be qualitatively the same as a diminishing return of male reproductive investment. Limitation of mating possibilities in space and time, low sperm competition, high fertilization probability and maternal size effects will thus enhance the diminishing return of males's reproductive investment (the *H2*-mechanism).

Diminishing returns of male reproductive investment (*H2*) might be the cause of reverse SSD in other teleost species where mating opportunities are limited. A mating system in which there is a strong male-male competition to fertilise eggs, and an increasing return on male reproductive investment with body size, a male-dominated SSD will evolve. In other words, the logic of the diminishing return can be inversed to obtain male-dominated SSD. If there is a size advantage in reproduction, sneaking of smaller males might arise as an alternative evolutionarily optimal strategy (Parker

1990, Fleming and Gross 1994), but only conditional on the predominance of larger successful males, which might lead to bimodal trait distributions.

Case-specific refinements. Mortality on the spawning ground leads to increased energy acquisition and delayed maturation. Males only take the risk of the increased mortality on the spawning ground (natural and fishing) if this risk is balanced by sufficiently high reproductive success, which is attained with relatively large size. This is in line with the finding that later maturation is observed when fisheries harvest only on the spawning grounds compared to harvesting the same population on the feeding grounds (Heino, et al. 2002). Hence, in the current situation for plaice, the spawning mortality prevents the males' sizes from decreasing to even smaller sizes.

Under exploitation, the lower relative reproductive investment γ / w (i.e. the energy used for reproduction relative to the energy content of the soma γ / w) observed in male plaice (Van Walraven, et al. 2009) could not be explained by the diminishing return effect alone (Fig. 1). In this case the lower relative male investment is explained by the time cost (*H1a*) in combination with mortality avoidance (*H1b*) leading to a reduced spawning duration t_{sg} and reduced reproductive investment rate c_{m}. Reproductive investment not only depends on the reproductive allocation rate c but also on the other metabolic rates (a and b) and on the weight change between the spawning seasons and thus also on the onset of maturation (see Eq. 3). Since energy acquisition rate a and onset of maturation t_{mat} both increase under the respective assumptions in *H1a*, *H1b* and *H1ab*, the decrease in relative reproductive investment γ / w must be due to the decrease in reproductive investment rate c_{m}. The loss in size due to a reduced growing season and the mortality due to spawning behaviour in *H1a* and *H1b* respectively are minimized by keeping the spawning season t_{sg} and correspondingly the reproductive investment rate c_{m} low. Although the dimorphism in body size at age and age and size at maturation can be obtained only with hypothesis *H2*, the mechanisms explored in hypotheses *H1a* and *H1b* and *H1ab* might be indispensable to understand specific cases where relative reproductive investment is lower in males than females.

Fisheries-induced selection and SSD. Fisheries-induced selection leads to a faster pace of life, namely to higher metabolic rates of energy acquisition a and reproductive investment c and an earlier onset of maturation or a lower PMRN intercept u. The decrease in the PMRN and the increase in reproductive investment lead to smaller body size at older ages, consistent with predictions from similar models (Dunlop, et al. 2009, Enberg, et al. 2009). Exploitation releases the density-dependent competition for food, restricted in this study to fish <25cm, and leads to higher phenotypic acquisition rates and an increase in body size of young fish. The effect on the increase of metabolic rates a and c is stronger for females, whereas the effect on the decrease in the maturation age and size is stronger in males. Exploitation thus enhances the differences in metabolic rates and maturation between males and females and for certain life stages it will also enhance the difference in body size.

Sex-specific effects on energy acquisition rate a: The selection for higher rates of energy acquisition a in females may be due to the selection for a higher reproductive investment. In males, the change in reproductive investment due to fishing is less important and so is the selection on the energy acquisition rate a. This may explain why the genetic energy acquisition rate a_g in males, in contrast to females, does not increase (Table 5).

Sex-specific effects on reproductive investment rate c: The increase in male reproductive investment rate c_m is less important than in females because it is proportional to the spawning duration t_sg. Increasing c_m therefore results in a reduced growing season (see *H1a*) and a higher mortality cost in males due to additional spawning mortality (see *H1b*). If the spawning duration t_sg was not coupled to the reproductive investment rate c_m (see Eq. 9), it would decrease to avoid additional spawning mortality (result not shown). Since reproductive investment rate c_m and spawning duration t_sg nevertheless increase due to exploitation, the fitness advantage of increased c_m must be more important than the advantage of mortality avoidance through a shorter spawning duration t_sg.

Sex-specific effects on the maturation trait u: The effect of exploitation to mature earlier is stronger in males than in females because in males the advantage of being a large spawner is discounted (see *H2*) and the advantage of delaying maturation, once exceeded the size targeted by predators (Henderson, et al. 2003, Rennie, et al. 2008), becomes relatively small under exploitation. The effect of spawning mortality (see *H1b*), leads to delayed maturation. But in combination with the diminishing return of male reproductive investment (see *H2*), this effect of spawning mortality might become opposite because the male mortality cost of reproduction (spawning mortality) becomes higher through fishing: Since the advantage of being a large spawner is not important it might become more advantageous to be a small spawner because additional spawning mortality can then be avoided. The effect will depend on the balance between the mortalities caused by spawning, predation and exploitation and might differ in other species-specific cases.

Sex-specific effects on size at age: The effect of exploitation to increase size at younger ages but to decrease size at older ages is more important for females than for males, which is caused by the respectively positive and negative selection for the genetic energy acquisition rate a_g. In contrast, the difference in size for later life stages between males and females becomes smaller, because the difference in the asymptotic size given by $a/(b+c)$ becomes smaller. This is a consequence of the more important increase in reproductive investment rate c (+14%) in females compared to males (+10%, Table 5). Because older fish are rarely observed under high exploitation rates, the observation from the younger fish in practice is more likely to confirm that exploitation enhances SSD.

Model fit to plaice data. The model overestimates female size at age and underestimates male size at age in the two years after maturation (Fig. 3). Empirical data suggest that male and female growth are similar up to age 5 and only thereafter the male growth lags behind, whereas in the model males grow slower from the beginning. Males might reduce their energy acquisition only after the onset of maturation. Relatively faster growth rates before maturation reduce the predation risk (Henderson, et al. 2003, Rennie, et al. 2008). If male size after maturation is already beyond the vulnerability size window for predators, high energy acquisition might pay off relatively less only after maturation, because that is where the effect of diminishing returns from reproductive investment kicks in. A switch in energy acquisition after maturation would thus make biological sense and improve the fit to data. However, evidence on these processes is scarce and we were interested in the general pattern for effects on energy acquisition, which is likely to be the same with or without such a switch.

On the individual level the relative reproductive investments γ / w increase with age and size. On the population level however, the investment decreases with age (Fig. 1 & 2), which is due to a demographic effect: the cost of reproduction (Eq. 15) induces a negative selection differential on reproductive investment. Consequently, the average reproductive investment within a cohort decreases over the ages.

The model predicts a more important decrease in the plaice PMRN for males (-38%) than for females (-22%). An earlier study using the same data set presented a more important change in the female PMRN of about -50% (Van Walraven, et al. 2009). The differences are due to different definitions of the PMRN: In this study the PMRN was defined prospectively and then refitted with a constant slope to period-specific maturation-critical ages, whereas in the other study it was defined retrospectively allowing for curvilinearity. When comparing PMRN estimates from different PMRN definitions, it has to be considered that the maturation-critical ages changed through time. This study offers for the first time an estimate of the relative change in the male PMRN between the early 1900s and the present, as there are no estimates of male PMRN estimates for the earlier period.

Model limitations. The model is built under the assumptions that the historic and current populations are at evolutionary equilibrium under a certain constant fishing selectivity. This assumption is certainly wrong. The ongoing decrease in PMRN (Grift, et al. 2003, Van Walraven, et al. 2009), suggest that the current population is still in a evolutionary transient state. Also fishing selectivity has changed during the last century (Rijnsdorp and Millner 1996). The parameter estimates would change if the assumption of an evolutionary equilibrium state is relaxed, but there is no alternative as the evolutionary initial and final state are unknown. The retrospective prediction of the unexploited population or the prospective prediction of the evolutionary endpoint therefore depends on the assumptions made in the model calibration. However, in this application we focused on the causes of SSD in the current situation and the assumption of evolutionary equilibrium was therefore sound.

Conditional on the fit to data, the model indicates that the historic state of the population was also already adapted to some level of exploitation ($F_{\max,H} = 0.27$). Indeed, exploitation rates were already well above natural mortality rates around 1900 (Rijnsdorp and Millner 1996). It might however also be that the estimate of natural mortality of M=0.1yr^{-1} is too low. A higher estimate of M would have resulted in lower estimates of $F_{\max}$ and furthermore, the growth-survival and reproduction-survival tradeoffs might have been modeled linearly instead of being accelerating functions.

Another alternative functionality not considered in our model involves different properties of the male and female gonad. The building up of gonads might be restricted by other factors than stored energy. Male gonad consists of a much higher density of DNA and therefore essential elements such as phosphate might be limiting in the stoichiometry of sperm produced in the restricted time of the spawning events. If so, an additional currency for energy should be considered.

Conclusions. To our knowledge this is the first study to explore the different evolutionary origins of SSD in a realistic ecological setting applied to a real population. It might provide an evolutionary explanation for female-biased SSD in many teleost species that display a similar mating behavior as North Sea plaice. We reject the hypothesis that males in this species are smaller due to higher activity costs. The SSD is caused by the relatively smaller benefit of increased reproductive investment in males. It is therefore likely that reproductive investment is generally smaller in males of fish with reverse SSD.

The study also presents the first of these type of models which is objectively fitted to age-specific observations of size, maturation probability and reproductive investment. Since it captures demographic processes realistically and is able to reproduce the observations for both the current and the historic situation in North Sea plaice, it provides the necessary tool for an evolutionary impact assessment (Jørgensen, et al. 2007).

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Chapter 6

A RECONSTRUCTION OF THE FISHERIES-INDUCED EVOLUTION OF NORTH SEA PLAICE (*PLEURONECTES PLATESSA*)

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(Manuscript)

Abstract

There is growing evidence that harvesting may lead to evolutionary changes in life-history traits over decadal time scales. This study analyzes fisheries-induced changes in life-history traits (growth, maturation and reproduction) using an individual based eco-genetic model that includes inheritance of quantitative genetic traits and frequency-dependent selection. The model is fitted to empirical life-history estimates in North Sea plaice in a historic (1900s) and a present time period (2000s) assuming an average harvesting rate during the 20th century. Harvesting leads to a genetic selection for maturation at a smaller size and younger age and to an increase in reproductive investment. Phenotypic growth potential temporarily increased due to a relaxation of density-dependent competition for resources (plastic response), and due to selection for higher genetic energy acquisition rates to support the higher reproductive investment. Over a longer time period however, the direction of selection for the genetic energy acquisition rate changes from positive to negative after about 100 years of exploitation. Long-term exploitation will thus lead to a population with smaller size at age, higher reproductive investment and earlier maturation. Whereas the younger age classes might increase in size due to density-dependent growth, the older age classes will decrease in size due to earlier maturation, higher reproductive investment and eventually lower energy acquisition rates. This is the first model of this type, fitted to empirical data of growth maturation and reproduction over various life stages. Since the evolutionary initial and final states are unknown, extrapolation outside the studied period is rather qualitative.

Key words: *fisheries-induced evolution, individual-based modeling, density-dependent growth, energy allocation, energy acquisition, reproductive investment, maturation reaction norm, North Sea plaice*

Introduction

Fisheries-induced life-history evolution. Exploitation of fish stocks is increasingly recognized as a driving force in the evolution of life-history traits (Law and Grey 1989, Rijnsdorp 1993, Stokes, et al. 1993). Higher size-independent mortality and positively size-selective mortality typical for fisheries, cause an organism's current reproduction to become relatively more important than its future reproduction (Heino and Kaitala 1999). It might therefore be expected that fish become mature earlier and invest more into reproduction as a response to fishing (Law 2000). Indeed, earlier maturation and increased reproductive investment has been found in empirical studies with fishing as the most likely cause (review in Jørgensen, et al. 2007, Kuparinen and Merilä 2007). The expectation for intrinsic growth rate might be in both directions and will depend on the size-selectivity: if the likelihood to survive the young ages and small sizes is low, it might be advantageous to increase energy acquisition to sustain higher reproductive investment rates, or if the PMRN has no more flexibility to decrease, earlier maturation can only be achieved by faster growth, otherwise selection would be on lower energy acquisition (Dunlop, et al. 2009).

Observed changes in life-history traits will be correlated since they are intricately linked in the energy allocation schedule of the individual. Selection on one trait will affect and may be affected by selection on another trait. However, measuring changes in co-varying life-history traits in the field is notoriously difficult, because one would ideally have to follow individuals throughout their life. Furthermore, changes in phenotypic life-history traits will be confounded by genetic effects and phenotypic plasticity due to environmental variation which are in praxis difficult to disentangle (Stokes, et al. 1993). Since it can be expected that life history changes due to size-selective fishing typically go along with a reduction of sustainable yield (Law and Grey 1989, Heino and Godø 2002), it is of interest to understand the evolutionary mechanisms of these changes and adopt management strategies to promote stock recovery, or at least to prevent further life-history evolution (Jørgensen, et al. 2007). Individual-based eco-genetic models (Dunlop, et al. 2009) provide a powerful tool for understanding and analyzing the evolution of life-history traits, their correlation structure, and the effects of different harvesting strategies.

North Sea plaice & exploitation history. North Sea plaice has been exploited for centuries but realized fishing mortality rate F_{real} only increased to substantial levels in the late 19th century when it increased from about $F_{\text{real}} = 0.3$ yr^{-1} around 1890 to above $F_{\text{real}} = 0.5$ yr^{-1} around 2000, three to five times the rate of natural mortality (Beverton 1964), with high variability in between (Fig. 1). In females, size and age at maturation decreased between the early 1900s to the mid-1980s by 10–16% and 30–35%, respectively, and in males by 35% and 50–60%, respectively (Rijnsdorp 1989). Using the probabilistic maturation reaction norm or PMRN (Heino, et al. 2002) that allows to disentangle a genetic change from phenotypic plasticity, supported that part of this change was due to fisheries-induced evolution (Grift, et al. 2003, Van Walraven, et al. 2010). Size-specific fecundity, indicative of reproductive investment, increased over the same period in females up to 40 cm, but not in larger females, making the interpretation ambiguous (Rijnsdorp, et al. 2005). Plastic changes in growth rate are mainly observed in the juvenile fish, most likely due to an increase in the productivity of the environment in the 1960s and 1970s (Rijnsdorp and Van Beek 1991). Growth rate of the larger sized plaice has not changed substantially (Rijnsdorp and van Leeuwen, 1996; Bolle et al., 2004) but the asymptotic size decreased since the 1900s (Van Walraven, et al. 2010). Density-dependent reduction in growth rate seem to be restricted to the juvenile plaice when they are concentrated in shallow coastal nursery areas (Rijnsdorp et al., 1996; Teal et al. 2008).

In this paper we use a recently developed eco-genetic model parameterized for North Sea plaice (Mollet, et al. submitted) to predict and elucidate the changes in key life history parameters (onset of maturation, reproductive investment, growth) over the last century. The original model aimed to explain the sexual size dimorphism, but for simplicity we only focus on the female life-history evolution here.

Material and methods

Model. The individual-based eco-genetic model described in Mollet, et al. (submitted) is used to reconstruct the female North Sea plaice population in an environment of size-selective mortality as experienced over the entire 20th century (Rijnsdorp and Millner 1996). Somatic growth and reproductive investment are described by an energy allocation model (West, et al. 2001):

$$\frac{\partial w}{\partial t} = \begin{cases} aw^{\alpha} - bw^{\beta} & \text{if} \quad t < t_{\text{mat}} \\ \\ aw^{\alpha} - bw^{\beta} + cw^{\gamma} & \text{if} \quad t \geq t_{\text{mat}} \end{cases} \tag{1}$$

whereas w is the somatic weight and t is the age in years. The potential energy acquisition rate a and reproductive investment rate c evolve, maintenance rate b is assumed to be constant. The asymptotic body weight is given by the ratio $w_{\infty}^{1-\alpha} = a/(b+c)$. Potential energy acquisition rate a of the smaller fish <25cm is reduced as a function of biomass of these corresponding sizes due to density-dependent competition for resources. Since the larger plaice move into the open North Sea where abundances are much lower, the density-dependence in energy acquisition of these larger fish is negligible (Rijnsdorp and Van Beek 1991, Bolle, et al. 2005). Since the model is run in yearly time steps we assume a constant length–weight relationship representing the size after spawning. Maturation is defined by the maturation reaction norm (Stearns and Koella 1986), which for simplicity is assumed to be linear with an intercept u and slope s:

$$l_{\mathrm{p50}}(t) = u + st \tag{2}$$

where the l_{p50}'s are the age-specific reaction norm midpoints, i.e. the body lengths at which probability of maturing is 50%, defining the probabilistic maturation reaction norm (PMRN). For any given age and size combination, the probability of maturing p_{mat} is given by

$$p_{\mathrm{mat}} = (l,t) = \frac{1}{1+e^{-(l(t)-l_{\mathrm{p50}}(t))/\Omega}} \tag{3}$$

where l is body length and Ω is a scaling parameter defining the probabilistic width d of the reaction norm as $d = 2\Omega \mathrm{logit}(p_{\mathrm{mat}})$, depending on the maturation probability p_{mat} for which this width is implemented. The natural mortality consists of the following components: (i) a constant mortality rate m_0; (ii) a size-dependent predation mortality rate m_{p}; (iii) an energy acquisition-dependent foraging mortality rate m_{f} also being caused by predation; (iv) a reproduction-mortality m_{γ} depending on the reproductive investment γ relative to body weight w, expressed in terms of gonadic over somatic weight to be comparable to the gonado-somatic index (GSI). The model is parameterized such that the average natural mortality equals the natural mortality of $M = 0.1$ yr^{-1}, as is assumed in the ICES stock assessment for plaice (ICES 2008). Recruitment was kept constant, because from empirical data there is no indication of a change in recruitment with changing spawning stock biomass (ICES 2008), and we wanted to avoid life-history parameters to be affected by changes in recruitment.

Exploitation & selectivity. Although the spatial distribution of fish and the fleet might affect the shape of the selectivity, fishing mortality rate is for simplicity determined by (i) mesh size selection and (ii) fishing effort only. Mesh size selection is described by a logistic curve, defined by the mesh size ψ, a selection factor λ and a selection range ϕ (Van Beek, et al. 1983). Fishing effort F_{max} determines the height of this logistic curve and might vary from year to year:

$$F(l) = \frac{F_{\mathrm{max},y}}{1+e^{-\pi(l(t)-\lambda\psi)}} \tag{4}$$

The realized fishing mortality F_{real} depends on the age and size distribution of the population and was calculated as the weighted average over the ages ≥2, similar to the ICES stock assessment (ICES 2008):

$$F_{real} = \frac{n_{F,y+1}}{n_{F,y+1} + n_{M,y+1}} \log\left(\frac{N_y}{N_y - n_{F,y+1} - n_{M,y+1}} \right) \tag{5}$$

where N_y is the population number in year y, and the number of these fish left in the following year N_{y+1} given by N_y minus the number of fish $n_{M,y+1}$ that died due to natural and the number $n_{F,y+1}$ that died due to fishing mortality during the course of the year.

For simplicity, we assume a constant realized fishing mortality F_{real} over the entire studied period. Since the size distribution in the exploited population changes with time due to exploitation, F_{real} can not be strictly controlled. To keep F_{real} at a constant targeted level $\varGamma_{\mathrm{real}}$, the level of $F_{\max}$ (Eq. 4) is retrospectively adjusted each year proportional to the deviation between F_{real} and $\varGamma_{\mathrm{real}}$ in the previous year:

$$F_{\max,y} = F_{\max,y-1}\left(1 + \frac{\varGamma_{\mathrm{real}} - F_{\mathrm{real},y-1}}{F_{\mathrm{real},y-1}}\right) \tag{6}$$

Fitting. Model predictions are fitted to empirical data: (1) size at age, (2) maturation reaction norms (Mollet, et al. submitted) and (3) reproductive investment. The oldest available data apply to the first decade of the 20th century (Rijnsdorp 1993). From the end of the 1950s onwards the population was intensively sampled and size at age and ovary weights have been monitored on a routine basis. Although the species was already exploited during the medieval times (Van Neer, et al. 1999), exploitation rates have increased substantially in the late 19th century (Rijnsdorp and Millner 1996). Exploitation rates before this time might already have influenced the population's life history, but the start of exploitation and its intensity are unknown. For simplicity we therefore assume that the start of exploitation was in the late 19th century, that the available data from the early 20th century represents a historic stock in the first few years after the start of exploitation, and that after about 100 years of exploitation the model prediction represents the currently observed population. Exploitation in the model is initiated after the initial unexploited population reached evolutionary equilibrium.

The pace of evolution depends on the fishing mortality level F_{real}, on the coefficient of variation CV of the additive genetic trait variance (of evolving traits) and on the strength of tradeoffs (Mollet, et al. submitted). For the model parameterization in Mollet, et al. (submitted), there are several combinations of F_{real}'s, CV's and tradeoff settings that might match the observed life-history evolution of the North Sea plaice stock. Empirical estimates of yearly F_{real}'s over the 20th century range from

0.05 yr^{-1} to 0.92 yr^{-1} and are on average about 0.5 yr^{-1} (Fig. 1). Exploitation rates increased in the first half of the century to $F_{\text{real}} > 0.6$ yr^{-1} before the second world war and thereafter increased from about $F_{\text{real}} = 0.3$ yr^{-1} to $F_{\text{real}} > 0.5$ yr^{-1} at present (Rijnsdorp and Millner 1996, ICES 2008). The F_{real} estimates turn out higher if the mortality rate is averaged over the ages 2-6 instead of the ages 4-8 and if they are deduced from all the fish caught (landings + discards) instead from the landed fish only (Fig. 1).

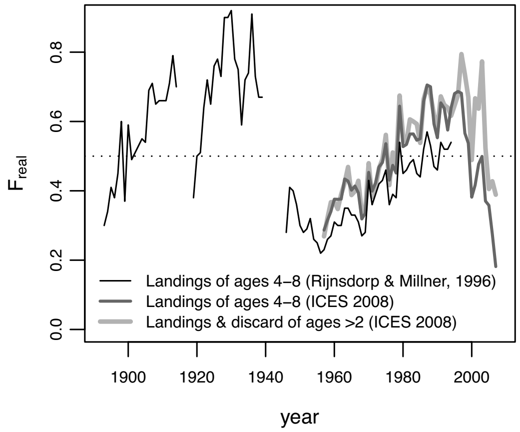

Figure 1: Fishing mortality rates of North Sea plaice (Rijnsdorp and Millner 1996) and (ICES 2008). The estimates by Rijnsdorp and Millner (1996) were based on the mortality rate averaged over the ages 4-8 not including discards (solid line). The analogue can be obtained from the (ICES 2008) estimates over ages 4-8 excluding discards (dashed line). The difference between these two estimates is likely due to that from Rijnsdorp and Millner (1996) used a plus group (the age group above which all ages are treated as the same age group) of 15+ while (ICES 2008) used an plus group of 10+. The mortality rate coming closest to the one used in the model is averaged over all ages above and with age 2 including discards, i.e. considering all fish that die due to fishing (dotted line). The estimates illustrate that assuming an average realized fishing mortality rate of 0.5 is unlikely an overestimation.

For simplicity we assumed a constant realized fishing mortality rate of F_{real} = 0.5 yr^{-1} throughout the course of exploitation. The fit of the predicted change in phenotypic life history to the observed change was evaluated over a grid of CV 's for the evolving traits: acquisition rate $CV(a)$; reproductive investment rate $CV(c)$; and PMRN intercept $CV(u)$. After the start of exploitation that supposedly occurred in the late 19th century, the evolutionary transient population states of the model were fitted to the observed population state in the early 1900s and in the 2000s. The fit to data was evaluated by a combined bias from size at age, PMRN midpoints at age and relative reproductive investment γ / w at age,

$$\Delta = \sum_{i=1}^{10}\left(\frac{\overline{w_i}^{\text{mod}} - \overline{w_i}^{\text{emp}}}{\overline{w_i}^{\text{emp}}}\right)^2 + \sum_{i=1}^{6}\left(\frac{\bar{l}_{\text{p50}i}^{\text{mod}} - \bar{l}_{\text{p50}i}^{\text{emp}}}{\bar{l}_{\text{p50}i}^{\text{emp}}}\right)^2 + \sum_{i=6}^{10}\left(\frac{\overline{(\gamma / w)_i}^{\text{mod}} - \overline{(\gamma / w)_i}^{\text{emp}}}{\overline{(\gamma / w)_i}^{\text{emp}}}\right)^2 \qquad (7)$$

where i indicates the ages over which the relative deviations between simulated (indexed by mod) and empirically estimated (indexed by emp) average characteristics were summed, w is the size (length or weight), l_{p50} are the reaction norm midpoints (Eq. 2 & 3) and γ / w is the relative reproductive investment (in terms of somatic over gonadic weight). The best solution was determined to minimize 1) this bias for the historic and the present population state at some years after exploitation, and 2) the deviation from 100 years between the distance in time of these historic and present population states where the bias was lowest. Further details on modeling and data estimation are given in Mollet, et al. (submitted).

To estimate the reaction norm, an ogive model was fitted by decade ($decade$) to market sample data with the ogive model

$$\mathrm{logit}(p_{\mathrm{mat}}) = \beta_0 + \beta_1 decade + \beta_2 t + \beta_3 l \qquad (8)$$

where p_{mat} is the probability of being mature, t is age and l is length. The probability of maturing was then obtained prospectively, i.e. is determined by the probability of maturing in the following (not in the previous) year for a given age and size (Mollet, et al. submitted), by the ratio of numbers that actually have over the ones that could have matured accounting for the effected growth, in each year (Barot, et al. 2004). To estimate a size-specific reproductive investment, an allometric relationship between relative reproductive investment γ / w and length l,

$$\gamma/w = \varphi l^{\rho} \qquad (9)$$

was assumed in both, empirical estimates and model predictions.

Results

The CV's of the evolving parameters of energy acquisition rate a, reproductive investment rate c and PMRN intercept u giving the best fit to data were $CV(a)$ = 0.20, $CV(c)$ = 0.23 and $CV(u)$ = 0.16. Due to the constant exploitation rate at $F_{\mathrm{real}} = 0.5$ yr^{-1}, population abundance drops to about 50% percent of the unexploited abundance after the start of exploitation in 1900 and thereafter stays relatively constant. Population biomass of the total population drops to 10% of the unexploited biomass as the larger fish disappear, whereas the biomass of the small fish <25cm drops to 50% (Fig. 2). The proportion of adults drops from 0.27 to 0.03 after 10 years of exploitation and from there subsequently increases to about 0.09 after 200 years of exploitation, as plaice evolves to mature at a smaller size. The population fecundity follows the trend of the adult's proportion (Fig. 4). To maintain the realized mortality rate of $F_{\mathrm{real}} = 0.5$ yr^{-1} the selectivity parameter $F_{\max}$ increases to about 0.67 yr^{-1} due to the changing size distribution in the population (Fig. 2).

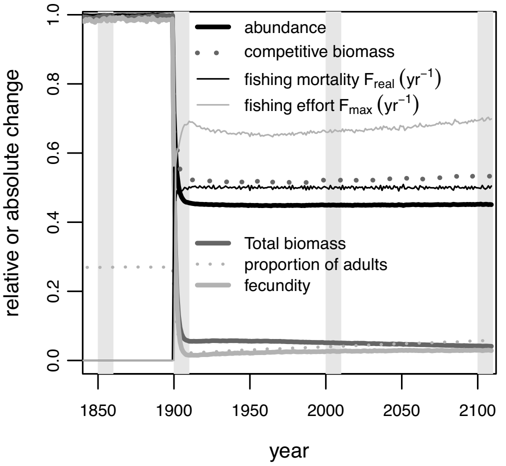

Figure 2: Demographic changes due to exploitation starting at year 1900 with $\Gamma_{\text{real}} = 0.5$ yr^{-1}: Changes in abundance (solid black), biomass (solid gray), competitive biomass of fish <25cm (dotted gray) and fecundity (light gray) are given as the percentage relative to the state in the unexploited population, the proportion of adults (dotted light gray), realized fishing mortality F_{real} (thin black) and fishing effort F_{max} (thin gray) are given on the absolute scale. The shadings represent the unexploited, historic, present and future population states (see Fig. 4).

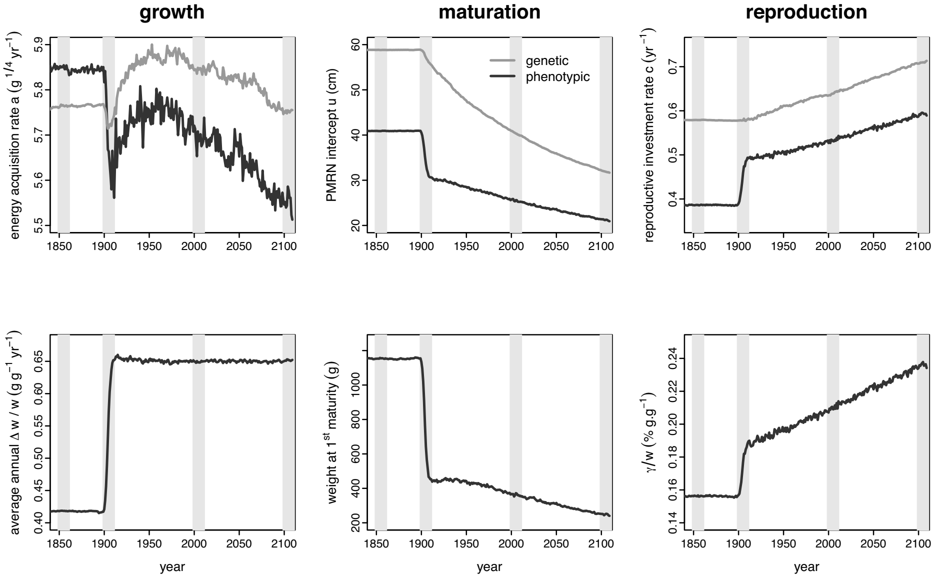

Figure 3: Evolution of evolving traits (energy acquisition rate, reproductive investment rate and PMRN intercept) and correlated emergent traits (growth rate, i.e. size increment relative to size, relative reproductive investment γ / w in terms of the % of gonadic over somatic weight, and age at first maturity). The gray line represents the evolving genetic trait values whereas the black line represents the corresponding phenotypic trait values. The vertical grey bars represent the four periods mainly represented in the results: the unexploited population before year 1900, the historic population in the 1900s, the present population in the 2000s and the predicted future population in the 2100s.

The evolution of traits of the adult population averaged over all adult ages and sizes is illustrated in Fig. 3. The relation of phenotypic and genetic trait values of energy acquisition rates a relatively changes at the start of exploitation in 1900 due to relaxation of density-dependent competition for food resources. The genetic as well as the phenotypic traits of energy acquisition rate a increase after the start of exploitation, but tend to decreases again after about 100 years of exploitation (Fig. 3).

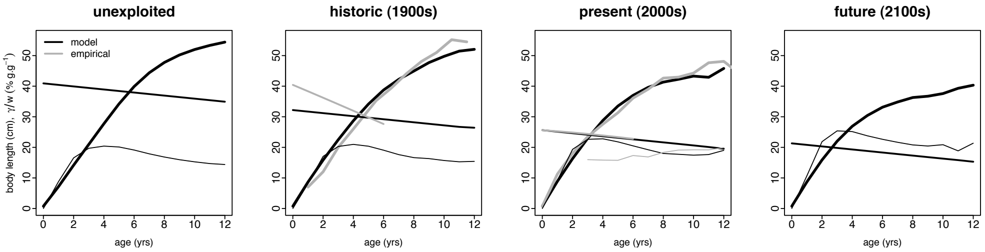

Figure 4: Size at age (thick), probabilistic maturation reaction norms (PMRNs, medium) and relative reproductive investment γ / w (thin) in terms of the % of gonadic over somatic weight, before the start of exploitation (unexploited) in the historic population in the early 1900s, in the present population in the 2000s and in the predicted future population in 100 year from now. Black lines indicate the model, gray lines the empirical data.

The genetic trait of the reaction norm intercept u decreases gradually after the start of exploitation from 59cm to 32cm after 200 years of exploitation, whereas its phenotypic trait value drops from 41cm to 30cm after 10 years of exploitation and thereafter gradually decreases to 21cm after 200 years of exploitation. The genetic traits of reproductive investment rate c increases gradually after the start of exploitation from 0.58 yr^{-1} to 0.71 yr^{-1} after 200 years of exploitation, whereas its phenotypic traits jumps from 0.39 yr^{-1} to 0.49 yr^{-1} after 10 years of exploitation and thereafter gradually increases to 0.59 yr^{-1} after 200 years of exploitation Average annual weight increment relative to body weight quickly increases from 0.40 to 0.65 g.g^{-1} after the first 10 years of exploitation and thereafter stays constant, the weight at the onset of first maturity drops from 1153g to less than 500g after 10 years of exploitation and thereafter gradually decreases to 200g after 200 years of exploitation and the average reproductive investment in terms of gonadic weight relative to body weight jumps from about 0.16 to 0.19 after 10 years of exploitation and thereafter gradually increases to 0.24 after 200 years of exploitation.

The model predictions for size at age, PMRN and relative reproductive investment γ / w are given in Fig. 4 for the unexploited population, the historic population in the early 1900s, the present population after 100 years of exploitation in the 2000s, and the future population after 200 years of exploitation (in the 2100s), together with the available empirical estimations of the historic and present population state.

Population characteristics of these 4 population states are given in Table 1. Gradual changes of size at age, PMRN midpoints at age and relative reproductive investment γ / w (gonadic over somatic weight) at length are shown in Fig. 5. The size at age increases for the younger age classes at the start of exploitation due to the relaxation of density-dependent competition for resources applying to the smaller fish of <25cm. The asymptotic size however decreases over the entire exploitation period after the start of exploitation and so does the size at age for the older age classes. Also the size at age of the younger age classes tends to decrease after the initial increase. After 200 years of exploitation the size at age is higher than before exploitation for ages 1-3, but for all older age classes the size has become smaller due to exploitation (Fig. 5). The PMRN shifts to lower levels and relative reproductive investment γ / w increases over the entire exploitation period after the start of exploitation. The decrease of the l_{p50}'s at age of the empirical estimations is not as gradual as in the model prediction and shows the highest rate of change in the last 20 years. The model prediction of relative reproductive investment γ / w at younger ages is higher than the corresponding empirical estimates.

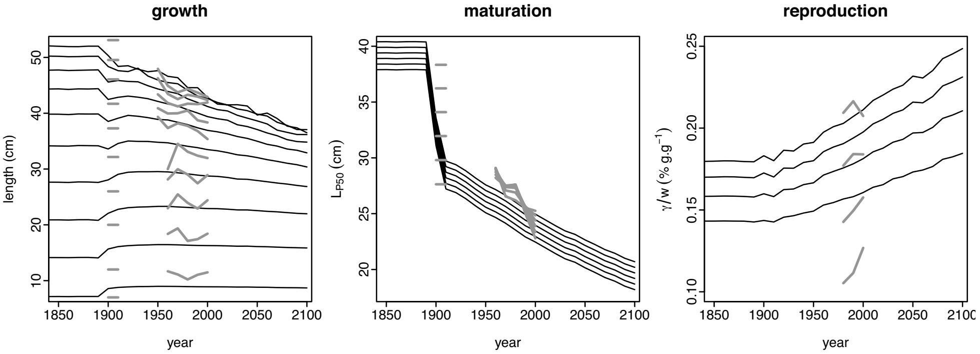

Figure 5: Temporal changes in size at age for ages 1-10, PMRN midpoint for ages 1-6 and γ / w in % of gonadic over somatic weight to be comparable with GSI (thin), for lengths 20, 30, 40 and 50cm of model predictions (black lines) and empirical data used to fit the model (gray lines).

Discussion

Fisheries-induced evolution. To our knowledge this is the first study to simulate fisheries-induced evolution fitting a true population in its key life-history characteristics of growth, maturation and reproductive investment over the entire lifespan over period of 100 years. Similar studies in Northeast arctic cod or smallmouth bass did not dispose of such detailed empirical estimates and therefore fitted size at age or a simplified proxy of the PMRN like age or size at 50% maturity (Dunlop, et al. 2007, Dunlop, et al. 2009, Enberg, et al. 2009). The model predicts how sizes at age and the onset of maturation decreased and reproductive investment increased after the start of exploitation and this prediction is in line with the empirical estimates. At the start of exploitation, energy acquisition for the younger age classes increases because of the relaxation of the density-dependent competition. Although growth of the younger age classes (up to age 3) is therefore not clearly affected, the decrease in growth of the older age classes is substantial. The asymptotic weight, given by the ratio of energy acquisition over energy expenditure rates $a/(b+c)$, decreases because reproductive investment rate c increases more importantly relative to energy acquisition rate a in the first 100 years of exploitation, because after 100 years of exploitation energy acquisition rate a furthermore decreases, and because also the onset of maturation tends to occur earlier in life. The model predicts a switch in the selection

	description	**symbol**	**unexploited**	**historic** first 10 yrs	**present** after 100 yrs	**future** after 200 yrs
Evolving traits	Phenotypic energy acquisition rate	a [$g^{1/4}$ yr^{-1}]	5.84	5.69	5.71	5.55
	reproductive investment rate	c [yr^{-1}]	0.39	0.45	0.53	0.59
	PMRN intercept	u [cm]	40.9	34.5	25.7	21.2
Emergent traits	Population number	N [1]	56443	27990	25433	25536
	fraction of adults	f_{adl} [1]	0.27	0.05	0.04	0.07
	Weight (at age 6)	w [g]	791	735	647	455
	Weight (at age 10)	w [g]	1631	1514	1001	635
	Length (at age 6)	l [cm]	39.8	38.4	37.1	32.9
	Length (at age 10)	l [cm]	52.0	50.2	43.6	36.5
	Age at 1st maturity	t_{mat} [yr]	6.8	5.0	3.4	3.6
	Length at 1st maturity	l_{mat} [cm]	48.6	41.0	33.2	29.1
	Weight at 1st maturity	w_{mat} [g]	1153	716	367	248
	Average annual relative growth rate	$\Delta w/w$ [yr^{-1}]	0.42	0.55	0.65	0.65
	Relative reproductive investment	γ/w [gg^{-1}]	0.156	0.174	0.209	0.236
	Cumulative juvenile mortality	$\overline{M}_j$ [t_{mat}^{-1}]	0.094	0.129	0.128	0.114

Table 1: Summary of population characteristics of the adult population in the four states of the population: initial state before exploitation, historic state in the first 10 years after the start of exploitation, the present state after 100 years of exploitation and a future state after 200 years of exploitation.

for the genetic trait of energy acquisition rates, from a selection for higher values towards a selection for lower values, to occur about now, after 100 years of exploitation. Energy acquisition in the first 100 years of exploitation might increase to cope with the earlier maturation and increased reproductive investment (see Dunlop, et al. 2009). The change in direction of the selection of energy acquisition is likely a consequence of the decreasing size at age, which was in the first 100 years of exploitation caused by the earlier maturation and the increasing reproductive investment. To maintain a certain level of realized fishing mortality $F_{\text{real}} = 0.5$ yr^{-1} the fishing effort $F_{\max}$ increases if the population evolves towards smaller sizes at age. It appears that the mortality cost for a certain growth pattern at some point becomes so high, that it no longer pays off to increase energy acquisition to cope with higher reproductive investment. A better strategy then seems to cut down the expenditure on somatic growth while keeping the level of reproductive investment and consequently less energy needs to be acquired.

Implications for productivity. These findings might be of interest to fisheries managers because populations that grow less, become mature earlier and invest more into reproduction will be less productive (Law and Grey 1989, Heino 1998). The consequences of fisheries-induced evolution may have severe repercussions on the long-term yield. As the fish mature earlier and stay smaller at size, the yield for a given realized mortality rate F_{real}, which is defined by population numbers, will decrease. Also the F_{MSY}, the mortality resulting in the maximal yield, is expected to change under exploitation due to these evolutionary effects (Mollet, et al. in review).
Fisheries-induced evolution may also influence the recruitment to the population. Although fisheries-induced evolution may lead to an increase in the proportion of available energy into reproduction, the fish may not necessarily be more fecund as they will remain smaller and fecundity is size dependent. This effect will be amplified if fish start to acquire energy at a lower rate, as the model predicts. Furthermore, there is evidence that the survival of the progeny is dependent on the maternal fish size (Trippel and Neil 2004). Because there is no empirical evidence that recruitment of plaice decrease at low spawning stock biomass, we assumed that recruitment is constant. However, it seems likely that, at some point, there will also be an impact on the recruitment when the population becomes less fecund and produces eggs of a lower quality. The effects of a negative impact on recruitment might then be deleterious and increase the probability of a stock collapse.

Model assumptions and prediction. For simplicity we assume a constant realized fishing mortality F_{real} over the first 100 years of fishing, although the fishing mortalities showed substantial changes in relation to the 1st and 2nd world war periods when fishing fleets and their activities were substantially reduced (Fig. 1). Fishing mortality increased from 0.3 to 0.8 yr^{-1} in the decades before the 1st world war. After the 1st world war, F_{real} increased again from about 0.4 to 0.9 yr^{-1} in the 1930s. Since the 2nd world war fishing mortality increased from a low in the 1950s of 0.24 to almost 0.6 yr^{-1} around 1990. The estimates for the years up to 1940 are relatively uncertain as these are based on data sets representing only part of the fishing fleets. Nevertheless they are likely to represent the trends in exploitation over the last century (Rijnsdorp and Millner 1996). The model is parameterized such that the natural mortality equals the natural mortality estimate of $M = 0.1$ yr^{-1} assumed in fish stock assessment, but the basis for this assumption is rather poor (Beverton 1964, Beverton and Iles 1992). Little is known about the effects of the variation in mortality on the evolutionary outcome but there is no basis to assume it would be qualitatively different than under a constant mortality regime. Because evidence on additive genetic variance of the modeled life-history traits is non existent, the variances of evolving traits were fitted in this study by adapting the corresponding CV 's to bring the pace of evolution in line with empirical observations. Alternatively, also the reported variable fishing mortality rates could have been used and the additive genetic variance (CV 's) would have been adapted accordingly. Since the model could be fitted to any other assumption on fishing mortality by adjusting the CV 's, we don't expect that a deviation from the made assumptions would alter the findings over the analyzed period. The simulated cumulative fishing mortality unlikely underestimates the true cumulative fishing because the reported exploitation rates since 1893 constitute a time series that is already longer than 100 years and it is likely that the stock was also already exploited to some degree before that. Furthermore, discarding was not accounted for in the fishing mortality estimates and the minimum landing size has varied across historic periods. The reported fishing mortality rates, in particular in the period since the 2nd world war therefore underestimate the true fishing mortality rates. This inference is supported by higher fishing mortality estimates including discards (ICES 2008).

The pace of evolution and the final equilibrium states of the population depend on the parameterization of the model. In the parameterization, different parameter combinations, e.g. the slopes in the asymmetric tradeoffs of energy acquisition and survival and reproductive investment and survival, may result to fit the data similarly well. The parameterization was furthermore based on the assumption that the historic and the present population state are at evolutionary equilibrium by varying the mortality rate and the degree of reduction in energy acquisition due to density dependent growth between these two states (Mollet, et al.submitted). This equilibrium assumption will not hold in reality because it will take more than 100 years to reach an evolutionary equilibrium. Nevertheless, the observed changes in life-history traits between 1900 and the current period could also have been modeled by adapting the CV 's for a different parameterization. In that case, the initial population would have been a different one and the population would have reached quantitatively a different final equilibrium. The direction of evolution would however not change and the future projection can therefore be used on a qualitative scale to compare management scenario's (Mollet, et al. in review).

Growth plasticity. Growth in reality is very plastic and was likely affected by other factors, not accounted for in the model, such as temperature and eutrophication. Yearly average surface temperatures in the North Sea have increased over the past 50 years by about 1°C (Van Aken 2003). Temperature will have a positive effect on all metabolic rates (see Van der Veer, et al. 2001) and temperature is known to have a positive effect on growth (Pepin 1991, Brown, et al. 2004). Also eutrophication and bottom trawling may have affected growth rate in plaice since the 1960s (Rijnsdorp and Van Beek 1991, Rijnsdorp and Van Leeuwen 1996). By including a relation of metabolic rates or growth with temperature, nutrient levels and bottom trawling, such effects could be accounted for. However, because we were interested here to study the evolutionary response separately, the environmental variation was simplified to random noise and to the evolutionary relevant effects of fishing and density-dependent growth. The sizes at age change abruptly to higher levels after the start of exploitation due to the relaxation of density-dependent food acquisition. In reality this density-dependent effect might have occurred more gradually since because fishing mortality increased more gradually than assumed here with the constant fishing mortality rate.

Sex-dependent evolution. For simplicity only the evolution of females was presented here. The original sex-structured model assumed that each individual carries a male and a female version of a trait and that only one of them is expressed according to its sex (Mollet, et al. submitted). Therefore the male and female traits evolve independently. However, if the genes coding for the modeled life-history traits were sex-linked, the evolution in the two sexes would not be independent. Empirical data suggest that males react even stronger in their life history to the harvesting regime (e.g. Rijnsdorp 1989, Van Walraven, et al. 2010). Hence, if the evolution of the sexes was not independent, the female evolution might even be accelerated by the faster male evolution. For the model presented here the consequence would be that the CV 's used need to be reduced to fit the pace of evolution.

Outlook & management advice. The model presented will be used for future projections to evaluate management scenarios (Mollet, et al. in review). It seems obvious that the fisheries-induced evolution has undesirable long-term effects on the productivity of the stock. This conclusion might also apply to many other stocks were similar patterns of decreasing growth, earlier onset of maturation and increased reproductive investment are observed (Jørgensen, et al. 2007). The evolutionary effects might be mitigated by changing the fishing effort or the size-dependence of the fishing mortality by protecting the large and late maturing fish. It seems therefore likely that short-term losses in yield would have to be accepted to reduce the long-term losses in yield due to the evolutionary effects of fishing.

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IV

Implications for management

Chapter 7

EVOLUTIONARY IMPACT ASSESSMENT OF COMMERCIAL FISHERIES: A CASE STUDY OF NORTH SEA FLATFISH FISHERIES MANAGEMENT

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(Manuscript)

Abstract

There is growing evidence that fishing causes evolution in life-history traits that affect the productivity of a fish stock. The impact of fisheries-induced evolution on the productivity of North Sea plaice is explored using an eco-genetic individual-based model by comparing management scenarios with and without an evolutionary response. Under the current management, plaice evolve towards smaller size at age, earlier maturation and higher reproductive investment, and as a consequence the biological reference points of maximal sustainable yield (MSY) and corresponding fishing mortality F_{MSY} will decrease. Hence, the current reference points, that are estimated ignoring fisheries-induced evolution, cannot be considered sustainable. The nature and extent of the evolutionary change depend on fishing effort and selectivity. The evolution can be reversed by implementing a dome-shaped exploitation pattern protecting the large fish, but this would result in a short term loss in yield. Hence, the long-term yield loss due to evolution trades off against the short-term yield of the management strategy. Depending on the time horizon considered, the increase in short-term yield of a strategy targeting on more large fish for a given mortality rate might therefore compensate for the yield loss due to the evolutionary impact but if time is long enough the long-term evolutionary impact will become more important. The long-term maximal yield lies somewhere in between.

Key words: *fisheries management, harvesting-induced evolution, maximum sustainable yield, fishing mortality rate, selectivity, exploitation pattern, mesh size, North Sea plaice*

Introduction

Fisheries management difficulties. The successful management of a resource requires that the processes causing variation in the potential yields of that resource are well understood. The dynamics of many harvested populations are routinely studied using stock assessment models (Gulland 1983, Deriso, et al. 1985) based on samples of the commercial catches and/or fisheries independent data. A harvesting regime is allowed based on the most recent perception of the stock trends. Optimally, a population would be harvested at a fishing mortality level for which population growth is maximal and stable in the long term. The yield analysis to study the dependence of yield on fishing mortality typically assumes constant population characteristics (growth, maturation, fecundity), a constant relationship of spawning stock biomass and recruitment, constant natural and constant exploitation pattern over the ages (Shepherd 1982). The aim is to find an exploitation pattern that avoids harvesting cohorts too early, when they have not yet realized their growth potential, but also not too late, when potential harvest is lost to natural mortality. Yield-fishing mortality relationships are then presented as diagrams where estimated realized fishing mortality rate is on the x-axis and yield is on the y-axis. The maximum sustainable yield (MSY) and the corresponding fishing mortality maximizing the yield, F_{MSY}, define two commonly used reference points (Beverton and Holt 1965). However, the estimates of F_{MSY} and MSY reference points have a high degree of uncertainty because the constancy assumptions are not met in nature. The reasons for the variation in the relationships are not well known and thus not captured by these models. Attempts to explain the variation in growth, maturation, fecundity, recruitment and mortality typically suppose the variation to be caused by abiotic factors (e.g. temperature, NAO, currents, nutrients) or in shifts in biotic factors (Basson 1999, De Oliveira and Butterworth 2005, Sinclair and Crawford 2005).

Fisheries-induced evolution. A Another factor that may affect growth, maturation, fecundity, recruitment and mortality is fisheries-induced evolution (Law and Grey 1989, Rijnsdorp 1993, Law 2000). In order to maximize fitness, organisms adapt their life-history depending on mortality (Stearns 1992). Fishing mortality rates have increased substantially with industrialization and concerns had been raised that life history of fish might evolve contemporarily on decadal time scales (Law and Grey 1989, Stokes, et al. 1993, Law 2000, Reznick and Ghalambor 2001). Fishing mortality rate is usually positively size-dependent, opposite to natural mortality rate, but often exceeds the latter about fourfold (Mertz and Myers 1998). A much stronger selection force in the opposite direction of the force of natural selection may cause evolution to occur at a higher pace than intuitively expected. From controlled experiments it is known that life-history evolution can occur within a few generations (Reznick, et al. 1990, Conover and Munch 2002), and substantial evidence had shown that harvesting-induced evolution can occur in wild populations within a few decades (Jørgensen, et al. 2007, Kuparinen and Merilä 2007). Other than changes in growth, maturation and fecundity caused by environmental variability, evolutionary changes caused by fishing are directional towards the evolutionary equilibrium under the higher mortality regime. Moreover, evolutionary changes caused by fishing are expected to reverse slower if the fishing mortality was lowered again (Law 2000, Enberg, et al. 2009). Fisheries-induced evolution can be studied with individual-based eco-genetic models: due to size-selective fishing typically an earlier maturation and higher reproductive investment is expected, whereas for growth rates both directions might be possible depending on the interaction of the population's size-distribution, mortality and maturation (Dunlop, et al. 2009). These findings are in line with life-history theory (Stearns 1992). It has however not yet been analyzed how these expected individual evolutionary changes would translate to the population level and what the consequences for the yield would be. Since maturation might occur earlier, reproductive investment might increase but growth might evolve in either direction, it seems not possible to make a general prediction for the long term MSY and F_{MSY}.

Traditional reference points based on a non-evolutionary model may thus not be sustainable if the evolutionary changes caused by fishing change the location of the points themselves. Instead of MSY and F_{MSY} we will therefore refer to MY and F_{MY} in the following. Only the yield that has stabilized after some years in the evolutionary model can be considered to be sustainable. To prevent the potentially negative effects of fisheries-induced evolution, the fisheries manager might determine the degree of evolution and its impact on the yield mainly by altering the fishing mortality and the size-dependence of the selectivity of fishing.

Evolutionarily enlightened management. In this paper we study the impact of harvesting-induced evolution on the long term evolutionarily sustainable yield in North Sea plaice. Fisheries-induced evolutionary changes have been reported in the onset of maturation (Grift, et al. 2003), reproduction (Rijnsdorp, et al. 2005) and growth rate has increased while the asymptotic size has decreased (Van Walraven, et al. 2010). We use an eco-genetic model that was parameterized for North Sea plaice and fitted to the exploitation history and corresponding empirical life-history estimates (Mollet, et al. in review, Mollet, et al. submitted). Management scenarios resulting in different fishing selectivity curves and fishing mortality rates are analyzed for their effect on harvesting-induced evolution and consequently on MY and F_{MY}. By comparing the evolving population to a population in which the life-history is static, the change in yield which is due to evolution is given and finally, a maximal evolutionarily sustainable long-term yield can be predicted in dependence of the management decision.

Material and methods

Concept. An individual-based eco-genetic model parameterized for North Sea plaice is used to reproduce the historical fisheries-induced life-history adaptation of the population over the last century until the present state of the population (Mollet, et al. in review). In accordance with the historical timeframe of the North Sea plaice exploitation the fishery was simulated for 100 years, and the model fits empirical data at the start of exploitation in the early 20th century as well as in its present state, after 100 years of exploitation, in terms of average body size at age, average gonad size at age and probabilistic maturation reaction norms. Based on this simulated current population, different management scenarios are evaluated from the present (year 0) onwards, and the faith of the population is projected for 1000 years into the future. The management scenarios affect the size-dependence and the intensity of the fishing mortality (see below).

Model. Somatic growth and reproductive investment follow an energy allocation model (West, et al. 2001):

$$\frac{\partial w}{\partial t} = \begin{cases} aw^{\alpha} - bw^{\beta} & \text{if} \quad t < t_{\text{mat}} \\ aw^{\alpha} - bw^{\beta} + cw^{\gamma} & \text{if} \quad t \geq t_{\text{mat}} \end{cases} \tag{1}$$

whereas w is the somatic weight and t is the age in years. Energy acquisition rate a and reproductive investment rate c are allowed to evolve, maintenance rate b is assumed to be constant. Energy acquisition rate a for the smaller fish <25cm is reduced by crowding as a function of biomass of these corresponding sizes (see Mollet, et al. submitted). Since the model is run in yearly time steps it is safe to assume a constant body length – body weight relationship. Maturation is defined by the maturation reaction norm (Stearns and Koella 1986), which is assumed to be linear with an intercept u and slope s:

$$l_{p50}(t) = u + st \tag{2}$$

Since maturation is a probabilistic process, l_{p50} is the slope through the reaction norm midpoints, i.e. the body lengths at which probability of maturing is 50%, defining the probabilistic maturation reaction norm (PMRN). For any given age and size combination, the probability of maturing is given by

$$p_{\text{mat}} = (l,t) = \frac{1}{1 + e^{-(l(t) - l_{\text{p50}}(t))/\Omega}} \tag{3}$$

where l is body length and Ω is a scaling parameter defining the probabilistic width d of the reaction norm as $d = 2\Omega \text{logit}(p_{\text{mat}})$, depending on the maturation probability p_{mat} for which this width is implemented. The natural mortality consists of the following components: (i) a constant mortality rate m_0; (ii) a size-dependent predation mortality rate m_{p}; (iii) an energy acquisition-dependent foraging mortality rate m_{f} also being caused by predation; (iv) a reproduction-mortality m_γ depending on the reproductive investment γ relative to body weight w, expressed in terms of gonadic over somatic weight to be comparable to the gonado-somatic index (GSI). Recruitment was kept constant, because from empirical data there is no indication of a change in recruitment with changing spawning stock biomass (ICES 2006), and we therefore wanted to avoid an effect on life history due to decreasing recruitment.

Exploitation & selectivity. Fishing mortality rate $F(l)$ is determined by (i) mesh size selection, (ii) fishing effort and (iii) the selectivity for size. Mesh size selection is described by a logistic curve, defined by the used mesh size ψ, a selection factor λ and a selection range ϕ. The maximal selectivity $F_{\max}$ determines the height of this logistic curve and indicates the fishing effort for a given management scenario (see below). The selectivity depends on the fishing gear and the availability of fish. If the gear is selective for intermediate sizes or if large fish are less available to fishers due to a size-dependent spatial distribution, the exploitation pattern is expected to be dome-shaped.

$$F(l) = \left(1 - \delta + \frac{\delta}{1 + e^{-\varepsilon(l_{disp} - l(t))}}\right) \frac{F_{\max}}{1 + e^{-\varphi(l(t) - \lambda\psi)}} \tag{4}$$

where δ represents the reduction of availability of the large fish, with l_{disp} standing for the size corresponding to the half-maximal availability range ε. The availability function decreases from 1 for small fish (100% availability) to a minimal value of $1 - \delta$. If $\delta = 0.0$, the selectivity does not decrease for the large fish (flat exploitation pattern), if $\delta = 1.0$, the selectivity decreases to 0 for the large fish (dome-shaped exploitation pattern, Fig. 1). The realized fishing mortality F_{real} over all sizes depends on the size distribution of the population. Similar to the ICES stock assessment, F_{real} is given by the number of fish of age 2 and older N_y in year y, and the number of these fish left in the following year N_{y+1}, accounted for the number of fish that died due to natural mortality $n_{M,y+1}$ and due to fishing mortality $n_{F,y+1}$ in the course of the year:

$$F_{\text{real}} = \frac{n_{F,y+1}}{n_{F,y+1} + n_{M,y+1}} \log\left(\frac{N_y}{N_y - n_{F,y+1} - n_{M,y+1}}\right) \tag{5}$$

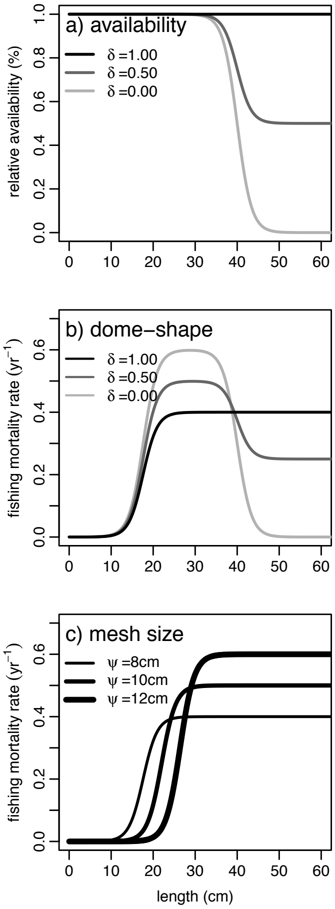

Figure 1: Illustration of different exploitation patterns: the availability of fish (a) given by the dome-shape parameter δ decreases with size (see Eq. 4) and determines the strength of the dome-shape (b) of the exploitation pattern. Increasing mesh size (c) shifts the selectivity curve to the right. The fishing effort $F_{\max}$ in b) and c) was varied to illustrate that F_{real} is kept constant for a given size distribution in the population.

For simplicity, we assume a constant realized fishing mortality F_{real} over the entire studied period, but due to stochastic and evolutionary effects, F_{real} cannot be strictly controlled. To keep F_{real} at a constant targeted level of fishing mortality Γ_{real}, the level of $F_{\max}$ (Eq. 4) is retrospectively adjusted each year by the degree of deviation between realized F_{real} and targeted Γ_{real} mortality in the previous year:

$$F_{\max,y} = F_{\max,y-1}\left(1 + \frac{\Gamma_{\mathrm{real}} - F_{\mathrm{real},y-1}}{F_{\mathrm{real},y-1}}\right) \tag{6}$$

Fishing effort $F_{\max}$ is consequently adjusted to result in the same realized fishing mortality F_{real} across different management scenarios.

Management options. Management decisions might affect the selectivity curve (Eq. 4) by changing the (i) mesh size regulations or (ii) the spatial and temporal dynamics of exploitation (given that the spatial and temporal distribution of fish is size-dependent). Fishing with larger mesh sizes would shift the selectivity curve to the right (larger ψ in Eq. 4) and fishing more on intermediate sizes would result in a more dome-shaped selectivity pattern ($\delta > 0.0$ in Eq. 4). To find the maximal sustainable yield MSY and the corresponding level of fishing mortality F_{MSY}, management scenarios with $\delta \in \{0.0, 0.25, 0.5, 0.75, 1.0\}$ and $\psi \in \{4, 6, 7, 8, 9, 10, 12\}$ cm are run over the 1000 years for a range of fishing mortalities $F_{\mathrm{real}} = \{0, 0.01, 0.02, ..., 1.2\}$ yr^{-1}. For the 100 years of exploitation before the present, it was assumed that $F_{\mathrm{real}} = 0.50$ yr^{-1}, $\delta = 0.0$ and $\psi = 8$ cm (Mollet, et al. in review). This scenario is used as reference scenario and represents in future extrapolations the case where management would not change.

Evolutionary impact assessment. To asses the loss in yield due to the fisheries-induced evolution, the yield Y_{evol} was compared to the yield Y_{static} of a population in which the life history remains constant at the present life-history trait values. The evolutionary impact EI was given by the relative yield change, i.e. the difference of these yields in year y at the realized fishing mortality F_{real} under the management scenario S, standardized for the yield at the start of the management evaluation ($y = 0$) with the respective fishing mortality F_{real} under scenario S:

$$EI = \frac{Y_{\mathrm{evol}}(y, F_{\mathrm{real}}, S) - Y_{\mathrm{static}}(y, F_{\mathrm{real}}, S)}{Y_{\mathrm{evol}}(y = 0, F_{\mathrm{real}}, S)} \tag{7}$$

Results

Yield, MY and F_{MY}. Under the reference scenario ($F_{\mathrm{real}} = 0.50$ yr^{-1}, $\delta = 0.0$ and $\psi = 8$ cm) the population life history evolves towards smaller size at age, earlier maturation and higher relative reproductive investment (see Mollet, et al. in review, Fig. 3). The maximum yield (MY) correspondingly evolves to become lower and the maxima evolve to occur at lower fishing mortalities (F_{MY}, Fig. 2): For another 100 years of exploitation the maximum yield is obtained at $F_{\mathrm{real}} = 0.31$ yr^{-1}, after 1000 years of exploitation at $F_{\mathrm{real}} = 0.10$ yr^{-1}, due to evolution.

Trait evolution under different scenarios. The management scenarios affect the evolution of life-history traits differently. The flat exploitation pattern induces evolution towards low energy acquisition rate, high reproductive investment rate and low PMRN with a stronger effect for the larger mesh size (Fig. 3). Under continuation of the reference scenario ($F_{\mathrm{real}} = 0.50$ yr^{-1}, $\delta = 0.0$ and $\psi = 8$ cm) the population evolves to a state of dwarfism after 500 years where the energy acquisition rate a is about three times lower, reproductive investment rate c about twice as high and the PMRN intercept about 5 times lower (Fig. 3). In this case the fish become practically mature after birth and invest all acquired energy into reproduction instead of somatic growth and consequently reach a small maximal body size of less than 10cm (result not shown).

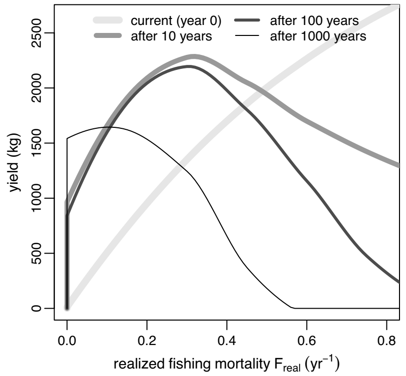

Figure 2: Evolution of yield under the (current) reference scenario with $F_{real} = 0.5$ yr^{-1}, $\delta = 0.0$ and $\psi = 8$ cm at year 0 and after 10, 100 and 1000 years of exploitation.

The switch to dwarfism is triggered by the increase in fishing effort F_{max} to maintain the realized fishing mortality of $F_{real} = 0.50$ yr^{-1}, when the individual body size evolves to be smaller (see below). If a larger mesh size is used under a flat exploitation pattern $\delta = 0.0$ and $F_{real} = 0.50$ yr^{-1}, the switch to dwarfism occurs even earlier (Fig. 3). If on the other hand the exploitation pattern is dome-shaped, the direction of evolution imposed by the flat exploitation pattern might be reversed (Fig. 3).

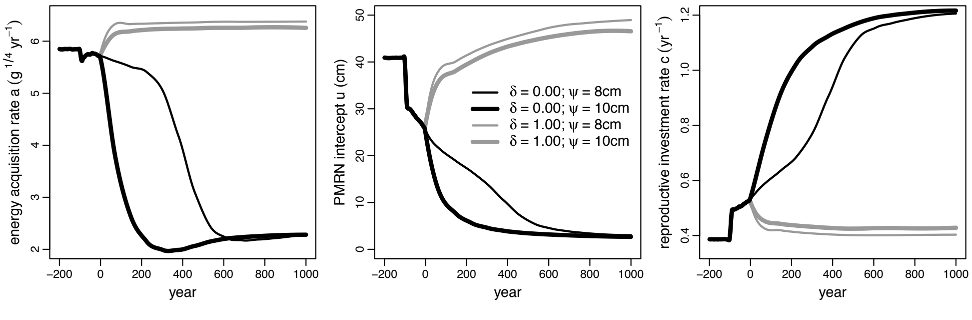

Figure 3: Evolution of energy acquisition rate a, PMRN intercept u and reproductive investment rate c at $F_{real} = 0.5$ yr^{-1} under four different management scenarios with $\delta \in \{0.0, 1.0\}$ and $\psi \in \{8, 10\}$ cm. Fishing is initiated at year -100 with $\delta = 0.0$ and $\psi = 8$ cm. At present (year 0) different management scenarios are implemented. Black lines represent the evolving traits under a flat exploitation pattern ($\delta = 0.0$), gray lines the traits under a dome-shaped exploitation pattern ($\delta = 1.0$), thin lines the traits using a mesh size of 8cm ($\psi = 8$ cm) and thick lines the traits using a mesh size of 10cm ($\psi = 10$ cm).

For a fully dome-shaped exploitation pattern ($\delta = 1.0$), the energy acquisition rate a evolves to even higher levels than in the unexploited population, and the reproductive investment rate c and the PMRN recovers to a similar level as in the unexploited population (Fig. 3) and the size at age remains correspondingly large. Using a larger mesh size under a dome-shaped exploitation pattern scenario has again the same effect of relatively decreasing energy acquisition, increasing reproductive investment and decreasing maturation. The trait distributions remained unimodal (not shown) and selection was thus not bidirectional as might have been expected under a dome-shaped exploitation pattern.

Evolution of effort and yield under different scenarios. If the population evolves towards smaller sizes at age, fishing effort $F_{\max}$ increases to maintain a realized fishing mortality F_{real}. Under a flat exploitation pattern ($\delta = 0.0$), $F_{\max}$ exceeds 2.0 yr^{-1}, an effort level that will be difficult to reach in practice, within 400 years (Fig. 4). Under a dome-shaped exploitation pattern ($\delta = 1.0$), a constant realized fishing mortality F_{real} can be reached with a constant effort $F_{\max}$. Alternatively, the stock could be managed by controlling fishing effort $F_{\max}$ instead of mortality rate F_{real} (Fig. 4, right panel). If fishing effort $F_{\max}$ is kept constant, the realized fishing mortality F_{real} decreases with increasing dome-shape or mesh size (Fig. 4). If the population moves towards lower sizes at age (reference scenario), the realized fishing mortality F_{real} will decrease over time. The initially higher realized fishing mortality F_{real} of the reference scenario therefore falls below the realized mortality rate obtained with a dome-shaped exploitation pattern after 500 years of exploitation (Fig. 4). Keeping the fishing effort $F_{\max}$ constant instead of the realized mortality F_{real} results in similar evolutionary trajectories of the yield (Fig. 4).

With the evolution towards smaller size at age, earlier maturation and increased reproductive investment, the yield decreases over time under the reference scenario (Fig. 2, Fig. 4). Reducing the realized fishing mortality rate in the reference scenario from $F_{\text{real}} = 0.50$ yr^{-1} to the level targeted by ICES of $F_{\text{real}} = 0.30$ yr^{-1}, results in a short-term increase of the yield, showing that population growth was overfished with $F_{\text{real}} = 0.50$ yr^{-1}. But also in the case of $F_{\text{real}} = 0.30$ yr^{-1}, selection in the long term is on lower energy acquisition, earlier maturation and increased reproductive investment and therefore reducing the yield under the flat exploitation pattern (Fig. 4). Changing the reference scenario to a fully dome-shaped exploitation pattern from $\delta = 0.0$ to $\delta = 1.0$ initially decreases the yield because less large fish are caught. However, under this dome-shaped exploitation pattern the yield then remains stable and constant over the 1000 years of exploitation such that it exceeds the decreasing yield of the reference scenario after 250 years of exploitation (Fig. 4). Changing the realized fishing mortality under the dome-shaped exploitation pattern from $F_{\text{real}} = 0.50$ yr^{-1} to $F_{\text{real}} = 0.30$ yr^{-1} has only a marginal effect on the yield (Fig. 4).

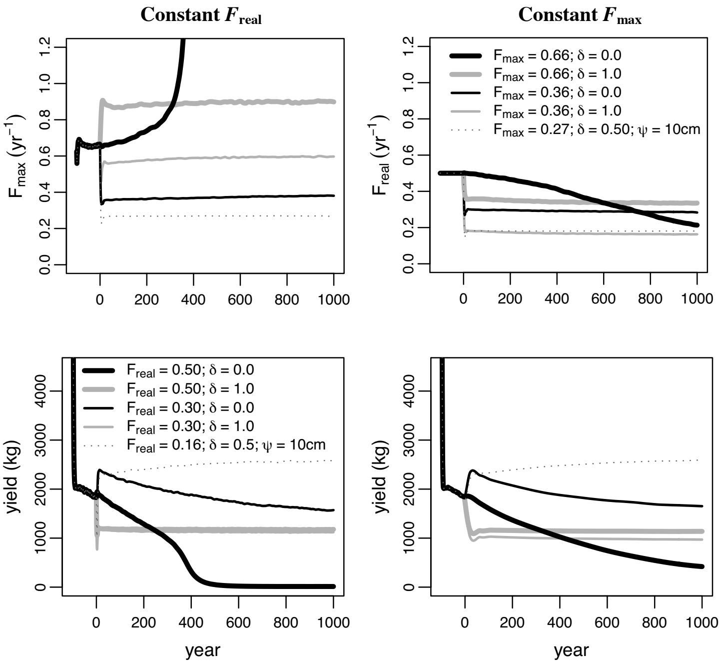

Fig. 4: The evolution of fishing effort $F_{\max}$ and yield using a constant realized fishing mortality rate F_{real} (left panel) and the evolution of realized fishing mortality F_{real} and yield using a constant fishing effort $F_{\max}$ (right panel) under five management options: $F_{\text{real}} \in \{0.3, 0.5\}$ yr^{-1} (representing the targeted and the current fishing mortality rate, thin and thick lines), $\delta \in \{0.0, 1.0\}$ (flat and dome-shaped exploitation pattern, black and gray lines) with $\psi = 8$ cm and additional the optimal management strategy (see Table 1) with $F_{\text{real}} = 0.16$ yr^{-1}, $\delta = 0.5$ and $\psi = 10$ cm (dotted) for comparison. Under constant fishing effort the level of fishing effort resulting in the reference mortality of $F_{\text{real}} = 0.5$ yr^{-1} under the reference scenario ($\delta = 0.0$, $\psi = 8$ cm) in the first 100 years of exploitation is shown (see legend).

			δ									
			0.00	0.25	0.50	0.75	1.00	0.00	0.25	0.50	0.75	1.00
			evolutionary					**static**				
ψ **(cm)**	4	**F_{MY} (yr^{-1})**	0.16	0.16	0.22	0.24	1.20	0.20	0.20	0.20	0.24	0.42
	6		0.15	0.16	0.20	0.30	0.68	0.20	0.20	0.21	0.27	0.32
	7		0.15	0.16	0.16	0.24	0.90	0.20	0.20	0.20	0.27	0.31
	8		0.16	0.16	0.17	0.24	0.87	0.20	0.21	0.20	0.24	0.37
	9		0.14	0.16	0.17	0.23	0.56	0.23	0.23	0.21	0.25	0.33
	10		0.07	0.11	0.16	0.21	0.90	0.27	0.25	0.24	0.24	0.35
	12		0.00	0.02	0.04	0.07	0.48	0.39	0.40	0.39	0.39	0.39
	4	**MY (kg)**	2321	2344	2208	1914	1033	2415	2251	2009	1695	1035
	6		2336	2396	2265	1973	1056	2476	2342	2100	1767	1101
	7		2364	2438	2338	2060	1113	2540	2400	2198	1845	1168
	8		2275	2431	2418	2159	1191	2581	2450	2257	1933	1248
	9		1947	2450	2504	2288	1286	2619	2527	2341	2038	1351
	10		1069	1737	2599	2397	1436	2524	2470	2448	2190	1475
	12		854	880	867	1076	1775	1886	1897	1875	1894	1709

Table 1: Maximal sustainable yield MY (kg) and corresponding fishing mortalities F_{MY} (yr^{-1}) leading to the MY for different settings of the dome-shape δ and mesh size ψ after 1000 years of exploitation.

Table 1 shows the maximal yields MY and the corresponding fishing mortality F_{MY} over the evaluated range of dome-shape δ and mesh size ψ. Because protecting the large fish with a dome-shaped selectivity or by smaller mesh sizes has long-term evolutionary benefits but drawbacks on the instantaneous yield as the large fish are not caught, the strategy to optimize the long-term yield is found at some intermediate level of dome-shape and mesh size, namely at $F_{\text{real}} = 0.16$ yr^{-1}, $\delta = 0.50$ and $\psi = 10$ cm (Table 1). In this case the yield, initially increases and thereafter continues to increase as the population evolves towards larger sizes at age again (Fig. 4).

Evolving vs. static MY and F_{MY} under different scenarios. The evolutionary yields Y_{evol} are shown in Fig. 5 as a function of F_{real} after 10, 100 and 1000 years of implementation of the scenarios with $\delta \in \{0.0, 1.0\}$ and $\psi \in \{8, 10\}$ cm, against the yields Y_{static}, corresponding to the yield curves routinely estimated in fish stock assessment assuming a constant life history. In the non-evolving population the maximal yield MY and the corresponding mortality rate F_{MY} at which this MY occurs, are roughly the same after 10, 100 and 1000 years (Fig. 2nd column, differences might be due to population dynamics and plastic effects). Under a flat exploitation pattern $\delta = 0$ the maximal yields MY might be higher than with a dome-shaped exploitation pattern $\delta = 1.0$ (Fig. 5), in the short term even if the population evolves, but occur at a much lower exploitation rate F_{MY}. When mortality levels are increased above F_{MY}, the yields drop quickly to 0, whereas under a dome-shaped exploitation the MY occurs at relatively high exploitation rates and the yield is stable over a wide range of F_{real}'s around F_{MY} (Fig. 5). Larger mesh sizes result in higher yields at lower exploitation rates F_{MY} in the short term. In the long term, flat exploitation pattern and larger mesh sizes reverse to result in lower MY's which occur at lower F_{MY}'s if the population evolves. Dome-shaped exploitation pattern and larger mesh size results in higher yields than with smaller mesh sizs over a range of F_{real}'s and these only drop to 0 in the vicinity of $F_{\text{real}} = 1$ yr^{-1}. If the population would be exploited at the F_{MY} of each management scenario, the evolution of traits is much less severe or in other words, the yield is maximal if the initial evolutionary effects are minimized or reversed (result not shown).

Evolutionary impact assessment. The difference between the yields from the evolving and the non-evolving population, Y_{evol} and Y_{static}, defines the relative change in yield due to evolution, in other words, the evolutionary impact (Fig. 5, 3rd column). This difference becomes already considerable after 100 years of exploitation. Under a flat exploitation pattern the Y_{evol} is lower than Y_{static} with maximal yields MY occurring at lower exploitation rates F_{MY}. The relative change in yield decreases by about 100% after 100 years if exploitation rate is $F_{\text{real}} > 0.4$ yr^{-1}, and after 1000 years if $F_{\text{real}} > 0.2$ yr^{-1}, whereas the decrease is stronger for the larger mesh sizes.

Under a dome-shaped exploitation pattern however, Y_{evol} is lower only at low exploitation rates but higher at high exploitation rates than Y_{static}, with maximal yields MY occurring at higher exploitation rates F_{MY}. In this case the relative change in yield increases if $F_{\text{real}} > 0.2\ \text{yr}^{-1}$. The increase is stronger for the larger mesh sizes but then drops again to negative levels when it is no longer possible to survive the size-window vulnerable to fishing at $F_{\text{real}} > 1.0\ \text{yr}^{-1}$. For the smaller mesh sizes the yield change stays positive.

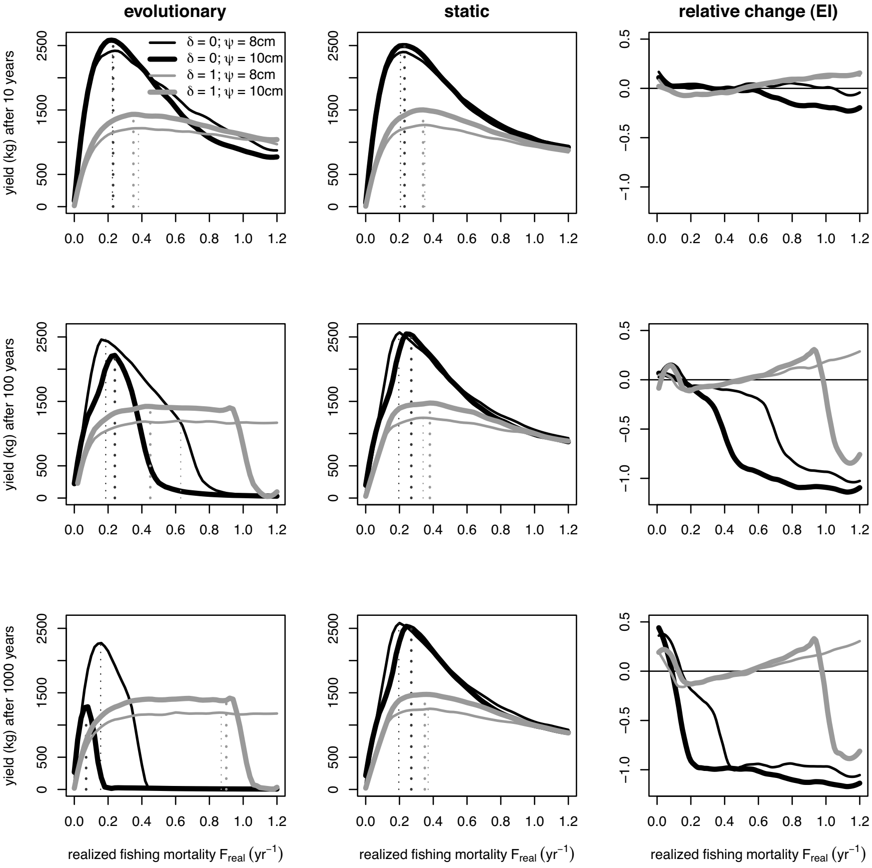

Figure 5: Yield with (fist column) and without (second column) evolution and relative yield change (third column) after 10, 100 and 1000 years (first-third row) of exploitation over a range of realized fishing mortalities F_{real} from 0 to 1.2 for the possible management scenarios with $\delta \in \{0.0,1.0\}$ and $\psi \in \{8,10\}$ cm, i.e. flat and fully dome-shaped exploitation pattern and mesh sizes 8cm and 10cm. Black lines represent the yield obtained with the flat exploitation pattern, gray lines the yield with the dome-shaped exploitation pattern, thin lines the yield obtained with a mesh size of 8cm and thick lines the yield with a mesh size of 10cm. Vertical dotted lines indicate the F_{MSY} of the respective management scenario.

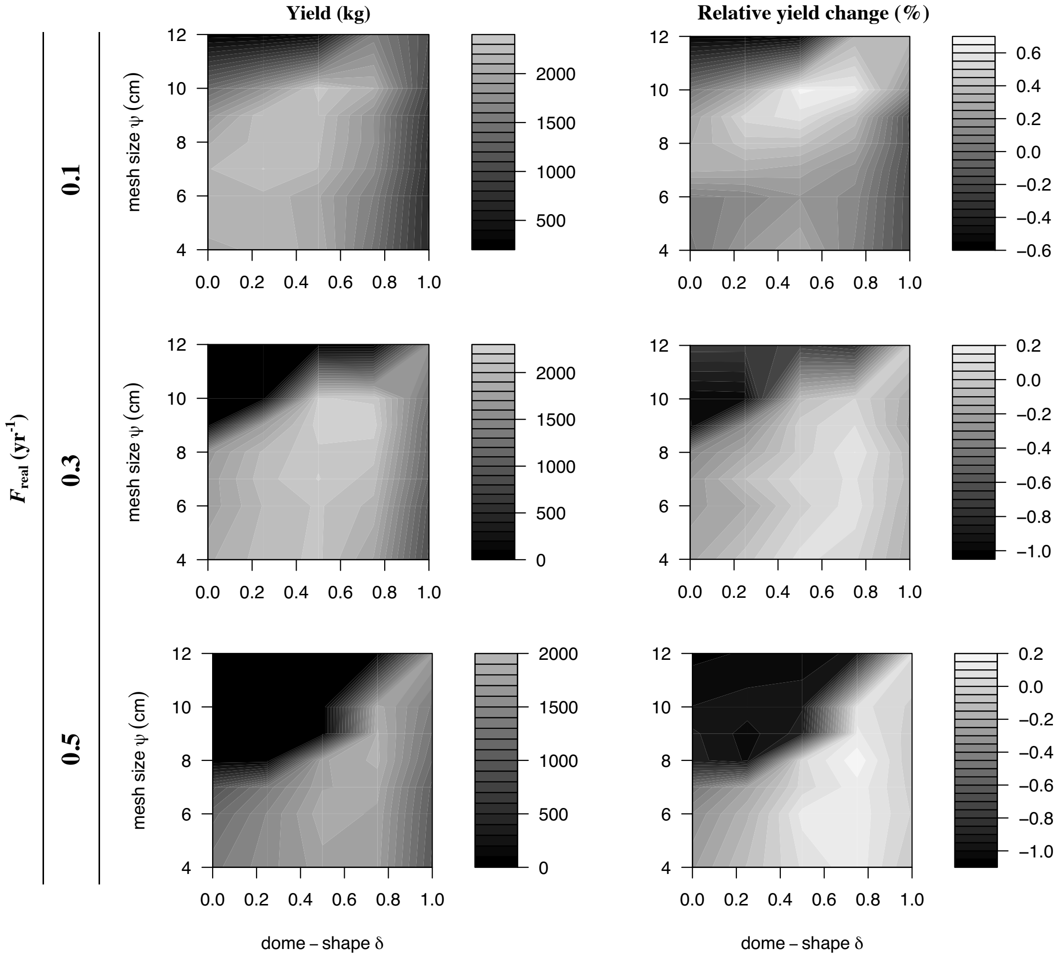

Figure 6: Absolute yield (kg) and relative yield change (%) after 1000 years of exploitation at $F_{\mathrm{real}} \in \{0.1, 0.3, 0.5\}$ yr^{-1} as a function of mesh size ψ, and dome-shape parameter δ.

Mitigation. Mitigation of evolutionary effects might be evaluated under certain future mortality regimes F_{real} for varying exploitation patterns δ and mesh sizes ψ (Fig. 6). As exploitation rates increase, the maximal relative yield change moves in Fig. 6 from left to right, i.e. from a flat exploitation pattern to a dome-shaped exploitation pattern, and from top towards the bottom, i.e. from large mesh sizes to small mesh sizes.

The behaviour of the maximal yield reflects the one of the relative yield change due to evolutionary effects: As exploitation rates increase, a higher yield is obtained with smaller mesh sizes and a more dome-shaped exploitation pattern. However, the maximal yield lies at higher mesh sizes and less important dome-shape than the maximum for the relative yield change due to evolutionary effects. This is because the long-term evolutionary benefit using smaller mesh sizes and dome-shaped exploitation patterns trades off against the short-term benefit in catching larger fish by using larger mesh sizes and flat exploitation patterns.

Discussion

Main findings. To our knowledge this is the first study to illustrate the cost in yield of evolutionary effects due to harvesting in a model framework that fits to a real population in its key life history aspects of growth, maturation and reproductive investment (see Mollet, et al. in review). It demonstrates how the yield is associated to the evolving population characteristics, which in turn depend on the imposed fishing regime. The evolutionary effects of the fishing regime that operated over the last 100 years has negatively affected the yield. Under a flat exploitation pattern and high fishing mortalities, the population evolves towards smaller sizes at age, earlier maturation and higher reproductive investment, resulting in lower long-term yields. Due to the evolution towards smaller sizes at age, the fishing effort $F_{\max}$ would have to increase to unrealistic levels to maintain a certain realized mortality rate F_{real}. This is unlikely to occur because the fishery will no longer be economically profitable if effort $F_{\max}$ becomes large in relation to the correspondingly resulting yield. Using larger mesh sizes for a given fishing mortality rate amplifies the selection towards small and slow growing fish. This result might be counter-intuitive but is a consequence of keeping realized mortality F_{real}, given by the proportion of fish harvested relative to the total number of fish, constant: The large fish with fast growth, late maturation, and low reproductive investment, are consequently removed more efficiently when using a larger mesh size. The evolutionary trend in life history could be reversed by protecting the large fish. i.e. by imposing a dome-shaped exploitation pattern. The fish then grow as fast as possible to outgrow the exploitation window of the intermediate sizes. The short-term yield in this scenario is lower because less large fish are caught, but the long-term yield is higher because the population growth rate does not decrease. The short-term benefits of catching large fish thus trades off against the long-term effects of protecting them, since in the latter case the relatively high growth rate (energy acquisition), late maturation and low reproductive investment are evolutionarily stable. The question for the optimal harvesting strategy depends on what time horizon is considered. This study shows that trying to obtain high yields in the short term may result in deleterious evolutionary effects. The current exploitation regime results in a reduction of the productivity of the stock and in a gradual downward trend in the maximum achievable yield. The life-history traits in this study stabilize after about 1000 years for each management scenario and the yields can therefore be considered evolutionarily sustainable only at this time horizon.

Effects on MSY and F_{MSY} resp. MY and F_{MY}. One of the main caveats of the currently imposed management is that it assumes constant life-history characteristics. The calculation of the "maximal sustainable yield" or "MSY" – quotation marks indicating the current naming but the inaccuracy of the word "sustainable" in it (see below) - is usually based on an average size at age, maturation and fecundity or based on intuitive estimates of these. Since the prediction of the yield is very uncertain precautionary approaches were introduced (Myers and Mertz 1998, Caddy 1999, Piet and Rice 2004), proposing more precautionary exploitation regimes by more precautionary reference points with which the exploitation of populations is likely on the safe side, i.e. is not overexploited with a high probability. However, because the life-history evolves, the target reference points of "MSY" and "F_{MSY}" evolve with it and become slipping targets. The estimated yields assuming a constant life-history are thus not sustainable and were therefore called here MY instead of MSY. In summary, under a flat exploitation pattern and larger mesh sizes, the population growth decreases and the MY's and F_{MY}'s decrease along with it. That is, even if the so-called "MSY" and "F_{MSY}" assuming a static population are correctly estimated and implemented (which is unlikely in practice) they are not sustainable as the evolving MY and F_{MY} might already be considerably lower within a few decades. Hence, if fishing at the currently estimated "F_{MSY}"'s, the population will still be overfished and a considerable part of the potential yield is lost due to the evolutionary effects. The currently expected yields are therefore likely all overestimated. The overestimation of MSY and F_{MSY} could be avoided by applying a more dome-shaped exploitation pattern in the future as the evolutionary F_{MSY} might then evolve to be higher. Furthermore, the yields under a dome-shaped exploitation are much more stable if the realized F_{MY} would deviate from the proposed "F_{MSY}". However, lower yields would have to be accepted by not catching the large fish.

The management objectives for the management of the North Sea plaice stock set by the EU are to reduce F_{real} to $F_{\mathrm{real}} = 0.3$ yr^{-1} within the following 10 years (COUNCIL REGULATION (EC) No 676/2007). However, our results show that even at a level of $F_{\mathrm{real}} = 0.3$ yr^{-1} a substantial part of the yield is lost due to evolutionary effects. In fisheries, exploitation patterns are typically flat and a flat exploitation pattern was therefore used as reference scenario that applied over the past 100 years. With this reference scenario, F_{real} would have to be reduced to below $F_{\mathrm{real}} < 0.2$ yr^{-1} to achieve a maximal yield in the longer-term future. At higher levels of F_{real} the evolutionary yield change is negative. Setting $F_{\mathrm{real}} = 0.3$ yr^{-1} only makes sense if the corresponding exploitation pattern was substantially dome-shaped, i.e. if a large part of the large fish were protected.

Evolutionarily enlightened management. At some point the long-term evolutionary loss might exceed the short-term gain in yield by not protecting the large fish. The management might be adjusted such that this switch occurs as far as possible in the future, and managers would have to make sure then that the fishing mortality is below a critical level such that the switch is not induced earlier. Optimally, the management is optimized by stabilizing the population's life history and hence the yield by protecting a part of the large fish by imposing a dome-shaped exploitation pattern. A tool apt to simulate life-history evolution is necessary to predict this optimum. Our plaice model predicts a maximal yield, if the selectivity of the large fish is half-maximal, $\delta = 0.5$, and if that the selection of larger fish is more efficient with $\psi = 10$ cm, but at a realized fishing mortality rate $F_{\text{real}} = 0.16\,\text{yr}^{-1}$ which is much lower than the currently imposed mortality rates. As the advantage in yield of a flat exploitation pattern and a large mesh size only holds for relatively lower F_{real}'s in the long term, there is a risk in proposing too flat exploitation patterns or too large mesh sizes. If the realized fishing mortality F_{real} is higher than the proposed fishing mortality, the consequences of a flatter exploitation pattern and larger mesh size might quickly become deleterious. Furthermore, we suggest to optimize the yields over time horizons over which the population life-history stabilizes, in this case over about 1000 years. The effect of not considering time horizons long enough to let the life-history traits stabilize would in the end have the same effects as not considering evolution, namely the "MSY" and "F_{MSY}" would be overestimated.

Applicability of scenarios. These findings could qualitatively hold for any exploited fish stock. The question is mainly whether an exploitation with dome-shaped selectivity is realistic. Demersal and pelagic and nets are generally positively size selective. Only gill nets are known to be selective for intermediate sizes. However, if a species is distributed in space in relation to its size, fishing in certain areas offers another opportunity to achieve a dome-shaped realized selectivity curve. Many flatfish species are distributed in space as a function of their size (Gibson 2005). During spawning, fish of all size classes concentrate on spawning grounds but during the growing season the larger fish migrate into the central North Sea and migration distances are proportional to body size (Rijnsdorp and Pastoors 1995). During the growing season, the large fish are thus less available to the gear when fishing close to the shore, except during spawning when fish of all size classes return to the spawning grounds closer to the coast. Hence, fishing closer to the coast thus increases the dome-shape of the selectivity pattern and the large fish can be protected by not fishing in the more central North Sea (Quirijns, et al. 2008, Aarts and Poos 2009). During spawning however a flat exploitation pattern could hardly be avoided, since fish of all sizes come to the same spawning grounds. Reducing fishing during spawning in the first quarter would thus lead to a rather dome-shaped exploitation pattern. On the other hand, a selection for mature fish might also have positive effects. It has been shown that selection for mature individuals results in a delayed maturation

(Ernande, et al. 2004, Mollet, et al. submitted). The individual tries to compensate the risk of a high mortality on the spawning ground by a high reproductive success by growing large before reproducing. The switch to lower growth rates, earlier maturation and higher reproductive investment resulting in lower yields is therefore unlikely if fishing is selective for mature fish. In general, fishing closer to the shore might be an evolutionarily stable exploitation strategy.

Model uncertainty. Caution is needed when using quantitative predictions of a model. The quantitative predictions here are conditional on the assumptions made in the parameterization (Mollet, et al. in review) and the fitting to the exploitation of the past 100 years. In the model parameterization, different parameter combinations would result in a similar fit, especially for the tradeoffs between growth and survival, and reproduction and survival. The historic exploitation was assumed to be characterized by a flat exploitation pattern, and a constant mortality rate of $F_{\text{real}} = 0.5\ \text{yr}^{-1}$. In reality, the exploitation was not exactly flat and the mortality rate not constant. Furthermore, changes in mesh size might in reality also affect the selection range (φ in Eq. 4) because if larger meshes are stretched in a full net, the smaller fish might still be retained. However, since we are interested in the general prediction of the effects of a flat *versus* a dome-shaped exploitation pattern and a low *versus* a high mortality rate, we think these were valid assumptions.

Recruitment may be modeled with a Beverton-Holt-type stock-recruitment relationship where recruitment increases with population fecundity asymptotically (Mollet, et al. in submitted). In this study this relationship was assumed so steep that recruitment was kept constant because we were interested in exploring the evolutionary effects independently from potential effects on recruitment. Population fecundity and recruitment however may increase with a dome-shaped exploitation pattern and relatively decrease for the flat exploitation pattern (not shown) and therefore recruitment might also relatively increase or decrease if the relationship of population fecundity and recruitment was assumed to be less steep. Since the model was previously fitted to the life-history evolution of the past 100 years, changes in these model assumptions would not affect the model prediction for the evolution in these 100 years but might lead to different evolutionary equilibria outside of the range for which empirical estimates are available.

Effort F_{max} and dwarfism. Above a certain level of fishing mortality and a sufficiently flat exploitation pattern, the model population switched to dwarfism along with the increase in fishing effort F_{max} to maintain a constant realized fishing mortality F_{real} under the shift in the distribution of individual body size towards lower sizes. In reality this is as mentioned unlikely to happen since the associated life-history evolution results in lower yields and higher fishing efforts would therefore not be economically possible. The fishery would likely have to close long before the potential switch to dwarfism occurs. A threshold of fishing effort relative to the yield for which the fishery is no longer economically viable could be included in the model, and the fishery would then likely collapse in this scenario.

Management and evolution. The cost of evolution might be high in the long term and should therefore clearly be taken into account for a sustainable management. Managers are currently aiming to take account of all possible effects of fishing on the ecosystem (trophic interactions in a multispecies context, habitat disturbance) by the so-called ecosystem-based approach (Caddy 1999, Butterworth and Punt 2003, Rice 2003). Evolution would thus be an important factor to consider therein and add yet another dimension of complexity. In any case, it should be acknowledged that the currently estimated F_{MSY} values based on constant life-histories are not sustainable, and that evolutionary F_{MSY} values can be considerably lower if the current direction of the stock's life-history evolution does not change. As shown in this study, management scenarios could luckily be adapted to reverse the current evolutionary trends which would result in an increase in the long-term yield, for instance by a dome-shaped exploitation pattern.

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Synthesis

NORTH SEA FLATFISH AND LIFE-HISTORY EVOLUTION

The North Sea flatfish offer a convenient case to study life-history evolution. First of all, the exploitation history is rather well documented and extensive samples are available over long time series. The biology of the species furthermore allows to follow life history closely. The distribution in space and time is well known and the flatfish migrate rather small distances relative to e.g. pelagic fish. The nursery grounds are close to the shore and as the fish grow larger, the further offshore they migrate for feeding and return after maturation each year to the stock-specific spawning grounds (Rijnsdorp and Pastoors 1995). Although there might be some gene flow between the stocks, there are reproductively distinct subpopulations (e.g. Exadactylos, et al. 1998, Exadactylos, et al. 2003). The benthic ecology of the species makes its traceability easier and would suggests rather low gene flow between these spawning populations. As such, the extensive monitoring of the exploitation and the traceability of the population in space and time, allows to postulate that observed changes in the observed life history are a response to changing environmental conditions of populations that are more or less separated by reproduction. The fishery might therefore be considered as a large scale experiment in life-history evolution (Rijnsdorp 1993). The environmental conditions experienced by the fish were considered here to consist of a part that is directly fisheries-induced, translating for the fish into a lower survival probability especially at larger sizes, causing the fitness maximum to change and thus leading to FIE, and another part that is indirectly induced by the fishery or not related at all. Since fishing typically affects various trophic levels, it may alter also predation mortality and prey availability on top of the effects on intraspecific competition for food, and all these factors and their interplay may affect the evolutionary optimum. Indicators for intraspecific competition may be obtained from stock abundance estimates but predator and prey interactions were ignored in this thesis, first of all, because too little is known about them. However, a change in predation mortality would in any case be of little importance for the evolutionary optimum relative to the overwhelming fishing mortality. The total natural mortality – of which predation mortality would only be a part – is in plaice and sole assumed to be $M=0.1$ yr^{-1}, whereas the fishing mortality was about $F=0.5$ over the past century, ranging from about $F=0.3$ to $F=0.9$ yr^{-1} (see introduction, chapter 6). Furthermore, there is no evidence for substantial predation of the larger flatfish except from seals in some areas (Hall, et al. 1998). The small benthic prey communities may have increased due to the seabed disturbance by the trawl favoring r- over k-strategists (Hiddink, et al. 2008) and *per capita* food availability may have furthermore increased due to the relaxation of intraspecific competition for food by lower population densities (Rijnsdorp and Van Beek 1991). Both may have increased the component of phenotypic plasticity in growth. Changes in other environmental factors that are not directly related to fishing activity may also have affected the phenotypic plasticity. Average temperatures increased over the study period by about 1°C (Van Aken 2008) and temperature likely has a positive effect on growth (Pepin 1991, Brown, et al. 2004). Temperature will also affect developmental rates (Baynes and Howell 1996, Fuiman, et al. 1998) and may for instance have a growth-independent effect on maturation. Eutrophication, indicated by nutrients in river discharges, peaked in the 1980s and may also have affected growth (Rijnsdorp and Van Leeuwen 1996).

If environmental trends affecting phenotypic plasticity persist over long time periods, the resulting life history might diverge from the evolutionary optimum and the population might therefore react genetically to compensate for the different conditions. The individual fitness is determined by the phenotype in growth, maturation and reproductive investment and the phenotype is thus evolutionarily optimized. If a population at evolutionary equilibrium for instance experiences an increase in temperatures, the optimal strategy, all other environmental conditions being constant, would still be the same but the population now diverges from this optimum because growth is faster due to the increase in temperature, maturation is earlier (as a consequence of increased growth or by a growth-independent effect on maturation). To compensate for this plastic effect, the population would have to adjust its genetic growth, maturation and reproduction components to achieve the optimal strategy again, i.e. by coding for slower growth and postponed maturation (higher PMRN). A similar phenomenon is known for species that are distributed along environmental gradients over which they display identical phenotypes despite the different conditions and is called counter-gradient variation. The field of a temporal counter-gradient variation is unexplored as it would require to perform common garden experiments (where environmental conditions are kept constant) of a species before and after the environmental change that may reveal underlying genetic differences and to assume that the evolutionary optimum did not temporally change, which is impossible in heavily exploited fish stocks. If organisms adapt quickly to phenotypic plasticity, the phenotype could be assumed to represent the optimal adaptation to the current environment. Prediction is furthermore complicated if mortality rates also change with environmental changes, e.g. temperature. The selection force from environmental changes can however generally be assumed negligible compared to the overwhelming fishing mortality.

In the modeling part (chapter 5-7) trends in phenotypic plasticity due to environmental trends that are not related to fishing were ignored, as phenotypic plasticity in this sense was merely expressed as random noise. It could however easily be included in the modeling framework. Fisheries-related phenotypic plasticity was included in terms of density-dependent intraspecific competition for food resources, changes in predator-prey interactions due to exploitation of various trophic levels was not considered. If sufficient information was available the model could be extended also in a food-web sense but this might stretch the limits of complexity. Since the research question on how exploitation affect the life history of a flatfish population, the simplifications made in this thesis seem appropriate.

EMPIRICAL EVIDENCE FROM SINGLE TRAITS

The single trait analysis of the studied flatfish univocally support the hypothesis of FIE. For sole, the PMRN midpoints decrease over four decades although fishing only substantially increased in the 1960s, and also after having included fish condition, an indicator of stored energy that may be used for reproduction, the trend persists (chapter 1). The seasonal timing of maturation, the reliability of its determination, and the individually linked availability of information on factors that may influence it, are critical aspects to bear in mind in all maturation studies (Wright 2007). In many cases, maturity will only be reliably determined shortly before spawning, but the individual development of maturation, i.e. the start of vitellogenesis, was initiated maybe 6 months before spawning, and therefore ideally the individual state determining maturation (age, length, weight and other factors) would have to be analyzed at this moment. As this information is commonly not available, the individual state at the moment when maturity can be determined, just prior to spawning, are analyzed instead for their influence on maturation, ignoring how this state had changed between the actual maturation and the moment of observation. If growth in length is seasonal and mainly occurs in summer, it might be acceptable to neglect the growth in length during winter before spawning, but for growth in weight it remains critical as energy reserves for reproduction are typically stored in body tissues and maturation will thus influence the weight at a given length. Furthermore, the PMRN method ignores that growth will be affected by the maturation initiation as energy is spent for reproduction instead of growth and maturing fish will consequently grow differently than juveniles. However, these drawbacks of the PMRN estimation do not likely affect the trends of in the estimated PMRN over time. Only if there was a temporal trend in growth during the maturation and the moment of maturity observation it might have confounded the temporal trends in PMRN midpoints.

The hypothesis of FIE is confirmed by the principle of exclusion of other potential explanations of observed trends and the criticism remains that maturation might be affected by factors independently of growth. This may be approached by a statistical test where annual averages of potential factors explain variation in the PMRN midpoints (chapter 1 & 4). If the temporal trend is always selected to maximize likelihood and the potential other factors only explain additional variation, FIE seems the most likely explanation. If the potential factors are regressed on the residuals of the temporal trend in PMRN midpoints (e.g. Kraak 2007), the test is whether the potential factor explains additional variation – this does not question the temporal trend itself relative to the other potential variables and does thus not strictly test the hypothesis of FIE statistically. By analyzing the residuals of the temporal trend, the temporal trend itself is already assumed to be the most important explanatory variable *a priori*, i.e. the FIE hypothesis is already accepted *a priori*, and it is thus not tested if some other environmental variable (e.g. temperature) explains the variation in the response better than the mere temporal trend, which would reject the FIE hypothesis. It is therefore not recommendable to sequentially test the likelihood of potentially explanatory variables, but these variables should be tested simultaneously with the temporal trend variable (see chapter 1 & 4). Unfortunately, the best indicators available for the tested variables represent annual averages, for e.g. temperature even at some fixed location. The mechanistic effect of these variables on maturation, if they have an effect at all, is in reality much more complicated than can be captured by these data. Ideally the variables would be included in the reaction norm but for this, taking temperature as an example, the individually experienced temperatures before or during the onset of vitellogenesis would be needed. Since this information is not available, averages have to be used to regress on cohort-wise PMRN midpoints. It is inelegant because many combinations of experienced temperatures and onsets of maturation could lead to the observed PMRN-temperature correlation, yet ignoring that the used temperature average does not even reflect the average of experienced temperatures since it was measured at a location and time different from the individuals when they became mature. A designed experiment to tackle the question of growth-independent temperature effects on maturation suggest that there is a temperature optimum for growth-independent maturation (Dhillon and Fox 2004), but if such an effect really plays a role in the wild remains speculative.

The study on plaice in chapter 2 overviews the life-history traits of growth, maturation and reproductive investment and extends the previous maturation analysis (Grift, et al. 2003) to the early 1900s and to males. The change in the onset of maturation over this time scale is in females of 45% and for males the maturity can hardly be estimated anymore because these mature already before they are caught. For reproductive investment, estimated by the loss in energy content during spawning, a temporal trend could not be tested, because only the analysis of the present period considered the size-dependence of reproductive investment. However, the changes of patterns in the growth curve can be interpreted relative to reproductive life history. All growth models incorporate some logic of energy allocation, and it is surprising that these corresponding interpretations are not put in context more widely. In the case of Von Bertalanffy growth, the underlying energy allocation assumes that the growth rate, the change in weight over time is given by the difference between the acquired available energy and the energy expended for reproduction (Von Bertalanffy and Pirozynski 1952):

$$\frac{\partial w}{\partial t} = aw^{\alpha} - cw$$

where w is the somatic weight, t is time, aw^{α} is the rate of energy acquisition (discounted for the cost of maintenance) and cw is the rate of reproductive investment. The lower exponent for the weight scaling in the energy acquisition than in the energy expenditure rate causes the slope of the corresponding somatic growth curve to decrease until reaching 0 at the asymptotic weight at $(a/c)^{1/(1-\alpha)}$. By integration of the above formula the somatic growth is obtained as a function of size. An immature individual would not have the energy expenditure of reproduction cw, resulting that the size $w^{1-\alpha}$ linearly increases with time:

$$w^{1-\alpha}(t) = w_0^{1-\alpha} + at$$

Where w_0 is the size at age 0. For adults the rate of growth in size $w^{1-\alpha}$ decreases with time:

$$w^{1-\alpha}(t) = \frac{a}{c} - \left(\frac{a}{c} - w_{\text{mat}}^{1-\alpha}\right)\mathrm{e}^{-c(1-\alpha)(t-t_{\text{mat}})}$$

where t_{mat} is the moment of the onset of maturation and w_{mat} is the weight at maturation (given by the juvenile growth curve at $t = t_{\text{mat}}$). Ideally, the juvenile and adult growth functions would be fitted simultaneously to growth data by using a switch function at the onset of maturation t_{mat} and thereby also estimating the parameter t_{mat} (see chapter 3 & 4). However, scientists commonly use the simplified Von Bertalanffy (VB) growth curve comprising the three parameters size at age 0 L_0, asymptotic size L_∞, and the velocity to reach L_∞, k. It may be written as :

$$l(t) = L_\infty - \left(L_\infty - L_0\right)\mathrm{e}^{-kt}$$

where $l(t)$ is the size in length. It becomes obvious that the VB equation is of the same structure as the adults growth curve above. In the VB growth curve the growth rate is a constant function of size because there is no mechanistic onset of maturation incorporated. In the biological interpretation, relating to the adults growth curve above, this means that with VB growth individuals are assumed to be mature since birth. This is a crude assumption but nevertheless, probably because data often consist of mainly adults, VB growth often seems a sound approximation. The above growth functions can thus be directly compared. Becoming mature at age 0 means that $t_{\text{mat}} = 0$ and that $w_0 = w_{\text{mat}}$. The ratio a/c thus relates to L_∞, w_{mat} to L_0 and $c(1-\alpha)$ to k. Because one formulation is based on size in terms of weight whereas the other in terms of length, the scaling of the parameters would change when translating the formulations to the same size unit (assuming a constant length-weight relationship). But in either case, k is directly related to reproductive investment whereas L_∞ is related to the ratio of energy acquisition over reproductive investment. This is the basis for interpretation of VB parameters in chapter 2.

The fitting of an energy allocation growth model with a juvenile and an adult growth curve switching at t_{mat} could be generally used to estimate indicators for intrinsic growth rate, the onset of maturation and reproductive investment (see chapter 3 & 4). For this, only size at age data is necessary and it would therefore significantly reduce the efforts rendered otherwise to directly determine maturity and reproductive investment. To correctly capture the correlation between energy acquisition, onset of maturation and reproductive investment, individual data, i.e. individual growth curves, are needed, because the tradeoffs generating these correlations apply only on the individual level. But if the research question is merely focused on whether there are temporal trends in life-history traits, such an energy allocation growth model might be fitted to cohorts separately. Details for such an analysis are given in chapters 3 & 4.

LIFE-HISTORY TRAIT CORRELATIONS OR TRADEOFFS

The correlated traits of energy acquisition, maintenance, reproductive investment and onset of maturation can be individually assessed at once, thereby also capturing the correlation between them, by fitting an energy allocation growth model to individual age and size data. In fish, individual growth curves can be obtained from otoliths or scales, but it could be applied also to any other organism, for which individual growth can be traced. The trait correlations are of particular interest because they reflect individual life history tradeoffs, which are postulated by fundamental metabolic constraints (Stearns 1992, Roff 2002), but are hardly ever directly measured. The technical drawback of the method is the confounding between the parameters, namely the confounding between maintenance and reproductive investment. Since the maintenance rate was interpreted as the resting metabolic rate (chapter 3), we might assume that it would not differ significantly between individuals of the same species. Mainly the individually experienced temperature regimes might cause some error to this assumption (Kooijman 2000, Brown, et al. 2004), but since these errors would be in the range of about 10% of the true value (chapter 3 & 4), the introduced error by assuming a constant maintenance is likely lower than the error introduced trough the confounding between maintenance and reproductive investment. The constant maintenance assumption inflates the correlation estimates quantitatively, but at least qualitatively the estimates are more stable. The positive correlation between reproductive investment and energy acquisition rate becomes evident assuming a constant maintenance, the onset of maturation correlates negatively with energy acquisition and reproductive investment rates, as was expected from theory.

The major strengths of this method are that life history tradeoffs that were formerly due to speculation can actually be measured and that the knowledge of these tradeoffs may be used to disentangle phenotypic plasticity from underlying genetic effects. In sampling, the probability of occurrence of a fish of a certain age and size is directly related to its survival to that age and size, which is in turn a consequence of its life history. Therefore, the distribution of life-history traits over the sampling ages informs us over the survival probability of certain life history strategies. The decrease in energy acquisition rate over the sampling ages for instance (chapter 4) represents a measure of a growth-survival tradeoff. Food acquisition is commonly assumed to be achieved with foraging activity, hence exposure to predators and therefore increased mortality risk (Stearns 1992, Roff 2002). In evolutionary modeling such a tradeoff is often indispensable because otherwise the growth potential might evolutionarily increase infinitely, but references of such tradeoffs are scarce if not nonexistent. With the individual estimation of life history, this tradeoff could be quantified. Similarly, also reproduction is commonly assumed to bear a survival cost, for instance through mating combats, predation exposure due to mating activity or due to the high energy expenses that have to be well timed with the energy availability in the environment (i.e. a fish that depletes all energy reserves in reproduction might starve if environmental conditions after reproduction are not favorable). The decrease in reproductive investment rate over the sampling ages therefore also quantifies a reproduction-survival tradeoff that could be used in modeling.

EMPIRICAL EVIDENCE FROM CORRELATED TRAITS

The sequence of the events in energy allocation, i.e. energy acquisition and subsequent allocation of acquired energy to growth or reproduction, likely determines the causality between these processes. As the results have shown (chapter 3 & 4), energy acquisition rate is positively correlated to reproductive investment rate and negatively to the onset of maturation. That is, a fish disposing of more energy matures earlier and can invest more into reproduction. Consequently, the onset of maturation and the reproductive investment depend on the surplus energy production. The analysis in chapter 4 presents for the first time an analysis using the information of life-history correlation to disentangle phenotypic plasticity from genetic effects. By allowing for individual statistical random effects, the life-history correlation is accounted for and the found temporal trends are thus conditional on these correlations. Environmental changes have likely caused an increase in energy acquisition which in turn has led to an earlier maturation and an increase in reproductive investment via correlation with energy acquisition. The study of temporal changes however shows that there is likely also a genetic component to these trait changes, the temporal trend being conditional on environmental variability and life-history correlation (chapter 4). Since various life-history traits are analyzed here by controlling for environmental variability and life-history correlation, this might be one of the most integrative studies on FIE in the wild so far. Also the viability selection differentials might be caused by life-history correlation. But controlling for this correlation also showed that viability is higher for low rates of energy acquisition and reproductive investment and late maturation, conditionally on the correlation.

The presented reaction norm for reproductive investment (chapter 4) aims to disentangle phenotypic plasticity in reproductive investment caused by variation in surplus energy over the lifespan. Former studies also postulated an increase in fecundity or reproductive investment but were inconclusive whether this change was due to a genetic effect, because also growth rates and the productivity of the whole system likely increased over the analyzed periods (Rijnsdorp 1991, Rijnsdorp, et al. 2005). If the life history mainly varies as function of surplus energy it appears likely that the life-history traits would vary annually because the surplus energy is mainly affected by the varying environmental conditions. An analysis at this level of resolution is however not possible with individual growth data as the estimated traits are individual lifetime averages. Our approach has thus the benefit to obtain size-specific estimates of surplus energy, which is otherwise difficult, but the disadvantage of not considering interannual variation. The method however elucidates that the energetic reproductive output is not a meaningful estimator of the energy allocation to reproduction, since all considered life-history traits are confounded in this reproductive output. A much purer estimate for the individual life-history "decision" on reproduction is therefore the size-specific reproductive investment rate c, not confounded by other traits. As this estimate is size-specific, it provides the best reproductive investment reaction norm, better than any reaction norm derived from size-dependent traits, because in these size-dependent traits the considered size-specific life-history traits will be confounded.

The conclusion is thus that fishing has selected for higher energy acquisition, higher reproductive investment and earlier maturation. For the onset of maturation and reproductive investment this is in line with predictions from life-history theory, for energy acquisition there is no straightforward prediction. Surprisingly, the viability differentials are opposite to the evolutionary response. The fecundity selection differentials therefore must be opposite to and relatively more important than the viability selection differentials. As for the other traits, the change in energy acquisition therefore must be due to an advantage in fecundity and not to an advantage through mortality avoidance.

FISHING IMPLICATIONS OF LIFE-HISTORY VARIATION

Sole has a higher turnover rate than plaice, i.e. has higher rates of energy acquisition, maintenance, reproductive investment, and an earlier onset of maturation. This result may be interpreted by differences in the spatial environment. Soles live in shallower waters and experience therefore higher temperatures, which at least partly explains the higher metabolic rates. It would be interesting to apply the method to other specimen of different environments. In general, deep sea species have a lower pace of life than species occurring in more shallow waters. The orange roughy (*Hoplostethus atlanticus*) for instance occurs in 200-2000m, matures at about age 25, has a relatively low fecundity and might become about 125 years old (Thresher and Proctor 2007). This slow paced life history makes these populations extremely vulnerable to overfishing, as fishing more likely removes all adults individuals in one run and thereafter it might take years until the adult population recruits to sustain reproduction again (Koslow 1996, Koslow, et al. 2000). Deep sea trawling has increased in the recent decades as a consequence of overfishing the shallower waters. Because of the slow paced life history these previously non-fished deepwater stocks were typically fished down within 5-10 years. Most of the deepwater stocks are today overfished or even depleted (Koslow, et al. 2000). If populations with a slower paced life history manage to adapt to exploitation, the selection pressure is higher than if their life history was of a faster pace. In a simplified perspective, the evolutionary pressure is given by the difference of the age at which the fishing mortality becomes substantial relative to their total lifespan and to their onset of maturation, i.e. by the number years in the juvenile or adult stage for which fishing is substantial. Evolution can only occur if individuals survive until reproduction. In a population with later maturation and/or faster growth, the evolutionary selection pressure for a life history change will therefore be higher for a given typical (size-selective) fishing regime. As plaice and sole are caught in a mixed demersal fishery, the fishing mortality can be expected the same for both species. However, plaice becomes mature later and is larger at a certain size, and therefore experiences a stronger evolutionary pressure. Hence, in a FIE perspective, larger life history changes in plaice can be expected, also for the future.

ORIGIN AND IMPORTANCE OF SSD

As in many other species, North Sea flatfish are sexually size dimorphic, the males growing slower, maturing earlier and investing less in reproduction (Rijnsdorp and Ibelings 1989). A general hypothesis suggests that male size will be determined by sperm competition, i.e. the probability that a female will be mating with another male (Parker 1992): High sperm competition might even result in combat where a large size is of advantage, whereas with low sperm competition, the male's only function is to deliver sufficient sperm to fertilize the available eggs. However, although this may explain differences in male sizes across species, it does not explain the male's size relative to the female's size in a specific species. It has been argued that males have a lower energy acquisition after maturation or once they grew out of the predator's preferred size window than females (Henderson, et al. 2003). Another explanation of female-biased dimorphism is that males have additionally to the energetic expenses for gonads a higher behavioural cost of spawning activity, e.g. due to courting (Rennie, et al. 2008). This would mean that despite the typically lower gonadic costs, the total reproductive investment, i.e. the sum of the gonadic and the activity cost, would be higher in males than in females leading to a lower somatic growth. However, the mechanistic origin of these potential explanations has not been explored nor have these been evolutionarily tested. Why would the males have a lower energy acquisition rate than females? And why would a higher activity cost, i.e. a higher reproductive investment not induce a higher energy acquisition rate to compensate for the energetic loss? The hypothesis of a higher activity cost in males was based on the assumption that males somewhere lose acquired energy relative to females, and on the competition during reproduction. The higher reproductive activity of males in reversed or female-biased sexual size dimorphic species has barely ever been measured in nature. The evidence in flatfish shows that males invest less into reproduction (chapter 2). The eco-energetic model (chapter 5) explored such mechanistic causes of female-biased sexual size dimorphism. Indeed, the results show that a higher male activity cost can not explain slower growth, because a higher reproductive investment would evolutionarily be compensated by a higher energy acquisition rate. It is rather because male reproductive investment is lower that males are not driven to acquire as much energy as females and also therefore achieve the threshold of disposing of enough energy reserves to become mature earlier. The reproductive investment in males is smaller because less investment, relative to females, is sufficient to maximize fitness. The basis for this lies in the reproductive biology of the flatfish but might be generally valid for species with similar reproductive constraints. In flatfish and other teleost taxa, reproduction occurs in restricted time windows. The mating opportunities of males are therefore limited and since the presence of females peaks in a certain time interval, the male spawning efficiency decreases if the spawning activity is extended beyond that interval and consequently, the benefit of increasing reproductive investment decreases. This causality was mechanistically included in the model (chapter 5) by a diminishing return of reproductive investment for the reproductive fitness, and this diminishing return is the necessary condition to explain reversed or female-biased SSD. This may not only apply to the North Sea flatfish but also likely plays a role in many other species.

The dimorphism could have consequences for differential responses to exploitation. Data from the early 1900s indicate that the dimorphism might have been weaker, and thus the relative change in life history might have been larger in males (Rijnsdorp 1989). Because of the diminishing return of reproductive investment and the higher mortality rates in males due to spawning activity, it might pay off relatively less to invest more into reproduction, to grow and to postpone maturation, as soon as mortality increases. The higher pace of evolution in males could be shown in a real time exploitation simulation (see chapter 6). However, the parameterization of such a model including males and females would be critical, since the model can only be fitted to data representing transitional evolutionary states. The initial state of the population as well as the evolutionary endpoint are not known but these would be necessary to fit a model apt for a quantitative prediction for the pace of male life history relative to females. By fitting transitional states, different model assumptions imply different assumptions on the initial state and the evolutionary endpoint, which would however be determinant for the evolutionary pace. Therefore, although fitting a sex-structured model for the real time exploitation might be complex but possible, the argument for the conclusions on the evolutionary pace would not be strong. It might also be possible that the life-history evolution in one sex might have influenced the evolution in another sex. Exploring this question would however require a much broader knowledge of the genetic basis of life-history traits and their inheritance and the corresponding modeling would likely become too complex to be grasped. For simplicity we assumed that males and females inherit two versions of a gene, a male and a female version, but only express the one corresponding to their sex. That is, we assumed perfect sex-linkage of the modeled life-history traits. Perfect sex-linkage is unlikely to be the case in reality but since there is no basis to assume anything else, which would furthermore only complicate the results, it seems a sound working hypothesis. As a consequence, male and female life history can as well be modeled separately in separate models. We might assume that the evolutionary consequences of fishing are at least quantitatively similar between the sexes.

MODELING FIE & MODEL ACCURACY

The focus for further investigations (chapters 6 & 7) was thus on females only. The model was fitted to a moment in the past and to the present by adapting the additive genetic variances. Fishing mortality rate could be adapted instead to adjust the evolutionary pace but since the genetic variance is not known whereas the level of fishing mortality is well reported, the simplification of a constant fishing mortality rate was made. Fishing mortality rates in reality varied substantially (see introduction, chapter 6) but assuming a constant fishing mortality seemed appropriate because the research question was not on the effect of variability in fishing mortality – a question that might be addressed in the future. The model is unique in using the realized fishing mortality rate F, given by the numbers of fish caught relative to the total numbers of fish in the sea, (and keeping it constant by updating the mortality function) which makes it directly comparable to the F's in fisheries management declared by ICES. Other models using a constant mortality-size relationship miss the fact that the realized fishing mortality changes if a population evolves as its size distribution changes and consequently ends up at a different position on the mortality size curve. The evolution of realized fishing mortality when assuming a constant mortality-size relationship would thus falsify the comparison with an estimated realized F. The model is furthermore unique by fitting the growth, the PMRN and reproductive investment all together over the individual lifespan. When fitting PMRNs it should be considered that the published estimates typically define the PMRN retrospectively, i.e. defining the maturation probability as the probability at an age and size of having become mature in the previous year. In the modeling however it will be more common to define the maturation probability prospectively, i.e. as the probability at an age and size of becoming mature in the subsequent year, because growth in the year of maturation might be modeled to be reduced as a consequence of the reproductive cost. A separate PMRN estimation is therefore necessary. The modeled life-history consequences of fishing are rather clear and as expected: (i) increase in the maturation probability at age and size; (ii) increased reproductive investment; (iii) energy acquisition rates initially increase but decrease thereafter, consequently resulting in smaller fish. The change in the direction of energy acquisition evolution is intriguing as growth rates in North Sea flatfish indeed tended to increase in the mid-century (Rijnsdorp and Van Beek 1991, chapter 4) but seem to decrease at present (after 100 years of exploitation in the model, see e.g. chapter 2). It might be explained by some threshold effect of the number of fish starting to become to mature at a size smaller than the minimally exploited size, because evading fishing mortality by diminishing growth only makes sense if maturation can be reached before achieving the vulnerable size window. If a size is reached as a juvenile already for which exploitation rate is maximal, it might be advantageous to be larger relative to other fish experiencing the same maximal mortality. As a general prediction, we might expect an earlier maturation at younger age and smaller size and an increased reproductive investment due to size-selective mortality. The prediction of the selection on energy acquisition depends rather on the specific case. Depending on the life-history prototype, the selection of intrinsic growth potential might go in both directions (Dunlop, et al. 2009). As shown here, the minimally exploited size and the pace of evolution of other traits might play a role additionally to the prototype.

However, caution is needed for quantitative interpretations of the model, because the model is fitted to states representing evolutionary transitions but the initially unexploited population and the evolutionary endpoint are not known. Parameter fitting was therefore based on the assumption that the fitted population is at evolutionary equilibrium (chapter 5). This is obviously not true but would affect the assumption on the initial and final population and thus also future projections (chapter 7). Although the model predictions fit the observations over about 100 years, the lack of knowledge of the initial and the final state of the population implies that the same fit might have been obtained with different parameters using different assumptions in the model calibration. This does however not really affect the questions on the life-history effect of exploitation. Future projections (chapter 7) might be quantitatively prone to error, but will be valid qualitatively. The eco-genetic model is a crude simplification of reality, despite its complexity, as it only considers life-history changes due to evolution and to demographic effects of fishing in the exploited species, although many other things may have changed in the environment. For instance food availability, temperature and the predator community are all factors that have changed over time and are likely to have influenced the observed life history. The model could incorporate these effects – the effect of food availability could be included by adding to the phenotypic plastic component of energy acquisition, the temperature adding to the phenotypic plastic effect of all metabolic rates with an appropriate relationship with temperature and the predation community with a change in the predation mortality curve – if these processes were known quantitatively. However, the interest here was to study which genetic changes could be expected and interactions with environmental changes would have complicated the question and would have obscured the results. This means that the effects of genetic selection might in reality not be as strong as predicted by the model, because in reality also another environmental change might have contributed to the observed life history change. It seems for instance likely, that some part (about 14%, chapter

2) of the decrease in the PMRN is attributable to the increase in temperature and the prediction of the model would therefore be too high by about 14%.

MANAGEMENT IMPLICATION AND RECOMMENDATIONS

The management implications of FIE for North Sea flatfish is shown by the relative yield change due to evolution (chapter 7), which translates directly into a monetary cost of evolution – which is likely the most straight forward motivation to convince managers to mitigate for it. It seems not surprising that the yield decreases if the population life history evolves towards earlier maturation, increased reproductive investment and decreased intrinsic growth rates, i.e. if the fish stay on average smaller. Nevertheless, as the long-term yield loss was so far rather speculative, the study on the yield change due to FIE (chapter 7) is unique as it provides for the first time a quantitative prediction for a specific fish stock. Because the modeling captures the relevant aspects of the species biology and the simulated exploitation rates are directly comparable to the ones estimated in virtual population analysis (VPA), also the relationships of fishing mortality and long-term yield resemble the ones estimated in VPA. As VPA assumes a constant, non-evolving life history, the results of the scenario where life history is "frozen" at the start of the management implication (chapter 7) relate to the VPA estimations of the mortality-yield relationships. Comparison with the scenario where life history evolves show that the VPA estimates must be, despite the large associated estimation error, substantially wrong. The yields of the evolving population are for the currently assumed flat exploitation pattern much lower, because the population life history will still evolve in the future and consequently the yield will decrease. The model might not represent reality mainly because it was parameterized without knowledge of the initial state and the evolutionary endpoint (see above) but the representation is valid qualitatively. Since yield evolves due to the changing population's life history, the yield calculated in VPA assuming constant life history can no longer be called sustainable and the terms of maximal sustainable yield MSY has therefore been replaced by maximal yield MY. In the model, the yield of the evolving population only stabilizes after about 1000 years of exploitation and might thus deserve to be called sustainable only at this time horizon. The relative yield loss due to FIE is given for a certain exploitation regime by the difference in yield-mortality curves between the evolving and the non-evolving populations, and might be standardized relative to the initial yield of the corresponding exploitation regime (see chapter 7). This approach might be used routinely for other stocks to determine the evolutionary impact assessment (Jørgensen, et al. 2007) as soon as a species specific eco-genetic model is available.

The exploration of different management scenarios affecting the selectivity of fishing mortality have shown that the evolution in the undesired direction, i.e. towards decreased energy acquisition rates, earlier maturation and increased reproductive investment rates, is amplified, if larger mesh sizes would be used, but might be reversed, if more medium-sized fish instead of large fish would be caught (dome-shaped exploitation pattern, chapter 7). With a constant realized exploitation rate – i.e. the number of fish caught relative to the total number is constant – using larger mesh size means that the larger fish are exploited more efficiently. The effect of mesh size might not be important if for instance a constant catch regime was applied, because then less of the larger fish would be needed to achieve the same catch of biomass. In either case, increasing mesh size could not mitigate for FIE. Mitigation of FIE only seems possible if the large fish are protected, i.e. by smaller mesh sizes or by a dome-shaped exploitation pattern. In the North Sea, a dome-shaped exploitation pattern can be realized due to the size-dependent spatial distribution of fish. The large fish would be protected by reducing fishing effort further offshore or during the spawning season when the adult fish aggregate on their localized spawning grounds. There is thus hope that something can be done against FIE and that thereby also the long term sustainable yield relatively increases. It has been shown that recovery of fish stocks that have undergone evolutionary changes can be slower than FIE (Law and Grey 1989, Law 2000, De Roos, et al. 2006, Conover, et al. 2009, Enberg, et al. 2009), because the selection pressure in the opposite direction of FIE in the absence of fishing is much lower. This would be certainly also the case in flatfish. But application of a dome-shaped exploitation pattern also shows that FIE may be reversed by applying a specific selection that protects larger fish, i.e. that recovery could be accelerated also by exploitation. The problem in practice is that protecting the large fish results in a loss in the instantaneous yield. There is thus a tradeoff between protecting the large fish, resulting in attenuated or even reversed FIE and consequently higher stable long-term yields, and targeting the large fish, resulting in a high instantaneous yield. The optimal strategy therefore lies somewhere in between at an intermediate dome-shape for the exploitation pattern at a relatively low exploitation rate $F<0.2\ \mathrm{yr}^{-1}$. This is thus still much lower than $F=0.3\ \mathrm{yr}^{-1}$ targeted by the European Union (being a political but not a scientific decision), which is obviously due to the lack of the impact assessment of FIE. It will mainly depend on the time horizon managers are apt to consider to maximize the yields of their fisheries. If they go on being worried about the short-term yield in the next 5-10 years, protecting the large fish will indeed not yet compensate for the short term gain in catching the large fish. However if they care that their children and grandchildren still might be able to consume the same fish, protecting the large fish appears indispensable to mitigate for the negative impact of FIE on the yield.

At some point the long-term evolutionary loss might exceed the short-term gain in yield by not protecting the large fish (chapter 7, Fig. 6 below). The duration t_{evol} after which this switch occurs depends on the imposed management scenario. The management might be adjusted such that t_{evol} is as far as possible in the future. The fishing mortality rate F_{evol} would have to be found at which the switch occurs at a given t_{evol}, and managers would have to make sure then that the fishing mortality $F< F_{\mathrm{evol}}$. Optimally, the management is optimized by stabilizing the population life history and hence the yield by protecting a part of the large fish by imposing a dome-shaped selection pattern. In any case, there is also a risk in proposing a too flat exploitation pattern or too large mesh sizes, which would result in a short-term yield advantage. If the realized fishing mortality is higher than the proposed fishing mortality, the consequences of a flatter exploitation pattern and larger mesh size might quickly become deleterious. The switch when the long-term evolutionary loss exceeds the short-term gain in yield by not protecting the large fish will occur earlier under higher mortality rates (chapter 7, Fig. 6 below).

The evolution towards dwarf morphs under high exploitation rates (chapter 7) might be seen as an extrapolation of the model, but its mechanistic basis is rather realistic. Dwarf morphs occur in the model due to a switch effect when the fishing effort needs to be increased exponentially as the population quickly evolves, in order to maintain a constant realized exploitation rate. It seems unlikely that in reality fishing effort increases that much such that dwarf morphs might actually evolve, because such a scenario would not be economically sustainable. The evolution towards dwarf morphs seems nevertheless intriguing, as for instance in flatfish dwarf morphs indeed exist (Gibson 2005). Even if it seems unlikely that this evolution would be human-induced, it can not be excluded that dwarf morphs evolved due to high (natural) mortality rates in a certain microenvironment. The evolution of fishing efforts is however realistic and troublesome. As the population evolves towards smaller size, fishing effort has to be increased to maintain a constant realized exploitation rate, also in reality. This has direct economic consequences since economic costs of fishing effort increase, whereas the yield, consisting of smaller and smaller fish, decreases. Fishing thus becomes less and less efficient and the cost-benefit calculation becomes more and more negative.

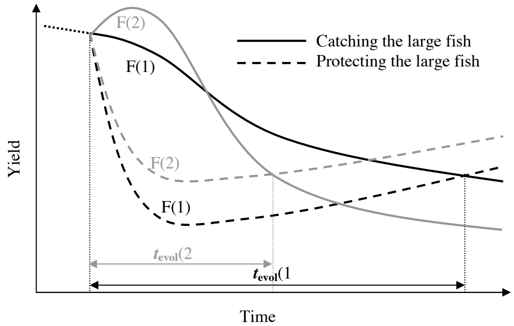

Fig. 6: Illustration for a concept of evolutionary enlightened management. If large fish are caught e.g. with a flat exploitation pattern or/and large mesh sizes the yield will continuously decrease due to life-history evolution (solid line) but if large fish are protected e.g. with a dome-shaped exploitation pattern or/and small mesh sizes the yield will initially drop but thereafter stabilize or even increase again due to reversion of evolutionary trends in life history (dashed lines) under a certain fishing mortality rate F(1). For a higher mortality rate F(2) the initial yield might be higher than if fishing with a lower mortality rate but the continuous decrease in yield for the scenario catching the large fish, and the increase in yield due to the reversion of the life history trend for the scenario protecting the large fish is likely steeper, resulting in a relatively lower and higher yield respectively in the long term. The time t_{evol} at which the yield of the scenario protecting the large fish exceeds the yield of the scenario catching the large fish thus depends on the fishing mortality rate F. Management might either target a F for a given t_{evol} or target a t_{evol} for a given F.

FURTHER DEVELOPMENT

Further evidence for FIE is thought to be brought from direct genetic analyses. Showing that genetic markers that are associated to certain life-history traits have changed over the time of exploitation might also support the hypothesis of FIE. Since there is a genetic background variation of neutral markers influencing the coding marker's variation, this neutral variation would have to be disentangled to infer on a change in the coding markers. The procedure to infer on FIE would thus be comparable to the disentangling of phenotypic plasticity presented in this thesis.

The idea of proving genetic change by analyzing the change in genetic markers is somehow compelling. However, the phenotypes of life histories are translated from genes by epigenetic mechanisms by several coding areas, which are never entirely understood. Because of the complex interaction between these coding areas, we could not explain how a set of coding bits results in a certain phenotype, even if the coding areas were known. The direct genetic analysis therefore faces the problem that when looking at something, it can not really be defined what it is in the perspective of the phenotype, a problem that obviously does not exist in the direct analysis of phenotypes. Furthermore, proving evidence for FIE by changes in genetic markers will still face the same problem about the causality of the fisheries-induction. As in the studies presented here, there will be no formal proof that an observed change was caused by selection due to higher exploitation, and the hypothesis of FIE can therefore only be supported by the principle of exclusion of other potential causes. But also a change in genetic markers might have been caused by other changes in the environment, such as a change in temperature. As in the studies presented here, the influence of such environmental influences would need to be disentangled, but this is unlikely achievable in practice on a genetic level.

The genetic analysis might be a nice complement to the existing evidence of FIE but does not seem necessary to corroborate its basis. It has been shown here that FIE is not fiction and that it has undesired consequences. The findings of this thesis should at least for North Sea flatfish cause enough worries to take action.

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TRAINING AND SUPERVISION PLAN

Fabian Mollet

The Graduate School
WAGENINGEN INSTITUTE of
ANIMAL SCIENCES

Description	**year**	**ECTS**[*]
Professional skills courses		
Techniques for scientific writing	2006	3.0
Statistical methods for longitudinal and incomplete data	2006	0.6
Applied geostatistics	2006	0.6
Introduction to FLR	2006	0.9
Evolutionary modeling	2006	0.6
Didactic skills training		
WIAS introduction course	-	W[**]
WIAS course on philosophy of science and ethics	2009	1.5
Organisation of FishACE meetings and workshops	2006	0.9
Tutorship of MSc students	2008	0.9
Scientific exposure		
Conferences		
International Council of Exploration of the Sea (ICES), Maastricht, Netherlands	2006	1.5
North Atlantic Fisheries Organization (NAFO), Lisbon, Portugal	2007	0.9
American Fisheries Society Symposium (AFS), Ottawa, Canada	2008	1.5
7th International Flatfish Symposium (IFS), Sesimbra, Portugal	2008	1.5
Diversification, Adaptation and Speciation (IGB), Berlin, Germany	2009	0.9
Meetings, seminars and workshops		
FishACE meetings and workshops within Europe	2006-2009	10.3
Marie-Curie secondments within Europe	2006-2009	6.9
Study group on fisheries-induced adaptive change (SGFIAC) within Europe	2007-2010	3.3
Young Scientists Summer Program (YSSP) at IIASA, Laxenburg, Austria	2007	5.7
FinE meetings and workshops within Europe	2007-2010	6.2
Oral presentations at international conferences and meetings	2006-2010	19.0
Total		**66.7**

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[*] One ECTS credit equals a study load of 28 hours

[**] Waiver granted by WIAS due to high international scientific exposure

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