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THINKING BEYOND THE DATA

Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence

Katja Enberg[1,2], Christian Jørgensen[1,5], Erin S. Dunlop[1,2,6], Øystein Varpe[1,3,7], David S. Boukal[1,2,8], Loïc Baulier[1,2,9], Sigrunn Eliassen[1] & Mikko Heino[1,2,4]

1 Department of Biology, University of Bergen, Bergen, Norway
2 Institute of Marine Research, Bergen, Norway
3 The University Centre in Svalbard, Longyearbyen, Norway
4 International Institute for Applied Systems Analysis, Laxenburg, Austria
5 Uni Research, Bergen, Norway
6 Present address: Aquatic Research and Development Section, Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada
7 Present address: Norwegian Polar Institute, Tromsø, Norway
8 Present address: Laboratory of Theoretical Ecology, Institute of Entomology, Biology Centre AS CR, České Budějovice, Czech Republic
9 Present address: Department of Fisheries Sciences and Technologies, Ifremer, Lorient, France

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Correspondence
Katja Enberg, Institute of Marine Research, Box 1870 Nordnes, N-5817 Bergen, Norway.
E-mail: katja.enberg@imr.no

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Abstract

The interest in fishing-induced life-history evolution has been growing in the last decade, in part because of the increasing number of studies suggesting evolutionary changes in life-history traits, and the potential ecological and economic consequences these changes may have. Among the traits that could evolve in response to fishing, growth has lately received attention. However, critical reading of the literature on growth evolution in fish reveals conceptual confusion about the nature of 'growth' itself as an evolving trait, and about the different ways fishing can affect growth and size-at-age of fish, both on ecological and on evolutionary time-scales. It is important to separate the advantages of being big and the costs of growing to a large size, particularly when studying life-history evolution. In this review, we explore the selection pressures on growth and the resultant evolution of growth from a mechanistic viewpoint. We define important concepts and outline the processes that must be accounted for before observed phenotypic changes can be ascribed to growth evolution. When listing traits that could be traded-off with growth rate, we group the mechanisms into those affecting resource acquisition and those governing resource allocation. We summarize potential effects of fishing on traits related to growth and discuss methods for detecting evolution of growth. We also challenge the prevailing expectation that fishing-induced evolution should always lead to slower growth.

Introduction

In recent years, the potential evolutionary consequences of fishing have received considerable attention (reviewed and discussed in Law 1991; Dieckmann & Heino 2007; Jørgensen *et al.* 2007; Kuparinen & Merilä 2007; Marshall & Browman 2007; Fenberg & Roy 2008; Hutchings & Fraser 2008; Naish & Hard 2008; Dunlop *et al.* 2009a). For harvested stocks, the requirements for harvest-induced evolution are typically fulfilled, namely that: (i) fishing is selective on phenotypic traits, either because the gear in use is actively targeting fish with certain traits (see Hamley 1975 for a review of gill net selectivity) or because elevated mortality in general favours traits expressed early rather than late in life; and (ii) there is heritable genetic variability for several of these traits (Gjedrem 1983;

Carlson & Seamons 2008). Furthermore, exploitation rates are often several-fold higher than natural mortality (Mertz & Myers 1998) so the overall selection might be strong. Fishing is therefore likely to influence the course of evolution, but what is not immediately obvious is which traits will evolve, in which direction and how quickly will evolution proceed, how important will it be relative to other forces causing phenotypic change, and, finally, how we can best manage any potential consequences.

One life-history trait that is expected to evolve in response to fishing is growth rate. Early literature on fishing-induced evolution of growth was dominated by the hypothesis that fishing would select against fast-growing, large fish because fishing mortality typically increases with body size (eventually exceeding natural mortality in most exploited stocks), and that growth could consequently evolve towards slower rates (Rutter 1902; Miller 1957; Favro *et al.* 1979; Kristiansen & Svåsand 1998). This hypothesis is intuitive and has been reiterated many times, but serious attempts to test or evaluate it were for a long time restricted to Ricker's (1981) classic work on the declining size of Pacific salmon. Within the last decade, there has been a resurgence of studies on fishing-induced evolution of growth, both from experiments (Conover & Munch 2002; Biro & Post 2008) and from examinations of wild populations (Edeline *et al.* 2007; Swain *et al.* 2007). The work by Conover & Munch (2002) drew considerable media attention and scientific debate (Hilborn 2006; Conover & Munch 2007). The same occurred with the study by Edeline *et al.* (2007), which was included among the journal *Nature*'s research highlights of 2007 (Anonymous 2007, see also Conover 2007) and was praised elsewhere (Coltman 2008). However, these studies have revealed that predictions on the direction of evolution of growth are more complex than was thought when the first hypotheses were formulated. In particular, many studies confuse growth rate with size-at-age, or treat growth rate as the evolving trait without considering other traits and processes that influence size-at-age. Here we aim to address the confusion by a concept-oriented review of mechanisms that affect growth (and consequently size-at-age) through their impact on the acquisition and allocation of resources. We further interpret each mechanism in light of fishing-induced evolution, and expose the difficulties associated with the measurement of growth rate from field data. Finally, we consider the achievements of the field as a whole and where future research is needed.

Definitions and Key Concepts

It is often deceptive to think of growth as a single trait, when instead it is the outcome of a complex suite of behavioural, morphological and physiological processes. These processes relate to both incoming resources and subsequent partitioning of those resources, and in particular to how surplus resources are allocated among competing needs. Different components of growth are therefore subject to various selection pressures, making evolutionary change in growth inherently difficult to predict and quantify from data. In this section, we first provide key definitions, and highlight areas where misconceptions typically occur. Our approach and definitions are inspired by foraging behaviour (Lima & Dill 1990), a life-cycle perspective to energy allocation (*e.g.* Roff 1983; Kozlowski 1992), and energy budgets and flows within individual organisms (*e.g.* Kooijman 2010).

Acquisition, allocation, and growth

Key processes involved in energy budgeting within an individual are resource acquisition, resource allocation, and growth (Figs 1 and 2). We define *resource acquisition* as the processes involved in foraging, ingestion and digestion. Resource acquisition controls the total amount of resources available to the organism, and these are *allocated* to various competing needs.

Some of the resources are allocated to running costs of the organism: mainly its basal metabolism (often quantified as resting metabolism), digestion and routine activity (Fig. 2). Basal metabolism represents a set of basic processes needed to remain alive and functional (*e.g.* maintenance, immune defence and cognition). Note that allocation to, for example, cognition, movement and digestion may increase the organism's potential for resource acquisition, so allocation and acquisition are not completely separable. Of special importance for this review is the availability of resources after basal metabolism and

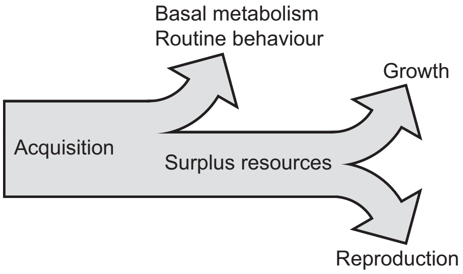

Fig. 1. Simplified representation of the basic logic of resource flow underlying growth. Acquired resources are allocated to three main components: (i) the 'running costs' of an individual including basal metabolism and routine behaviour, (ii) somatic growth including structures and stores, and (iii) reproduction. Before maturation, changes in surplus resources will translate directly into changes in growth, whereas a proportion of the surplus resources is allocated towards reproduction from maturation onwards. A more comprehensive flowchart is shown in Fig. 2.

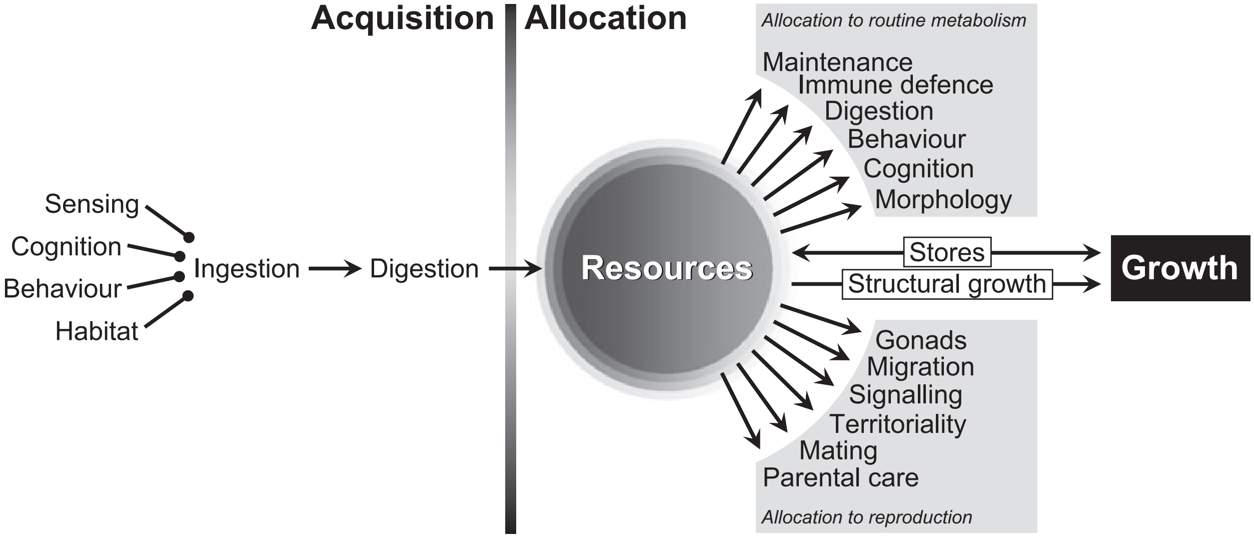

Fig. 2. Resource acquisition (left) and allocation (right) are both adaptive processes. The amount of acquired resources is affected by many processes influencing foraging and ingestion, which after digestion translates into available resources. Resources allocated to routine metabolism, reproduction and structural growth are generally not available for later use, whereas resources deposited in stores can be utilized later. Changes in any of the components affecting resource acquisition or in how the acquired resources are allocated may lead to altered growth.

routine activity have been accounted for, and we term these *surplus resources* (Fig. 1). Surplus resources are often termed 'surplus energy' (Ware 1975; Roff 1983) or 'growth effort' (Abrams & Rowe 1996); by referring to 'resources' we acknowledge that not only is the total energy important, but the nature of that energy (*e.g.* its nutrient composition) has consequences as well (*e.g.* Pulliam 1975; Blount *et al.* 2000; Grandison *et al.* 2009). During the immature phase of the life cycle, surplus resources will result in *somatic growth*, which includes the growth of all tissues in the body except for germ cells; it is therefore distinguished from *reproductive investment*, which allocates a proportion of the surplus resources to reproduction as the individual becomes sexually mature.

Size is a state, growth is a process

Individual body size is of profound ecological importance. Larger individuals usually have increased survival, are more successful at attracting mates, have higher fecundity, have an enhanced capability to withstand starvation, and are better in competition for resources (Peters 1983). However, food requirements are generally higher for larger animals, and growing big takes time and resources. There are thus several components in a cost–benefit budget that jointly determine the evolutionary advantages and disadvantages of having a particular size. Behavioural and life-history strategies will therefore often be size-dependent and change as an animal grows (McNamara & Houston 1996). From a fisheries perspective, the size distribution of individuals also has a strong influence on population dynamics, including recruitment (Persson *et al.* 2007) and fisheries yield (Law & Grey 1989; Conover & Munch 2002).

Growth and size are intimately linked and often correlated (for example, fast-growing individuals are often big) but, obviously, they are not the same. For example, large individuals may, when they use their resources for reproduction, grow more slowly than smaller fish. Thus, whereas body size characterizes an individual's *state*, growth is the *process* that leads to that state. For example, it can be risky to grow fast, but once a certain size is attained, the payback in terms of survival or reproduction can be good.

It is tempting to think that selection on growth could be fully understood by studying selection on size, or *vice versa*, but this is not the case. To be able to grow to a certain size, an individual needs to acquire resources through foraging, usually at a cost of exposure to predators, parasites and infections. From an evolutionary perspective, it is therefore important to separate between the advantages of being big and the costs of growing to a large size. Consequently, there can be selection not only on body size but also on the growth-related processes that allow the individual to attain a certain size. Growth and size are coupled, so selection on one may lead to indirect selection on the other, and growth and size may also be correlated with other traits under selection.

Observing growth directly implies measuring changes in size over time, and growth per unit of time is referred to as *growth rate*. The most common measures of growth rate in fish are length increment or body mass increment per time (for other definitions see Dmitriew 2011). These measures differ in one important aspect: increase in length is usually irreversible, whereas weight can increase or decrease as stores are deposited and utilized, or as gonad mass is built and spawned.

Growth is evolutionarily optimized, not maximized

In the past, growth was often regarded as a trait that should, under natural selection, evolve towards maximum rates, within the limits of physiological constraints (*e.g.* Ricklefs 1969). However, there may be several benefits of sub-maximal growth, and it was surprisingly recently that growth became more widely regarded as being evolutionarily optimized rather than maximized (in large part due to the review by Arendt 1997; but see also Case 1978). Two well-documented phenomena clearly support this conclusion in fish. First, when individuals are given excess food after a period of food deprivation, they often grow faster than control groups that are fed *ad libitum*. This phenomenon, referred to as compensatory growth or catch-up growth (reviewed in Metcalfe & Monaghan 2001; Ali *et al.* 2003), illustrates how growth rate is normally well below the physiological capacity (Sundström *et al.* 2007). A wide spectrum of delayed and immediate costs of compensatory growth have been identified (Arendt 1997; Metcalfe & Monaghan 2001; Arendt & Reznick 2005; Mangel & Munch 2005), further suggesting that although faster growth is possible, it implies costs, particularly in terms of survival. The ability for fast growth may, for example, be costly in terms of starvation tolerance: a recent study in European sea bass *Dicentrarchus labrax* identified a positive correlation between the rate of mass loss during a starvation period and the growth during a subsequent compensatory period (Dupont-Prinet *et al.* 2010).

Countergradient variation is another phenomenon that shows a clear role for local adaptations in growth (Conover & Present 1990). In the wild, populations experiencing different growth conditions may show comparable growth within a season, even though there might be considerable differences, for example, in the length of the growing season or temperature along a latitudinal gradient. One species where countergradient variation has been studied is the Atlantic silverside, *Menidia menidia*, a small annual fish found along the east coast of North America: in common garden experiments, individuals from the northern populations grow faster than their southern counterparts, indicating a genetic basis for the difference (Conover & Present 1990). The northern population's increased growth rate in the lab compensates for shorter growing season in the wild, so that when different populations are sampled in their native environment, the differences in size-at-age are smaller than the local environment would prescribe (Conover & Present 1990). Countergradient variation has also been observed in a number of other fish species and other taxa (Conover & Schultz 1995).

Compensatory growth and countergradient variation demonstrate that growth is evolutionarily 'optimized' at levels below the physiological capacity. Which trade-offs cause adaptive differences in growth between individuals, populations and species? Is it possible to predict how the mechanisms underlying growth may evolve in response to fishing? In the remainder of this paper we try to answer these central questions by splitting growth into several processes and analyzing each process separately. We describe selection on growth-related traits in a natural setting, and how that selection may be modified due to fishing. In practice we do this mainly by identifying the underlying trade-offs and evaluating how the costs and benefits change from the natural setting to one in which fishing occurs.

Factors Affecting Growth

Even though growth is usually observed as one variable (the rate of change in size) the process of growth consists of two main components: acquisition of resources and subsequent allocation to different needs. Below we provide a conceptual review of factors affecting observed growth rate. Although we attempt to break growth down into component processes, it is important to keep in mind that there are developmental constraints, shared mechanisms, delayed effects, variable heritabilities, and genetic correlations that may influence phenotypic expression as well as the ability of each trait to evolve. On top of this, growth is also very sensitive to environmental conditions, so for any phenotypic effect one needs to bear in mind that there might be genetic influences as well as phenotypic plasticity.

Key processes: resource acquisition and allocation

Organisms have a limited amount of resources they can use, not only for growth, but also for storage, reproduction and maintenance. That resources are finite can, as illustrated by Reznick *et al.* (2000), be depicted as a pie where allocation decisions are represented as slices, with the sum of all slices necessarily constrained by the size of the whole pie. Consequently, increasing the 'growth-slice' will decrease the size of some other slice(s), for instance the amount of resources allocated to reproduction. This paradigm underlies much of life-history theory (*e.g.* Roff 1992) and energy allocation modelling (*e.g.* Roff 1983; Kozlowski 1992).

However, the total size of the pie depends on resource acquisition. If an individual is efficient in gaining resources, the pie becomes larger (Reznick *et al.* 2000). Constraints on acquisition may, however, arise through avoidance of predation or through food limitation. Here, we highlight the many traits which could be traded-off with growth rate. We group basic mechanisms into two categories: those affecting resource acquisition (the size of the whole pie) and those governing resource allocation (the relative size of each slice).

Resource acquisition revolves around the processes of foraging leading up to ingestion and digestion (Fig. 2). Foraging involves behavioural and morphological adaptations related to finding and capturing prey, as well as physiological and anatomical adaptations involved in sensing and cognition. Many trade-offs have been extensively studied within the field of foraging ecology (*e.g.* Stephens *et al.* 2007), and most of these relate to behaviour and risk-taking. In Table 1, we list many of the trade-offs relating to resource acquisition, and how they may be perturbed by fishing activities.

To illustrate that there are also less intuitive costs related to acquisition, consider the example of digestion. In fish, the entire digestion process typically consumes some 10% of the energy content of the ingested food (Tandler & Beamish 1979). However, digestion also requires oxygen and, as aquatic respiration is costly, this is often in conflict with other purposes such as escaping predators (Arnott *et al.* 2006). This conflict has been demonstrated in a comprehensive set of experiments on the Atlantic silverside along the axis of countergradient variation of growth described above. Northern silverside populations, which experience short growing seasons, increase their growth rate by voluntarily ingesting larger meals (Lankford *et al.* 2001) and consequently have higher metabolic rates and consume more oxygen (Arnott *et al.* 2006). In common garden experiments, northern populations are poorer swimmers (Billerbeck *et al.* 2001), which gives them poorer escapement responses and they are consequently eaten more often by predators (Lankford *et al.* 2001; Munch & Conover 2003). Physiological mechanisms related to digestion thus translate increased growth rate into higher predation rates. Similar results have also been obtained from experiments by Suzuki *et al.* (2010), who hypothesized that individual medaka *Oryzias latipes* being predated upon by an ambush predator might trade off cautiousness to forage more intensely. When fishing elevates mortality rates, speeding up growth rate and reproduction by digesting faster might be favoured, even if it means being exposed to some extra predation mortality. Through this mechanism, fishing might thus increase acquisition rates and, if allocation does not change, also growth rate. Further trade-offs related to resource acquisition and how these may respond to fishing are listed in Table 1.

The allocation of acquired resources is also a dynamic and multifaceted process. Owing to its direct relevance for fitness, allocation to reproduction has received considerable attention, often contrasted with allocation to growth as the only other recipient of energy (*e.g.* Roff 1983; Kozlowski 1992). Growth trajectories are split in two broad categories depending on the age-schedule of allocation to growth and reproduction: determinate (a sharp transition from allocation to growth to allocation to reproduction, leading to growth curves resembling a hockey-stick) and indeterminate (more gradual transition from allocation to growth to allocation to reproduction and more von Bertalanffy-like growth curves; reviewed in Heino & Kaitala 1996; see also Von Bertalanffy and Pirozynski 1953). In fish, indeterminate growth is common, giving extra degrees of freedom to adult life histories.

Although growth and reproduction can receive a large proportion of resources, they are only two of several resource-demanding processes in an individual. In a more complete picture, investment in other components such as maintenance, immune defence, digestion, morphology, cognition, behaviour, and storage also need to be considered (Fig. 2). Each of these components receives energy and resources in an amount that is likely adaptive in the environment in which the organism has evolved. By down-regulating any of these components, energy and metabolic capacity can be freed for somatic growth. Examples of components with competing demands for energy and resources are given in Table 2.

Developmental constraints and delayed effects of growth

Having outlined how resource acquisition (Table 1) and resource allocation (Table 2) are malleable processes that can respond to selection pressures (including those from fishing), it is necessary to understand that constraints may act directly on growth rate. In particular, the development rate of certain body structures may constrain the growth rates of other structures or induce costs related to rapid growth. For instance, rapidly growing snails have thinner shells because the rate of calcium deposition does not keep up with increased growth rates, and individuals with thin shells are more vulnerable to predators (Palmer 1981). Similarly, rapid growth may result in compromised morphology, such as suboptimal body proportions, increased fluctuating asymmetry, and skeletal deformities (see Arendt 1997). For example, a positive correlation between rapid growth rates and the degree of coronary lesions was reported in Atlantic salmon (Saunders *et al.* 1992). Such effects may be exacerbated by energy-maximizing diets,

Table 1. Processes involved in resource acquisition and their relation to natural and fisheries selection. Mechanisms are grouped by general category, below which more specific mechanisms are listed. The last two columns contain potential consequences for fishing-induced adaptations, and relevant literature examples, preferably on fish.

Category *Process*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Habitat choice	Habitats differ in food availability and exposure to predators, resulting in trade-offs between food intake and survival	Strong preference of fish for a given area may direct fishing effort to such locations	Fish frequenting certain habitats where fishing occurs will be selected against, causing, for example, changes in the distributional patterns of the population	Biro *et al.* (2006) observed differences in habitat use between domestic and wild rainbow trout – with higher growth rates and reduced survival in the risk-prone domesticated strain
		Fish that hide, for example flatfish on the bottom, generally move when approached by active gears such as trawls	Leaving the hiding place may expose fish to predators	A classical review of risk in relation to foraging behaviour is Lima & Dill (1990)
Temporal light regime	As most fish are visual predators, both foraging rates and piscivore predation change as light levels vary throughout the day (and season)	Many types of fishing gear, *e.g.* baits, lures, and gillnets, are most efficient at times of the day when fish are foraging or active	Fish that are active foragers may be caught more often. Could cause reduced growth or shifting foraging to less optimal times of the day	Juvenile sockeye salmon feed most intensively at dawn and dusk, when the ratio between foraging rates and predation risk are most favourable (Clark & Levy 1988). A model suggested reduced growth if passive gears harvest the most active swimmers (Favro *et al.* 1979)
Vertical light regime	Light extinction down the vertical column creates a visual habitat that changes with depth as well as time. Deeper habitats are safer, but may restrict foraging rates for visual feeders	Some pelagic fishing gear is deployed close to the surface, for example purse seines	Fish that avoid surface waters could have a a selective advantage but might suffer suboptimal foraging rates	The best time and depth windows are used first, for example in crepuscular feeding where small pelagic fish come close to the surface to fill their stomachs before nightfall (Strand *et al.* 2002)
Diet choice	Food items differ in size, energy content, digestibility, and handling time. Several trade-offs between food intake and survival are involved	Fishing may change availability of food	Foraging can become safer or riskier as a result of fishing	Bottom trawling may increase food availability for plaice (Hiddink *et al.* 2008)
Handling time	Including food items larger or smaller than the optimal size may increase energy intake but at a cost of increased handling time, during which the forager may be vulnerable to predators	Longer handling time may lead to higher exposure to certain types of fishing gear	To avoid gear, fish that forage less or reject items that require extra handling time may be favoured. This might lead to decreased acquisition	Juvenile coho salmon forage less and avoid large food items just after a predator has been sighted (Dill & Fraser 1984)
			Alternatively, fish may evolve reduced handling times at a cost of less energy extracted or increased digestion times	Several bird species reduce handling time in the open, presumably at a cost of reduced digestion rates (Valone & Lima 1987)

Table 1. Continued.

Category *Process*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Search time	There is often a trade-off between ingesting an encountered food item and continuing searching for a more profitable one. This trade-off is influenced by exposure to predators during search and handling	Fish that search more have a higher risk of encountering passive gear such as gillnets or baited hooks	Fish with reduced food search behaviour may be more likely to survive fishing, leading to reduced acquisition rates	Vulnerability to angling is heritable, suggesting that consistent differences in feeding motivation or food search behaviour affect experienced mortality in a fishery (Cooke *et al.* 2007, Philipp *et al.* 2009)
Ingesting pathogens	Food items differ in the likelihood of containing parasites, pathogens, or toxins. Individuals that discriminate less may increase energy intake, but also suffer reduced survival or other long-term negative effects	Increased mortality from fishing shortens lifespan, discounting long-term negative effects of disease, toxins, or parasites	Fishing may favour fish that ignore long-term consequences and instead forage indiscriminately, thus leading to elevated mortality rates late in life	Oystercatchers *Haematopus ostralegus* avoid large and energy-rich cockles because these have higher infection intensities of a helminth parasite (Norris 1999). Sheep *Ovis aries* that are strongly motivated to feed include also patches infested with parasite-infected faeces (Hutchings *et al.* 1999)
Nutrient composition	Diets that maximize energy intake can be low in essential nutrients (*e.g.* Pulliam 1975). Increasing growth through a diet that focuses more on energy can thus compromise other crucial processes	Because fishing reduces life-span, short-term energy gains may outweigh long-term consequences of a poor diet	Fish that maximize short-term benefits such as high growth or elevated reproduction through an energy-rich diet may be favoured, although these adaptations may incur costs in terms of *e.g.* sexual traits, development, or immune defence due to deficits of essential nutrients	Carotenoids are important for immune defence and the expression of sexually selected traits in many fish (Maan *et al.* 2006)
Ingestion rate	Digestion elevates metabolic rate and therefore occupies part of the aerobic oxygen budget. This, in turn, leads to reduced swimming performance and increased predation rates	Fishing reduces life-span and favours fast life histories, which may require higher ingestion rates	Higher ingestion rates may be selected to sustain faster growth and more intense reproduction	Atlantic silversides adapted to high overwintering mortality forage more intensely, digest faster, but are also predated upon more often (Billerbeck *et al.* 2001; Lankford *et al.* 2001)
		Avoidance of active fishing gear may be more difficult for fish that digest at high rates	Fish that consume less may be more successful at avoiding fishing gear, which could select for decreased energy acquisition	Fish that digest fast are eaten more often in predation experiments because their swimming performance is poorer (Lankford *et al.* 2001)
		Baited fishing hooks or traps may be most attractive to hungry fish or individuals with high feeding motivation	Fish that forage more cautiously may be favoured. This could lead to lower acquisition rates	In a whole-lake experiment, a bold and fast-growing genotype of rainbow trout was selectively harvested by angling with lures (Biro & Post 2008; see also Dupont-Prinet *et al.* 2010)

Table 1. Continued.

Category *Process*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Social behaviour	Groups often confer advantages to all the individuals that belong to it	With echosounders, fishermen have the ability to target groups of fish rather than individual fish dispersed over larger volumes of water	Fish that are less often in groups may have an advantage in the presence of fishing, but less gregarious behaviour may lead to loss of group benefits	Social and group behaviour is reviewed in Giraldeau & Caraco (2000) and Krause & Ruxton (2002)
Group foraging	Small to moderate-sized groups often find food more efficiently than solitary individuals	Fishing that targets groups of fish may favour solitary feeding	Energy acquisition rates may drop. This may be compensated by riskier foraging that leads to increased predation	Minnows and goldfish find food faster as group sizes increase up to 20 individuals (Pitcher *et al.* 1982)
Predator defence	Predation risk is diluted in groups (Inman & Krebs 1987). Several anti-predator behaviours involve co-operation between individuals	Fishing that targets groups may favour individuals that face predators alone	Fish that encounter predators alone may escape less often, leading to more risk-averse foraging strategies and reduced energy acquisition and growth	Guppies inspect predators in pairs, thus mapping risk as part of efficient foraging behaviour (Griffiths & Magurran 1998)
Schooling	Individual foraging rates may drop in dense and large schools as is often seen in marine pelagic fish species	Fishing that targets schools may favour solitary fish or fish at the outskirts of a school if that enabled escape from the fishing gear	Fish that are more often outside the school may have higher resource acquisition rates, but will presumably suffer higher predation rates	Reduced foraging performance in schools takes place because visual fields and search volumes overlap (Eggers 1976)

Table 2. Traits associated with resource allocation and their relation to natural and fisheries selection. Traits are grouped by general category, below which more specific mechanisms are listed in some cases. The last two columns contain potential consequences for fishing-induced adaptations, and relevant literature examples, preferably on fish.

Trait group *Specific trait*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Maintenance	Repair of genetic material, replacement of damaged proteins (Hawkins 1991), and renewal of cells and tissue help maintain a well-functioning soma. For example, the theory of aging partly ascribes senescence to build-up of damage inflicted by mutations (Medawar 1952) and reactive oxygen molecules (Harman 1956)	Fish investing less in maintenance could be less able to escape active fishing gear such as trawls	Often there is a trade-off between investment in somatic growth and investment into maintenance, such that fishing might favour fish investing less in growth	Ferox trout is a morph that lives longer and grows larger in co-existence with regular brown trout, presumably due to piscivory allowing a different allocation to growth and maintenance (Mangel & Abrahams 2001). Reduction in allocation to maintenance was hypothesized to enable lower assimilation efficiency but higher conversion efficiency, allowing better predator avoidance, in fast growing damselfly larvae under time and predation stress (Stoks *et al.* 2005)
Immune defence	Building and maintaining general and specific immune defence is energetically costly (Lochmiller & Deerenberg 2000). Down-regulating these mechanisms can increase the costs of having an infection and the probability of injury or death (Møller & Saino 2004)	Fishing reduces lifespan and hence the benefits from investment in immune defence	Individuals that reduce investment in immune defence (for long-term survival) may have more resources for growth and reproduction	De Block *et al.* (2008) found reduced investment in immune defence in damselflies with compensatory growth
		Individuals with reduced immune defence may be more often infected, which could lead to reduced escapement ability, especially from active gears Fish with low immune defence may be more prone to fatal damage due to contact with fishing gear	Fish with stronger immune defence would be selected for. Increased investment in immune defence could lead to lower growth rates	Similarly, the damselflies with higher immune investment had lower rates of compensatory growth (De Block *et al.* 2008)
Neural development and cognition	Cognition enhances food-finding, anti-predator behaviours, and within-species social interactions, but sensory organs, neural tissue, and investment in learning are costly. The brain alone usually requires 2–8% of the metabolic rate in vertebrates, but can demand as much as 60% in some species of electric fish (Nilsson 1996)	It might be speculated that 'smarter' fish would be better at avoiding fishing	If more resources were to be diverted to neural development and cognition, the resources would no longer be available for growth or other resource-demanding processes	Miller (1957) suggested that angling would select for intelligence. Haddock have learned to swim through gillnet mesh but the relationship to cognition has not been studied (Özbilgin & Glass 2004).

Table 2. Continued.

Trait group *Specific trait*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
		Learning often involves a short-term cost to acquire a long-term gain. Because fishing reduces lifespan, it also reduces the potential for the long-term gain	Costly learning for long-term benefits may evolve to lower levels	Increasing mortality rate in a model led to reduced levels of learning but faster learning rates (Eliassen *et al.* 2007)
Morphology	Anti-predator strategies can involve spines, large or sharp fins, and other morphological features. Feeding on specific types of resources can require specialized mouth parts. These structures can be energetically costly to build, use, or carry	Catching fish with gillnets is based on individuals getting tangled in the net, thus this kind of gear might select against spines, large or sharp fins	Reduced investment in costly morphological features may free resources for growth or reproductive investment	Gillnet selectivity curves, including their dependence on body profiles, are reviewed in Hamley (1975)
	A stout body shape causes swimming to be more costly when compared to more streamlined fish (Petrell & Jones 2000; Boily & Magnan 2002)	Good swimming performance improves avoidance of active fishing gears, but is often low for stout fish	By selectively fishing the roundest or stoutest fish, nets could select for more streamlined body shapes. This could cause adaptive changes in growth or reproductive investment	Female guppies carrying large internal broods have poorer swimming performance than females without broods (Ghalambor *et al.* 2004)
	Fish also differ in their general body plan, from being long and slim to stout and round	Gillnets are often selective on body shape, with slim fish better at escaping, but also with very deep-bodied fish such as *Tilapia* having narrower selectivity curves (Hamley 1975)	Slimmer fish could be favoured. That could lead to reduced growth, reduced reproductive investment, or reduced energy storage	Trends, presumably evolutionary, towards leaner fish have been observed in Pacific salmonids (Ricker 1981, 1995) and lake whitefish (Thomas & Eckmann 2007; Thomas *et al.* 2009)
Migrations	Many species move extensively between foraging areas and spawning areas, or follow prey on feeding migrations	Fishing concentrated in space or time may cause variation in mortality that can cause selection	Migration patterns may evolve to avoid fishing	Increased marine fishery on anadromous species may delay seawards migration or cause increased freshwater residency (Thériault *et al.* 2008)
		Fishing may cause changes in size distribution, which may have effects on migrations because swimming costs are size-dependent	Earlier maturation at smaller size may have correlated consequences for migrations	Fishing-induced evolution of smaller adult size was correlated with shorter spawning migrations in a model for Atlantic cod (Jørgensen *et al.* 2008)

Table 2. Continued.

Trait group *Specific trait*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Energy storage	Food availability is often unpredictable, or predictably bad in certain periods. Energy storage may function as a buffer against poor conditions, but also as capital allocated to reproduction at a later stage (see Reproduction below)	Gillnets select on girth and could remove fish with large energy stores faster than fish with smaller energy stores	Individuals investing less in stores would be favoured. These individuals could be at higher risk of starvation, but could allocate more to growth or income breeding. If energy stores are for capital breeding, selection towards income breeding would be expected	Compensatory growing juvenile halibut decreased energy storage, presumably resulting in increased starvation risk (Hurst *et al.* 2005)
Somatic growth	Large size is advantageous for many purposes including survival and foraging, but growth requires time and resources	Fishing gear or practice may be directly or indirectly selective on size or on any process related to growth	Fishing can cause slower or faster growth (Fig. 3A)	Pink salmon declined in size over time, and fastest in areas with the most size-selective gear (Ricker 1981). In cod, selection on size fluctuated (Swain *et al.* 2007)
Reproduction	Reproduction is among the most dominant processes diverting energy away from growth. In fish, allocation to reproduction is negligible in early life, and it is therefore convenient to characterize reproductive investment through its ontogenetic dimension (timing) and intensity	Fishing reduces life-span, implying that events later in life matter less for fitness	Reduced longevity selects for increased reproductive output early in life	Law (1979a) showed theoretically that shorter lifespan favours increased reproductive investment
		Fishing activities may also target more specific phenotypes or reproductive behaviours	Any adaptation would be case-specific	Some fishing-induced evolutionary effects are listed in Dieckmann *et al.* (2009)
Timing of maturation	Fish spend energy and time on the maturation process to develop primary and secondary sexual characters. When reproduction begins, it occupies resources that otherwise could have been used for growth or other purposes	Fishing reduces life span	Fish that mature earlier can reproduce more times before they are fished, and could be favoured by selection. Earlier maturation will normally lead to reduced size-at-age in post-mature fish (Fig. 3B)	Fishing-induced evolution towards earlier maturation was reviewed by Dieckmann & Heino (2007). The influence of earlier maturation on size-at-age has been quantified in Pardoe *et al.* (2009)
		Some fisheries target spawning aggregations	Fish may lower their exposure to fishing gear by delaying maturation or spawning less frequently	One of the first papers to suggest delayed maturation if fish were harvested on spawning grounds was Law & Grey (1989)
		Fishing gear is often size-selective or targets specific phenotypes in other ways	Size-selective gear may create refuges for certain maturation sizes and ages. Gear selective on other traits may cause other refuges	Gillnets have bell-shaped size-selectivity, and may favour maturation large and late in life (Boukal *et al.* 2008; Jørgensen *et al.* 2009)

Table 2. Continued.

Trait group *Specific trait*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Reproductive investment	Reproductive investment determines the amount of resources channelled towards maturation and reproduction. In the broad sense this includes not only gonads but also spawning migrations, competition for mates, and parental care	Fishing reduces lifespan	With short lifespan it is more beneficial to increase reproductive investment than to grow, which can be seen as an investment in future reproduction (Law 1979b). Higher investment in reproduction will lead to slower post-maturation growth and a more determinate growth pattern (see Fig. 3C)	Increased fecundity or reproductive investment has been demonstrated in several harvested species in the wild, for example plaice (Rijnsdorp 1991; Rijnsdorp *et al.* 2005), cod (Yoneda & Wright 2004), and haddock (Wright 2005). The reverse trend has been observed in experiments where populations have been translocated to environments with lower predation rates (Reznick *et al.* 1990)
Skipped spawning	Indeterminate growth in fish implies a phase following maturation where there is a gradual transition from both growth and reproduction to only reproduction. For late-maturing fish, skipping spawning seasons may be adaptive	Fishing reduces lifespan	Individuals that skip spawning may prioritize growth over reproduction even after maturation. If expected lifespan is reduced, the delayed benefit may never materialize and skipped spawning become less common	Temporal trends in skipped spawning driven by fishing was investigated in an energy allocation model, leading to reduced rates of skipped spawning as an adaptation to modern fishing pressure (Jørgensen & Fiksen 2006; Jørgensen *et al.* 2006)
Capital-versus income-breeding	Reproductive tactics are represented along the whole continuum from pure capital breeding to income breeding. Capital breeders rely on stored resources for reproduction whereas income breeders rely on concurrent food intake. Salmon, herring and capelin are examples of capital breeders	Large gonads or large energy stores in preparation for spawning typically make fish rounder, with higher probabilities of being caught with *e.g.* gillnets	Fish that have leaner body shapes may better slip through gillnets, but will reproduce less or depend on income breeding to a greater extent. Trade-offs involving internal resource storage are complex and link to a range of life history traits (*e.g.* Varpe *et al.* 2009)	Lake whitefish got leaner over time, presumably as a response to a gillnet fishery (Thomas & Eckmann 2007; Thomas *et al.* 2009)
Parental care	Post-fertilization care of offspring requires parental presence and investments of time or energy	Fish that guard offspring may be easy to find or aggressive and active and therefore easy to fish	Fishing may select for reduced parental care. Alternatively, the selection pressure induced by parental care may slow fishing-induced evolution on other traits	(Dunlop *et al.* 2007) found that maturation tendency evolved less when paternal care was included in their model. Drake *et al.* (1997) found reduced parental care and increased cuckoldry among bluegills in heavily harvested lakes, presumably a side-effect of decreasing maturation size and age

Table 2. Continued.

Trait group *Specific trait*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Mating success	Females are often choosy about whom they mate with. In such cases of sexual selection, mating success and thereby reproductive success among males depends on the expression of a display trait or another phenotypic trait Male–male competition for mates may favour traits that have no survival value in their environment, for example display traits, a large body size, or weaponry	In many species females prefer larger males. Size-selective fishing gear can then remove the most sexually attractive partners In many species males fight for territories, for a central position in a lek, or for access to females, an often size is important for the outcome	If larger partners are preferentially chosen as mates, this selection pressure acts in opposition to the most normal fishing-induced selection towards smaller size. This may slow evolutionary rates	In a model, size advantage among males, be it through female choice or male-male competition, slowed evolutionary rates under moderate fishing pressures but not when harvesting was very strong (Hutchings & Rowe 2008)
Hermaphroditism	Sequential hermaphrodites reproduce as one sex early in life and thereafter change sex and reproduce as the other sex. If one sex is rare then it may pay off to change to that sex	Fishing often truncates age- and size-structure so that the later sex may become under represented	Because each sex contributes equally to the next generation, the rarer sex is selected for. Fishing can therefore cause evolution towards sex change at smaller size	In an individual-based model, maturation to the first sex and sex change both evolved to become earlier, and in some cases hermaphroditism was lost and the populations evolved separate sexes (Sattar *et al.* 2008)
Phenology	Fish are adapted to the seasonality in their living environment, for example, timing of spawning run is usually dependent on suitable water flow in the river allowing for upward migration. Likewise, spawning in general is often timed to benefit the survival and growth of eggs and larvae	Fisheries sometimes have consistent seasonality caused by fishing within regulated or preferred time-windows, seasonal weather conditions, or closing of fisheries after a quota is reached	Selective harvesting on seasonal timing could cause a shift in the timing of important events such as migration or spawning run, possibly with related changes in resource acquisition and allocation, and thereby change the life history strategy (McNamara & Houston 2008)	Late sockeye salmon migrants have been fished the most, and the run has become progressively earlier presumably as an evolutionary adaptation (Quinn *et al.* 2007)

Table 2. Continued.

Trait group *Specific trait*	Mechanism or trade-off in nature	Relation to fishing	Potential fishing-induced adaptation	Relevant literature
Phenology			If variation in size is correlated with variation in phenology (*e.g.* if large individuals arrive earlier at the spawning grounds), then selection on size and potentially growth could arise. For example, large and fast-growing coho salmon smolts migrated earlier than their smaller and slower-growing conspecifics (Sundström *et al.* 2010)	Complex patterns of natural and fishing-induced selection arise on local populations of salmon harvested in different parts of their spawning migration (Kendall & Quinn 2009)

which may lead to deficiency of essential nutrients (Pulliam 1975). Another study, on zebra finches *Taeniopygia guttata*, showed that individual variation in resting metabolic rate may be a consequence of the growth trajectory during early ontogeny, with high metabolic rates in adulthood being caused by accelerated growth during earlier life stages (Criscuolo *et al.* 2008). These examples emphasize that not all costs of growth are immediate, which can make it harder to identify the trade-off in nature.

Effects of the environment

Growth rate is also influenced by environmental conditions such as temperature or the type and abundance of food items. The latter may, in turn, be influenced by density dependence, for example if a large population depletes its food resource. There is also a potential for social effects, for example, reduced numbers of old and large individuals in a population may release an inhibition of maturation on smaller and younger individuals (Kolluru & Reznick 1996). Fishing affects many of these relationships directly, for example by decreasing the number of fish, which can induce an increase in prey abundance and lead to more resources becoming available. Furthermore, phenotypic expression may depend on the environmental conditions through developmental channelling or phenotypic plasticity. It is therefore difficult to conclude whether detectable changes in size-at-age during a period of fishing are due to fishing-induced evolution or indirect effects of fishing on environmental characteristics. The method of Swain *et al.* (2007) offers one good example of how one may work around this problem. They included proxies for the biotic and abiotic environment, and estimated their effects on growth trajectories.

In this paper we do not aim to review the environmental influences of growth, as there is a general awareness of the phenomenon and it is often corrected for in studies. We merely want to emphasize that whenever a phenotypic trait is quantified, one needs to correct for environmental influences before one can make inferences about underlying genetic differences, be it between populations or trends in time-series analyses. Whenever genetic variation underlies some of the phenotypic variation in a trait, the trait is heritable, and natural or artificial selection may mould that trait over time. However, modelling studies suggest that phenotypic plasticity in growth and maturation dominate the picture, especially over short time scales, and that these may mask underlying evolutionary change that takes place at a comparatively slower pace (see Dunlop *et al.* 2009b; Enberg *et al.* 2009). Probably due to such plastic effects, the analysis by Hilborn & Minte-Vera (2008) did not reveal any clear pattern between change in size and fishing mortality in a large number of marine fish stocks.

Fishing-Induced Evolution of Growth

Up until this point, we have been discussing the processes and mechanisms involved in growth with the hope of providing the necessary context for studying how fishing might affect these processes. We argue that an understanding of the fundamentals of resource acquisition and allocation is crucial to being able to predict the direction and extent of fishing-induced evolution of growth and to interpret trends in size-at-age or growth from phenotypic data. For the remainder of this paper, we direct our attention to fishing-induced evolution of growth more specifically, and in particular describe what previous research on the topic has taught us.

Expectations

Although several studies have suggested that fishing will result in reduced growth rates (*e.g.* Miller 1957; Conover & Munch 2002; Edeline *et al.* 2007), these predictions have often been based on the influence of size on survival. If one considers a larger set of mechanisms, as listed in Tables 1 and 2, it becomes more difficult to devise general expectations for how fishing-induced selection might change growth rates (see also Heino & Godø 2002). As is evident from Tables 1 and 2, there are fishing-induced effects that could lead to higher or lower acquisition rates, or to allocation of a greater or lesser share to somatic growth, and there might be selection on several of these mechanisms simultaneously.

The most fundamental consequence of increased mortality from fishing is reduced expected life-span. Fish that accelerate their life history through earlier maturation, increased reproductive investment, or increased resource acquisition and faster growth are thus likely to be favoured. For example, Biro *et al.* (2005) found that juvenile trout raised in low-food lakes took high risks to achieve rapid growth and thereby shortened their duration of exposure to high predation at small size.

In general, a faster life history (higher acquisition rate and earlier reproduction) will be favoured if the mortality risk associated with it is lower than the extra mortality accumulated with a slower life history (lower acquisition rate and later reproduction) (Williams 1966). Increased mortality from fishing may thus lead to the evolution of faster resource acquisition and altered allocation patterns to accelerate growth, as suggested by Case (1978). This prediction is in contrast to the frequently cited expectation that fishing will cause evolution towards slower growth. Most likely there will be selection pressures acting in both directions simultaneously, and depending on relative strengths, evolution of growth may go in either direction. Models have indeed supported our hypothesis, with some predicting evolution of slower growth (Favro *et al.* 1979), some predicting evolution of faster growth (Enberg *et al.* 2009; Jørgensen & Fiksen 2010), and others predicting evolution of either faster or slower growth depending on the size-selectivity of the fishery (Boukal *et al.* 2008; Andersen & Brander 2009; Dunlop *et al.* 2009b). These model findings challenge the prevailing notion that fishing will always lead to evolution of slower growth.

Challenges in quantifying growth evolution from field data

Fishing-induced evolution of growth has been well documented in selection experiments (*e.g.* Conover & Munch 2002). In observational field studies, the task is more challenging. In an ideal setting, allelic frequencies at the loci that determine growth rate would be monitored to detect whether growth is evolving (as suggested by Kuparinen & Merilä 2007). Unfortunately, we are still years away from identifying all the genes that contribute to the complex suite of processes and mechanisms affecting growth of wild fish. Until then, much of our analysis of growth evolution in wild populations will have, at best, to focus on a restricted number or genes (or their products) of which various alleles have been associated with differential growth rates (*e.g.* Case *et al.*, 2006), or more frequently rely on observational phenotypic data, which can provide only indirect evidence for evolution. However, rather than giving up in the absence of genetic data, we believe much can still be learned about fishing-induced evolution of growth from the analysis of phenotypic data. The reality is that phenotypic data are most readily available, notably time-series data for commercial species, and we can still obtain valuable insight as long as the various caveats and challenges are kept in mind.

The first challenge to consider when analyzing phenotypic field data is that size at a given age is influenced by how much resources are diverted to reproduction, if any. In Fig. 3 we give a simplified schematic of how it is possible to attain the same distribution of size-at-age through three different mechanisms: variable growth rate (Fig. 3A), variable timing of maturation (Fig. 3B), and variable investment into reproduction (Fig. 3C). The energetic demands of reproduction are ubiquitous and have strong effects on growth rate that only rarely can be ignored. The challenge of understanding the processes behind changes in size-at-age can be partly overcome by studying juvenile growth because it is not affected by reproductive investment (Heino *et al.* 2008; Swain *et al.* 2008).

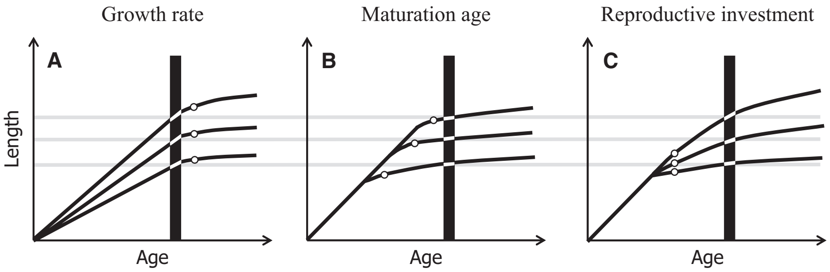

Fig. 3. Size at a given age (indicated by the black vertical bars) is influenced not only by growth rate but also by the timing of maturation and the subsequent investment into reproduction. Black lines show growth trajectories for individuals with different trait values, and open circles indicate timing of first reproduction. (A) Different juvenile growth rates, due to adaptive differences in either resource acquisition or allocation to routine metabolism, lead to different growth trajectories and sizes at a given age even before maturation. (B) When the maturation schedule can evolve, individuals with the same juvenile growth rate may have different post-maturation size-at-age depending on their maturation schedule. (C) Variation in reproductive investment can also cause variation in size-at-age later in life, even among individuals with the same growth rate and maturation age. In particular, increased reproductive investment will cause a more determinate growth pattern with a sharp transition between juvenile growth and a more or less fixed adult size (lower growth curve), in contrast to indeterminate growth (top growth curve). In reality, these three different processes are likely to interact and need to be accounted for before changes in size-at-age are equated to evolution of growth. Worth highlighting is that all of these different processes could lead to similar patterns in size-at-age (where the growth trajectories cross the black vertical bar).

Secondly, obtaining representative samples of a fish population to estimate growth rate is difficult. Virtually all sampling methods are size-selective, which is an obvious problem for estimating growth rate, although some biases can be corrected for. The origin of the data makes an important difference: the fishing fleet intentionally targets a certain size range of fishes (usually the larger end of the size spectrum), determined by landing size and gear regulations, geographical distribution, and market valuation of differently sized fish (see Pardoe *et al.* 2009). Studies based on catch data inherit these biases, and the nature of those biases may change over time as the population or fishing practices change. Scientific surveys are intended to be less selective and more consistent over time, as they follow deliberately designed sampling schemes, aiming also for segments of the population that are not specifically targeted by fisheries (for example smaller and younger individuals). Nevertheless, unbiased sampling over the entire population is virtually impossible.

Thirdly, purely demographic effects confound the estimation of population parameters. Even unselective fishing leads to higher mortality, leaving on average younger and therefore smaller individuals. On top of this, selective harvesting may lead to differential mortalities within a cohort, for example when the largest members of a given age class are harvested and the smaller ones survive, leading to demographic change in mean trait values over time even within one cohort (Sinclair *et al.* 2002; Swain *et al.* 2007).

Fourthly, as we have emphasized above, growth rate is generally not a directly observable trait but needs to be inferred from observations of size-at-age. Repeated individual measurements of size-at-age are preferable, for example from recaptures of tagged individuals or through back-calculations of growth patterns from scales or otoliths (*e.g.* Edeline *et al.* 2007; Swain *et al.* 2007), but such samples are more laborious and costly to obtain and are therefore relatively rare.

Last but not least, growth is notoriously plastic, being influenced by both abiotic factors (*e.g.* temperature) and a range of biotic factors such as predator and prey distributions and density dependence. Conceptually, phenotypic plasticity can for example be accounted for by estimating reaction norms describing how growth varies with environmental factors, similar to what has been proposed to help disentangle phenotypic plasticity and evolutionary change in maturation (Heino *et al.* 2002; Dieckmann & Heino 2007). In practice, using a similar methodology for growth may turn out to be more difficult because whereas observations of maturation often carry along with them individual-level information on growth (a major source of plasticity in maturation), sources of growth plasticity are many and mostly difficult to measure even at the level of a population, not to mention that of an individual.

Empirical Evidence of Fishing-Induced Evolution of Growth: What Have We Learned?

The body of literature relating to fishing-induced evolution of growth is diverse in both the species studied and the methodology used (Table 3). Most investigations rely on the analysis of time-series data from field studies, but

Table 3. Studies examining evolutionary changes in growth caused by fishing. We have included studies where the authors themselves acknowledge fishing-induced evolution as a possible cause for the observed changes, and some studies which in our opinion suggest evolutionary changes in growth due to fishing.

Species	Type of study	Proxy for growth	Agent of selection	Main finding	Reference
Pink salmon *Oncorhynchus gorbuscha*	Commercial catch statistics and data from sampling program	Size at maturation (fixed maturation age and semelparous life history indicate that size at maturation reflects juvenile growth rate)	Gillnetting, trolling	Decreased size at maturation over time	Ricker 1981, 1995
Rainbow trout *Oncorhynchus mykiss*	Experimental (semi-natural ponds)	Specific growth rate	Gillnetting	Bold and fast-growing individuals with active foraging behaviour were first to be fished out from the experimental ponds	Biro & Post 2008
Atlantic salmon *Salmo salar*	Time series data from trapping fish on their spawning run	Weight and length at age	Angling	Declines in body weight and length due to selection caused by angling	Saura *et al.* 2010
Lake whitefish *Coregonus clupeaformis*	Mostly commercial catch data, some from sampling program	Weight at age	Gillnetting	Somatic growth rate and condition factor had decreased as a result of girth-selective gillnet fishery	Handford *et al.* 1977
Common whitefish *Coregonus lavaretus*	Commercial catch data and surveys	Back-calculated length at age	Gillnetting	Declining somatic growth and increased investment into reproduction due to gillnet harvesting	Thomas & Eckmann 2007; Thomas *et al.* 2009
Alpine whitefish *Coregonus palaea*	Data from monitoring program, sampled with gillnets	Back-calculated length at age 1 (reflecting juvenile growth rate), back calculated growth rate from age 1 to capture (reflecting adult growth rate)	Gillnetting	Significantly negative selection differentials were detected for a coefficient that described growth in the adult phase. No selection on juvenile growth	Nusslé *et al.* (2009)
Atlantic silverside *Menidia menidia*	Laboratory experiment over four generations	Length at age 190 days (before maturation)	Artificial selection	Selective harvesting on large individuals led to decreased size-at-age, whereas selective harvesting on small individuals led to increased size-at-age	Conover & Munch (2002); see also Walsh *et al.* (2006); Conover *et al.* (2009)
Atlantic cod *Gadus morhua*	Bottom-trawl survey data	Back-calculated length at ages 3 and 4 years	Trawling	Fisheries-induced evolution towards slower growth rate had likely occurred	Swain *et al.* (2007, 2008)
Pike *Esox lucius*	Time series of gillnet fishing (culling and scientific sampling)	Asymptotic length from von Bertalanffy growth curve fitted to individual back-calculated length-at-age data	Gillnetting	A pattern of selection towards reduced asymptotic length during some periods was observed	Edeline *et al.* (2007, 2009)

Table 3. Continued.

Species	Type of study	Proxy for growth	Agent of selection	Main finding	Reference
Plaice *Pleuronectes platessa*	Otolith data from surveys and market samples	Energy allocation model fitted to back-calculated individual growth trajectories	Trawling	The method specifies a growth model based on allometric scaling functions for acquisition, maintenance, and reproduction, with growth emerging as the resultant outcome of these processes. It enables quantifying temporal changes in each of these processes as well as maturation age	Mollet *et al.* (2010)
Haddock *Melanogrammus aeglefinus*	Survey data, 1965–2001 year-classes	Year-class-specific length-at-day of ages 5–10	Trawling	Declined length at age and age at maturity not explained by temperature or population density	Neuheimer & Taggart (2010)

also include experiments performed in laboratory settings (Conover & Munch 2002) and in semi-natural ponds (Biro & Post 2008). In our view, growth evolution has been most rigorously documented in pink salmon (Ricker 1981, 1995) and in the experiments on silversides (Conover & Munch 2002, Conover *et al.*, 2009). Part of the reason these two studies were able to clearly document fishing-induced evolution of growth was because both species examined had a constant maturation age; thus, the confounding factors of maturation and reproductive investment (Fig. 3) could be excluded. However, at the same time that a constant maturation age makes the results easily interpretable, it also limits the generality of the conclusions because most fished species have more flexible reproductive schedules. In the case of silversides, declining food consumption rates were indicative of evolving resource acquisition, and changes in fecundity and egg size indicated that allocation to reproduction had evolved as well (Walsh *et al.* 2006). In addition, food conversion efficiency in the silversides declined, suggesting changed allocation also to some of the more subtle costs such as immune defence or maintenance.

Despite the difficulty of generalization to many commercial species, the case studies on pink salmon and silversides nonetheless make a strong case that fishing has the capability to induce evolutionary change in resource acquisition and allocation. In the silverside experiment where most confounding factors were controlled, the strength of the evidence approaches proof that fishing can cause evolution of growth, both in terms of changes in resource acquisition and allocation.

The influence of reproduction

As we hope is now appreciated, observing change in size-at-age is not sufficient evidence that growth rate has evolved, as there are many potential factors that could cause those changes. In particular, one needs to exhibit caution when interpreting changes in size-at-age or growth in a species where age at maturation or reproductive investment might change in response to fishing. Such caution seems warranted in the study of Lake Windermere pike by Edeline *et al.* (2007, 2009) where changes in von Bertalanffy growth parameters (including asymptotic length) were seen as evidence for growth evolution. The von Bertalanffy parameters aggregate size-at-age information and do not allow the separation of resource acquisition from resource allocation. This is a problem because, as Edeline *et al.* (2007) point out themselves, gonad weight decreased over time, especially in smaller young female pike. This leaves open the possibility that changes in reproductive investment could be underlying the reported trend in asymptotic length. Therefore, although the Windermere pike study has been lauded as providing evidence for fishing-induced evolution of growth (Conover 2007; Coltman 2008), the conclusions that can be drawn are not so straightforward.

Increased reproductive investment is a commonly predicted response to fishing mortality (Law & Grey 1989; Rijnsdorp *et al.* 2005). The most common explanation for this type of pattern is that those individuals that invest more in current reproduction (even at the cost of slower growth) produce higher numbers of offspring over their lifetime than those that invest less in reproduction. However, it is important to keep in mind that selection could act on reproductive investment in other ways. For example, in pink salmon (Ricker 1981, 1995) and whitefish (Handford *et al.* 1977; see also Hamley 1975) the high condition factor and high ratio of maximum girth over body length, respectively, imply that gillnets could select on reproductive investment either directly, by removing fish with large gonads, or indirectly, by fishing out individuals with large energy stores that later would be used for reproduction. It is thus interesting to observe that in a fished population of lake whitefish, reproductive investment increased over the same period as sizes decreased (Thomas *et al.* 2009). Thus, simultaneous change towards lower condition and larger gonads suggests that fecundity selection acts simultaneously with viability selection imposed by the fishing gear.

Correlations between traits

Size-selective fishing lead to changes in life-history, behavioural and morphological traits in the experiments on silversides (Conover & Munch 2002; Walsh *et al.* 2006; Chiba *et al.* 2007), and it will be interesting to see whether further experiments can reveal to what degree these concurrent responses are due to genetic correlations (Naish & Hard 2008) as opposed to being independent processes of adaptation. In the pond experiments on rainbow trout by Biro & Post (2008), growth was correlated with behavioural traits; because gillnetting harvested the most active fish, there was selection on feeding behaviour that also led to selection on other physiological traits related to growth. These studies suggest that considering different classes of traits together (*e.g.* behavioural, morphological, physiological) is necessary to paint the full picture of how fishing can lead to evolutionary growth changes in harvested species.

Selective gear, but on which trait?

A surprisingly diverse range of fishing gear has been shown to exert selection on growth and size-at-age (Table 3).These gears are both active (trawls, angling with lures) and passive (gillnets) and can select directly on girth (trawls, gillnets), feeding motivation (angling with lures), activity (gillnets), and potentially also on swimming and escape ability (trawls). Indirectly, selection on morphological traits such as girth may affect the mechanisms of building stores, growing large gonads and expressing prominent secondary sexual characters. Thus, the ultimate goal in understanding how gear selection may lead to changes in growth rate or size-at-age is piecing together a mosaic of the many mechanisms mentioned in Tables 1 and 2. This perspective may at first glance seem discouraging, but in our opinion it can also inspire new experiments and statistical analyses of available data, which will move the entire field of fishing-induced evolution forward.

Accounting for the environment

As phenotypic plasticity can have strong effects on growth rate, it is important to account for environmental factors. Studies of fishing-induced evolution often rely on time-series analysis or at least on consistent comparisons between separate periods. Unfortunately, appropriate environmental data are often unavailable or only available for part of the time-series. For example, one of the earliest studies of fishing-induced evolution showed that somatic growth rate and condition factor of lake whitefish had decreased, just as one would expect as an evolutionary response to the highly girth-selective gillnet fishery with a large mesh size (Handford *et al.* 1977). However, the data did not permit Handford to draw strong conclusions about whether the observed changes were evolutionary or caused by phenotypic plasticity, as only limited information about the environment was available. The whitefish population had concurrently undergone a collapse with delayed recovery, indicating large changes in density dependence and potentially also other ecological changes (Bell *et al.* 1977).

Despite the obvious challenges posed by studying a highly plastic process such as growth, it is encouraging that several recent studies have been able to account for important abiotic and biotic environmental factors such as ambient temperature, eutrophication and conspecific biomass (*e.g.* Swain *et al.* 2007; Thomas & Eckmann 2007; Neuheimer & Taggart 2010). Even after adjusting for certain environmental factors, these studies suggest residual trends in size-at-age that are the result of selection pressures from fishing (Swain *et al.* 2007; Thomas & Eckmann 2007; Neuheimer & Taggart 2010).

Conclusions and Future Directions

A promising avenue for future investigations is to build on the approach taken by Swain *et al.* (2007, 2008) and study selection differentials. The response R of a trait to selection S (the difference in the trait in the parents of the next generation compared to the trait distribution in the same cohort at birth) is $R = h^2S$, where h^2 is the heritability that typically takes values around 0.2–0.3 for life-history traits, at least in gadoids and salmonids (Gjedrem 1983; Carlson & Seamons 2008). Heritabilities in this range imply that the selection differential S is three to five times stronger than the evolutionary response R (comparing one generation with the next), and S may therefore be easier to quantify, including the separation of effects of fishing from effects of the environment. Another advantage is that selection differentials can be quantified by cohort. Individuals belonging to the same cohort often experience similar environmental conditions, hence comparison within a cohort reduces the influence of environmental variation on phenotypically plastic traits.

However, there are two inherent problems when studying phenotypic selection differentials. First, one has to measure a given trait for fish of different ages. For size this may be accomplished through back-calculations of size-at-age from scales, otoliths or other structures (as in Swain *et al.* 2007). The second challenge is that the sampling method should ideally be unselective for all types of fish sampled. For gears with baits there is likely a correlation between acquisition and catchability. If growth rate decreases in the population, one may catch fewer and fewer fish but the samples (collected with baited gear) could be dominated by the fastest growing fish along the entire time-series, meaning that the change in growth could be underestimated or not detected at all. Most fishing gear, even the types used in research surveys, are selective on size, condition, satiation, activity or swimming speed, and arriving at the correct conclusions may turn out to be sensitive to any deviations from random sampling.

Another promising method is the process-based bioenergetics method that fits process parameters to individual growth trajectories (Mollet *et al.* 2010). The data requirements are similar to that of Swain *et al.* (2007), and it will be interesting to see how the method performs when used to study temporal change and when applied to other species.

In summary, studying fishing-induced evolution of growth rate requires careful consideration of the many processes involved in resource acquisition and allocation. As with all aggregated phenomena, a deeper understanding requires that the intertwined sub-processes are teased apart and studied in more detail. Accounting for all the components will, at least in field studies, remain impossible. However, this difficulty should not dissuade us from trying to identify the main components. One important point from our review is that one should distinguish between size, which describes a state, and growth, which is a multitude of processes leading to a given size. This includes acknowledging and correcting for plasticity and environmental effects and simultaneously accounting for changes in other important life-history traits, particularly maturation schedule and reproductive investment. For example, developing methods to apply reaction norms to traits other than maturation and thereby incorporating effects of environmental variables on growth will likely help detect evolutionary changes. By involving other approaches we can hope to expand the range of suitable data also for species and stocks where environmental data are otherwise unavailable, and broaden the scope of studies of fishing-induced evolution of growth. Examples of these other approaches include stable isotope analyses from scales and otoliths or oceanography modelling for hind-casting environmental conditions and environmental monitoring of potential prey or predator species. Because growth integrates many dimensions of environmental influence with physiological function, it will be exciting and necessary to see how the phenotypic view of life history changes compares with genetic data when those become available.

Many of the mechanisms that can lead to increased growth rate due to fishing-induced evolution entail a riskier life and could increase natural mortality rates (*e.g.* Jørgensen & Fiksen 2010). Growth evolution will affect both species ecology and fisheries economics but the devil is in the detail: the consequences will depend on which traits are adapting and how. While increased individual growth is sometimes seen as beneficial for the productivity of a fish stock, the positive effects could be counteracted by a larger loss through predation and other sources of natural mortality (Swain 2011). And while slow growth means smaller fish, these adaptations are likely to help individuals survive to reproduce and populations persist in an environment dominated by fishing. Earlier maturation may also have a positive influence on stock reproduction, although this does not necessarily propagate to an increase in harvestable biomass or catches (Enberg *et al.* 2009). Whether productivity and viability will increase or decrease will thus depend on the evolution of multiple life-history traits, and no thorough analysis exists yet. Many challenges of demonstrating and interpreting growth evolution and its consequences lie ahead, and an increased understanding requires that multiple biological disciplines together colour the rich picture of intertwined mechanisms and the complex layers of confounding factors.

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