The value of size

Bioeconomic consequences of size-dependent pricing and fishing-induced evolution

Fabian B. Zimmermann

Dissertation for the degree philosophiae doctor (PhD)

at the University of Bergen

2011

SCIENTIFIC ENVIRONMENT

This study was mainly conducted in the Evolutionary Fisheries Ecology (EvoFish) group at the Department of Biology, University of Bergen, and was financed by the Research Council of Norway through the project *Socio-economic consequences of fishing-induced evolution*. Parts of the study were carried out at the School of Economics and Finance, University of Tasmania, and in collaboration with the Institute for Research in Economics and Business Administration in Bergen.

ACKNOWLEDGMENTS

Finishing this thesis means that an interesting and important period of my life enters a final stage. Therefore I would like to dedicate these line to all those who contributed to the successful completion of this work with their supervision, support or friendship.

First of all, I would like to thank my supervisors Mikko Heino, Christian Jørgensen and Stein Ivar Steinshamn for giving me the opportunity to come to Bergen, introducing me to fisheries science and providing guidance whenever possible. Mikko, I would like to thank particularly for always going to the effort and time of in-depth analysis, tough revision and debate. This was certainly the essential factor for most progress in my scientific working and writing. Christian, for all this as well, but maybe even more for always being there with useful advice. Your research enthusiasm was a constant source of motivation and inspiration. Stein Ivar, thank you for giving me an understanding of economics and contributing the crucial perspective to complete this thesis. I could not have asked for better supervision than from all of you.

A vital part of good work is certainly a pleasant working environment in general, therefore my gratitude to all of the current and former members of EvoFish and Modelling group for their contributions. Thanks to Bea for all the help from start to finish, to Ingrid for all the uplifting words, to Agur, Nico, Nicolás and Loïc for all the coffee breaks, advice, fun and everything else. Thanks to Katja for taking care of me when most needed, Øyvind, Anders, Dorothy, Jennifer, Olav, Sigrunn and everybody else for input, seminars and social events.

This extends to all those who had their part in making Bergen a nice place, even in rainy times, with all the lunch breaks, parties and the other activities. Ana, Anders, Antonio I and II, Carol, Cindy, Jan, Jon, Laurent, Mahaut, Mari, Mia, Paolo, Sara, Sofia, Sam, Valentina and all those who became victim of limited space or memory loss: You have certainly made sure that there is always room for the fun parts of life!

I would also like to thank Satoshi for inviting me to UTAS in Hobart and providing together with everybody else from the School of Economic and Finance the opportunity for a great and informative time in Tasmania.

Furthermore danke and merci to friends in Hamburg and anywhere else, my hockey mates and everybody else who would deserve to be mentioned here, but most importantly my friends from Bern: Thank you guys for all the awesome times back home, here in Norway or wherever!

Last but definitely not least, none of this would have been possible without the support of my parents and my brother, so I would like to dedicate this work most of all to them.

Bergen, June 2011

Fabian Zimmermann

It was the Law of the Sea, they said. Civilization ends at the waterline.
Beyond that, we all enter the food chain, and not always right at the top.
Hunter S. Thompson

CONTENTS

LIST OF PAPERS

PAPER I

Zimmermann F., Heino M., and Steinshamn S. (2011)

Does size matter? A bioeconomic perspective on optimal harvesting when price is size-dependent. *Canadian Journal of Fisheries and Aquatic Sciences (in press)*

PAPER II

Zimmermann F., Steinshamn S., and Heino M. (2011)

Optimal harvest feedback rule accounting for the fishing-up effect and size-dependent pricing. *Natural Resource Modeling (in press)*

PAPER III

Zimmermann F., and Heino M.

Size-dependent pricing in Norwegian fisheries. *Manuscript*

PAPER IV

Zimmermann F., and Jørgensen C.

The bioeconomic consequences of fishing-induced evolution: A model predicts limited impact on net present value. *Manuscript*

ABSTRACT

The influence of fishing on the dynamics of fish stocks is a core element in fisheries management. One of the most notable characteristics in this context is the size-structure of a fish stock, composed by the individual and its body size. From a biological perspective, individual size is directly linked to most relevant life-history traits like growth, maturation or reproductive output, connecting it to evolutionary processes. In the context of fisheries, individual fish constitute the harvested biomass and therefore its overall value. In addition, individual size possesses an intrinsic economic value: Commonly, bigger fish are more valuable than smaller ones and fetch higher prices per weight unit. Thus, size-dependent pricing underlines in economic terms the relevance of individual size, and suggests at the same time an interaction with demographic shifts through fishing. Generally, policies accounting for individual growth and size structure can improve yield and economic returns, therefore an interactive influence of size-dependent pricing on optimal harvest strategies is likely. Similarly, to take into account the impact of potential evolutionary changes in stock composition through fishing could improve the long-term economic benefits from fisheries.

In paper I and II, the influence of size-dependent pricing on optimal harvest strategies is evaluated. Positive relationships between individual sizes of fish and the prices per weight unit fishermen receive are widespread in commercial fisheries. This underlying hypothesis is evaluated in **Paper III** with a statistical analysis of price data from Norwegian fisheries. Furthermore it is commonly assumed that such size-dependent pricing can influence the optimal catch composition maximizing economic rent. This raises the question whether the impact on optimal harvest strategies and corresponding maximum economic yield is of significant magnitude, and hence should be considered in management decisions. **Paper I** addresses this issue with age-structured models parameterized for two pelagic fisheries in Norway, targeting Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*). Here positive size-dependent pricing results in lower optimal harvest, higher average catch size and influences net

present value. On the other hand, **paper II** provides an analytical approach, introducing size effects into a generic Gordon-Schaefer type model. The assumption of a negative relationship between fishing effort and average individual size emulates a fishing-induced truncation of size structure, while mean catch size is positively related to price to account for size-dependent pricing. This allows for tracing how such size-dependent effects change the patterns of optimal harvest paths and sustainable revenue in fish stocks. The results show a decrease of optimal effort and harvest with increasing strength of size effects. Therefore, **Paper I** and **II** suggest that ignoring the impact of fishing on size structure of fish stocks as well as size-dependent pricing could result in suboptimal management strategies and rent dissipation. **Paper III** underlines this conclusion and demonstrates that size-dependent pricing is indeed relevant in Norwegian fisheries.

In **Paper IV**, a simplified evolutionary life-history model was utilized to explore potential economic consequences of fishing-induced evolutionary changes. The underlying assumption is based on evidences that harvesting of fish stocks changes survival probabilities and therefore selection landscape for life-history strategies, resulting in adaptations of corresponding traits like maturation age. Hence, the model focuses on age at maturation as basis of stock dynamics for a cod-like species, while fishing is described by fishing mortality and size selectivity. Combined, these parameters determine the resulting yield and net revenue of the simulated fishery. A comparison of this model with a non-evolutionary version allows for an impact analysis of harvest strategies on life history evolution and the long-run economic consequences. The results predict an influence of fishing-induced evolution on stock biomass and composition as well as yield and economic rent. However, the quantitative impact is marginal even under low discount rates and the consequences for optimal harvest patterns moderate. Negative economic consequences are present for stocks managed within the range of maximum economic yield, while evolutionary adaptation provides beneficial resilience towards high fishing pressure. Nevertheless, under consideration of fishing-induced evolution fishing mortalities maximizing economic rent remain nearly the same for most parameter values, implying that optimal harvest strategies are not significantly affected by an evolutionary component. Additionally, the results show high sensitivity to discounting: Increasing discount rates render the influence of fishing-induced evolution irrelevant even on the level of low to moderate discount rates. This highlights the problematic effect of discount rates in long-term cost-benefit calculations, and calls for a careful use of discounting in view of small but detrimental changes over long time periods.

THE ECONOMICS OF FISHING

"It will appear, I hope, that most of the problems associated with the words "conservation" or "depletion" or "overexploitation" in the fisheries are, in reality, manifestations of the fact, that the natural resources of the sea yield no economic rent."

H. Scott Gordon, 1954

FISH – A NATURAL RESOURCE

Aquatic organisms are one of the world's pivotal renewable resources, providing food, employment and other benefits on a global scale. Most prominent are commercial fisheries and aquaculture with a total production volume of 145.1 million tones in 2009 (FAO 2011), whereof marine fisheries contribute the main part (55%) with a stable production. Aquaculture has become increasingly important, now accounting for 38% of the total volume, while inland fisheries remain a minor factor (7%). Fisheries and aquaculture provide direct or indirect livelihoods for estimated 540 million people, and human consumption represents the primary utilization (81%), resulting in all-time high of 17.2 kg per capita annual fish supply in 2009. Correspondingly, fish contributed 15.7% to the global population's intake of animal protein in 2007 (FAO 2011).

Fish is a particularly important food source in developing countries, therefore a key component for future food security in view of population growth and environmental threats (Kent 1997, Garcia and Rosenberg 2010). However, the progression from artisanal to industrial fishing resulted in four-fold increase of total catch over the second half of last century, threatening fish as a future resource (Pauly et al. 2002). Today, unsustainable exploitation and habitat degradation peril global fish stocks, and therefore the natural capital and food source they represent (Pauly et al. 2005, Godfray et al. 2010).

In summary, there is substantial wealth generated globally in connection with fish and fisheries. At the same time, mismanagement and detrimental utilization put the continuity of those resources at risk and squander potential benefits on massive scale

(World Bank 2009). The study of these systems at the intercept point between biology and economics is therefore not only of scientific value but embodies high socioeconomic relevance. The disciplines of bioeconomics and fisheries management may provide here important answers for the problems and challenges to achieve sustainability and efficiency.

EVOLUTION OF FISHERIES ECONOMICS

From today's perspective, the sweeping absence of scientific and political debate until mid 20th century on the utilization and management of fish stocks may be puzzling. However, it illustrates impressively how the way society bears upon the environment and natural resources has changed, as well as the scientific progress that has been made in the past decades. The levity of previous generations in this matter becomes more understandable in view of a vast resource and limited technological possibilities of past fishermen. Hence, the fallacy that fishing cannot cause a significant impact on fish stocks was common even among biologists. A drastic change in the situation began with large-scale industrial fisheries after World War II, accentuating the need for a paradigm shift.

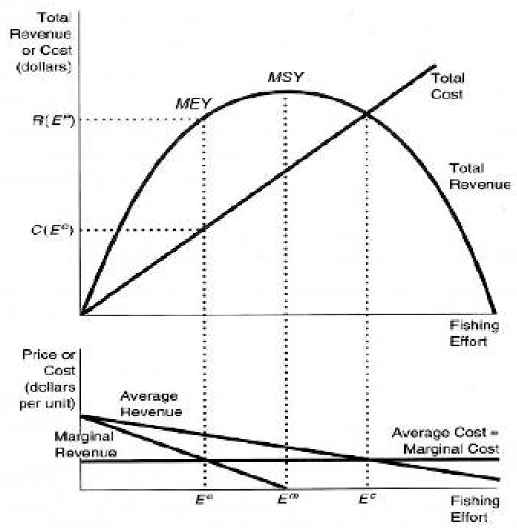
The technological development of fisheries found its echo in several corner stones of modern fisheries management published in the same period (Gordon 1954, Schaefer 1954, Scott 1955, Beverton and Holt 1957). Conceptually, the ideas may be divided into a biological approach contrasting the economic perspective: R. Beverton and S. Holt, as well as M.B. Schaefer focused on dynamics of exploited stocks while A. Scott's book contained a "then confusing notion of conservation of natural resources in terms of stewardship of assets" (Wilen 2000). Gordon on the other hand discussed the problem of overexploitation in an open-access resource and thus portended what later became more generally known as the "tragedy of the commons" (Hardin 1968). Particularly the work of Gordon and Schaefer offered with their perceptive simplicity an essential understanding of key mechanisms in a fishery – and still do. This is easily underlined by the fact that the Gordon-Schaefer model remains until today the pedagogical tool of choice to explain characteristics of a common-property resource (Tietenberg and Lewis 2008).

The main achievements of the Gordon-Schaefer model are the concepts of maximum sustainable yield (MSY), maximum economic yield (MEY) and open-access equilibrium. MSY describes the stock size and corresponding fishing effort where yield is highest, i.e. a simple maximization of biological productivity. MEY on the other hand incorporates economics as part of the fishery, defining the yield where economic rent is maximized. This is contrasted by the open-access equilibrium, characterized by zero economic returns from additional harvest and therefore full rent dissipation (Gordon 1954, Gardner et al. 1990).

Yet, the static framework's disregard for the temporal component of resource exploitation was cause for some concern, as already Scott had recognized (Scott 1955).

THE GORDON-SCHAEFER MODEL

The Gordon-Schaefer model (Schaefer 1954, Tietenberg and Lewis 2008) combines a logistic growth model with simple economic assumptions to an equilibrium model of a fishery, describing stock productivity and corresponding fishing effort under assumption of constant price and constant marginal cost. Under effort E^m biological yield is maximized, while with E^e the efficient allocation of effort is achieved (marginal cost = marginal revenue) and economic rent highest. Without regulation effort is increased until rent is fully dissipated, i.e. total cost equals total revenue, defining the open access situation. Limitations are the simplified stock dynamics, ignoring ecosystem interactions, demographics and genetics, as well as fleet dynamics.



Therefore, fisheries economics progressed significantly with the introduction of dynamic solutions to the problem of optimal resource utilization and an elaborated capital theory. The first model accounting for dynamics dates back to Crutchfield and Zellner (1962), concluding, however, little influence on the outcome. This dissented Scott's notion that high discount rates could shift MEY towards the effort level of an open-access situation. Consequently, dynamic solutions to fisheries problems were considered to be of little relevance (Turvey 1964), even by Scott himself (Christy and Scott 1965). Optimal control-theory (Pontryagin et al. 1962) provided here a new powerful tool, but its implementation into resource economics towards the end of the decade was viewed as mere complication (Munro 1992). It was mainly C.W. Clark who caused a paradigm shift as he demonstrated the impact of dynamic solutions: Effort yielding MEY can surpass MSY-effort (Clark 1971) and the difference between discount rate and intrinsic growth rate can affect optimal harvest strategies (Clark 1973). Based on this, Clark highlighted the peculiarity of fish stocks as natural capital (Clark and Munro 1975). Collecting those threads, "Mathematical bioeconomics" (Clark 1976) proved itself as a seminal work that provided strong argument for the interdisciplinarity of fisheries science. In spite of the more recent scientific and political advancements (Wilen 2000, Bjørndal et al. 2007, Clark 2010), the basic principles and questions remained rather perpetual. Foremost the quest for MEY is still the dominating thread for fisheries economists (Grafton et al. 2007, Dichmont et al. 2010).

CURRENT STATUS AND MANAGEMENT PERSPECTIVE

The conclusive and aging theoretic directives to optimal resource utilization are contrasted by prevalent management failure in reality as well as a poor state of the world's fisheries and marine resources today (Jackson 2008, Holt 2009, World Bank 2009, FAO 2011). Renowned fisheries scientists draw a bleak picture, attesting a trophic down-fishing (Pauly et al. 1998), "worldwide crisis in fisheries" (Clark 2006a), the collapse of all fisheries in near future (Worm et al. 2006) and ultimately the "end of fish" (Pauly 2009). These assessment are not unchallenged (Murawski et al. 2007, Branch

INDIVIDUAL TRANSFERABLE QUOTAS

Individual transferable quotas are one type of dedicated access rights, distributing total allowable catches (TAC) as quota shares to private individuals (Squires et al. 1995, Grafton 1996, Branch et al. 2006). The quota share is fully transferable and can therefore be traded. First described by F.T. Christy (1973), ITQs remained a theoretical concept for almost two decades until first implementations in Icelandic and New Zealand fisheries (Sissenwine and Mace 1992, Annala 1996, Arnason 1996). Since then they gained increasing acceptance as a management tool. The key advantage of ITQs is their transferability: More efficient fishermen can buy quota shares from less efficient fishermen. This results in a overall increase of economic efficiency in the fishery. Additionally, future rents promote stewardship for the fish stock among the quota owners. But there is a downside to both points: Quota trading can lead to monopolization, and potentially huge increases in values raise questions of social equity (Clark 2006a). In particular, critics point out that free endowment of fishermen and lack of temporal restrictions can lead to substantial private profits from a public good (Macinko and Bromley 2003). ITQs also do not guarantee biological sustainability, but generate solely economic efficiency. Therefore successful ITQ management still relies on an adequate TAC and strict enforcement of quota and gear restrictions.

2008, Daan et al. 2011, Hilborn 2011), and recent studies come to more complex conclusions (Dankel et al. 2008, Mora et al. 2009, Worm et al. 2009). In particular, there are widespread counterexamples of successful management (Beddington et al. 2007, Hilborn 2007a, c, Costello et al. 2008). Furthermore, flawed conclusion based on unclear objectives (Hilborn 2007d), arbitrary reference points (Hilborn and Stokes 2010) or inconclusive catch data (De Mutsert et al. 2008, Branch et al. 2010) require consideration. Nonetheless, the overall performance of global fisheries is mediocre at best, raising the question: What went wrong?

The reasons for overfishing, unsustainable practices and economic underperformance are diverse and rarely straight-forward. From an economic perspective, the problems in fisheries originate in market failures connected to deficient property rights, quota system designs, user conflicts or insufficient enforcement (Clark 2006b, Grafton et al. 2008). Thus, a common symptom of fisheries mismanagement is overcapitalization, often caused by subsidies (Munro and Sumaila 2001, Clark et al. 2005, Sumaila et al. 2008, Sumaila et al. 2010). This problem is strongly linked to unsustainable total allowable catches (TACs) due to political decisions instead of scientific advice (Pauly, et al. 2002). Catch restrictions are further undermined by illegal, unreported and unregulated (IUU) fishing activities, particularly in absence of an adequate legal framework or sufficient enforcement (Gallic and Cox 2006, Sumaila et al. 2006, Agnew et al. 2009)

A key role in overfishing and rent dissipation can be attributed to improper access, property and use rights (Schlager and Ostrom 1992, Scott 2008). Hence, fishermen behaviour and fleet dynamics are a crucial factor (Branch, et al. 2006). However, previous quota systems often provided improper incentives and therefore failed in reality (Hilborn et al. 2005, Clark 2006a): A race-to-fish, high-grading and discarding as some of the most notable unwanted effects of unsound quota system designs (Pascoe 1997, Sutinen 1999, Hilborn 2007b). A potential cause is the prevalent management focus on biological reference points and the health of fish stocks, disregarding economic objectives as driving force of fisheries (Wilen 2000, Hilborn 2002, Branch, et al. 2006). Yet economic factors are from society's viewpoint a key purpose of fisheries and demand adequate attention in fisheries management. In this context, catch shares in form of individual fishing quotas (IFQs) or individual transferable quotas (ITQs) gain increasing acceptance as potential remedy (Squires, et al. 1995, Grafton 1996, Grafton et al. 2006). Signs of success substantiate this notion (Chu 2009, Costello et al. 2010), although a cautious implementation is required (Bromley 2009, Grafton et al. 2009, Gibbs 2010, Sumaila 2010), and the appropriate choice of management instruments depend on specific situations and challenges (Kompas et al. 2008, Hannesson 2011).

ALTERNATIVE USES AND ECOSYSTEM BENEFITS

The direct benefits from commercial fisheries are supplemented by alternative use values and non-use values of fish, frequently leading to stakeholder conflicts over the resources. Particularly recreational fishing generates substantial benefits (Connelly and Brown 1991, Pitcher and Hollingworth 2002), but may also contribute to stock depletion (Post et al. 2002, Coleman et al. 2004, Cooke and Cowx 2004) and is commonly understudied. Furthermore, recreational fishing is connected to benefits through tourism, and therefore relates to non-consumptive use values of aquatic systems and the ecosystem services they provide (Costanza 1997).

Ecological economics define ecosystem services as a flow of energy, information and material from natural capital within ecosystems to the benefit of human welfare (Costanza 1997, Millennium Ecosystem Assessment 2005). This includes direct and indirect use and non-use values, ranging from food production and recreational purposes to climate regulation, pollution control or sediment retention. Commonly markets captures these services only partially or not all, and quantitative valuation is often difficult. In fisheries management some ecosystem approaches attempt to account for additional ecosystem services, but globally most policies focus solely on (single) fish stocks as food source. Here integration of ecological economics and alternative stakeholder interests could result in improved sustainability and alignment of objectives as part of a “new consensus” (Hilborn 2007).

THE BIOLOGY BEHIND ECONOMICS

"I think the major opposition to ecology has deeper roots than mere economics; ecology threatens widely held values so fundamental that they must be called religious"

Garrett Hardin, 1982

FISH STOCKS AS BIOLOGICAL SYSTEMS

As fisheries biologists tend to underestimate the economic complexity of a fishery, so are fish rarely grasped as the biological entities they are in fisheries economics. Fish stocks are subpopulations of a fish species, and therefore subject to population dynamics and demographics. Furthermore, a fish stock exists in an ecological and evolutionary context, including all biological interactions in the framework of an ecosystem, as well as the underlying environmental determinants. The resulting inherent complexity of a fish stock elevates it above more trivial resources. Consequently, harvesting fish involves much more than a mere removal of biomass as economic models traditionally suggest. Thus, simplifications of low-dimensional lumped-biomass models could be a reason for unsatisfactory management results (Krysiak and Krysiak 2002, Tahvonen 2008).

IMPACT OF FISHING

Fishing imposes additional mortality on a fish stock, commonly enhanced by size selectivity, and alters the demographic composition of the stock. Truncations of size structure may impair the recruitment potential of fish stocks (Murawski et al. 2001, Berkeley et al. 2004b), destabilize population dynamics (Anderson et al. 2008) and increase population variability (Longhurst 2002, Hsieh et al. 2006) as well as natural mortality (Jørgensen and Fiksen 2010). This generally results in reduced productivity of fish stocks and higher vulnerability towards environmental changes and fluctuations. These dynamics feedbacks could be particularly problematic in view of potential threats through climatic changes (Perry et al. 2005, Brander 2007).

Reduced stock densities are another major factor to take into account in harvested populations. Density-dependence in larval and juvenile survival is commonly acknowledged as an essential part of population dynamics in fish (Rothschild 1986, Hilborn and Walters 1992, Houde 1994, Cowan et al. 2000). This is extensively implemented in most stock assessment models as density-dependent recruitment, i.e. a spawning stock-recruitment relationship, and long established in fisheries science (Ricker 1946, Beverton and Holt 1957). In comparison, density-dependent individual growth among recruited fishes has received little attention, despite evidence for its relevance in the regulation of fish stocks (Jenkins Jr et al. 1999, Lorenzen and Enberg 2002, Vincenzi et al. 2008) and its potential management implications (Helser and Brodziak 1998). In general, density-dependence results in increased growth potentials under low densities and may reinforce resilience of fish stocks towards fishing mortality.

There is increasing evidence that fishing may cause evolutionary changes (Law and Grey 1989, Conover and Munch 2002, Jørgensen et al. 2007, Law 2007, Hutchings and Fraser 2008, Allendorf and Hard 2009). Fishing mortality reduces the overall chance of survival and imposes a shift in the selection landscape of life-history traits. The mechanism and resulting adaptations have been documented in time-series analysis (Ricker 1981, Heino et al. 2002, Swain et al. 2007), experimental (Reznick and Ghalambor 2005, Conover et al. 2009, Conover and Baumann 2009) and modelling approaches (Ernande et al. 2004, Dunlop et al. 2009b). Today most commercial fish stocks are heavily exploited (Worm, et al. 2009, FAO 2011), fishing mortalities may therefore outnumber natural mortalities significantly (Mertz and Myers 1998) and cause rapid evolution (Darimont et al. 2009). Potential negative consequences for biomass and yield (Law and Grey 1989, Conover and Munch 2002), adult body size (Heino 1998, Enberg et al. 2011) or the recovery of depleted fish stock (Enberg et al. 2009) are contrasted by indications for heightened resilience towards fishing pressure (Enberg, et al. 2009, Enberg et al. 2010).

As ecosystems are subject to fluctuations and changes up to drastic regime shifts (Scheffer and Carpenter 2003, Mayer and Rietkerk 2004, Carpenter et al. 2008), fishing has been suggested as an indirect or direct cause for trophic shifts and ecological transitions (Jackson et al. 2001, Folke et al. 2004). In particular, predominant targeting of large predatory species and overfishing may cause cascading effects on the food web and result in alternative trophic regimes (Scheffer et al. 2005, Daskalov et al. 2007, Österblom et al. 2007, Casini et al. 2009). This corresponds with an observed decrease of mean trophic level of catches that indicates a dwindling of high-trophic level fisheries and increasing exploitation of lower trophic levels (Pauly, et al. 1998, Pauly and Palomares 2005, Essington et al. 2006, Branch, et al. 2010). It has been shown that this could create alternative stable states (Persson et al. 2007).

MANAGEMENT IMPLICATIONS

The complexity of marine ecosystems with multi-layered feedbacks to fishing reveals another major reason for failing fisheries. Correspondingly, the comprehensive understanding of the underlying biological system is a crucial component of successful fisheries management. But in reality most approaches are still rather simplistic. Traditionally, management efforts target on concepts like MSY (Larkin 1977) and preventing growth or recruitment overfishing (Beverton and Holt 1957, Sissenwine 1987, Myers et al. 1994). The corresponding biological reference points (Gabriel and Mace 1999) and size limits remain therefore predominant. However, the crude single-species perspective neglects evolutionary and plastic consequences as well as the ecosystem point of view.

The proportion of big individuals in a population could be one major parameter for improved sustainability (Berkeley, et al. 2004b, Birkeland and Dayton 2005). This idea is based upon the avoidance of recruitment overfishing, but links to concerns of growth overfishing too. The concept of growth overfishing dates back to Beverton and Holt (1957) who pointed out the relevance of age structure and the growth of corresponding cohorts. When individuals of a cohort are allowed to grow sufficiently, the resulting yield per recruit is optimized and a biologically efficient harvest is achieved. More recent studies add the additional dimension of maternal effects. There is evidence for higher larval survival of older female spawners (Berkeley et al. 2004a) with impacts on lifetime reproduction (O'Farrell and Botsford 2006). Here, considering individual growth and age-dependent effects can therefore not only maximize the harvested yield from a cohort, but increase recruitment and overall population stability (Murawski 2000, Anderson, et al. 2008). Thus, several threads of evidence suggest that taking into account age structure and individual size may be crucial parameters to determine optimal sustainable harvest (Tahvonen 2008, Diekert et al. 2010).

The potential impact of fishing-induced evolutionary changes is a similar management concern (Heino 1998, Ashley et al. 2003, Jørgensen, et al. 2007, Dunlop et al. 2009a). As fishing has the ability to affect the evolution of life-history traits, consequences for the biomass of fish stocks and their resilience towards environmental change are likely, ultimately derogating sustainable yields of fisheries. Because evolutionary changes may be difficult or even impossible to reverse (De Roos et al. 2006), a careful assessment of evolutionary impacts and their mitigation with evolutionary sensitive reference points is necessary (Hutchings 2009).

The ecosystem perspective of fisheries management has gained much attention recently (Pikitch et al. 2004, Garcia and Cochrane 2005). In spite of the fast dissemination of the term itself, including FAO guidelines and others, the concept remained rather vague. Generally, ecosystem-approaches to fisheries imply a holistic perspective and aim for by-catch mitigation, multi-species management, avoidance of ecosystem degradation or integrated approaches (Morishita 2008). Hence, single-species stock assessments and reference points need to be replaced by appropriate metrics and management goals (Brodziak and Link 2002, Hall and Mainprize 2004, Jennings 2005). However, scientific progress and partial implementations initiated a potential paradigm shift (Murawski 2007).

In general, the management instruments to address biological challenges are limited. Specific management questions may obscure that the underlying mechanisms are restricted to gear selectivity and – overall, spatial or temporal – reductions of fishing mortality. Because gear selectivity is imperfect and very limited in some fisheries, e.g.

purse-seining, fishing mortality becomes often the only biological lever of regulatory control. At the same time, overfishing is the key driver of unsustainable fisheries, stock collapse and evolutionary or ecological changes. Accordingly, lowered fishing pressure can be considered as straight-forward remedy, addressing all described problems to some degree. Two threads take this up in particular: Precautionary approach and marine protected areas (MPAs). The precautionary approach focuses on uncertainty directly, using risk-minimizing reference points to ensure long-term sustainability (Garcia 1996, Hilborn et al. 2001). Similarly, MPAs attempt to mitigate uncertainties, consolidate stock productivity and resilience and reduce ecosystem impacts with no-take zones (Sumaila et al. 2000, Grafton et al. 2005, Edgar et al. 2007).

BIOECONOMIC SYNTHESIS

> "The current state of affairs, in which most professional economists ignore resource limitations and in which most ecologists maintain a proud disdain of economics, must give way to a science of renewable resource management based on sound principles of bioeconomics. "
>
> Colin W. Clark, 1989

In view of the biological and socio-economic dynamics of fisheries, it becomes clear that only an interdisciplinary approach enables successful management. Bridging the gap, bioeconomics provide a crucial discipline to achieve the goal of sustainable, yet profitable fisheries and marine ecosystems (Hannesson 1993, Anderson and Seijo 2010, Clark 2010). In this respect, bioeconomic models are a useful tool to combine stock and fleet dynamics, balance biological precaution with economic efficiency, and generate comprehensive policy advice. However, implementing theory in practice has its pitfalls. In particular, adequate complexity in biological and economic parameters is crucial, or as in the canonical saying, models should be as simple as possible, but as sophisticated as necessary. Hence, to reach this goal while balancing the different perspectives summarizes the key challenge of bioeconomic models. It comes as no surprise that the previously described discipline biases, i.e. lack of biological or economic insight, respectively, is a key problem. To unify the different perspectives and explore potentially relevant mechanisms at the boundary of biology and economics is therefore crucial for successful bioeconomics. The research in the framework of this thesis was conducted in this spirit.

THESIS APPROACH

RESEARCH RATIONALE

To this point I discussed the biological and economic complexities of fisheries management, highlighting the need for integral bioeconomic research that combines both perspectives. This represents the root idea of this thesis: The basic quest throughout to bring more biology into economic questions and vice-versa, and thereby to improve utilization of fish stocks. In detail, the general research questions are:

- What is the value of body size?
- What is the economic impact of fishing-induced evolution?

The first question (**paper I**, **II**, **III**) ties in with the topic of growth overfishing and general importance of size-structure for fisheries. With a focus on size-dependent pricing, we emphasise the intrinsic economic value of body size directly. Thus, we provide a change of perspective with this previously understudied topic and underline the overall relevance of body size for fisheries. The second problem (**paper IV**) centres on potential evolutionary consequences of fishing by amending previous research with an economic assessment. This offers a first evaluation of possible evolutionary cost, and introduces at the same time an evolutionary dimension into fisheries economics.

THE VALUE OF SIZE

Individual growth has been long established as a key parameter in population dynamics of fish, and therefore also the prevention of growth overfishing for fisheries management (Beverton and Holt 1957). More recent studies corroborate the biological relevance of stock structure in context of survival and reproductive success further (Murawski, et al. 2001, Berkeley, et al. 2004b, Birkeland and Dayton 2005). Similarly, age and size structure are increasingly acknowledged as crucial factor for harvest optimization (Tahvonen 2008, 2009, Diekert, et al. 2010). However, another aspect has drawn little attention: The intrinsic economic value of body size, or size-dependent pricing.

It is common that ex-vessel prices for fish are weight-structured with increasing prices per weight unit for larger individuals. Simply speaking, big fish often fetch higher relative prices than smaller one. Correspondingly, an influence of size-dependent pricing on optimal harvest strategies has been suggested for a long time (Hilborn and Walters 1992). Yet just a few studies regarded this aspect to some extent (Gallagher et al. 2004, Holland et al. 2005, Tahvonen 2009). More frequently, size-dependent pricing was considered as a fixed component of fisheries without further analysis (e.g.Helser et al. 1996, De Leo and Gatto 2001, Katsukawa 2005). Therefore the goal was to fill this gap and demonstrate in two different approaches the influence of size-dependent pricing on optimal harvesting, as well as assess its prevalence in Norwegian fisheries. This involved quantifications in the framework of age-structured models (**paper I**) as well as an analytical approach (**paper II**) and a statistical analysis (**paper III**).

Paper I uses Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) as example fisheries for the influence of size-dependent pricing on optimal fishing mortalities and resulting net present value (NPV). We use age-structured population models with size-dependent harvesting, and apply a price function based on a linear approximation of Norwegian price per weight class data (**paper III**) to allow for a smooth variation of the size-price relationship. This quantifies how size-dependent pricing may alter optimal fishing mortalities, and the resulting mean catch weight and NPV.

Paper II combines fishing-induced truncations of size structure with size-dependent pricing to study the consequences of size-dependent effects on sustainable rent and harvest paths. To permit an analytical approach we chose a lumped-biomass model, extended with relationships between fishing effort and mean individual size as well as size and price. This enables us to trace on a generic level how size-dependent effects change optimal harvest paths and sustainable rent.

Paper III contains an analysis of price data from Norwegian fisheries in respect to size dependence. This takes up the point of origin in paper I, but uses instead statistical methods to determine the overall prevalence and strength of size-dependent pricing in Norwegian fisheries. Because all previous work in this topic was mostly conceptual or restricted to mere case studies, **paper III** offers a first systematic approach. Moreover, it underlines the key assumption of **paper I** and **II** and therefore their conclusions.

Both modelling approaches conclude a reduction of optimal effort or fishing mortality under consideration of size structure and size-dependent pricing. This suggests that ignoring body size could lead to flawed strategies to achieve MEY, potentially causing rent dissipation and suboptimal performance of fisheries. From our results it follows that the impact of fishing on stock demographics and size-structured market prices should receive more attention in bioeconomic modelling and management policies.

THE COST OF EVOLUTION

As evidences for evolutionary consequences of fishing have been substantiated (e.g. Conover and Munch 2002, Law 2007, Hutchings and Fraser 2008, Allendorf and Hard 2009), the debate has shifted towards possible management implications of fishing-induced evolution (FIE) (Jørgensen, et al. 2007, Dunlop, et al. 2009a, Hutchings 2009). In summary, there is concern that FIE may impair stock biomass, stability and recovery potential, and therefore result in negative consequences for fisheries, particularly reduced yield and higher vulnerability to environmental change. However, existing work is mainly focused on biological consequences of FIE for fish stocks, their conclusiveness and adequate management response. On the other hand, there was little attention for the economic perspective, in spite of its crucial role for fisheries. Therefore, in **paper IV** we contribute an evaluation of potential economic impacts of FIE.

Our study contains a basic quantification of the economic impact FIE might have. In doing so, we extend traditional bioeconomic models not only with dynamics of a structured population, but with trait variation as well. Changeable traits have been rarely part of bioeconomic studies; therefore our approach includes general novelty in this context. In **paper IV** we compare an age-structured population dynamics model with evolutionary life-history to the same model with fixed traits. Maturation age acts as the only evolving trait in a key role and affects here growth, reproduction and survival directly, and is genetically inherited. Natural mortality and fishing are size-dependent and act as selective force. Additionally, the input parameters of fishing, size-selectivity and maximum fishing mortality, determine the catch and corresponding economic output. The parameterization is adjusted to the stock of Northeast Arctic cod (*Gadus morhua).*

The model shows a clear long-term impact of fishing-induced evolution on economic rent. However, the quantitative influence is generally rather insignificant. In particular, the differences between optimal fishing mortality and resulting MEY are low even under assumption of low discount rates. With higher discount rates, the effect of FIE becomes even negligible. Furthermore, in our model the fish stock demonstrates a higher resilience towards overfishing with FIE, pointing out potential advantages through evolutionary adaptation in specific situations. Our results predict also an evolutionary shift in size composition of stock and catch. This may be a concern in context of general fishing-induced changes in stock structure and consolidate related negative effects like reduced productivity and population stability on a genetic level. In economic terms, consequences of FIE could be enhanced when considering the value of size. Therefore a future extension of the model with size-dependent pricing is likely to predict more pronounced economic consequences.

The influence of discounting on the economic relevance of FIE underlines a problematic aspect with dynamic solutions to problems of optimal resource utilization. Traditionally, reasonable low discount rates, e.g. a social discount rate, demonstrated little influence on optimal harvest of fish stocks. However, precondition is a sufficient difference of magnitude between discount rate and intrinsic growth rate. Otherwise, optimal economic harvest can shift to levels higher than MSY or even suggest extinction (Clark 1973). Similarly, even high rates of human-induced evolutionary change are rather subtle and slow from a fisheries perspective. Therefore, as we have shown in **paper IV**, economic impacts of FIE may be very sensitive to choice of discount rate. This implies that FIE is for fisheries economics and in view of overall uncertainty rather irrelevant. Yet it appears ethically problematic to diminish the productivity of a fish stock for future generations, which raises the question if a conventional approach can do justice to such intergenerational problems (Lande et al. 1994, Weitzman 1998, Ainsworth and Sumaila 2005). This transcends to usage of natural resources and impact of environmental changes in general, and will require future research and debate. In particular, alternative concepts of discounting like e.g. decreasing discount rate over time await further exploration.

REFERENCE LIST

Agnew, D.J., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J.R. and Pitcher, T.J. 2009. Estimating the worldwide extent of illegal fishing. PLoS One **4**(2): e4570

Ainsworth, C.H. and Sumaila, U.R. 2005. Intergenerational valuation of fisheries resources can justify long-term conservation: a case study in Atlantic cod (Gadus morhua). Can. J. Fish. Aquat. Sci. **62**(5): 1104-1110

Allendorf, F.W. and Hard, J.J. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. Proc. Natl. Acad. Sci. USA **106**(Supplement 1): 9987-9994

Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M. and Sugihara, G. 2008. Why fishing magnifies fluctuations in fish abundance. Nature **452**(7189): 835-839

Anderson, L.G. and Seijo, J.C. 2010. Bioeconomics of fisheries management. Wiley-Blackwell, Hoboken, NJ.

Annala, J.H. 1996. New Zealand's ITQ system: have the first eight years been a success or a failure? Rev. Fish. Biol. Fish. **6**(1): 43-62

Arnason, R. 1996. On the ITQ fisheries management system in Iceland. Rev. Fish. Biol. Fish. **6**(1): 63-90

Ashley, M.V., Willson, M.F., Pergams, O.R.W., O'Dowd, D.J., Gende, S.M. and Brown, J.S. 2003. Evolutionarily enlightened management. Biol. Conserv. **111**(2): 115-123

Beddington, J.R., Agnew, D.J. and Clark, C.W. 2007. Current problems in the management of marine fisheries. Science **316**(5832): 1713-1716

Berkeley, S.A., Chapman, C. and Sogard, S.M. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, Sebastes melanops. Ecology **85**(5): 1258-1264

Berkeley, S.A., Hixon, M.A., Larson, R.J. and Love, M.S. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries **29**(8): 23-32

Beverton, R. and Holt, S. 1957. On the dynamics of exploited fish populations Ministry of Agriculture, Fisheries and Food, London **533**

Birkeland, C. and Dayton, P. 2005. The importance in fishery management of leaving the big ones. Trends Ecol. Evol. **20**(7): 356-358

Bjørndal, T., Munro, G.R., Arnason, R. and Sumaila, R.U. 2007. Advances in fisheries economics: festschrift in honour of Professor Gordon R. Munro. Wiley-Blackwell.

Branch, T.A., Hilborn, R., Haynie, A.C., Fay, G., Flynn, L., Griffiths, J., Marshall, K.N., Randall, J.K., Scheuerell, J.M. and Ward, E.J. 2006. Fleet dynamics and fishermen behavior: lessons for fisheries managers. Can. J. Fish. Aquat. Sci. **63**(7): 1647-1668

Branch, T.A. 2008. Not all fisheries will be collapsed in 2048. Mar. Pol. **32**(1): 38-39

Branch, T.A., Watson, R., Fulton, E.A., Jennings, S., McGilliard, C.R., Pablico, G.T., Ricard, D. and Tracey, S.R. 2010. The trophic fingerprint of marine fisheries. Nature **468**(7322): 431-435

Brander, K.M. 2007. Global fish production and climate change. Proc. Natl. Acad. Sci. USA **104**(50): 19709-19714

Brodziak, J. and Link, J. 2002. Ecosystem-based fishery management: what is it and how can we do it? B. Mar. Sci. **70**(2): 589-611

Bromley, D.W. 2009. Abdicating responsibility: the deceits of fisheries policy. Fisheries **34**(6): 280-290

Carpenter, S., Brock, W., Cole, J., Kitchell, J. and Pace, M. 2008. Leading indicators of trophic cascades. Ecology Letters **11**(2): 128-138

Casini, M., Hjelm, J., Molinero, J.C., Lövgren, J., Cardinale, M., Bartolino, V., Belgrano, A. and Kornilovs, G. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proc. Natl. Acad. Sci. USA **106**(1): 197-202

Christy, F. 1973. Fisherman quotas: a tentative suggestion for domestic management, Occ. Pap. 19: 6 pp. Law of the Sea Institute, Univ. Rhode Island,.

Christy, F.T. and Scott, A. 1965. The common wealth in ocean fisheries: some problems of growth and economic allocation. The Johns Hopkins Press, Baltimore.

Chu, C. 2009. Thirty years later: the global growth of ITQs and their influence on stock status in marine fisheries. Fish and Fisheries **10**(2): 217-230

Clark, C.W. 1971. Economically optimal policies for the utilization of biologically renewable resources. Mathematical biosciences **12**(3-4): 245-260

Clark, C.W. 1973. Profit maximization and the extinction of animal species. J. Polit. Economy **81**(4): 950-961

Clark, C.W. and Munro, G.R. 1975. The economics of fishing and modern capital theory: A simplified approach* 1. J.Environ.Econ.Manage. **2**(2): 92-106

Clark, C.W. 1976. Mathematical bioeconomics: the optimal management of renewable resources. John Wiley, New York.

Clark, C.W., Munro, G.R. and Sumaila, U.R. 2005. Subsidies, buybacks, and sustainable fisheries. J.Environ.Econ.Manage. **50**(1): 47-58

Clark, C.W. 2006a. The worldwide crisis in fisheries: economic models and human behavior. Cambridge University Press, Cambridge, UK.

Clark, C.W. 2006b. Fisheries bioeconomics: why is it so widely misunderstood? Springer, Tokyo.

Clark, C.W. 2010. Mathematical Bioeconomics: The Mathematics of Conservation. Wiley, Hoboken, NJ.

Coleman, F.C., Figueira, W.F., Ueland, J.S. and Crowder, L.B. 2004. The impact of United States recreational fisheries on marine fish populations. Science **305**(5692): 1958

Connelly, N.A. and Brown, T.L. 1991. Net economic value of the freshwater recreational fisheries of New York. T. Am. Fish Soc. **120**(6): 770-775

Conover, D., Munch, S. and Arnott, S. 2009. Reversal of evolutionary downsizing caused by selective harvest of large fish. Proc. R. Soc. B

Conover, D.O. and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. Science **297**(5578): 94

Conover, D.O. and Baumann, H. 2009. The role of experiments in understanding fishery induced evolution. Evol. Appl. **2**(3): 276-290

Cooke, S.J. and Cowx, I.G. 2004. The role of recreational fishing in global fish crises. Bioscience **54**(9): 857-859

Costanza, R. 1997. The value of the world's ecosystem services and natural capital. Nature **387**(6630): 253-260

Costello, C., Gaines, S.D. and Lynham, J. 2008. Can catch shares prevent fisheries collapse? Science **321**(5896): 1678

Costello, C., Lynham, J., Lester, S.E. and Gaines, S.D. 2010. Economic incentives and global fisheries sustainability. Res. Econ. **2**: 299-318

Cowan, J., Rose, K. and DeVries, D. 2000. Is density-dependent growth in young-of-the-year fishes a question of critical weight? Rev. Fish. Biol. Fish. **10**(1): 61-89

Crutchfield, J.A. and Zellner, A. 1962. Economic aspects of the Pacific halibut fishery. Fish. Ind. Res **1**(1): 23-24

Daan, N., Gislason, H., Pope, J.G. and Rice, J.C. 2011. Apocalypse in world fisheries? The reports of their death are greatly exaggerated. ICES J. Mar. Sci.

Dankel, D.J., Skagen, D.W. and Ulltang, O. 2008. Fisheries management in practice: review of 13 commercially important fish stocks. Rev. Fish. Biol. Fish. **18**(2): 201-233

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. and Wilmers, C.C. 2009. Human predators outpace other agents of trait change in the wild. Proc. Natl. Acad. Sci. USA **106**(3): 952-954

Daskalov, G.M., Grishin, A.N., Rodionov, S. and Mihneva, V. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proc. Natl. Acad. Sci. USA **104**(25): 10518-10523

De Leo, G.A. and Gatto, M. 2001. A stochastic bioeconomic analysis of silver eel fisheries. Ecol. Appl. **11**(1): 281-294

De Mutsert, K., Cowan, J.H., Essington, T.E. and Hilborn, R. 2008. Reanalyses of Gulf of Mexico fisheries data: Landings can be misleading in assessments of fisheries and fisheries ecosystems. Proc. Natl. Acad. Sci. USA **105**(7): 2740-2744

De Roos, A.M., Boukal, D.S. and Persson, L. 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. Proceedings of the Royal Society B: Biological Sciences **273**(1596): 1873

Dichmont, C., Pascoe, S., Kompas, T., Punt, A. and Deng, R. 2010. On implementing maximum economic yield in commercial fisheries. Proc. R. Soc. B **107**(1): 16-21

Diekert, F.K., Hjermann, D., Nævdal, E. and Stenseth, N.C. 2010. Spare the young fsh: Optimal harvesting policies for North-East Arctic cod. Environ. Resource Econ. **47**(4): 455-475

Dunlop, E.S., Enberg, K., Jørgensen, C. and Heino, M. 2009a. Toward Darwinian fisheries management. Evol. Appl. **2**(3): 245-259

Dunlop, E.S., Heino, M. and Dieckmann, U. 2009b. Eco-genetic modeling of contemporary life-history evolution. Ecological Applications **19**(7): 1815-1834

Edgar, G.J., Russ, G.R. and Babcock, R.C. 2007. Marine protected areas. Marine Ecology: 533-555

Enberg, K., Jørgensen, C., Dunlop, E., Heino, M. and Dieckmann, U. 2009. Implications of fisheries-induced evolution for stock rebuilding and recovery. Evol. Appl. **2**(3): 394-414

Enberg, K., Jorgensen, C. and Mangel, M. 2010. Fishing-induced evolution and changing reproductive ecology of fish: the evolution of steepness. Can. J. Fish. Aquat. Sci. **67**(10): 1708-1719

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S. and Heino, M. 2011. Fishing-induced evolution of growth: concepts, mechanisms, and the empirical evidence. Mar. Ecol. in press

Ernande, B., Dieckmann, U. and Heino, M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proc. R. Soc. B **271**(1537): 415

Essington, T., Beaudreau, A. and Wiedenmann, J. 2006. Fishing through marine food webs. Proc. Natl. Acad. Sci. USA. **103**(9): 3171-3175.

FAO. 2011. The state of world fisheries and aquaculture 2010 FAO Fisheries and Aquaculture Department, Rome.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. and Holling, C. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. **35**: 557-581

Gabriel, W.L. and Mace, P.M. 1999. A review of biological reference points in the context of the precautionary approach. Northeast Fisheries Science Center, Woods Hole, MA.

Gallagher, C., Hannah, R. and Sylvia, G. 2004. A comparison of yield per recruit and revenue per recruit models for the Oregon ocean shrimp, Pandalus jordani, fishery. Fish. Res. **66**(1): 71-84

Gallic, B.L. and Cox, A. 2006. An economic analysis of illegal, unreported and unregulated (IUU) fishing: Key drivers and possible solutions. Mar. Pol. **30**(6): 689-695

Garcia, S. 1996. The precautionary approach to fisheries and its implications for fishery research, technology and management: an updated review. FAO Fisheries Technical Paper: 1-76

Garcia, S.M. and Cochrane, K.L. 2005. Ecosystem approach to fisheries: a review of implementation guidelines. ICES J. Mar. Sci. **62**(3): 311

Garcia, S.M. and Rosenberg, A.A. 2010. Food security and marine capture fisheries: characteristics, trends, drivers and future perspectives. Proc. R. Soc. B **365**(1554): 2869

Gardner, R., Ostrom, E. and Walker, J.M. 1990. The nature of common-pool resource problems. Rationality and Society **2**(3): 335

Gibbs, M.T. 2010. Why ITQs on target species are inefficient at achieving ecosystem based fisheries management outcomes. Mar. Pol. **34**(3): 708-709

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M. and Toulmin, C. 2010. Food security: the challenge of feeding 9 billion people. Science **327**(5967): 812-818

Gordon, H. 1954. The economic theory of a common-property resource: the fishery. J. Polit. Economy **62**: 124-142

Grafton, R., Kompas, T. and Schneider, V. 2005. The bioeconomics of marine reserves: a selected review with policy implications. Journal of Bioeconomics **7**(2): 161-178

Grafton, R.Q. 1996. Individual transferable quotas: theory and practice. Rev. Fish. Biol. Fish. **6**(1): 5-20

Grafton, R.Q., Arnason, R., Bjorndal, T., Campbell, D., Campbell, H.F., Clark, C.W., Connor, R., Dupont, D.P., Hannesson, R. and Hilborn, R. 2006. Incentive-based approaches to sustainable fisheries. Can. J. Fish. Aquat. Sci. **63**(3): 699-710

Grafton, R.Q., Kompas, T. and Hilborn, R.W. 2007. Economics of overexploitation revisited. Science **318**(5856): 1601

Grafton, R.Q., Hilborn, R., Ridgeway, L., Squires, D., Williams, M., Garcia, S., Groves, T., Joseph, J., Kelleher, K. and Kompas, T. 2008. Positioning fisheries in a changing world. Mar. Pol. **32**(4): 630-634

Grafton, R.Q., Campbell, D., Costello, C., Hilborn, R. and Kompas, T. 2009. Comment on Abdicating Responsibility: The Deceits of Fisheries Policy. Fisheries **34**(6): 292-294

Hall, S.J. and Mainprize, B. 2004. Towards ecosystem based fisheries management. Fish and Fisheries **5**(1): 1-20

Hannesson, R. 1993. Bioeconomic analysis of fisheries. Fishing News Books Ltd., Oxford, UK.

Hannesson, R. 2011. Rights based fishing on the high seas: Is it possible? Mar. Pol.

Hardin, G. 1968. The tragedy of the commons. Science **162**: 1243-1248

Heino, M. 1998. Management of evolving fish stocks. Can. J. Fish. Aquat. Sci. **55**(8): 1971-1982

Heino, M., Dieckmann, U. and Godo, O.R. 2002. Estimating reaction norms for age and size at maturation with reconstructed immature size distributions: a new technique illustrated by application to Northeast Arctic cod. ICES J. Mar. Sci. **59**(3): 562-575

Helser, T.E., Thunberg, E.M. and Mayo, R.K. 1996. An age-structured bioeconomic simulation of US silver hake fisheries. N. Am. J. Fish. Manage. **16**(4): 783-794

Helser, T.E. and Brodziak, J.K.T. 1998. Impacts of density-dependent growth and maturation on assessment advice to rebuild depleted US silver hake (Merluccius bilinearis) stocks. Can. J. Fish. Aquat. Sci. **55**(4): 882-892

Hilborn, R. and Walters, C. 1992. Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty. Chapman & Hall, New York.

Hilborn, R., Maguire, J.J., Parma, A.M. and Rosenberg, A.A. 2001. The Precautionary Approach and risk management: can they increase the probability of successes in fishery management? Can. J. Fish. Aquat. Sci. **58**(1): 99-107

Hilborn, R. 2002. The dark side of reference points. Bull. Mar. Sci. **70**(2): 403-408

Hilborn, R., Orensanz, J. and Parma, A.M. 2005. Institutions, incentives and the future of fisheries. Philosophical Transactions of the Royal Society B: Biological Sciences **360**(1453): 47

Hilborn, R. 2007a. Defining success in fisheries and conflicts in objectives. Mar. Pol. **31**(2): 153-158

Hilborn, R. 2007b. Moving to sustainability by learning from successful fisheries. Ambio **36**(4): 296-303

Hilborn, R. 2007c. Managing fisheries is managing people: what has been learned? Fish and Fisheries **8**(4): 285-296

Hilborn, R. 2007d. Reinterpreting the state of fisheries and their management. Ecosystems **10**(8): 1362-1369

Hilborn, R. and Stokes, K. 2010. Defining Overfished Stocks: Have We Lost The Plot? Fisheries **35**(3): 113-120

Hilborn, R. 2011. Let Us Eat Fish. *In* The New York Times, New York. p. A27.

Holland, D.S., Bentley, N. and Lallemand, P. 2005. A bioeconomic analysis of management strategies for rebuilding and maintenance of the NSS rock lobster (Jasus edwardsii) stock in southern New Zealand. Can. J. Fish. Aquat. Sci. **62**(7): 1553-1569

Holt, S. 2009. Sunken Billions-But how many? Fisheries Research **97**(1-2): 3-10

Houde, E. 1994. Differences between marine and freshwater fish larvae: implications for recruitment. ICES J. Mar. Sci. **51**(1): 91

Hsieh, C., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M. and Sugihara, G. 2006. Fishing elevates variability in the abundance of exploited species. Nature **443**(7113): 859-862

Hutchings, J.A. and Fraser, D.J. 2008. The nature of fisheries-and farming-induced evolution. Mol. Ecol. **17**(1): 294-313

Hutchings, J.A. 2009. Avoidance of fisheries induced evolution: management implications for catch selectivity and limit reference points. Evol. Appl. **2**(3): 324-334

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J. and Estes, J.A. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**(5530): 629

Jackson, J.B.C. 2008. Ecological extinction and evolution in the brave new ocean. Proceedings of the National Academy of Sciences **105**(Supplement 1): 11458

Jenkins Jr, T.M., Diehl, S., Kratz, K.W. and Cooper, S.D. 1999. Effects of population density on individual growth of brown trout in streams. Ecology **80**(3): 941-956

Jennings, S. 2005. Indicators to support an ecosystem approach to fisheries. Fish and Fisheries **6**(3): 212-232

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M. and Rijnsdorp, A.D. 2007. Managing evolving fish stocks. Science **318**(5854): 1247-1248

Jørgensen, C. and Fiksen, Ø. 2010. Modelling fishing-induced adaptations and consequences for natural mortality. Can. J. Fish. Aquat. Sci. **67**(7): 1086-1097

Katsukawa, T. 2005. Evaluation of current and alternative fisheries management scenarios based on spawning-per-recruit (SPR), revenue-per-recruit (RPR), and yield-per-recruit (YPR) diagrams. ICES J. Mar. Sci. **62**(5): 841-846

Kent, G. 1997. Fisheries, food security, and the poor. Food Policy **22**(5): 393-404

Kompas, T., Che, T.N. and Grafton, R.Q. 2008. Fisheries instrument choice under uncertainty. Land economics **84**(4): 652

Krysiak, F.C. and Krysiak, D. 2002. Aggregation of Dynamic Systems and the Existence of a Regeneration Function* 1. J.Environ.Econ.Manage. **44**(3): 517-539

Lande, R., Engen, S. and Saether, B.E. 1994. Optimal harvesting, economic discounting and extinction risk in fluctuating populations. Nature **372**(6501): 88-90

Larkin, P.A. 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. **106**(1): 1-11

Law, R. and Grey, D.R. 1989. Evolution of yields from populations with age-specific cropping. Evolutionary Ecology **3**(4): 343-359

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Mar. Ecol.-Prog. Ser. **335**: 271-277

Longhurst, A. 2002. Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fisheries Research **56**(2): 125-131

Lorenzen, K. and Enberg, K. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proc. R. Soc. B **269**(1486): 49-54

Macinko, S. and Bromley, D.W. 2003. Property and fisheries for the twenty-first century: seeking coherence from legal and economic doctrine. Vt. L. Rev. **28**: 623

Mayer, A.L. and Rietkerk, M. 2004. The dynamic regime concept for ecosystem management and restoration. Bioscience **54**(11): 1013-1020

Mertz, G. and Myers, R.A. 1998. A simplified formulation for fish production. Can. J. Fish. Aquat. Sci. **55**(2): 478-484

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis 1597260401 World Resources Institute, Washington, DC.

Mora, C., Myers, R.A., Coll, M., Libralato, S., Pitcher, T.J., Sumaila, R.U., Zeller, D., Watson, R., Gaston, K.J. and Worm, B. 2009. Management effectiveness of the world's marine fisheries. PLoS Biol. **7**(6): e1000131

Morishita, J. 2008. What is the ecosystem approach for fisheries management. Mar. Pol. **32**(1): 19-26

Munro, G.R. 1992. Mathematical bioeconomics and the evolution of modern fisheries economics. Bull. Math. Biol. **54**(2): 163-184

Munro, G.R. and Sumaila, U.R. 2001. Subsidies and their potential impact on the management of the ecosystems of the North Atlantic. Fish. Cent. Res. Rep. **9**(5): 10-27

Murawski, S., Methot, R. and Tromble, G. 2007. Biodiversity loss in the ocean: how bad is it? Science **316**(5829): 1281

Murawski, S.A. 2000. Definitions of overfishing from an ecosystem perspective. ICES J. Mar. Sci. **57**(3): 649

Murawski, S.A., Rago, P.J. and Trippel, E.A. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES J. Mar. Sci. **58**(5): 1002-1014

Murawski, S.A. 2007. Ten myths concerning ecosystem approaches to marine resource management. Mar. Pol. **31**(6): 681-690

Myers, R., Rosenberg, A., Mace, P., Barrowman, N. and Restrepo, V. 1994. In search of thresholds for recruitment overfishing. ICES J. Mar. Sci. **51**(2): 191

O'Farrell, M.R. and Botsford, L.W. 2006. The fisheries management implications of maternal-age-dependent larval survival. Can. J. Fish. Aquat. Sci. **63**(10): 2249-2258

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R. and Folke, C. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems **10**(6): 877-889

Pascoe, S. 1997. Bycatch management and the economics of discarding FAO Fisheries Technical Paper, Rome.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and Torres Jr, F. 1998. Fishing down marine food webs. Science **279**(5352): 860-863

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. and Zeller, D. 2002. Towards sustainability in world fisheries. Nature **418**(6898): 689-695

Pauly, D. and Palomares, M.L. 2005. Fishing down marine food web: it is far more pervasive than we thought. Bull. Mar. Sci. **76**(2): 197-212

Pauly, D., Watson, R. and Alder, J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. Philos. Trans. R. Soc. B-Biol. Sci. **360**(1453): 5

Pauly, D. 2009. Aquacalypse now: the end of fish. The New Republic **240**(18): 24-27

Perry, A.L., Low, P.J., Ellis, J.R. and Reynolds, J.D. 2005. Climate change and distribution shifts in marine fishes. Science **308**(5730): 1912

Persson, L., Amundsen, P.A., De Roos, A.M., Klemetsen, A., Knudsen, R. and Primicerio, R. 2007. Culling prey promotes predator recovery—alternative states in a whole-lake experiment. Science **316**(5832): 1743

Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D. and Heneman, B. 2004. Ecosystem-based fishery management. Science **305**(5682): 346

Pitcher, T.J. and Hollingworth, C.E. 2002. Recreational fisheries: ecological, economic, and social evaluation. Wiley-Blackwell, Hoboken, NJ.

Pontryagin, L., Boltyanskii, V., Gamkrelidze, R. and Mishchenko, E. 1962. The mathematical theory of optimal processes. Interscience, New York.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L. and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries **27**(1): 6-17

Reznick, D.N. and Ghalambor, C.K. 2005. Can commercial fishing cause evolution? Answers from guppies (Poecilia reticulata). Can. J. Fish. Aquat. Sci. **62**(4): 791-801

Ricker, W.E. 1946. Production and utilization of fish populations. Ecological Monographs **16**(4): 373-391

Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. **38**(12): 1636-1656

Rothschild, B.J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, MA.

Schaefer, M. 1957. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. J . Fish. Res. Board Canada **14**: 669-681

Scheffer, M. and Carpenter, S.R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol. Evol. **18**(12): 648-656

Scheffer, M., Carpenter, S. and Young, B. 2005. Cascading effects of overfishing marine systems. Trends Ecol. Evol. **20**(11): 579-581

Schlager, E. and Ostrom, E. 1992. Property-rights regimes and natural resources: a conceptual analysis. Land economics **68**(3): 249-262

Scott, A. 1955. Natural resources: the economics of conservation. University of Toronto Press, Toronto.

Scott, A. 2008. The evolution of resource property rights. Oxford University Press, USA.

Sissenwine, M. 1987. An alternative perspective on recruitment overfishing and biological reference points. Can. J. Fish. Aquat. Sci **44**(6987): 913

Sissenwine, M.P. and Mace, P.M. 1992. ITQs in New Zealand: the era of fixed quota in perpetuity. Fish. Bull. **90**(1): 147-160

Squires, D., Kirkley, J. and Tisdell, C.A. 1995. Individual transferable quotas as a fisheries management tool. Rev. Fish. Sci. **3**(2): 141-169

Sumaila, U.R., Guénette, S., Alder, J. and Chuenpagdee, R. 2000. Addressing ecosystem effects of fishing using marine protected areas. ICES J. Mar. Sci. **57**(3): 752

Sumaila, U.R., Alder, J. and Keith, H. 2006. Global scope and economics of illegal fishing. Mar. Pol. **30**(6): 696-703

Sumaila, U.R., Teh, L., Watson, R., Tyedmers, P. and Pauly, D. 2008. Fuel price increase, subsidies, overcapacity, and resource sustainability. ICES Journal of Marine Science: Journal du Conseil **65**(6): 832

Sumaila, U.R. 2010. A cautionary note on individual transferable quotas. Ecology and Society **15**(3): 36

Sumaila, U.R., Khan, A.S., Dyck, A.J., Watson, R., Munro, G., Tydemers, P. and Pauly, D. 2010. A bottom-up re-estimation of global fisheries subsidies. Journal of Bioeconomics: 1-25

Sutinen, J.G. 1999. What works well and why: evidence from fishery-management experiences in OECD countries. ICES J. Mar. Sci. **56**(6): 1051

Swain, D.P., Sinclair, A.F. and Mark Hanson, J. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proc. R. Soc. B **274**(1613): 1015-1022

Tahvonen, O. 2008. Harvesting an age structured population as biomass: Does it work? Natural Res. Modeling **21**(4): 525-550

Tahvonen, O. 2009. Optimal harvesting of age-structured fish populations. Mar. Resour. Econ. **24**(2): 281–299

Tietenberg, T. and Lewis, L. 2008. Environmental and natural resource economics. Addison Wesley, Boston.

Turvey, R. 1964. Optimization and suboptimization in fishery regulation. The American economic review **54**(2): 64-76

Vincenzi, S., Crivelli, A.J., Jesensek, D. and De Leo, G.A. 2008. The role of density-dependent individual growth in the persistence of freshwater salmonid populations. Oecologia **156**(3): 523-534

Weitzman, M.L. 1998. Why the far-distant future should be discounted at its lowest possible rate. J.Environ.Econ.Manage. **36**(3): 201-208

Wilen, J.E. 2000. Renewable resource economists and policy: What differences have we made? J.Environ.Econ.Manage. **39**(3): 306-327

World Bank. 2009. The sunken billions: The economic justification for fisheries reform. World Bank, Washington D.C., USA.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F. and Palumbi, S.R. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science **314**(5800): 787

Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A. and Jennings, S. 2009. Rebuilding global fisheries. Science **325**(5940): 578