Darwinian fisheries science needs to consider realistic fishing pressures over evolutionary time scales

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ABSTRACT: The apparently intense selective differentials imposed by many fisheries may drive the rapid evolution of growth rates. In a widely-cited laboratory experiment, Conover & Munch (2002; Science 297:94–96) found considerable evolutionary change in the size of harvested fish over 4 generations. Their empirical model has since been used to estimate the impact of fishery-driven evolution on fishery sustainability. Using a mathematical, individual-based model (IBM) that simulates that experiment, we showed that the selection imposed in the Conover & Munch (2002) model is unrealistically strong when compared to harvest rates in wild fisheries. We inferred the evolutionary change that could be expected over the timescale used by Conover & Munch (2002), had they simulated more realistic harvest regimes, and found that the magnitude in their original experiment was 2.5 to 5 times greater. However, over evolutionary timescales of 30 generations and with realistic fishing pressure, the results of Conover & Munch (2002) are comparable to wild fisheries. This simulation result provides support for the use of empirical models to predict the impacts of fishery-driven evolution on yields and sustainability. Future models should consider the timing of fishing events, the trade-off between size, maturation and growth, and density-dependent effects for a comprehensive analysis of the consequences of fishery-driven evolution.

KEY WORDS: Fishery-driven evolution · Evolution · Fisheries · Heritability · Life history · Selection · Individual-based model

INTRODUCTION

Strong fishing selection pressure, in combination with moderate levels of heritable genetic variation, have been shown to drive the Darwinian evolution of life history traits such as growth rate and size-at-maturity in numerous fished populations (Jørgensen et al. 2007). The magnitude of change in these life-history traits is so great that it will most likely result in lower sustainable yields (Law 2000) and may even have contributed to stock collapse in some fisheries (Olsen et al. 2004). Hence, the Darwinian fishery paradigm can no longer be ignored if fish stocks are to be managed for sustainability or recovery from over-exploitation (Conover 2000).

When predicting the magnitude of evolutionary change, it is important to consider what proportion of the variance in the life-history trait can be attributed

to genetic variation, the selective strength of fishing, and appropriate timescales. The genetically controlled proportion of life history traits is probably moderate, estimated at 0.2 to 0.3 for fish (Law 2000, Stokes & Law 2000). The selective pressure exerted by different fisheries is variable and depends upon the harvest rate and the degree to which the fishery targets particular components of the population. Gillnets can be highly size selective (Sinclair et al. 2002), and focussing fishing effort on particular fish life history stages, such as the spawning aggregations, can also exert strong selective pressures for delayed maturity (Law & Grey 1989). Given these factors, fishery-driven evolution is highly likely in fish stocks that have been fished for tens to hundreds of generations. A review of empirical studies of fishery-driven evolution suggests that, in heavily fished populations, a 25% evolutionary change in life-history traits over 30 to 40 generations is possible (Jørgensen et al. 2007).

The gradual nature of evolutionary trends, as well as confounding environmental factors such as density-dependent growth compensation, impede the detection of life-history evolution in wild fisheries. A number of studies, using a variety of methods, have tried to separate environmental from genetic effects in wild fisheries (e.g. Rijnsdorp 1993, Heino et al. 2002, Swain et al. 2007). However, the statistical techniques used to identify potential evolutionary trends necessarily make important simplifying assumptions (Dieckmann & Heino 2007, Wright 2007). Thus, it is necessary to consider a wide variety of sources of evidence and study techniques. Predictions of fishery-driven evolution in wild fisheries are complemented by models, because they enable the simulation of processes driving evolutionary change in life history traits without other confounding forces. Both mathematical and empirical models have been used to explore the impacts of fishery-driven evolution on life-history traits and fishery sustainability (Conover & Munch 2002, Reznick & Ghalambor 2005, Williams & Shertzer 2005, de Roos et al. 2006, Andersen et al. 2007).

The empirical study by Conover & Munch (2002) has received a particularly great amount of attention (148 citations on ISI Web of Knowledge, March 2008, http://wok.mimas.ac.uk). This could largely be attributed to the evidence for rapid evolutionary change, resulting in a reduction of 25% in size at age over 4 generations, presented in the study. Such drastic changes in size would have severe implications for yields in wild fisheries and would reduce sustainability through the evolution of genetically correlated life-history traits such as fecundity (Conover & Munch 2002, Conover et al. 2005, Munch et al. 2005, Walsh et al. 2006). However, Conover & Munch (2002) have been criticised for using extreme harvest rates and

artificially constraining age at maturity, conditions that may produce unrealistically great evolutionary change over short timescales (Hilborn 2006, Conover & Munch 2007, Hilborn 2007). Thus, they may overestimate the impact of fishery-driven evolution on sustainability and yields in wild fisheries.

To determine the relevance of their studies to wild fisheries, we developed a mathematical, individual-based model (IBM) that simulated the Conover & Munch (2002) experiment and considered the evolutionary change in growth under different harvesting regimes and over more realistic evolutionary timescales. This enabled us to compare the results of Conover & Munch (2002) with those that might have been expected had their experiment used fishery pressures and evolutionary timescales that occur in wild fisheries.

METHODS

Model structure. Our IBM simulated growth, fishing, spawning and inheritance cycles from Conover & Munch (2002). Similar to their empirical model, replicate populations of 1000 larval fish of the same age 'grew' for 190 d in our simulation. On the 190th day, each population was 'harvested' according to one of 3 rules: fishing removed either the (1) largest (large-harvested), (2) smallest (small-harvested), or (3) a random (random-harvested) 90% of individuals. Conover & Munch (2002) artificially induced the surviving 100 individuals to spawn, and their offspring were taken to breed the next generation of 1000 fish. This fishery pattern was repeated for 4 generations. In our IBM, in contrast, surviving individuals 'spawned' and contributed equal numbers of model offspring to the next generation of 1000 individuals. This cycle was repeated for up to 100 generations (Fig. 1).

Individual growth and size. Each individual in the IBM simulations grew on a daily time-step. Growth was simulated using a function relating size (length in mm) and age (in d), following the description of growth of Atlantic silverside *Menidia menidia* in Munch et al. (2005):

$$S_a = Da^2 + \theta a + G \tag{1}$$

where S_a is the size at age a; D is the age-squared growth coefficient; θ is the growth coefficient and G is the size-at-birth for an individual.

Variable size at age (upon which harvesting selection acts) was simulated by assigning individual growth coefficients. Individuals with greater growth coefficients grew faster. The age-squared coefficient was kept constant, because small changes in its value effect much greater changes than the growth coefficient in the

growth curve. Assumptions about static or evolving size at birth were tested in sensitivity analyses.

In the first generation, growth coefficient values were randomly selected from a normal distribution (for parameter values see Table 1). The distribution was generated using the mean and standard deviation of size-at-190 d in the first generation of random-harvested trials from the Conover & Munch (2002) experiment. In following generations, the growth constant was inherited from individuals that spawned. All individuals that survived fishing spawned, and all spawning individuals contributed equal numbers of offspring to the next generation. Individual length was converted to harvested yield in weight, making IBM results directly comparable with those reported by Conover & Munch (2002). This equation followed the form typical for length–weight relationships:

$$W = \alpha L^{\beta} \qquad (2)$$

where α and β are constants.

Parameters for Eq. 2 (Table 1) were calculated using the mean weight of harvested fish in first generation random-harvested trials from Conover & Munch (2002) and the mean size of unselectively harvested fish in Munch et al. (2005). The power parameter β, was set at a typical level for length–weight relationships (Blueweiss et al. 1978).

Table 1. *Menidia menidia*. Parameters and values used in the individual-based model (IBM). CV: coefficient of variation

Parameter	Value	Source
Age-squared growth coefficient, D (mm d^{-2})	0.002	Munch et al. (2005)
Mean growth coefficient, θ (mm d^{-1})	0.047	Munch et al. (2005)
CV of the growth coefficient, θ	0.70	Conover & Munch (2002)[a]
Size at birth, G (mm)	4.63	Munch et al. (2005)
Generation time (d)	190	Conover & Munch (2002)
Length–weight conversion constant, α (g mm^{-1})	5.25×10^{-6}	Conover & Munch (2002)[a]
Length–weight conversion constant, β	3	Blueweiss et al. (1978)
Heritability, h^2	0.2	Conover & Munch (2002)

[a]No exact values given for the parameters; values estimated from published results. See 'Methods' for details
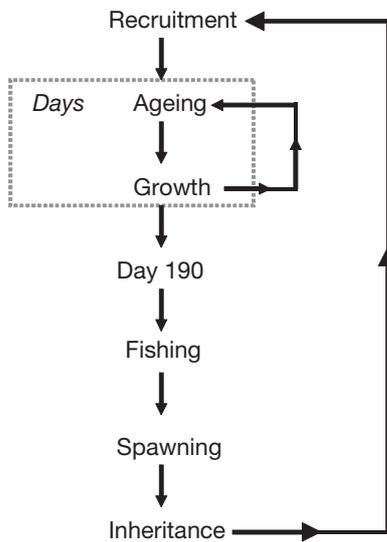

Fig. 1. Schematic of individual-based model components cycled each generation in the Atlantic silverside model. Components inside the dashed box were updated each model day

Inheritance of growth. Individual phenotypes are determined by a combination of environmental and genetic effects. The genetic component of the variance of a quantitative trait is composed of additive, dominant and epistatic components and interactions between these components (broad-sense heritability *sensu* Falconer & Mackay 1996). The additive component is of greatest interest in selection experiments, since additive genes combine cumulatively to influence the phenotypical expression of a trait; hence, the evolutionary response is predictable under selection (Falconer & Mackay 1996). The narrow-sense heritability (henceforth referred to as heritability, h^2) is the proportion of phenotypic variance observed in a quantitative trait that can be explained by additive genetic variation:

$$h^2 = V_a / V_p \qquad (3)$$

where V_a is the proportion of phenotypic variance that is explained by additive genetic variance and V_p is the total phenotypic variance in a population.

Conover & Munch (2002) set the age at maturity by artificial induction of spawning in all individuals that survived harvesting; hence, it was only necessary to simulate heritability of size at age. In our IBM simulations, the growth coefficient representing size at age was inherited with a heritability of 0.2, based on the estimates by Conover & Munch (2002). Inheritance of the growth coefficient was simulated by using the 'breeders equation' to calculate the evolutionary response R to the selection of a trait in a population:

$$R_T = h^2{}_T \Delta S_T \qquad (4)$$

where T is the trait, $h^2{}_T$ is the heritability of the trait T and ΔS_T is the difference in the mean number of parents displaying the phenotype for trait T before and after selection.

The breeders equation has commonly been used in other models of fishery-driven evolution (Munch et al. 2005, de Roos et al. 2006, Andersen et al. 2007). In our model, it was used to calculate the phenotypic mean for a normal distribution of possible offspring trait values for each new generation, given the mean trait values for all parents after selection. The phenotypic standard deviation was estimated from Conover & Munch (2002) and assumed to be constant in all our IBM simulations (Table 1). The trait values for growth of individuals in the new generation were then randomly selected from this distribution. In real animal populations, selection tends to erode additive genetic diversity, decreasing the phenotypic variability on which selection can act (Falconer & Mackay 1996). The evolutionary rate in Conover & Munch (2002) showed no sign of slowing over the timescales considered; hence, simulating genetic diversity as a constant is a valid assumption for our model, provided the evolutionary rate of change does not exceed that observed in Conover & Munch (2002).

The evolution of adult size may also be expected to be correlated with the evolution of size at other ages. The growth equation (Eq. 1) includes a term for size at birth, so it is important to consider co-evolution of this trait. We considered the co-heritability of size at birth and size at age 190 d. Co-heritability describes the expected change in a trait given selection of another trait. Thus, the evolutionary response R of a genetically correlated trait can be calculated based on the selection of another trait:

$$R_P = h^2_{T,P} \Delta S_T \qquad (5)$$

where P is the correlated trait, $h^2_{T,P}$ is the co-heritability of the traits T and P, and ΔS_T is the difference of the mean number of parents displaying the phenotype for trait T before and after selection (Falconer & Mackay 1996).

The breeders equation for co-heritability was used to calculate the size at birth parameter G for each individual specific growth coefficient. The effect of different co-heritability values was explored in sensitivity analyses.

Heritability of the growth trait in our IBM was confirmed to represent heritability of the size at age 190 d by plotting the cumulative selective differential for different heritability values. The slope of this plot is an estimate of heritability of size at age (Falconer & Mackay 1996). The estimates match the heritability values for the growth constant used in our simulations (Fig. 2). Furthermore, our simulations confirm that the model represented evolution linearly for the magnitude of change considered, which was a necessary assumption for a heritability equation that does not consider changes in genetic variance. When the cumulative selection differential is plotted against the mean
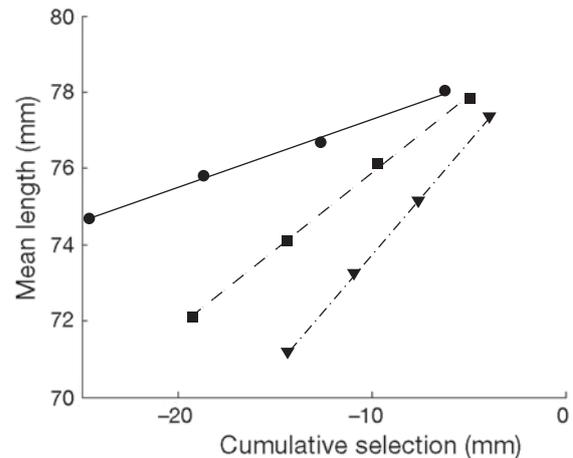

Fig. 2. Cumulative changes in the mean phenotype of parents caused by selection over 4 generations (cumulative selection) against the mean length of the population at different heritability values. Slopes of the lines give the heritability of size at age 190 d for each generation. If all of the variability in growth was genetically controlled ($h^2 = 1$), the change in mean length would correspond exactly with changes in cumulative selection. The slopes of the fitted lines are 0.20 (—●—), 0.40 (--■--) and 0.60 (-·▼-·) for trials with heritability of 0.2, 0.4 and 0.6, respectively

length, our IBM shows less residual variance than the experimental results of Conover & Munch (2002) (Fig. 2, $R^2 = 0.99$ for all scenarios), due to the averaging approach taken in the breeders equation (Eq. 4).

Model simulations. Initially, a base-case simulation, using parameters from Conover & Munch (2002), was compared with results from that study. Then, simulations were conducted to test sensitivity of our IBM to parameter assumptions about the variance in growth rates in a generation, the heritability of growth rates and the co-heritability of growth rates and size at birth. In order to contextualise the selective pressure indicated by the Conover & Munch (2002) experiment, it was necessary to compare the results from their experiment with selective pressures from a wide range of wild fisheries. Because it is complicated and data-intensive to calculate selective pressure in wild fisheries (Sinclair et al. 2002), we used the maximum estimated yearly harvest rates (proportion of fishable stock removed per year) for different wild fisheries as an indicator of fishery pressure. Maximum yearly harvest rates in 82 wild fisheries were calculated from the maximum fishing mortality rate (instantaneous rate) from the literature and databases of fishery mortality rates (Appendix 1). We then simulated evolution in the Conover & Munch (2002) experiment with our IBM, applying harvest rates of 0 to 1 to the vulnerable proportion of the population, which included 5 to 100 % of the largest individuals. Thus, the evolutionary change expected in the original Conover & Munch (2002)

experiment could be compared with the evolutionary change expected when using more realistic harvest rates from wild fisheries. To calculate realistic evolutionary timescales, we considered the number of generations required to reproduce the result from Conover & Munch (2002) across the range of fishery selective pressures.

RESULTS

Comparison of our model with the Conover & Munch (2002) experiment

A comparison of the Conover & Munch (2002) experiment (Fig. 3A) with our results (Fig. 3B) shows that the IBM approximates the general trends of increasing size in small-harvested trials and decreasing size in large-harvested trials observed in the empirical exper-
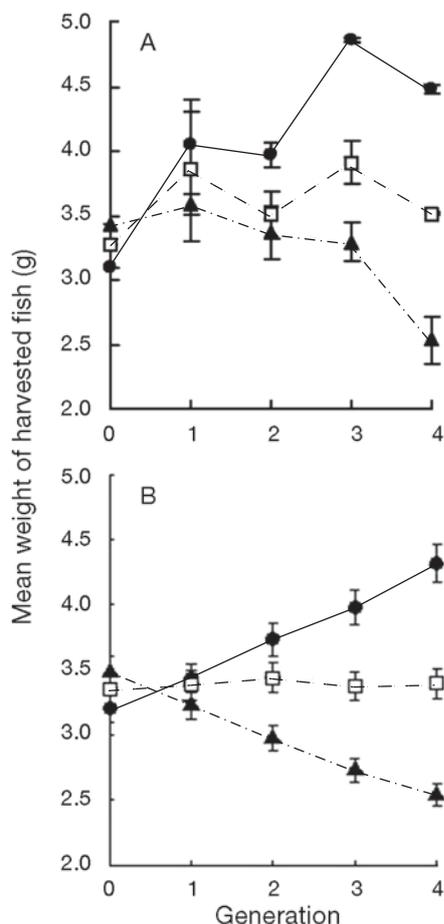

Fig. 3. Change in mean weight (± SE) of harvested fish; (A) from Conover & Munch (2002), reprinted with permission from AAAS, and (B) individual-based model (IBM) populations. Populations are either large-harvested (▲), small-harvested (●) or random-harvested (□)

iment. Our simulated evolutionary trends are more consistent and slightly underestimated when compared with Conover & Munch (2002). The extra variation in Conover & Munch (2002) could be explained by random genetic sampling effects or non-genetic inter-annual variation, factors not accounted for in our simple additive genetic model. Underestimation of evolutionary change by our IBM could be due to underestimation of key IBM parameters, evolution of other life-history traits genetically correlated with size at age 190 d, or non-additive genetic effects in the empirical experiment. Whilst evolutionary models of non-additive genetic effects are achievable (e.g. Hallander & Waldmann 2007), not enough is known about non-additive genetic effects in silverside to include them in this simple model.

The minor underestimation of the evolutionary magnitude in Conover & Munch (2002) may also be caused by the assumption of constant size at birth in all generations. Thus, we also considered the co-heritability of size at birth and size at age 190 d for co-heritability values ranging from 0 to 0.01. Munch et al. (2005) published values for co-heritability of size at age 190 d and earlier ages for the model system used by Conover & Munch (2002). The magnitude of the co-heritability decreased for younger ages (Munch et al. 2005). Thus, the upper limit for this sensitivity exploration (0.01) was chosen as twice the estimate of co-heritability of size at age 190 d and size at age 7 d published in Munch et al. (2005). After 4 generations, there is no difference between the mean weight of harvested fish for simulations with co-heritability values ranging from 0 and 0.01. Simulations of longer time-scales produced similar results. Thus for simplicity, in subsequent simulations constant size at birth is assumed over all generations.

The sensitivity of evolutionary change to 2 other key parameters in our IBM was also tested. Sensitivity of evolutionary change to heritability (h^2 = 0 to 1) was conducted, whilst holding population variability constant at CV = 0.7. Sensitivity to population variability (CV = 0.05 to 1) was also tested whilst holding the heritability constant at 0.2. The IBM showed low sensitivity to both parameters. An increase in heritability of 0.1 resulted in a linear decrease of 8.3% (0.31 g) in the mean weight of harvested fish after 4 generations, compared to the harvest size in the first generation. An increase in population variability of 0.1 resulted in a linear decrease of 2.3% (0.09 g). Linear sensitivity to key parameters means that, if population variability or heritability were underestimated in the IBM, the relative magnitude of evolutionary change in the Conover & Munch (2002) would not change for fishery scenarios with alternative selective pressures. Based on these results, our IBM was then used to compare evolutionary change under different fishery conditions.
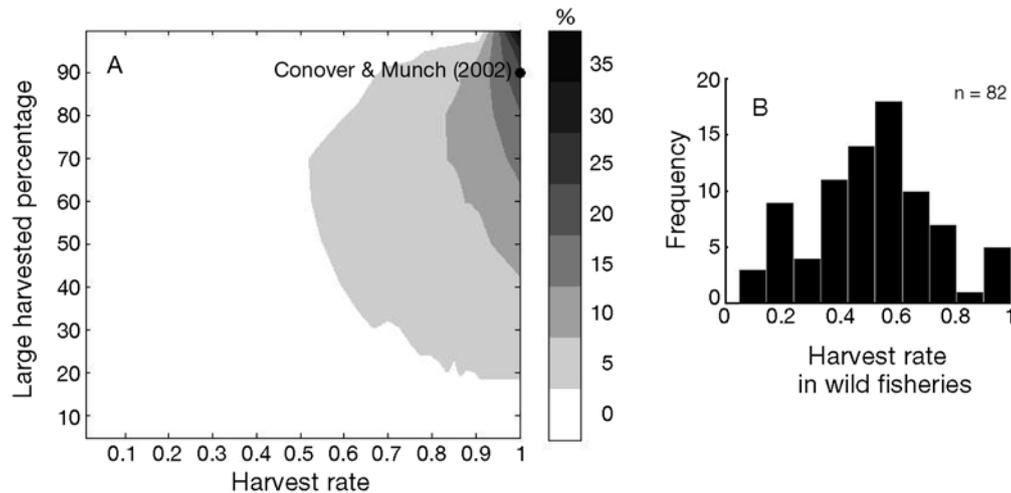
Fig. 4. (A) Contour plot of the change in mean weight (%) of all fish after 4 generations of harvesting, using different fishery scenarios, in the individual-based (IBM) model. The dot indicates size selectivity and harvest rate in Conover & Munch (2002) (B) Histogram of the maximum yearly harvest rate in 82 wild fisheries for comparison with the harvest rate used in Conover & Munch (2002). For sources of fisheries data see Appendix 1

Selection in the IBM compared to wild fisheries

Individual-based model scenarios for evolutionary change under different fishery scenarios indicated strong effects of both the harvest rate and large-harvested percentage, and an interaction between these 2 variables (Fig. 4A). Evolutionary change was reduced for lower harvest rates at all large-harvested percentages. Evolutionary change was also reduced for lower large-harvested percentages, but only at high harvest rates. For intermediate harvest rates, evolutionary change was greatest at intermediate large-harvested percentages. This pattern can be attributed to a balance between low removal rates for very low large-harvested percentages and a weakened selective strength at very high large-harvested percentages, due to the harvesting effort being spread across a greater number of individuals in the population.

Our IBM predicted evolutionary change in the Conover & Munch (2002) experiment to be higher than 25% only under a combination of extremely high harvest rates and large-harvested percentages (Fig. 4A). However, in reducing the harvest rates from 1 to 0.8, for example, the evolutionary change drops from 25% to below 10% for any large-harvested percentage. A review of several fishery databases suggests that maximum harvest rates in most fisheries do not exceed 0.8 and are generally around 0.6 (Fig. 4B). Several salmon fisheries did have maximum harvest rates similar to the Conover & Munch (2002) harvest rate (Appendix 1); however, harvest rates in salmon species are generally not consistently high (Labelle et al. 1997, Quinn et al. 2007).

Thus, the magnitude of evolutionary change in the Conover & Munch (2002) experiment is 2.5 to 5 times the magnitude that would be expected had they used harvest rates more commonly estimated in wild fisheries, such as 0.7 for plaice *Pleuronectes platessa* or 0.45 for gemfish *Rexea solandri* (Appendix 1) over the same timescales.

The number of generations required to achieve the magnitude of evolutionary change observed in Conover & Munch (2002) under different fishery scenarios is illustrated in Fig. 5. With fishing pressures similar to those found in wild fisheries (see above), 15 to 50 or more generations are required to observe the 25% change in size observed by Conover & Munch (2002).

DISCUSSION

The fishing pressure used in Conover & Munch (2002), which removes 90% of the largest fish, is unrealistically high and consequently produces unrealistically rapid evolutionary change, approximately a 25% change in size at age over 4 generations. Individual-based model simulations with more realistic harvest rates in the range of 0.5 to 0.8 suggest that evolutionary change over 4 generations would be less than 10%. Based on these results, either Atlantic silverside are a unique species, and hence, generalizations are not appropriate, or selection pressures are too strong to extend to wild fisheries. Either way, it is important to consider timescales relevant to wild fisheries. A review of empirical studies of fishery-driven evolution sug-
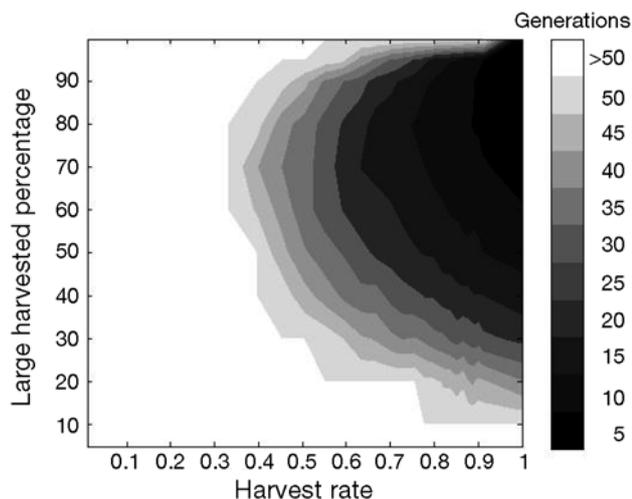
Fig. 5. Contour plot of the number of generations required in the individual-based model (IBM) to reach the same magnitude of evolutionary change in size (25%) for different fishery scenarios as Conover & Munch (2002). Black areas indicate regions where the time scale of change is similar to Conover & Munch (2002), the lightest areas indicate regions where a time-scale of 50 generations or longer is required

gests that, in wild fisheries, a 25% evolutionary change in trait values over 30 generations is possible (Jørgensen et al. 2007). Simulations of the Conover & Munch (2002) experiment over longer timescales with more realistic fishery scenarios suggest that the magnitude of change they observed is comparable to the magnitudes of evolutionary change occurring at slower rates over longer timescales in wild fisheries. Furthermore, the Conover & Munch (2002) heritability estimate of 0.2 is within the range of 0.2 to 0.3 predicted for wild fish stocks. These results suggest that the magnitude of evolutionary change in the Conover & Munch (2002) experiment is comparable to that in wild fisheries.

In reality, environmental variability and co-evolution of genetically correlated traits confound evolutionary trends in wild fisheries. Thus, the Conover & Munch (2002) experimental design also makes 3 further simplifications: (1) maturity is artificially fixed at a constant age; (2) fishing is limited to a single day, just prior to spawning; and (3) individual growth and spawning are density independent (Conover et al. 2005). The Conover & Munch (2002) experiment has already received criticism for these simplifications, because these patterns of fishing and life-histories are rare in wild fisheries (Hilborn 2006, 2007). In semelparous species, such as Atlantic salmon *Salmo salar*, age at maturity can vary across a season and selective exploitation of late-running fish may result in a shift towards earlier-running genotypes (Consuegra et al. 2005). Thus, evolution of size at age also depends upon

life history trade-offs with age at maturity (Roff 1992). In iteroparous species, predicting the evolutionary response to selective fishing is more complicated: growth, age-at-maturity and size at maturity are all expected to evolve under selective fishing (Kuparinen & Merila 2007). Furthermore, the evolutionary response of these traits to the spatial and temporal patterns in fishing pressure can affect the direction of evolution. Evolution of earlier or later age-at-maturity depends upon whether sexually mature or immature fish are targeted by the fishery (Law & Grey 1989). Furthermore, fishery-induced changes in stock density of wild fish populations affect growth and maturity traits (Lorenzen & Enberg 2002), and changes in stock fecundity affect recruitment in subsequent generations (Jennings et al. 2001). For instance, a study of lake pike *Esox lucius* has suggested that the evolutionary response of growth and reproductive traits to fishing depended upon a balance between fishing selective pressure and natural selection driven by density-dependent processes (Edeline et al. 2007).

Despite the limitations, the simplified fishery pressure and life-history pattern that Conover & Munch (2002) applied is also the main strength of their experiment. Unconfounded life-history evolution enabled them to study fishery-driven evolution of traits that are genetically correlated with size at age. Further studies using the Conover & Munch (2002) model system have found that early life-history traits, such as larval size and larval survival, can evolve when size at age is acted on by fishery pressure (Munch et al. 2005, Walsh et al. 2006). Munch et al. (2005) were also able to use the experimental results to predict that the evolution of genetically correlated early-life history traits was unlikely to affect recruitment in wild fisheries, and hence fishery yields and sustainability. These results indicate that further empirical and modelling studies should focus on how fishery-driven evolution of size at age may impact fecundity of spawning fish, rather than the impact of fishery-driven evolution on offspring quality (Munch et al. 2005).

The model system of Conover & Munch (2002) has provided important insights into how severe fishery-driven evolution may impact upon yields and sustainability; however, alone it does not provide evidence that fishery-driven evolution is a common problem for wild fisheries. The simulations used in this study demonstrate that the magnitude of evolutionary change observed in Conover & Munch (2002) is similar to that in wild fisheries, with change occurring more slowly in wild fisheries due to weaker fishery selection pressures. Future model systems that build on the Conover & Munch (2002) empirical model and their subsequent research (Munch et al. 2005, Walsh et al. 2006) should take realistic features of fisheries into

account, such as the life history trade-offs between size, maturation and growth, the timing of fishing events and density dependence. Model systems that can explicitly consider the impact of life-history evolution on fishery sustainability and yields will provide fishery managers with the information required to assess the costs of fishery-driven evolution and implement management strategies to ensure evolutionary sustainability of fisheries.

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Appendix 1. Data sources for the review of maximum harvest rates (proportion of the population removed by fishing each year) in wild fisheries. Included are 82 stocks of 51 different species

Common name	Scientific name	Region	Location	Harvest rate (yr^{-1})	Source
Albacore	*Thunnus alalunga*	Central Pacific	General estimate	0.15	Cox et al. (2002)
Bigeye tuna	*Thunnus obesus*	Central Pacific	General estimate	0.14	Cox et al. (2002)
Billfish	*Makaira* sp.	Central Pacific	General estimate	0.21	Cox et al. (2002)
	Tetrapturus sp.				
	Istiophorus platypterus				
Blue marlin	*Makaira* sp.	Central Pacific	General estimate	0.27	Cox et al. (2002)
Blue shark	*Prionace glauca*	Central Pacific	General estimate	0.18	Cox et al. (2002)
Blue whiting	*Micromesistius poutassou*	NE Atlantic	ICES Sub-areas I-IX, XII & XIV	0.66	ICES CIEM (2007)
Bluefish	*Pomatomus saltatrix*	USA	East Coast	0.40	Ransom Myers' Stock Recruitment Database[a]
Bocaccio	*Sebastes paucispinis*	USA	West coast	0.24	Ransom Myers' Stock Recruitment Database[a]
Brazilian sardine	*Sardinella brasiliensis*	Brazil	South-east	0.77	Ransom Myers' Stock Recruitment Database[a]
Brown shark	*Carcharhinus longimanus*	Central Pacific	General estimate	0.08	Cox et al. (2002)
Chum salmon	*Oncorhynchus keta*	Canada	Johnstone Strait	0.67	Ransom Myers' Stock Recruitment Database[a]
Cod	*Gadus morhua*	NE Atlantic	ICES Divisions VIIe-k	0.67	ICES CIEM (2007)
			ICES Sub-divisions 22 to 24	0.86	ICES CIEM 2007
			ICES Sub-divisions 25 to 32	0.75	ICES CIEM (2007)
			Faroe Plateau	0.56	ICES CIEM (2007)
			ICES Division Va	0.59	ICES CIEM (2007)
			Norwegian Coast	0.46	ICES CIEM (2007)
Coho salmon	*Oncorhynchus kisutch*	Canada	Strait of Georgia	0.96	Labelle et al. (1997)
False scad	*Decapterus rhonchus*	NW Africa	–	0.58	Ransom Myers' Stock Recruitment Database[a]
Gemfish	*Rexea solandri*	Australia	West Australia	0.45	Smith & Wayte (2004)
Haddock	*Melanogrammus aeglefinus*	NE Atlantic	Faroe Islands	0.51	ICES CIEM (2007)
			West of Scotland	0.60	ICES CIEM (2007)
			Rockall	0.61	ICES CIEM (2007)
			ICES Divisions VIIb-k	0.53	ICES CIEM (2007)
			North Sea	0.68	ICES CIEM (2007)
			Icelandic	0.54	ICES CIEM (2007)
			NE Arctic	0.60	ICES CIEM (2007)
Hake	*Merluccius merluccius*	Atlantic Ocean	South-west	0.44	Ransom Myers' Stock Recruitment Database[a]
Hake	*Urophycis earllii*	NE Atlantic	ICES Divisions IIIa, IV, VI, VII, VIIIa,b	0.35	ICES CIEM (2007)
			ICES Divisions IIIa, IV, VI, VII, VIIIa,b	0.54	ICES CIEM (2007)
			ICES Divisions Divisions VIIIc and Ixa	0.40	ICES CIEM (2007)
Halibut	*Hippoglossus hippoglossus*	NE Atlantic	Greenland	0.48	ICES CIEM (2007)
Herring	*Clupea harengus*	NE Atlantic	ICES Division Via	0.65	ICES CIEM (2007)
			ICES Divisions VIId & IIIa	0.77	ICES CIEM (2007)
			Bothnian Sea	0.21	ICES CIEM (2007)
			ICES Sub-divisions 22-24 and Division IIIa	0.54	ICES CIEM (2007)
			ICES Sub-divisions 25 to 29 and 32	0.37	ICES CIEM (2007)
			Gulf of Riga	0.51	ICES CIEM (2007)
			Archipelago and Bothnian Seas	0.20	ICES CIEM (2007)
			Icelandic	0.34	ICES CIEM (2007)
			Norway	0.42	ICES CIEM (2007)
Horse mackerel	*Trachurus trachurus*	NW Africa	–	0.72	Ransom Myers' Stock Recruitment Database[a]
Horse mackerel	*Trachurus mediterraneus*	Black Sea	–	0.73	Ransom Myers' Stock Recruitment Database[a]
King mackerel	*Scomberomorus cavalla*	USA	Gulf of Mexico	0.53	Ransom Myers' Stock[a] Recruitment Database
Mackerel	*Scomber scombrus*	Black Sea	–	0.75	Ransom Myers' Stock[a] Recruitment Database
		NE Atlantic	North Sea	0.32	ICES CIEM (2007)
Mahimahi	*Coryphaena hippurus*	Central Pacific	General estimate	0.05	Cox et al. (2007)
Megrim	*Lepidorhombus whiffiagonis*	NE Atlantic	ICES Divisions VIIIc and IXa	0.55	ICES CIEM (2007)

Appendix 1 (continued)

Common name	Scientific name	Region	Location	Harvest rate (yr^{-1})	Source
New Zealand snapper	*Pagrus auratus*	New Zealand	–	0.36	Ransom Myers' Stock Recruitment Database[a]
NE Arctic cod	*Arctogadus glacialis*	NE Atlantic	NE Arctic	0.64	ICES CIEM (2007)
Pink salmon	*Oncorhynchus gorbuscha*	Canada	Dean Channel	1.00	Ransom Myers' Stock Recruitment Database[a]
Plaice	*Pleuronectes platessa*	NE Atlantic	Celtic Sea plaice	0.53	ICES CIEM (2007)
			Irish Sea	0.57	ICES CIEM (2007)
			Western Channel	0.49	ICES CIEM (2007)
			North Sea	0.56	ICES CIEM (2007)
			Eastern Channel	0.55	ICES CIEM (2007)
Sablefish	*Anoplopoma fimbria*	Canada	West coast	0.24	Ransom Myers' Stock Recruitment Database[a]
Saithe	*Pollachius virens*	NE Atlantic	NE Arctic	0.49	ICES CIEM (2007)
			Faroe Islands	0.50	ICES CIEM (2007)
			ICES Sub-area IV, Division IIIa & Sub-area VI	0.44	ICES CIEM (2007)
Sardine	*Sardinops sagax*	Western USA	California	0.91	Ransom Myers' Stock Recruitment Database[a]
Sardine	*Sardinella* sp.	NE Atlantic	ICES Divisions VIIIc and IXa	0.97	ICES CIEM (2007)
Sharks	*Alopias superciliosus Isurus oxyrinchus Galeocerdo cuvieri*	Central Pacific	General estimate	0.17	Cox et al. (2007)
Skipjack	*Euthynnus affinis*	Central Pacific	General estimate	0.66	Cox et al. (2007)
Sockeye salmon	*Oncorhynchus nerka*	USA	Bristol Bay	1.00	Quinn et al. (2007)
Sole	*Solea solea*	NE Atlantic	ICES Division IIIa	0.45	ICES CIEM (2007)
			Irish Sea	0.70	ICES CIEM (2007)
			Eastern Channel	0.50	ICES CIEM (2007)
			Western Channel	0.71	ICES CIEM (2007)
			Celtic Sea	0.35	ICES CIEM (2007)
			Bay of Biscay	0.37	ICES CIEM (2007)
			North Sea	0.54	ICES CIEM (2007)
South Pacific horse mackerel	*Trachurus symetricus*	South Pacific	–	0.59	Ransom Myers' Stock Recruitment Database[a]
Southern blue whiting	*Micromesistius australis*	New Zealand	Campbell Island	0.48	Ransom Myers' Stock Recruitment Database[a]
Spanish sardine	*Sardina pilchardus*	NE Atlantic	West Iberian peninsula	0.42	ICES CIEM (2007)
Sprat	*Sprattus sprattus*	NE Atlantic	ICES Sub-divisions 22 to 32	0.38	ICES CIEM (2007)
Striped bass	*Morone saxatilis*	USA	East Coast	0.32	Ransom Myers' Stock Recruitment Database[a]
Swordfish	*Xiphias gladius*	Central Pacific	General estimate	0.31	Cox et al. (2007)
White croaker	*Argyrosomus argentatus*	China	East China Sea	0.77	Ransom Myers' Stock Recruitment Database[a]
Whiting	*Merlangius merlangus*	NE Atlantic	North Sea & Eastern Channel	0.65	ICES CIEM (2007)
Widow rockfish	*Sebastes entomelas*	USA & Canada	West coast	0.44	Ransom Myers' Stock Recruitment Database[a]
Yellowfin tuna	*Thunnus albacares*	Central Pacific	General estimate	0.16	Cox et al. (2007)

[a]http://ram.biology.dal.ca./~myers/data.html

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